

Selective feeding by coral reef fishes on coral lesions associated with brown band and black band disease

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Abstract Recent studies have suggested that corallivorous fishes may be vectors for coral disease, but the extent to which fishes actually feed on and thereby potentially transmit coral pathogens is largely unknown. For this study, in situ video observations were used to assess the level to which fishes fed on diseased coral tissues at Lizard Island, northern Great Barrier Reef. Surveys conducted at multiple locations around Lizard Island revealed that coral disease prevalence, especially of brown band disease (BrB), was higher in lagoon and backreef locations than in exposed reef crests. Accordingly, video cameras were deployed in lagoon and backreef habitats to record feeding by fishes during 1-h periods on diseased sections of each of 44 different coral colonies. Twenty-five species from five fish families (Blenniidae, Chaetodontidae, Gobiidae, Labridae and Pomacentridae) were observed to feed on infected coral tissues of staghorn species of *Acropora* that were naturally infected with black band disease (BBD) or brown band disease (BrB). Collectively, these fishes took an average of 18.6 (± 5.6 SE) and 14.3 (± 6.1 SE) bites per hour from BBD and BrB lesions, respectively. More than 40% (408/948 bites) and nearly 25% (314/1319 bites) of bites were observed on lesions associated with BBD and BrB, respectively, despite these bands each representing only about 1% of the substratum available. Moreover, many

corallivorous fishes (*Labrichthys unilineatus*, *Chaetodon aureofasciatus*, *C. baronessa*, *C. lunulatus*, *C. trifascialis*, *Cheiloprion labiatus*) selectively targeted disease lesions over adjacent healthy coral tissues. These findings highlight the important role that reef fishes may play in the dynamics of coral diseases, either as vectors for the spread of coral disease or in reducing coral disease progression through intensive and selective consumption of diseased coral tissues.

Keywords Coral disease · Corallivores · Butterflyfishes · Feeding selectivity · Disease transmission

Introduction

Coral diseases have increased greatly in prevalence and impact over recent years, contributing substantially to accelerating coral loss and reef degradation throughout the world (Green and Bruckner 2000; Rosenberg and Ben-Haim 2002; Harvell et al. 2007, 2009). For example, white plague and white band diseases have caused extensive depletion of Caribbean species of *Acropora*, leading to marked shifts in Caribbean coral community structure (Aronson and Precht 2001; Miller et al. 2006, 2009; Weil et al. 2006). Explanations for the recent increases in the prevalence of coral disease are often related to ocean warming (Bruno et al. 2007; Harvell et al. 2007), although the abundance of coral disease is also known to be enhanced by stressors, such as increased nutrients, sedimentation and pollution (Harvell et al. 2009). Alternatively, Raymundo et al. (2009) attributed the increased prevalence of coral disease, in part, to overfishing and trophic cascades among coral reef fishes, whereby increased abundance of corallivorous fishes following

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declines in predatory fishes might contribute to the spread of pathogens among corals. However, the nature of interactions between coral-feeding fishes and coral pathogens is unclear (Rotjan and Lewis 2008), and very little is known about the etiology and transmission of most major coral diseases.

The influence of vectors in coral diseases is uncertain, but such knowledge would enhance prediction of coral disease distribution patterns (Green and Bruckner 2000; Work et al. 2008). Three species of invertebrate corallivores have been implicated in the initiation of new disease cases involving the coral-bleaching pathogen *Vibrio shiloi* and unknown pathogen(s) causing tissue sloughing (Sussman et al. 2003; Williams and Miller 2005; Dalton and Godwin 2006). Corallivores implicated in these studies encompass a range of taxa, including a fireworm (*Hermodice carunculata*), a snail (*Coralliophila abbreviata*) and a nudibranch (*Phestilla* sp.). The fireworm also serves as a disease reservoir, enabling the pathogen to survive unfavourable winter conditions inside the worm's epidermis (Sussman et al. 2003). While the likelihood that corallivorous invertebrates spread certain coral diseases seems clear, interactions between coral-feeding fishes and coral pathogens are more obscure (Rotjan and Lewis 2008); in particular, evidence that fishes actually feed on, and thereby potentially transmit, putative disease pathogens is equivocal.

Most corallivorous fishes feed on numerous different coral colonies within their feeding territories and are constantly moving between colonies (Pratchett 2007); thus, they may contribute to the spread of coral diseases if they interact directly with coral pathogens. Within recirculating aquarium studies, Aeby and Santavy (2006) showed that the presence of the Caribbean butterflyfish *Chaetodon capistratus* increased the transmission of black band disease (BBD) among non-adjacent corals, although they could not directly attribute this transmission to fishes feeding on and then moving between diseased and healthy coral fragments. The specific mechanism by which transmission occurred and the roles that fishes played in this experiment remain unknown, but it is possible that feeding by butterflyfishes on diseased corals simply displaced pathogens into the water column, increasing waterborne transmission (Aeby and Santavy 2006). On the Great Barrier Reef (GBR), Australia, observations of six species of coral-feeding fishes (*Chaetodon* butterflyfishes and *Labrichthys unlineatus*) feeding on disease bands associated with black band disease on acroporid corals led to the speculation that corallivorous butterflyfishes might be important in reducing the abundance and severity of BBD on the GBR (Cole et al. 2009). A short pilot study suggested that rather than contributing to increasing abundance of this disease, intensive feeding by corallivorous

fishes actually slowed the progression of BBD. Detailed observations of the feeding behaviour of corallivorous fishes are needed, however, to further explore their potential role as either vectors or mitigators of coral disease spread.

