Host preference and specialization in *Gnathia* sp., a common parasitic isopod of coral reef fishes

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A gnathiid species (Crustacea: Isopoda; one of the most common ectoparasites of coral reef fishes) from the Great Barrier Reef, Australia, was allowed to choose among fishes from three different families to feed on (using two species of fishes per family). Gnathiids showed a strong preference for labrids, rarely feeding on pomacentrids or apogonids. In a separate experiment, gnathiid host preference did not vary among three labrid fish species. Gnathiids that fed on labrids had higher survival than those that fed on apogonids. Male gnathiids that fed on labrids also moulted to the adult stage more quickly. This suggests that host specialization and local adaptation might be occurring between these ectoparasites and their host fishes at the host fish family level. © 2007 The Authors

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INTRODUCTION

Coral reef fishes are parasitized by a wide range of ectoparasites (Rohde, 1993) that can have significant detrimental effects on their growth, survival and reproduction (Cusack & Cone, 1986; Adlard & Lester, 1994). Gnathiid isopods are the main food item of many obligate cleaner fishes in marine cleaning symbioses (Côté, 2000; Grutter, 2002). They attach to the skin and gills with piercing mouthparts and use a muscular oesophagus and grooved paragnath to feed on blood and plasma (Monod, 1926). Gnathiids can inflame and destroy mucosal tissue (Honma & Chiba, 1991), lower blood volume (Jones & Grutter, 2005), and kill captive fishes (Paperna & Por, 1977; Mugridge & Stallybrass, 1983).

Despite an extensive descriptive study of their biology early in the last century (Monod, 1926), little progress has been made in understanding aspects of their basic biology such as taxonomy and host specificity. Only 12 species from

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the Great Barrier Reef (GBR), and nearby Queensland coast have been described (Holdich & Harrison, 1980), although identification of more species from this area is currently underway (N. Smit, pers. comm.). These species descriptions are based on the morphology of adult males, which do not feed (Monod, 1926; Cohen & Poore, 1994). Adult males are found only in benthos and cannot be matched easily with the ectoparasitic juvenile stages, which are remarkably similar across taxa (Grutter *et al.*, 2000; Smit & Davies, 2004).

The three highly mobile juvenile stages, *c*. 1–3 mm long, feed briefly on their host and then return to the benthos to moult to the next stage (Monod, 1926; Grutter, 2003). Because the juveniles are difficult to identify to species, little is known about their host specificity. Thus it is unclear if fishes in a given area are parasitized by a few gnathiid taxa that are host generalists, or many taxa that are host specialists. Gnathiids have been found on 70% of 56 species of reef fishes surveyed on the GBR (Grutter & Poulin, 1998), and turnover rates on host fishes were rapid (12–24 h) (Grutter, 1999, 2003; Grutter & Hendrikz, 1999). Among large (>20 cm total length, L_T) wild reef fishes, gnathiids regularly occur on some fish families (*e.g.* Labridae and Acanthuridae) but not on others (*e.g.* Serranidae, Haemulidae and Lutjanidae) (Smit *et al.*, 2006). The thick-lipped wrasse, *Hemigymnus melapterus* (Bloch), is the only fish on the GBR whose gnathiid parasites have been well documented. When caught during the day near Lizard Island, it consistently hosted two undescribed gnathiid species (*Gnathia* sp. *A* and sp. *B*) (Smit *et al.*, 2006), but not any of the other undescribed *Gnathia* spp. that occur there (A. S. Grutter, unpubl. data). This suggested that some gnathiids may specialize on particular host fish taxa.

Parasite specialization is influenced by the abundance and predictability of hosts (Thompson, 1994; Combes, 1997; McCoy *et al.*, 2001; Tripet *et al.*, 2002). Coral reefs are highly productive ecosystems, with many potential host fishes usually present at any time on even very small reefs (Sale, 2002). Reef fishes on the GBR differ in many characteristics that may affect their susceptibility to gnathiid parasitism [*e.g.* feeding guilds, social behaviour and time of the day or night that they are active (Randall *et al.*, 1997)]. Therefore, there may be natural selection on gnathiid preferences for hosts that differ in any of these characteristics if they offer fitness benefits to the gnathiids.

