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A. Marshall & P. J. Mumby

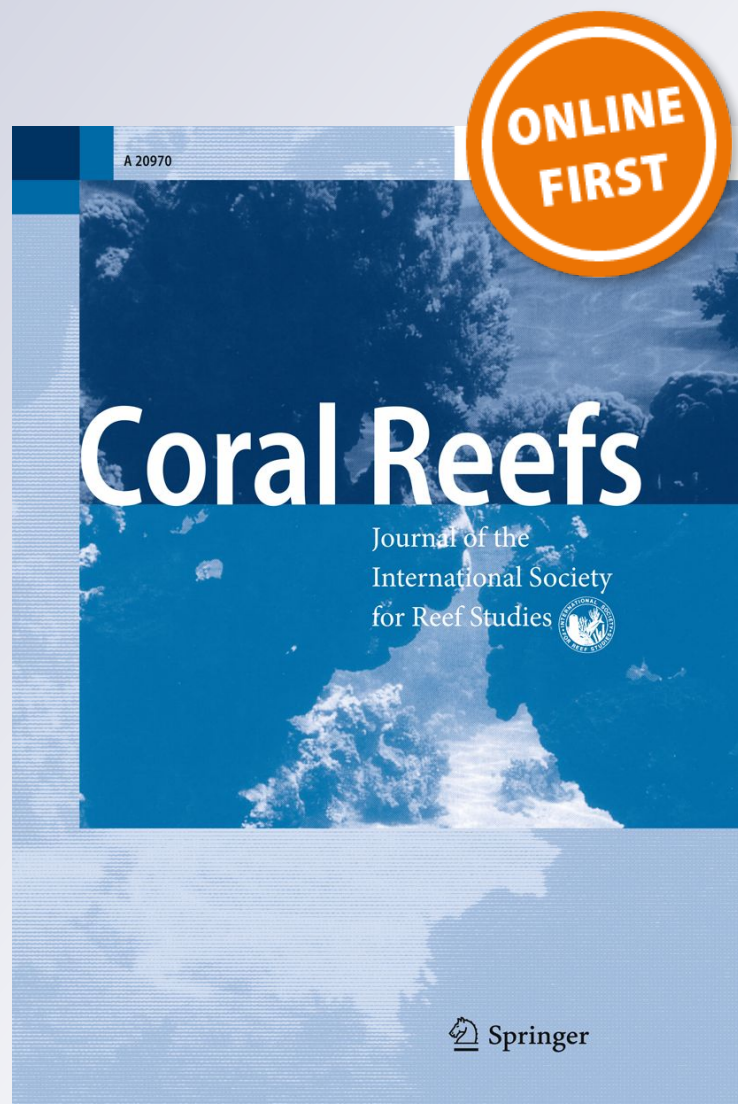
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Revisiting the functional roles of the surgeonfish *Acanthurus nigrofuscus* and *Ctenochaetus striatus*

A. Marshall · P. J. Mumby

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Abstract Investigating the functional role of herbivorous fish species is important for understanding reef resilience and developing targeted management plans. Among the most abundant fish species on Indo-Pacific coral reefs are the surgeonfishes *Acanthurus nigrofuscus* and *Ctenochaetus striatus*. *A. nigrofuscus* is an herbivorous grazer that crops filamentous algae from the epilithic algal matrix, while *C. striatus* is detritivorous and was thought to ‘brush’ detritus from the surface of filamentous algae, causing little damage to algal strands. Although the foraging mechanisms and general diet of these surgeonfishes have been established, their grazing impact on epilithic algal turfs has been unclear. This is the first study to quantify the grazing impact of *A. nigrofuscus* and *C. striatus* on algal turfs. Through aquaria trials using epilithic algal turf grown on experimental tiles, we found that both *A. nigrofuscus* and *C. striatus* consistently fed more intensively upon sparse/short algal turfs even though the yield of algae per bite was greater for dense/long algal turfs. As there was no difference in the nutritional value of sparse and dense algal turfs, we hypothesise that *A. nigrofuscus* avoided dense turf due to its significantly greater sediment load than sparse turf, while *C. striatus* likely avoided dense turf as it would become entangled in their bristle-like teeth. Unexpectedly, despite its dental morphology, *C. striatus* removed significantly more algal turf per hour than *A. nigrofuscus*, irrespective of canopy height. The capability of *C. striatus* to

remove significant quantities of algal turf through their foraging activity implies that this abundant and widespread species may substantially affect algal turf dynamics. If this is the case, the exclusion of detritivorous *Ctenochaetus* species from herbivorous fish functional groups used in resilience monitoring will need to be re-evaluated.

