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ORIGINAL ARTICLE

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Trade-offs for the butterflyfish, *Chaetodon multicinctus*, when feeding on coral prey infected with trematode metacercariae

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Abstract Predators that feed on prey infected with larval parasites risk parasitic infection and the subsequent costs parasites extract from their hosts. It has been hypothesized that selection could favor predators that feed on infected prey if there were some benefit from feeding on such prey that outweighed the risk of and/or costs associated with parasitic infection. I tested this hypothesis using a parasite–host system involving the coral-feeding butterflyfish, *Chaetodon multicinctus*, which preferentially feeds on coral polyps infected with trematode metacercariae. Infected polyps appear as obvious, swollen nodules on the coral colony. Coral is a relatively energy-poor food source and so the choice made by *C. multicinctus* to feed on infected coral might represent a trade-off between benefits gained from feeding on infected prey and the risk of acquiring and/or the costs of harboring the parasite. The rate of establishment of the trematode within *C. multicinctus* was low, especially compared to the fish's rate of consumption of infected coral. The low intensity of trematode infection, in field-caught fish, suggests that parasite acquisition may not be increasing linearly through time. There was no measurable effect of parasitic infection on the body condition or liver energy reserves of fish. The swollen nature of infected polyps allowed fish to obtain more coral tissue per bite when feeding on infected compared to uninfected coral. It is suggested that the benefits gained from enhanced feeding offset the costs associated with infection and thus may help explain why *C. multicinctus* chooses to feed on infected coral.

Keywords Butterflyfish · Infected coral prey · Predator choice · Trade-offs

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Introduction

Optimal foraging models assume that efficient predators will choose prey items that maximize their net rate of energy gain (MacArthur and Pianka 1966; Krebs and Davies 1991). However, foraging behavior can be constrained by a number of factors such as the risk of feeding on prey infected with larval parasites (Lozano 1991; Lafferty 1992; Norris 1999; Hutchings et al. 2000). Predators feeding on infected prey risk acquiring both parasitic infection and the subsequent costs that parasites impose on their hosts. A potential host could reduce its risk of parasitism by simply avoiding food that is the source of parasites (Lozano 1991; Hart 1994). Grazing herbivores have been found to avoid foraging near feces, which reduces the risk of infection (Hart 1994; Hutchings et al. 2000), and Keymer et al. (1983) demonstrated that rats learned to avoid foods with certain flavors, which were associated with the acquisition of nematode infection. Yet, many predators do feed on infected prey; trophic transmission is a common strategy among gut parasites (Moore 1983; Lafferty 1999; Brown et al. 2001).

Parasites that are trophically transmitted often alter the appearance or behavior of intermediate hosts resulting in increased predation by definitive hosts (see reviews by Holmes and Bethel 1972; Moore and Gotelli 1990; Combes 1991; Poulin 1994). For example, Lafferty and Morris (1996) found that killifish infected by larval trematodes exhibited conspicuous behaviors that resulted in a 30-fold increase in rate of predation by definitive host birds. Why would a predator choose to feed on infected prey? It may simply be that predators are unable to distinguish between infected and uninfected prey. Alternatively, parasite alteration of the intermediate host may allow for easier predation by an appropriate definitive host (Holmes and Bethel 1972; Lafferty 1992; Poulin 1993). If so, then selection could favor predators that feed on infected prey if the risk of becoming parasitized were low or if there were some benefit derived from feeding on infected prey that outweighed the

costs associated with parasitic infection (Holmes and Bethel 1972; Moore 1983; Lozano 1991; Lafferty 1992; Thomas et al. 2000). A potential benefit would especially be likely if competition among parasites in the gut or a host immune response limit the number of parasites that can successfully establish in the host. In fact, using a theoretical model, Lafferty (1992) concluded that predators should only avoid infected prey if the cost of parasitism were high and modification of prey were low. He also points out that avoidance of infected prey would carry its own cost in terms of lost foraging opportunities. Hence, foraging decisions made by predators, whether or not to feed on infected prey, should be based upon the trade-offs between enhanced foraging and costs of parasitic infection.

I tested this hypothesis using a marine host–parasite system in which a definitive host for a parasite species can differentiate between infected and uninfected prey, yet still prefers to feed on infected prey. In Hawaii, the reef corals, *Porites* spp., serve as intermediate hosts for the digenetic trematode, *Podocotyloides stenometra* Pritchard (Cheng and Wong 1974; Aeby 1998a). Encystment of the metacercarial stage of the parasite in coral results in alteration of the coral's appearance and behavior. Infected polyps appear as pink, swollen nodules on the coral colony, which are no longer able to adequately retract into their protective coral skeletons (Aeby 1998b). Infected coral polyps are, therefore, both conspicuous and quite vulnerable to predation. Completion of the parasite's life cycle occurs when coral-feeding fish ingest the infected polyps (Aeby 1998a). The adult worm subsequently resides in the intestinal tract of the host fish (Pritchard 1966, cited after Bray and Cribb 1989; Aeby 1998a). *Porites* corals are the dominant corals on the reefs of Hawaii (Jokiel 1987) and, as such, constitute a large proportion of the diet of many species of coral-feeding fishes (Hourigan 1987; Tricas 1989a; Reese 1991; Kosaki 1999). Therefore, coral-feeding fish would be faced with the decision of whether or not to feed on the infected coral prey.

