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REPORT

Clarifying functional roles: algal removal by the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus*

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Abstract The lined bristletooth, *Ctenochaetus striatus*, and the brown surgeonfish, *Acanthurus nigrofuscus*, are among the most abundant surgeonfishes on Indo-Pacific coral reefs. Yet, the functional role of these species has been the focus of an ongoing debate lasting at least six decades. Specifically, to what extent are *C. striatus* herbivorous like the visually similar *A. nigrofuscus*? To address this question, we used natural feeding surfaces, covered with late successional stage reef-grown algal turfs, to examine turf algal removal by the two species. Surfaces exposed to *C. striatus* in laboratory experiments exhibited no significant reductions in turf length or area covered by turfing algae. In marked contrast, *A. nigrofuscus* reduced turf length by 51% and area covered by turfing algae by 15% in 1 h. The gut contents of specimens from the reef revealed that *A. nigrofuscus* predominantly ingests algae (the dominant item in 79.6–94.7% of gut content quadrats), while *C. striatus* ingests detritus and sediments (dominant in 99.6–100% of quadrats). Therefore, *C. striatus* ingests detritus and sediment, leaving mature algal turfs relatively intact, while *A. nigrofuscus* directly removes and ingests turf algae. The function of *C. striatus* differs from cropping herbivorous surgeonfishes such as *A. nigrofuscus*. On coral reefs, *C. striatus* brush detrital aggregates from algal turfs, removing microorganisms, organic detritus and inorganic sediment. Confusion over the functional role of *C. striatus* may stem from an inability to fit it into a single functional category.

Keywords Coral reef · Herbivory · Detritivory · Epilithic algal matrix · Algal turfs

Introduction

Investigating functional roles on coral reefs and classifying fish species into broad functional groups has received considerable attention in recent years (Graham et al. 2011; Pratchett et al. 2011; Chong-Seng et al. 2012; Plass-Johnson et al. 2015). The identification of functional components within this complex ecosystem provides a clearer perspective of reef resilience and facilitates ecosystem-based management approaches (Bellwood et al. 2004; Nyström 2006; Nash et al. 2013). However, broad functional classifications may conceal important interspecific variation that could be vital in understanding the ecology of fishes (Clements et al. 2009; Brandl and Bellwood 2014; Streit et al. 2015; Kelly et al. 2016). This is particularly important when examining common species that play important roles in ecosystems. This issue has come to the fore with the conflicting classifications of two key fishes in Indo-Pacific reef ecosystems, the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus*.

The lined bristletooth, *C. striatus*, and the brown surgeonfish, *A. nigrofuscus*, are both abundant on Indo-Pacific coral reefs (Randall 2005; Cheal et al. 2012). Together they

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comprise a core component of the herbivorous/detritivorous fish community that feeds on the epilithic algal matrix (EAM) on these reefs (Russ 1984; Choat and Bellwood 1985; Randall 2005; Cheal et al. 2012). Their abundance means that the two species are highly influential in quantitative assessments of reef resilience based on functional groups (Cheal et al. 2012; Johansson et al. 2013). Furthermore, with the recent move towards modelling complex coral reef ecosystems, the two species often influence the outputs of models used to assess herbivory on reefs (Brandl and Bellwood 2016; Doropoulos et al. 2016). However, considerable debate persists over the functional role of these species, especially *C. striatus*. The key question is: to what extent is *C. striatus* herbivorous and how does it compare to *A. nigrofuscus*?

Numerous ecological studies have classified *C. striatus* as a herbivorous fish along with the other surgeonfishes (e.g. Hiatt and Strasburg 1960; Bouchon-Navaro and Harmelin-Vivien 1981; Montgomery et al. 1989; Polunin and Klumpp 1989). Under this classification, the degree to which *C. striatus* has been considered herbivorous has ranged from being pooled with *A. nigrofuscus* due to their superficial similarity in appearance (Bouchon-Navaro and Harmelin-Vivien 1981), to examples such as Montgomery et al. (1989) who classified *C. striatus* as herbivores but noted that they ingested large quantities of sediment and detritus. More recently Marshell and Mumby (2012, 2015) suggested *C. striatus* could remove more algae than *A. nigrofuscus* when feeding on early successional algal communities (a maximum of 6 weeks old) on artificial substrata, highlighting its potential role as a functional herbivore on coral reefs. Reports of *C. striatus* bioeroding the reef matrix in the Red Sea (Schuhmacher et al. 2008; Krone et al. 2011) have also been presented as evidence of their ability to remove significant amounts of algae (Marshell and Mumby 2015). These independent lines of evidence all suggest that *C. striatus* predominantly functions as a herbivore.

