Parasitic isopod *Anilocra apogonae*, a drag for the cardinal fish *Cheilodipterus quinquelineatus*

Sara Östlund-Nilsson[1,4,*], Lynda Curtis[2], Göran E. Nilsson[3], Alexandra S. Grutter[2]

[1]Vision, Touch and Hearing Research Centre (VTHRC), School of Biomedical Sciences, and [2]Department of Zoology
and Entomology, University of Queensland Brisbane, Queensland 4072, Australia

[3]Physiology Programme, Department of Molecular Biosciences, University of Oslo, PO Box 1041, 0316 Oslo, Norway

[4]*Present address:* Department of Biology, University of Oslo, PO Box 1066, 0316 Oslo, Norway

ABSTRACT: Cymothoid isopods *Anilocra apogonae* are regular ectoparasites of the cardinal fish *Cheilodipterus quinquelineatus* on the Great Barrier Reef. To determine whether this large isopod, attached to the head of the fish, affects the physiology and behaviour of its host, we conducted morphological measurements to obtain a condition index and several laboratory experiments on fish with and without isopods. The condition index did not vary between parasitised and non-parasitised wild fish. However, we found that parasitised fish lost more weight than unparasitised fish when fed a low food ration. Parasitised fish also had a higher rate of oxygen consumption than non-parasitised fish. When maintaining body posture in calm water, parasitised fish had an elevated pectoral fin beat frequency, probably because the isopod attaches asymmetrically, causing an asymmetrical weight balance for which the fish needs to compensate. Moreover, the sustained aerobic swimming speed as well as the swimming endurance at high water speeds were reduced in parasitised fish, possibly because of the drag from the parasite. The results suggest that parasites can have significant effects on fish even if this is not revealed by their body condition index in the wild. The metabolic effects found imply that parasitised fish may have to spend more time foraging to compensate for their higher metabolism. This could expose them to a higher risk of being eaten, a situation made worse by an impaired swimming ability that may reduce their capacity to escape a predator.

KEY WORDS: Parasite · Isopod · Apogonidae · Cardinal fish · Condition index

INTRODUCTION

Members of the isopod family Cymothoidae are among the largest parasites of fishes and are highly host specific (Brusca 1981). Adult cymothoids are usually ectoparasitic on fish, being attached to the skin, gills or oral cavity of their hosts, whereas their juveniles are often free living (Bunkley-Williams & Williams 1998). Like most isopods, cymothoids are considered to feed principally on blood, but they may consume the mucus, epithelium and subcutaneous tissues of their host (Bunkley-Williams & Williams 1998). The lifespan of isopods appears to vary from species to species, with most living for 1 to 2 yr (Brusca 1981), while others may live for over 9 yr on the host fish (Maxwell 1982).

In some field studies, fish parasitised with isopods have been found to suffer from reduced condition index and growth (Krykhtin 1951, Kroger & Guthrie 1972, Sadzikowski & Wallace 1974, Lanzing & O'Connor 1975, Romestand & Trilles 1979, Adlard & Lester 1994), impaired reproduction and a reduced lifespan (Adlard & Lester 1994). Several studies have found no harmful effects on the host fish (Weinstein & Heck 1977, Maxwell 1982, Chang 1999). However, such an apparent lack of effect on the host condition index from the association with the isopod could be explained by the host compensating for a higher rate of energy loss by feeding more than non-parasitised individuals.

At Heron Island, on the Great Barrier Reef, Adlard & Lester (1994) showed that the cymothoid isopod

Fig. 1. The host fish *Cheilodipterus quinquelineatus* and its isopod *Anilocra apogonae* (photo: G. E. Nilsson)

Anilocra pomacentri depressed the growth, reproduction and survivorship of its host, the damsel fish *Chromis nitida*. Other fishes also carry similar parasites (Brusca 1981), yet little is known of their effect on their host. In particular, no studies have been done on their effect on host metabolism or swimming performance.

