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Corallivorous Reef Fishes as Potential Vectors of Coral Disease Based on a Study of Dietary Preferences

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Abstract

The prevalence of coral disease appears to be increasing worldwide, although little is known about how these diseases are transmitted between coral colonies. To examine whether corallivorous fishes could potentially act as disease vectors, this study examined whether and which fish species feed on diseased coral, and whether these fishes actively target diseased coral sections. Branches of *Acropora muricata* with brown band disease were filmed in the field, and bites taken by fishes on different sections of the coral (live tissue, tissue margin, disease band, dead skeleton, and algae) were recorded. For each fish species, electivity indices were calculated for each coral section to determine feeding preferences. Additionally, feeding preferences for diseased or healthy coral fragments were determined for the corallivorous butterflyfish *Chaetodon lunulatus* and wrasse *Labrichthys unilineatus* in aquaria. Many fishes, including non-corallivores, consumed diseased coral and exhibited a preference for the disease band and adjacent live tissue margin. Butterflyfishes, including *C. lunulatus*, and particularly *Chaetodon aureofasciatus*, showed a strong preference for the tissue margin, while *L. unilineatus* showed a clear preference for the disease band. The obligate corallivores (*Chaetodon* spp. and *L. unilineatus*) are most likely to act as disease vectors, as they were the only fishes to feed substantially on live tissue in addition to the disease band, and they are known to repeatedly feed on multiple coral colonies in their territories. The non-corallivores are unlikely to be spreading disease, and may actually slow the disease progression by selectively consuming brown band ciliates.

Keywords: coral disease, corallivory, feeding selectivity, coral reef fish

Table of Contents

List of Figures

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1 Introduction

1.1 Coral diseases and brown band disease

The prevalence of coral disease appears to be increasing worldwide, perhaps because of the increasing environmental stresses corals are facing (Willis et al. 2004). In the Caribbean, coral diseases are a major cause of reef deterioration, known to decrease coral abundance and reproductive potential and to change community composition (Boyett 2006). Much less in known about the effects of coral disease in the Indo-Pacific, including the Great Barrier Reef (GBR), where disease has only recently become an important area of research.

Coral diseases can be caused by a range of fungi, bacteria, cyanobacteria, and protozoans, and of the more 29 described coral diseases, very few have been examined in detail (Willis et al. 2004). On the GBR, the most common scleractinian (hard) coral diseases are black band disease (caused by filamentous cyanobacteria), skeletal eroding band disease (caused by the ciliate *Halofolliculina corallasia*), brown band disease (also caused by a ciliate), and white syndrome (multiple potential causes) (Willis et al. 2004).

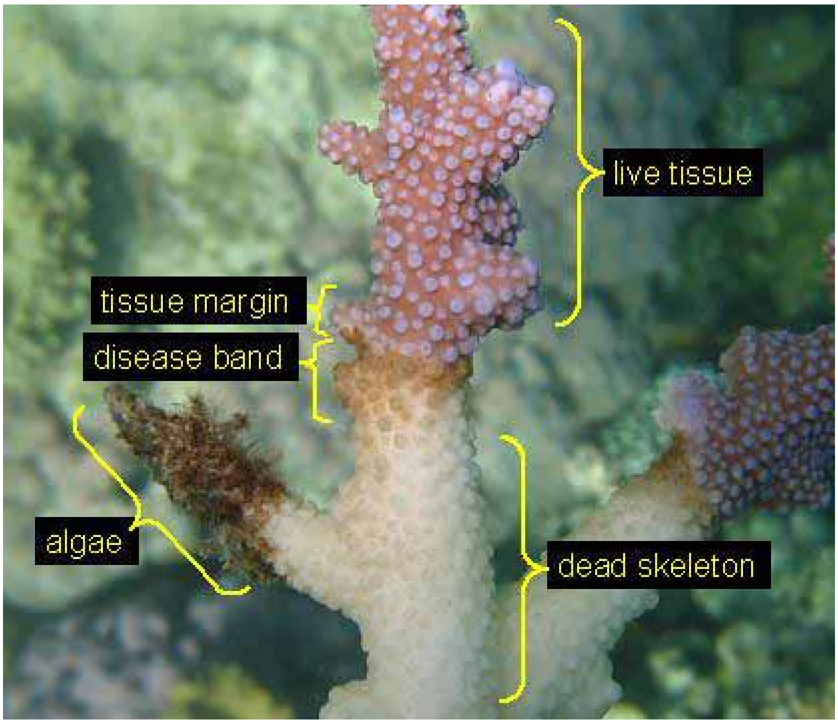

Figure 1. Brown band disease on a branch of *Acropora muricata*, showing the different sections used to define the location of bites by fishes. (Photo: Morgan Pratchett)

Brown band disease was first described from the GBR in 2004, and appears as a brown band on the coral surface bordered on one side by healthy tissue, and the other side by white, dead skeleton (Willis et al. 2004, Figure 1). The band moves along the branch in the direction of the healthy tissue at variable but potentially rapid rates of 0.3 to 6.1 cm/day in the northern GBR (Boyett 2006). The brown color of the band comes from a high density of ciliates (class Oligohymenophora, subclass Scuticociliatia), which are filled with zooxanthellae from coral tissue they have consumed (Boyett 2006). In addition to the ciliates, an array of bacteria are associated with brown band disease that may compromise the coral tissue before the ciliates invade (Boyett 2006, Bourne et al. 2008). Not much is known about the disease, including how it is transmitted, and how it affects interactions between the corals and the fish that feed on them.

