



Indirect effects of cleaner fish *Labroides dimidiatus* on fish grazing per reef area and benthic community structure

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Abstract

Grazing fishes farm algae, and consume algae, detritus and sediment and consequently differentially modify benthic communities. Manipulations of cleaner fish *Labroides dimidiatus* on reefs show that cleaners affect fish abundance differently according to grazer functional group. Accordingly, whether reefs are grazed differently, with consequences for the benthos (fouling material tile⁻¹), was tested using reefs kept free of *L. dimidiatus* for 10 years compared with undisturbed control reefs. We recorded on video the grazing density (bites tile⁻¹ h⁻¹ reef⁻¹) on settlement tiles and the natural benthos (roving fishes only), according to territorial algal farmer (Pomacentridae) and roving grazer (Acanthuridae, Labridae, Siganidae) functional groups, and measured the accumulation of fouling material tile⁻¹ after 10 months. Grazing density on tiles (dominated by ‘indeterminate’ farmers, and roving ‘sediment-removing’ detritivore *Ctenochaetus striatus*) and the natural benthos (dominated by *Ct. striatus* and other grazers) was not measurably affected by cleaner presence. The composition of fouling material (dominated by detritus > turf algae > sediment > other) and organic and inorganic dry weight of material tile⁻¹ were also not measurably affected by cleaner presence. This points to resilience of the benthic community to loss of cleaners. The likely complex interactions between cleaner fish presence, grazer abundance and mobility, and the often-opposite effects of territorial farmers and roving grazers on the benthos underscore the challenge in determining indirect effects of cleaners on benthic community structure. However, a lack of cleaners has negative ramifications for fish populations and physiology and thus their loss remains problematic for client fishes.

Keywords Herbivory · Coral reef ecology · Fish behaviour · Cleaning symbiosis

Introduction

All species are involved in complicated webs of ecological interactions. A continuing challenge in ecology is to untangle the functions species perform in shaping these webs. This involves identifying the links among species, how they affect each other, and what happens when the functions they provide are altered or lost. Key species and functional groups of species perform ecological processes that are disproportionately important in maintaining an ecosystem’s function (Wolfe et al. 2021). Many ecological interactions are indirect

ones, where the impact of one organism on another depends upon a third party. Indirect effects can modify species interactions, including predation, grazing, competition, parasitism, and mutualism (Bernot and Lamberti 2008; Bruno et al. 2003; Grutter and Irving 2007; Malmqvist 1993; Soluk and Collins 1988; Stachowicz 2001; Wootton 1994).

Coral reefs are highly complex systems, with many trophic levels where a change in one level can influence another (Elmhirst et al. 2009; Munday et al. 2009). Grazing by fishes, predation, and many symbioses are key ecological processes involving trophic interactions that contribute to both habitat (e.g., bioerosion, calcification) and production (e.g., fisheries, nutrient cycling) functioning on coral reefs (Houk and Musburger 2013; Vermeij et al. 2010; Wolfe et al. 2021). Most grazing fishes are not strictly herbivorous, but also ingest detritus or animal matter (Choat et al. 2002). Grazers are often grouped into large roving grazers, which forage across large areas and reduce algal growth, and small territorial ‘farmers’ that defend rich algal turfs against

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roving grazers and harvest algae inside the territory. Both groups influence benthic community structure in different ways (Ceccarelli 2007; Clements et al. 2009; Eurich et al. 2018; Goatley and Bellwood 2010; Mantyka and Bellwood 2007; Mumby et al. 2006).

The influences of grazers on the benthos has often been predicted using functional groups (Wolfe et al. 2021). Territorial farming species have been grouped into ‘intensive’ and ‘extensive’ farmers, according to the composition of their farms (mixed culture vs monoculture), their behaviour (e.g., weeding, excluding other grazers) and territory size, and into ‘indeterminate’ farmers (farms are not readily distinguished) (Hata and Ceccarelli 2016). Roving grazers have been grouped according to what they remove (e.g., turf algae, sediment, sponge; Bejarano et al. 2019; Siqueira et al. 2019). Variation in grazing rates is associated with changes in the substrate grazed upon (Bonaldo and Bellwood 2011; Bruggemann et al. 1996). Algal farmers and other grazers, by interacting with algae, can also indirectly impact other organisms such as urchins or corals (Graham and Nash 2013; White and O'Donnell 2010).

