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1 **Clarifying functional roles: algal removal by the surgeonfishes**

2 ***Ctenochaetus striatus* and *Acanthurus nigrofuscus***

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21 **Abstract**

22 The lined bristletooth, *Ctenochaetus striatus*, and the brown surgeonfish, *Acanthurus nigrofuscus*, are
23 among the most abundant surgeonfishes on Indo-Pacific coral reefs. Yet the functional role of these
24 species has been the focus of an ongoing debate lasting at least six decades. Specifically, to what
25 extent are *C. striatus* herbivorous, like the visually similar *A. nigrofuscus*? To address this question
26 we used natural feeding surfaces, covered with late successional stage reef-grown algal turfs, to
27 examine turf algal removal in the two species. Surfaces exposed to *C. striatus* in laboratory
28 experiments exhibited no significant reductions in turf length or area covered by turfing algae. In
29 marked contrast, *A. nigrofuscus* reduced turf length by 51 % and area covered by turfing algae by 15
30 % in one hour. The gut contents of specimens from the reef revealed that *A. nigrofuscus*
31 predominantly ingests algae (the dominant item in 79.6 – 94.7 % of gut content quadrats) while *C.*
32 *striatus* ingests detritus and sediments (dominant in 99.6 – 100 % of quadrats). The results suggest
33 that *C. striatus* ingests detritus and sediment, leaving mature algal turfs relatively intact, while *A.*
34 *nigrofuscus* directly removes and ingests turf algae. The function of *C. striatus* differs from cropping
35 herbivorous surgeonfishes such as *A. nigrofuscus*. On coral reefs *C. striatus* brush detrital aggregates
36 from algal turfs, removing microorganisms, organic detritus and inorganic sediment. Confusion over
37 the functional role of *C. striatus* may stem from an inability to fit it into a single functional category.

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45 **Introduction**

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

57 The lined bristletooth, *C. striatus*, and the brown surgeonfish, *A. nigrofuscus*, are both
58 abundant on Indo-Pacific coral reefs (Randall 2005; Cheal et al. 2012). Together they comprise a core
59 component of the herbivorous/detritivorous fish community which feeds on the epilithic algal matrix
60 (EAM) on these reefs (Russ 1984; Choat and Bellwood 1985; Randall 2005; Cheal et al. 2012). Their
61 abundance means that the two species are highly influential in quantitative assessments of reef
62 resilience based on functional groups (Cheal et al. 2012; Johansson et al. 2013). Furthermore, with the
63 recent move towards modelling complex coral reef ecosystems, the two species often influence the
64 outputs of models used to assess herbivory on reefs (Brandl and Bellwood 2016; Doropoulos et al.
65 2016). However, considerable debate persists over the functional role of these species, especially *C.*
66 *striatus*. The key question is: to what extent is *C. striatus* herbivorous and how does it compare to *A.*
67 *nigrofuscus*?

68 Numerous ecological studies have classified *C. striatus* as a herbivorous fish along with the
69 other surgeonfishes (e.g. Hiatt and Strasburg 1960; Bouchon-Navaro and Harmelin-Vivien 1981;
70 Montgomery et al. 1989; Polunin and Klumpp 1989). Under this classification the degree to which *C.*

71 *striatus* has been considered herbivorous has ranged from being pooled with *A. nigrofuscus* due to
72 their superficial similarity in appearance (Bouchon-Navaro and Harmelin-Vivien 1981), to examples
73 such as Montgomery et al. (1989), where it is noted that *C. striatus* ingest large quantities of sediment
74 and detritus, but they are still classified as herbivores. More recently it has been suggested that when
75 feeding on early successional algal communities (a maximum of 6 weeks old) on artificial substrata,
76 *C. striatus* can remove more algae than *A. nigrofuscus*, highlighting its potential role as a functional
77 herbivore on coral reefs (Marshall and Mumby 2012, 2015). Reports of *C. striatus* bioeroding the reef
78 matrix in the Red Sea (Schuhmacher et al. 2008; Krone et al. 2011) have also been presented as
79 evidence of their ability to remove significant amounts of algae (Marshall and Mumby 2015). These
80 independent lines of evidence all suggest that *C. striatus* predominantly functions as a herbivore.

81 Within the literature there is also evidence suggesting that *C. striatus* does not remove
82 significant amounts of algae on coral reefs and instead that it functions primarily as a detritivore
83 (Robertson and Gaines 1986; Choat and Clements 1998; Choat et al. 2002; Crossman et al. 2005;
84 Clements et al. 2009). Behavioural observations show that *C. striatus* often feed within the territories
85 of the herbivorous, lined surgeonfish, *Acanthurus lineatus*. This suggests that these fishes do not
86 compete for the same food resource (Choat and Bellwood 1985). Subsequent gut contents and short
87 chain fatty acid analyses have suggested that *A. lineatus* and *A. nigrofuscus* ingest substantial
88 quantities of algal matter, while *C. striatus* predominantly ingest detritus and sediment (Robertson and
89 Gaines 1986; Choat 1991; Choat and Clements 1998; Choat et al. 2002; Crossman et al. 2005). *C.*
90 *striatus* was subsequently classified as a detritivore (Robertson and Gaines 1986; Choat and Clements
91 1998; Choat et al. 2002; Crossman et al. 2005; Clements et al. 2009). In addition, comparative
92 examination of the morphology and bite capabilities of *C. striatus* and *A. nigrofuscus* have revealed
93 marked differences (Purcell and Bellwood 1993). The key morphological feature of *Ctenochaetus*
94 species is the possession of highly modified comb-like teeth, which are reportedly used to brush
95 detritus from the EAM (Randall 1955; Jones 1968; Purcell and Bellwood 1993; Bellwood et al. 2014).
96 Randall (1955) and Purcell and Bellwood (1993) suggested that the comb-like teeth of *Ctenochaetus*
97 species (Fig. 1a) are ineffective at removing algae, particularly when compared to the spatulate teeth