1.2 Effects of corallivorous fishes on coral reefs

The impact of corallivory, or the consumption is live coral, is predicted to increase as coral cover decreases in response to stressors such as coral disease, as well as rising water temperature and bleaching events, increased storm intensity, pollution, sedimentation, and eutrophication (Rotjan & Lewis 2008). Although corallivory by fishes was not considered important historically, as it often causes little apparent damage to reefs, chronic tissue removal by fish can be energetically costly to prey corals and have a significant influence on their distribution, abundance, growth, fitness, and competitive ability (Cole et al. 2008). In addition to directly affecting coral condition by mechanical damage and tissue removal, corallivory can have indirect effects on coral colonies, including the facilitation of algal competitors, boring organisms, or disease pathogens (Rotjan & Lewis 2008). Synergistic effects with other stressors may also have important consequences for corals. For instance, the recovery of corals affected by a bleaching or storm event can be highly impaired by predation (Cole et al. 2008). In turn, declines in coral cover can negatively affect populations of corallivorous fishes, especially obligate feeders (Cole et al. 2008).

Fishes in 11 families are known to consume coral, and the damage they inflict on coral colonies varies with the amount of coral tissue and skeleton the fish removes (Rotjan &

Lewis 2008). Corallivorous fishes can be obligate of facultative, and most target scleractinian corals. Fish are often very selective in the corals they consume (Pratchett 2005, 2007), perhaps because of differences in coral morphology, physical or chemical defenses, or nutriment (Cole et al. 2008). Some fish species have a known preference for physically damaged coral, perhaps because of increased mucous production (Pratchett 2005, McIlwain & Jones 1997), but the preference of fishes for other types of stressed corals, such as those with disease, and the consequences for those corals, has not been examined in depth.

1.3 Corallivorous fishes as potential vectors of coral disease

Many coral diseases, such as black band disease, are known to be spread by direct contact and possibly by prevailing currents, but animal vectors have yet to be thoroughly investigated (Aeby & Santavy 2006). Corallivorous fish, snails, worms, and nudibranchs have been recently suggested as potential vectors of coral bacterial infection (Rotjan & Lewis 2008). Butterflyfishes (family Chaetodontidae), which comprise 69 of the 128 known corallivorous fish species (Cole et al. 2008), are the most well studied corallivorous fishes and are likely candidates for disease vectors. Butterflyfishes feed on corals in home territories by removing coral tissue with fleshy, pointed mouths, generally without damaging the coral skeleton (Rotjan & Lewis 2008). In Florida, the butterflyfish *Chaetodon capistratis* was observed feeding on coral with black band disease, and the presence of a *C. capistratis* individual enabled infection to spread from diseased to healthy coral fragments in the same aquarium, suggesting oral and/or fecal transmission (Aeby and Santavy 2006). Since corallivorous fishes are known to feed preferentially on damaged coral (Pratchett 2005, McIlwain & Jones 1997), they may also prefer diseased tissue or tissue on the edge of disease band. After feeding on diseased coral, a fish may be able to transmit the pathogen to other colonies (particularly damaged or stressed parts of non-diseased corals, which may be more prone to infection) on which it subsequently feeds or defecates.

1.4 Objectives of study

To determine whether reef fishes, particularly corallivores, could act as potential vectors of coral disease on the GBR, it is first useful to investigate the actual consumption of diseased corals by these fishes. This preliminary study attempted to determine (1) whether and which fish species feed on diseased coral, (2) whether fishes actively target diseased coral or feed indiscriminately on the coral branch, and (3) which fish species are most likely to act as disease vectors based on these results. Fish species with a high preference for diseased coral, but which also consume healthy coral, were predicted to have the most potential to transmit disease between coral colonies.

2 Methods

2.1 Study sites and species

This study was conducted in November 2008 at Lizard Island, a mid-shelf continental island in the northern Great Barrier Reef, Australia (Figure 2). Field observations were performed at various fringing reefs around the island, and aquarium studies were conducted at the Lizard Island Research Station. Brown band disease was the focal coral disease of this study, as it was the most prevalent disease at the time. Although brown band disease could be found occasionally at almost all reefs, Horseshoe Reef and Little Vicki's Reef appeared to have the highest number of infected colonies (Figure 2). The vast majority of infected coral colonies were the branching staghorn coral *Acropora muricata*, so this was the coral species used for all disease feeding observations and trials (Figure 1).

Diseased branches of *A. muricata* were vertically divided into sections (live tissue, tissue margin, disease band, dead skeleton, and algae), which were used to define the location of each fish bite (Figure 1). Live tissue was defined as all parts of the coral appearing healthy and normal (bluish or olive in color) that were presumably not infected. The disease band was

