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Indirect effects of an ectoparasite reduce successful establishment of a damselfish at settlement

Alexandra S. Grutter*[,1], Angela J. Crean[1], Lynda M. Curtis[1], Armand M. Kuris[2], Robert R. Warner[2] and Mark I. McCormick[3]

[1]*School of Biological Sciences, The University of Queensland, St. Lucia, Queensland 4072, Australia;* [2]*Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, and Marine Science Institute, Santa Barbara, California 93106, USA; and* [3]*ARC Centre of Excellence for Coral Reef Studies and School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia*

Summary

1. The sublethal impact of parasites on host behaviour and the mechanism linking them to population level effects remain largely unquantified. On the Great Barrier Reef, juvenile gnathiid isopods (mobile ectoparasites) are one of the most common ectoparasites of fishes. Previous laboratory studies on damselfishes suggest that a single gnathiid can kill settlement-stage larvae and very young juveniles, while repeated attacks affect the growth of a juvenile damselfish. Nothing, however, is known of how gnathiids affect the performance, and the survival of settlement stage fishes in the wild.

2. We sampled juveniles of the damselfish *Pomacentrus amboinensis* for gnathiids and tested the effect of a single gnathiid (*Gnathia auresmaculosa*) on juvenile survival in the laboratory. We also tested the effect of this gnathiid on the swimming performance, oxygen consumption, and successful establishment in the wild of settlement-stage larvae.

3. Of the juvenile fish sampled at dawn, 3·5% had a gnathiid attached; at other times of the day, fish had no gnathiids. In the laboratory, most gnathiids (79%) remained attached to juvenile fish for up to 6 h and all fish survived exposure to one gnathiid.

4. When tested in pairs in a double-lane swim chamber, fish that had previously been fed on by one gnathiid ceased swimming first in 77% of the trials and had a lower critical swimming speed compared to fish not exposed to a gnathiid. Previously parasitized fish had a 35% higher oxygen consumption rate than did unexposed fish. When tagged fish were placed in pairs on dead coral patches in the wild and monitored, the previously parasitized fish disappeared from the reef first in 67% of the trials.

5. Our analysis indicates that a single ectoparasitic gnathiid isopod significantly decreases the performance of young *P. amboinensis* and their persistence on the reef. Gnathiids, by affecting fish performance, may therefore indirectly affect the successful establishment of fishes on the reef at settlement, a critical transitional stage for most coral reef fishes. Unsuccessful establishment on the reef most likely increases the interactions of settling fish with predators and thus gnathiids may contribute to the high mortality observed at this time.

Key-words: coral reefs, fish behaviour, Gnathiidae, parasites, Pomacentridae, recruitment, settlement, trait-mediated indirect effects

Introduction

Indirect effects are those where the impacts of one species on another are mediated by a third species (Wooton 2002). To understand and ultimately predict community and ecosystem-level phenomena, it is important to identify and predict the outcome of a wide range of indirect effects which can be either positive (Grutter & Irving 2007) or negative (Benedetti-Cecchi 2000). Impacts may involve density-mediated indirect interactions (Offenberg, Macintosh & Nielsen 2006). Or, in 'trait-mediated indirect effects' (Werner & Peacor 2003), one species changes the traits of individuals of a

*Correspondence author. E-mail: a.grutter@uq.edu.au

second species, and the altered trait(s) change how the second species interacts with a third species. Traits can involve morphological, physiological, life-history, and behavioural changes. While most of the research on trait-mediated indirect effects has concentrated on predator–prey interactions, they can also be mediated by parasites (Hatcher, Dick & Dunn 2006). For example, the parasitic trematode *Curtuteria australis* inhibits the burrowing behaviour of infected cockles *Austrovenus stutchuryi*, thereby exposing them to predation by the avian definitive host (Mouritsen & Poulin 2003).

Parasites are common on fishes and can directly affect hosts at individual and population levels by reducing growth and reproduction (e.g. Rohde 1993), or indirectly by altering behaviour (e.g. Dobson 1988; Poulin 1995; Lafferty & Morris 1996; Fenton & Rands 2006). Parasite induced changes in fishes may manifest themselves in a variety of ways (Barber, Hoare & Krause 2000). If parasitized fish have increased energy requirements they may alter their time budget to increase time spent foraging. Parasites may affect foraging if they occupy sites that impair sensory or motor systems, by affecting fish diet composition and prey selection, or by impairing competitive ability, often through reductions in maneuverability, swimming speed, and prey detection (Barber, Hoare & Krause 2000). Energy expended by the host to maintain parasites may be further drained as infections increase metabolic costs, particularly when these costs are associated with increased energetic demands of the immune system, or impair behavioural defences against predators. Consequently, fishes infected with strongly debilitating parasites may exhibit markedly reduced activity levels, conserving energy. Although the causal mechanisms of parasite manipulation of host behaviour in most fish-parasite interactions remain largely unknown, Shaw *et al*. (2009) show that the brain chemistry of a killifish is altered in association with behavioural modification by a trophically transmitted larval trematode.