98 of *A. nigrofuscus* (Fig. 1b). These studies of the behaviour, nutritional ecology and morphology of *C.*
99 *striatus* have all suggested that *Ctenochaetus* are unlikely to remove significant amounts of turf algae
100 from coral reefs.

101 Although research involving *Ctenochaetus* and *Acanthurus* has spanned at least six decades it
102 is evident that considerable disagreement persists over the functional role of *C. striatus* on coral reefs.
103 As *C. striatus* are highly abundant and widespread on coral reefs across the Indo-Pacific, determining
104 their functions is critical to understanding ecological processes such as detritivory and herbivory. Our
105 aim is to examine the functional role of *C. striatus* and *A. nigrofuscus*, answering the question: to
106 what extent is *C. striatus* a herbivore when feeding on mature turf algal communities and how does it
107 compare with the superficially similar species, *A. nigrofuscus*?

108 **Methods**

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

114 **Experimental procedures**

115 *Fish collection and husbandry*

116 Ten *C. striatus* and ten *A. nigrofuscus* were collected using barrier nets. The average total
117 length of the *C. striatus* and *A. nigrofuscus* specimens was 124.0 ± 4.5 mm (\pm SE) and 127.7 ± 2.3
118 mm, respectively. The fish were transported to Lizard Island Research Station where they were
119 individually housed in 90 L containers (620 × 400 × 380 mm) with flow-through water in an
120 aquarium room. Fish were acclimated to experimental conditions by offering them EAM-covered
121 rocks each day and placing a video camera (GoPro) inside each aquarium to record behaviour. The
122 camera indicator lights and sound were turned off to minimise the effect of the camera on behaviour.

123 This process was repeated for at least three days to ensure fish were accustomed to the addition of
124 GoPros to their tanks before treatments were offered. Each afternoon the aquaria were syphoned to
125 remove waste material. The fish readily acclimatised to aquarium conditions (usually within two
126 days) and trials were started once they fed repeatedly from EAM-covered rocks.

127 *Feeding surface preparation*

128 To ensure experiments closely replicated field conditions, natural feeding surfaces were used
129 which supported mature reef-grown algal turfs. These feeding surfaces were flat EAM-covered coral
130 rocks measuring approximately 50 cm² (Gordon et al. 2016) collected from a single area of reef. Upon
131 collection, feeding rocks supported natural algal turfs (indistinguishable from adjacent reef EAMs).
132 To ensure that the algal turfs were similar on all rocks and supported mature algal turfs (later
133 successional stage turf algal communities i.e. well-grazed, stable algal turfs less than 10 mm in
134 height) rocks were conditioned on the reef for an extra six months prior to use. All rocks were placed
135 in an area measuring approximately 5 m², at approximately chart datum (i.e. submerged all of the time
136 apart from the lowest astronomical tides), and away from the territories of damselfish, but within the
137 range of grazing herbivorous/detritivorous fishes. Both *C. striatus* and *A. nigrofuscus* were present in
138 this location. Rocks were collected the morning before use in the experiment and held in flow-through
139 aquaria.

140 *Benthic particulate preparation*

141 To standardise the other components of the EAM (sediment and detritus) benthic particulate
142 loads were created. The loads were equivalent to 150 g m⁻² of sediment with an organic percentage of
143 14 %, to replicate loads found naturally on Lizard Island reef crests (Purcell 2000; Purcell and
144 Bellwood 2001), the preferred reef habitat of the two study species at Lizard Island (Goatley and
145 Bellwood 2010, 2012). A value of 150 g m⁻² falls mid-way within the range of average sediment
146 loads reported for Lizard Island reef crest EAMs (75 - 236 g m⁻²) (Purcell 2000; Goatley and
147 Bellwood 2010, 2012).