Keywords Surgeonfish · Herbivore · Detritivore · Functional groups · Ecological role · Algal turf

Introduction

Herbivory can be more intense on coral reefs than in any other marine or terrestrial habitat (Hatcher and Larkum 1983; Carpenter 1986; Lewis 1986; Choat 1991). Herbivorous fish are generally the main consumers of coral reef primary production, potentially consuming between 50 and 100 % of total daily algal production (Hatcher 1981; Carpenter 1986). Herbivorous fish exert top-down controls on algal biomass (Lewis 1986; Hughes et al. 2007; Burkepile and Hay 2008), productivity (Russ 2003), and succession (Hixon and Brostoff 1996), thus reducing the establishment and growth of algal communities that compete with coral for space and inhibit coral recruitment, especially post-disturbance (Carpenter 1986; Hughes et al. 2007). Disturbances such as cyclones, bleaching, and outbreaks of crown of thorns starfish often lead to the loss of coral cover and increase of algal cover on coral reefs. Following disturbances, herbivorous fish play an important role in removing algae and promoting reef resilience and recovery (Nyström and Folke 2001; Bellwood et al. 2004; Ledlie et al. 2007). Therefore, herbivory is widely acknowledged as a key ecological process that structures benthic communities and is important for the resilience of coral reefs (Steneck 1988;

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Bellwood et al. 2004; Mumby and Steneck 2008). Determining the nature of top-down controls of grazers upon algae is important as part of a holistic analysis of all the drivers that might promote or mitigate an algal bloom on reefs (Russ 2003). On coral reefs across the mid- and outer Great Barrier Reef, the epilithic algal matrix (EAM) covers 50–80 % of reef flats and back reefs and 30–70 % of reef slopes (Hatcher and Larkum 1983; Klumpp and McKinnon 1992; Wismer et al. 2009). The EAM is a major source of primary production and is the predominant grazing surface for many herbivorous fishes (Hatcher 1997; Wilson et al. 2003). The EAM is a complex assemblage consisting of microalgae (e.g. diatoms, cyanobacteria), filamentous algal turfs < 1 cm high, juvenile stages of macroalgae, crustose algae, and detrital material (dead organic matter, inorganic material, microbes, meiofauna) (Steneck 1988; Choat 1991). More than 70 % of the detrital component of the EAM is derived from decaying filamentous algae, which is more nutritious than live algal turf because of the addition of bacteria and microalgae, and this dissolved organic matter is also more palatable and easier to digest (Wilson et al. 2003). The EAM primarily forms short, sparse mats of algal turfs < 1 cm high that have a high turnover rate because of intense grazing (Hatcher and Larkum 1983; Carpenter 1986). Long, dense mats of algal turfs > 1 cm high are generally only found within damselfish territories (Wilson and Bellwood 1997), or areas with heavy sediment load. Long, dense algal turfs trap more sediment than short, sparse algal turfs, resulting in a relatively stable, sediment-rich algal turf mat (Bellwood and Fulton 2008).

Herbivorous fish are a diverse ecological group (Choat 1991), and broad functional categories were established to aid development of general models of plant–herbivore interactions (Steneck 1988). Functional groups are formed based on species roles in ecosystem processes (Bellwood et al. 2004; Green and Bellwood 2009), and species are assigned to functional groups based on their ability to carry out similar ecosystem functions, regardless of their taxonomic classification (Steneck and Dethier 1994). Fish species are categorised into functional groups depending on how they feed, what they consume, and how they affect the structure of benthic communities (Green and Bellwood 2009). The most widely recognised functional groups of herbivorous fish are small excavators/scrapers, large excavators/bioeroders, grazers/detritivores, and browsers (Green and Bellwood 2009). Herbivorous fishes that feed on the EAM are an important trophic link between algal primary production and secondary consumers (Horn 1989; Choat 1991). However, it is often difficult to determine the trophic class or functional group of fishes that feed upon the EAM because of its complex species assemblage and physical structure. Consequently, EAM grazing fishes are classified into the single functional group of grazers/

detritivores. Yet, species that are considered exclusively detritivorous, causing little damage to algae through their grazing (e.g. *Ctenochaetus* species), are recommended to be excluded from resilience monitoring, as they are thought to not limit the establishment and growth of algal communities (Green and Bellwood 2009).

Inevitably, the categorisation of organisms into functional groups requires a compromise between highlighting major differences among groups and recognising the existence of heterogeneity within individual groups. Unfortunately, the functional role of some herbivorous fish species remains somewhat obscure (Fox et al. 2009), which prevents the adequacy of some functional classes from being evaluated. A case in point are the numerically dominant herbivores on many Indo-Pacific reefs, the surgeonfishes (Acanthuridae) that feed upon the EAM (Steneck 1988). Recent work has highlighted the ecological importance of acanthurid browsers in macroalgal dynamics (Hoey and Bellwood 2009), and acanthurid detritivores in sediment dynamics (Goatley and Bellwood 2010), but the functional role of highly abundant, diminutive acanthurid grazing species in algal turf dynamics is less understood.