The vulnerability of hosts to individual parasites is greater in small than in large hosts because a given parasite individual is often proportionately large relative to small hosts. Thus parasite effects on small coral reef fishes hosts may be proportionately large which may decrease condition and increase the probability of death. Condition is an important determinant of survival in juvenile reef fishes transitioning between pelagic to benthic habitats (e.g. McCormick 1998; Searcy & Sponaugle 2001; Hoey & McCormick 2004; Grorud-Colvert & Sponaugle 2006; Gagliano, McCormick & Meekan 2007). Parasites may directly cause mortality in small hosts or they can lower condition, affect behaviour, or alter physiology, thus indirectly raising the probability of death from other agents (such as predators). Understanding factors that affect larval condition is important because condition at metamorphosis is an important determinant of the successful survival to the juvenile stage and subsequent recruitment to adult populations. The end of the pelagic stage, when larvae metamorphose into juveniles, is termed the settlement stage. An estimated 56% of coral reef fishes die within 2 days of settlement onto the reef (Almany & Webster 2006). Attributes affecting survival during and after settlement include size (Booth 1995), growth history (Shima & Findlay 2002), swimming speed (McCormick & Molony 1993), lipid content (Booth & Hixon 1999) and behaviour (McCormick 2009). Natural intraspecific variation in these attributes (Hoey & McCormick 2004) may be further compounded when parasites affect the condition of fishes. Although predation may provide the proximal mechanism of mortality in the early stages of settlement on the reef (Leis & McCormick 2002), parasites may determine their susceptibility to predators. If parasites affect individual quality then they may also contribute to this variation. Parasite-associated behavioural changes in reef fishes have seldom been studied and even less so for the younger life stages.

A common ectoparasite found in reef fishes are gnathiid isopods. The high prevalence, attack rate, and mobility of such blood-feeding ectoparasites on adult fishes (Grutter 1995, 1996, 2008; Grutter & Poulin 1998; Jones & Grutter 2007) suggest that gnathiids may also significantly affect fishes at settlement. However, nothing is known of how gnathiids affect the performance or behaviour, and thus indirectly, the survival of young fishes in nature. Our aim was to determine whether gnathiids affect the behaviour and performance of young fishes and indirectly their survival on the reef. We sampled the ambon damselfish, *Pomacentrus amboinensis* Bleeker, to determine whether fish are infested with gnathiids as juveniles; we then observed the behaviour of gnathiids (*Gnathia auresmaculosa,* Ferreira and Smit) (Fig. 1) feeding on juvenile fish and monitored the mortality of these fish compared to control fish. We also monitored the performance (swimming and oxygen consumption) of these fish compared to unparasitized control fish. We hypothesized that gnathiid-induced reductions in performance likely decrease the survival of settlement stage ambon damselfish. We tested this prediction by introducing pairs of settlement stage fish (one fish that had been fed on by gnathiids, and one fish that had not) to patch reefs and comparing their persistence.

Fig. 1. Gnathid isopod. Engorged third stage juvenile *Gnathia aureusmaculosa*. Photo by G. Wilson.

Materials and methods

STUDY SPECIES

Gnathiid isopods feed on fish blood once during each of the three juvenile stages, and before returning to the benthos to moult to the next stage (Smit & Davies 2004). Gnathiids can readily detach from teleosts and so they often escape detection in parasite surveys (Grutter 1995). In the laboratory, gnathiids reduce the growth of a juvenile damselfish (Jones & Grutter 2008) and can also kill some settling and juvenile damselfishes, usually involving more than one gnathiid or a very small host fish (< 10 mm standard length) (Grutter *et al.* 2008; Jones & Grutter 2008; Penfold *et al.* 2008). Gnathiids are also potential vectors of haemogregarine blood parasites in fishes on the Great Barrier Reef (GBR) (Smit *et al.* 2006). *Gnathia auresmaculosa*, a common gnathiid on adult fishes (*Gnathia* sp. A in Smit *et al.* 2006) at the study site (Lizard Island, GBR, Australia,14°40′S, 145°28′E), were cultured (Grutter 2003) and used in the performance tests. Third stages (Ferreira *et al.* 2009) were used because their larger size (mean ± SE, range, unengorged: 1·1 ± 0·01, 1·1–1·3 mm; engorged: 1·6 ± 0·007, 1·5–2·0 mm, unpublished data, Grutter 2003) made them more visible for collection and to confirm that feeding had taken place. *Pomacentrus amboinensis* was used as the model fish because it has been used in several other studies on larval fish condition at settlement, is relatively site-attached (McCormick & Makey 1997), is common at the study site, and they settle onto small patch reefs in densities where they likely interact with each other (McCormick 2009). All fish in the performance tests were settlement-stage fish collected using light traps (Meekan *et al.* 2001) moored off the reef edge and approximately 500 m from shore. Traps were placed in the water around 18.00 h and emptied around 07.00 h each day. Fish were transferred to holding aquaria (65 × 35 × 30 cm maximum size) with constant aeration and water flow.