The purpose of this study was to explore the range of coral reef fishes that feed on naturally diseased coral tissues, thereby identifying species that potentially act as vectors of coral pathogens. In situ feeding observations were conducted with the aid of video cameras focussed on disease lesions characteristic of both brown band disease (BrB) and BBD (Fig. 1). The proportion of bites taken on lesions could then be quantified relative to nearby healthy coral tissues. If fishes feed directly on diseased coral tissues followed by feeding on nearby healthy coral tissues, they would be capable of spreading putative disease pathogens on their mouthparts or potentially through faeces (Aeby and Santavy 2006). Although the potential for pathogens to successfully infect new coral hosts when transmitted in either of these manners needs to be tested, a critical first step in clarifying the role of coral reef fish as vectors of coral disease is identifying the range of candidate vector species for targeted experiments.

Materials and methods

Study site and sampling design

This study was conducted at Lizard Island (14°40'S, 145°27'E), a mid-shelf reef on the Great Barrier Reef, Australia, during the 2008/2009 austral summer when disease prevalence is typically at its highest (Willis et al. 2004; Page and Willis 2006). Coral disease prevalence (percentage of colonies with disease signs) was assessed using replicate 20 × 2 m belt transects following the study by Willis et al. (2004). Three replicate transects were surveyed at 5 reefs within each of 3 distinct habitats: exposed reef crests, on shallow reef fronts within the lagoon and on the tops of individual patch reefs in the backreef (Fig. 2). Local densities of corallivorous fishes were also surveyed concurrently along replicate 50 × 4 m belt transects ($n = 3$ per site). All butterflyfishes (family Chaetodontidae) known to feed on live corals at Lizard Island, following Pratchett (2005), were recorded, as well as other corallivorous fishes, following Cole et al. (2008).

Spatial variation in the prevalence of both BrB and BBD was analysed using a nested ANOVA, with location (5 levels, random factor) nested within habitat-type (3 levels: crest, lagoon and backreef, fixed factor). Data on the prevalence of coral disease was square root-arcsine transformed, as required for percentage data (Zar 1984), although the proportion of colonies infected was

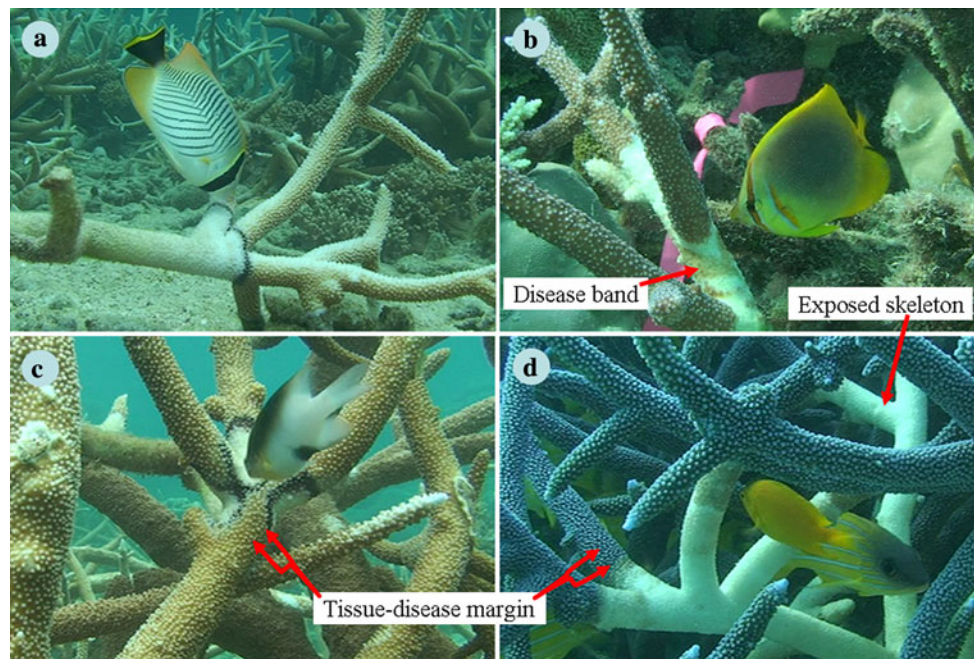


Fig. 1 Video stills of fishes feeding on colonies of *Acropora muricata* infected with **a, b** black band disease and **c, d** brown band disease. Fishes observed to feed on diseased corals included the

following: **a** *Chaetodon trifascialis*, **b** *Chaetodon aureofasciatus*, **c** *Dischistodus melanotus*, **d** *Pomacentrus moluccensis*. Categories used to characterise locations of fish bites are also depicted

consistently less than 5%. Local densities of corallivorous fishes were also analysed using a nested ANOVA, comparing abundance of coral-feeding butterflyfishes as well as all other known corallivores ('others') among locations and habitat types.