148 To ensure similar properties to sediment found naturally in EAMs, benthic particulates were
149 created from sediment collected from Lizard Island lagoon. Organic material was produced from
150 Hikari Marine A, which approximates the nutritional composition of EAM detrital aggregates (Tenore
151 1981; Wilson et al. 2003) and acts as a substitute for detritus in reef particulates (Gordon et al. 2016).
152 Sediment and Hikari Marine A were prepared following Gordon et al. (2016). Sediments were
153 bleached using hydrogen peroxide (H_2O_2) to remove residual organic matter. Bleaching continued
154 until no bubbles were released in a 24 hour period. Sediment was then dried to a constant weight at
155 $60^\circ C$ and sieved through a sieve stack (2000 - 63 μm). Hikari Marine A was ground using a pestle and
156 mortar and then passed through a 125 μm sieve to ensure similar particle sizes to natural detrital
157 material (Wilson et al. 2003; Gordon et al. 2016). Using this prepared sediment and organic material,
158 benthic particulate loads were created by weighing out individual grain size fractions to simulate grain
159 size distributions in Lizard Island reef crest EAM sediments (Purcell 2000). All grain sizes under
160 2000 μm were considered sediment (sands-clays; ISO 14688-1:200). This procedure ensured
161 equivalent sediment and organic loads on all experimental surfaces, as these may influence rates of
162 herbivory/detritivory (Goatley et al. 2016; Gordon et al. 2016; Tebbett et al. 2016a).

163 *Experimental process*

164 Immediately prior to use, feeding rocks were rinsed in seawater to remove existing sediment
165 and detritus, and visually inspected to ensure they were evenly covered with turfing algae and free of
166 macroalgae (> 10 mm) or encrusting organisms. 30 haphazardly selected algal filaments, from the flat
167 upper surface of each rock were measured using the depth probe of vernier calipers (measuring the
168 filament closest to the caliper probe). This distance was then immediately recorded by pushing the
169 tips of the calipers into saltwater-resistant pressure-sensitive poster adhesive (Blu-tack). This distance
170 was then measured using digital calipers following Bonaldo and Bellwood (2009) and Goatley and
171 Bellwood (2013). Following algal turf measurements, all rocks were photographed to quantify the
172 area covered by turfing algae. This was achieved by overlaying a grid of 30 randomly distributed
173 points over each photograph noting if turfing algae was present or absent under each point.

174 One rock was placed at the end of each aquarium and concealed within a 500 mm length of
175 90 mm diameter polyvinyl chloride (PVC) pipe to prevent feeding by fishes. To ensure sediment and
176 organic loads were consistent, the pre-prepared benthic particulates were wetted and then poured into
177 the PVC pipe and allowed to settle for at least 12 hours (overnight) onto the feeding surfaces
178 (following Gordon et al. 2016). At approximately midday the following day a video camera (GoPro,
179 with indicator lights and sound turned off) was placed into each aquarium, to quantify the number of
180 bites taken by each fish. Following the addition of the camera, the PVC pipe was removed and a 10
181 mm high 90 mm diameter, PVC ring was placed over the rock to restrict feeding to the upper surface.
182 Following an exposure period of 60 minutes the feeding rocks were removed, photographed for
183 quantification of algal coverage and the algal turf lengths remeasured. To control for potential losses
184 of algae, due to handling, an additional 20 rocks were exposed to identical experimental procedures in
185 aquaria without fishes. On each rock, the mean length of algae before experimental exposure to *C.*
186 *striatus*, *A. nigrofuscus* or the control was 4.1 ± 0.1 mm (\pm SE), 4.0 ± 0.2 mm and 3.8 ± 0.1 mm,
187 respectively (ESM S1). The mean percentage area of algal turfs on each rock before exposure was
188 50.7 ± 3.4 %, 59.7 ± 3.1 % and 53.3 ± 2.7 %, respectively (ESM S1).

189 **Video and statistical analysis**

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

199

200 **Examination of ingested material**

201 Five *C. striatus* and five *A. nigrofuscus* were collected using barrier nets and immediately
202 euthanised (clove oil), placed on ice and then frozen for later examination. The average total length of
203 *C. striatus* and *A. nigrofuscus* specimens was 188 ± 12.6 mm (\pm SE) and 145.2 ± 8.7 mm,
204 respectively. Ingesta from the anterior portion of the intestines and the stomach were examined
205 separately under a dissecting microscope (10-40 \times) for each specimen. The stomach and anterior
206 intestine were examined separately to ensure any differences between species were not a result of
207 variation in the anatomical structure of the stomach (Choat 1991). Following Wilson and Bellwood
208 (1997), a 15×15 square grid was fixed to the underside of a glass petri dish, with 50 randomly
209 marked quadrats. Samples were spread evenly over the petri dish and the dominant item (by area) in
210 each quadrat was recorded as well as any other material present. Material was categorised into
211 detritus, algae or sediment, with the term detritus used in the broad sense to describe amorphous
212 organic material with no visible structure, in all cases consisting of opaque, flocculent material
213 (following Wilson and Bellwood [1997]). This material is not detritus *sensu stricto*, as it is likely to
214 have contained some living material such as bacteria, microalgae and fungi (Wilson and Bellwood
215 1997). To analyse the differences in the frequency of occurrence of algal material compared to other
216 matter (sediment or detritus) in the gut contents of *C. striatus* vs. *A. nigrofuscus* Pearson's Chi-
217 squared tests with Yates' continuity correction were performed separately on stomach and intestinal
218 data. The tests were performed in the statistical software R (R Core Team 2014).