There is also evidence suggesting that *C. striatus* does not remove significant amounts of algae on coral reefs and instead functions primarily as a detritivore (Robertson and Gaines 1986; Choat and Clements 1998; Choat et al. 2002; Crossman et al. 2005; Clements et al. 2009). Behavioural observations show that *C. striatus* often feed within the territories of the herbivorous, lined surgeonfish, *A. lineatus*. This suggests that these fishes do not compete for the same food resource (Choat and Bellwood 1985). Subsequent gut contents and short-chain fatty acid analyses have suggested that *A. lineatus* and *A. nigrofuscus* ingest substantial quantities of algal matter, while *C. striatus* predominantly ingest detritus and sediment (Robertson and Gaines 1986; Choat 1991; Choat and Clements 1998; Choat et al. 2002; Crossman et al. 2005). *Ctenochaetus striatus* was subsequently classified as a detritivore (Robertson and Gaines 1986; Choat and Clements 1998; Choat et al. 2002; Crossman et al. 2005; Clements et al. 2009). In addition, comparative examination of the morphology and bite capabilities of *C. striatus* and *A. nigrofuscus* have revealed marked differences (Purcell and Bellwood 1993). The key morphological feature of *Ctenochaetus* species is the possession of highly modified comb-like teeth, which are reportedly used to brush detritus from the EAM (Randall 1955; Jones 1968; Purcell and Bellwood 1993; Bellwood et al. 2014). Randall (1955) and Purcell and Bellwood (1993) suggested that the comb-like teeth of *Ctenochaetus* species (Fig. 1a) are ineffective at removing algae, particularly when compared to the spatulate teeth of *A. nigrofuscus* (Fig. 1b). These studies of the behaviour, nutritional ecology and morphology of *C. striatus* have all suggested that *Ctenochaetus* are unlikely to remove significant amounts of turf algae from coral reefs.

Although research involving *Ctenochaetus* and *Acanthurus* has spanned at least six decades, it is evident that considerable disagreement persists over the functional role of *C. striatus* on coral reefs. As *C. striatus* is highly abundant and widespread on coral reefs across the Indo-

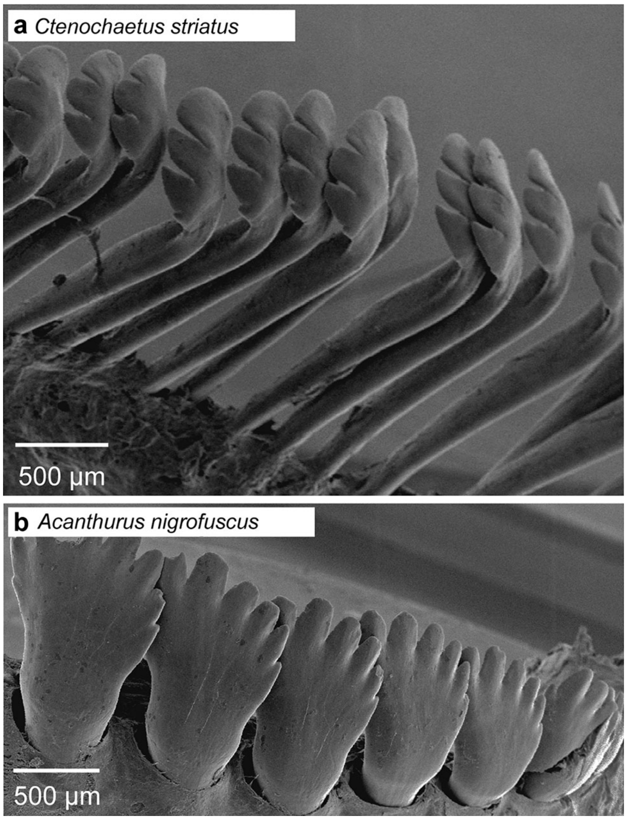

Fig. 1 Scanning electron micrographs of the teeth of **a** the lined bristletooth, *Ctenochaetus striatus* (anterior view of dentary) and **b** the brown surgeonfish, *Acanthurus nigrofuscus* (anterior view of dentary)

Pacific, determining its functions is critical to understanding ecological processes such as detritivory and herbivory. Our aim was to examine the functional role of *C. striatus* and *A. nigrofuscus*, answering the question: to what extent is *C. striatus* a herbivore when feeding on mature turf algal communities and how does it compare with the superficially similar species, *A. nigrofuscus*?

Methods

Algal removal and ingestion by *C. striatus* and *A. nigrofuscus* were examined at Lizard Island Research Station (14°40′8.04″S, 145°27′33.84″E), on the mid-shelf of the Great Barrier Reef. To examine algal removal, an aquarium-based before/after control/impact-style experiment was performed using natural feeding surfaces, i.e. late successional stage EAM-covered dead coral rocks. Gut contents analyses were also performed on fishes from the reef to examine ingested material.

Experimental procedures

Fish collection and husbandry

Ten *C. striatus* and ten *A. nigrofuscus* were collected using barrier nets. The average total length of the *C. striatus* and *A. nigrofuscus* specimens was 124.0 ± 4.5 mm (±SE) and 127.7 ± 2.3 mm, respectively. The fish were transported to Lizard Island Research Station where they were individually housed in 90-L containers (620 × 400 × 380 mm) with flow-through water in an aquarium room. Fish were acclimated to experimental conditions by offering them EAM-covered rocks each day and placing a video camera (GoPro) inside each aquarium to record behaviour. The camera indicator lights and sound were turned off to minimise the effect of the camera on behaviour. This process was repeated for at least 3 d to ensure fish were accustomed to the addition of GoPros to their tanks before treatments were offered. Each afternoon the aquaria were syphoned to remove waste material. The fish readily acclimatised to aquarium conditions (usually within 2 d) and trials were started once they fed repeatedly from EAM-covered rocks.

