

# Effects of the cleaner fish *Labroides dimidiatus* on grazing fishes and coral reef benthos

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**ABSTRACT:** Territorial and roving grazing fishes farm, and feed on, algae, sediment, or detritus, thus exerting different influences on benthic community structure, and are common clients of cleaner fish. Whether cleaners affect grazing-fish diversity and abundance, and indirectly the benthos, was tested using reefs maintained free of the bluestreak cleaner wrasse *Labroides dimidiatus* for 8.5 yr (removals) compared with controls. We quantified fish abundance per grazing functional group, foraging rates of roving grazers, cleaning rates of roving grazers by *L. dimidiatus*, reef benthos composition, and fouling material on settlement tiles. Abundances of 'intensive' and 'extensive' territorial farmers, non-farmers, parrotfishes and *Acanthurus* spp. were lower on removal than control reefs, but this was not the case for 'indeterminate' farmers and *Ctenochaetus striatus*. Foraging rates of *Acanthurus* spp. and *C. striatus* were unaffected by cleaner presence or cleaning duration. This suggests some robustness of the grazers' foraging behaviour to loss of cleaners. *Acanthurus* spp. foraged predominantly on sediment and detritus, whereas *C. striatus* and parrotfishes grazed over algal turfs. Nevertheless, benthic community structure and amount of organic and inorganic material that accumulated over 3.5 mo on tiles were not affected by cleaner presence. Thus, despite greater abundances of many roving grazers, and consequently higher grazing rates being linked to the presence of cleaners, the benthos was not detectably affected by cleaners. This reveals that the positive effect of cleaners on fish abundance is not associated with a subsequent change in the benthos as predicted. Rather, it suggests a resilience of benthic community structure to cleaner-fish loss, possibly related to multiple antagonistic effects of different grazer functional groups. However, losing cleaners remains a problem for reefs, as the lack of cleaning has adverse consequences for fish physiology and populations.

**KEY WORDS:** Herbivory · Coral reef ecology · Fish behaviour · Cleaning symbiosis

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## 1. INTRODUCTION

With a steady increase in environmental perturbations damaging ecosystems and leading to species loss, identifying drivers of ecosystem resilience that allow for ecosystem persistence or recovery is urgently needed. For instance, to manage the ongoing coral reef crisis, identifying the drivers of ecosystem functions that contribute to preventing or reversing shifts from coral-to-algal dominance is essential

(Bellwood et al. 2004, Hughes et al. 2018, Bruno et al. 2019). Nominally herbivorous grazing fish inhabiting coral reefs are functionally diverse, and their roles are key determinants of the structure and dynamics of benthic algal assemblages and the maintenance of coral-dominated systems (Mumby et al. 2006, Clements et al. 2009, Goatley & Bellwood 2010, Eurich et al. 2018). Interspecific interactions of fishes, which may be hindered by species loss, could play a key role in sustaining the functions fish perform on

coral reefs. Crucial for fish health and common across reef habitats are the multispecies interactions between client fishes and cleaner fishes (Vaughan et al. 2017, Grutter et al. 2019). Quantifying the role of cleaner fish as drivers of grazer diversity and herbivory levels is therefore of pivotal importance.

Herbivory levels sustained by nominally herbivorous reef fishes has profound effects on benthic community structure by influencing algal biomass, enhancing substrate for coral settlement, and modifying sediment deposition (Mumby et al. 2006, Clements et al. 2009, Goatley & Bellwood 2010, Eurich et al. 2018). The relationship between algae and corals is mostly regulated by herbivorous grazers as they can affect algal succession. However, different functional groups of grazers may have opposing effects on succession, which may affect recovery of reefs after disturbance (Emslie et al. 2008, Ceccarelli et al. 2011). Grazers can be classified into 2 broad functional groups: small territorial farming grazers and large roving grazers that usually feed over broad areas (Eurich et al. 2018). The ecological effects and ecosystem functions supported by these different groups are likely to vary depending on their taxonomic composition, distribution, and feeding behaviour.

Territorial farming damselfishes (Pomacentridae) feed on algae, invertebrates, and detritus within their territories, thus modifying the structure of the benthic community (Hata & Ceccarelli 2016). Farming species have been classified into 3 distinct functional groups: intensive, extensive, and indeterminate farmers. These groups differ in the types of algae they maintain, the strength of their defensive and weeding behaviours, and their impact on juvenile corals and the propagation of algal turfs (Emslie et al. 2012, Casey et al. 2015, Hata & Ceccarelli 2016). Variation in the functional composition of farmer assemblages may therefore differentially impact benthic community structure.

Roving grazer fishes, such as surgeonfishes (Acanthuridae), parrotfishes (Labridae), and rabbitfishes (Siganidae), feed on sessile and symbiotic algae, detritus, and other micro-organisms within the epilithic algal matrix (EAM) and sediments (Clements et al. 2009). Roving grazers have been classified into various functional groups according to traits related to food processing (alimentary tract and tooth morphology) and food acquisition (feeding habitat, feeding mode, diet, and schooling behaviour) (Bejarano et al. 2019, Siqueira et al. 2019). The combination of such traits is an indication of each species' role in ecosystem processes, including the cycling of nutrients and material on coral reefs.

Because of their close association with the benthos, grazers are themselves also relatively sensitive to disturbances that affect the benthic community. For example, an increase in the abundance of algal farmers occurred after an outbreak of crown-of-thorn starfish *Acanthaster planci*, whereas reductions occurred after a storm (Emslie et al. 2012). Fish assemblages have also shifted towards more algal-farmer-dominated species after a bleaching event (Cheal et al. 2008, Richardson et al. 2018). Populations of roving herbivores are also influenced by bleaching and storms (Cheal et al. 2008, Emslie et al. 2008), but these effects can depend on fishing pressure (Graham et al. 2007).

Another factor that can cause a similar magnitude of change in the abundance and diversity of coral reef fish is the presence/absence of a key mutualistic partner of many coral reef fishes: the cleaner fish *Labroides dimidiatus*. Cleaner fish remove and eat ectoparasites from client fish, which include most common coral reef fishes (Grutter & Poulin 1998). Experimental removals of a few adult *L. dimidiatus* individuals led to substantial reductions in the abundance and diversity of fishes (Bshary 2003, Grutter et al. 2003, Waldie et al. 2011). Such cleaner-affected species belong to a diverse group of fishes, including territorial and roving grazers (Acanthuridae, Ephippidae, Labridae, Pomacentridae, Siganidae) (Bshary 2003, Grutter et al. 2003, Waldie et al. 2011). Whether the absence of cleaner fish affects distinct functional groups differently, and if the influence is strong enough to impact feeding rates and benthic community structure, remain to be tested. Such information would provide a better understanding of the indirect effects of mutualistic relationships on ecosystem processes and functioning (Mouritsen & Haun 2008, Madin et al. 2010, Sotomayor & Lortie 2015). Importantly, steep decreases in cleaner fish density may occur following extreme weather events such as the consecutive cyclones and El Niño event that affected the Great Barrier Reef in 2016 (Triki et al. 2018). In that case, reduced densities of cleaner fish impacted the behaviours of cleaners and of clients, with cleaners failing to display previously documented behaviours. Although these results herald important ecological consequences of cleaner species loss, a rigorous long-term experimental approach to test the implications for coral reef functioning is currently lacking.

Most territorial and roving grazers engage in cleaning behaviour (Grutter & Poulin 1998), with many seeking cleaners numerous times on a daily basis (Grutter 1995). The rabbitfish *Siganus doliatus*, surgeonfish *Ctenochaetus striatus*, and parrotfish *Chlorurus spilurus*, for instance, seek the cleaner fish

*L. dimidiatus* an average of 144, 108, and 82 times a day, for 32, 22, and 11 min a day, respectively (Grutter 1995). This raises the question of whether time spent at cleaning stations results in reduced foraging activity. For example, the foraging rates of the carnivorous *Hemigymnus melapterus* (Labridae) on reefs with cleaners decrease with increasing frequency and duration of cleaning interactions (Grutter et al. 2002). Hence, it is important to test whether a herbivorous client getting cleaned comes at a cost to the client, as cleaning could reduce foraging opportunities for grazers. If, however, cleaning does not affect foraging activity, then grazing rates can be assumed to be proportional to grazer abundance (but see Steenack 1983, Bellwood et al. 2019, Tebbett et al. 2020).