GNATHIID OCCURRENCE ON WILD FISH

To determine if settled juvenile fish naturally become parasitized with gnathiids and other crustacean ectoparasites, fish were captured with a handnet at dawn (06.00–07.00 h, over five different days between 5 and 18 January 2005) and during the day (10.00–13.00 h, over 4 days between 24 December and 2 January, 2005) from several sites in the Lizard Island lagoon. Each site consisted of a collection of patch reefs and a different site was sampled each day. Fish were immediately placed into individual quick-sealing plastic bags, and transported in a slurry of ice and water (which euthanized the fish). In the laboratory, fish were transferred to 80% ethanol and the contents of the plastic bag rinsed and examined under a dissecting microscope (70-100×). For each fish, the body, fins, and gills were examined for gnathiids and other isopods, the former measured excluding the uropods and telson.

GNATHIID FEEDING BEHAVIOUR AND EFFECT ON MORTALITY

Juvenile fish were exposed to a gnathiid and the feeding behaviour of the gnathiid recorded. To determine if there was any parasite-induced mortality, survival of the hosts in the absence of predators, compared to those not exposed to a gnathiid, was recorded. Juvenile fish were collected on the reef using a handnet and localized sprays of 1 : 2 clove oil : ethanol, which anaesthetized fish, placed in plastic bags for transport, and then held overnight in aquaria with running water until tested. The mean size of fish exposed to a gnathiid was 17·4 ± 0·2, 12·35–22·5 mm (SL ± SE, range) or not exposed to a gnathiid was 17·3 ± 0·3, 13·0–27·0 mm; and fish SL did not differ between treatments (ANOVA, $F_{1,163} = 0{\cdot}053$, $P = 0{\cdot}819$). Fish were then placed in black plastic containers (16 × 11 × 4 cm) holding 365 mL of seawater. Fish were randomly allocated to a treatment (one gnathiid: total $n = 79$, no gnathiid: total $n = 86$). Every hour, for 10 h, we recorded the status of fish and (for trials with a gnathiid) the location of the gnathiid (attached to fish or not, and location of attachment site). This also provided an estimate of the time elapsed before gnathiids infected fish. Since fish were sampled hourly it was not possible to determine the exact times of attachment and detachment. However, it was possible to estimate the number of hours that gnathiids required to attach and feed. To determine if gnathiids that never attached and then disappeared were hiding in the gills, we euthanized these fish in a plastic bag placed in an ice slurry and examined their gills under a dissecting microscope.

GNATHIID INFECTIONS PRIOR TO PERFORMANCE EXPERIMENTS

Individual settlement stage fish used in the experiments below were placed in individual black plastic containers, as above, and randomly assigned to a treatment (one or no gnathiid). The gnathiid was added to the container 3–39 h after the removal of fish from light traps. The swimming performance and oxygen consumption of fish were tested after the gnathiid had fed (presence of engorged gut) and dropped off the fish, between 07.00 and 19.00 h. In cases where the gnathiid disappeared (presumed to have been eaten by the fish), the gnathiid or fish had died, or the gnathiid had not fed in time for the fish to be tested the fish was discarded.

SWIMMING PERFORMANCE

Swimming performance was measured for fish that were previously parasitized or unparasitized by a gnathiid ($n = 30$ per treatment). Mean standard length (SL) of previously parasitized fish was 11·4 ± 0·1 mm (SL ± SE) and of unparasitized fish it was 11·5 ± 0·1 mm and fish size did not differ between treatments (ANOVA, $F_{1,58} = 0{\cdot}005$, $P = 0{\cdot}946$). Half of the former fish had the gnathiid introduced on the previous night (19.00–21.30 h) and half the morning (10.00–11.20 h) of the day they were tested. Swimming trials were done using a clear Perspex, two-lane swim chamber (modified after Stobutzki & Bellwood 1997). An 8000 L h^{-1} submersible pump (Resum SP96005, Guangdong Risheng Group, Raoping, China) circulated water through the system and a calibrated gate valve controlled the water volume. Speed was calibrated by recording the volume of water passing over the weir in a set period of time, and dividing that by the sum of the cross-sectional area of each channel. Laminar flow was verified using a video camera (Sony DSR PD100AP, Kensington, Victoria, Australia) and neutral-density particles (unexpanded styrofoam balls).

Critical swimming speed (*U*-crit), an index of maximum swimming speed maintainable over short periods (Plaut 2001; Leis 2006), was used to determine the effect of gnathiids on the swimming performance of settlement-stage fish. The critical swimming speed of larvae was calculated as: $U\text{-crit} = U + (t/t_i \times U_i)$, where U is the penultimate speed, U_i is the velocity increment, t is the time swum in the final velocity increment and t_i is the set time interval for each velocity increment. Critical swimming speed has often been found to be correlated with other measures of swimming performance critical to the survival of larval fishes (Fisher *et al.* 2005).

One fish per lane was tested and fish of the two treatments were randomly allocated in equal numbers to each lane and allowed to acclimatize for 2 min before the start of the trial. The water speed was then increased by approximately three body lengths per second (4·5 cm s^{-1}) every 2 min until one fish could no longer maintain its position in front of the retaining mesh (Bellwood & Fisher 2001). This protocol involved fish swimming for up to 18 min. Experimental effects were controlled by using a paired design such that each trial involved a fish that was previously parasitized and one that was not.