One of the most abundant coral-feeding fish found on the reefs in Hawaii is the butterflyfish, *Chaetodon multicinctus* Garret (Tricas 1986). *C. multicinctus* occurs in male–female pairs that vigorously defend permanent feeding territories against intrusion by other corallivores (Tricas 1985, 1989b; Kosaki 1999). Coral tissues have a relatively low energy content (Tricas 1989a; Reese 1991) and so, in order for *C. multicinctus*, which feeds exclusively on coral polyps, to harvest sufficient energy, over 90% of its time is spent in feeding-related activities (Hourigan et. al. 1988; Tricas 1989a; Reese 1991). In addition, *C. multicinctus* have a small mouth that only allows for the removal of single polyps (Motta 1988, 1989; Tricas 1989a), limiting their ability to harvest their coral prey.

In a prior study, I found that *C. multicinctus* showed a preference for feeding on infected over uninfected coral (Aeby 1992). Given a choice between similar-sized colonies of infected and uninfected *Porites compressa* Dana, *C. multicinctus* directed over 80% of their bites toward the infected coral colony as compared to the 50% that would be expected if the fish were feeding randomly. In addition, when *C. multicinctus* feeds on an infected coral colony, they feed predominantly on the infected polyps (Aeby 1998b). Field observations also found that fish repeatedly fed on infected corals within their feeding territories (Aeby, unpublished data). *C. multicinctus* serves as a definitive host for *Podocotyloides stenometra* (Pritchard 1966, cited after Bray and Cribb 1989; Aeby 1998a), and so the choice made by *C. multicinctus* to feed on infected prey might represent a trade-off between risk of acquiring the infection and/or cost of harboring the parasite and the benefits gained from feeding on the swollen, infected coral polyp. Therefore, I first examined the susceptibility of *C. multicinctus* to infection from feeding on infected coral. I then examined the cost imposed on the definitive host fish by *P. stenometra* and determined if there was a benefit to the fish from feeding on infected coral instead of uninfected coral.

Methods

Susceptibility to infection

The risk of becoming parasitized depends on the susceptibility of *C. multicinctus* to this parasite species. Susceptibility to parasites can vary within and among host species (Esch et al. 1990; Esch and Fernandez 1993). I determined the susceptibility of *C. multicinctus* to infection from feeding on infected coral by estimating the proportion of ingested trematode metacercariae that could establish as juveniles in the guts of fish. The small size (average 0.3 mm) (Aeby 1998b) and nature of the metacercarial cysts made it impossible to feed fish a known number of cysts. Hence, I estimated the number of metacercarial cysts fish consumed during a 30-min feeding period and compared that quantity to the subsequent number of juvenile trematodes found in their gut after 24 h. Juvenile trematodes are shorter and rounder than older worms and easily distinguished from the latter.

Prior to the experiment, fish were deprived of food for 18–24 h in order to empty their guts. Fish were then allowed to feed on infected corals for 30 min. Subsequently, fish were again deprived of food for another 24 h. This allowed time for excystment of any ingested metacercariae and time for the establishment of immature worms in the intestines (Smyth and Halton 1983). The following day, fish were once again allowed to feed on infected corals for 30 min. They were sacrificed immediately afterwards and the number of metacercarial cysts found in the stomach contents was recorded. The number of bites taken by fish on coral was recorded for both feeding periods. The entire alimentary tract was examined for the presence of juvenile and adult trematodes. The hindgut, which is quite distinct in *C. multicinctus*, was also examined for the presence of undigested metacercarial cysts or juvenile trematodes. Nine butterflyfish were tested.

From these data, I calculated the estimated proportion of cysts consumed on day 1 that were able to establish as juveniles by day 2. To estimate the number of cysts fish consumed on experimental day 1, I compared the number of bites taken on coral during experimental day 2 with the number of cysts subsequently found in their stomachs. I then calculated the number of cysts consumed per bite taken on the coral for each fish. This corrected for the fact that the proportion of bites directed towards infected polyps varies among individual fish. Combining the ratio cysts consumed/bites taken with the number of bites taken by each fish on day 1, I calculated an estimate of the number of cysts that were ingested. This estimate was then compared with the number of juvenile trema-

todes found in their gut. In this way, I was able to estimate the percentage of consumed cysts that were able to establish as juvenile worms by day 2.

Cost to fish: effect of trematode on condition of fish

Energy diverted from the host by the parasite or expended by the host in response to the parasite could result in a reduction in overall fitness of the fish host. *C. multicinctus* are pelagic spawners with a protracted spawning season (Hourigan 1987; Tricas 1989b). Consequently, the direct measurement of reproductive output as a measure of fitness would be difficult. Spawning in these fish is thought to be limited by food availability (Tricas 1989b); if the energetic demands of parasitism results in a reduction in the body condition or energy reserves of the fish, this could translate into reduced energy available for reproductive output. Therefore, I examined the effect of parasite infection on both the body condition and energy reserves of *C. multicinctus*.