Here, we asked whether grazing activity is influenced by the functional role of cleaner fish and if the effect is strong enough to drive changes in the coral reef benthos. We tested this question by establishing a field experiment in which cleaner fish were regularly removed (~every 3 mo) from selected patch reefs for 8.5 yr and compared these reefs to nearby unmanipulated controls (Waldie et al. 2011). After this long-term manipulation, on both manipulated and control patch reefs we measured the (1) diversity and abundance of territorial grazers once and roving grazers once at 3 times of the day; (2) cleaning duration and foraging rates (per substratum type) of common roving grazers (*Ctenochaetus striatus*, *Scarus ghobban*, *S. globiceps*, *S. niger*, *S. rivulatus*, *S. schlegeli*, *Siganus doliatus*, and *Acanthurus* spp.); and (3) benthic community structure on the reef and on terracotta settlement tiles (fouling material accumulated over 3.5 mo). We hypothesized that (1) the taxonomic diversity and abundance of territorial and roving grazers would be highest on reefs with cleaner fish; (2) the more time individual roving grazers spent being cleaned, the lower their foraging activity would be; and (3) both benthic community structure on the reef and organic and inorganic weight of fouling material on tiles would differ between reefs with and without cleaner fish.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study was conducted at Lizard Island, Great Barrier Reef, Australia (14° 40' 9" S, 145° 28' 9" E). We used 16 small, spatially isolated patch reefs (3–7 m depth) at 2 sites: in the southern lagoon ('Lagoon'; 11 reefs) and off the research station ('Casuarina Beach'; 5 reefs). The presence of cleaner fish per reef was ini-

tially manipulated between 20 August and 5 September 2000, and has since been maintained involving removals approximately every 3 mo. For more details on reef areas, map of reefs, dates sampled, and number of cleaner fish present or removed, see Waldie et al. (2011). Whether reefs had cleaners present or absent is hereafter referred to as cleaner presence.

### 2.2. Grazer fish diversity and abundance

The diversity and abundance of small territorial grazing fish species was quantified in visual censuses conducted once per reef in April 2009 (Waldie et al. 2011). We only counted them once because, compared with roving counted by a snorkeler, territorial grazers are sedentary, their abundance was not expected to change throughout the day, their relatively high abundance required a significant amount of time to census, and these counts were done by a SCUBA diver with greater time constraints. The abundance per functional group (see below, this Section) per reef, and Simpson's diversity ( $D$ ) index per reef were calculated. Farmers modify the algal community structure in their territory by 'weeding' out undesirable algae and selectively consuming some species (Emslie et al. 2012, Hata & Ceccarelli 2016). They also aggressively defend their territories, curtailing the feeding activities of other herbivorous grazers. Consequently, they can increase the standing crop of algae within their territories, affect algal diversity and algal nitrogen fixation, enhance growth of fouling organisms, and reduce parrotfish bioerosion, which in turn may influence coral survival, recruitment, distribution, and diversity (Emslie et al. 2012, Hata & Ceccarelli 2016). Territorial grazers were categorised into 1 of the 3 functional farming groups (i.e. intensive, extensive, and indeterminate; Hata & Ceccarelli 2016) or as non-farmers (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m643p099\\_supp.pdf](http://www.int-res.com/articles/suppl/m643p099_supp.pdf)). Intensive farmers aggressively defend small territories containing low diversity algal turfs and weed them intensively. Extensive farmers maintain relatively large territories and defend and weed their territories less intensively. The territories of both of these groups are distinguishable from the surrounding area (Hata & Kato 2004). In contrast, indeterminate farmers weed and defend territories much less, with more subtle effects on algal assemblages within territories, and hence their territories are not distinguishable from the surrounding area (Emslie et al. 2012). The  $D$  index of all territorial grazers combined was calculated following Pielou (1969), where 0 indicates low diversity:

$$1 - D = 1 - \sum_{i=1}^s [n_i(n_i - 1) / N(N - 1)] \quad (1)$$

with  $n_i$  being the number of individuals of species  $i$ ,  $N$  being the total number of individuals in the sample, and  $s$  being the number of species in the sample.

The diversity (excluding *C. striatus*; see below, this Section) and abundance of all roving grazer fish species was obtained as above, but counted by snorkelers and not SCUBA divers, 3 times per day per reef, from Waldie et al. (2011). Abundance per functional group and the  $D$  index per reef were calculated as for territorial grazers. Initially, *C. striatus* were counted at the same time as the territorial grazers. However, the counts appeared to be an underestimate (*C. striatus* individuals were only observed on 7 of the 16 reefs in April 2009) compared with previous observations there on the 16 reefs (A. S. Grutter pers. obs.), so these counts were omitted. *C. striatus* were recounted 3 times per day per reef between 18 and 21 December 2012 as for the other roving grazers, but by a SCUBA diver as *C. striatus* can be relatively cryptic and wary (A. S. Grutter pers. obs.). In these second counts, *C. striatus* individuals were observed on all reefs. The 2012 *C. striatus* counts, however, were not included in the  $D$  index as they were counted at a different time. *Melichthys vidua* (Balistidae;  $n = 2$  on control reef 9), although known to eat algae, was not included as its functional role is not well known (Green & Bellwood 2009).

Roving grazers were categorized into 6 ecosystem functional groups (Siqueira et al. 2019) supporting (1) macroalgae removal, (2) turf (algae) removal, (3) sediment removal (including sediment transport and reworking), (4) crevice cleaning, (5) bioerosion, and (6) spongivory. These ecosystem functions were assigned to all species, with some species performing more than one function concurrently (Table S2).

*Acanthurus auranticavus*, *A. blochii*, *A. dussumieri*, *A. nigricauda*, and *A. xanthopterus*, which graze on the EAM, removing algal turfs, sand, and detritus (Choat et al. 2002, 2004), were difficult to distinguish; therefore, they were grouped together and are hereafter referred to as *Acanthurus* spp. This group was considered here as supporting both turf and sediment removal (Table S2). Many parrotfishes graze on the EAM while scraping or excavating the calcareous reef matrix and contributing to sediment removal and bioerosion. Rabbitfishes crop algae, leaving the basal portions intact, and graze on the EAM while feeding mostly within concealed crevices (Choat et al. 2002). They were considered here as supporting turf removal and crevice cleaning (Table S2). *C. striatus* (Acanthuridae) were considered here as principally detritivorous (Clements et al. 2009), capable

of removing sediment (Goatley & Bellwood 2010) (Table S2). *Zebrasoma veliferum* (Acanthuridae), a turf remover and crevice cleaner, was not included with rabbitfishes due to its rarity and classification in a different family, and was omitted (Table S2). Several rare, unidentified Acanthuridae and non-parrotfish macroalgal removers were also omitted. For the abundance of the omitted species, see Text S1 in the Supplement.

### 2.3. Foraging and cleaning behaviour of roving grazers

Foraging and cleaning behaviour of roving grazers were recorded visually by 2 SCUBA divers between 08:30 and 16:30 h over 12 d (29 April–10 May 2009). Observations were done at haphazard times throughout the day, and thus include potential variation in diurnal behaviour. Observations were possible on all reefs except for Reefs 1, 3, and 11 (for map, see Waldie et al. 2011) and focussed on common roving grazers (i.e. *C. striatus*, *Scarus ghobban*, *S. globiceps*, *S. niger*, *S. rivulatus*, *S. schlegeli*, *Siganus doliatus*, and *Acanthurus* spp.). Individual fish were carefully followed from a distance of at least 5 m to avoid interfering with natural behaviours. The number of feeding bites on the reef benthos was recorded per substratum type (i.e. hard coral, dead coral, soft coral, turf algae, fleshy algae, coralline algae, sand, or sponge), and fish total length (TL) was visually estimated to the nearest 1 cm. At the same time that bites were recorded, for all individuals on control reefs only, the duration of each cleaning event involving *L. dimidiatus* was also recorded. Each individual grazer was observed for up to 5 min, or less (median: 4.5 min; 25<sup>th</sup>/75<sup>th</sup> quantiles: 5/3.5 min) if it left the reef during that time period. The sum of the duration of cleaning time per observation was computed. Grazing bites and cleaning duration rates were scaled to bites (or seconds cleaned) min<sup>-1</sup> of observation duration. Mean estimated grazing bites min<sup>-1</sup> m<sup>-2</sup> per fish type, called 'overall bite rate', were calculated by multiplying the mean bite rate min<sup>-1</sup> by the abundance of fish reef<sup>-1</sup>, and dividing this by reef area in m<sup>2</sup>, for the 2 fish types (*Acanthurus* spp. and *C. striatus*) for which fish abundance was also available.