OXYGEN CONSUMPTION

Oxygen consumption is a measure of an animal's resting metabolic rate (Brett 1964). This was measured for settlement-stage fish that were previously parasitized by a gnathiid or not (n = 16 per treatment). Mean weight (wt) of previously parasitized fish was 0·059 ± 0·001 g (wt ± SE) and of unparasitized fish it was 0·061 ± 0·001 g and fish weight did not differ between treatments (ANOVA, $F_{1,30}$ = 0·956, P = 0·336). Weight was used here to standardize measurements according to fish mass. Fish from both treatments were tested each day, one at a time, over 7 days. The gnathiid was added to the fish at 1730 h on the day previous to the trials. Closed respirometry, following Nilsson (1996), was used to measure oxygen consumption. Fish were acclimatized to the 59 mL chamber in running water for at least 30 min. An oxygen electrode (WTW Oximeter Oxi 340i; Wissenschaftlich Technische Werkstätten, Weilheim, Germany) was inserted into the chamber which was submerged in running water to maintain a stable temperature (30 ± 1 °C). Oxygen concentration was recorded with MULTILAB PILOT software (Weilheim Germany, Cary, NC, USA) and until oxygen levels fell below 60% of air saturation (47–149 min).

PERSISTENCE IN THE WILD

The effect of a gnathiid on the performance, or survival, of settlement-stage larvae in the wild was measured by placing a pair of tagged fish (n = 71), consisting of a previously parasitized and an unparasitized fish, on a patch of coral rubble and monitoring which individual of the pair survived the longest, up to 48 h from being placed on the reef. Fish, randomly selected from holding aquaria and held in a bucket, were measured and tagged with a pink or black subcutaneous fluorescent elastomer tattoo (Northwest Marine Technology) on the anterior dorsal musculature using a 29-gauge hypodermic needle (McCormick & Hoey 2004). The colour of tag used per treatment was randomly allocated on each day. After tagging, fish were placed in a black container as above, and a gnathiid was added to half of the containers and gnathiids allowed to engorge and drop off the fish. Fish were exposed to a gnathiid the previous night, overnight or on the same day they were tested. Fish that had been previously fed upon by a gnathiid were paired with a randomly selected control fish from the same group and placed in a plastic bag for transport to the reef. Several trips were made to the reef each day as engorged gnathiids dropped off fish and those fish became available for pairing with control fish. Fish were placed on the reef over six consecutive days (7, 5, 10, 19, 21, 9 pairs each day, respectively) between 08.57 and 17.50 h. Confounding effects due to spatial and temporal differences between trials were controlled by using a paired design.

Pairs of fish were placed on labelled small patch reefs of dead coral rubble (25 cm diameter × 15 cm high) on sand, 1·5–3·6 m from the reef edge and 2–3 m apart. Patch reefs were at the back of the reef in 2·5–5 m depth. Pairs of fish were surveyed up to four times a day from 10.00 to 18.00 h. In 23% of the trials, both fish in the pair had disappeared before they were re-surveyed or between one survey and another; in 10% of the trials both fish still remained on reefs after 48 h, at which time the experiment was terminated. For the final 48 pairs having one survivor, mean size of previously parasitized fish was 12·7 ± 0·1 mm (SL ± SE) and of unparasitized fish it was 12·7 ± 0·1 mm and fish size did not differ between treatments (ANOVA, $F_{1,94}$ = 0·047, P = 0·828).

For the single surviving fish found on the reef, the duration since the time the gnathiid dislodged from the previously parasitized fish and time the pair of fish was placed on the reef was 196, 149, 228 min (median, 25th,75th quantile) for fish which had been exposed to a gnathiid and it was 144, 125, 259 min for fish which had not been exposed to a gnathiid and this did not vary between treatments (Wilcoxan test Z = 0·766, P = 0·444); this indicated time from when the gnathiid had dropped off fish did not affect the rate of fish persistence on the reef.