Mutualisms structure many ecological communities (Palmer et al. 2015). Their interactions can directly affect the fitness of individuals, and thus their local diversity and abundance, which in turn can influence trophic cascades (Palmer et al. 2015; Pringle and Gordon 2013). Services or goods traded by partners in mutualistic interactions determine the outcome of direct interactions (Bronstein 1998, 2015). But the indirect consequences of their outcomes on other organisms is relatively unexplored. Exclusion experiments show that services exchanged can affect the abundance of a third party (Del-Claro and Oliveira 2000; Grutter et al. 2018). For example, exclusion experiments show that ant presence reduces the abundance of the enemies of honeydew-producing tree-hopper (Membracidae) on host plants, and ants' protection services increase tree-hopper survival and the reproductive output of females (Del-Claro and Oliveira 2000).

On coral reefs, a common mutualistic interaction involves small-bodied fishes or crustaceans cleaning larger fishes, the clients. A client fish seeks cleaners for their ectoparasite-removal and wound-cleaning services (Grutter et al. 2020a; Vaughan et al. 2017). Cleaner organisms exchange this service for food in the form of ectoparasites and client tissues, and in the process attract many client fishes to their cleaning stations (Narvaez et al. 2021). Dedicated species feed exclusively by cleaning and are key in shaping the structure of marine cleaning mutualistic networks (Quimbayo et al. 2018; Vaughan et al. 2017). By relying on cleaning to feed, dedicated cleaners interact with most of the available clients, adding to the links among biotic interactions at the reef community level (Quimbayo et al. 2018).

The bluestreak cleaner wrasse *Labroides dimidiatus* (hereafter ‘cleaners’) is a dedicated cleaner fish common throughout Indo-Pacific coral reefs. It cleans a diverse range

of fishes, feeding on their ectoparasites (especially gnathiid isopods) and it is relatively well-studied (Bansemmer et al. 2002; Grutter 1996; Quimbayo et al. 2018; Randall et al. 1997). Cleaners' role in ecosystems is increasingly being considered by ecologists. Their abundance along with their biotic and abiotic influences, for instance, are important predictors of the abundance of other reef fish species and species richness (Wagner et al. 2015). In fact, *L. dimidiatus* function like ecosystem engineers, as they modify their habitat by attracting preferred clients to their cleaning station (Adam 2011). An assessment of coral reef functional groups and their vulnerability indicates *L. dimidiatus* is a high priority species for reef management (Wolfe et al. 2021). There was little redundancy in the ecosystem services *L. dimidiatus* provides to reef fishes, and of concern was the fish themselves were vulnerable to climate warming and cyclones (Wolfe et al. 2021).

Cleaning behaviour has direct and indirect consequences for fishes and other organisms. Cleaners directly reduce client stress levels and parasite loads and modify clients' movements (Clague et al. 2011; Gorlick et al. 1987; Grutter 1999, 2001; Grutter et al. 2003; Soares et al. 2011). Natural variation in access or experimental manipulations of the presence of cleaner *L. dimidiatus* reveal indirect effects. These involve changes in client physiological and morphological measures—most likely via a reduction of parasites (Binning et al. 2018; Bshary et al. 2007; Clague et al. 2011; Demaire et al. 2020; Paula et al. 2022; Ros et al. 2011, 2020; Waldie et al. 2011). Cleaner presence affects the populations of client fishes (Adam 2011; Adam 2012; Bshary 2003; Grutter 2012; Grutter et al. 2003; Sun et al. 2015; Wagner et al. 2015; Waldie et al. 2011), though this may involve direct and indirect processes. Cleaner presence indirectly affects the demersal stages of gnathiid isopods, but not other demersal zooplankton (Grutter et al. 2018, 2019, 2022; Sikkkel et al. 2019). Therefore, while *L. dimidiatus* are small and not abundant (< 12 cm maximum length, 2 individuals 100 m⁻², Randall et al. 1997; Triki et al. 2018), their effects on fish communities are disproportionately large. These effects could result in cascading effects on the food sources of their clientele. Cleaners can also indirectly influence habitat functioning by attracting to cleaning stations fishes that bioerode or predate on coral, with effects on local communities (Adam 2012). However, how cleaners influence the structure and dynamics of benthic communities remains relatively understudied.