Feeding surface preparation

To ensure experiments closely replicated field conditions, natural feeding surfaces that supported mature reef-grown algal turfs were used. These feeding surfaces were flat EAM-covered coral rocks measuring approximately 50 cm^2 (Gordon et al. 2016) collected from a single area of reef. Feeding rocks supported natural algal turfs indistinguishable from adjacent reef EAMs. Rocks were conditioned on the reef for an extra 6 months prior to use to ensure that the algal turfs were similar on all rocks and that rocks supported mature algal turfs (later successional stage turf algal communities, i.e. well-grazed, stable algal turfs <10 mm high). All rocks were placed in an area measuring approximately 5 m^2, at approximately chart datum (i.e. submerged all the time apart from the lowest astronomical tides), and away from the territories of damselfish, but within the range of grazing herbivorous/detritivorous fishes. Both *C. striatus* and *A. nigrofuscus* were present in this location. Rocks were collected the morning before use in the experiment and held in flow-through aquaria.

Benthic particulate preparation

To standardise the other components of the EAM (sediment and detritus) benthic particulate loads were created. The loads were equivalent to 150 g m^{-2} of sediment with an organic percentage of 14%, to replicate loads found naturally on Lizard Island reef crests (Purcell 2000; Purcell and Bellwood 2001), the preferred reef habitat of the two study species at Lizard Island (Goatley and Bellwood 2010, 2012). A value of 150 g m^{-2} falls mid-way within the range of average sediment loads reported for Lizard Island reef crest EAMs (75–236 g m^{-2}) (Purcell 2000; Goatley and Bellwood 2010, 2012).

To ensure similar properties to sediment found naturally in EAMs, benthic particulates were created from sediment collected from Lizard Island lagoon. Organic material was produced from Hikari Marine A, which approximates the nutritional composition of EAM detrital aggregates (Tenore 1981; Wilson et al. 2003) and acts as a substitute for detritus in reef particulates (Gordon et al. 2016). Sediment and Hikari Marine A were prepared following Gordon et al. (2016). Sediments were bleached using hydrogen peroxide (H_2O_2) to remove residual organic matter. Bleaching continued until no bubbles were released in a 24-h period. Sediment was then dried to a constant weight at 60 °C and sieved through a sieve stack (2000–63 µm). Hikari Marine A was ground using a pestle and mortar and then passed through a 125-µm sieve to ensure similar particle sizes to natural detrital material (Wilson et al. 2003; Gordon et al. 2016). Using this prepared sediment and organic material, benthic particulate loads were created by weighing out individual grain size fractions to simulate grain size distributions in Lizard Island reef crest EAM sediments (Purcell 2000). All grain sizes under 2000 µm were considered sediment (sands-clays; ISO 14688-1:2002). This procedure ensured equivalent sediment and organic loads on all experimental surfaces, as these may influence rates of herbivory/detritivory (Goatley et al. 2016; Gordon et al. 2016; Tebbett et al. 2017a).

Experimental process

Feeding rocks were rinsed in seawater immediately prior to use to remove existing sediment and detritus, and visually inspected to ensure they were evenly covered with turfing algae and free of macroalgae (>10 mm) or encrusting organisms. Thirty haphazardly selected algal filaments from the flat upper surface of each rock were measured using the depth probe of vernier calipers (measuring the filament closest to the caliper probe). This distance was immediately recorded by pushing the tips of the calipers into saltwater-resistant pressure-sensitive poster adhesive (Blu-tack). The distance was then measured using digital calipers following Bonaldo and Bellwood (2009) and Goatley and Bellwood (2013). Following algal turf measurements, all rocks were photographed to quantify the area covered by turfing algae. A grid of 30 randomly distributed points was overlaid over each photograph, and the presence or absence of turfing algae under each point was recorded.

One rock was placed at the end of each aquarium and concealed within a 500-mm length of 90-mm-diameter polyvinyl chloride (PVC) pipe to prevent feeding by fishes. To ensure sediment and organic loads were consistent, the pre-prepared benthic particulates were wetted and then poured into the PVC pipe and allowed to settle onto the feeding surfaces for at least 12 h (overnight) (following Gordon et al. 2016). At approximately mid-day the following day, a video camera (GoPro, with indicator lights and sound turned off) was placed into each aquarium, to quantify the number of bites taken by each fish. Following the addition of the camera, the PVC pipe was removed and a 10-mm-high 90-mm-diameter PVC ring was placed over the rock to restrict feeding to the upper surface. Following an exposure period of 60 min, the feeding rocks were removed, photographed for quantification of algal coverage and the algal turf lengths remeasured. To control for potential losses of algae due to handling, an additional 20 rocks were exposed to identical experimental procedures in aquaria without fishes. On each rock, the mean length of algae before experimental exposure to *C. striatus*, *A. nigrofuscus* or the control was 4.1 ± 0.1, 4.0 ± 0.2 and 3.8 ± 0.1 mm, respectively (Electronic supplementary material, ESM Table S1). The mean percentage area of algal turfs on each rock before exposure was 50.7 ± 3.4, 59.7 ± 3.1 and 53.3 ± 2.7%, respectively (ESM Table S1).

Video and statistical analysis

The total number of bites taken by fishes from the surface of the rock over the entire hour was recorded. The difference in average turf length before and after feeding was analysed using paired t tests. Normality was assessed using Shapiro–Wilks tests; all data were normally distributed. The difference in algal turf coverage before and after feeding was analysed using generalised linear mixed-effects models (GLMMs) with a binomial error distribution and logit link. Condition (before vs. after) was treated as a fixed effect, and rock ID was treated as a random effect to account for non-independence arising from measuring from the same rocks. Assumptions of the models were assessed using residual plots. All statistical analyses used the statistical software R (R Core Team 2014) using the *lme4* package (Bates et al. 2015).