If the parasite represents a nutritional drain on its fish host, there should be a negative relationship between parasite intensity [defined by Margolis et al. (1982) as number of parasites/host] and body condition of individual fish. Fulton's condition index (K) is believed to be a good indicator of general well-being of a fish (Bolger and Connolly 1989; Wang and Houde 1994) based on their weight/length relationship ($K=100\times$weight/standard length^3) (Fulton 1904, cited after Wang and Houde 1994). Therefore, I examined the relationship between parasite intensity and condition index of individual *C. multicinctus*. *P. stenometra* is a small worm (average total length=1 mm) and so it was assumed that the weight of the parasite did not significantly contribute to the weight of the fish host.

All *C. multicinctus* were caught by divers using handnets from reefs offshore of Kaneohe Bay, Oahu, Hawaii. Standard length (mm), body weight (g) and number of trematodes (adult and juvenile) were recorded for each fish. Measurements from 29 fish were taken throughout a 2-year period. Fish were held in flow-through seawater tanks at the Hawaii Institute of Marine Biology (HIMB) and given fresh, uninfected coral ad libitum prior to examination. The fish used in this analysis were first used for various behavioral studies and so were held in captivity for different lengths of time before they were examined. The condition indices of experimental fish held for the longest time period (4 weeks) were compared to other fish that had been sacrificed immediately after capture. They were found to be similar so it was assumed that body condition of experimental fish was not significantly affected by captivity.

In order to provide a broader range of parasite intensities, an additional 16 fish from a prior experiment were included in the analysis. Eight of the 16 fish (experimental group) fed on parasitized corals for 3–4 weeks resulting in fish having higher parasite intensities (adult plus juvenile trematodes) than those found in naturally infected fish. The other eight fish (control group) fed on uninfected coral and thus had field levels of parasite intensity. Therefore, a total of 45 fish were analyzed, with 37 fish having natural intensities of parasite infection (range 1–23, mean=6.7 trematodes/fish) and eight fish having high intensities of infection (range 5–156, mean=47.1 trematodes/fish).

Many species of fish store excess energy (glycogen and lipid) in the liver (Smith et al. 1990; Sayer et al. 1995; Zamal and Ollevier 1995). Reduced liver size has been associated with nutritional deficiency in *C. multicinctus* (Hourigan 1987); therefore an additional analysis was performed to determine if parasite infection affected the liver energy reserves of the fish host. The hepatosomatic index (liver weight as a percentage of body weight) indicates differences in liver size and, as such, has been used as a measure of the condition of fish (Bolger and Connolly 1989). Therefore, I examined the relationship between the parasite intensity and the hepatosomatic index of individual *C. multicinctus.*

Standard length (mm), body weight (g), wet liver weight (g) and number of trematodes were recorded for 12 fish. The fish used for this analysis were caught in the field and maintained in seawater tanks for similar amounts of time (7–10 days). Fish were given uninfected coral ad libitum and harbored natural levels of parasite intensities (range 2–18, mean=11.2 trematodes/fish).

Benefit to fish: coral tissue accessibility

C. multicinctus searches for and feeds upon the expanded coral polyps on a coral colony (Hourigan 1987; Tricas 1989a). Expanded polyps are consumed before they can contract back into their coral skeleton (Hourigan 1987; Motta 1988; Tricas 1989a). Infected coral polyps are swollen and can no longer completely withdraw into their protective calices. This may allow fish to access tissue that would otherwise be unavailable to them. I compared the amount of coral tissue that a fish could obtain per bite when feeding on infected *P. compressa* with that obtained when feeding on uninfected *P. compressa*.

Fish were maintained without food for 18–24 h in order to ensure an empty digestive tract. They were then allowed to feed on either an infected coral or an uninfected coral for a 15-min time period, during which the number of bites was recorded. Fish feeding on infected coral were observed to feed predominantly on infected polyps. Fish were sacrificed immediately following the test period and dissected. Dried weight of the stomach contents was recorded. Ten fish were tested with infected coral and ten fish with uninfected coral. This method was used successfully by Hourigan (1987) to document the amount of coral obtained per bite by *C. multicinctus*.

Results

Susceptibility of fish to trematode infection

An average of 167.8 (SE±40.3) metacercarial cysts were found in the stomachs of fish that had fed for 30 min on infected corals (range 20–340) (n=9). In contrast to the high number of cysts ingested, an average of only 9.8 (SE±4.6) juvenile trematodes were found in their guts (range 0–45). Thus, it was estimated that an average of only 8.1% (SE±2.5%) of consumed cysts were able to establish as juvenile worms. The rate of establishment of the trematode varied among fish from 0% to 21.7%. Only two of the nine fish had juvenile trematodes or cysts in their hindguts. One fish had ten juvenile trematodes and ten metacercarial cysts in the hindgut. Another fish had one cyst in the hindgut.

Cost to fish: effect of trematode on condition of fish

Parasitic infection did not negatively affect the overall body condition of the fish host. In fact, fish condition index was positively correlated with number of trematodes (least squares regression, r^2=0.15, P=0.004, n=45; Fig. 1). In addition, no statistically significant relationship was found between the intensity of infection and the hepatosomatic index of individual fish (Spearman rank correlation, r_s=0.28, P=0.35, n=12; Fig. 2).