219 **Results**

220 **Algal removal experiment**

221 Feeding by *C. striatus* did not result in a significant decrease in turf length ($t_9 = 1.72$, $p =$
222 0.12 ; Fig. 2a) or in the cover of turf algae (GLMM; $z = 0.33$, $p = 0.74$; Fig 2b; ESM S2). On rocks
223 exposed to *C. striatus*, algal turfs appeared largely unchanged following feeding (Fig. 3c, e) with an
224 average decrease in turf length of only 0.2 ± 0.1 mm (\pm SE) representing a reduction of 5.2 ± 2.7 % (\pm

225 SE). Additionally, the mean proportion of area covered by turfing algae decreased by only 1.3 ± 3.9
226 %. Visually, the only change was a reduction in particulate loads.

227 By contrast, feeding by *A. nigrofuscus* significantly decreased turf length ($t_9 = 11.59, p <$
228 0.0001 ; Figs 2a, 3d, f) and the area covered by turf algae (GLMM; $z = 3.59, p = < 0.001$; Fig. 2b, 3d,
229 f; ESM S2). On average, *A. nigrofuscus* reduced turf length by 2.1 ± 0.2 mm (\pm SE) representing a
230 reduction of 51.2 ± 2.4 % in one hour of feeding (Fig. 2a). The mean area covered by turf algae was
231 also reduced by 14.7 ± 4.0 %. Only short, well-cropped algal turfs remained following exposure to *A.*
232 *nigrofuscus*.

233 On control rocks there was no significant difference in turf length ($t_{19} = 0.62, p = 0.55$; Fig.
234 2a) or proportion of area covered (GLMM; $z = -0.17, p = 0.86$; Fig. 2b; ESM S2). During the one hour
235 feeding trials, *C. striatus* took an average of 592.5 ± 108.8 bites (\pm SE) on the rocks while *A.*
236 *nigrofuscus* took an average of 1583.2 ± 159.2 bites.

237 **Ingested material**

238 The material ingested by *C. striatus* on the reef was dominated by detritus and sediment (Fig.
239 4a, c; ESM S3). In *C. striatus* intestinal contents, detritus was the dominant category in 68.0 ± 8.2 %
240 (\pm SE) of quadrats. In the stomach of *C. striatus*, detritus was dominant in 64.4 ± 2.7 % of quadrats.
241 Algae were never the dominant category in intestinal contents quadrats and were only dominant in 0.4
242 ± 0.4 % of stomach sample quadrats. Although algae were present in 37.6 ± 10.8 % and 54 ± 4.7 % of
243 quadrats for *C. striatus* intestine and stomach samples, respectively, this was generally due to the
244 presence of a single algal filament (ESM S4). By contrast, in *A. nigrofuscus*, algae were the dominant
245 category in 79.6 ± 3.8 % and 94.7 ± 2.9 % of quadrats for intestine and stomach samples, respectively
246 (Fig. 4b, d; ESM S3). Algal material was dominant in quadrats significantly more in *A. nigrofuscus*
247 than in *C. striatus* in both stomach ($\chi^2 = 327.25, df = 1, p = < 0.0001$) and intestinal samples ($\chi^2 =$
248 $358.60, df = 1, p = < 0.0001$).

249

250 Discussion

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

265 Visually *C. striatus* and *A. nigrofuscus* are similar, however, they interact with algal turfs in
266 distinctly different ways. The spatulate teeth (Fig. 1b), small jaw opening (113°) and rapid biting
267 behaviour of *A. nigrofuscus* is well suited to nipping off algal filaments (Purcell and Bellwood 1993).
268 By contrast, *C. striatus* take slower bites, but can open their jaws to nearly 180° (Purcell and
269 Bellwood 1993), allowing fish to come in close contact with the substratum and to selectively brush
270 fine particulate material from turfing algae (EAM) using their comb-like teeth (Purcell and Bellwood
271 1993; Tebbett et al. 2016 [Fig. 1a]). This feeding behaviour and morphology does not appear to be
272 consistent with cropping algae.

273 *C. striatus* does not crop algal turfs but it could be argued that the wide gape (178°) of *C.*
274 *striatus*, which allows extended contact with the benthos (Purcell and Bellwood 1993), could increase
275 removal of entire algal filaments as in scraping parrotfishes (Bonaldo et al. 2014). However, in *C.*

276 *striatus* the morphology and teeth make this unlikely. Indeed, no significant reduction in algal turf
277 coverage on rocks exposed to *C. striatus* was recorded and it appears that mature algal turfs, which
278 are firmly attached to the substratum, are not readily removed by the brushing feeding behaviour.
279 While *C. striatus* may remove small amounts of loose or long filamented turfing algae, an expected
280 consequence of feeding on the EAM, such removal is minimal when compared to turf-feeding
281 herbivorous fishes like *A. nigrofuscus*. Observations in both the field and aquaria suggest that when *C.*
282 *striatus* dislodge algae it often becomes caught in their teeth, causing visible annoyance to the fish
283 (Randall 1955; Purcell and Bellwood 1993). This may explain the slight (non-significant) reduction in
284 mean algal turf length and proportional area covered on surfaces exposed to *C. striatus*, as longer
285 algal filaments are more likely to become entangled in their teeth. Such removal appears to be
286 incidental as no significant reductions in algae were recorded even after an average of 592.5 (\pm 108.8;
287 SE) bites in an area of approximately 50 cm² in one hour.