The objective of this study was to determine if there was evidence for host preference and host specialization in a gnathiid species. If gnathiids prefer to feed on some hosts and also have higher success after feeding on them, there may be some degree of host specialization. Evidence for host specialization would suggest the potential for local adaptation and coevolution between gnathiids and host fishes. Although this might be expected in many host–parasite interactions, this system is unusual because the host fishes and parasites are part of a complex cleaning mutualism involving cleaner fishes that eat gnathiids from the bodies of co-operating host fishes, the client fishes (Côté, 2000). The bluestreak cleaner wrasse *Labroides dimidiatus* (Valenciennes), a common cleaner wrasse in the Indo-Pacific and Red Sea, has significant effects on diversity of reef fishes and abundance through its role in reducing gnathiid loads on reef fishes (Bshary, 2003; Grutter *et al.*, 2003). Cleaner fishes, host fishes and parasites are each likely to be influenced by selective pressures from the other members of the cleaning symbiosis. If gnathiids prefer some hosts to others,

this may influence interactions among the partner fishes; for example, cleaner fishes may prefer to clean heavily infested client species, resulting in selection on clients to compete for access to cleaner fishes.

Understanding the host specificity of gnathiids is an important step in evaluating the ecological and evolutionary relationships of all of the members of this cleaning symbiosis. Host specificity or specialization can take place at several levels, from the breadth of a parasite's choice of spatial position on a host to differences in parasite success on different host fishes. In this study, host specialization was considered to be a parasite having higher success in a correlate of fitness (*e.g.* survival to the adult stage) after feeding on different hosts.

Gnathiids of an undescribed species (*Gnathia* sp. *A*) were allowed to interact in aquaria with potential host fishes from three different families, and which family they fed on at the end of a set period of time was scored as their preferred host. Gnathiid success (measured as survival and number of days for males to moult to the adult stage) was then evaluated after feeding on hosts from a preferred and a non-preferred fish family.

MATERIALS AND METHODS

PARASITE DESCRIPTION AND STUDY SITE

This research was conducted at the Lizard Island Research Station on the GBR, Australia, in April and November 2003. The gnathiids used were descended from individuals isolated in captivity after collection from a wild host labrid, *H. melapterus*, in November 2001. This population of gnathiids was held with *H. melapterus* at the Research Station until April 2003 (*i.e.* 17 months later). Moulting to the non-feeding adult stage after a last blood meal takes *c*. 8 days for males and 12 days for females in this species. Females carry 15–30 fertilized eggs for another 12–16 days, which hatch as fully formed 1st instars. The life cycle takes *c*. 6 weeks from hatching until death: females die after giving birth, and males a short time later (unpubl. obs.). These captive gnathiids were morphologically and genetically similar to wild diurnal gnathiids found on reefs near Lizard Island (unpubl. obs.). Unfed third stage juveniles were used because they were largest and thus most easily seen, and because of the need to control for potential differences in feeding behaviour among different stages. Each gnathiid was used once in the experiments.

HOST FISH COLLECTION

Host fishes were caught by divers using hand- and barrier-nets. The fishes belonged to three families found in large numbers on coral reefs: Apogonidae (cardinalfish), nocturnal planktivores; Pomacentridae (damselfish), diurnal and largely herbivores or planktivores; Labridae (wrasses), diurnal carnivores (Randall *et al.*, 1997). All fishes were captured from the same area, and were given a 2 min freshwater bath to kill external parasites (Kinne, 1984) before being held in outdoor 60 l flow-through seawater tanks for at least 2 days prior to testing. Fishes were fed minced shrimp or commercial fish flakes. All host fishes were used once (except for the family no-choice experiment, see below), and were released afterwards.

GNATHIID INFECTION

Three host preference experiments were conducted in which the protocols differed slightly. The following methods, however, were common to all three experiments: for

each trial, gnathiids were captured haphazardly from the culture tank and placed in an opaque aquarium containing 8 l of sea water and a plastic tube (5 × 10 cm) to provide shelter for the host fishes. Only third stage gnathiids in the culture are readily visible to humans, and these are easily captured with a small pipette. After 2 min, the host fishes were added to the experimental aquaria using a hand-net. After 30 or 60 min in the aquarium with the gnathiids, each fish was moved by hand to a smaller individual container (500 ml) full of sea water for 5 min. The fish was then gently scraped and rinsed with sea water from a squirt bottle, and engorged gnathiids in the fluids were collected with a pipette. The water used was filtered with a 62 μm mesh to ensure that all gnathiids were accounted for. Trials were conducted between 0700 and 1400 hours.

Family no-choice experiment

To ensure that no physiological or mechanical barriers were present that would prevent gnathiid attachment and feeding on a particular host fish family, an experiment was conducted to determine if gnathiids would feed on host fishes from each family. One gnathiid and one host fish were held together for 1 h. Ten trials for each host family were conducted, where each family was represented by two species (sample sizes in parentheses): Pomacentridae, *Dascyllus reticulatus* (Richardson) (5) and *Dascyllus aruanus* (L.) (5); Labridae, *H. melapterus* (4) and *Thalassoma lunare* (L.) (6); Apogonidae, *Apogon novemfasciatus* Cuvier (4) and *Cheilodipterus quinquelineatus* (Cuvier) (6). These fish hosts had been used (but not fed on) in the family choice experiment (below).