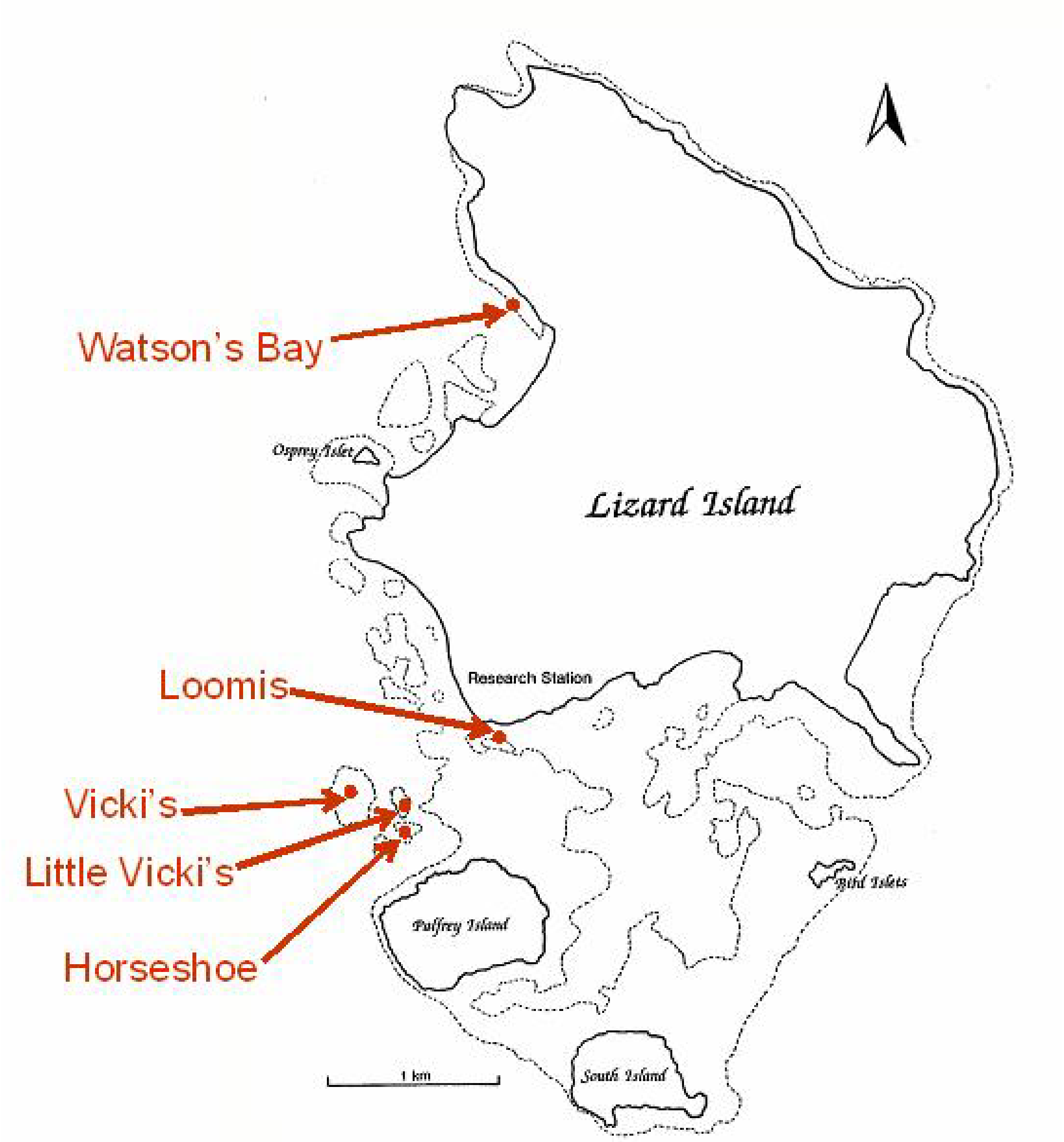

Figure 2. Map of Lizard Island showing the location of field sites. (Image: Anne Hoggett)

defined as any brown parts of the coral, where brown band ciliates were in high densities. The dead skeleton included all white sections of the coral below the disease band, where the coral tissue is dead and ciliates are no longer abundant. The tissue margin was defined as the 1 cm (for videos) or 5 mm (for aquaria trials) of live tissue at the edge of the disease band. The margin was differentiated from live tissue because this section of the coral may have the beginnings of infection and may be stressed or damaged in some way. Algae included all algal growth at the base or tips of branches.

Corallivorous butterflyfishes (family Chaetodontidae) and wrasses (family Labridae), including *Chaetodon aureofasciatus* (golden-striped butterflyfish), *Chaetodon baronessa* (triangular butterflyfish), *Chaetodon lunulatus* (redfin butterflyfish), *Chaetodon plebeius* (bluespot butterflyfish), *Chaetodon rainfordi* (Rainford's butterflyfish), and *Labrichthys unilineatus* (tubelip wrasse) were observed to consume *A. muricata* and the diseased portion of the coral during preliminary field observations. These fish species are all obligate corallivores, and generally rove between coral colonies within a feeding territory (Pratchett 2005, McIlwain & Jones 1997), so these were the focal species of the study and primary disease vector candidates. Territorial, herbivorous damselfishes (family Pomacentridae), such as *Stegastes* spp., frequently defended algal turfs at the bases of *A. muricata* branches, including infected colonies, and planktivorous damselfishes, such as *Chromis atripectoralis* and *Pomacentrus moluccensis*, often swam above and within the branches.

2.2 Video observations of feeding on diseased coral

To determine whether and which fish species feed on diseased coral, and whether these fishes actively target the diseased coral sections, diseased branches of *A. muricata* (n = 17) were located and filmed at Horseshoe Reef, Little Vicki's Reef, Vicki's Reef, and Loomis Reef (Figure 2). A video camera (Sony Handycam DCR-SR300E) in underwater housing was positioned approximately 0.5 m from the diseased branch so the disease band and surrounding healthy branches were in view. The camera was left to record unattended for at least 70 minutes. The first 10 minutes of footage were ignored to allow fish to acclimatize to the presence of the camera. For the next 60 minutes of footage, all fishes seen feeding on the coral were identified, and the number of bites taken by fishes on each section of the coral was recorded (Figure 1). Live tissue included the healthy coral on the diseased branch and on healthy neighboring branches. Bites were only recorded when the location of the bite was clear and within the frame of the camera.

Preference or avoidance of each section of the coral was calculated for each fish species using Ivlev's electivity index (McIlwain & Jones 1997), which is defined as:

$$E = (r - p) / (r + p)$$

where r is the proportion of a food type consumed and p is the proportion of this food type available in the environment. E values range from -1 to +1. A value of 0 indicates no selection (proportion consumed equal to proportion available), positive values indicate preference, and negative values indicate avoidance. E values were calculated for all videos combined, rather than each video, because of high variation in feeding rates. Total number of bites on each section was used to obtain the proportional consumption by each fish species. E values were only calculated for fishes that took more than 30 bites in total. Proportional availability of each coral section was calculated by placing a transparent grid of evenly-spaced points on the viewing screen, and counting the number of points intersecting each section for each video. There were 558 points covering the entire viewing screen. Background areas and background branches not examined for bites were excluded from the count. The number of points in each section was added across all videos to obtain the proportion available.