Cardinal fishes (family Apogonidae) are abundant members of tropical and temperate reef fish communities. They are also known to be very site-specific (Marnane 2000). At Lizard Island (Great Barrier Reef), the 5-lined cardinal fish *Cheilodipterus quinquelineatus* lives sympatrically with several other cardinal fish species among the framework of branching corals, under ledges or in caves. This species is frequently parasitised with the cymothoid isopod *Anilocra apogonae* (Fig. 1), a strikingly large parasite in the population we studied, its length being about a quarter that of its host. The large size of this parasite relative to the size of the fish raises the question of what affect it has on its host.

To determine the effect of the isopod *Anilocra apogonae* on the condition of 5-lined cardinal fish, we measured the condition index of wild fish. To examine the effect on host metabolism and behaviour, we tested in the laboratory whether (1) parasitised fish required a higher nutritious input compared to non-parasitised fish, if (2) the isopod affected the metabolism of the host, measured as oxygen consumption, and (3) whether the isopod affected the swimming performance of the fish.

MATERIALS AND METHODS

The study was conducted during October and November 2000, and continued in February and March 2001 at Lizard Island (14 40' S, 145 28' E), in the northern section of the Great Barrier Reef, Australia. Five-lined cardinal fish *Cheilodipterus quinquelineatus* with and without an attached *Anilocra apogonae* were caught while on SCUBA using localised sprays of clove oil to temporarily anaesthetise the fish. The fish were then caught with a small hand net and put into plastic bags, in which they were transported to the laboratory at Lizard Island Research Station (approximately 30 min). Fish were placed in aquaria continuously supplied with seawater pumped directly from the ocean. The temperature was 29 to 31°C.

Body condition index in wild fish. To examine the effect of *Anilocra apogonae* on the condition index of *Cheilodipterus quinquelineatus*, parasitised and non-parasitised fish were collected in the field and within 24 h of capture, fish were killed with an overdose of clove oil solution. For all fish sampled, standard length (mm) (the tip of the snout to the caudal peduncle) and total dry weight (mg) were measured and recorded. Dry weight was measured after drying the fish at 60°C for 24 h. In addition, the length (including the uropods) (mm) of the isopods of parasitised *C. quinquelineatus* was recorded.

Feeding experiment and nutritional status. To determine whether parasitised fish incur a greater reduction in condition factor when fed a low food ration, we conducted a feeding experiment. Parasitised and non-parasitised fish were matched in size (standard length). They were randomly assigned to either a high food ration or to a low food ration. Fish were held individually in opaque aquaria (length × width × height = 33.7 × 30.2 × 27.5 cm) divided into 4 equal sections (L × W × H = 16.85 × 15.1 × 27.5 cm). All fish were supplied with a shelter made from PVC pipe (length = 6 cm, diameter = 5.5 cm). Fish in the high-food group were fed twice a day for the duration of the 14 d experiment. At each feeding, they were fed 3 small pieces of pilchard fish flesh (mean wet weight per piece = 0.200 g, mean dry weight = 0.032 g). Fish in the low-food group were fed the same quantity of food (i.e. in 3 × 0.200 g in mean weight) but only once on the seventh day of the 14 d trial. At the conclusion of the experiment, wet weights and standard length measurements of the fish were recorded, while the fish were anaesthetised.

Effect of isopods on fish metabolism. To determine whether an attached isopod was energetically demanding for the fish, we measured the resting oxygen consumption of parasitised (n = 10) and non-parasitised (n = 8) fish in a closed respirometer, as described by Nilsson (1996). The volume of the respirometer chamber was 600 ml, and the consumption of O_2 was registered with an O_2 electrode. Each fish was allowed to acclimate in the respirometer for at least 2 h. The measurement of O_2 consumption was

started by turning off the water supply to the chamber. All fish remained virtually motionless during respirometry, which lasted 50 to 70 min. The experiments were terminated when the water oxygen level fell below 60% of air saturation.

In addition, the oxygen consumption rates of a subgroup of parasitised fish were measured both before and 48 h after the removal of the isopod, to quantify the immediate effect of the isopod on the host. We also measured the oxygen consumption rates of isopods (n = 4) that we removed from the fish in order to determine how much the isopod itself contributed to the measured oxygen consumption. The volume of the isopod respirometer was 12 ml. The estimated O_2 consumption per isopod was subtracted from the total oxygen consumption of each fish with a parasite (taking the parasite weight into account) to obtain the O_2 consumption of the fish itself.