Family choice experiment

To determine if gnathiids had preferences for different host families, trials were conducted in which three gnathiids were allowed to choose among three host fishes in an aquarium. This experimental design was chosen to best represent the possible foraging options of a gnathiid in a natural reef environment. Three gnathiids were used in each trial instead of one because preliminary tests showed that not every gnathiid fed when exposed to fishes. This experiment was conducted in April 2003 ($n = 20$) and repeated in November 2003 ($n = 13$) to increase the sample sizes of each of the host fish families. Most teleost gnathiids from the GBR become engorged in <60 min when held with captive host fishes (Grutter & Hendrikz, 1999; Grutter, 2003). For trials conducted in November, the time that gnathiids were kept with host fishes was reduced from 60 to 30 min because gnathiids fed more quickly than in trials conducted in April (this may be a natural seasonal variation in gnathiid feeding behaviour). Host choice by gnathiids was scored as '0' if no gnathiids fed on that host fish. A score of 1–3 defined the number of engorged gnathiids found on a host fish or in the water in a host's container at the end of a trial. The gnathiids were tested with host fishes in a randomized combination of six species from three families (Table I). The following host fish species

TABLE I. Combinations of the host fish species used for each host fish family (Labridae, Pomacentridae, Apogonidae) in the 33 family choice experiment trials

#	Labrid host	% fed	Pomacentrid host	% fed	Apogonid host	% fed
20	*Thalassoma lunare*	74·1	*Dascyllus aruanus*	22·2	*Apogon novemfasciatus*	3·7
8	*Thalassoma lunare*	90	*Dascyllus reticulatus*	10	*Cheilodipterus quinquelineatus*	0
5	*Hemigymnus melapterus*	85·7	*Dascyllus reticulatus*	14·3	*Cheilodipterus quinquelineatus*	0

#, the total number of trials conducted of each combination; % fed, the percentage of times that a gnathiid fed on that host fish species of all the gnathiids that fed in the trials conducted of that combination.

from each family were used (sample sizes in parentheses): Labridae, *H. melapterus* (5) and *T. lunare* (28); Pomacentridae, *D. aruanus* (20) and *D. reticulatus* (13); Apogonidae, *A. novemfasciatus* (20) and *C. quinquelineatus* (13).

Wrasse species choice experiment

To determine if the gnathiids held in captivity with the host fish *H. melapterus* would prefer this species to other species in the wrasse family, 30 min trials were conducted in which one gnathiid was allowed to choose between two wrasses. Since the objective was to determine whether gnathiids would prefer the host fish species with which they had prior exposure, one of the host fish was always *H. melapterus* (mean $\pm$ s.d. total length, $L_T = 10\cdot2 \pm 2\cdot7$ cm, $n = 20$). The other host was either *Halichoeres melanurus* (Bleeker) (mean $\pm$ s.d. $L_T = 9\cdot6 \pm 1\cdot2$ cm, $n = 9$) or *T. lunare* (mean $\pm$ s.d. $L_T = 11\cdot7 \pm 2\cdot5$ cm, $n = 11$).

Host specialization experiment

To determine if some correlates of gnathiid fitness would differ if they had fed on host fishes from a preferred host family *v.* a non-preferred family, a final experiment was conducted to measure gnathiid survivorship and number of days until moulting to the adult. Two hundred third stage gnathiids were held for 2 h during 9–12 December 2003 with *H. melapterus* (Labridae) ($n = 5$) and 200 with *C. quinquelineatus* (Apogonidae) ($n = 5$). All 10 host fishes were captured the previous day and were not used in previous experiments. Engorged gnathiids were collected and held in groups of five in 70 ml vials filled with sea water and kept at a constant temperature of 25° C. Moulted exoskeletons and other debris were removed daily and fresh sea water was added to the vial as needed. Gnathiids were examined with a dissecting microscope daily until they moulted to the adult, when they were preserved in 80% ethanol and the total length (from telson to gnathopods) was measured for a haphazardly chosen sample of males from each group.