Examination of ingested material

Five *C. striatus* and five *A. nigrofuscus* were collected using barrier nets and immediately euthanised (clove oil), placed on ice and then frozen for later examination. The average total length of *C. striatus* and *A. nigrofuscus* specimens was 188 ± 12.6 and 145.2 ± 8.7 mm, respectively. Ingesta from the anterior portion of the intestines and the stomach were examined separately under a dissecting microscope (10–40×) for each specimen. The stomach and anterior intestine were examined separately to ensure any differences between species were not a result of variation in the anatomical structure of the stomach (Choat 1991). Following Wilson and Bellwood (1997), a 15 × 15 square grid with 50 randomly marked quadrats was fixed to the underside of a glass petri dish. Samples were spread evenly over the petri dish, and the dominant item (by area) in each quadrat was recorded as well as any other material present. Material was categorised into detritus, algae or sediment, with the term detritus used in the broad sense to describe amorphous organic material with no visible structure, in all cases consisting of opaque, flocculent material (following Wilson and Bellwood 1997). This material is not detritus sensu stricto, as it is likely to have contained some living material such as bacteria, microalgae and fungi (Wilson and Bellwood 1997). To analyse the differences in the frequency of occurrence of algal material compared to other matter (sediment or detritus) in the gut contents of *C. striatus* versus *A. nigrofuscus,* Pearson's Chi-squared tests with Yates' continuity correction were performed separately on stomach and intestinal data. The tests were performed in the statistical software R (R Core Team 2014).

Results

Algal removal experiment

Feeding by *C. striatus* did not result in a significant decrease in turf length ($t_9 = 1.72$, $p = 0.12$; Fig. 2a) or in

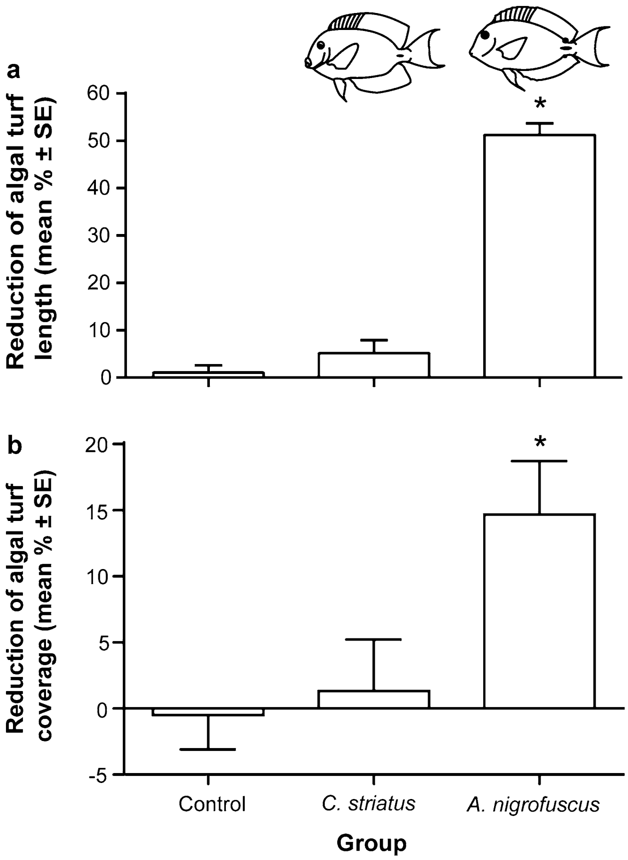

Fig. 2 Mean (percentage ± SE) reduction of algal turf **a** length and **b** area coverage following 1 h of exposure without fish present (control) and after 1 h of feeding by the lined bristletooth, *Ctenochaetus striatus,* and the brown surgeonfish, *Acanthurus nigrofuscus*. *Asterisk* denotes a significant difference before versus after exposure ($\alpha = 0.05$)

the cover of turf algae (GLMM; $z = 0.33$, $p = 0.74$; Fig. 2b; ESM Table S2). On rocks exposed to *C. striatus*, algal turfs appeared largely unchanged following feeding (Fig. 3c, e) with an average decrease in turf length of only 0.2 ± 0.1 mm representing a reduction of 5.2 ± 2.7%. Additionally, the mean proportion of area covered by turfing algae decreased by only 1.3 ± 3.9%. Visually, the only change was a reduction in particulate loads.

By contrast, feeding by *A. nigrofuscus* significantly decreased turf length ($t_9 = 11.59, p < 0.0001$; Figs. 2a, 3d, f) and the area covered by turf algae (GLMM; $z = 3.59$, $p = < 0.001$; Figs. 2b, 3d, f; ESM Table S2). On average, *A. nigrofuscus* reduced turf length by 2.1 ± 0.2 mm representing a reduction of 51.2 ± 2.4% in 1 h of feeding (Fig. 2a). The mean area covered by turf algae was also reduced by 14.7 ± 4.0%. Only short, well-cropped algal turfs remained following exposure to *A. nigrofuscus*.

There was no significant difference in turf length on control rocks ($t_{19} = 0.62$, $p = 0.55$; Fig. 2a) or proportion of area covered (GLMM; $z = -0.17$, $p = 0.86$; Fig. 2b; ESM Table S2). During the 1-h feeding trials, *C. striatus* took an average of 592.5 ± 108.8 bites on the rocks while *A. nigrofuscus* took an average of 1583.2 ± 159.2 bites.