STATISTICAL METHODS

Where the statistical assumptions of ANOVA were met, this analysis was used to test for differences in fish SL and weight between treatments; where these assumptions were not met, a Wilcoxan (rank) test was used. To test whether the proportion of wild fish infected with a gnathiid varied between fish collected at dawn and during the day, a Fisher's exact test was used. In the gnathiid feeding behaviour trials, a logistic regression was used to determine whether fish SL was a significant predictor of whether a gnathiid had disappeared (was presumably eaten) before attaching to a juvenile fish. To test whether the critical swimming speed of a pair of fish (a previously-parasitized and an unparasitized fish) differed according to parasite treatment, separate paired two-sample t-tests were done for the situations where the fish had had the gnathiid added to its container on the previous night of the test day and on the morning of the test day; an ANOVA was used to test whether the swimming speed of parasitized fish differed between fish where the gnathiid was added in the morning of the test and where the gnathiid was added the previous night. To determine whether parasite treatment affected which fish from the pair tested (a previously parasitized and unparasitized fish) in the two-lane swim chamber gave up swimming first, the proportion of fish which gave up swimming first for previously parasitized and unparasitized fish was compared to the hypothesized probabilities of random behaviour (50% and 50%) using a Pearson's chi square test. A full factorial analysis of covariance (ANCOVA), with oxygen consumption as the response, parasite presence as the factor, and time of day as the covariate was used to test whether oxygen consumption varied between parasitized and unparasitized fish and whether this was affected by the time of day the fish was tested; the assumptions of the analysis were examined using the residuals. To determine whether parasite treatment affected which individual fish from a pair (a previously parasitized and unparasitized fish) disappeared from the coral rubble patch reef first, the proportion of fish which disappeared first for previously parasitized and unparasitized fish was compared to the hypothesized probability of random behaviour (50% and 50%) using a Pearson's chi square test; to determine whether the proportion of previously parasitized and unparasitized fish that had disappeared first from the reef above differed between fish tag colours, the proportions per treatment for each colour were compared in a two by two contingency table using a Fisherman's exact test. Statistics were performed using the software JMP 8.0 (Cary, NC, USA).

Results

GNATHIID OCCURRENCE ON WILD FISH

Of 113 fish collected at dawn, 4 (3·5%) had a gnathiid juvenile; no other crustacean parasites, except for an unidentified immature parasitic copepod, were found. Gnathiids (gnathiid length mm per fish SL mm) found attached to fish were: a half-engorged gnathiid (0·90/11·6), an unengorged gnathiid (0·90/12·4), and two engorged gnathiids (0·98/18·1; 1·16/12·4); the latter was identified as *Gnathia falcipenis* Holdich and Harrison (Holdich & Harrison 1980) by comparing it to a photo library of various stages and moulted adults to determine which larvae belonged to which adult (A.S.G. and C. Jones, unpublished data), but the remaining three could not be identified. The mean SL ± SE, range of fish with no gnathiid was 15·8 ± 0·3, 11·0–28·3 mm. Of 80 fish collected during the day, none had a gnathiid and no other crustacean parasites were found; the mean SL ± SE, range of the fish was 12·9 ± 0·2, 10·5–17·3 mm. Gnathiid distribution did not differ significantly between dawn and during the day (Fisher's exact test, $P = 0{\cdot}140$).

GNATHIID FEEDING BEHAVIOUR AND EFFECT ON MORTALITY

In 23% of trials, the gnathiid disappeared before it attached to the juvenile fish and was presumed to have been eaten as no shelter for the gnathiid was available (four gnathiids immediately disappeared within the first hour; and 14 were never observed attaching to fish, disappeared during the trial, and were not found in gills afterwards). In the other trials ($n = 62$), gnathiids attached to a fish. Gnathiids attached to the body (61%), a fin (25%), an eye (3%), or an unobserved site (11%) which could have involved unobserved feeding in the gill cavity or elsewhere as these were later found engorged. Internal bleeding at the site of attack was occasionally noted. After detaching from fish, 87% of gnathiids disappeared and were presumed eaten. Most (71%) gnathiids attached within 2 h of being exposed to the fish, and 24% and 5% attached after 2–3 h and 6–7 h, respectively. Gnathiids remained attached to fish up to 3 h (42%), 3–6 h (37%), and 6–10 h (21%). A logistic regression showed that fish SL was not a significant predictor of a gnathiid disappearing (presumably eaten) before attaching ($\chi^2 = 0{\cdot}067$, d.f. = 1, $P = 0{\cdot}795$, $n = 79$). In the absence of predators, there was no mortality in fish exposed or not to a gnathiid. The volume of an engorged third stage *G. aureusmaculosa* gnathiid gut is 2 mm^3 (Grutter 2003). This is 85% of the total blood volume of a settlement stage *P. amboinensis* weighing 0·06 g or 5% of the total body volume of each individual (40 mm^3), estimated from the volume of a group of five fish (Grutter 2008). Third stage gnathiids each weighed a mean 0·0003 g, estimated by weighing 10 groups of 10 gnathiids; hence the ratio of gnathiid to *P. amboinensis* weight was 1 : 200.

SWIMMING PERFORMANCE

When tested in pairs in a double-lane swim chamber, the critical swimming speed of previously-parasitized settlement stage fish was significantly lower than in unparasitized fish in both situations where the fish had had the gnathiid added to its container on the previous night of the test day (paired two-sample *t*-test, $t = 2{\cdot}264$, d.f. = 14, $P = 0{\cdot}040$; Fig. 2a) and on the morning of the test day ($t = 4{\cdot}555$, d.f. = 14, $P = 0{\cdot}0004$; Fig. 2b). The time when fish had a gnathiid added to their container affected the swimming speed of fish, with the speed (mean ± SE) of fish tested being lower for those where the gnathiid was added in the morning of the test (25 ± 1·4 cm sec^{-1}) than those where the gnathiid was added the previous night (29 ± 1·1 cm sec^{-1}) (ANOVA, $F_{1,28} = 4{\cdot}888$, $P = 0{\cdot}035$) indicating that the latter fish had begun to recover from the infection. The previously parasitized fish gave up swimming first 77% of the time compared with the unparasitized fish; this response is significantly different from 50% (Pearson $\chi^2 = 8{\cdot}53$, d.f. = 1, $P = 0{\cdot}003$), the predicted value if the behaviour were random.