STATISTICAL ANALYSIS

Statistical analyses were performed using JMP version 5.1 (SAS, 2002). The data from the family choice experiment trials conducted in April and November were pooled because there were no differences in gnathiid feeding preference either within a host family or among host families in the two months (χ^2 goodness of fit, d.f. $= 1$, $P > 0\cdot05$). The data were also pooled for both host fish species used within a family because there were no differences in gnathiid feeding preference among fish species (χ^2, Pomacentridae: d.f. $= 1$, $P > 0\cdot05$; Labridae: d.f. $= 1$, $P > 0\cdot05$; Apogonidae: d.f. $= 1$, $P > 0\cdot05$). The results from two other experiments, family no-choice and wrasse species choice (see below), corroborated that gnathiids showed no preference for particular species within a host fish family. A nominal logistic regression model was used to determine if host fish family or host fish L_T were significant predictors of whether or not a gnathiid fed on a host. Host L_T was included in the model because it is not known if it affects gnathiid host preference.

RESULTS

FAMILY NO-CHOICE EXPERIMENT

Gnathiids fed on host fishes from each of the three families when tested with no other potential host fishes in the aquaria: 70% of the gnathiids tested with wrasse hosts fed on them, 60% fed on the damselfish hosts and 40% fed on the apogonids. Each species of host fish in a family was fed on at least twice in the 10 trials for that family.

FAMILY CHOICE EXPERIMENT

Only 44% of the 99 gnathiids tested in the experiment ($n = 33$) were engorged at the end of a trial. In 70% of trials, only one of the three gnathiids had fed on a host fish. There were no cases where all three gnathiids had fed. In 10 trials (30%), two of the three gnathiids were engorged. In four of these cases, two gnathiids fed on the same host fish individual (which was always the wrasse). In two trials, no gnathiids were engorged, and these were excluded from the analysis. Gnathiids were sometimes missing when a trial ended; in four trials (12%), one of the three gnathiids was missing, and it was assumed that one of the host fishes ate them. This is not unusual in laboratory tests with gnathiids and planktivorous fishes (especially pomacentrids) (unpubl. obs.).

Thirty-five per cent of gnathiids tested fed on hosts from the labrid family, while <10% fed on the other two families combined (8% on pomacentrids and 1% on apogonids). This preference for wrasses was significant (likelihood ratio χ^2, d.f. $= 6$, $P < 0.001$; Wald effect test, d.f. $= 4$, $P < 0.01$). Host fish L_T had no effect on gnathiid preference (Wald effect test, d.f. $= 2$, $P > 0.05$). The L_T of all the host fishes used was (mean $\pm$ S.D.): Labridae (12.6 ± 1.8 cm); Pomacentridae (7.0 ± 1.1 cm); Apogonidae (9.4 ± 1.3 cm).

WRASSE SPECIES CHOICE EXPERIMENT

Only trials in which one gnathiid fed on a host fish were included in the analysis (there were three trials where two gnathiids fed and one where none fed; all four were excluded). Gnathiids showed no preference for the species of wrasse with which they were familiar, *H. melapterus*: *H. melapterus v. H. melanurus* (χ^2, $n = 9$, $P > 0.05$); *H. melapterus v. T. lunare* (χ^2, $n = 11$, $P > 0.05$). The effect of host fish size on gnathiid preference was tested with a logistic regression of host fish L_T v. the number of gnathiids that fed on the fish. There was no significant effect when each fish species was plotted separately: *H. melapterus* ($r^2 = 0.04$, $n = 20$, $P > 0.05$); *H. melanurus* ($r^2 = 0.02$, $n = 9$, $P > 0.05$); *T. lunare* ($r^2 = 0.08$, $n = 11$, $P > 0.05$), so the data for all three species were combined for a single test ($r^2 = 0.02$, $n = 40$, $P > 0.05$).

HOST SPECIALIZATION EXPERIMENT

Only 20% of the 200 gnathiids that were held with apogonid hosts fed on them. In contrast, 59.5% of gnathiids held with labrid hosts fed on them. Twenty-five of the 40 gnathiids that fed on apogonid hosts survived to become adult (60%), compared to 93/119 (78%) that had fed on labrids (Pearson χ^2, $n = 159$, $P = 0.0503$). After removing from the dataset one female gnathiid that moulted but died within minutes (all others survived for at least 2 days), this difference was statistically significant (Pearson χ^2, $n = 158$, $P < 0.05$).

Of the 93 juveniles that fed on labrid hosts and survived to become adult, 61 were males and 32 were females. Of the 25 juveniles that fed on apogonids, 22 males moulted. Since only three females moulted in this group, no comparisons were made between females that fed on different hosts due to the unbalanced sample sizes.