In the calculations where parasitised and non-parasitised fish were compared, the oxygen consumption of the isopod was subtracted from the parasitised fish data.

Effect of isopods on fish swimming performance. A swimming chamber was constructed essentially as described by Stobutzki & Bellwood (1994) and consisted of a 200 mm long Perspex tube (inner diameter = 52 mm). The water was fed into the chamber using a submersible pump (Davey Sump Pump DC10A-2) placed in a 300 l reservoir below the chamber. The reservoir was continuously supplied with seawater at 30 ± 1°C. Maximum water flow was 1200 ml s^{-1}, which corresponded to a linear speed of 565 mm s^{-1}. A gate valve regulated the speed, and flow rates were calibrated to the angle of the valve. The water was forced through a number of densely packed plastic drinking straws (diameter = 5 mm, length = 45 mm) to create a laminar flow in the chamber. The fish was retained in the chamber by the flow straightener in front of the fish and by a plastic mesh (2.5 mm mesh size) placed 20 cm downstream from the flow straightener. The water speed was determined by measuring the volume of water leaving the chamber per unit of time divided by the cross sectional area of the chamber. A single fish was placed in the chamber, the water velocity was set to 25 mm s^{-1} and the fish was allowed to acclimate for 10 min. Like the other cardinal fishes, this species displays a labriform swimming mode (pectoral fin swimming), and therefore uses its pectoral fins for sustained aerobic propulsion, only utilising the caudal fin for very rapid anaerobic swimming bouts (Evans 1997).

Two measures of swimming performance were taken. To measure the maximum sustainable swimming speed, the water velocity was slowly increased until the first bouts of caudal fin beating occurred, then the water speed was lowered until no caudal fin beating occurred, and the water flow at this point was measured. This was considered to be a fully aerobic swimming mode, which was also confirmed in an initial experiment on 4 fish which showed that they were able to maintain this speed for at least 4 h, during which time no caudal fin beating occurred. The water flow was then decreased to 25 mm s^{-1} and fish were allowed to rest for 15 min. The time to fatigue (in seconds) was then measured for the maximum water speed of the swimming apparatus (565 mm s^{-1}), which in this case corresponded to 7.4 to 10.3 standard body lengths s^{-1}, since the length of the fish varied between 55 and 76 mm. This water speed was approximately 1.5 to 2.7 times faster than the maximum sustained swimming speed, and forced the fish to continuously use their caudal fin. The fish was considered exhausted when it came to rest against the rear plastic mesh in the chamber, at which point the experiment was terminated.

Effect of isopods on pectoral fin beat frequency. We investigated whether an attached *Anilocra apogonae* affected the pectoral fin beat frequency of the resting host. *Cheilodipterus quinquelineatus* beat continuously with their pectoral fins also at rest, probably to maintain their body posture. *C. quinquelineatus* are commonly seen standing in the water column with their head facing the corals. All individuals seem to have a specific position in the coral and this behaviour makes them very difficult to spot at a distance.

Parasitised and non-parasitised (n = 28) *Cheilodipterus quinquelineatus* were collected from the field. Each fish was placed in a separate aquarium (L × W × H = 20 × 30.5 × 20 cm) and allowed to acclimate for 24 h. Trials were conducted each day between 14:00 and 15:00 h to avoid possible variability caused by diurnal changes in activity levels of the fish. The water flow was turned off and the air stone removed 10 min prior to the beginning of each trial to eliminate water currents. The pectoral fin beat of each fish was counted over a 5 min period.

To determine whether the removal of the isopod resulted in a change in pectoral fanning, a second group of parasitised (n = 5) and non-parasitised (n = 5) *Cheilodipterus quinquelineatus* were subjected to this same procedure both before and 24 h after the removal of the isopod from the fish. The isopods were generally removed with a pair of forceps after lightly anaesthetising the parasitised fish in clove oil.