Ingested material

The material ingested by *C. striatus* on the reef was dominated by detritus and sediment (Fig. 4a, c; ESM Fig. S1). In *C. striatus* intestinal contents, detritus was the dominant category in 68.0 ± 8.2% of quadrats. In the stomach of *C. striatus*, detritus was dominant in 64.4 ± 2.7% of quadrats. Algae were never the dominant category in intestinal contents quadrats and were only dominant in 0.4 ± 0.4% of stomach sample quadrats. Although algae were present in 37.6 ± 10.8 and 54 ± 4.7% of quadrats of *C. striatus* intestine and stomach samples, respectively, this was generally due to the presence of a single algal filament (ESM Table S3). By contrast, in *A. nigrofuscus,* algae were the dominant category in 79.6 ± 3.8 and 94.7 ± 2.9% of quadrats of intestine and stomach samples, respectively (Fig. 4b, d; ESM Table S3). Algal material was significantly more dominant in quadrats in *A. nigrofuscus* than in *C. striatus* in both stomach ($\chi^2 = 327.25$, $df = 1$, $p = < 0.0001$) and intestinal samples ($\chi^2 = 358.60$, $df = 1$, $p = < 0.0001$).

Discussion

Ctenochaetus striatus removed little algae from mature algal turfs, even after a period of intensive feeding. In marked contrast, *A. nigrofuscus* removed substantial quantities of algae, leaving noticeably cropped algal turfs. These differences were mirrored by the material ingested by wild-caught specimens. The gut contents of *C. striatus* predominantly contained detritus and sediment, while *A. nigrofuscus* predominantly contained algae. Our findings support conclusions drawn from behavioural (Choat and Bellwood 1985), nutritional (Randall 1955; Choat et al. 2002; Crossman et al. 2005; Clements et al. 2009; Brandl et al. 2015) and morphological studies (Randall 1955; Jones 1968; Purcell and Bellwood 1993; Bellwood et al. 2014), in that *C. striatus* did not remove significant amounts of algae from mature algal turfs and therefore are unlikely to be significant herbivores on coral reefs. The apparent inability of *Ctenochaetus* species to remove mature turfing algae was noted in several early ecological studies of coral reefs (Randall 1955, 1961). Indeed, our findings highlight the fundamental differences in the way two superficially similar surgeonfishes affect algal turfs on coral reefs and the interspecific variability which may occur between fishes that have been classified under the same functional identity, i.e. herbivorous fishes.

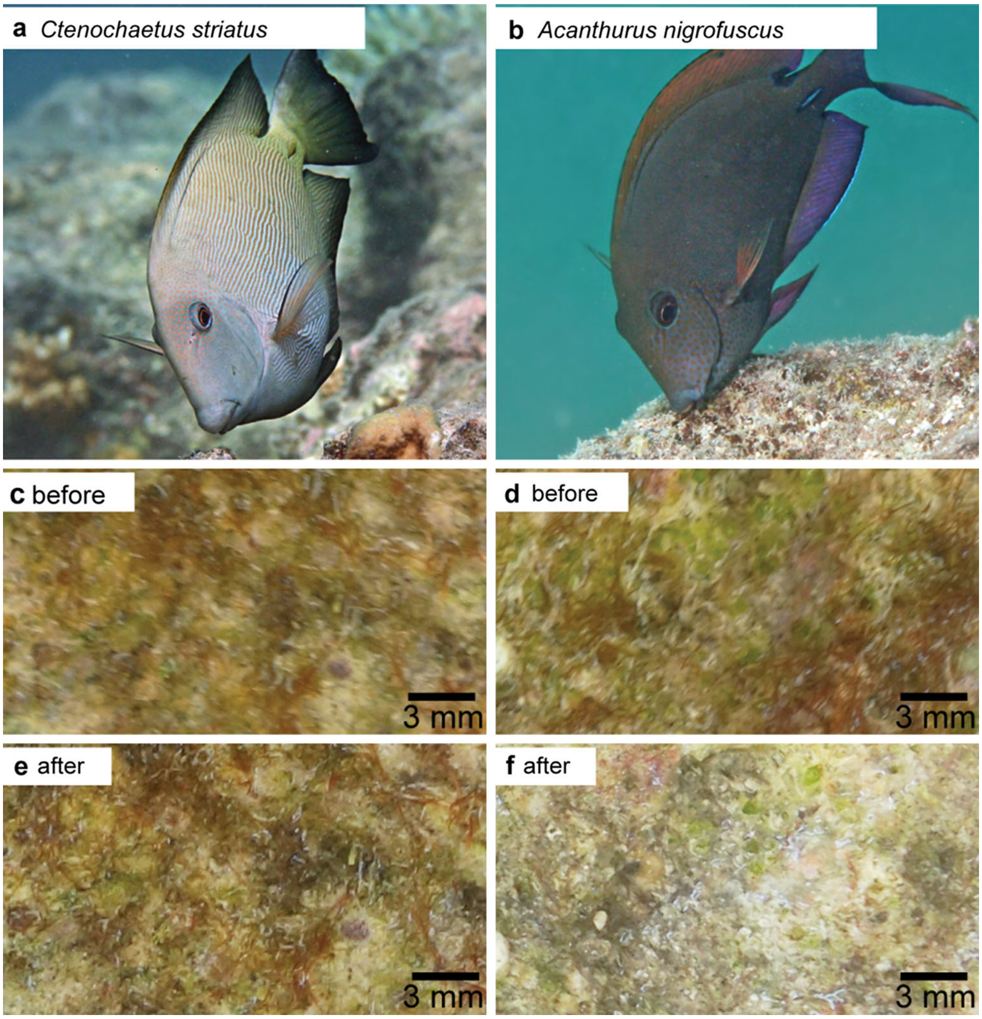

Fig. 3 **a** Lined bristletooth, *Ctenochaetus striatus*. **b** The brown surgeonfish, *Acanthurus nigrofuscus* (photographs by CHRG). **c** Feeding surface before exposure to *C. striatus*. **d** Feedings surface before exposure to *A. nigrofuscus*. Feeding surfaces after 1 h of feeding by **e** *C. striatus* and **f** *A. nigrofuscus*. *Scale bars* are approximate