Benefit to fish: coral tissue accessibility

Fish were able to obtain significantly more coral tissue per bite when feeding on infected coral (mean=8.2×

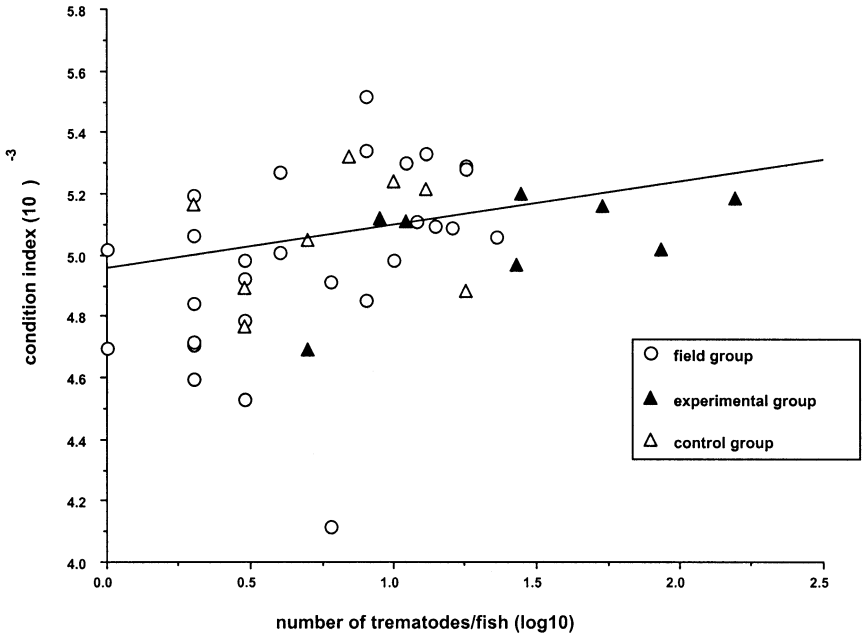

Fig. 1 Relationship between parasite intensity and body condition of individual butterflyfish *Chaetodon multicinctus* (*n*=45). Experimental group of fish were fed infected coral in the laboratory before examination (*n*=8). Control group of fish were fed uninfected coral in the laboratory before examination (*n*=8). Field group of fish were examined shortly after capture (*n*=29)

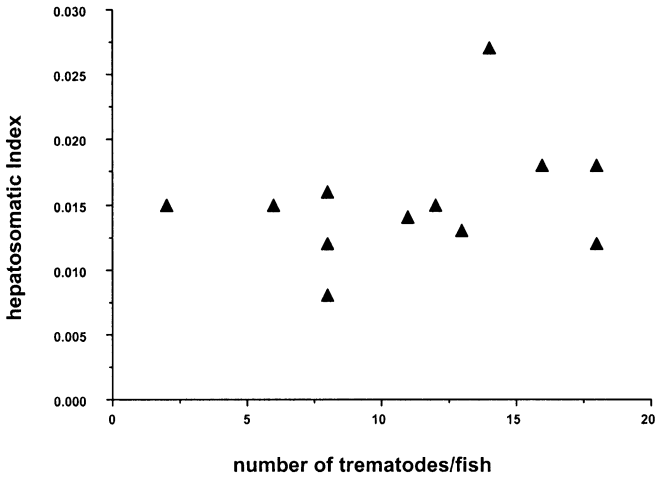

Fig. 2 Relationship between parasite intensity and liver energy reserves of individual butterflyfish *C. multicinctus* (*n*=12)

10^{-5} g/bite; SE±1.2×10^{-5}) than when feeding on the uninfected coral (mean=4.7×10^{-5} g/bite; SE±0.44×10^{-5}) (ANOVA, F=12.7, P=0.0025, n=20). This was especially apparent for larger fish (>80 mm SL; n=5) feeding on infected coral which were able to obtain an average of 10.8×10^{-5} g/bite (SE±1.3×10^{-5}) compared to similar sized fish feeding on uninfected coral (mean =4.94×10^{-5} g/bite; SE±0.5×10^{-5}; n=7) (Mann-Whitney U, P=0.0057, n=12)(Fig. 3). The total amount of coral tissue obtained by fish during a 15-min foraging bout was similar for both infected (mean=1.3×10^{-2} g; SE±0.17) and uninfected corals (mean=1.2×10^{-2} g; SE±0.16) (ANOVA, F=1.23, P=0.28). Fish took approximately one third fewer bites when feeding on infected coral (average 177; SE±16) versus uninfected coral (average 259 SE±35) (ANOVA, F=4.1, P=0.06, n=20).

Discussion

When *C. multicinctus* fed on infected coral, they were found to consume surprisingly high numbers of metacercarial cysts (up to 340 cysts/30 min.). Yet, relatively few juvenile trematodes were found in their guts. It was estimated that less than 10% of the ingested metacercariae were able to establish as juvenile trematodes. This estimated rate of parasite establishment is quite low compared to what has been found in other parasite–host systems. For example, Bates and Kennedy (1990) looked at the establishment of two species of acanthocephalans (thorny-headed worms) in trout that were fed a known number of infective cystacanths. They found that 7 days post-infection, 68% of the cystacanths of one parasite species and 47% of another species were established within fish. Ballabeni (1994) exposed minnows to a known number of cercariae of the digenetic trematode, *Diplostomum phoxini*, and found that 50% of the cercariae at low doses (10 cercariae) and 42% of the cercariae at high doses (40 cercariae) were successful at encysting in the fish host.