Male gnathiids that fed on labrids moulted an average of 8·03 ± 0·60 days (mean ± S.D.) after feeding compared to 8·68 ± 0·77 days for those that fed on apogonids (*t*-test, $n = 81$, $P < 0.001$). There was no significant difference in adult male size (*t*-test, $n = 19$, $P > 0.05$) between gnathiids that fed on labrids ($n = 8$, mean ± S.D. = 3·13 ± 0·14 mm) and those that fed on apogonids ($n = 11$, mean ± S.D. = 3·07 ± 0·09 mm).

DISCUSSION

The experiment in which gnathiids had no choice of host fishes demonstrated that they were capable of feeding on all of the host species used, making unlikely the possibility of mechanical or physiological barriers that prevented feeding on non-preferred host fish families. The experiment that tested for gnathiid preference among labrid species revealed no preference for the species with which gnathiids were held prior to the experiments, showing that host specificity does not occur at the host species level.

At the host family level, however, gnathiids clearly preferred wrasses to the two other fish families. One explanation for this pattern is that the gnathiids used to initiate the laboratory culture were wrasse specialists, and the preference that they showed was present prior to isolation with this host in culture. In this situation, host preference in gnathiids may be genetically determined, resulting in lineages of gnathiids that specialize on particular families of host fishes. Most examples of genetically determined host preferences come from phytophagous insects (Emelianov *et al.*, 1995; Via, 1999; Groman & Pellmyr, 2000), but there are some examples of terrestrial ectoparasites (ticks) with ecological similarities to gnathiids where sympatric host races that prefer different seabird hosts are genetically distinct (McCoy *et al.*, 2001).

Alternatively, these gnathiids could be generalists that regularly feed on the wrasse *H. melapterus* (from which they were captured to establish the culture). Host preference could have then either evolved in captivity, or else gnathiid feeding behaviour may be plastic (*e.g.* allowing for changes in phenotype to specialize on hosts that are commonly encountered in an area). A final possibility, however, is that wrasses are simply superior hosts, and that gnathiids always prefer them to other fishes. It is common for generalist parasites to show preferences for certain hosts (Tripet & Richner, 1997; Johnson *et al.*, 2002) (but of course this depends upon how 'generalist' is defined).

A potentially confounding factor in the experimental design was that gnathiids might choose the first host fish that they encounter. For example, wrasses typically swam or remained stationary near the bottom of an aquarium during a trial, and if gnathiids also stayed near the bottom, then what appears to be preference may simply be a result of proximity. During these experiments, however, gnathiids were observed on the sides of the aquarium and at the surface of the water. In addition, gnathiids appeared to have very good vision or other sensory abilities (or both) as they immediately swim towards items placed in the culture tank (unpubl. obs.), so they should have had the opportunity to see (or otherwise sense) all of the host fishes in the aquarium with them. It would also be unusual to see a difference in parasite performance after feeding on an arbitrarily chosen host.

Host fishes may be able to resist gnathiid parasitism by using behavioural or physiological adaptations or both; for example, this population of gnathiids has been shown experimentally to avoid toxic areas on the bodies of adult gobies (Munday *et al.*, 2003). It is not known if fishes develop the ability to resist gnathiid parasitism as they age, so using initial phase wrasses (*i.e.* younger stages) in tests with older individuals from the other families may have resulted in wrasses being fed upon disproportionately.

Although host fish size was correlated with host family (*e.g.* wrasses are larger than damselfish), the effect of size was not a significant predictor of gnathiid preference in the experiment that tested for gnathiid preference among different host families. Gnathiids fed on hosts from a range of sizes in the wrasse and damselfish families, but avoided cardinalfish, which were intermediate in size between wrasses and damselfish. Neither was host fish size a significant predictor of gnathiid preference within each of the three families in this experiment when analysed separately. This was also the case in the experiment that tested for gnathiid preference among different wrasse species. These results suggest that gnathiids may use cues other than host size when choosing host fishes. This contradicts findings from ecological studies on the GBR, which show that larger fishes have higher gnathiid loads (Grutter, 1999; Muñoz *et al.*, 2006). The present result may be an artefact of the laboratory test conditions (*e.g.* all of the three potential host fishes were of relatively similar size and were confined in a small aquarium with the gnathiids).

Little is known about the mechanics of how gnathiids or any other marine isopods find their host fish (*e.g.* vision *v.* olfaction), or the basis of host fish preferences (*e.g.* host size, colour and behaviour). Poulin *et al.* (1990) demonstrated that parasitic copepods (*Salminicola edwardswii*) were attracted to moving shadows and disturbance. Salmon lice (*Lepeoptheirus salmonis*) respond to chemicals from their host fish in water (Devine *et al.*, 2000). In terrestrial ticks and fleas, a combination of vibrations, shadows and chemical concentration appear to aid in host recognition (Cox *et al.*, 1998; Ostercamp *et al.*, 1999).