### 2.4. Surveys of reef benthic community structure

Benthic cover was assessed by a SCUBA diver, between 09:30 and 15:00 h over 5 d (24–28 April

2009), using  $1 \times 1 \times 1.5$  cm polyvinyl chloride pipe quadrats divided with 3 vertical and 3 horizontal strings to yield 25 equally spaced (20 cm) intersects where strings crossed. A quadrat was placed at a random point on the reef, and the benthos directly under each string intersect was classified into one of the following categories: hard coral, dead coral, soft coral, turf algae, fleshy algae, coralline algae, sand, or sponge. The number of quadrats per reef was dependent on reef size, with one quadrat for every  $10 \text{ m}^2$  of reef, limited to between 5 and 10 quadrats reef<sup>-1</sup> (total  $n = 124$ ).

## 2.5. Fouling material on settlement tiles

Clean, numbered terracotta tiles ( $19 \times 19 \times 4$  cm) were placed on the reefs on 12–13 May 2009 by researchers using SCUBA gear. Tiles were haphazardly placed on relatively stable (not live hard or soft coral) surfaces on the reefs, with the number of tiles per reef varying depending on reef size (i.e. 1 tile for every  $10 \text{ m}^2$  of reef) and limited to 5–10 tiles reef<sup>-1</sup> ( $n = 124$ ). Tiles were placed on the reef without regard to territories of farming damselfish.

Tiles remaining after 3.5 mo ( $n = 113$ ) were collected over 6 d (25–31 August 2009). This period allowed sufficient time for algal settlement and growth, sedimentation, and herbivory to occur. Tiles were retrieved and transported to the lab inside sturdy, sealed plastic bags. All fouling material was scraped off and filtered on  $62 \mu\text{m}$  plankton mesh together with all the water retained in the corresponding plastic bag. Filters were then dried in a drying oven at  $80^\circ\text{C}$  until weight was reduced by  $<0.01 \text{ g min}^{-1}$  of drying time (i.e. in  $\sim 15$  min), and then weighed. To obtain organic content, samples were burned at  $550^\circ\text{C}$  for 6 h using a Lenton 2250 Watt oven (Heiri et al. 2001). For the initial 11 samples, the entire sample was burned, but these burns were not successful and thus were omitted. A  $0.75 \text{ g}$  subsample resulted in consistent and successful burning, and was used thereafter. The final number of samples successfully burned was 99. Based on the number of tiles per reef, on average each reef was covered by tiles over  $0.22\%$  (SE 0.02;  $n = 99$ ) of its total area.

## 2.6. Statistical analyses

For territorial grazer abundance, a generalized linear mixed-effect model (GLMM) was used with a Poisson distribution, as data involved counts. The

fixed effects of site (Casuarina Beach or Lagoon), cleaner presence (present or absent), and functional group were fitted as categorical fixed factors, with reef area as a fixed continuous factor, and reef as a random factor. We considered site in all analyses as a fixed factor, as they were not selected at random (only these sites were available at this location) and habitat differed between the 2 sites. One site was a shallow lagoon (Lagoon) and the other was a deeper back reef habitat (Casuarina Beach) and therefore we expected there to be differences between them; furthermore, this allowed integration with other data from studies on the same reefs that involved only one of the sites (Grutter et al. 2019, Sikkell et al. 2019). To interpret a significant interaction between site, cleaner presence, and functional group, the analysis was then repeated separately by functional group. The 'lme4' package was used (R Core Team 2012). When present, overdispersion was accounted for by including an observation level random factor in the model (a sequential value starting at 1 up to the total number of observations). This was required for the territorial grazers' full model and the *Acanthurus* spp. only model below (see Text S2 in the Supplement for R coding). The most parsimonious model was selected using the function 'drop1' and a chi-squared test (R Core Team 2012). Separate Wilcoxon rank sum tests, using JMP v.10.0.0 (SAS Institute), were used to test for an effect of cleaner fish presence at each site for (1) the abundance of the intensive farmer group, and (2) the Simpson's taxonomic diversity index for all territorial grazers, as these data did not satisfy the assumptions of the GLMM.

To test whether the abundance of roving grazers was affected by *L. dimidiatus* removals, separate GLMMs for each functional group were required. The effects of site, cleaner presence, and time of day were fitted as fixed categorical factors, with reef area as a fixed continuous factor, and reef as a random factor. The most abundant 'turf and sediment removers' observed on the reefs was the *Acanthurus* spp. complex, so this group was analysed separately. The 'turf remover and crevice cleaners', all Siganidae, were combined (except for *Z. veliferum* and unidentified Acanthuridae, which were excluded; see above) and summed across the 3 times of day to reduce the number of zeros in the data. To test for an effect of cleaner fish presence on the *D* index of roving grazers, the same factors for abundance were used, but with a linear mixed effect model (LME, fit by restricted maximum likelihood estimation [REML] using the 'lme4' package in R version 3.6.1; R Core Team 2019).



To test for an effect of cleaner removals on the roving grazer foraging rates (mean bite rate  $\text{min}^{-1}$ ), a LME model was fit by REML. Cleaner presence, site, and fish species were used as fixed categorical factors, fish TL as a covariate, and reef as a random factor. Only the 5 species that were observed at both sites and in both cleaner presence treatments were included in the analyses.

For data from control reefs, where cleaning by *L. dimidiatus* during the foraging observations was recorded, Spearman's correlations (JMP v.10.0.0) were used to examine the relationships between foraging and cleaning rates and between cleaning rate and fish TL. This correlation was used because the data contained many zeros. Sites were pooled to obtain an adequate sample size for correlation analysis.

To test whether cleaner removals had an indirect effect on benthic community structure on the reef, percent cover of turf algae, live-, soft-, and dead coral, and other (remaining categories combined), we used a permutational multivariate analysis of variance (PERMANOVA) using PERMANOVA+ for PRIMER (Anderson et al. 2008). Cleaner presence and site were fixed factors; reef was a random factor. The response was the proportion of intersects out of 25 per  $\text{m}^2$  quadrat per habitat type. The results were interpreted using the nonmetric multidimensional scaling (nMDS) analysis ordination method obtained using PRIMER 7 (Clarke & Gorley 2015).

A LME model with REML was used to test for an effect of cleaner removals on the  $\log_{10}$ (organic weight of fouling material per settlement tile), with cleaner presence and site as fixed factors, the covariate  $\log_{10}$ (dry weight of fouling material), and reef as a random factor. Including  $\log_{10}$ (dry weight of fouling material) allowed organic weight to be adjusted for this variable. A similar model was used to test for an effect of cleaner presence on  $\log_{10}$ (inorganic weight of fouling material), but without  $\log_{10}$ (dry weight of fouling material) in order to examine unadjusted inorganic (sediment) load per tile. This allowed the effect of cleaners on total sediment load to be examined. Data were  $\log_{10}$  transformed to satisfy the assumption of homogeneity of variance and to linearise the response variable with the covariate.

All statistical analyses, unless otherwise stated, were carried out in R v.2.15.0 (R Core Team 2013) using the 'nlme' package (Pinheiro et al. 2012). For all parametric analyses, quantile–quantile plots of the residuals were examined to check for normality, and plots of the residuals versus the fitted values

were examined to check for homogeneity of variance. In all models, a full model was initially fitted, then any non-significant interaction terms omitted to obtain a final simplified model. As the sample sizes were unequal, Type III sums of squares were used in the linear models, as these are based on unweighted marginal means and thus are not influenced by sample size (Quinn & Keough 2002). All results are presented as raw means  $\pm$  SE, except where least square means ( $\pm$  SE) obtained from the full model were used (using the package 'eemmeans' in R version 3.6.1; R Core Team 2019).