288 As commonly reported, the gut contents of *C. striatus* specimens from the reef did contain
289 some algae (Polunin and Klumpp 1989; Choat and Clements 1998; Choat et al. 2002). This algae may
290 be partly from incidental removal and ingestion, as above. However, it may also be the result of
291 secondary ingestion of algal material through coprophagy. Many herbivorous fishes, including *A.*
292 *nigrofuscus*, void their faeces over the reef (Fishelson et al. 1985; Clements 1991; Bonaldo et al.
293 2014) and much of the algal material contained within the faeces remains structurally intact and can
294 continue to grow (Vermeij et al. 2013; Tâmega et al. 2016). *C. striatus* feeds over the same substrata
295 as these fishes, especially herbivorous acanthurids (Choat and Bellwood 1985) and it is likely that *C.*
296 *striatus* may ingest a considerable amount of faecal matter (Clements 1991). Indeed, *C. striatus*
297 consumed 42 % and 37 % respectively of the faeces consumed from the herbivorous surgeonfishes *A.*
298 *nigricans* and *A. lineatus* (Robertson 1982). Rather than directly removing mature turfing algae from
299 the reef, *C. striatus* may act as a secondary herbivore ingesting algae and detritus from the faeces of
300 other reef organisms.

301 It the experiments *A. nigrofuscus* did take substantially more bites during the exposure period
302 than *C. striatus*, however, this is unlikely to contribute significantly to the differences observed. The

303 bites of each species are fundamentally different and although a slower feeder, the bite area of *C.*
304 *striatus* is much larger than *A. nigrofuscus* (Purcell and Bellwood 1993). A similar disparity in bite
305 rates is seen in the wild, with *A. nigrofuscus* having a higher bite rate than *C. striatus* (Clements 1991;
306 Polunin et al. 1995). In an experimental study by Marshall and Mumby (2012) examining algal turf
307 removal by *C. striatus* and *A. nigrofuscus* differences in bite rates were also recorded; *A. nigrofuscus*
308 took six times more bites than *C. striatus*. Although a disparity in bite rates was reported, like the
309 present study, it is interesting to consider the contrasting results in terms of the fishes' effects on algal
310 turfs.

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

318 The second difference lies in the nature of the algae examined. The current study used reef-
319 grown algal turfs which were at least six months old growing on planar dead coral rocks.
320 Consequently the coral rocks supported mature algal turfs. By contrast, the algal turfs used by
321 Marshall and Mumby (2012) were grown on artificial surfaces (rough "limestone" tiles, orange in
322 colour) which were "preconditioned on the reef". These tiles were, however, scrubbed following
323 conditioning to begin with an algal biomass of zero. They were then placed in flow-through aquaria to
324 develop sparse algal turfs after two weeks and dense algal turfs after six weeks (Marshall and Mumby
325 2012). The algal communities in the two studies were likely to differ in two fundamental ways. First,
326 differences in algal communities may arise due to variation in the texture and chemistry between the
327 two settlement substrata (natural coral rocks vs. artificial tiles), which can impact the species of algae
328 which settle and develop (Harlin and Lindbergh 1977; Borowitzka et al. 1978; Hixon and Brostoff
329 1985; Diaz-Pulido and McCook 2002; Smith et al. 2010). Indeed, coral rock substrata tend to support

330 more later successional algae compared to artificial settling substrata and as algal turfs can penetrate
331 coral rock substrata they may be more firmly attached (Hixon and Brostoff 1996; Diaz-Pulido and
332 McCook 2002).

333 The second major difference between these studies lies in the age of the algal turfs used. The
334 algal community used by Marshall and Mumby (2012) was less than six weeks old and consequently
335 was likely to be dominated by early successional algae which are only superseded by more mature
336 forms after several months (Borowitzka et al. 1978; Diaz-Pulido and McCook 2002). Early
337 successional algal communities are dominated by diatoms, coccoids and blue-green filamentous algae,
338 while later successional stage turf algal communities are more species rich and include complex algal
339 forms (Borowitzka et al. 1978; Scott and Russ 1987; Diaz-Pulido and McCook 2002). Early
340 successional algal communities are less firmly attached to substrata (Borowitzka et al. 1978; Diaz-
341 Pulido and McCook 2002) and consequently may be removed far more easily than later-successional
342 algal turfs such as those used in our study. As *Ctenochaetus* are able to open their jaws to nearly 180°
343 to feed on planar surfaces (Randall 1955; Purcell and Bellwood 1993) they are likely to remove loose
344 algae from planar, smooth artificial tiles far more effectively than *A. nigrofuscus*. Indeed early
345 successional “algal turfs” (diatoms and cyanobacteria) may form an important component of the
346 nutritional ecology of *C. striatus* where available (Polunin et al. 1995; Choat et al. 2002; Wilson et al.
347 2003). This is particularly likely if they feed on smooth surfaces covered with calcareous algae where
348 the removal of microalgal fouling may be important. However the feeding activity of *C. striatus*
349 appears to have a minimal effect on later successional stage algal turfs, which are often the dominant
350 benthic covering on coral reefs (Wismer et al. 2009).