Local adaptation to a host occurs when the mean fitness of a parasite is higher on the host with which it has co-evolved than on a novel host (Gandon *et al.*, 1998). Resulting specialization on these hosts could lead to genetically distinct populations of parasites if they are reproductively or geographically isolated from other parasite populations that utilize different hosts (Jaenike, 1981; Rice, 1987). The host specialization experiment showed that gnathiid survival was lower in the group of gnathiids that fed on apogonids (the non-preferred host fish) than in those that fed on labrids (the preferred host). In addition, very few females moulted to become adult after feeding on apogonids, and males took longer to moult. This gnathiid species therefore appears to prefer and to be specialized for feeding on host fishes from the wrasse family. Although it is desirable to know if there is a direct effect on gnathiid fitness (*e.g.* the number of offspring produced), there are good reasons to expect that moulting earlier may translate into higher fitness for males. Little is known about sexual behaviour in gnathiids, but the mating system of other marine isopods such as *Paracerceis sculpta* involves intense competition among males for access to females (Shuster, 1992). Breeding gnathiids are found in cavities in

corals or sponges, where several females are usually found with one male (Rohde, 2005). Males have greatly enlarged mandibles that may be used in intrasexual conflict, and they probably mate with more than one female (Monod, 1926; Upton, 1987; Rohde, 2005). When males of this species are kept together in 250 ml vials, one male often ends up with many of its appendages missing (A. S. Grutter, unpubl. obs.). Moulting earlier may allow males to obtain higher reproductive success if they are able to out compete males that emerge later, especially if the mating system is haremic and mate guarding occurs. Gnathiids that took longer to moult after feeding on apogonids were not larger than the gnathiids that fed on labrids. This is important because moulting at a larger size might confer an advantage in a system where male–male competition occurs (Shuster, 1992).

Although the host specialization experiment demonstrated that this species of gnathiid has strong host preferences and that they have higher success after feeding on this preferred host, an ecological definition of specialization would require illustrating that there is variation in the degree of parasite specialization in this system. For example, most studies on the evolution of host specialization take into account at least two hosts and two parasites. This study has shown that one gnathiid species prefers one host fish family (labrids) to others (apogonids), but does not show that some other gnathiid species or race prefer to feed on (and has higher fitness on) apogonids (or some other fish family). It would also be desirable in this case to determine if there are gnathiids that feed and perform equally on several different fish groups (*i.e.* a generalist).

When sympatric host fishes (such as the apogonids and labrids used in this study) have different effects on parasite fitness, there should be selection on the parasites to prefer the hosts that result in higher fitness for them. A preference for labrid hosts could lead to genetically distinct populations of gnathiids if they are reproductively or geographically isolated from other parasite populations that utilize different host fishes.

In general, parasites with complex life cycles that are intimately associated with their host tend to be specialists, while those with simple, direct life cycles occurring away from the host are less host-specific (Noble *et al.*, 1989; Combes, 1991). It is therefore surprising to find specialization in a parasite that feeds only briefly on its host. This may be explained partly by the high abundance of reef fish hosts that are present at predictable times on coral reefs. Several studies have suggested that evolution favours specialization in parasites when hosts are abundant and predictable (Thompson, 1994; Combes, 1997; McCoy *et al.*, 2001; Tripet *et al.*, 2002).

Further studies of some basic aspects of gnathiid ecology (*e.g.* dispersal) and behaviour (*e.g.* sexual selection) in this and other gnathiid species will greatly improve understanding of the processes affecting gnathiid evolution. It is also important to determine how gnathiid evolution is shaped by selection pressure from their main predators, cleaner fishes. Cleaner fishes, host fishes and parasites each have the potential to be influenced by selective pressures from the other partners in the cleaning symbiosis. Understanding host specificity in gnathiids is an important step in evaluating the ecological and evolutionary dynamics among host fishes and these ectoparasites.

References

Adlard, R. D. & Lester, R. J. G. (1994). Dynamics of the interaction between the parasitic isopod *Anilocra pomacentri*, and the coral reef fish, *Chromis nitida*. *Parasitology* **109,** 311–324.

Bshary, R. (2003). The cleaner wrasse, *Labroides dimidiatus*, is a key organism for reef fish diversity at Ras Mohammed National Park, Egypt. *Journal of Animal Ecology* **72,** 169–176.

Cohen, G. F. & Poore, G. C. B. (1994). Phylogeny and biogeography of the Gnathiidae (Crustacea; Isopoda) with descriptions of new genera and species, most from south eastern Australia. *Memoirs of the Museum of Victoria* **54,** 271–397.