Having established that disease prevalence was highest in lagoon and backreef locations, colonies of *Acropora* (*A. muricata*, *A. abrolhosensis*, *A. intermedia*) that were infected with either BrB or BBD were then located in these two habitats, to assess the extent to which fishes consumed diseased versus healthy sections of infected corals. BrB and BBD are two of the most widespread and distinctive of the coral diseases known to infect Indo-Pacific corals (Willis et al. 2004) and among the few Indo-Pacific diseases for which putative disease pathogens have been identified (Carlton and Richardson 1995; Bourne et al. 2008). BrB is associated with ciliates (class Oligohymenophorea: Scuticociliatia; Bourne et al. 2008), which move over the surface of coral tissues, while BBD mats are composed of a consortium of microbes, including cyanobacteria, sulphate-reducing and sulphide-oxidizing bacterial species (reviewed by Richardson 2004). Digital video cameras were placed a minimum of 50 cm away from a colony infected with either BrB or BBD and focussed on the distinctively coloured bands bordering disease lesions adjacent to seemingly healthy coral tissues. A total of 44 different infections, divided evenly between BrB and BBD and spread across 8 reefs, were filmed in 44 1-hr-long video recordings.

Data collection from videos and statistical analysis

All species of fishes that took bites from substrata within the field of view of each camera were recorded during analyses of the videos. The number of bites taken by each fish was recorded within each of the following five categories: algae on substrata near colonies monitored, exposed skeleton on diseased corals, disease bands comprised of pathogens and necrotic coral tissue, coral tissue bordering lesions (defined as the 1-cm band of live tissue adjacent to disease bands) and apparently healthy coral tissue greater than 1 cm from lesions (Fig. 1). Visits without feeding were also recorded. Bites were counted only when the observer could see the mouth and food source; all bites obscured by branches were omitted. Bite rates within the first and last 10 min of recordings were compared to check, whether a period of acclimation to the presence of the cameras was required before normal feeding patterns were established; however, a *U* test showed no statistical difference in bite rates, $U = 220.5$, $P > 0.05$. Mean bite rates on the disease bands were compared between BrB and BBD videos and between corallivores and non-corallivores using non-parametric Mann–Whitney *U* tests, as assumptions of normality and homogeneity of variances were not met.

To assess whether fish species were actively choosing to feed on the bands of pathogens and necrotic coral tissue associated with BBD and BrB lesions, the proportion of bites taken on each of the five resource categories described previously was compared with their proportional

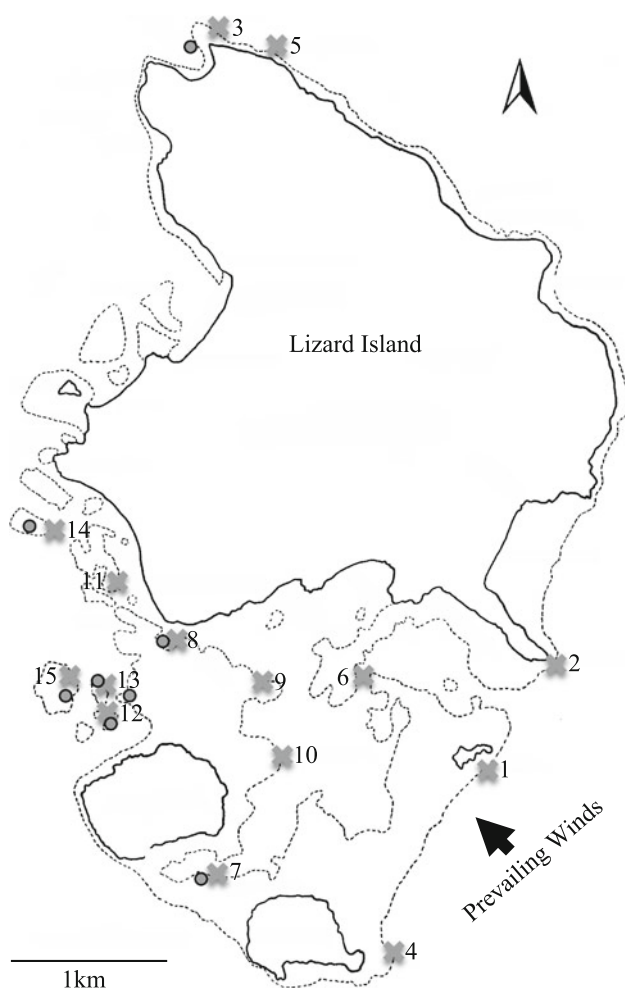


Fig. 2 Sites used for surveys of black band (BBD) and brown band (BrB) coral disease prevalence and corallivorous fish abundance (x) and video recordings of infected coral colonies (o) at Lizard Island, northern Great Barrier Reef, Australia. Dashed lines indicate approximate reef outline. Numbers correspond to reef names used in Fig. 3