OXYGEN CONSUMPTION

Previously parasitized settlement-stage fish had a 35% higher oxygen consumption rate (least square mean 2023 ± SE 140 mg $Kg^{-1}h^{-1}$) compared with unparasitized fish (1499 ± 140 $Kg^{-1}h^{-1}$) (ANCOVA: $F_{1,1} = 6{\cdot}997$, $P = 0{\cdot}013$; Fig. 2c); oxygen consumption also increased with the covariate time of day ($F_{1,1} = 4{\cdot}514$, $P = 0{\cdot}043$); and this slope did not vary with parasite presence ($F_{1,1} = 0{\cdot}120$, $P = 0{\cdot}731$).

PERSISTENCE IN THE WILD

When tagged settlement-stage fish were placed in pairs on coral rubble patches and monitored over 48 h, the previously parasitized fish disappeared from the reef first 67% of the time, compared with unparasitized fish (Fig. 2d). This response was significantly different (Pearson $\chi^2 = 5{\cdot}33$, d.f. = 1, $P = 0{\cdot}020$) from 50%, the predicted value if the behaviour were random. The proportion of previously parasitized fish that disappeared first did not differ between tag colours (Fisherman's exact test $P = 0{\cdot}125$). On some occasions, soon (often just seconds) after the two fish had been placed on the coral patch, one would aggressively approach the other and attempt to chase it away from the reef.

Discussion

ECTOPARASITES AFFECT HOST BEHAVIOUR AND PHYSIOLOGY

Attack by a single gnathiid isopod on a juvenile coral reef fish, in the absence of predators, did not directly kill captive resting juveniles over the time frame examined. Gnathiid attack, however, resulted in an increased respiration in resting individual fish and a reduced swimming speed of fish in captivity,

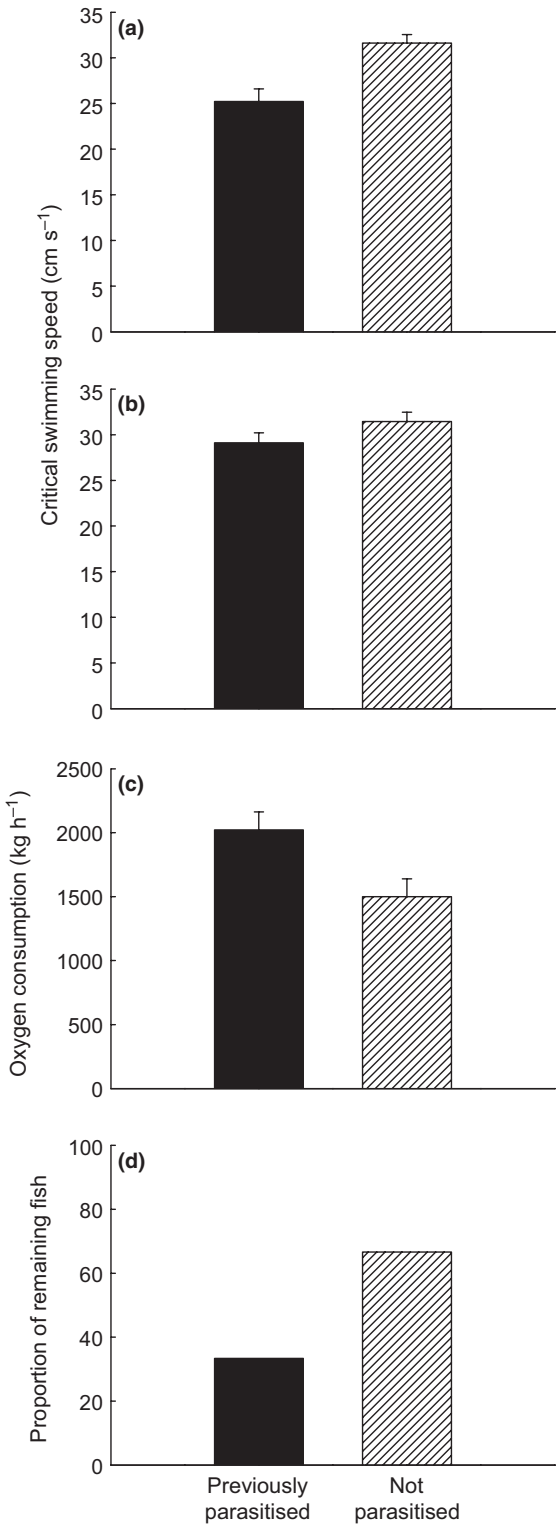

Fig. 2. Measures of performance of settlement-stage *Pomacentrus amboinensis*. The fish had been held in a container and was either previously parasitized (black bar) or not (hatched bar) by a *Gnathia aureusmaculosa* gnathiid isopod before being tested. Critical swimming speed of fish previously held in the container since (a) the morning of the day tested or (b) the previous night of the day tested; (c) Least square mean (adjusted for time of day tested) oxygen consumption of fish and (d) remaining single fish of a pair placed on a coral reef patch and surveyed for up to 48 h. Error bars are standard errors.

and affected the successful establishment of juvenile fish in a natural setting. These findings reveal ectoparasites affect several behavioural and physiological processes which are important in juvenile fish survival and thus they may contribute to some of the high mortality of fishes observed during the transition from the pelagic environment to the reef.