Combes, C. (1991). Evolution of parasite life cycles. In *Parasite-host Associations: Coexistence or Conflict?* (Toft, C. A., Aeschlimann, A. & Bolis, I., eds), pp. 62–82. London: Oxford University Press.

Combes, C. (1997). Fitness of parasites: pathology and selection. *International Journal of Parasitology* **27,** 1–10.

Côté, I. M. (2000). Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology: an Annual Review* **38,** 311–355.

Cox, R., Stewart, P. D. & Macdonald, D. W. (1998). The ectoparasites of the European badger, *Meles meles*, and the behaviour of the host-specific flea, *Paracercas meles*. *Journal of Insect Behaviour* **12,** 245–265.

Cusack, R. & Cone, D. K. (1986). A review of parasites as vectors of viral and bacterial diseases of fish. *Journal of Fish Disease* **9,** 169–171.

Devine, G. J., Ingvarsdottir, A., Mordue, W., Pike, A. W., Pickett, J., Duce, I. & Mordue, A. J. (2000). Salmon lice (*Lepeoptheris salmonis*), exhibit specific chemotactic responses to chemicals originating from the salmonid, *Salmo salar*. *Journal of Chemical Ecology* **26,** 1833–1847.

Emelianov, I., Mallet, J. & Baltensweiler, W. (1995). Genetic differentiation in the larch budmoth *Zeiraphera diniana* (Lepidoptera: Tortricidae): polymorphism, host races or sibling species? *Heredity* **75,** 416–424.

Gandon, S., Ebert, D., Olivieri, I. & Michalakis, Y. (1998). Differential adaptation in spatially heterogeneous environments and host-parasite coevolution. In *Genetic Structure and Local Adaptation in Natural Insect Populations* (Mopper, S. & Strauss, S., eds), pp. 325–341. London: Chapman & Hall.

Groman, J. D. & Pellmyr, O. (2000). Rapid evolution and specialisation following host colonization in a yucca moth. *Journal of Evolutionary Biology* **13,** 223–236.

Grutter, A. S. (1999). Infestation dynamics of parasitic gnathiid isopod juveniles on a coral reef fish *Hemigymnus melapterus*. *Marine Biology* **135,** 545–552.

Grutter, A. S. (2002). Cleaning behaviour from the parasite's perspective. *Parasitology* **124,** S65–S81.

Grutter, A. S. (2003). Feeding ecology of the fish ectoparasite *Gnathia* sp. (Crustacea: Isopoda) from the Great Barrier Reef, and its implications for fish cleaning behaviour. *Marine Ecology Progress Series* **259,** 295–302.

Grutter, A. S. & Hendrikz, J. (1999). Diurnal variation in the abundance of parasitic gnathiid isopod larvae on coral reef fish: its implications in cleaning interactions. *Coral Reefs* **18,** 187–191.

Grutter, A. S. & Poulin, R. (1998). Intraspecific and interspecific relationships between host size and the abundance of parasitic larval gnathiid isopods on coral reef fishes. *Marine Ecology Progress Series* **164,** 263–271.

Grutter, A. S., Morgan, J. A. T. & Adlard, R. (2000). Characterising gnathiid isopod species and matching life stages using ribosomal DNA ITS2 sequences. *Marine Biology* **136,** 201–205.

Grutter, A. S., Murphy, J. M. & Choat, A. (2003). Cleaner fish drives local fish diversity on coral reefs. *Current Biology* **13,** 64–67.

Holdich, D. M. & Harrison, K. (1980). The crustacean isopod genus *Gnathia* (Leach) from Queensland waters with descriptions of nine new species. *Australian Journal of Marine and Freshwater Research* **31,** 215–240.

Honma, Y. & Chiba, I. (1991). Pathological changes in the brachial chamber wall of stingrays, *Dasyatis* spp., associated with the presence of juvenile gnathiids (Isopoda, Crustacea). *Gyobyo Kemkyu* **26,** 9–16.

Jaenike, J. (1981). Criteria for ascertaining the existence of host races. *American Naturalist* **117,** 830–834.

Johnson, K. P., Weckstein, J. D., Witt, C. C., Faucett, R. C. & Moyle, R. G. (2002). The perils of using host relationships in parasite taxonomy: phylogeny of the *Degeeriella* complex. *Molecular Phylogenetics and Evolution* **23,** 150–157.

Jones, C. M. & Grutter, A. S. (2005). Parasitic isopods (*Gnathia* sp) reduce haematocrit in captive blackeye thicklip (Labridae) on the Great Barrier Reef. *Journal of Fish Biology* **66,** 860–864.