Even with a low rate of infection for *C. multicinctus* when feeding on infected coral, one might expect that, with time, fish would accumulate high numbers of parasites. Butterflyfish do live for many years (Reese 1991) and many studies have found that larger, hence older, fish commonly have more parasites than younger fish (Koie 1984; Bean and Winfield 1989; Karlsbakk 1995; Poulin 2000). In addition, the intensity of other gut parasites within marine fishes can be quite high. For example, Campos and Carbonell (1994) found that the wrasse, *Laburs merula*, harbor an average of 222 trematodes (*Diphtherostumum brusinae*) per fish with the range being 1–1,007 trematodes.

However, this was not true for populations of *C. multicinctus*. In this study, the 37 fish with natural

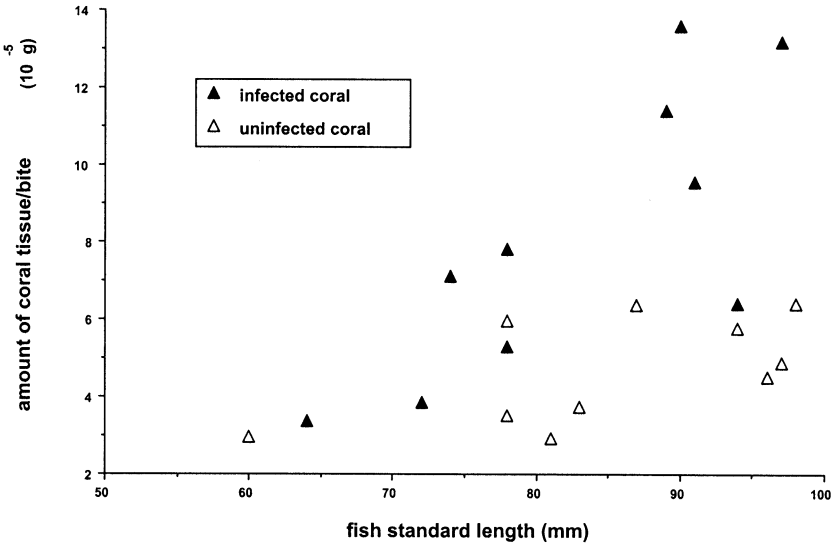

Fig. 3 Comparison of foraging efficiency of *C. multicinctus* feeding on infected versus uninfected coral (*n*=20)

intensities of parasite infection harbored an average of only seven trematodes per fish. In another study, Aeby (unpublished data) examined the parasite intensity of 25 *C. multicinctus* from the Big Island of Hawaii, which were known to have infected coral within their feeding territories. These fish were examined for parasites shortly after capture, and they showed an average of only two worms per fish. This suggests that when *C. multicinctus* feed on infected polyps, they can acquire the infection, but that the rate of parasite acquisition is much lower than their relative rate of consumption of infected prey.

Parasite abundance within hosts can be affected by a number of factors either external or internal to the host (Esch and Fernandez 1993). One factor that may affect establishment of *P. stenometra* within *C. multicinctus* is variability in the viability of metacercariae. Encysted metacercariae do not feed and instead depend on endogenous reserves while awaiting transmission to the final host (Smyth and Halton 1983; Smyth 1994). The amount of time that *P. stenometra* metacercariae can survive before senescence occurs varies from several weeks to several months (Aeby 1998b). Therefore, it may be that a high proportion of the metacercariae consumed by the fish in this study were already senescent.

Alternatively, factors such as parasite–parasite interactions, immunity and host genetics are known to affect parasite establishment (Holmes 1986; Esch and Fernandez 1993; Kennedy-Stoskopf 1993). Intraspecific competition has been found to affect the rate of establishment of other intestinal helminthes (Brown 1986; Kennedy 1996). Some butterflyfish were found to have consumed hundreds of cysts at a single feeding so it is possible that competition among juvenile trematodes reduced survival. The presence of adult trematodes in the gut could also affect the survival of juvenile trematodes. These hypotheses warrant further investigation.

Host immune response may also be important in limiting parasite establishment. The intestinal mucosa contains immunoglobulins, lymphocytes and a wide variety of non-lymphoid effector cells that can quickly respond to antigenic materials such as parasites (Kennedy-Stoskopf 1993). Meguid and Eure (1996) found hyperplasia of goblet cells in sunfish heavily infected by two species of gut nematodes. This resulted in large quantities of mucus covering the intestines in these regions. Meguid et al. (1995) speculated that the accumulation of mucus creates a physical barrier to the establishment of enteric helminthes or that the mucus may contain antibodies directed at the parasites.

Similar mechanisms may be operating in *C. multicinctus* in response to *P. stenometra*. Within two of the nine experimental fish, no juvenile trematodes were found, even though both fish had been observed feeding heavily on infected polyps the day before. In addition, ten juvenile trematodes were found in the hindgut of another fish. This suggests that although these worms were able to successfully excyst in the stomach, they were not able to subsequently establish in the fishes' gut. These observations suggest that there could be some host-mediated mechanism limiting the establishment of *P. stenometra* in *C. multicinctus*.