351 In addition to the differences outlined above, other factors may also have contributed to the
352 disparity in the results. In particular, the sediment loads within the algal turfs in the present study were
353 approximately six to thirteen times lower than those in Marshall and Mumby (2012) and were more
354 similar to loads found in reef crest algal turfs (Purcell 2000; Goatley and Bellwood 2012), the
355 predominant feeding habitat of the two surgeonfishes (Russ 1984; Goatley and Bellwood 2010). As
356 sediments suppress the feeding rates of herbivorous/detrivorous fishes (Goatley and Bellwood 2012;

357 Gordon et al. 2016; Tebbett et al. 2016a, 2016b) this may explain why we found higher bite rates in
358 both fish species. Importantly, this means that any effect the fishes may have had on algal turfs in the
359 present study should have been more pronounced.

360 It should be noted that we did not directly examine if *C. striatus* were ingesting and
361 assimilating the particulate material used in the experiments, such an examination may have provided
362 supporting evidence of their ability to brush detritus from algal turfs. However, visual observations
363 and video recordings both strongly suggest that particulates were removed; although this reduction
364 was not quantified it may have yielded interesting results. Nevertheless, the chief aim of this study
365 was to assess the extent of algal removal from mature algal turfs by the two species, which is
366 evidently minimal in the case of *C. striatus*.

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

379 When brushing detrital aggregates from the EAM, *C. striatus* also removes and ingests
380 inorganic sediments, making it a key player in EAM sediment dynamics (Goatley and Bellwood 2010;
381 Krone et al. 2011; Tebbett et al. 2016b). Unlike many fishes, *C. striatus* have distinct defecation
382 areas, off the reef and/or in deeper water (Krone et al. 2008; Goatley and Bellwood 2010). They

383 therefore export ingested sediment away from feeding areas (Krone et al. 2008, 2011; Goatley and
384 Bellwood 2010). This role may be vital to coral reefs as EAM sediments suppress herbivory (Goatley
385 and Bellwood 2012; Gordon et al. 2016) and coral recruitment (Birrell et al. 2005; Diaz-Pulido et al.
386 2010; Perez III et al. 2014). By reducing EAM sediment loads, *C. striatus* may facilitate herbivory in
387 these environments (Choat 1991; Goatley and Bellwood 2010) underpinning both the preservation of
388 short productive algal turfs (SPATs *sensu* Goatley et al. 2016) and coral replenishment (Brandl and
389 Bellwood 2016). Interestingly, if *C. striatus* also ingests viable algal material from the faeces of other
390 fishes (as discussed above) their defecation behaviour may also incidentally help limit algal
391 development and expansion. *C. striatus* may therefore perform a secondary “herbivory” function on
392 coral reefs by harvesting loose, but viable, algal material and exporting it off the reef. Exploring the
393 potential for *C. striatus* to act as a secondary herbivore in this manner may be an important topic for
394 future research.

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

405 In addition to the functional roles discussed so far, in the Red Sea *C. striatus* have also been
406 suggested to play a role in bioerosion, through the use of a hard palate structure that could be used to
407 rasp the substratum (Schuhmacher et al. 2008; Krone et al. 2011), although, Krone et al. (2011)
408 conclude that bioerosion by *C. striatus* is only a minor role compared to the removal of loose
409 sediments. It is interesting that although *C. striatus* is abundant, widely distributed and often studied,

410 bioerosion and the presence of a hard palate structure has not been reported outside of the Red Sea.
411 Further investigation of bioerosion and the anatomy of *C. striatus* in other geographic localities could
412 be worthwhile.

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

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

435

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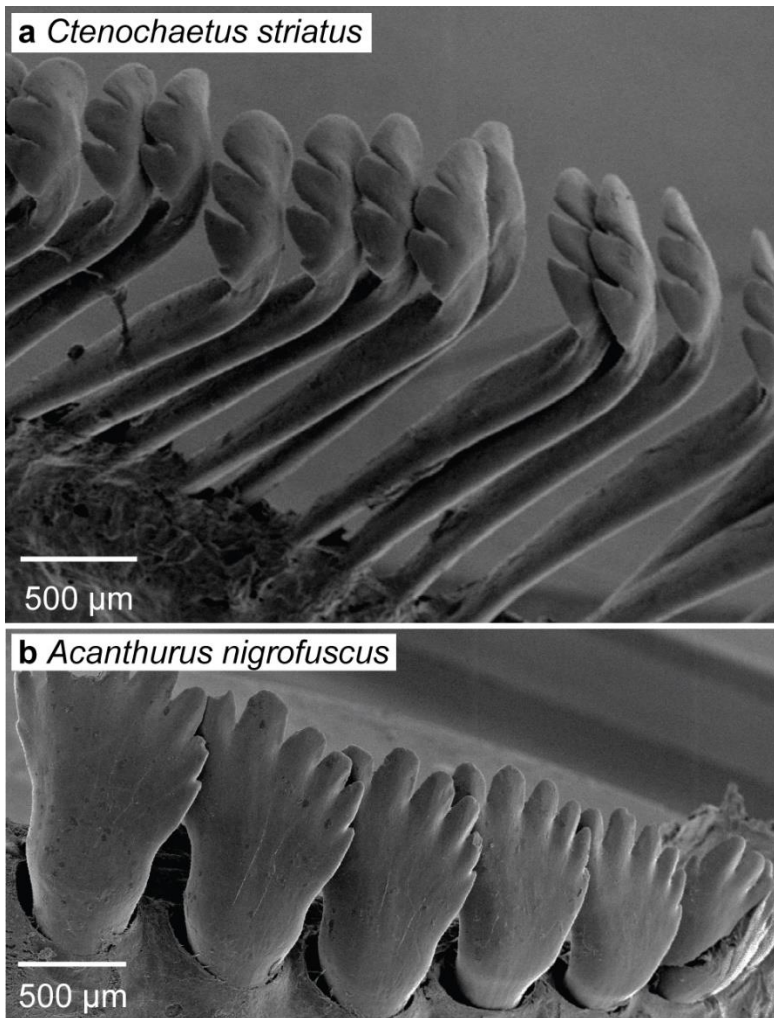
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643 **Figures**