Throughout the Indo-Pacific, two of the most abundant reef fishes that feed upon the EAM are the brown surgeonfish, *Acanthurus nigrofuscus*, and the lined bristletooth, *Ctenochaetus striatus* (Russ 1984; Choat and Bellwood 1985; Trip et al. 2008; Cheal et al. 2012). *A. nigrofuscus* is classified as a grazer that feeds upon sparse algal turfs, tearing epilithic microalgal turf filaments from the substratum (Horn 1989; Purcell and Bellwood 1993; Polunin et al. 1995). *C. striatus* is classified as a detritivore that feeds upon sparse algal turfs and calcareous algae, ‘brushing’ detritus off the substratum surface and causing little damage to algal turfs (Choat 1991; Purcell and Bellwood 1993; Polunin et al. 1995; Choat et al. 2002, 2004; Goatley and Bellwood 2010). Given the abundance of *C. striatus* and *A. nigrofuscus*, which can dominate fish communities and attain average densities on sheltered reefs of up to 33 and 13 individuals per 300 m², respectively (Choat and Bellwood 1985), it is important to establish the foraging impact of these species on algal turf communities. A key functional question, from an ecosystem perspective, is whether these species can physically remove algal turfs from the EAM. If a species simply ‘brushes’ the algal turf surface for detritus, then it may have little or no direct impact on algal dynamics. However, should the action of their foraging effectively remove significant algal turf biomass—even if targeting detritus rather than living algal turf, then the functional impact on algal dynamics will be very different.

Here, we study the grazing impact of *A. nigrofuscus* and *C. striatus* on algal turfs. Through experimental trials, we aim to: (1) investigate the potential grazing impact of acanthurid grazer *A. nigrofuscus* and detritivore *C. striatus* on epilithic

algal turfs, (2) establish whether these species prefer to feed upon different stages (sparse/short: 2-week growth, or dense/long: 6-week growth) of algal turfs, and examine whether this is correlated with differing algal nutritional value or sediment load, and (3) determine the average amount of algal turfs ingested per bite by these fishes.

Methods

Fish capture and husbandry

This study was undertaken at Heron Island Research Station (HIRS), southern Great Barrier Reef, Queensland, Australia (23.44°S, 151.91°E). Individuals of *Acanthurus nigrofuscus* and *Ctenochaetus striatus* were captured from northern Heron reef slope, in shallow spur-and-groove habitat (23°26'23"S, 151°58'37.2"E), using a barrier net (25 × 1.5 m) herding technique. The average fork lengths (cm ± SE) of captured *A. nigrofuscus* and *C. striatus* were 16.7 ± 0.4 and 19.7 ± 0.6, respectively. Captured fish were transported to the HIRS laboratory where they were kept in outdoor, partly shaded aquariums. *C. striatus* individuals were kept in a large circular aquarium (2.05 m diameter × 0.6 m deep, 1,980 l), while *A. nigrofuscus* individuals were kept in an oval aquarium (2.15 m long × 1 m wide × 0.5 m deep, 878 l), both with a continuous supply of unfiltered flow-through seawater pumped directly from the reef. Both species were fed a natural diet of algal turf-covered coral rubble and sediment collected daily from the nearby reef flat. Rectangular aquariums for experimental trials (1.85 m long × 0.7 m wide × 0.25 m deep, 324 l) were divided in half using black plastic 2.5 cm² mesh, to create two experimental areas per aquarium. Each experimental area had a concrete block housing and was partly covered with shade cloth. Individual fish were removed from the holding aquaria on the evening prior to their experimental trials and placed into the experimental areas. Experimental trials were conducted the following day between 0800 and 1200 hours. If the fish fed and there was a noticeable reduction in algal turf biomass, they were released post-trial, otherwise, on rare occasions, the trial was cancelled and the fish were returned to holding aquaria to be retried on another day. If the fish did not feed on a second attempt, they were released without being used in trials.

Feeding preference aquaria experimental trials

To develop epilithic algal turf growth on experimental tiles, preconditioned limestone tiles (13 × 13 × 1.5 cm) with a rough textured surface were scrubbed gently (to begin with an algal biomass of zero) and placed in aquarium troughs

(1.85 m long × 0.7 m wide × 0.25 m deep, 324 l) with continuous flow-through unfiltered sea water pumped directly from the reef flat. To allow different stages of algal turf development to be achieved, the tiles were placed into troughs in phases, resulting in tiles with sparse (<1 cm, 2 weeks old) and dense (>1 cm, 6 weeks old) algal turf growth. To determine the average algal turf biomass (g C cm⁻²) and sediment/inorganic biomass (g cm⁻²) on each tile before and after each experimental trial, eight random 2.5 × 2.5 cm squares were scraped, dried to constant weight at 60 °C, and weighed to the nearest 0.0001 g. The organic weight of each scraped algal turf sample was determined by reweighing the sample after ashing at 500 °C for at least 6 h (Paine and Vadas 1969), and subtracting the ash-free dry weight (AFDW) from the constant dry weight. The inorganic weight of each scraped sample was determined by subtracting the AFDW after the trial from the AFDW before the trial to give an indication of sediment removed during the trial. The surface area (cm²) was determined by measuring the length and width of each tile.

Each experimental trial consisted of two experimental tiles (one with sparse/short and one with dense/long algal turf growth) offered to an individual fish (*A. nigrofuscus*: $n = 9$; *C. striatus*: $n = 8$) by randomly placing them in the experimental tank a few centimetres apart. Experimental tiles were left in the tank for 60 min, or until there was a noticeable reduction in algal biomass. Each feeding trial was filmed using a Sanyo Xacti HD2000 camcorder, and subsequent video analysis permitted the number of bites taken to be counted. To control for loss of algal turf biomass due to handling during each experimental trial, control sparse ($n = 11$) and dense ($n = 11$) tiles were scraped and kept under identical conditions as experimental tiles, but without fish present. Experimental tiles were also individually photographed before and after each trial.