The above hypotheses are not mutually exclusive, and it may be a combination of factors that affect the rate of establishment of *P. stenometra* in *C. multicinctus*. Regardless of what the mechanisms may be, the end result is that *C. multicinctus* are able to feed on infected coral polyps with only a limited proportion of the ingested metacercariae resulting in parasite acquisition.

When *C. multicinctus* do harbor *P. stenometra*, there is no measurable effect of the trematode on either body condition or on liver energy reserves of the host fish. Reproductive output in *C. multicinctus* is limited by food availability (Tricas 1989a). However, since *P. stenometra* was found to have a minimal affect on the energy reserves of *C. multicinctus*, the probability of parasitism affecting the fitness of the host, in terms of reproductive output, would probably also be minimal.

For many parasite species, the potential for pathological effect in a host is related to the relative mass of the parasite compared to that of their host (McPhail and

Peacock 1983). *P. stenometra* is quite small (average 1 mm total length) compared to *C. multicinctus* (average 85 mm total length), and so the mass of the trematodes, even in heavy infections, would be small compared to that of its host. Therefore, it is probable that the nutritional drain *P. stenometra* has on its fish host is quite small and may be compensated for by increased feeding. In fact, for *C. multicinctus*, the energetic gains from feeding on infected coral appear to outweigh the costs incurred from parasitic infection. A positive relationship was found between condition index and parasite intensity of butterflyfish. This suggests that fish which feed on infected coral are potentially acquiring higher parasite intensities but are also receiving even greater energetic gains.

If parasitic infection is not very costly to the fish then there is no selective advantage to avoid infected prey. In fact, avoidance of infected prey could carry a cost to the fish in terms of lost foraging opportunities (Lafferty 1992). However, unless there was a benefit to feeding on infected coral, one would expect fish to feed on infected polyps at random. Since *C. multicinctus* shows a strong preference for feeding on infected coral (Aeby 1992), if such selectivity is adaptive this suggests that there must be a benefit gained by the fish. Consistent with this, I found that fish were able to consume more coral tissue per bite when feeding on infected coral than when feeding on uninfected coral. I also found that larger fish with their larger mouths were able to take advantage of the increased tissue availability more so than smaller fish.

Feeding by *C. multicinctus* is energetically expensive in that it requires a rapid lunge of the entire body (Motta 1988; personal observation). By feeding on infected coral, fish are able to increase the amount of food consumed per unit effort expended. In the laboratory, fish feeding on infected coral took approximately one third fewer bites than fish feeding on uninfected coral (average 177 vs 259), yet they were still able to obtain a similar amount of food. Hence, the rate of return was greater for fish feeding on infected coral.

C. multicinctus has to feed constantly and the amount of food obtained each day is constrained primarily by the time available for feeding (Hourigan 1987; Tricas 1989a). This is due, in part, to the fact that once a fish removes individual polyps from a colony, surrounding polyps respond rapidly by withdrawing into their protective calices (Gochfeld 1997). When feeding on normal, uninfected coral, *C. multicinctus* is usually limited to taking 4–5 bites on a coral colony before moving on to another colony to search for suitable (i.e. expanded) polyps (Hourigan 1987; Tricas 1989a, b). As such, *C. multicinctus* has been found to show a preference for feeding on coral species that have the highest energetic profit in terms of energy intake per unit foraging time (Hourigan 1987; Tricas 1989a, b). For example, Tricas (1989a) found *C. multicinctus* showed a preference for feeding on the reef coral *Pocillopora meandrina* over *Porites* sp. *P. meandrina*, in contrast to *Porites* sp., has an imperforate skeleton which leaves much of the coral tissue vulnerable to predation and their polyps have a clustered distribution allowing fish to harvest more polyps in a shorter amount of time (reduced handling time).

Similarly, when *C. multicinctus* feed on infected polyps, they are getting more food per bite, and since infected polyps are unable to retract, they would also be able to harvest more coral tissue (reduced handling time) before having to move onto the next colony. In the laboratory, it was observed that fish were able to take from 5–10 bites on an infected polyp compared to the single bite obtained from an uninfected polyp. When *C. multicinctus* feed on infected coral, they benefit not only from an increased amount of coral tissue per bite but also in terms of higher harvestibility of infected polyps.

Trade-offs between energy intake and exposure to parasites have been found in a number of other systems. For example, Norris (1999) examined the foraging choice of oystercatchers feeding on cockles. Cockles serve as an intermediate host to larval parasites and parasite intensity was found to increase with the size of the cockle. To maximize energy intake, birds should feed on the larger cockles but to minimize the risk of parasite acquisition they should feed on the smallest cockles. He found that oystercatchers selectively consumed an intermediate size class of cockles and concluded that this choice was a compromise between the conflicting demands.

C. multicinctus is a predator that feeds on a calorically poor food source and has morphological constraints on foraging. As such, when faced with the choice of whether or not to feed on infected prey *C. multicinctus* preferentially feeds on infected coral and in so doing is able to obtain more coral food. However, infection rate does not increase linearly with exposure rate. Therefore, whereas the benefits of that foraging choice (increased food intake) accrue with time, the cost of that choice (parasite acquisition) does not. It is suggested that the benefits gained from enhanced foraging offset the costs associated with infection and thus may offer some explanation as to why *C. multicinctus* preferentially feeds on infected coral.