Gnathiids detrimentally affected settlement-stage ambon damselfish *Pomacentrus amboinensis* in several ways. First, fish previously parasitized by a gnathiid had a lower critical swimming speed (*U*-crit) compared with unparasitized fish. The blood ingested by the gnathiids, estimated at 85% of the fish's blood (Grutter 2008), would have likely made fish anaemic – a symptom that typically decreases fish swimming performance (Gallaugher, Thorarensen & Farrell 1995). Fish swimming performance can determine survival (Plaut 2001), the ability to find food or avoid unfavourable conditions (Videler 1993; Von Herbing, Gallager & Halteman 2001), and the encounter rate with prey and avoidance of predators (Videler 1993). *U*-crit provides a measure of the maximum speeds at which fish can swim, and therefore estimates the ability of fish to cover relatively short distances (< 500 m) at high speeds, over short time scales (< 30 min), which includes moving among and within habitats (Fisher, Bellwood & Job 2000). *U*-crit can also be regarded as a measure of relative stamina. If gnathiids cause a reduction in a fish's stamina, then such fish may re-disperse after the initial settlement choice to areas where energy demands are less (e.g. low flow environments) to offset the negative effects of gnathiids. This will have the strongest influence on fish species that demonstrate a settlement transition period involving movement among a number of microhabitats after their initial association with the reef (e.g. McCormick & Makey 1997), and also in species that preferentially settle to high energy habitats such as the reef crest (Fulton, Bellwood & Wainwright 2001). If gnathiids ultimately affect a juvenile's habitat choice and/or result in differential post-settlement mortality among habitats, this may affect the adult population distribution and abundance. The faster swimming rate of fish tested after they had a gnathiid added to their container the previous night, compared to fish tested the day of the trial, suggests that they had begun to recover from the gnathiid's attack.

Second, settlement-stage fish that were previously parasitized by a gnathiid had, when adjusted for the time of day they were tested, 35% higher oxygen consumption rates than unparasitized ones. Because fish were tested after having been exposed to a gnathiid overnight, and thus several hours after gnathiids had detached from fish, it means this physiological response was maintained for some time after the gnathiid attack. *Cheilodipterus quinquelineatus* cardinalfish harbouring one *Anilocra apogonae* isopod also have a higher oxygen consumption (Östlund-Nilsson *et al.* 2005), attributed to the hydrodynamic resistance of the parasite and increased energy consumption in parasitized hosts. Although our *P. amboinensis* were tested after the gnathiid had detached, the gnathiid would have likely provided a significant hydrodynamic resistance during the several hours it was attached to the fish prior to testing because the ratio of gnathiid volume to fish volume

(5%) is relatively high. Indeed, in other larval and juvenile damselfishes, swimming behaviour was affected by a gnathiid, particularly when attached to the fins or gills (Grutter *et al*. 2008). The slight increase in oxygen consumption over the course of the day, regardless of parasite treatment, may be due to a corresponding increase in aquarium water temperature which is known to increase oxygen consumption in damselfishes (Nilsson *et al*. 2009).

Third, gnathiids decreased the persistence of fish individuals in natural conditions. When pairs of fish on small coral rubble patches were surveyed over 48 h, the fish that was previously parasitized by a gnathiid persisted less often than the unparasitized fish. Therefore, gnathiids affected the ability of *P. amboinensis* to stay in one place on the reef and is thus a measure of successful establishment on the reef. Our laboratory experiments highlight possible explanations for this pattern. One is that previously parasitized fish became more fatigued and so could not swim fast enough to maintain their position on the coral patch. Indeed, oxygen demand increases with increasing swimming speeds in fishes (Brett 1964; Nilsson *et al*. 2007). Because the coral patches were positioned in the open sand to isolate fish, and this resulted in maximal exposure to tidal currents, fish often had to swim to remain on the patch. On several occasions, fish were observed being slowly swept away from the coral patch into open sand by the current despite their attempts to remain on the patch. The previously parasitized fish may also have been poor competitors for access to refuges, similar to that shown in bridled reef gobies *Coryphopterus glaucofraenum* infected with *Pharodes tortugensis* copepods (Forrester & Finley 2006). Since our fish were in pairs, this may have arisen out of competitive interactions between the two individuals. Indeed, field observations revealed aggressive interactions between the two. Fish persistence was not affected by the duration of time since gnathiid dislodged and time fish were tested. This suggests that, although increased recovery times resulted in faster swimming rates in laboratory fish, no such effect was apparent when fish were tested in the wild. Gnathiids may therefore have a greater effect on fish physiology than was detected in this study. A loss of an estimated 85% of the total blood volume of settlement-stage *P. amboinensis* as a result of a gnathiid attack is likely to have a variety of other affects on the host than those measured here and suggests an avenue for future research.