### 3. RESULTS

#### 3.1. Grazer fish diversity and abundance

A total of 18 species (in 9 genera and 2 families) of territorial grazers were identified across all reefs. The vast majority were damselfishes (Pomacentridae, 16 species) (Table S1, Fig. S1). Of the identified species, 0, 3, and 15 were observed only on removal reefs, only at control reefs, or at both removal and control reefs, respectively. For a summary of the effect of cleaner presence, see Table 1. The *D* index for these territorial grazing species did not differ with cleaner presence at the Casuarina Beach site (median, 25<sup>th</sup>/75<sup>th</sup> quantile: with *Labroides dimidiatus*: 0.77, 0.75/0.78; without: 0.83, 0.77/0.89; Wilcoxon rank sum test,  $\chi^2_1 = 0.33$ ,  $p = 0.564$ ) but did at the Lagoon, with diversity being higher on reefs with (0.85, 0.83/0.86) than without *L. dimidiatus* (0.80, 0.61/0.83; Wilcoxon rank sum test,  $\chi^2_1 = 7.50$ ,  $p = 0.006$ ).

The abundance per reef of intensive farming damselfish differed with cleaner presence at the Lagoon (Wilcoxon rank sum test:  $\chi^2_1 = 5.03$ ,  $p = 0.025$ ), with fewer fish on reefs without than with *L. dimidiatus* (Fig. 1a); whereas at Casuarina Beach they were too rare to test for an effect of cleaner removals ( $n = 4$ ; control reef 16). For the remaining farming functional groups, there was a significant interaction between site, cleaner presence, and functional group (GLMM, likelihood ratio test,  $\text{LRT} = 6.84$ ,  $\text{df} = 2$ ,  $p = 0.033$ ) and reef area was significant ( $\text{LRT} = 11.63$ ,  $\text{df} = 1$ ,  $p = 0.0007$ ). When analysed separately for each farming functional group to interpret this interaction, the abundance per reef of extensive farming damselfish differed with cleaner presence ( $\text{LRT} = 17.04$ ,  $\text{df} = 1$ ,  $p < 0.0001$ ), with fewer fish on reefs without than with *L. dimidiatus* at both sites. There were also more fish at the Lagoon than Casuarina Beach ( $\text{LRT} = 10.27$ ,  $\text{df} = 1$ ,  $p = 0.001$ ) (Fig. 1b); abundance

Table 1. Fish diversity and abundance in relation to the effect of cleaner fish treatment (present or absent). (+) Higher fish diversity or abundance on reefs with cleaners relative to reefs without at the site(s); NA: fish too rare to analyse; C: cleaner presence; S: site; T: time of day; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

Fish functional group sampled	Response measured	Effect tested	Casuarina Beach p-value	Cleaner presence effect	Lagoon p-value	Cleaner presence effect	Casuarina and Lagoon p-value	Cleaner presence effect
<b>Territorial grazers</b>								
All territorial grazers	Diversity	C	0.564		0.006**	+		
Intensive	Abundance	NA	NA		0.025*	+		
Extensive	Abundance	C					<0.001***	+
Indeterminate	Abundance	C × S				+ <sup>b</sup>	0.056	
Non-farmer	Abundance	C × S		+			0.037*	
<b>Roving grazers</b>								
All roving grazers	Diversity	C					0.125	
<i>Acanthurus</i> spp.	Abundance	C × T					0.024*	+ <sup>a</sup>
Rabbitfishes	Abundance	C					0.056	+ <sup>b</sup>
Parrotfishes	Abundance	C					0.015*	+
<i>Ctenochaetus striatus</i>	Abundance	C					0.419	
<sup>a</sup> Significant cleaner presence treatment effect occurred in the morning and midday, but not in the afternoon								
<sup>b</sup> Marginally significant cleaner presence treatment effect								

was positively related to reef area (LRT = 7.38, df = 1,  $p = 0.007$ ). There was a marginally significant interaction between site and cleaner presence on abundance of indeterminate farmers (LRT = 3.67, df = 1,  $p = 0.056$ ), due to a tendency toward fewer fish on reefs without than with *L. dimidiatus* at the Lagoon but not at Casuarina Beach (Fig. 1c). There was an interaction between site and cleaner presence for the abundance of non-farming grazers (LRT = 4.36, df = 1,  $p = 0.037$ ), with fewer fish on reefs without than with *L. dimidiatus* at Casuarina Beach but no effect of cleaner removals at the Lagoon (Fig. 1d). Non-farmer abundance was positively related to reef area (LRT = 9.40, df = 1,  $p = 0.002$ ).

Of the 26 types of roving, grazing fishes found across all reefs, 23 were identified to species, 2 only to genus, and 1 only to family (total 9 genera and 4 families; Table S2, Fig. S2). For a summary of the effect of cleaner presence, see Table 1. The *D* index for these fishes did not differ with cleaner presence (LRT = 0.483, df = 1,  $p = 0.487$ ), with the diversity being  $0.326 \pm 0.098$  (least square mean  $\pm$  SE) on reefs without in contrast to with *L. dimidiatus* ( $0.404 \pm 0.088$ ). The effects of site (LRT = 0.462, df = 1,  $p = 0.496$ ) and time of day (LRT = 0.196, df = 2,  $p = 0.906$ ) were also not significant. However, roving grazer diversity increased with reef area (LRT = 3.988,  $p = 0.046$ ).

The most abundant turf and sediment removers observed on the reefs belonged to the *Acanthurus* spp. complex (Fig. S2). There was a significant interaction between cleaner presence and time of day on *Acanthurus* spp. (LRT = 9.46, df = 3,  $p = 0.024$ ), with fewer fish on reefs without in contrast to with *L. dimidiatus* in the morning and midday, but not in the afternoon (Fig. 2). There was also an interaction between site and time of day due to a difference between sites at midday and afternoon (Fig. 2b,c) but not in the morning (LRT = 16.53, df = 3,  $p = 0.001$ ; Fig. 2c). The turf-removers and crevice-cleaners, all Siganidae (but see Table S2), belonged to 7 rabbitfish species (Fig. S3) and, when summed over the 3 times, their abundance was marginally non-significant with respect to cleaner presence, with a tendency towards fewer fish on reefs without than with *L. dimidiatus* (LRT = 3.55, df = 1,  $p = 0.056$ ); there was a positive relationship with area (LRT = 12.71, df = 1,  $p = 0.0004$ ).

A total of 12 parrotfishes (Labridae) belonging to the category turf and sediment remover were observed on the reefs (Table S2, Fig. S2). Their abundance per reef differed with cleaner presence (LRT = 5.91, df = 1,  $p = 0.015$ ), with fewer fish on reefs without than with *L. dimidiatus*, and did not differ with site (LRT = 3.78, df = 1,  $p = 0.052$ ) or among times of day (LRT = 2.83, df = 2,  $p = 0.244$ ; Fig. 3).

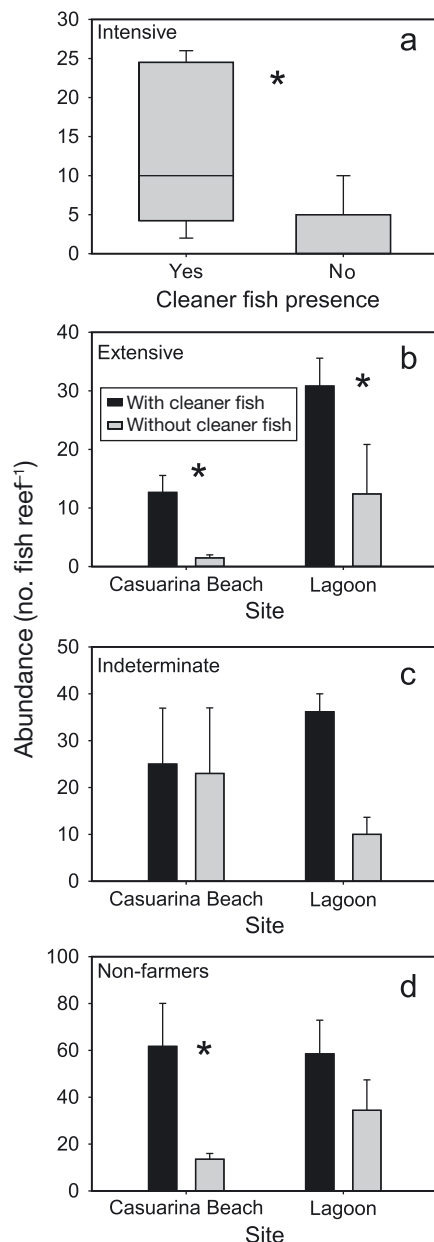


Fig. 1. Mean (SE) abundance of territorial grazers on reefs with and without cleaner fish at Casuarina Beach and Lagoon, according to farming functional group: (a) intensive (note this was only analysed at Lagoon; data are summarized in boxplots), (b) extensive, (c) indeterminate, and (d) non-farmers. Boxplots show the median, 25<sup>th</sup> and 75<sup>th</sup> quantiles, and 90<sup>th</sup> quantiles. \* $p < 0.05$  for cleaner presence treatment

In 2012, the abundance of the sediment remover *Ctenochaetus striatus* per reef did not differ according to cleaner presence (LRT = 0.65, df = 1,  $p = 0.419$ ), site (LRT = 0.05, df = 1,  $p = 0.820$ ), or time of day (LRT = 3.07, df = 2,  $p = 0.215$ ; Fig. S4). Its abundance per reef was positively related to reef area (LRT = 5.95, df = 1,  $p = 0.015$ ).