To investigate the nutritional quality of the algal turf growth on experimental tiles, ten samples of both sparse and dense algal turfs were scraped from random tiles, frozen immediately, and their energy contents determined from C and N mass fraction analysis. Nitrogen is a limiting nutrient for the growth of herbivores (Choat 1991). Therefore, C/N ratios of food sources have been extensively used as an indicator of nutritional quality to consumers and provide a useful measure for comparing the potential nutritional significance of food sources (Purcell and Bellwood 2001).

Data analysis

The potential grazing intensity (m² h⁻¹) of *A. nigrofuscus* and *C. striatus* was calculated for both sparse and dense algal turf treatments by:

mean number of bites (h⁻¹) × mean bite size (cm²).

The mean bite size of each species was calculated by measuring the area (cm²) of grazing scars left on experimental tiles using freeware image analysis program 'Image J', and then scaling up the mean grazing scar area to m². Combined error terms were calculated using Goodman's estimator (Travis 1982; Marnane and Bellwood 2002):

$$SE(\bar{x} \times \bar{y})^2 = \bar{x}^2 \times SE_{\bar{y}}^2 + \bar{y}^2 \times SE_{\bar{x}}^2 + SE_{\bar{x}}^2 \times SE_{\bar{y}}^2$$

where \bar{x} = mean number of bites; \bar{y} = mean bite size; $SE_{\bar{x}}$ = standard error of mean number of bites; $SE_{\bar{y}}$ = standard error of mean bite size.

The average amount of algal turf removed per bite by *A. nigrofuscus* and *C. striatus* was determined by calculating the average decrease in algal turf biomass after a known number of bites on experimental tiles with epilithic algal turf growth (Bruggemann et al. 1994b). Food intake per bite was calculated as (g algal AFDW):

$$\text{mean algal biomass}_{\text{before}} - \text{mean algal biomass}_{\text{after}} / \text{no. of bites cm}^{-2}.$$

All results are presented as mean \pm standard error, unless stated otherwise. To investigate whether differences existed between sparse and dense turf tile treatments, normal distribution of the data was established using a Shapiro–Wilk test, and paired t-tests were used to compare between the two treatments. Log-transformation of samples achieved normal distributions and/or obtained equal variances when required.

Results

Both *Acanthurus nigrofuscus* (grazer) and *Ctenochaetus striatus* (detritivore) preferred sparse/short algal turf to dense/long algal turf growth, with 88 % of *A. nigrofuscus* bites ($n = 5,648/6,430$) and 74 % of *C. striatus* bites ($n = 1,734/2,351$) taken on sparse algal turfs.

On average, *A. nigrofuscus* took significantly more bites on sparse than dense algal turfs (Fig. 1a-i; $t_8 = 4.782$, $p = 0.001$) and removed more algal turf per bite when feeding on dense algal turf (Fig. 1b-i; $t_8 = -3.761$, $p = 0.006$). Although *A. nigrofuscus* removed more algal turf per bite when feeding on dense algal turf, the fish consistently invested a greater proportion of their time (>80 %) and effort feeding upon sparse algal turf throughout the experimental trial (Fig. 1c).

The results from *C. striatus* were qualitatively similar to *A. nigrofuscus* in that: (1) their grazing rate was higher on sparse algal turf than on dense algal turf (Fig. 1a-ii; $t_7 = 3.529$, $p = 0.01$), (2) they removed more algal turf per bite when feeding on dense algal turf (Fig. 1b-ii; $t_7 = -3.463$, $p = 0.01$), and (3) the investment of time feeding on sparse algal turfs was consistently greater

(>70 %) over the duration of the trial despite a larger harvest per bite on dense algal turfs (Fig. 1d). The data in Fig. 1a and 1c, d are directly related (number of bites = time/effort spent on a treatment); however, Fig. 1c/d displays how the fish behaved over the duration of the trial, with both species preferring to feed consistently upon the sparse turf treatment.

A. nigrofuscus was observed to remove turf and leave sediment behind, whereas *C. striatus* removed both turf and sediment indiscriminately from the experimental tiles (Fig. 2a, b). *C. striatus* removed more inorganic sediment biomass (g cm⁻² h⁻¹) per trial than *A. nigrofuscus* for both sparse ($t_{15} = -4.531$, $p < 0.001$) and dense ($t_{15} = -3.435$, $p = 0.004$) algal turf treatments (Fig. 2c). On average, the detritivorous species *C. striatus* also removed significantly more algal turf biomass (g C cm⁻² h⁻¹) than the grazing species *A. nigrofuscus*, for both sparse (Fig. 3; $t_{15} = -5.171$, $p < 0.001$) and dense (Fig. 3; $t_{15} = -4.226$, $p < 0.001$) algal turf treatments.