availability within the field of view. For some species (e.g. small gobies and blennies), it was not always possible to discern the specific number or location of bites, and so these species were excluded from analyses. The proportional availability of each resource was calculated using a point-intercept method based on 714 points placed equidistance across the field of view of each video camera. Selectivity for each fish species was analysed using the log-likelihood statistic (C_{L2}^2), calculated using the formula:

$$X_{L2}^2 = 2 \sum_{j=1}^n \sum_{i=1}^l u_{ij} \ln [u_{ij}/E(u_{ij})],$$

where u_{ij} is the use of each resource (i) by each individual (j), and $E(u_{ij})$ is the expected number of bites taken from resource i by the j th individual if use is proportional to availability (Manly et al. 2002). The significance of selectivity was ascertained by comparing overall levels of

selectivity (C_{L2}^2) to a chi-square distribution with $n(I-1)$ degrees of freedom, where I is the total number of resources used across all fish species (Manly et al. 2002). Resource selection functions (w_i) were used to determine which resource (i) was consumed more or less frequently than expected, based on its availability to each fish species, and calculated as:

$$\hat{w}_i = (u_{i+}/u_{++})/(\pi_i)$$

The resource selection functions calculated compared the proportional use (u_{i+}/u_{++}) of each substrate category by all individuals of a species with the proportional availability of that substrate category (π_i) within the local area (where the local area is defined as the field of view of the video camera; Manly et al. 2002). To interpret the selection function values obtained, 95% confidence intervals around each selection function were calculated, and the use of each resource was deemed disproportionate to availability if the 95% confidence interval did not include 1 (Manly et al. 2002). Selectivity functions distinguished between fish actively targeting diseases on the colonies on which they fed and fish consuming diseased tissues randomly and in proportion to their availability; they do not represent measures of selectivity for disease across the entire territories of these fish species.

Results

Disease prevalence and corallivorous fish abundance around Lizard Island

BrB prevalence on all corals varied significantly between locations (ANOVA, $F = 0.001$, $df = 0.007$, $P < 0.05$) and was between 8 and 34 times higher in lagoon and backreefs than in exposed reef crests (Fig. 3). While BBD prevalence did not vary significantly between locations (ANOVA, $F = 9.91E^{-5}$, $df = 0.001$, $P > 0.05$), prevalence was 5–6 times higher in lagoon and backreefs than in exposed reef crests (Fig. 3). The average prevalence of BrB on acroporid corals ranged from 0 to 4.0% (± 2.0 SE) in backreefs, 0 to 10.3% (± 1.5 SE) in lagoon reefs and 0 to 0.2% (± 0.2 SE) in exposed reefs. By comparison, BBD prevalence on acroporid corals ranged from 0 to 3.4% (± 1.7 SE) in backreefs, 0 to 3.0% (± 3.0 SE) in lagoon reefs and 0 to 0.5% (± 0.5 SE) in exposed reefs. BBD and BrB prevalence on other genera was negligible; no cases were found in the backreef locations, and only one case of BrB and no BBD cases were found at exposed reefs. For lagoon reefs, BBD prevalence was $0.2 \pm 0.2\%$, while BrB prevalence was $0.8 \pm 0.5\%$.

Corallivorous butterflyfish abundance showed no significant variation between locations (ANOVA, $F = 5.689$,