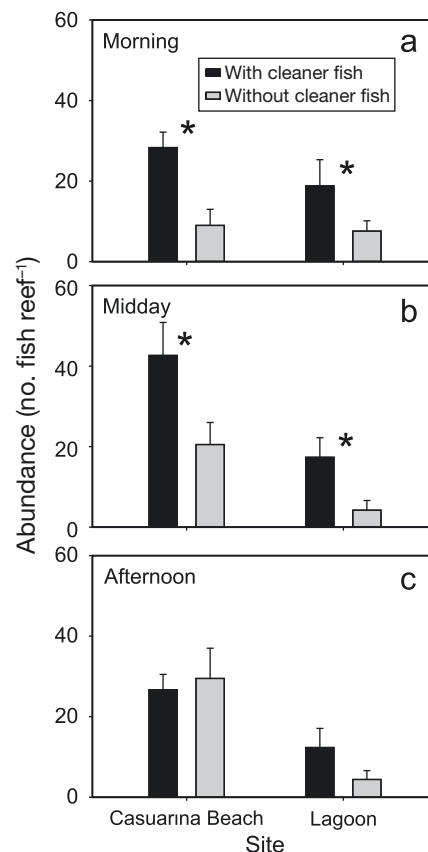


Fig. 2. Mean (SE) abundance of roving turf- and sediment-removing *Acanthurus* spp. surgeonfishes on reefs with and without cleaner fish at Casuarina Beach and Lagoon in (a) morning, (b) midday, and (c) afternoon. \* $p < 0.05$  for cleaner presence treatment

### 3.2. Roving grazer fish foraging behaviour

The foraging rate of roving grazers (*Acanthurus* spp., *C. striatus*, *Scarus globiceps*, *S. rivulatus*, *Siganus dolia*) was not affected by cleaner removals (LME, REML:  $F_{1,9} = 2.00$ ,  $p = 0.190$ ) and was comparable between sites ( $F_{1,9} = 1.87$ ,  $p = 0.205$ ; Table S3), but did differ among species ( $F_{1,61} = 2.54$ ,  $p = 0.048$ ; Fig. 4), and decreased with fish size ( $F_{1,61} = 4.70$ ,  $p = 0.034$ ) (Table S3). *Acanthurus* spp. had the lowest total bite rates ( $3 \pm 0.6$  bites min<sup>-1</sup>), and were observed feeding largely on sand/detritus directly adjacent to the patch reefs, and on turf algae, coralline algae, and fleshy algae (once) (Fig. 4). *C. striatus*, in contrast, had the highest total bite rate ( $17 \pm 1.4$  bites min<sup>-1</sup>), and fed largely on turf algae; the parrotfishes and the rabbitfish also largely fed on turf algae (Fig. 4). The overall bite rate per reef area (bites min<sup>-1</sup> m<sup>-2</sup>) by all *Acanthurus* spp. on reefs with and without cleaners was  $0.5 \pm 0.05$  and  $0.2 \pm 0.05$ , respectively; for all *C. striatus* it was  $0.9 \pm 0.1$  and  $0.8 \pm 0.1$ , respectively.



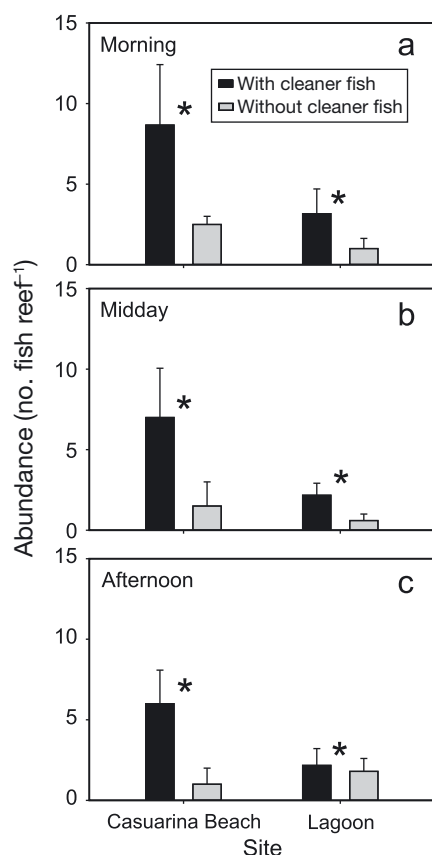


Fig. 3. Mean (SE) abundance of roving turf- and sediment-removing parrotfishes on reefs with and without cleaner fish at Casuarina Beach and Lagoon in (a) morning, (b) midday, and (c) afternoon. \* $p < 0.05$  for cleaner presence treatment

### 3.3. Cleaning activity on roving grazers

The 5 roving grazer species were observed being cleaned in 25, 41, 29, 33, and 0% of all foraging observations, respectively, for *Acanthurus* spp., *C. striatus*, *Scarus globiceps*, *S. rivulatus*, and *Siganus doliatus*. For the species observed being cleaned most frequently (i.e. with the largest sample size), *Acanthurus* spp. and *C. striatus*, cleaning rates ( $s\ min^{-1}$ ) were not correlated with foraging bites (Spearman's correlation,  $\rho = -0.085$ ,  $n = 24$ ,  $p = 0.692$ ;  $\rho = 0.054$ ,  $n = 22$ ,  $p = 0.812$ , respectively; for the remaining species, samples sizes were too small [ $n = 7, 6, 5$  respectively] to conduct this test). Cleaning rate and fish TL within a species were correlated for *Acanthurus* spp. (Spearman's correlation,  $\rho = 0.361$ ,  $p = 0.008$ ) but not *C. striatus* ( $\rho = -0.232$ ,  $p = 0.299$ ). Mean (SE) cleaning rates were 22 (0.5) and 17 (0.4) s per 5 min for *Acanthurus* spp. and *C. striatus* that were cleaned, or 7 and 6% of their total time budget, respectively.

### 3.4. Percent cover of the reef benthos and fouling material on tiles

Nine years after the presence of cleaner fish per reef was manipulated, there was no effect of cleaner presence on the composition of the benthos, when measured using the percent cover of 5 benthic categories (PERMANOVA: pseudo- $F = 0.90962$ ,  $p = 0.444$ ; Fig. 5a, Table S4). There was, however, an effect of site on the benthic composition (pseudo- $F = 9.2846$ ,  $p = 0.001$ ). The effect of site, when interpreted using nMDS plots, was largely due to a higher percent cover of soft coral at Casuarina Beach compared with the Lagoon (Fig. 5b).

Tiles were largely covered by a film of sediment, micro-algae, and detritus. Organic weight ( $\log_{10}$ ) of fouling material on settlement tiles did not differ with cleaner presence ( $F_{1,11} = 0.006$ ,  $p = 0.938$ ) or site ( $F_{1,11} = 2.07$ ,  $p = 0.177$ ), but increased with the covariate dry weight ( $\log_{10}$ ) ( $F_{1,84} = 208.03$ ,  $p < 0.0001$ ; Fig. 6). The inorganic weight ( $\log_{10}$ ) also did not vary with cleaner presence ( $F_{1,11} = 0.85$ ,  $p = 0.377$ , removals: 6.92, 1.72/1.38 g; controls: 5.36, 0.98/0.83 g; back-transformed mean +SE/-SE) and site ( $F_{1,11} = 0.94$ ,  $p = 0.353$ ).