Although both species preferred sparse algal turfs, the higher yield of algae per bite from dense algal turfs meant that the total amount of turf removed over time did not differ between turf classes (Fig. 3; *A. nigrofuscus*: $t_8 = -1.237$, $p = 0.251$; *C. striatus*: $t_7 = 0.495$, $p = 0.636$).

From the functional perspective of grazing intensity, calculated as the product of grazing rate per treatment and mean bite area, it is clear that the grazing intensity (m² h⁻¹) is greater for sparse turf algae than dense turf algae for both species (Fig. 4). Although the differences in grazing intensity between algal turf classes are similar to the proportions in Fig. 1a-i and 1a-ii, the grazing intensity plotted in Fig. 4 allows a clearer comparison of the 2-dimensional grazing intensity by both algal density and fish species.

Prior to experimental trials, dense algal turf contained a significantly greater average sediment load (0.19 \pm 0.018 g cm⁻², \pm SE) than sparse algal turf (0.09 \pm 0.008 g cm⁻², \pm SE; $t_{32} = -4.658$, $p < 0.001$). However, there was no difference in the average nutritional value of sparse (7.8:1 \pm 0.23, mean \pm SE) and dense (7.4:1 \pm 0.28) algal turfs, as evidenced by statistically indistinguishable ratios of total organic carbon (TOC) to total nitrogen (TN) ($t_{19} = -1.326$, $p = 0.201$). Control tiles (controlling for experimental handling effects) showed that there was no significant difference in algal turf biomass before and after experimental trials in the absence of herbivorous fish ($t_{20} = 1.536$, $p = 0.140$).

Discussion

This is the first study to quantify the grazing impact of *A. nigrofuscus* and *C. striatus* on algal turfs. Both *Acanthurus*