2.3 Preference of fishes for diseased or healthy coral in aquaria

To supplement observations from the video recordings, the feeding preferences of two obligate corallivores, *C. lunulatus* and *L. unilineatus*, were also measured in aquaria. *C. lunulatus* and *L. unilineatus* individuals were collected from Watson's Bay (Figure 2) using barrier nets and clove oil, and then kept in large tanks for 6-8 days before the experiment with an ample supply of *A. muricata* and *Pocillopora damicornis* for food. One day before the experiment, diseased and healthy fragments of *A. muricata* approximately 10-15 cm in length were collected from Loomis Reef (Figure 2). Two healthy fragments or two diseased fragments were affixed upright to the opposite corners of a 10 × 10 cm tile with plasticine clay and superglue. Healthy fragments were kept in tanks in the lab, and diseased fragments were kept on racks near Loomis Reef before retrieval. No algae were present on any of the fragments.

Fish were starved for at least 2 hours, and then a pair of *C. lunulatus* (n = 7) or *L. unilineatus* (n = 5) was placed into one side of a glass aquarium (60 × 26 × 38 cm, 59 l) with flow-through seawater divided in half by a removable partition. Fish were paired because they typically do not feed when alone (Pratchett, personal comm.). A tile with diseased coral fragments and a tile with healthy coral fragments were placed into the other half of the tank. Fish were allowed to acclimate for at least one hour before the partition was removed and the tiles with corals were moved to opposite ends of the tank. All bites on the corals taken by both fish (as a pair) were recorded for 30 minutes starting at the first bite. The number of bites and the location of each bite was recorded (Figure 1).

Preference for each section of coral was calculated using Ivlev's electivity index (see Section 2.2). E values were calculated for each pair of fish and then averaged for the species. Proportional consumption was based on the number of bites taken from each section. The vertical length (mm) of each section relative to the length of the coral fragment was used to determine the proportional availability. Lengths from the two corals on each tile were combined. Measuring only the linear dimensions did not consider the absolute surface area of each section available to the fish, but provided an approximate index.

3 Results

3.1 Video observations of feeding on diseased coral

A total of 15 identifiable fish species from 4 families were observed feeding on any part of the coral branch: 5 butterflyfish (Chaetodontidae), 8 damselfish (Pomacentridae), 1 wrasse (Labridae), and 1 leatherjacket (Monacanthidae). 12 species took at least one bite from the disease band or tissue margin (the diseased sections). Only 6 species took more than a total of 30 bites.

The two species with the most number of bites on the disease band and tissue margin were *Pomacentrus moluccensis* and *C. aureofasciatus* (Figure 3). *P. moluccensis* took more bites on the disease band than the tissue margin, while *C. aureofasciatus* did the opposite. Unidentified, juvenile striped wrasses took the third most number of bites on these two sections, followed by *Stegastes* spp., *Cheiloprion labiatus*, *C. lunulatus*, and *C. rainfordi*. Juvenile wrasse took almost no bites from the tissue margin.

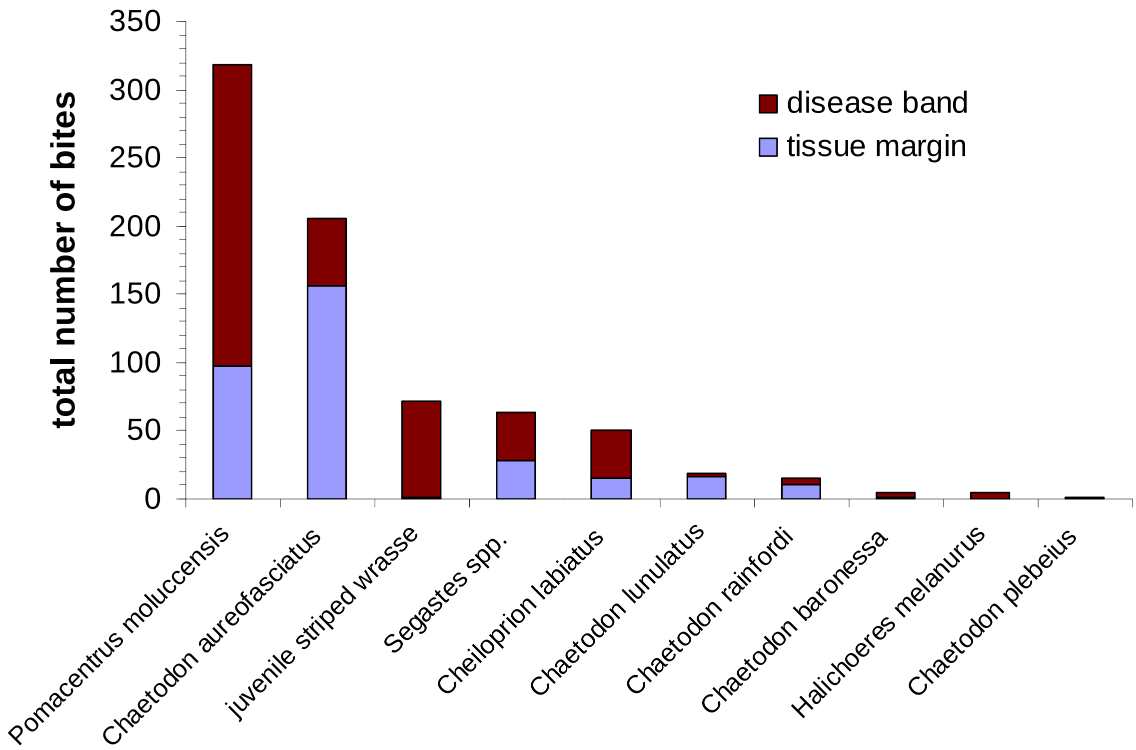

Figure 3. Total number of bites taken by different fish species on disease band and tissue margin during video observations of *A. muricata* branches with brown band disease. Data were combined from 17 different videos, each 1 hour long.

The proportional availability of each coral section was 67% live tissue, 20% algae, 8% dead skeleton, 4% disease band, and 1% tissue margin. All fish species for which electivity indices were calculated showed selective consumption of different sections. The three butterflyfish *C. aureofasciatus*, *C. rainfordi*, and *C. lunulatus* all exhibited a strong preference for the tissue margin (E ≈ 0.9), and avoidance of dead skeleton and algae (E < -0.5) (Figure 4). Of the three butterflyfish, *C. aureofasciatus* showed the most preference for the disease band and the least preference for live tissue, followed by *C. rainfordi*, and then *C. lunulatus*, which showed the least preference for the disease band and the most preference for live tissue.