## 4. DISCUSSION

### 4.1. Summary

Using reefs where cleaner fish *Labroides dimidiatus* were experimentally manipulated for 8.5 yr, we determined whether the diversity and abundance of their grazing fish clients from various functional groups differed with cleaner removals, and if so, whether this subsequently translated into an effect on the benthic community that the clients farm and or graze upon. Of our 3 predictions, only the first—that the abundance of territorial and roving grazers should be higher on reefs with cleaner fish—was supported. Where cleaner fish were absent, fish abundance was reduced substantially for many territorial and roving grazing functional groups. The second prediction—that foraging activity of roving grazers should decrease with increasing time spent being cleaned—was not supported, as individual foraging rates did not differ with cleaner presence or with cleaning duration where cleaners were present. This suggests that the cleaners' grazing pressure on the reef is therefore proportional to their abundance on the reef, as there are no costs to foraging rates associated with being cleaned on reefs with cleaners.

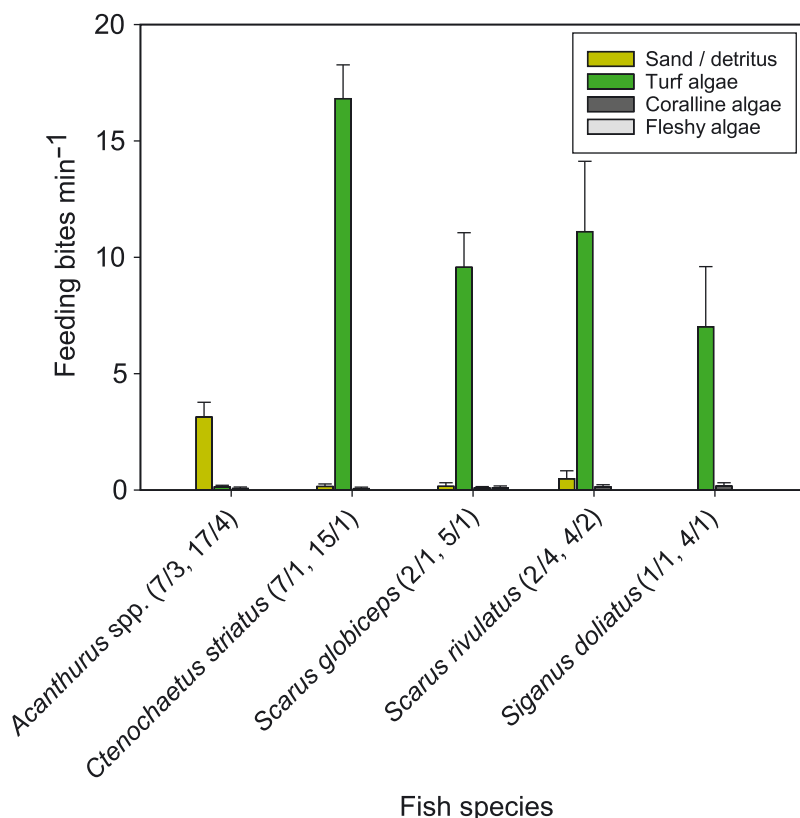


Fig. 4. Mean (SE) number of feeding bites  $\text{min}^{-1}$  by individual fish in each benthic habitat type for the 5 most common roving grazer fishes (number of observations for reefs with/without cleaners at Casuarina Beach, Lagoon, respectively)

Finally, the third prediction—that the natural benthic habitat and growth of fouling material should differ with cleaner presence/absence—was not supported, as the composition of the natural benthos and amount of fouling material on settlement tiles did not differ with cleaner presence. Therefore, despite there being fewer grazers, and thus lower farming and or feeding interactions with certain benthic substrates where cleaners were removed, no associated differences in the benthic community were detected.

#### 4.2. Fish diversity and abundance

Diversity was higher on reefs with cleaners than on those without, for territorial grazers at the Lagoon site only. For roving grazers, diversity was not affected by cleaner presence. Thus, observed increases in fish abundance for roving grazers (see below, this Section) were generally spread across multiple species and not due to increased numbers in a few species

only, as appears to be the case for territorial grazers.

Territorial grazer abundance was reduced on removal reefs compared with controls at one or both sites for intensive farmers, extensive farmers, and non-farmers, but not for indeterminate farmers, although the latter showed a tendency to be lower on reefs without cleaners at one site (Fig. 1). Intensive farmers cultivate a monospecific turf and keep out macroalgae, while extensive farmers cultivate a mix of filamentous and macroalgae turf (Ceccarelli 2007). Thus, it would be predicted that more area should be farmed and thus the percent cover of algae should be higher on reefs with cleaners. However, territory sizes vary among farming species, and competition with nearby individuals or other fish in the community and the amount of food availability may vary with fish density, which may affect territory size (Grant 1997, Ceccarelli et al. 2006). Non-farmer grazers largely feed on algae (Table S1) and so would be predicted to reduce algal cover on reefs with cleaners. How the apparent opposing pressures on algae of farmers and non-farmers interact and influence the benthos remains unclear.

The foraging behaviour of farmers was not quantified due to time constraints. Future studies of their behaviour, for example, their territory size, individual cleaning rates, and foraging bites off the benthos and settlement tiles, may reveal whether their behaviour differs with cleaner presence.

Compared with the other roving grazer groups, the turf and sediment remover *Acanthurus* spp. complex was the most abundant type, but it should be noted it consisted of 5 surgeonfish species (*A. auranticavus*, *A. blochii*, *A. dussumieri*, *A. nigricauda*, and *A. xanthopterus*) (Fig. S2). Roving grazer abundance was reduced on removal reefs for *Acanthurus* spp. in the morning and midday but not in the afternoon (Fig. 2). The species in this group tend to graze over sand and sediment and feed on a combination of algae and detritus (Choat et al. 2002, 2004). Over the reef substrata *Acanthurus* spp. likely also feed on EAM and, because of its high abundance, they could consume significant amounts of algal turf. Thus, they would be predicted to reduce algal abundance and detritus. However, *Acanthurus* spp. tended to feed on sand/detritus