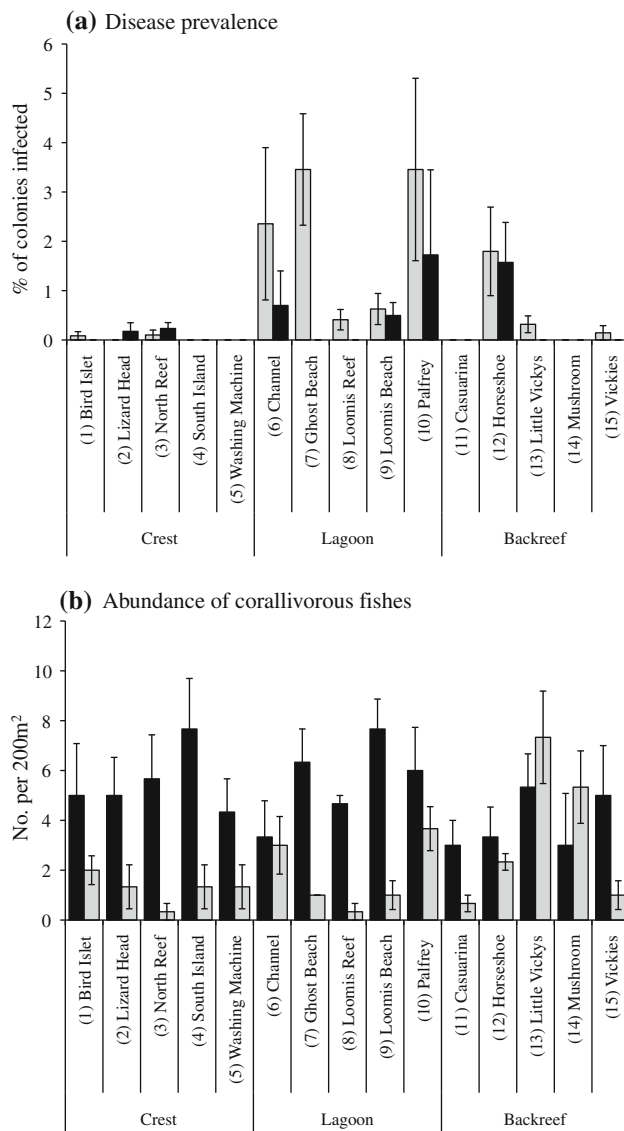


Fig. 3 Spatial variation in **a** mean (\pm SE) prevalence of brown band disease (BrB; grey bars) and black band disease (BBD; black bars) and **b** densities of coral-feeding butterflyfishes (black bars) versus other known corallivores (grey bars). Numbers prefixing reef names correspond to locations on map, Fig. 2

$df = 68.3$, $P > 0.05$), and average abundances were between 3 and 7 fish per reef (Fig. 3). By comparison, all other corallivorous fishes showed a significant variation in abundance with location (ANOVA, $F = 10.883$, $df = 130$, $P < 0.01$), and average abundances ranged from 1 to 9 fish per reef (Fig. 3).

Range of fishes observed to interact with corals and disease lesions

A total of 25 fish species from five families (Blennidae, Chaetodontidae, Gobiidae, Labridae and Pomacentridae) were observed to feed on disease bands associated

with BBD and BrB lesions, presumably consuming both necrotic coral tissue and the putative causative agents of each of these diseases (Table 1). A further five corallivorous species, from three families (Chaetodontidae: *Chaetodon auriga*, *C. melannotus* *C. vagabundus*; Ostraciidae: *Ostracion cubicus*; and Monacanthidae: *Oxymonacanthus longirostris*) were observed during the videos, but never fed on disease bands or on coral tissue bordering lesions. Of those species that fed on disease bands, the following seven fed only on BrB: the obligate corallivorous species *Chaetodon rainfordi* and *Cheiloprion labiatus*, and five non-corallivorous species (*Gomphosus varius*, *Pomacentrus moluccensis*, *Stegastes apicallis*, *S. nigricans* and juvenile scarids). Eight fish species fed only on BBD, specifically two obligate corallivorous species (*Chaetodon trifascialis*, *Labrichthys unilineatus*), two facultative corallivorous species (*Chaetodon citrinellus*, *C. klenii*) and four non-corallivorous species (*Acanthochromis polyacanthus*, *Dischistodus melanotus*, *Pomacentrus amboinensis* and *P. chrysurus*). A further 10 species fed on both BrB and BBD, these being three obligate corallivorous species (*Chaetodon aureofasciatus*, *C. baronessa*, *C. lunulatus*), one facultative soft coral-feeder species (*Neoglyphidodon melas*) and six non-corallivores (*Amblyglyphidodon curacao*, *Coris batuensis*, *Pomacentrus wardii*, *Escenius stictus*, *Bryaninops erythrops*, *Gobiodon okinawae*).

Selective consumption of diseased coral tissues

Coral reef fishes exhibited strong preference for disease bands bordering lesions, based on bite rates on corals and other substrata visible within the fields of view for each of the 44 videos. Of bites taken by fishes feeding on diseased coral tissues, 23.9% (314/1319 bites) and 43% (408/948 bites) were taken directly on disease bands associated with BrB and BBD lesions, respectively, even though BrB and BBD disease bands accounted for only 1.20 and 0.96%, respectively, of available substratum. Furthermore, fishes were recorded to feed on disease bands in 64% of BrB videos ($n = 22$ videos) and in 91% of BBD videos ($n = 22$ videos). Overall, mean feeding rates on disease bands by all fishes combined did not differ between the two diseases (14.3 ± 6.1 bites h^{-1} for BrB vs. 18.6 ± 5.6 bites h^{-1} for BBD; $U = 183.0$, $P > 0.05$). However, considering each feeding guild separately, corallivorous fishes fed nearly threefold more frequently on BBD than on BrB lesions (15.8 ± 5.44 bites h^{-1} on BBD lesions vs. 3.7 ± 2.04 bites h^{-1} on BrB lesions; $U = 143.5$, $P < 0.05$), taking 57.8% of their total bites during video observations of BBD-infected corals from the disease band itself (Fig. 4). In contrast, non-corallivores fed most frequently on BrB, taking four times as many bites from disease bands on BrB-infected corals compared to BBD-infected corals