Statistical procedure. Data are given as means ± SD and were checked for normality. Parametric and non-parametric tests were chosen accordingly. In some figures, percentage values are displayed, but in the statistical calculations, percentages/proportions were arcsine-square-root-transformed. Fish condition index was estimated by the residuals from the correlation

between wet weight and standard length. We used Fulton's condition index (weight/length^3) since this is a common method of measuring condition in fish.

RESULTS

Body condition index in wild fish

The isopods were always found attached just posterior and dorsal to the eye of the host fish, on either side of the midline (never centrally). Host and isopod standard length were positively correlated (n = 24, r = 0.49, p < 0.02). The average host parasite length ratio was 1:0.26 mm (54.4 ± 8.45 mm, n = 24 and isopod length 14.3 ± 1.69 mm, n = 24, respectively). There was no difference in condition index, between parasitised (n = 23, Fulton's condition index ± SD: $5.04 \times 10^6 \pm 5.06 \times 10^7$) and non-parasitised (n = 23, $5.13 \times 10^6 \pm 8.93 \times 10^7$) *Cheilodipterus quinquelinatus*, measured directly after being caught (unpaired *t*-test, t = 0.38, p = 0.70).
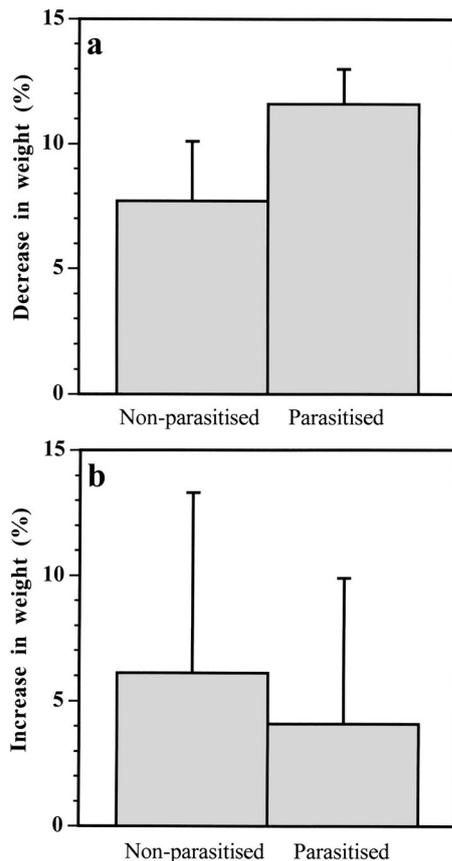

Fig. 2. *Cheilodipterus quinquelineatus*. Percent of weight change over 14 d for the cardinal fish *C. quinquelineatus* with and without the parasitic isopod *Anilocra apogonae* exposed to either (a) a low-food treatment or (b) a high-food treatment
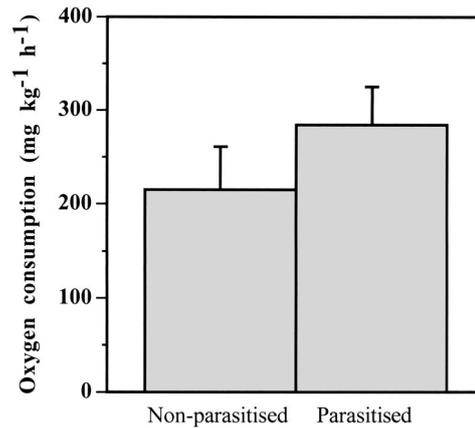

Fig. 3. *Cheilodipterus quinquelineatus*. Resting rate of oxygen consumption for cardinal fish *C. quinquelineatus*, with and without the parasitic isopod *Anilocra apogonae*

Feeding experiment and nutritional status

In the low-food treatment, we found that the parasitised fish (n = 13) lost significantly more weight (calculated as the weight difference between the start and end of the experiment and then divided by the start weight) compared to the non-parasitised fishes (n = 13) (unpaired *t*-test, *t* = 5.1, p < 0.0001, Fig. 2a). In the high-food treatment, both parasitised and non-parasitised fishes gained weight (both n = 11), but there was no difference between the parasitised and non-parasitised group in weight change during the trial (unpaired *t*-test, *t* = 0.51, p = 0.613, Fig. 2b).