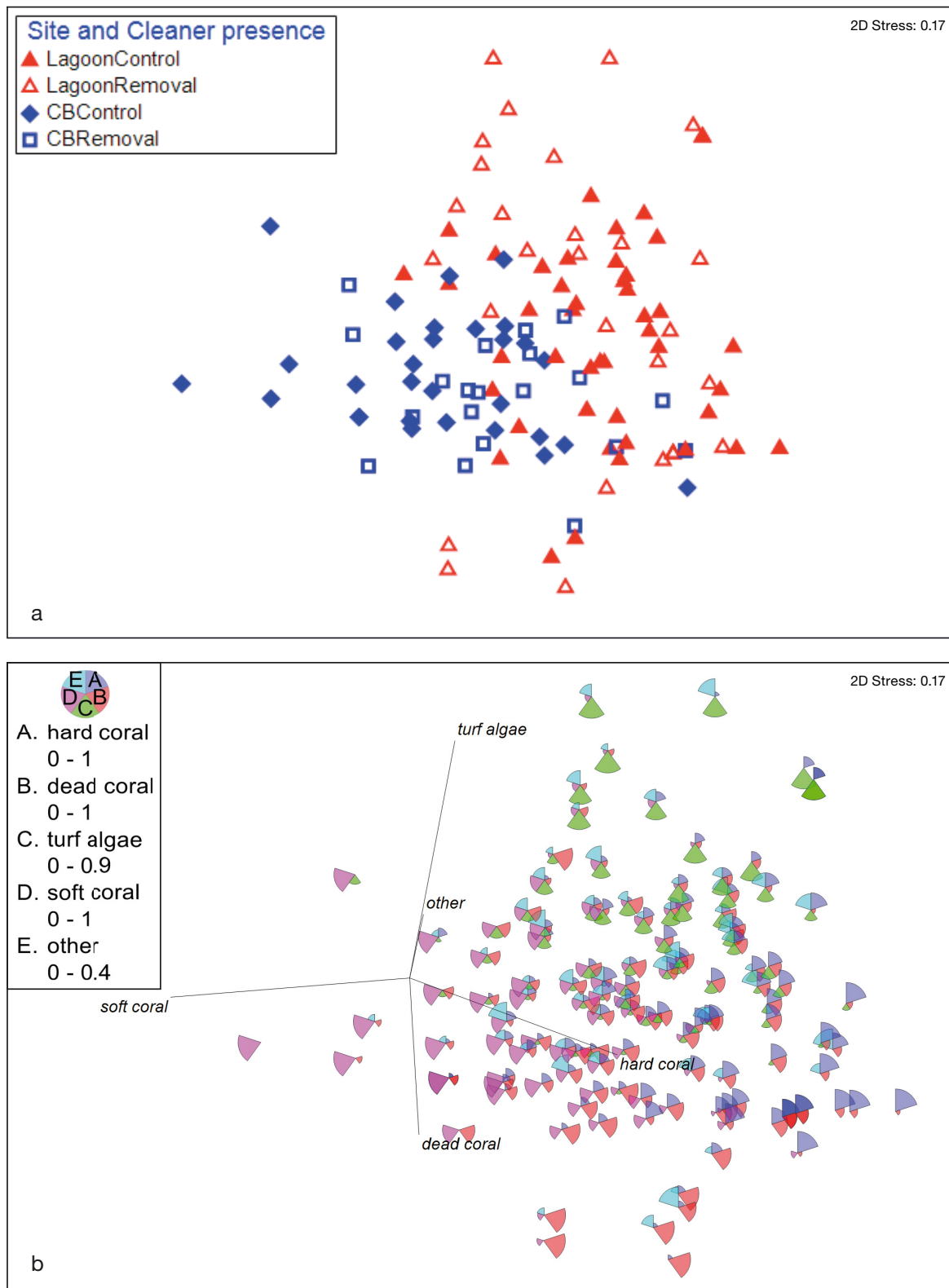


Fig. 5. Non-parametric multidimensional scaling analysis. Each sample is labelled by (a) site and cleaner fish presence (control: reefs with cleaners; removal: reefs with no cleaners) and (b) by benthic type using segmented balloons representing the proportion of each benthic type per sample; key shows minimum and maximum proportions per benthic type

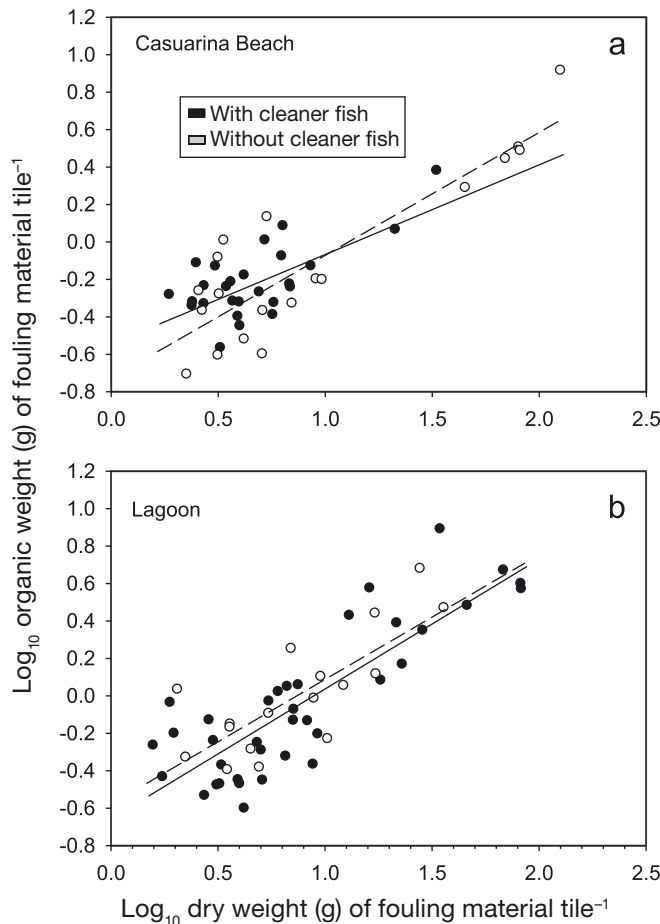


Fig. 6. Organic weight ( $\log_{10}$ ) relative to the initial dry weight ( $\log_{10}$ ) of the same sample for fouling material per settlement tile ( $19 \times 19 \times 4$  cm surface) on reefs with (solid circles, solid lines) and with no (open circles, dotted lines) cleaner fish at (a) Casuarina Beach and (b) Lagoon

directly adjacent to the patch reefs. The fouling material growing on the settlement plates consisted largely of a layer of a matrix of sediment with detritus within it, which would have been a potential food source for *Acanthurus* spp. The extent to which fish fed on the tiles was not quantified, due to the rarity of this behaviour occurring, given that the mean percent of total reef area covered by tiles was only 0.22%. Note that at least one of these species (*A. dussumieri*), which shelters on reefs during the day at Lizard Island, is nocturnal and disperses over a large distance at night (Khan et al. 2017). It is possible that reefs with cleaners represent preferred daytime resting locations for *Acanthurus* spp., with nocturnal foraging occurring elsewhere. If so, the daytime abundance of *Acanthurus* spp. would have minimal effect on the benthic composition of sampled reefs. Another turf and

sediment remover grazer group, consisting of 12 parrotfish species, occurred in relatively lower numbers than did *Acanthurus* spp. (Fig. 2). Their abundance was also reduced on removal reefs, and at all times of day (Fig. 3). Some parrotfish species also bioerode some of the substratum while feeding (Table S2) (Bellwood & Choat 1990). All intensely graze on epilithic algal turf, and occasionally sediment and live coral.

In contrast, turf-removing and crevice-cleaning rabbitfishes (Fig. S3) and the sediment remover surgeonfish *Ctenochaetus striatus* (Fig. S4) were not significantly affected by cleaner presence, although the former showed a tendency towards lower abundance on reefs with cleaners. Rabbitfishes, which had low abundances like those of parrotfishes (Fig. S2), feed intensively on epilithic algal turfs and limit macroalgae (Green & Bellwood 2009). Although *C. striatus* was relatively less abundant compared with the *Acanthurus* spp. (a 5 species complex) and parrotfishes (12 species) groups (Fig. S2) which were affected by cleaner presence, *C. striatus* was the most abundant single roving grazing species. Although they were counted later in 2012, they are long-lived (maximum 37 yr; Trip et al. 2008) so their abundances are likely to have been similar in April 2009 when all the other fishes were counted. *C. striatus* also had a higher bite rate than that of *Acanthurus* spp. All *C. striatus*, therefore, took more overall bites off each reef. *C. striatus* brush detritus from algal turf, removing organic detritus, microorganisms, and inorganic sediment (Tebbett et al. 2017a). Therefore, they may facilitate algal growth (and thus herbivory) and also the establishment of coral. By defecating off the reef, *C. striatus* also move sediment off the reef. Hence, they play a key role in biological sediment flux (Tebbett et al. 2017a). The numerical dominance of the single species *C. striatus* makes it one of the most likely candidate roving species for influencing the benthos on the experimental reefs, and suggests that it could overpower effects of other functional groups.

Despite the differences between sites, both in the form of habitat (lagoon or back reef) and abundances of some functional groups found here, the effect of cleaner removals on the abundance of fish across functional groups tended to be consistent at both sites. When abundance and diversity were affected at one site only, this tended to be at the Lagoon site—a site where more reefs were also sampled and diversity was higher for territorial grazers.

### 4.3. Roving grazer foraging behaviour

The foraging bite rates of individuals of common roving grazers belonging to 4 different grazing functional groups (*Acanthurus* spp., *C. striatus*, *Scarus globiceps*, *S. rivulatus*, *Siganus doliatus*; Table S2) differed among species but not with cleaner presence (Fig. 4). The importance of this result is that their bite rate can be assumed to be proportional to their abundance on the reef. Except for *Acanthurus* spp., which were observed mainly feeding on sand and detritus and had the lowest bite rate ( $3 \pm 0.6$  bites  $\text{min}^{-1}$ ), the other species largely fed over turf algae at a relatively similar rate, though *C. striatus* had the highest rate ( $17 \pm 1.4$  bites  $\text{min}^{-1}$ ).