Only two studies have examined the indirect effect of cleaner fish on the sessile benthic community. In French Polynesia, Adam (2012) examined *L. dimidiatus*' effect on a corallivore fish (*Chaetodon ornatissimus*, Chaetodontidae) and its coral prey and found that cleaning caused localised overuse of space near cleaning stations, and thus increased local coral predation and reduced corals growth rates. Thus,

cleaners indirectly affected corals locally, by concentrating corallivory (Adam 2012). In Australia, Grutter et al. (2020b) examined *L. dimidiatus*' effect on abundance of territorial and roving grazer functional fish group, individual grazing rates of rovers (bites min^{-1}), natural benthos composition, and accumulation of fouling material on settlement tiles after 3.5 months. They used reefs maintained free of *L. dimidiatus* for 8.5 years (removals) compared with controls located off Lizard Island, Great Barrier Reef (GBR). Cleaner removal resulted in a lower number of territorial 'non-farmer', 'extensive' and 'intensive' farmer fish individuals, but not 'indeterminate' farmers (Pomacentridae), and fewer roving 'algal turf-removing' and or 'sediment removing' parrotfishes (Labridae) and *Acanthurus* spp. surgeonfishes (Acanthuridae), but not the surgeonfish *Ctenochaetus striatus* (Grutter et al. 2020b). Grazing rates (bites min^{-1}) of *Acanthurus* spp. and *Ct. striatus* were unaffected by cleaner presence or, on control reefs, by cleaning duration. Based on the latter, they assumed that grazing pressure (bites area^{-1}) could be inferred from fish abundance, i.e., that more fish individuals per reef would result in more bites area^{-1} , regardless of cleaner presence treatment. Nevertheless, benthic community structure and the amount of organic and inorganic material accumulated on tiles were unaffected by cleaner presence. Thus, despite greater abundances of many roving grazers, and consequently presumed higher grazing density (i.e., bites area^{-1}) being linked to the presence of cleaners, the fouling material on tiles and natural benthos was not detectably affected by cleaners (Grutter et al. 2020b). Here, we build on these studies to further examine the indirect effect of cleaner presence on the sessile benthic community.

A direct measure of grazing pressure involves focal observations of the benthos where the number of bites per area is computed, i.e., grazing density (bites area^{-1}). However, in an earlier study on the same Lizard Island reefs used here, only the grazing rates per unit time (bites min^{-1}) were measured (Grutter et al. 2020b). These involved focal observations of natural benthos by individual roving grazers. In addition, to date, the effect of cleaner presence on the accumulation of the fouling material on settlement tiles on the aforementioned reefs has been examined after 3.5 months only, with this material consisting of a film of sediment, micro-algae, and detritus (Grutter et al. 2020b). Most grazers interact with a more complex community of fouling organisms, such as the above rovers, observed grazing mostly over turf algae, and territorial farmers which farm algal turfs (Grutter et al. 2020b). However, complex communities like these require a relatively longer period than 3.5 months to establish in controlled studies using uncolonized surfaces.

Therefore, to better understand how cleaners affect reef functioning, we investigated the consequences of their experimental removal on grazing density (bites area^{-1}) and

benthic colonization by sessile biota. We tested whether (1) grazing density is affected by cleaner presence and grazer functional group, specifically by sampling grazing on an intermediate fouling community on tiles (after 10 month) and the natural benthos, and (2) whether the composition of the tile fouling community is affected by cleaner presence. We used the above long-term depopulation experiment, where patch reefs have been kept free of *L. dimidiatus* since September 2000. Here, reefs were sampled 10-year post-removal. We hypothesized that, lacking an important fish ecosystem function (i.e., fish cleaning behaviour services), reefs without *L. dimidiatus* would (1) receive a reduced grazing density compared to controls, due to a lower abundance of grazers and (2) the indirect consequence of the alteration of cleaners' presence would be an altered sessile benthic community structure.

Methods and materials

Cleaner fish presence manipulations

We used 16 patch reefs (61 to 285 m^2) off Lizard Island, GBR (14°40'0"S, 145°28'0"E) from a long-term *Labroides dimidiatus* depopulation study (for map, see Fig. S1). Since 2000, reefs were inspected approximately every 3 months over 10 years, and any adult or juvenile *L. dimidiatus* removed (removal reefs) or counted on control reefs. Cleaners were removed (initially 1 to 5 adults reef $^{-1}$) from reefs using barrier nets and hand nets and released elsewhere. For number of cleaners removed or counted over time and detailed methods, see (Grutter et al. 2022; Waldie et al. 2011). Removals are highly effective, with 90% of all inspections finding reefs remained free of adults (Grutter et al. 2022).

Grazing on tiles and natural benthos

Terracotta brick tiles ($N = 15$, 19 × 19 × 4 cm) were haphazardly placed on each reef by a snorkeller or scuba diver (initial $N = 240$) following Grutter et al. (2020b), between December 23 and 29, 2009, with placement constrained to locations where the tiles would remain stable and not damage coral.