Visually, *C. striatus* and *A. nigrofuscus* are similar but they interact with algal turfs in distinctly different ways. The spatulate teeth (Fig. 1b), small jaw opening (113°) and rapid biting behaviour of *A. nigrofuscus* are well suited to nipping off algal filaments (Purcell and Bellwood 1993). By contrast, *C. striatus* take slower bites, but can open their jaws to nearly 180° (Purcell and Bellwood 1993), allowing fish to come in close contact with the substratum and to selectively brush fine particulate material from turfing algae using their comb-like teeth (Fig. 1a; Purcell and Bellwood 1993; Tebbett et al. 2017b). This feeding behaviour and morphology does not appear to be consistent with cropping algae.

Ctenochaetus striatus does not crop algal turfs, but it could be argued that their wide gape (178°), which allows extended contact with the benthos (Purcell and Bellwood 1993), could increase removal of entire algal filaments as in scraping parrotfishes (Bonaldo et al. 2014). However, the morphology and teeth of *C. striatus* make this unlikely. Indeed, no significant reduction in algal turf coverage on rocks exposed to *C. striatus* was recorded and it appears that mature algal turfs, which are firmly attached to the substratum, are not readily removed by the brushing feeding behaviour. While *C. striatus* may remove small amounts of loose or long-filamented turfing algae, an expected consequence of feeding on the EAM, such removal is minimal compared to turf-feeding herbivorous fishes like *A. nigrofuscus*. Observations in both the field and aquaria suggest that when *C. striatus* dislodge algae it often becomes caught in their teeth, causing visible annoyance to the fish (Randall 1955; Purcell and Bellwood 1993). This may explain the slight (nonsignificant) reduction in mean algal turf length and proportional area covered on surfaces exposed to *C. striatus*, as longer algal filaments are more likely to become entangled in their teeth. Such removal appears to be incidental as no significant

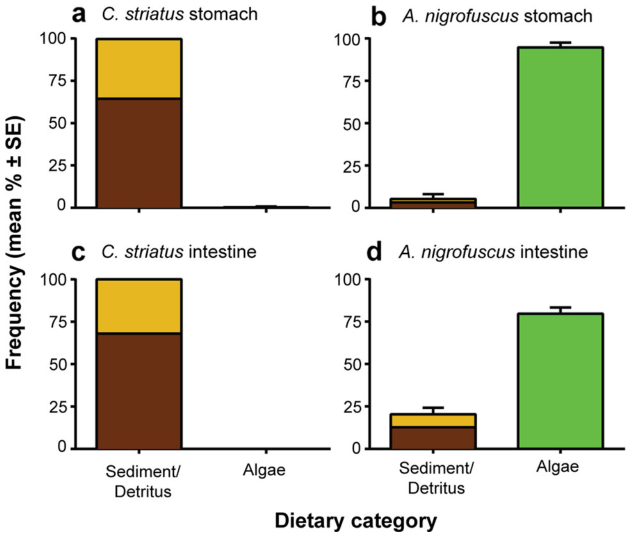

Fig. 4 Analysis of ingested material showing the percentage (mean ± SE) of quadrats in which each dietary category (detritus [*brown*], sediment [*yellow*] and algae [*green*]) was dominant by area in **a** the gizzard-like stomach of the lined bristletooth, *Ctenochaetus striatus* ($n = 5$), **b** the stomach of the brown surgeonfish, *Acanthurus nigrofuscus* ($n = 3$) and in the intestinal tract of **c** *C. striatus* ($n = 5$) and **d** *A. nigrofuscus* ($n = 5$)

reductions in algae were recorded even after an average of 592.5 (±108.8) bites in an area of approximately 50 cm^2 in 1 h.

As commonly reported, the gut contents of *C. striatus* specimens from the reef did contain some algae (Polunin and Klumpp 1989; Choat and Clements 1998; Choat et al. 2002). This algae may be partly from incidental removal and ingestion, but it may also be the result of secondary ingestion of algal material through coprophagy. Many herbivorous fishes, including *A. nigrofuscus*, void their faeces over the reef (Fishelson et al. 1985; Clements 1991; Bonaldo et al. 2014) and much of the algal material contained within the faeces remains structurally intact and can continue to grow (Vermeij et al. 2013; Tâmega et al. 2016). *Ctenochaetus striatus* feeds over the same substrata as these fishes, especially herbivorous acanthurids (Choat and Bellwood 1985), and it is likely that *C. striatus* may ingest a considerable amount of faecal matter (Clements 1991). Indeed, of the faeces from the herbivorous surgeonfishes *A. nigricans* and *A. lineatus* that was eaten by fishes, 42 and 37%, respectively, was consumed by *C. striatus* (Robertson 1982). Thus, rather than directly removing mature turf algae from the reef, *C. striatus* may act as a secondary herbivore ingesting algae and detritus from the faeces of other reef organisms.