Effect of isopods on fish metabolism

The resting rate of oxygen consumption for parasitised *Cheilodipterus quinquelineatus* (n = 10, weight = 5.51 ± 0.82 g) was 25% higher than that of non-parasitised individuals (n = 8; weight = 5.86 ± 0.96 g; Mann-Whitney *U*-test, *U* = 70, p = 0.008, Fig. 3).

The removal of the isopod from another group of fish resulted in a 23% fall in their oxygen consumption, from 292 ± 41.8 to 224 ± 26.9 mg O_2 kg^{-1} h^{-1} (measured after 24 h, n = 7, weight = 4.84 ± 1.05 g; Wilcoxon signed rank test; *Z* = 2.4, p = 0.018). When the oxygen consumption rate of these fish that had had their isopods removed was compared to that of the above non-parasitised fish (from Fig. 3), the difference was not significant (Mann-Whitney *U*-test, *U* = 25.0, p = 0.73).

Interestingly, the mass-specific O_2 consumption of the isopod parasite (294 ± 95.2 mg O_2 kg^{-1} h^{-1}, n = 4, weight of isopod = 103 ± 8 mg) was similar to that of its host.

Effect of isopods on fish swimming performance

The maximum sustainable (aerobic) swimming speed of the isopod-parasitised fish (n = 12) was approximately 13% lower than that of non-parasitised fish (n = 15; unpaired *t*-test: *t* = 2.66, p = 0.014, Fig. 4a). At the maximal speed that could be produced by the swim tunnel, the parasitised fish also swam for a much shorter time before reaching fatigue (n = 22) compared to the non-parasitised individuals (n = 20; unpaired *t*-test: *t* = 2.05, p = 0.047, Fig. 4b).

The measures of swimming performance did not correlate with fish standard length for parasitised and non-parasitised fish (maximum sustained swimming speed: parasitised, n = 13, r = 0.23, p = 0.46; non-parasitised, n = 15, r = 0.23, p = 0.43; time to fatigue: parasitised, n = 11, r = 0.24, p = 47; non-parasitised, n = 16, r = 0.30, p = 0.26). Thus, fish size did not have to be taken into account.

Fig. 5. *Cheilodipterus quinquelineatus*. Pectoral fin beat frequency of the cardinal fish *C. quinquelineatus* with and without the parasitic isopod *Anilocra apogonae*, while standing still in the water column
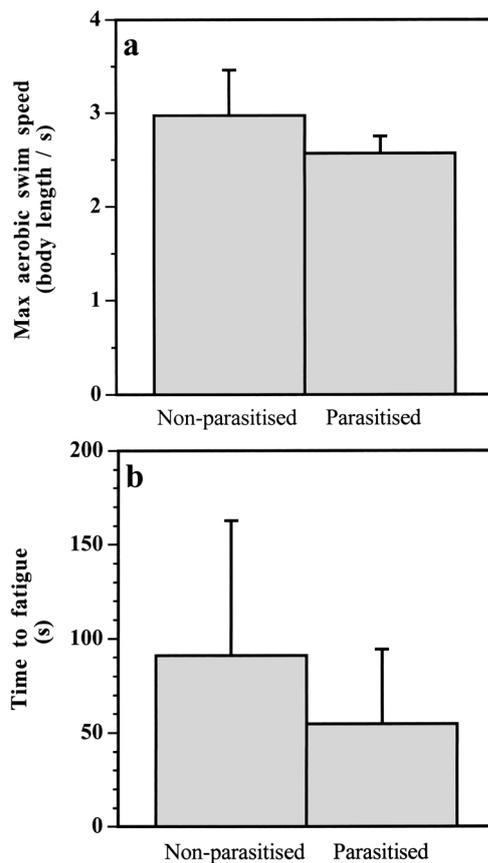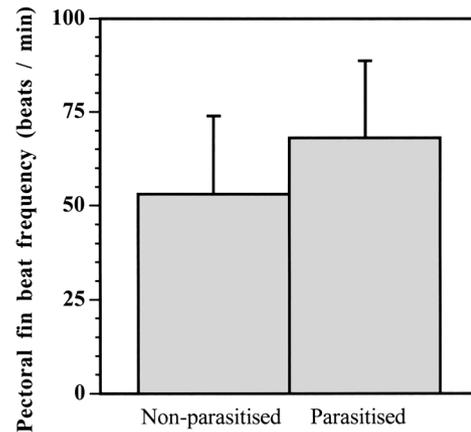