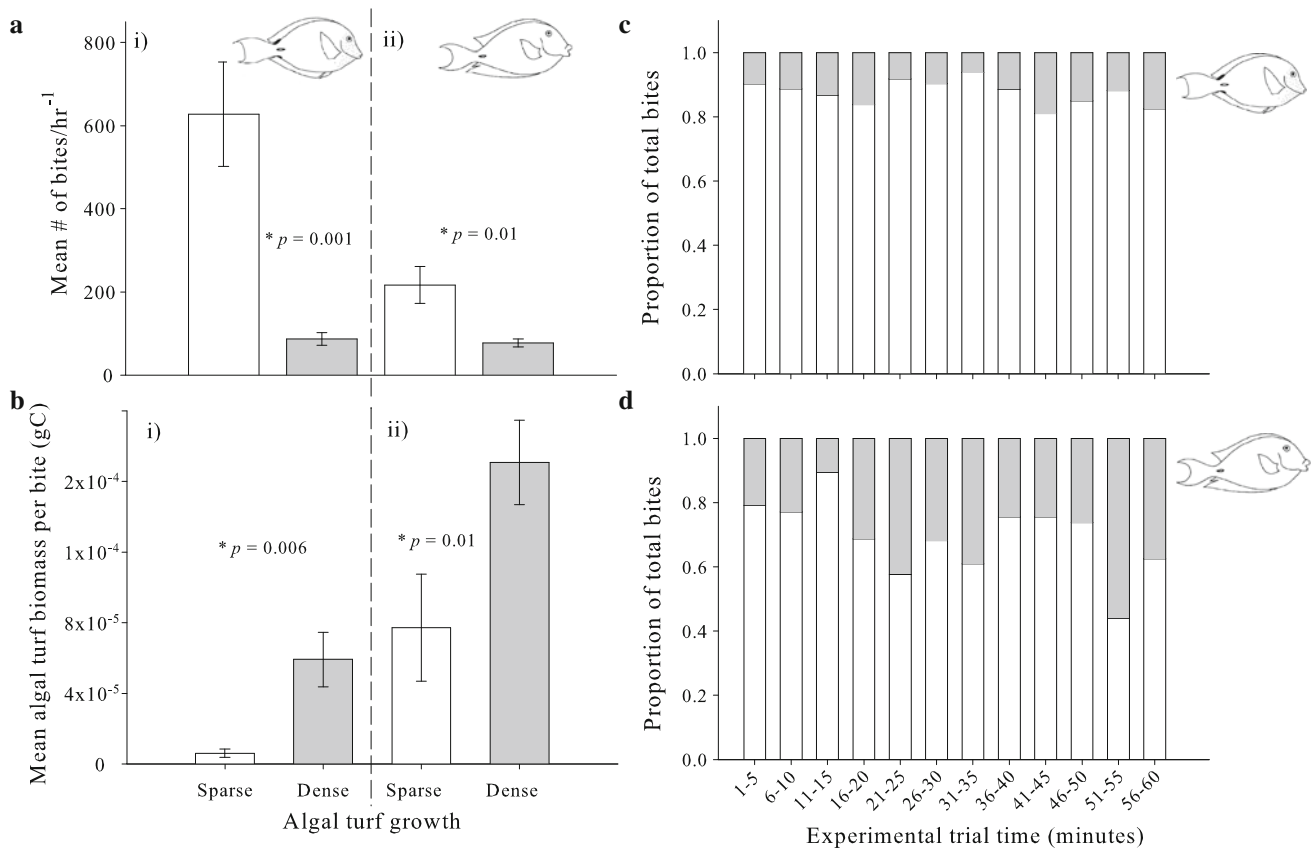


Fig. 1 **a** (i) The mean number of bites taken on sparse (white bar) and dense (grey bar) algal turf by *Acanthurus nigrofuscus* ($n = 9$) per 60-min experimental trial. (ii) The mean number of bites taken on sparse (white bar) and dense (grey bar) algal turf by *Ctenochaetus striatus* ($n = 8$). Error bars indicate standard error. **b** (i) The mean algal turf biomass per bite (g/Carbon) taken by *A. nigrofuscus* ($n = 9$). (ii) The mean algal turf biomass per bite (g/Carbon) taken by

C. striatus ($n = 8$). Error bars indicate standard error. **c** The proportion of total *Acanthurus nigrofuscus* ($n = 9$) bites taken on sparse (white) and dense (grey) algal turf, per 5-min time period of the trials. **d** The proportion of total *Ctenochaetus striatus* ($n = 8$) bites taken on sparse (white) and dense (grey) algal turf, per 5-min time period of the trials

nigrofuscus and *Ctenochaetus striatus* fed more intensively on sparse/short algal turfs even though the yield of algae per bite was greater for dense/long algal turfs. Unexpectedly, the detritivorous species, *C. striatus*, removed significantly more algal turf per hour than the grazing species, *A. nigrofuscus*, irrespective of canopy height.

The ecological importance of *C. striatus* in reef sediment dynamics has been investigated extensively (e.g. Nelson and Wilkins 1988; Krone et al. 2008; Goatley and Bellwood 2010). However, its impact on epilithic algal turf dynamics had previously not been studied. Given their elongate, flexible teeth with incurved tips, it was thought that *C. striatus* were limited to ‘brushing’ loose particulate matter off the substratum surface and unable to crop attached algal turfs, thereby causing little damage to the epilithic algal turf community overall (Robertson 1982; Purcell and Bellwood 1993). However, here we show that *C. striatus* are capable of removing significant quantities of epilithic algal turf through their foraging activity. Being one of the most abundant fishes on Indo-Pacific reefs

and having one of the highest maximum bite rates (30 bites min^{-1} ; Polunin et al. 1995) of detritivorous fishes (Wilson et al. 2003), their ability to remove significant quantities of algal turfs has important implications for their functional role in driving EAM dynamics, and potentially in driving interspecific interactions among herbivores.

In this study, detritivorous *C. striatus* removed significantly more epilithic algal turf per hour than the grazing species *A. nigrofuscus*. *C. striatus* individuals were 3 cm bigger (on average) than *A. nigrofuscus* in this study, and their larger body size and bite size likely contributed to this result. However, it remained surprising to observe such a strong impact of *C. striatus* on turfs, given that it was expected to cause little damage to algal turfs. Although we did not test whether *C. striatus* ingested or assimilated the algal turf, it is functionally important that they have the capability to remove significant quantities of it through their foraging activity. On outer reef flats, *C. striatus* have been observed foraging across sparse filamentous algal turf-covered rocks and crustose coralline algal surfaces

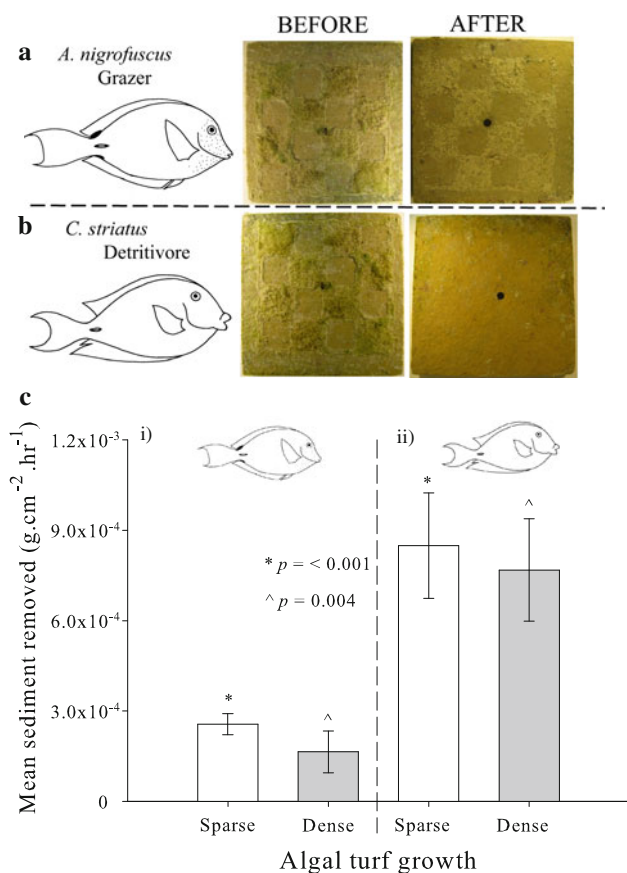


Fig. 2 Examples of sparse algal turf experimental tiles before and after an experimental trial for **a** grazer *Acanthurus nigrofuscus* and **b** detritivore *Ctenochaetus striatus*. *A. nigrofuscus* generally removed turf and left sediment behind, while *C. striatus* generally removed both turf and sediment. **c** The mean inorganic sediment biomass ($\text{g}\cdot\text{cm}^{-2}\cdot\text{hr}^{-1}$) removed per sparse and dense treatment by (i) *Acanthurus nigrofuscus* and (ii) *Ctenochaetus striatus*. Error bars indicate standard error