When the bite rate per reef area was calculated taking into account the abundance of all the individuals per reef (i.e. the 'overall bite rate'), the overall bite rate of all *Acanthurus* spp. was lower on reefs without cleaners than with them, implying that their grazing pressure on the benthos should also be lower on reefs without cleaners. In contrast, the overall bite rate for *C. striatus* did not differ with cleaner presence. This implies *C. striatus*' grazing effect on the benthos should not be affected by cleaner presence. Its higher bite rate, compared with *Acanthurus* spp. regardless of cleaner treatment, suggests *C. striatus* could have obscured any cleaner presence effect on *Acanthurus* spp. grazing rates. However, it should be noted that this does not account for the negative effect of size on bite rates observed here across all species, and that *Acanthurus* spp. are larger than *C. striatus*. Furthermore, although larger fish take fewer bites, they likely also take larger bites and thus have a greater impact on the benthos than smaller fish, which could compensate for the lower bite rates of larger species like *Acanthurus* spp. Thus, the larger *Acanthurus* spp., although foraging at a lower rate than the relatively smaller *C. striatus*, could also play an important role in overall grazing pressure. Thus, simply considering 'overall bite rate' may artificially inflate the importance of smaller fishes. While territorial damselfishes can modify the foraging patterns of roving grazers by excluding them from their territories (Hata & Ceccarelli 2016), despite the greater abundance of some of these territorial damselfishes on reefs with cleaners, individual roving grazers' foraging rates were not reduced on reefs with cleaners. Furthermore, the abundance of some roving grazers was higher on reefs with cleaners despite there being more territorial fishes there also.

### 4.4. Roving grazers: foraging and cleaning

On control reefs, foraging rate was not correlated with cleaning time for 2 roving grazer species (*Acanthurus* spp., *C. striatus*). Indeed, they often continued to feed while being cleaned (P. A. Waldie pers. obs.). Therefore, time spent being cleaned did not appear to come at a cost of reduced bite rate. This further supports the above finding that individuals' foraging rates do not differ with cleaner presence. *Acanthurus* spp. ( $22 \pm 0.5$ ) and *C. striatus* ( $17 \pm 0.4$ ) had similar combined cleaning durations (s per 5 min of observation) which comprised 7 and 6% of individuals' total time budgets observed on the reef, respectively; hence, they spent relatively little time being cleaned. This is likely to be different for more site-attached cleaners, such as Caribbean cleaner gobies (Sikkel et al. 2004).

The findings that individuals foraged at the same rate regardless of cleaner presence, and that if they were cleaned, it did not appear to reduce the time they spent foraging, suggest that changes in grazer abundance should result in changes in grazing pressure on the benthos. Hence, reefs with *L. dimidiatus* (and thus more of some grazers) should have been exposed to more grazing pressure from those grazers. Indeed, estimated overall bite rates  $\text{min}^{-1} \text{m}^{-2}$  by *Acanthurus* spp. were higher on reefs with cleaners than on those without.

While territorial farmers' foraging rates and cleaning behaviours were not investigated due to time constraints, their interaction with the benthos is complex (Hata & Ceccarelli 2016). Furthermore, they are likely cleaned less often than roving grazers, as similar Great Barrier Reef species (i.e. other damselfishes) are cleaned less frequently than some roving grazers (i.e. *C. striatus*; Grutter 1995, P. A. Waldie et al. unpubl. data). In the Caribbean, whether territorial damselfish are cleaned depends on whether there are cleaning stations nearby (Sikkel et al. 2004). Even travelling short distances (<2 m) from the territory appears to be costly to these damselfish due to attacks by conspecific territory holders and territorial intrusions.

### 4.5. Natural reef benthos

The composition of the natural benthos (percent cover of turf algae, soft-, hard-, and dead coral, and other items) did not differ with cleaner presence. Since roving grazers mostly foraged on turf algae, as did non-farmer grazers, this benthic category was



predicted as being the most likely to be indirectly reduced on reefs with cleaner fish. Yet this clearly did not occur. However, it should be noted that farming species tend to enhance various algal species (Hata & Ceccarelli 2016), so it was also predicted that such farmed algae should be higher on reefs with cleaner fish. Thus, while high numbers of roving grazers on controls might remove algae, higher numbers of territorial farmers might enhance it and in doing so, possibly compensate for its removal. However, interactions among algal species and their responses to grazing are highly complex (Green & Bellwood 2009, Hata & Ceccarelli 2016). It is likely that any relationships between cleaners and the benthos involve multiple level interactions. Therefore, this complexity and the multiple drivers involved could obscure any potential cleaner effect. Alternatively, the decrease in grazers observed may be under the threshold where they produce an ecologically significant effect on the benthic composition. No evidence of a change in the benthos could also be due to opposing effects of different functional groups of grazers. Additionally, other ecological processes (e.g. algal–coral interactions) may be more important than grazing as drivers of benthic composition.

Algal growth dynamics and turnover rate may also be more important than simply measuring their percent cover at one point in time. Indeed, the turnover rate of turf algae on coral reefs can be extremely high, their density and height may vary, and the species compositions of algae and fish and the interactions among them likely also vary (e.g. Hoey & Bellwood 2010, Hurd et al. 2014, Hata & Ceccarelli 2016, Tebbett et al. 2017a). These factors would make it difficult to detect a disturbance effect. Future studies should better quantify algae and increase the taxonomic resolution of all benthic organisms.

#### 4.6. Fouling material on settlement tiles

Settlement tiles used as substitutes for benthic surfaces were initially homogeneous, unlike the natural benthos which was heterogeneous and inhabited by various organisms, so they allowed us to sample the effect of cleaners on identical surfaces free of fouling organisms. After 3.5 mo, the living fouling material consisted largely of a mat of sediment and detritus along with the microorganisms living within this matrix. Both the organic and inorganic weights of fouling material were unaffected by cleaner presence. The organic component likely consisted of detritus and associated microorganisms, whereas the

inorganic component involved sediment including sand. These components are essential to understanding detrital and sediment flux on coral reefs (Purcell & Bellwood 2001). The organic weight of material per tile was positively correlated with the initial dry weight of the sample (organic plus inorganic weight) and this relationship was not affected by cleaner presence. This indicates that the proportion of organic material in the fouling material was not affected by cleaner presence. Furthermore, the inorganic weight per tile was also unaffected by cleaner presence.

Detritivores such as *Acanthurus* spp. and *C. striatus* feed on material similar to that found on tiles (Choat et al. 2002, 2004, Tebbett et al. 2017a). Yet despite the estimated higher bite rate per reef area of all *Acanthurus* spp. on reefs with cleaners, and that parrotfishes (which are known to transport sediment off reefs; Bellwood 1996) were also more abundant on reefs with cleaners, no reduction in organic (detritus) or inorganic (sediment) material on the tiles was detected on reefs with cleaners. *C. striatus* also transport sediment off the reef (Goatley & Bellwood 2010). While their abundance was not affected by cleaner presence, their bite rate per reef area was higher than that of *Acanthurus* spp. This uniform foraging pressure exerted by *C. striatus* on reefs with and without cleaners could have overpowered other species' impacts on sediments. While *C. striatus* is very sensitive to increasing sediment loads within the EAM (Tebbett et al. 2017b), the amount on tiles was within the range that causes little suppression of detritivory (Tebbett et al. 2017b). Therefore, whether or not cleaner presence is an indirect biological mechanism mediating sediment flux on coral reefs remains unclear.

## 5. CONCLUSIONS

The key question in this study was: To what extent does the presence of cleaner fish and its effect on the distribution of their client fish indirectly influence the benthic community? The answer appears to be that, for this system, the abundance of fishes that farm and/or graze on the benthos was negatively impacted by the long-term removal of the cleaner fish *Labroides dimidiatus*, yet this did not indirectly lead to measurable changes in the benthos. In light of the lack of an indirect relationship between cleaners and the benthos, we suggest that a range of complex mechanisms (e.g. involving environmental effects and interactions among benthic organisms) may play a stronger direct role in shaping benthic com-

munity structure. While it is generally assumed that higher abundances of key herbivorous fishes translate to more function (i.e. grazing pressure on the benthos), this assumption is increasingly being questioned (Steneck 1983, Bellwood et al. 2019, Tebbett et al. 2020). Instead, feeding by fishes can be more heterogeneous than assumed; i.e. fewer herbivorous fishes does not necessarily mean less grazing pressure, as found in this study, suggesting the link between the abundance of herbivores and impact on the benthos is tenuous at this site.

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