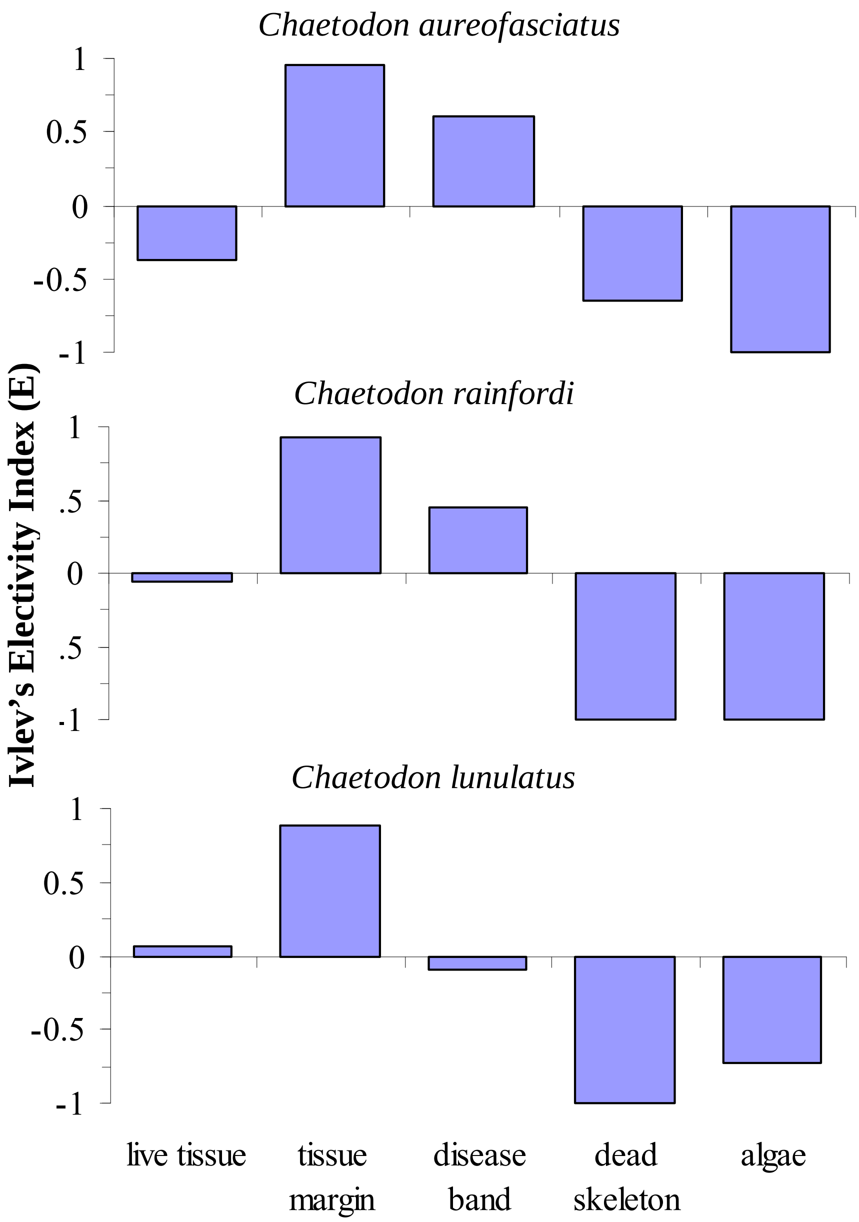

Figure 4. Selective consumption of different coral sections by 3 species of butterflyfishes during video observations of *A. muricata* branches with brown band disease using Ivlev's electivity index. Positive values indicate preference and negative values indicate avoidance. Data were combined from 17 different videos, each 1 hour long.

Three damselfish species all showed a strong preference for the tissue margin and disease band, and avoidance of live tissue (Figure 5). *Cheiloprion labiatus* (biglip damsel), a corallivore, additionally preferred the dead skeleton and avoided algae. Conversely, the herbivorous *Stegastes* spp. preferred algae and avoided the dead skeleton. *P. moluccensis*, a planktivore, avoided both the dead skeleton and algae. Juvenile striped wrasses tended to