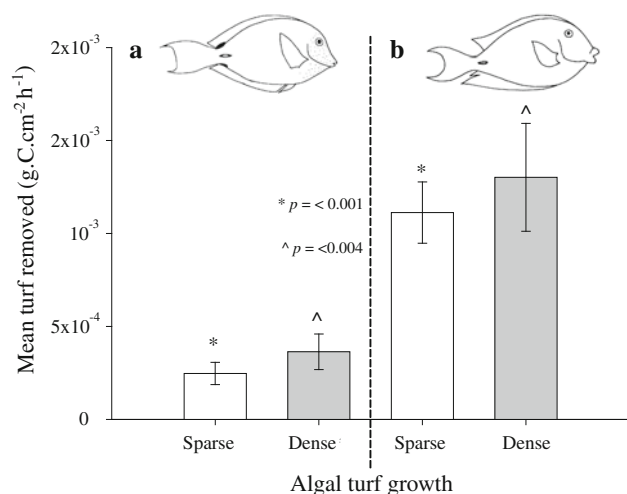


Fig. 3 The mean sparse and dense algal turf biomass removed per trial ($\text{g}\cdot\text{C}\cdot\text{cm}^{-2}\cdot\text{h}^{-1}$) by **a** *Acanthurus nigrofuscus* and **b** *Ctenochaetus striatus*. Error bars indicate standard error

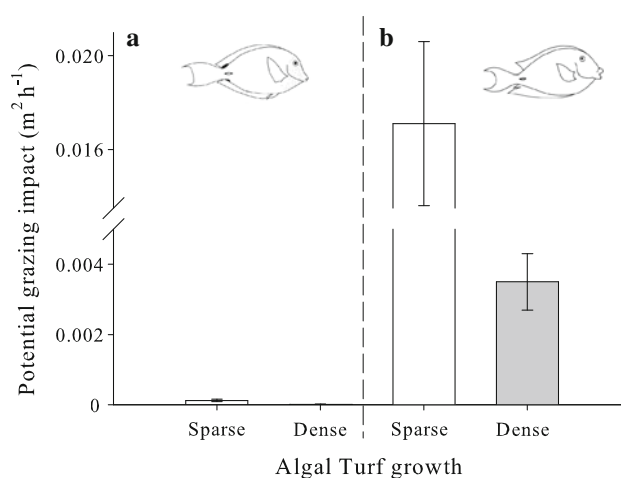


Fig. 4 The potential grazing intensity ($\text{m}^2\cdot\text{h}^{-1}$) upon sparse and dense algal turf by: **a** *Acanthurus nigrofuscus* and **b** *Ctenochaetus striatus*. Potential area grazed = mean number of bites per hour \times mean bite size (measured from grazing scar area). Error bars indicate combined error using Goodman's estimator (Travis 1982, Marnane and Bellwood 2002)

(Polunin and Klumpp 1989). Algal filaments represented $\sim 20\%$ of the dietary items found in organic matter in *C. striatus* gizzards from the northern Great Barrier Reef (Choat et al. 2002). However, it was unclear whether these filaments were 'grazed from the substratum or represented detrital elements', and most studies of *C. striatus* stomach contents show that they ingest calcareous sediments and organic detritus with little evidence of algal consumption (Robertson and Gaines 1986; Nelson and Wilkins 1988; Montgomery et al. 1989; Choat et al. 2002). Therefore, if they are not ingesting and assimilating the algae that they possibly remove, it is likely that they are contributing to the production of organic detritus by dislodging living turfs. Previous studies have found that a substantial amount of the algal material removed by reef herbivores is not digested (Purcell and Bellwood 2001) and fishes assimilate only between 20 and 70% of algae consumed (Horn 1989; Galetto and Bellwood 1994; Bruggemann et al. 1994b). We hypothesise, therefore, that *C. striatus* may contribute to the detrital pool ($>70\%$ derived from filamentous algae, Wilson et al. 2003) by harvesting and depositing large amounts of turf. Moreover, it is possible that *C. striatus* is effectively contributing to the creation of their own detrital pool within their relatively small (average, 12.1 m^2) home range (Krone et al. 2008).