Fig. 4. *Cheilodipterus quinquelineatus*. Swimming performance of the cardinal fish *C. quinquelineatus* with and without the parasitic isopod *Anilocra apogonae* measured as (a) the maximum sustained (aerobic) swimming speed and (b) the time to fatigue

Effect of isopods on pectoral fin beat frequency

When remaining still, the pectoral fin beat frequency of parasitised (n = 29) *Cheilodipterus quinquelineatus* was approximately 23% higher than that of non-parasitised fish (n = 28) (unpaired *t*-test; *t* = 2.7, p = 0.008, Fig. 5). The fin beats, after the removal of the isopod from a second group of parasitised fish, decreased but not significantly (parasitised fish before removal of isopod: n = 12, mean ± SD: 60.1 ± 12.6 fin beats min^{-1}; same individuals after removal of the isopod: n = 12, mean ± SE: 56.5 ± 17.3 fin beats min^{-1}, paired *t*-test; *t* = 0.7, p = 0.49). However, the fin beat frequency of these previously parasitised fish (n = 12, mean ± SD: 56.5 ± 17.4 fin beats min^{-1}) was not significantly different from that of naturally nonparasitised fish (n = 28, mean ± SD: 53.1 ± 20.8 fin beats min^{-1}; unpaired *t*-test; *t* = 0.5, p = 0.62), indicating that the removal of *Anilocra apogonae* resulted in recovery with regard to pectoral fanning.

There were no differences in the standard length between the parasitised group (54.4 ± 9.0 mm, n = 22) and the non-parasitised group (56.3 ± 8.8 mm, n = 18) of fish used in the experiment (unpaired *t*-test, *t* = 0.68, p = 0.51).

DISCUSSION

We found that the condition index of wild-caught *Cheilodipterus quinquelineats* did not differ between fish with and without the parasitic isopod *Anilocra apogonae*. Our laboratory experiments, however, show that this does not necessarily mean that these parasites have no effect on their host. The results of our feeding

experiment suggest that this apparent lack of effect in the wild might be due to an ability of the fish to compensate for the energetic drain of the parasites by increasing food intake. The feeding experiment showed that the parasitised fish lost 35% more weight than non-parasitised fish when held on a low-food regimen. By contrast, the fish receiving large rations of food, all gained a similar amount of weight regardless of being parasitised or not. Thus, *A. apogonae* only had a significant effect on fish weight when food supply was limited. This clearly indicates that the isopods do affect the energy balance of the host, but that this can be compensated for with high levels of food intake; thus, it is possible that fish surviving the parasite association may be high quality individuals that normally would have had a higher condition index than the population average.

However, if parasitised fish have to increase their foraging efforts, this could have drastic consequences for their survival, as foraging is often associated with the risk of being eaten. Previous studies have shown that fish which are under energetic stress due to parasites have a greater need for energy and are, therefore, more willing to compromise safety from predation for foraging gains (Giles 1987, Godin & Sproul 1987).

The fact that the isopod infection increased the demand for energy was corroborated by our measurements of resting oxygen consumption, suggesting that the resting metabolic rate was 25% higher in parasitised fish. Sticklebacks bloated by *Schistocephalus cestodes*, have also been found to have an elevated oxygen consumption (Lester 1970). This was attributed to the energy involved in overcoming the extra hydrodynamic resistance encountered by the bloated fish. The crabs *Hemigrapsus crenulatus*, when parasitised by the acanthocephalan parasite *Profilicollis antarcticus*, also have a higher metabolic rate (Haye & Ojeda 1998). Several studies have indicated that parasitised fish have greater energy requirements as a result of the parasite's use of a portion of their assimilated energy stores (Walkey & Meakins 1970, Giles 1987, Godin & Sproul 1987, Lozano 1991).