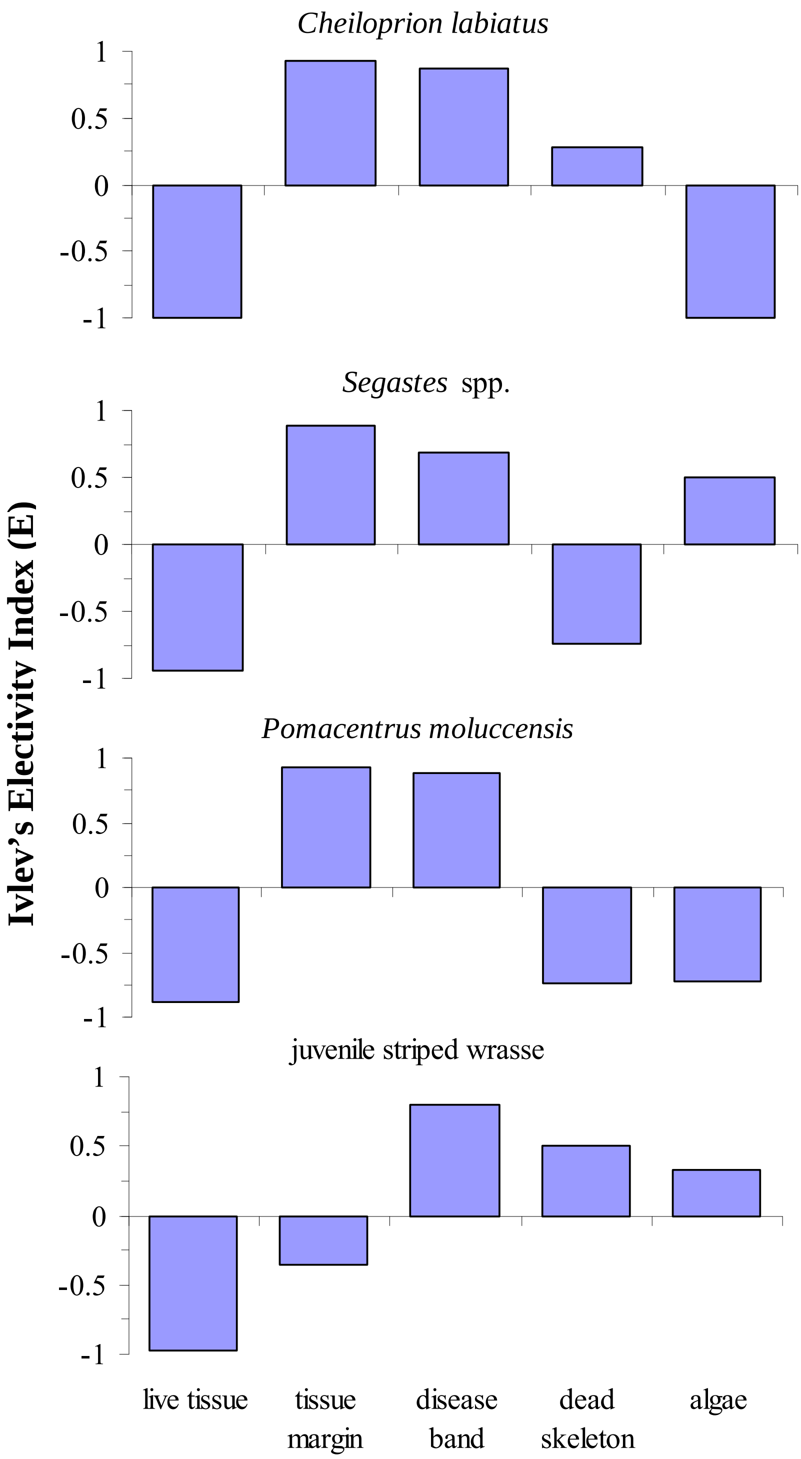

Figure 5. Selective consumption of different coral sections by 3 species of damselfishes and striped juvenile wrasse during video observations of *A. muricata* branches with brown band disease using Ivlev's electivity index. Positive values indicate preference and negative values indicate avoidance. Data were combined from 17 different videos, each 1 hour long.

avoid live tissue and tissue margin, preferring the disease band, dead skeleton, and algae.

Gobies (probably *Eviota* sp.) were often observed sitting on and biting the disease band and tissue margin in the videos. It was difficult to count the number of bites taken, and difficult to spot the gobies on healthy branches for comparison, so they were not included in the electivity analysis, but they appeared to have a strong preference for the diseased sections.

3.2 Preference of fishes for diseased or healthy coral in aquaria

Feeding rates varied considerably between the two fish species (Figure 6). *C. lunulatus* fed much more frequently than *L. unilineatus* in total, and took many more bites on live tissue than *L. unilineatus*. However, both fed approximately the same absolute amount on the tissue margin and disease band, and *L. unilineatus* took more bites of the dead skeleton than *C. lunulatus*.

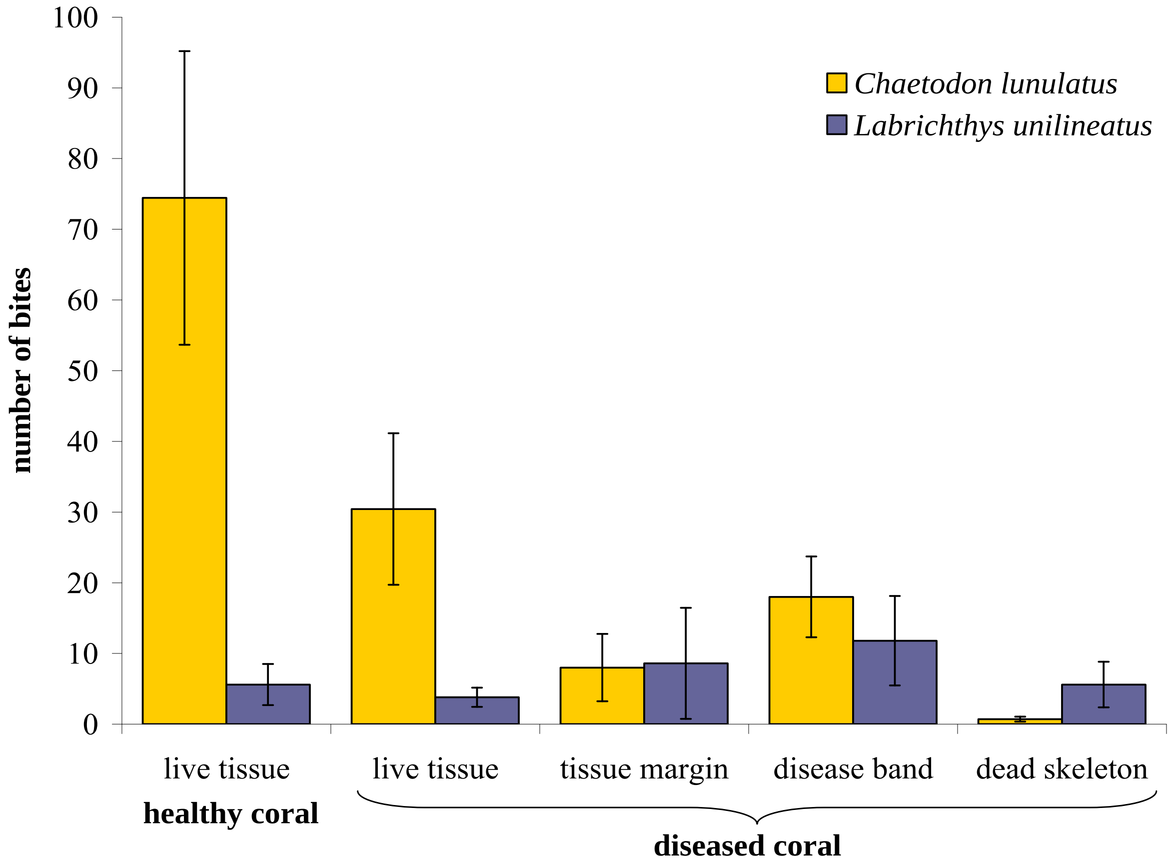

Figure 6. Number of bites (mean ± SE) by a pair of *C. lunulatus* (n = 7) and *L. unilineatus* (n = 5) on healthy coral and different sections of diseased coral during a 30 min time period. Fish were presented with two diseased and two healthy *A. muricata* fragments in an aquarium.