Traditionally, optimal foraging models assume that the primary goal of foragers is the maximization of energy intake ((MacArthur and Pianka 1966; Krebs and Davies 1991). However, trade-offs between energy intake and parasite acquisition can occur. Therefore, the predictive power of optimal foraging models may be enhanced by the inclusion of parasite factors within the optimal foraging framework (Lafferty 1992).

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References

Aeby GS (1992) The potential effect the ability of a coral intermediate host to regenerate as had on the evolution of its association with a marine parasite Proc 7th Int Coral Reef Symp 2:809–815

Aeby GS (1998a) A digenean metacercaria from the reef coral, *Porites compressa*, experimentally identified as *Podocotyloides stenometra*. J Parasitol 84:1259–1261

Aeby GS (1998b) Interactions of the digenetic trematode, *Podocotyloides stenometra*, with its coral intermediate host and butterflyfish definitive host: ecology and evolutionary Implications. PhD dissertation, University of Hawaii, Honolulu

Ballabeni P (1994) Experimental differences in mortality patterns between European minnows, *Phoxinus phoxinus*, infected with sympatric or allopatric trematodes, *Diplostomum phoxini*. J Fish Biol 45:257–267

Bates R, Kennedy C (1990) Interactions between the acanthocephalan *Pomphorhynchus laevis* and *Acanthocephalus anguillae* in rainbow trout: testing an exclusion hypothesis. Parasitology 100:435–444

Bean CW, Winfield IJ (1989) Biological and ecological effects of a *Ligula intestinalis* (L.) infestation of the gudgeon, *Gobio gobio* (I.), in Lough Neagh, Northern Ireland. Fish Biol 34:135–147

Bolger T, Connolly PL (1989) The selection of suitable indices for the measurement and analysis of fish condition. J Fish Biol 34:171–182

Bray RA, Cribb TH (1989) Digeneans of the family Opecoelidae Ozaki, 1925 from the southern Great Barrier Reef, including a new genus and three new species. J Nat Hist 23:429–473

Brown A (1986) Evidence for density-dependent establishment and survival of *Pomphorhynchus laevis* (Muller 1776) (Acanthocephala) in laboratory infected *Salmo gairdneri* Richardson and its bearing on wild population in *Leuciscus cephalus* (L). J Fish Biol 28:659–669

Brown S, Renaud F, Guegan J, Thomas F (2001) Evolution of trophic transmission in parasites: the need to reach a mating place. J Evol Biol 14:815–820

Campos A, Carbonell E (1994) Parasite community diversity in two Mediterranean labrid fishes *Symphodus tinca* and *Labrus merula*. J Fish Biol 44:409–413

Cheng TC, Wong AK (1974) Chemical, histochemical and histopathological studies on corals, *Porites* spp. parasitized by trematode metacercariae. J Invert Pathol 23:303–317

Combes C (1991) Ethological aspects of parasite transmission. Am Nat 138:866–880

Esch G, Fernandez C (1993) A functional biology of parasitism. Chapman and Hall, New York

Esch G, Bush A, Aho J (eds) (1990) Parasite communities: patterns and processes. Chapman and Hall, New York

Fulton TW (1904) The rate of growth of fishes. Fish Bd Scotl Annu Rep 22:141–241

Gochfeld DG (1997) Mechanisms of coexistence between corals and coral-feeding butterflyfishes: territoriality, foraging behavior and prey defense. PhD dissertation, University of Hawaii, Honolulu

Hart BL (1994) Behavioral defense against parasites: interaction with parasite invasiveness. Parasitology 109:S139-S151

Holmes JC (1986) The structure of helminth communities. Int J Parasitol 17:203–207

Holmes JC, Bethel WM (1972) Modification of intermediate host behavior by parasites. In: Canning EU, Wright CA (eds) Behavioral aspects of parasite transmission. Academic Press, London, pp 123–149

Hourigan TF (1987) The behavioral ecology of three species of butterflyfishes (Family Chaetodontidae). PhD dissertation, University of Hawaii, Honolulu

Hourigan TF, Tricas TC, Reese ES (1988) Coral reef fishes as indicators of environmental stress in coral reefs. In: Soule DF, Kleppel G (eds) Marine organisms as indicators. Springer, Berlin Heidelberg New York, pp 107–135

Hutchings MR, Kyriazakis I, Anderson DH, Gordon IJ, Coop RI (1998) Behavioural strategies used by parasitized and non-parasitized sheep to avoid ingestion of gastro-intestinal nematodes associated with faeces. Anim Sci 67:97–106

Hutchings MR, Kyriazakis I, Papachristou TF, Gordon IJ, Jackson F (2000) The herbivores' dilemma: trade-offs between nutrition and parasitism in foraging decisions. Oecologia 124:242–251

Jokiel PL (1987) Ecology, biogeography and evolution of coral in Hawaii. Trends Evol Ecol 2:333–336

Karlsbakk E (1995) The occurrence of metacercariae of *Buciphaloides gracilescens* (Digenea: Gasterostomata) in an intermediate host, the four-bearded rockling, *Enchelyopus cimbrius* (Gadidae). J Fish Biol 46:18–27

Kennedy C (1996) Establishment, survival and site selection of the cestode *Eubothrium crassum* in brown trout, *Salmo trutta*. Parasitology 112:347–355