In the experiments, *A. nigrofuscus* took substantially more bites during the exposure period than *C. striatus*; however, this is unlikely to contribute significantly to the differences observed. The bites of each species are fundamentally different and although a slower feeder, the bite area of *C. striatus* is much larger than *A. nigrofuscus* (Purcell and Bellwood 1993). A similar disparity in bite rates is seen in the wild, with *A. nigrofuscus* having a higher bite rate than *C. striatus* (Clements 1991; Polunin et al. 1995). In an experimental study examining algal turf removal, *A. nigrofuscus* took six times more bites than *C. striatus* (Marshell and Mumby 2012). Although a disparity in bite rates was reported, similar to the present study, it is interesting to consider the contrasting results in terms of the fishes' effects on algal turfs.

In feeding trials conducted by Marshell and Mumby (2012), *C. striatus* removed significantly more algae than *A. nigrofuscus*. Such contrasting results may be explained by two key differences between our study and the work of Marshell and Mumby. First, the two studies examined different metrics. Marshell and Mumby (2012) examined algal turf biomass, while we used measurements of algal turf length and area coverage. Although these metrics are not the same, if *C. striatus* were removing significant amounts of algal biomass it would be expected that at least one of our metrics would show a significant decrease. Clearly, this was not the case.

The second difference lies in the nature of the algae examined. The current study used reef-grown algal turfs that were at least 6 months old growing on planar dead coral rocks. Consequently, the coral rocks supported mature algal turfs. By contrast, the algal turfs used by Marshell and Mumby (2012) were grown on artificial surfaces (rough "limestone" tiles, orange in colour) which were "preconditioned on the reef." These tiles were, however, scrubbed following conditioning to begin with an algal biomass of zero. They were then placed in flow-through aquaria to develop sparse algal turfs after 2 weeks and dense algal turfs after 6 weeks (Marshell and Mumby 2012). The algal communities in the two studies were likely to differ in two fundamental ways. First, differences in algal communities may arise due to variation in the texture and chemistry between the two settlement substrata (natural coral rocks vs. artificial tiles), which can affect the species of algae that settle and develop (Harlin and Lindbergh 1977; Borowitzka et al. 1978; Hixon and Brostoff 1985; Diaz-Pulido and McCook 2002; Smith et al. 2010). Indeed, coral rock substrata tend to support more later successional algae compared to artificial settling substrata and, as algal turfs can penetrate coral rock substrata, they may be more firmly attached (Hixon and Brostoff 1996; Diaz-Pulido and McCook 2002).

The second major difference between these studies lies in the age of the algal turfs used. The algal community used by Marshell and Mumby (2012) was less than 6 weeks old and consequently was likely to be dominated by early successional algae which are only superseded by more mature forms after several months (Borowitzka et al. 1978; Diaz-Pulido and McCook 2002). Early successional algal communities are dominated by diatoms, coccoids and blue-green filamentous algae, while later successional stage turf algal communities are more species rich and include complex algal forms (Borowitzka et al. 1978; Scott and Russ 1987; Diaz-Pulido and McCook 2002). Early successional algal communities are less firmly attached to substrata (Borowitzka et al. 1978; Diaz-Pulido and McCook 2002) and consequently may be removed far more easily than later successional algal turfs such as those used in our study. As *Ctenochaetus* are able to open their jaws to nearly 180° to feed on planar surfaces (Randall 1955; Purcell and Bellwood 1993), they are likely to remove loose algae from planar, smooth artificial tiles far more effectively than *A. nigrofuscus*. Indeed, early successional "algal turfs" (diatoms and cyanobacteria) may form an important component of the nutritional ecology of *C. striatus* where available (Polunin et al. 1995; Choat et al. 2002; Wilson et al. 2003). This is particularly likely if they feed on smooth surfaces covered with calcareous algae where the removal of microalgal fouling may be important. However, the feeding activity of *C. striatus* appears to have a minimal effect on later successional stage algal turfs, which are often the dominant benthic covering on coral reefs (Wismer et al. 2009). The early successional algae used by Marshell and Mumby (2012) are also likely to be particularly amenable to the use of biomass as a metric (discussed above), due to the ease with which these algae can be scraped from the substratum for measurement.

In addition to the differences outlined above, other factors may also have contributed to the disparity in the results. In particular, the sediment loads within the algal turfs in the present study were approximately six to thirteen times lower than those in Marshell and Mumby (2012) and were more similar to loads found in reef crest algal turfs (Goatley and Bellwood 2012; Tebbett et al. 2017c), the predominant feeding habitat of the two surgeonfishes (Russ 1984; Goatley and Bellwood 2010). Sediments suppress the feeding rates of herbivorous/detritivorous fishes (Goatley and Bellwood 2012; Gordon et al. 2016; Tebbett et al. 2017a, b) which may explain why we found higher bite rates in both fish species. Importantly, this means that any effect the fishes may have had on algal turfs in the present study should have been more pronounced.

It should be noted that we did not directly examine whether *C. striatus* was ingesting and assimilating the particulate material used in the experiments. Such an examination may have provided supporting evidence of their ability to brush detritus from algal turfs. However, visual observations and video recordings both strongly suggest that particulates were removed. Nevertheless, the chief aim of this study was to assess the extent of algal removal from mature algal turfs by the two species, which is evidently minimal in the case of *C. striatus*.