A. nigrofuscus and *C. striatus* are thought to coexist in 'synergistic cohabitation' because of their ability to exploit different resources (filamentous algae and detritus, respectively) from the EAM, given major differences in their jaw morphologies (jaw bones, gape, tooth structure) and foraging actions (Purcell and Bellwood 1993). Additionally, *C. striatus* generally exhibit weak territorial

aggression (Polunin and Klumpp 1989), and their distributions commonly overlap spatially with territorial surgeonfish and parrotfish, while *A. nigrofuscus* are often aggressively excluded from herbivorous fish territories (Choat and Bellwood 1985; Robertson and Gaines 1986). Future studies will need to manipulate turf composition and substrate type simultaneously to investigate any partitioning that may occur among species. Prior studies have suggested that the relationship between *C. striatus* and territorial fishes (e.g. *Acanthurus lineatus*) could be mutually advantageous in that *C. striatus* removes sediments from algal turfs for territorial fish and in return is permitted access to actively defended territories with a large algal standing crop (Purcell and Bellwood 1993). However, in some regions, cohabitation between *Ctenochaetus* species and territorial herbivorous fishes is rare and habitat specific (Robertson and Gaines 1986). Therefore, if *C. striatus* are removing significant quantities of algal turfs, then their interspecific relationships may be more complex than has previously been proposed. Future studies are needed to establish whether interspecific relationships between *Ctenochaetus* species and herbivorous fishes are region and/or habitat specific.

Algae are generally low in protein and energy. Therefore, herbivorous fish may spend time and effort to select algae with the highest nutritional quality and obtain the best diet available (Lobel and Ogden 1981; Horn 1989; Choat 1991; Bruggemann et al. 1994a) or alternatively may be less selective and consume greater quantities of algae with lower nutritional quality. Although new algal growth is generally more nutritious and palatable than older growth (Cronin and Hay 1996), we found no difference in C/N ratios among our two classes of algal growth. The C/N ratios of algal turfs in this study (6:1–9:1) were comparable to field ratios of Lizard Island epilithic filamentous algae within lagoonal damselfish (*Stegastes nigricans* and *Hemiglyhidodon plagiometopon*) territories (6:1–9:1, Wilson and Bellwood 1997), and windward, sub-tidal reef zones (8:1–10:1, Purcell and Bellwood 2001). Therefore, as there were no differences in nutritional content of the algal turf classes, *A. nigrofuscus* likely preferred sparse/short turf because of its relatively low sediment content. Grazers are deterred by inorganic sediments that accumulate in the EAM (Choat 1991), and inorganic sediment loads are directly related to canopy height (Purcell 2000). Although the dense/long algal turf had a greater sediment load, it is also likely that *C. striatus* fed less frequently on this substratum because the elongated filaments would become entangled in their teeth and they would often forcefully reject it (Marshall, *personal observation*). *C. striatus* has previously been observed to avoid areas with long filamentous algae (>5 mm) and reject long filaments that became entangled

in their teeth when feeding on algae-covered substratum in aquaria (Purcell and Bellwood 1993). The inorganic sediment load of algal turfs in this study (sparse, 0.09; and dense, 0.19 g cm⁻²) was within the lower range of sediment loads found across natural reef zones (0.1–0.56 g cm⁻²), excluding the low values of the reef crest (0.01–0.02 g cm⁻²; Purcell 2000).

Herbivory is inversely related to sediment load of the EAM (Steneck et al. 1997; Purcell and Bellwood 2001), with increased sediment having a direct negative effect on grazing activity (Bellwood and Fulton 2008). By finding both a grazer and detritivore preference for sparse algal turfs with significantly less sediment load, our data support an earlier hypothesis that fishes contribute to the development and maintenance of a sediment-dominated substrate by avoiding such areas while foraging. Bellwood and Fulton (2008) proposed that positive feedbacks between increased sediment load and decreased grazing lead to a grazing-resistant, sediment-laden algal mat. The overwhelming surgeonfish preference for sparse/short algal turfs with reduced sediment load provides further evidence for this potential mechanism for the development and maintenance of these stable sediment-rich algal turf mats, which likely limit both coral and macroalgal colonisation and may represent an alternative degraded stable state to macroalgal dominance on coral reefs (Bellwood and Fulton 2008). Future studies could manipulate sediment load within the same algal canopy to determine whether this affects surgeonfish preference.

The results of this study only represent surgeonfish grazing on algal turfs grown on limestone tiles in aquaria, and further work is needed to investigate the removal rates and preference for algal turfs on the reef. Exploring long-term trophodynamics of *C. striatus* using stable isotopes techniques may determine whether *C. striatus* is ingesting/assimilating live algal turfs in significant quantities on the reef, as it has been difficult to determine this unequivocally using 'snapshot' stomach content analyses where algal turfs are often only a minor component. Regardless of whether *C. striatus* is ingesting and assimilating live algal turfs in significant quantities, it is important to recognise that this widespread and abundant detritivore, previously thought to cause little damage to algal turfs, is capable of removing significant quantities of algal turf through their foraging activities. Consequently, despite their detritivorous diet, *C. striatus* may play an important functional role in grazing pressure on Indo-Pacific reefs and their grazing impact would need to be considered when assessing the consequences of grazing fishes on EAM dynamics. If this is the case, the exclusion of detritivorous *Ctenochaetus* species from herbivorous fish functional groups used in resilience monitoring would also need to be re-evaluated.

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