Table 1 Dietary selectivity of 19 coral reef fishes observed to have taken at least one bite on the disease band of a coral infected with black band and/or brown band disease

| Species | X_{L2}^2 * | | Disease band w_i | | Selectivity | | | | | | | | | | | |
|---------------------------------|--------------|------|--------------------|-------|-------------|-----|-----|-----|----|-----|----|----|----|----|----|----|
| | | | | | BrB | | | | | BBD | | | | | | |
| | | | | | BrB | BBD | BrB | BBD | A | S | B | M | T | A | S | B |
| Obligate corallivores | | | | | | | | | | | | | | | | |
| <i>Labrichthys unilineatus</i> | | 552 | | 79.06 | | | | | | | | NU | NU | + | + | NU |
| <i>Chaetodon aureofasciatus</i> | 736 | 135 | 15.8 | 42.94 | NU | 0 | + | + | 0 | – | + | + | + | + | – | NU |
| <i>Chaetodon baronessa</i> | 87.5 | 1134 | 9.08 | 27.08 | NU | 0 | 0 | 0 | NU | – | + | + | + | + | – | – |
| <i>Chaetodon lunulatus</i> | 154 | 348 | 5.76 | 76.48 | – | NU | 0 | + | 0 | NU | 0 | + | NU | NU | – | – |
| <i>Chaetodon rainfordi</i> | 73.6 | | 9.83 | | NU | 0 | + | + | + | | | | | | | |
| <i>Chaetodon trifascialis</i> | | 553 | | 102.3 | | | | | | | NU | NU | + | NU | NU | – |
| <i>Cheiloprion labiatus</i> | 286 | | 20.7 | | – | + | + | + | – | | | | | | | |
| Facultative corallivores | | | | | | | | | | | | | | | | |
| <i>Chaetodon citrinellus</i> | | 159 | | 83.43 | | | | | | | NU | NU | + | 0 | NU | – |
| <i>Chaetodon klenii</i> | | 210 | | 104.3 | | | | | | | NU | NU | + | NU | NU | – |
| <i>Neoglyphidodon melas</i> | 12.9** | 974 | | 93.76 | | | | | | | – | + | + | 0 | NU | – |
| Non-corallivores | | | | | | | | | | | | | | | | |
| <i>Dischistodus melanotus</i> | 57.2 | 649 | 0 | 29.8 | + | – | NU | NU | NU | 0 | – | + | NU | NU | – | – |
| <i>Pomacentrus amboinensis</i> | | 98.3 | | 4.85 | | | | | | | – | + | + | NU | NU | – |
| <i>Pomacentrus chrysurus</i> | | 219 | | 10.12 | | | | | | | + | + | + | – | – | – |
| <i>Pomacentrus moluccensis</i> | 1049 | | 36.2 | | – | + | + | + | 0 | | | | | | | |
| <i>Pomacentrus wardi</i> | 241 | 104 | 11.9 | 10.7 | + | + | 0 | + | NU | + | NU | 0 | + | NU | – | – |
| <i>Stegastes apicalis</i> | 70.5 | | 35.8 | | 0 | NU | + | + | NU | | | | | | | |
| <i>Stegastes nigricans</i> | 133 | | 5.06 | | + | 0 | 0 | NU | NU | | | | | | | |
| <i>Gomphosus varius</i> | 125 | | 20.9 | | 0 | + | + | NU | NU | | | | | | | |
| Juvenile scarids | 652 | | 16.3 | | 0 | + | + | + | – | | | | | | | |

A Algae, S exposed skeleton, B disease band, M tissue-disease margin, T live tissue, + resource used significantly more than expected, – resource avoided, 0 resource used in approximate proportion to its availability, NU resource unused. Six more species were observed to feed on disease bands, but either (1) total bites could not be accurately quantified (i.e. for *E. stictus*, *B. erythroptus* and *G. okinawae*) or (2) no selectivity was displayed (i.e. by *A. polyacanthus*, *A. curacao*, *C. batuensis*)