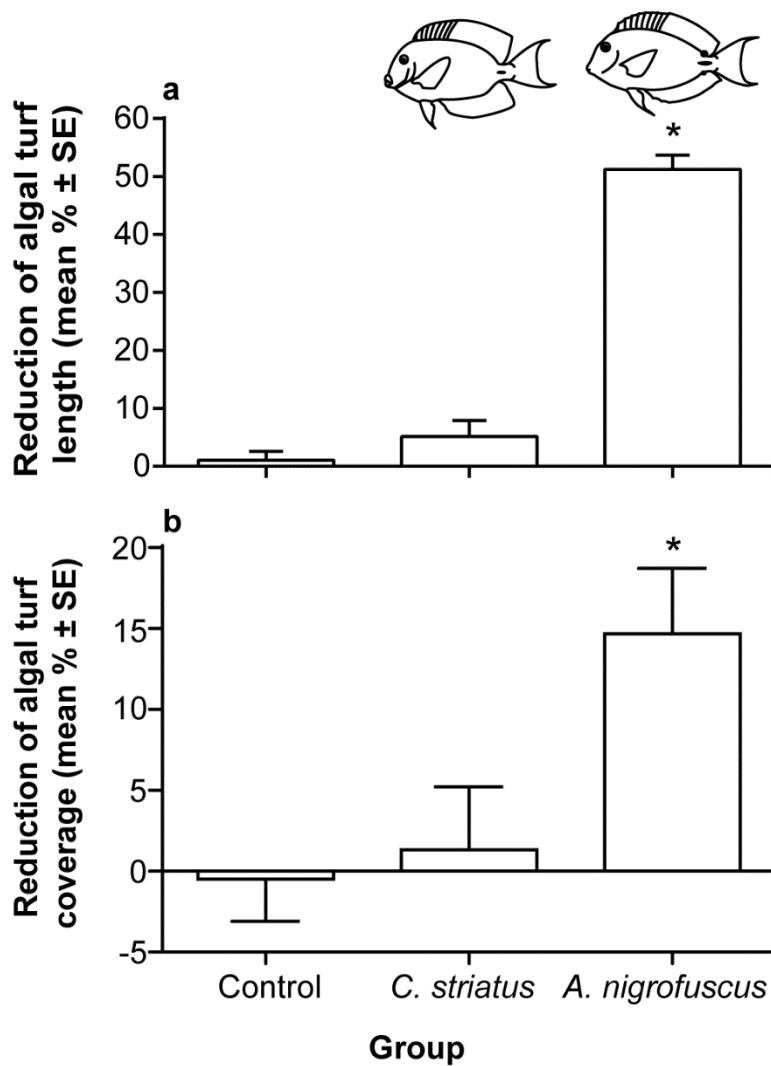
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646 **Fig. 1** Scanning electron micrographs of the teeth of **a** the lined bristletooth, *Ctenochaetus striatus*
647 (anterior view of dentary) and **b** the brown surgeonfish, *Acanthurus nigrofuscus* (anterior view of
648 dentary)