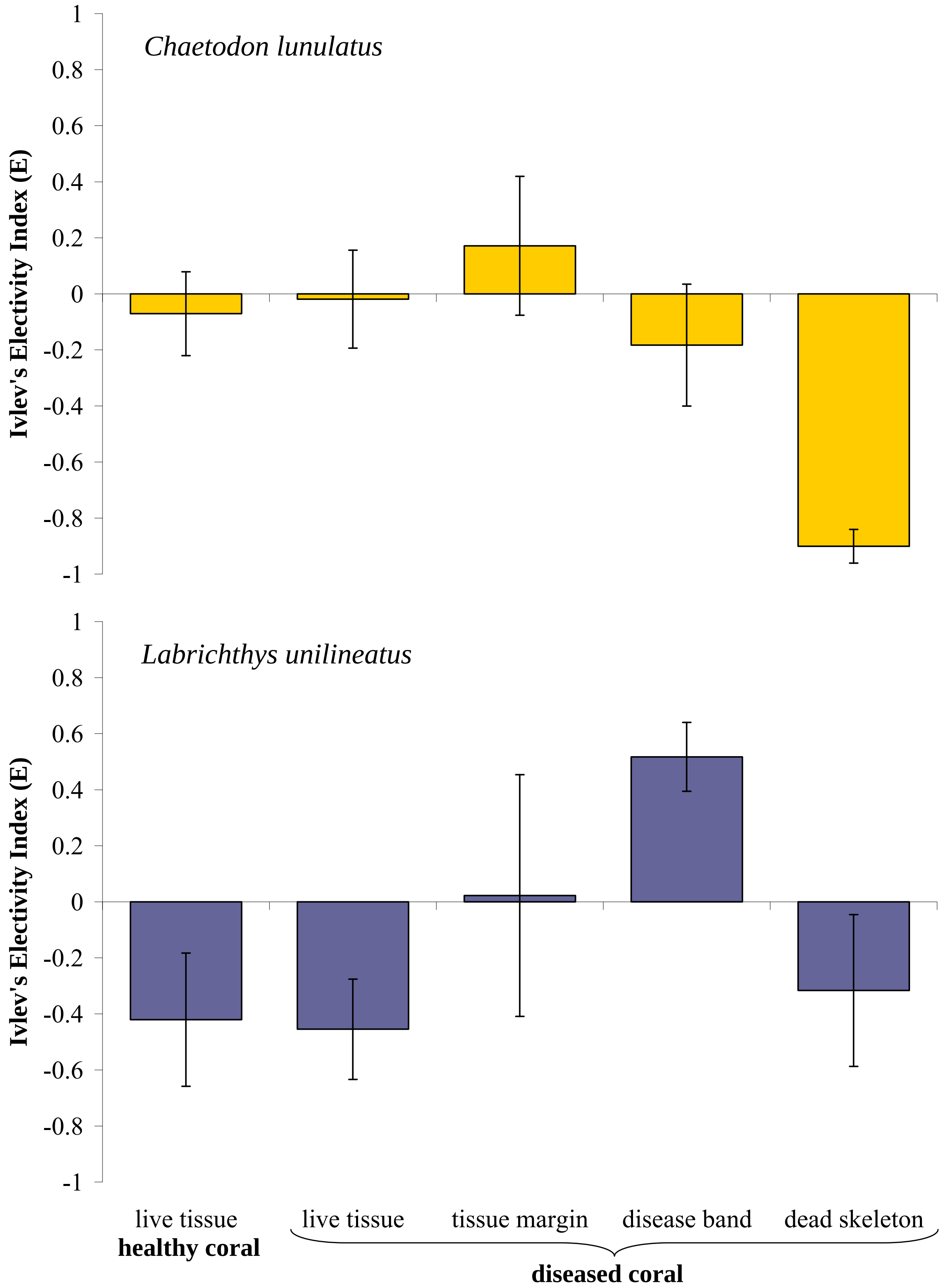

Figure 7. Selective consumption of healthy coral and different sections of diseased coral by a pair of *C. lunulatus* (n = 7) and *L. unilineatus* (n = 5) during a 30 min time period using Ivlev's electivity index (mean ± SE). Fish were presented with two diseased and two healthy *A. muricata* fragments in an aquarium. Positive values indicate preference and negative values indicate avoidance.

The proportional availability of each coral section was 20% live tissue on healthy coral, 15% live tissue on diseased coral, 18% disease band, 16% dead skeleton, and 2% tissue margin. *C. lunulatus* showed preferences in the aquarium trials (Figure 7) similar to those it exhibited in the video observations (Figure 4). It had a close to neutral preference for live tissue, both on healthy and diseased coral, a slight avoidance of the disease band, and a strong avoidance of the dead skeleton. *C. lunulatus* had a potential preference for the tissue margin, although it was not as extreme as in the video observations ($E = 0.17 \pm 0.25$ as opposed to 0.88). Because of variation in the data from the aquarium trials, however, zero is included in the SE range for all sections except the dead skeleton.

The preferences of *L. unilineatus* were very different from those of *C. lunulatus* (Figure 7). *L. unilineatus* avoided live tissue on both healthy and diseased coral, and may or may not prefer the tissue margin, as there was large variation. Like *C. lunulatus*, it avoided the dead skeleton, but unlike *C. lunulatus*, it showed a definite preference for the disease band.