* $P < 0.001$ for all chi-square statistics, except ** where $P > 0.05$

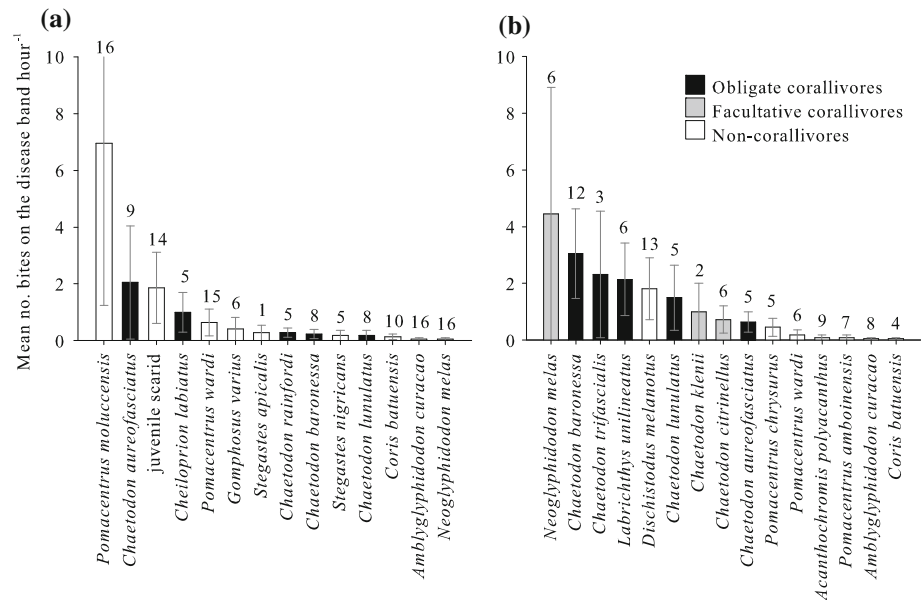
(10.5 ± 5.9 vs. 2.7 ± 1.1 bites h^{-1}); however, bite rates were highly variable among video recordings, and this difference was not statistically significant ($U = 225.5$, $P > 0.05$). Considering each disease type separately, corallivorous fishes had a fivefold greater mean bite rate per hour than non-corallivorous fishes on BBD (15.8 ± 5.4 vs. 2.8 ± 1.1 bites h^{-1} ; $U = 139.5$, $P < 0.05$), whereas non-corallivores took three times as many bites as corallivorous species on BrB (10.5 ± 5.9 vs. 3.8 ± 2.1 bites h^{-1}), although this latter difference was not statistically significant ($U = 230.0$, $P > 0.05$).

Resource selection functions highlighted the selectivity that the majority of fishes displayed for disease bands. Significant feeding selectivity was displayed by 86% of fishes ($n = 22$ species) for which bites could be accurately recorded during feeding and which fed on disease bands (Table 1). Significant selectivity for at least one type of disease band (BrB or BBD) was exhibited by 89.5% of

species that fed selectively ($n = 19$ species), i.e. they consumed diseased tissue in proportions significantly greater than expected given its availability (Table 1). Only one species (*Chaetodon aureofasciatus*) showed significant selection for both types of disease band. Six and ten species showed significant selection for only BrB or BBD, respectively (Table 1). Two species that fed on the disease band but only in proportion to its availability showed significant selection for the tissue margin and/or the exposed skeleton (*Pomacentrus wardi* on both BBD and BrB and *C. lunulatus* on BrB).

Based on the number of bites on a given substratum in relation to its availability, fishes feeding on BrB-infected corals ($n = 12$ species) were more likely to avoid live coral tissue (75% of species) and algae (50% of species), while simultaneously selecting for disease bands (58.3% of species), tissue-disease margins (66.7% of species) and exposed skeleton (41.7% of species). In comparison, fishes

Fig. 4 Mean (\pm SE) number of bites on disease bands by fish species observed in 22 videos of **a** brown band disease and **b** black band disease. The number of videos in which each species was observed to feed is displayed above the relevant histogram



feeding on BBD ($n = 12$ species) tended to avoid all resource categories except the specific disease band (selected by 91.7% of species).

Discussion

This study revealed that there are at least 25 species of coral reef fishes from five families that actively feed on diseased coral tissues, raising the possibility that a large number of reef fishes may contribute to either the spread (Aeby and Santavy 2006) or containment (Cole et al. 2009) of coral diseases. Previous discussions about the role of fishes as vectors for coral disease have focussed almost entirely on *Chaetodon* butterflyfishes (e.g. Raymundo et al. 2009), but clearly there are many more species and families potentially involved. Moreover, because this study only investigated two diseases that are especially common on staghorn corals in the genus *Acropora* from sheltered lagoon and backreef habitats, the actual number of coral reef fishes that feed on diseased coral tissue is likely to be considerably higher if the full range of different diseases, habitats and coral species are considered. At the time of study, disease prevalence values for both BBD and BrB were low (<5%); thus it would be interesting to observe how fish community dynamics might change if disease prevalence were to reach outbreak proportions.

Fishes that feed on diseased coral tissues are not limited to obligate or facultative corallivores (Table 1). Indeed, most of the bites on specific sites of BrB infection were taken by the planktivorous damselfish *Pomacentrus moluccensis*. In contrast, several corallivorous fishes, most notably the obligate corallivores *Oxymonacanthus*

longirostris and *C. melannotus* (Cole et al. 2008), were seen to consume healthy tissue of corals monitored, but never fed on or near diseased tissue. Territorial species are likely to have played a role in the species composition of fishes that eat diseased coral tissue. There were two highly territorial butterflyfishes (*C. baronessa*, *C. trifascialis*) and damselfishes (*S. nigricans*, *S. apicalis*), none of which were recorded feeding in the same video as their territorial congeners. Territoriality among corallivorous butterflyfishes (especially for *C. baronessa*) is, however, much lower in lagoonal and backreef habitats than in exposed reef crests (Berumen and Pratchett 2006).