ECTOPARASITES CONTRIBUTE INDIRECTLY TO MORTALITY

This study most resembles parasite-induced trait-mediated indirect interactions involving predators-prey interactions where the parasite infects the prey (Hatcher, Dick & Dunn 2006). Effects of blood-feeding gnathiids on fish behavioural and physiological traits may have increased the susceptibility of fish to predators. In a similar study, recently-settled *P. amboinensis* suffered high levels of predation by relatively small predatory fishes (Holmes & McCormick (2006). *Pomacentrus amboinensis* that were compromised by a previous attack by a gnathiid may have been more vulnerable to predators when on patch reefs or if unable remain on patch reefs when in the open sand. Energy depletion caused by the infection may have also affected their foraging behaviour such that it increased their risk of predation, a common occurrence in other parasitized fishes (Barber, Hoare & Krause 2000). Indeed, two observations revealed that fish were preyed upon by the fish *Thalassoma lunare* when they left the patch reef (A.S.G. pers. obs.). Similarly, branchiurids *Argulus canadensis* increase the predation risk of juvenile *Gasterosteus aculeatus* and *G. wheatlandi* sticklebacks (Poulin & Fitzgerald 1989). The observed changes in the traits of individuals may also affect its interactions with other species resulting in more complex trophic cascades (Offenberg, Macintosh & Nielsen 2006). For example, if gnathiid attack indirectly reduces the foraging efficiency or competitive ability of individual fish, this may affect the fish's prey and competitors, respectively.

IMPLICATIONS

Mortality rates of coral reef fishes at settlement are generally very high (Almany & Webster 2006). Gnathiids may indirectly contribute to this mortality. Since selective predation of infected hosts removes a disproportionate fraction of parasites, Hudson, Dobson & Newborn (1992) argued that it reduces the regulatory role of parasites. Gnathiids, however, do not remain on the host for long (Grutter 2003). Importantly, the behavioural and physiological effects were observed even after the gnathiid had finished feeding and dropped off the host. Higher predation rates of parasitized animals often facilitate trophic transmission, although this only appears to occur in parasites with indirect life cycles (Lafferty 1999), which does not include gnathiids. The higher predation rates of parasitized fish in this study appear to be the result of the pathology due to infection, without being adaptive to the parasite (Poulin 1994).

Gnathiid isopods are ubiquitous on the reef and occupy most microhabitats (Jones & Grutter 2007), and spend much of their life in the benthos (Smit & Davies 2004) making them difficult to avoid. Our low detection rates of gnathiids at dawn and during the day, compared to the rapid rate at which gnathiids fed in the laboratory and the finding in another study that gnathiids were associated with caged settlement-stage *Pomacentrus moluccensis* at night only (Jones & Grutter 2008), suggests that the presence of gnathiids on young fish can change over short time scales. Thus this study may have underestimated gnathiid abundance and is therefore conservative. Their effects may therefore be larger than the 3·5% infection rate at dawn suggested here, with more fish likely attacked than was detected here, possibly even repeatedly, in the first few days after settling. The cumulative effects are thus likely to be much greater than the ones shown here. The wild juvenile fish (11·6–18·1 mm SL) infected with a gnathiid are likely to have been on the reef for 0–10 days (M.I. McCormick unpublished data). There is already a huge variation in

the condition of fishes at settlement that can affect fish survival (e.g. Jones & McCormick 2002; Grorud-Colvert & Sponaugle 2006; Gagliano, McCormick & Meekan 2007; Hamilton, Regetz & Warner 2008). Our study suggests that infection by a gnathiid may compound variability in fish condition at settlement. Why fish larvae migrate to from the reef to the pelagic environment is highly debated (Strathmann *et al*. 2002). It has been posited that it may disrupt, avoid, or lower transmission of infectious agents (Strathmann *et al*. 2002). This study suggests that one of these agents may be gnathiid isopods.

Despite their prevalence and ubiquity in natural systems as diverse as terrestrial systems (e.g. Arthur 1965; Keiper & Berger 1982), salt marshes (Poulin & Fitzgerald 1989) and the sea (e.g. Stepien & Brusca 1985; Grutter & Poulin 1998; Fogelman & Grutter 2008), the impact of highly mobile ectoparasites on host population dynamics, particularly during the early life-history stages, remains largely unquantified. Our study isolated the sublethal impact of blood-feeding gnathiid isopods on their hosts (prey) and exposes the mechanism that may link them to population level impacts. Although mortality in the young stages of fishes is generally attributed to predation (Leis & McCormick 2002), our study shows how gnathiid isopods can indirectly affect the population dynamics of organisms during critical early-life history stages by affecting their behaviour and physiology and their subsequent establishment in the wild. The relatively ephemeral nature of the association between highly mobile blood-feeding ectoparasites and their hosts, means such ectoparasites are a relatively 'invisible' group whose effects remain long after they have left.

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