Kinne, O. (1984). *Diseases of Marine Animals*, Vol. I. Hamburg: Biologische Anstalt Helgoland.

McCoy, K. D., Boulinier, T., Tirard, C. & Michalakis, Y. (2001). Host specificity of a generalist parasite: genetic evidence of sympatric host races in the seabird tick *Ixodes uriae*. *Journal of Evolutionary Biology* **14,** 395–405.

Monod, T. (1926). Les Gnathiidae. Essai monographique (morphologie, biologie, systématique). *Mémoires de la Société des Sciences Naturelles du Maroc* **13,** 1–661.

Mugridge, R. E. R. & Stallybrass, H. G. (1983). A mortality of eels (*Anguilla anguilla*. L.) attributed to Gnathiidae. *Journal of Fish Biology* **6,** 81–82.

Munday, P. L., Schubert, M., Baggio, J. A., Jones, G. P., Caley, M. J. & Grutter, A. S. (2003). Skin toxins and external parasitism of coral-dwelling gobies. *Journal of Fish Biology* **62,** 976–981.

Muñoz, G., Grutter, A. S. & Cribb, T. H. (2006). Endoparasite communities of five fish species (Labridae: Cheilininae) from Lizard Island: how important is the ecology and phylogeny of the hosts? *Parasitology* **132,** 363–374.

Noble, E. R., Noble, G. A., Schad, G. A. & MacInnes, A. J. (1989). *Parasitology: the Biology of Animal Parasites*. Philadelphia, PA: Lea & Febiger.

Ostercamp, J., Wahl, U., Schmalfuss, G. & Haas, W. (1999). Host-odour recognition in two tick species is coded in a blend of vertebrate volatiles. *Journal of Comparative Physiology* **185,** 59–67.

Paperna, I. & Por, F. D. (1977). Preliminary data on the Gnathiidae (Isopoda) of the Northern Red Sea, the Bitter Lakes and the Eastern Mediterranean and the biology of *Gnathia piscivora*. *Rapports de la Commission Internationale pour la Mer Méditerranée* **24,** 195–197.

Poulin, R., Curtis, M. A. & Rau, M. E. (1990). Responses of the fish ectoparasite *Salmonicola edwardsii* (Copepoda) to stimulation, and their implications for host-finding. *Parasitology* **3,** 417–421.

Randall, J. E., Allen, G. R. & Steene, R. C. (1997). *Fishes of the Great Barrier Reef and Coral Sea*. Honolulu, HI: University of Hawaii Press.

Rice, W. R. (1987). Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *Evolutionary Ecology* **1,** 301–314.

Rohde, K. (1993). *Ecology of Marine Parasites; an Introduction to Marine Parasitology*. Wallingford: CAB International.

Rohde, K. (2005). *Marine Parasitology*. Wallingford: CABI Publishing.

Sale, P. F. (2002). *Coral Reef Fishes: Dynamics and Diversity in a Complex System*. San Diego, CA: Academic Press.

SAS (2002). *JMP, Version 5*. Cary, NC: SAS Institute Inc.

Shuster, S. M. (1992). The reproductive behaviour of α-, β-, and γ-male morphs in *Paracerceis sculpta*, a marine isopod crustacean. *Behaviour* **121,** 259–287.

Smit, N. J. & Davies, A. J. (2004). The curious life-style of the parasitic stages of gnathiid isopods. *Advances in Parasitology* **58,** 289–391.

Smit, N. J., Grutter, A. S., Adlard, R. D. & Davies, A. J. (2006). Hematozoa of teleosts from Lizard Island, Australia with some comments on their possible mode of transmission. *Journal of Parasitology* **92,** 778–788.

Thompson, J. N. (1994). *The Coevolutionary Process*. Chicago, IL: University of Chicago Press.

Tripet, F. & Richner, H. (1997). The coevolutionary potential of a 'generalist' parasite, the hen flea *Ceratophyllus gallinae*. *Parasitology* **115,** 419–427.

Tripet, F., Jacot, A. & Richner, H. (2002). Larval competition affects the life histories and dispersal behaviour of an avian ectoparasite. *Ecology* **83,** 935–945.

Upton, N. P. D. (1987). Asynchronous male and female life cycles in the sexually dimorphic, harem-forming isopod *Paragnathia formica* (Crustacea: Isopoda). *Journal of Zoology* **212,** 677–690.

Via, S. (1999). Reproductive isolation between sympatric races of pea aphids. I. Gene flow restriction and habitat choice. *Evolution* **53,** 1446–1457.