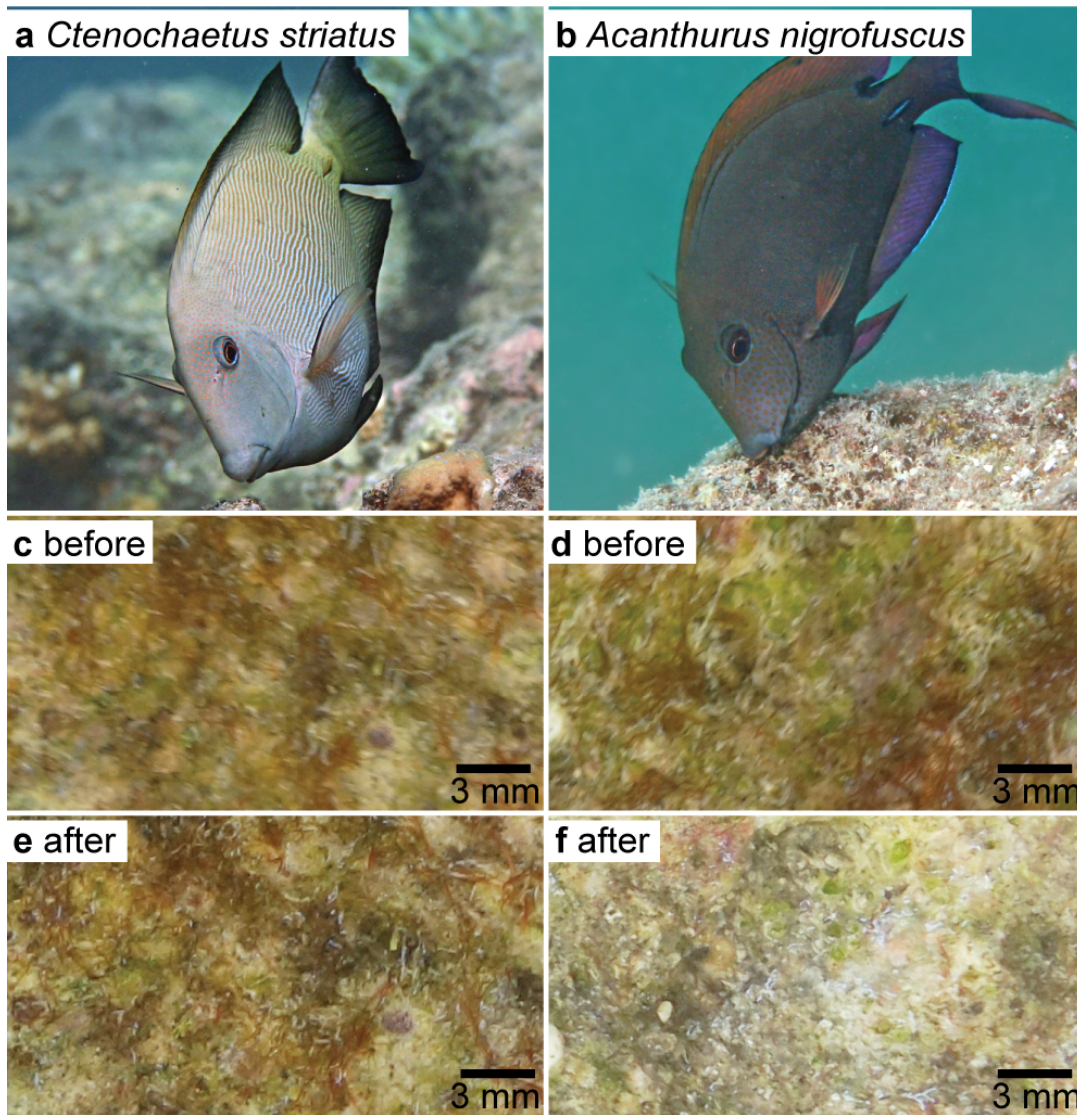
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651 **Fig. 2** The mean (% ± SE) reduction of algal turf **a** length and **b** area coverage following one hour of
 652 exposure without fish present (control) and after one hour of feeding by the lined bristletooth,
 653 *Ctenochaetus striatus*, and the brown surgeonfish, *Acanthurus nigrofuscus*. * denotes a significant
 654 difference before versus after exposure ($\alpha = 0.05$)

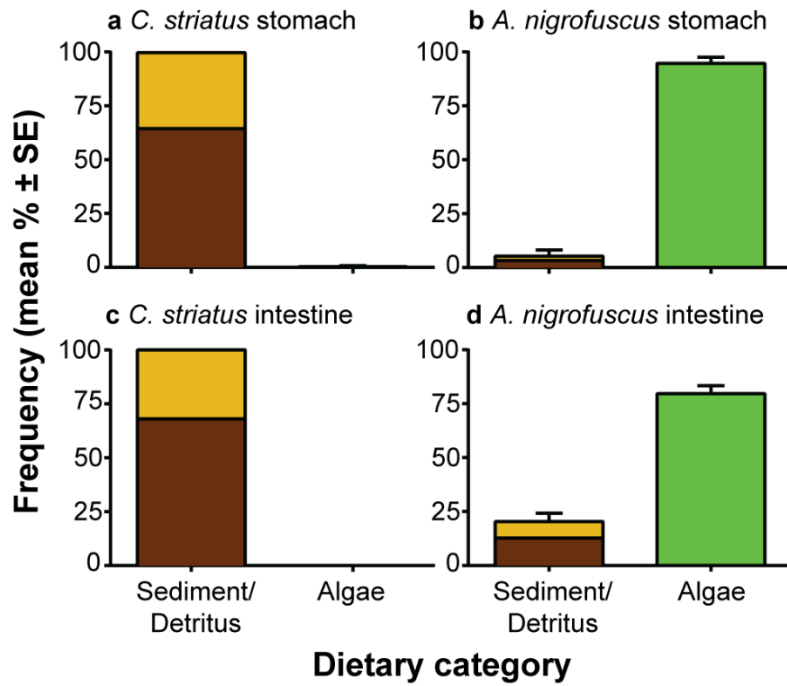
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657 **Fig. 3** **a** the lined bristletooth, *Ctenochaetus striatus*, **b** the brown surgeonfish, *Acanthurus*
 658 *nigrofuscus*, (photographs by CHR) **c** feeding surface before exposure to *C. striatus* and **d** *A.*
 659 *nigrofuscus*. Feeding surfaces after one hour of feeding by **e** *C. striatus* and **f** *A. nigrofuscus*. Scale
 660 bars are approximate.

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

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