4 Discussion

Most fish species, including non-corallivores, took bites from the disease band and/or tissue margin and showed a preference for at least one of these two sections. However, it was only corallivores (*Chaetodon* spp. and *L. unilineatus*) that appeared to feed on live tissue in addition to these diseased sections, and so would be mostly likely to spread disease to healthy corals. The disease band is known to contain the brown band ciliates (Boyett 2006), and fishes may be picking them up by feeding on this section. The fish might then transmit the pathogens to other corals they feed on, as found by Aeby and Santavy (2006). By feeding on the tissue margin, which may have the onset of infection by ciliates or associated bacteria, the fish may also pick up pathogens, or the fish might further stress this tissue and increase the rate of progression of the disease. It is also possible that by feeding on the disease band, the fish (including non-corallivores) could remove the disease from the coral. In Hawaii, the butterflyfish *Chaetodon multicinctus* preferentially fed on coral polyps infected with a parasitic trematode (Aeby 2002). Feeding removed the parasite from a colony, but fish then propagated the parasite to more colonies through their feces. Oral and fecal transmission, and the effect consuming the disease band or margin on the coral itself, are all worthy of future investigation.

The preference of fishes for the disease band and tissue margin is consistent with other studies showing a preference for damaged corals (Pratchett 2005, McIlwain & Jones 1997), but why fishes prefer these diseased sections is uncertain. It has been suggested that damaged coral tissue emits olfactory attractants or increases mucous production in a way that makes it more appealing to fish (McIlwain & Jones 1997). Perhaps the ciliates themselves offer some nutritional value, or the damaged tissue is easier to remove.

It is interesting that many non-corallivores, such as *P. moluccensis*, fed so frequently on the disease band and tissue margin (Figure 5). Perhaps they were targeting the ciliates, as opposed to the coral tissue, which would be interesting to examine in the laboratory. It is possible that the small gobies and juvenile wrasse seen in the videos were consuming ciliates, as both fish seemed to bite preferentially on the disease band with their tiny mouths. The herbivorous *Stegastes* spp. were naturally one of the only fishes to prefer algae, but it was unexpected that they also preferred the diseased sections. Perhaps they thought the brown band resembled algae, or were biting at potentially weakened coral tissue to try and promote algal growth. Because many of the damselfishes and other non-corallivores did not consume live coral, and often resided within well-defended territories in a single coral colony, these species are not likely to be transmitting disease. It is possible they may even reduce the prevalence of disease by selectively feeding on and removing the ciliates.

The corallivores (*Chaetodon* spp. and *L. unilineatus*) are known to feed repeatedly on the multiple colonies within their feeding territories (Pratchett 2005, McIlwain & Jones 1997), which makes them more likely to transmit disease between colonies. To better understand which of these corallivores are most capable of acting as disease vectors, it would be useful to investigate the number of coral colonies and coral species visited by these fishes after feeding on the diseased coral. Assuming fishes can act as oral or fecal disease vectors after feeding on a diseased colony in their territory, fishes that then visit a large number of different coral species and colonies would have the most potential to spread the disease. Of particular interest would be the number of different *A. muricata* colonies a fish feeds from, since this species appears most susceptible to disease. Why *A. muricata* is affected so much by brown band disease is another subject that could be examined. Being a rapidly growing coral species, perhaps it has fewer defenses against damage and infection.

Of the butterflyfishes, *C. aureofasciatus* has the most potential to be a disease vector. Not only did this species take the most bites of the disease band and tissue margin (Figure 3), it also showed the most preference for the disease band relative to live tissue (Figure 4). *C. rainfordi* would follow as the next most likely vector, as it showed the next most preference for the disease band relative to live tissue, and then *C. lunulatus* (Figure 4). The other butterflyfishes observed feeding on diseased coral, *C. baronessa* and *C. plebeius*, fed only rarely on the diseased sections in the videos (Figure 3), so it was not possible to determine their feeding preferences and potential to transmit disease. It is likely that their preferences are similar to those of the other butterflyfishes.

Although the feeding preferences of *C. lunulatus* were similar for video and aquarium observations, suggesting reliability, it is possible that both trials were biased. Diseased coral was likely represented in higher proportions than would be available to the fish in its natural environment. The feeding behavior of fishes away from the diseased branches was not observed. To most accurately confirm feeding preferences, one would ideally follow the feeding behavior of individual fishes in the field and relate their prey choice to the availability of diseased and healthy corals in the surrounding reef as determined by a coral survey, as done by Pratchett (2007).

McIlwain and Jones (1997) found that *L. unilineatus* preferred the damaged edges of live corals, which included edges caused by disease. This preference was particularly pronounced in males. *L. unilineatus* showed no definite preference for the tissue margin in this study, instead preferring the disease band (Figure 7). Although this is still a preference for damaged over healthy tissue, the slight discrepancy may ontogenetic, since all the fish used in this study were females. Unfortunately, *L. unilineatus* was not observed feeding on the corals in the videos, so no comparison could be made with the aquarium trials.

5 Conclusions

Although many fishes fed upon and showed a preference for diseased coral sections, the obligate corallivores (mainly *Chaetodon* spp. and *L. unilineatus*) have the most potential to act as disease vectors, as they were the only fishes to feed substantially on live tissue in addition to targeting the diseased sections, and they are known to repeatedly visit multiple colonies in their feeding territories. Other fishes, such as *P. moluccensis*, which do not feed on live coral and typically reside within a single colony, are unlikely to be spreading the disease through their feeding activities. These species may actually reduce the prevalence or slow the progression of brown band disease by selectively consuming the ciliates. The potential effects of corallivory on diseased coral, including both transmission and inhibition, would need to be confirmed using appropriate experiments. To understand the ecology of coral diseases and their ultimate effect on coral persistence, it appears important to consider the additional effects of corallivory by reef fishes.

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