Kennedy-Stoskopf S (1993) Immunology. In: Stoskopf M (ed) Fish medicine. Saunders, London, pp 149–159

Keymer A, Crompton DT, Sahakian BJ (1983) Parasite-induced learned taste aversion involving *Nippostrongylus* in rats. Parasitology 86:455–460

Koie M (1984) Digenetic trematodes from *Gadus morhua* L. (Osteichthyes, Gadidae) from Danish and adjacent waters, with special reference to their life-histories. Ophelia 23:195–222

Kosaki RK (1999) Behavioral mechanisms of coexistence among coral-feeding butterflyfishes. PhD dissertation, University of Hawaii, Honolulu

Krebs JR, Davies NB (1991) Behavioural ecology: an evolutionary approach, 3rd edn. Blackwell, Oxford

Lafferty KD (1992) Foraging on prey that are modified by parasites. Am Nat 140:854–867

Lafferty KD (1999) The evolution of trophic transmission. Parasitol Today 15:111–115

Lafferty KD, Morris AK (1996) Altered behavior of parasitized killifish greatly increases susceptibility to predation by bird final hosts. Ecology 76:110–117

Lozano GA (1991) Optimal foraging theory: a possible role for parasites. Oikos 60:391–395

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

Margolis LE, Esch GW, Holmes JC, Kuris AM, Schad GM (1982) The use of ecological terms in parasitology. J Parasitol 68:131–133

McPhail JD, Peacock SD (1983) Some effects of the cestode (*Schistocephalus solidus*) on reproduction in the three-spine stickleback (*Gasterosteus aculeatus*): evolutionary aspects of a host-parasite interaction. Can J Zool 61:901-908

Meguid MA, Eure HE (1996) Pathobiology associated with the spiruroid nematodes *Camallanus oxycephalus* and *Spinitectus carolini* in the intestine of green sunfish, *Lepomis cyanellus*. J Parasitol 82:118–123

Meguid MA, Esch GW, Eure HE (1995) The distribution and pathobiology of *Neoechinorhynchus cylindratus* in the intestine of green sunfish, *Lepomis cyanellus*, Parasitology 111: 221–231

Moore J (1983) Responses of an avian predator and its isopod prey to an acanthocephalan parasite. Ecology 64:1000–1015

Moore J, Gotelli NJ (1990) A phylogenetic perspective on the evolution of altered host behaviors: a critical look at the manipulation hypothesis. In: Barnard CJ, Behnke JM (eds) Parasitism and host behavior. Taylor and Francis, London, pp 193–233

Motta PF (1988) Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. Environ Biol Fish 22:39–67

Motta PF (1989) Dentition patterns among Pacific and Western Atlantic butterflyfishes (Perciformes, Chaetodontidae): relationship to feeding ecology and evolutionary history. Environ Biol Fish 25:159–170

Norris K (1999) A trade-off between energy intake and exposure to parasites in oystercatchers feeding on a bivalve mollusk. Proc R Soc Lond Ser B 266:1703–1709

Poulin R (1993) Age-dependent effects of parasites on anti-predator responses in two New Zealand freshwater fish. Oecologia 96:431–438

Poulin R (1994) Meta-analysis of parasite-induced behavioral changes. Anim Behav 48:137–146

Poulin R (2000) Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. J Fish Biol 56:123–137

Pritchard MH (1966) Studies on digenetic trematodes of Hawaiian fishes: family Opecoelidae. Zool Jahrb (Syst) 93:158–172

Reese ES (1991) How behavior influences community structure of butterflyfishes (Family Chaetodontidae) on Pacific coral reefs. Ecol Int Bull 19:29–41

Sayer MDJ, Gibson RN, Atkinson RJA (1995) Growth, diet and condition of goldsinny on the west coast of Scotland. J Fish Biol 46:317–340

Smith RL, Paul AJ, Paul JM (1990) Seasonal changes in energy and the energy cost of spawning in Gulf of Alaska Pacific cod. J Fish Biol 36:307–316

Smyth JD (1994) Introduction to animal parasitology, 3rd edn. Cambridge University Press, Cambridge

Smyth JD, Halton DW (1983) The physiology of trematodes, 2nd edn. Cambridge University Press, Cambridge

Thomas F, Poulin R, Guegan J, Michalakis Y, Renaud f (2000) Are there pros as well as cons to being parasitized? Parasitol Today 16:533–536

Tricas TC (1985) The economics of foraging in coral-feeding butterflyfishes of Hawaii. Proc 5th Int Coral Reef Symp 5:409–414

Tricas TC (1986) Life history, foraging ecology, and territorial behavior of the Hawaiian butterflyfish, *Chaetodon multicinctus*. PhD thesis, University of Hawaii, Honolulu

Tricas TC (1989a) Prey selection by coral-feeding butterflyfishes: strategies to maximize the profit. Environ Biol Fish 25:171–185

Tricas TC (1989b) Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*. Anim Behav 37:830–841

Wang SB, Houde ED (1994) Energy storage and dynamics in bay anchovy *Anchoa mitchilli*. Biology 121:219–227

Zamal H, Ollevier F (1995) Effect of feeding and lack of food on the growth, gross biochemical and fatty acid composition of juvenile catfish. J Fish Biol 46:404–414