Ctenochaetus striatus may be herbivorous in regards to their ability to remove early successional algal communities from planar surfaces or microalgae from algal turfs, but they do not appear to play a significant role in the removal of algae from mature algal turfs. Inevitably, this raises the question: what are the main functional roles of *C. striatus*? The most likely answer lies in their contribution to detritivory and EAM sediment dynamics. Detritivory is a central trophic pathway on coral reefs, and given the size, abundance and volume of detritus removed by *C. striatus*, this species is probably one of the most important detritivorous fish species on Indo-Pacific coral reefs (Wilson et al. 2003; Crossman et al. 2005). However, the term "detritus" encompasses items such as diatoms, microalgae, microbes, cyanobacteria and faeces which may also be important nutritional resources (Polunin et al. 1995; Choat et al. 2002; Wilson et al. 2003; Clements et al. 2016). While acknowledging these other resources, given their main feeding mode, we consider *C. striatus* to be "detrital aggregate brushers."

When brushing detrital aggregates from the EAM, *C. striatus* also removes and ingests inorganic sediments, making it a key player in EAM sediment dynamics (Goatley and Bellwood 2010; Krone et al. 2011; Tebbett et al. 2017b). Unlike many fishes, *C. striatus* has distinct defecation areas, off the reef and/or in deeper water (Krone et al. 2008; Goatley and Bellwood 2010). They therefore export ingested sediment away from feeding areas (Krone et al. 2008, 2011; Goatley and Bellwood 2010). This role may be vital to coral reefs as EAM sediments suppress herbivory (Goatley and Bellwood 2012; Gordon et al. 2016) and coral recruitment (Birrell et al. 2005; Diaz-Pulido et al. 2010; Perez et al. 2014). By reducing EAM sediment loads, *C. striatus* may facilitate herbivory in these environments (Choat 1991; Goatley and Bellwood 2010) underpinning both the preservation of short productive algal turfs (SPATs sensu Goatley et al. 2016) and coral replenishment (Brandl and Bellwood 2016). Interestingly, if *C. striatus* also ingests viable algal material from the faeces of other fishes (as discussed above) their defecation behaviour may also incidentally help limit algal development and expansion. *Ctenochaetus striatus* may therefore perform a secondary "herbivory" function on coral reefs by harvesting loose, but viable, algal material and exporting it off the reef. Exploring the potential for *C. striatus* to act as a secondary herbivore in this manner may be an important topic for future research.

The importance of the different functional roles that *C. striatus* fulfil could also change depending on the specific context. Specifically, the ability of *C. striatus* to remove early successional algae may be important following major disturbance events. By removing early successional algae that colonise dead coral skeletons, *C. striatus* could slow or prevent the development of mature algal turfs (Hixon and Brostoff 1996; Steneck 1997). This may assist the recovery of coral reefs, as mature algal turfs impede coral recruitment (Arnold et al. 2010; Diaz-Pulido et al. 2010). However, as *C. striatus* predominantly feeds on smooth surfaces (Choat and Bellwood 1985; Brandl et al. 2015), removal of early successional algae from complex or branching dead coral skeletons by *C. striatus* is unlikely. Once mature algal turfs develop that are not readily removed by *C. striatus*, the functional roles of *C. striatus* are predominantly detritivory and sediment transport.

In addition to the functional roles discussed so far, it has also been suggested that *C. striatus* plays a role in bioerosion in the Red Sea, through the use of a hard palate structure that could be used to rasp the substratum (Schuhmacher et al. 2008; Krone et al. 2011), although Krone et al. (2011) concluded that bioerosion by *C. striatus* was only a minor role compared to the removal of loose sediments. It is interesting that although *C. striatus* is abundant, widely distributed and often studied, bioerosion and the presence of a hard palate structure has not been reported outside of the Red Sea. Further investigation of bioerosion and the anatomy of *C. striatus* in other geographic localities could be worthwhile.

Assigning a single overarching functional role to *C. striatus* is difficult. Indeed, the debate and confusion surrounding the functional role of this species may stem from a desire to simplify and apply broad categorisations to complex ecosystems. Evidently, *C. striatus* plays a variable role in many functions on coral reefs; categorising it into a single functional group may overlook the contribution that this species makes to other functions. While functional classifications are useful management tools (Bellwood et al. 2004) care should be taken in their use to assess ecological processes as they may conceal intra-functional group variability (Clements et al. 2009; Streit et al. 2015; Kelly et al. 2016). Functional classifications fail to consider that the role a fish fulfils is rarely “black and white” and in some cases the contribution a fish makes to a particular function is better viewed as a sliding scale, particularly evident in the extent to which *C. striatus* functions as a herbivore on coral reefs.

The key question in our study was: to what extent is *C. striatus* herbivorous and how does this compare to *A. nigrofuscus*? The answer appears to be that compared to *A. nigrofuscus*, *C. striatus* has a minimal effect on mature algal turfs with only small amounts of algae ingested under natural settings. The way these two fishes interact with algal turfs and consequently the functional roles they perform on coral reefs are distinctly different. Although *C. striatus* may remove loosely attached early successional algal communities, predominantly composed of diatoms and cyanobacteria, categorising them as significant herbivores on coral reefs should be done with caution. *Ctenochaetus striatus* is unlikely to directly remove significant amounts of algae from mature algal turfs. *Ctenochaetus striatus* appears to be predominantly detritivorous removing particulates from the EAM or reef surface. However, as *C. striatus* appears to fulfil numerous functional roles on coral reefs, classifying this species into a single functional category may underestimate the extent of its importance in other ecological processes.

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