In our population, however, we speculate that this may not be the main cost, especially since brooding isopods do not feed and *Anilocra* are brooding most of the time. Unfortunately, we could not control for this in our study. In our population, no fish were ever observed with more than 1 isopod and the body mass of the isopod was only about $\frac{1}{60}$ of that of the fish. Since the isopod had a mass specific rate of metabolism that was virtually identical to that of the host, the relationship of host to parasite metabolic rate should therefore be 1:60; thus, the metabolic effect from a possible non-brooding and feeding isopod would probably have been negligible.

Another and probably more noteworthy factor that could account for a substantial part of the energetic cost of being parasitised could be the hydrodynamic consequences of such a relatively bulky and asymmetrically attached parasite. The parasite was always situated off-centre, on either side of the midline. Our measurements of pectoral fin beat frequency in resting fish showed that parasitised fish were beating their pectoral fins at a rate 23% higher than non-parasitised individuals. Pectoral fins are used to maintain balance in fish (Jobling 1995). Most likely, the increased activity in pectoral fin beats was related to a need for increased fanning to maintain the equilibrium of the body posture when burdened with an asymmetrically placed parasite. During the day, *Cheilodipterus quinquelineatus* primarily occupied territories within the coral, where they remained relatively stationary rather than constantly swimming; thus, much of the energy devoted to fin movements is possibly used for posture control rather than sustained movement in this species.

Non-parasitised adult *Cheilodipterus quinquelineatus* reacted violently if an *Anilocra apogonae* larva was placed on the head; parasitised fish did not exhibit erratic behaviour. This may be because cymothoid isopods attach to juvenile fish and become permanent parasites (Menzies et al. 1955, Weinstein & Heck 1977, Maxwell 1982, Adlard 1989), and parasitised *C. quinquelineatus* may, over time, become behaviourally 'acclimated' to the presence of the isopod (Williams et al. 1982). This suggests that the increase in pectoral fin beats of parasitised fish is less likely to be due to a stress response and more likely to be caused by the off-centred position of the parasite.

We also found that the maximum sustainable (aerobic) swimming speed, and the swimming endurance at a very high (anaerobic) speed, were both lower in parasitised *Cheilodipterus quinquelineatus*. This implies that the impaired swimming performance was related to the increased hydrodynamic drag caused by the parasite. There is a striking parallel in studies showing that external tagging devices on fish reduce swimming performance by acting as a hydrodynamic drag burden (Lewis & Muntz 1984, Mellas & Hayes 1985, Serafy et al. 1995, Adams et al. 1998) or the impact of sea lice infection on the swimming performance of Atlantic salmon (Wagner et al. 2003).

Slower sustained swimming speeds and more rapid times to fatigue may have a number of implications for fish. As *Cheilodipterus quinquelineatus* travel to feeding grounds at night (Marnane 2000), their ability to migrate could be affected due to a reduction in mobility and endurance (Sprengel & Luchtenberg 1991) caused by the parasite.

Their ability to swim against water currents may also be compromised by the isopod *Anilocra apogonae*.

At Lizard Island, water currents can reach 100 to 300 mm s^{-1} (Frith et al. 1986), which for *Cheilodipterus quinquelineatus* correspond to 1.2 to 6 body lengths s^{-1}. In other words, the fish have to swim actively against the high and low tide currents to avoid drifting away from their home territory. This could potentially affect the range of habitats that parasitised fish can choose from if they need to avoid currents. Perhaps parasitised individuals may live closer to foraging grounds to minimise the cost of travel from their resting place. Moreover, a decrease in rapid anaerobic swimming bursts may reduce an individual's ability to avoid and escape predation (Sprengel & Luchtenberg 1991, Coleman 1993, Serafy et al. 1995, Adams et al. 1998), and to capture live food (Coleman 1993, Serafy et al. 1995). This may be especially detrimental for parasitised *C. quinquelineatus* as they may have to spend more time foraging for food due to the energetic stress caused by the association of the isopod, as shown by the feeding experiments. In contrast, parasitised individuals might have a reduced conspicuousness in the presence of a predator due to behavioural changes, as is the case in the grass shrimp *Palaemonetes pugio* (Bass & Weis 1999).

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