Of those fishes that fed on diseased coral tissues, the most likely vectors for direct transmission of coral diseases would be the obligate corallivores (i.e. *Labrichthys unilineatus*, *Chaetodon aureofasciatus*, *C. baronessa*, *C. lunulatus*, *C. rainfordi*, *C. trifascialis*, *Cheilopriion labiatus*). Obligate corallivores forage on many different coral colonies throughout their feeding ranges (Pratchett 2005; Gregson et al. 2008). During this study, several pairs of obligate corallivores were observed to return frequently to the disease band of an infected coral, followed by visits to other apparently healthy colonies. In this way, disease-causing agents may be carried on mouthparts and deposited at several sites within and among adjacent corals (e.g. Aeby and Santavy 2006). Similarly, several small goby and blenny species were observed to sit on disease bands, potentially picking up pathogens on their fins and body and carrying them among corals as they constantly move within and between adjacent colonies. However, effective transmission of coral disease pathogens by reef fishes is yet to be tested, and the transmission of causative disease agents will not in itself necessarily lead to new sites of infection.

Furthermore, predation upon the diseased coral tissues by fishes that do not otherwise feed on live corals (e.g. *Pomacentrus moluccensis*) may facilitate either water transmission by mechanical disturbance (Bruckner et al. 1997) or faecal transmission, assuming the agents of disease can remain infective after passing through the digestive system of these fishes (Aeby and Santavy 2006).

The range of reef fishes that fed on diseased coral tissue encompassed several feeding guilds, including corallivores, planktivores, herbivores and omnivores. Many reef fishes are highly versatile and capable of opportunistically exploiting a wide range of seasonally available resources (e.g. Pratchett et al. 2001; McCormick 2003), but it is unknown why these fishes are targeting lesions on diseased corals. The nutritional content of the microbial community associated with BrB and BBD is currently unknown but may represent a nutritious and readily accessible source of prey for benthic feeding fishes with small mouths, such as butterflyfishes. Several obligate coral-feeding butterflyfishes have recently been shown to supplement their diet with food sources other than coral tissue (Nagelkerken et al. 2009). *Chaetodon baronessa* and *C. lunulatus*, for example, appear to supplement their coral diet with polychaete worms and macroalgae, thereby increasing the intake of several essential nutrients (Nagelkerken et al. 2009). Similarly, BrB ciliates and the microbial consortium associated with BBD may represent a source of nutrients that are low in abundance or not provided by coral tissue. Importantly, bacteria involved in sulphur cycling associated with the BBD consortium produce trace elements that are often scarce in oligotrophic coral reef waters (Sato et al. 2010). Alternatively, fishes (especially corallivorous species) may feed on or near sites of BrB and BBD infection owing to compromised defences of the coral and increased access to necrotic coral tissue. Several species of corallivorous fishes are well known to target sites of recent injury on corals (McIlwain and Jones 1997; Pratchett 2005), which would account for feeding observed on disease margins, as well as bites taken within the specific band of infection.

High rates of feeding on BrB and BBD (14.3 and 18.6 bites h^{-1} , respectively, by all fishes combined) indicate that coral reef fishes are important players in the dynamics of coral diseases. In addition to potentially spreading the causative agents of coral diseases, chronic feeding at the site of infection may restrict the progression of established BrB and BBD infections. In a pilot aquarium study, Cole et al. (2009) showed that intensive feeding by *Chaetodon plebeius* at sites of BBD lesions on *Acropora muricata* effectively halted progression of the disease along the branch, whereas BBD progressed at 1.1 mm h^{-1} and eventually killed equivalent coral nubbins in aquaria without *C. plebeius*. Depending on whether they are

feeding on the infected coral tissue or specific causative agents of these diseases (e.g. BrB ciliates), different fishes may be more or less effective at halting progression of BrB and BBD. It seems likely that unusually high densities of coral-feeding butterflyfishes, for example due to trophic cascades (Raymundo et al. 2009), would be likely to reduce the impact of these two diseases on individual coral hosts, while simultaneously increasing the incidence of coral diseases on nearby corals.

This study provides evidence that many species of reef fishes actively, and often selectively, feed on specific sites of infection for two of the most common and widespread coral diseases on the Great Barrier Reef: BrB and BBD. Further research is required to establish the specific role of different fishes in potentially spreading and/or containing coral diseases, but it is clear that fishes must be considered as important contributors to the dynamics of diseases on corals. Assuming that these fishes are targeting the putative pathogens when feeding at sites of active infection, it is likely that high abundance and diversity of small reef fishes will be critical in managing the increasing prevalence and impact of coral diseases throughout the world's coral reefs.

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