After 10 months, grazing density was recorded between 21 October and November 1, 2010. Grazing density surveys were done using two unmanned stationary high-definition video cameras (Sanyo Xacti, in a Sanyo housing) per reef. Cameras were mounted on a tripod attached to a weighted plastic crate at a height of ~45 cm, and usually placed at the edge of the reef on the sand. Continuous recordings (~45 min; mean, SE: 44.4, 0.6 min) were done. Video surveys were done in the morning and afternoon to account

for potential diel variability in fish bite rates (Zemke-White et al. 2002). Each camera recorded one of the tiles, if it was a tile not constrained by reef structure and thus visible to the camera, and the surrounding field of view of natural benthos. The camera was placed at a distance of 2 to 3 m. Each day, usually a control-removal pair of reefs was sampled.

During the analysis of video recordings, the number of bites and the identity of the grazers were recorded separately for feeding on tiles and surrounding natural benthos. Tiles were visible in 45 of the 64 video replicates [Casuarina Beach: $N=6/4$, Lagoon: $N=19/16$; controls/removal reefs, respectively; 33.3 h recorded (for details see supplementary methods)]. Number of bites per recording were adjusted to grazing density (bites tile⁻¹ h⁻¹) and thus was treated as a continuous variable. During the observations focussed on feeding bites on the natural benthos ($N=64$, 47.4 h recorded) only roving species were quantified due to visibility constraints. Territorial farmers were often too distant and small to unequivocally detect feeding or identity. Due to the variable reef terrain, it was not possible to quantify the area recorded. All values were standardised to bites field of view⁻¹ h⁻¹. Fish were grouped into functional groups within broader groups: i) territorial farmers and other site-attached species, mainly damselfishes according to Hata and Ceccarelli (2016), ii) roving grazers using Siqueira et al. (2019), and iii) other large species (carnivores) following Randall et al. (1997). For grazer species within functional groups, see Table S1.

Fouling material on tiles

After recording grazing behaviour, between 23 October and 2 November 2010, each tile including all loose material on tiles, was placed by a scuba diver into a plastic bag and promptly sealed. Between 11 and 15 tiles were recovered from each reef (final total = 228 tiles).

At the Lizard Island Research Station laboratory, all fouling material on tiles was scraped off the upper surface and sides. All material was placed into a sieve (62 microns) and rinsed with freshwater to remove excess salt, transferred to a Petri dish and allowed to settle to the bottom before decanting excessive liquid. It was then dried in an oven at 60°C for one to two days, until achieving a constant weight. The dried sample was transferred to a quick-sealing plastic bag, and the empty dish weighed again. The dry sample weight of the algae was obtained by subtracting the weight of the empty dish from the combined sample and dish weight. As reference samples, one dried sample per most reefs ($N=15$) was also retained. Four unsuccessfully dried samples were discarded.

To quantify the percent cover of scraped fouling material, the dried samples were rehydrated in freshwater in an 18.5 cm diameter Petri dish (for details see supplementary

methods). A quadrat (75×75 mm, with a 15 by 15 grid of squares printed on clear plastic sheets within this area) was used to randomly quantify the dominant item within each square. Fifty squares were randomly selected, and the squares' outline printed in a different colour. Eight different quadrats were generated with 50 different randomly selected squares and quadrats were used haphazardly. The dominant item was used as this permitted the best identification of items at the magnification used (25 to 45×), but this may have underestimated small or rare items. The variables were summed per quadrat and a percent calculated for each item type.

To obtain the organic weight of fouling material, the above rehydrated samples were bleached using a 12.5% sodium hypochlorite solution following (Bellwood 1996), leaving only inorganic sediments. These were rinsed, allowed to fully settle, and dried to constant weight as above. The inorganic sediment weight was subtracted from the unbleached dry weight to obtain the organic weight of fouling material. Eight unsuccessfully bleached samples were discarded (final $N=201$).

Statistical analyses

Grazing on tiles and natural benthos

To determine whether farmer grazing density composition varied with cleaner presence, we analysed the grazing density per tile of the eight damselfish (Pomacentridae) species using a permutational multivariate analysis of variance (PERMANOVA) using the software PERMANOVA + for PRIMER 7 (Anderson et al. 2008). Cleaner presence and site were fixed factors; reef was a random factor. Values per species for each video were used as replicates in the model ($N=45$). Data were square root transformed, which allows intermediate values to contribute to the similarity. A Bray–Curtis dissimilarity index was calculated for the distance measure analysed. To assess significant differences among groups and their interactions, a model with cleaner presence treatment and site as fixed effects and reef as a random effect was analysed. Sums of Squares Type III (partial) was used, with the permutation of residuals under a reduced model, and a maximum number of permutations of 9999. A principal coordinate analysis (PCO) ordination plot was used to visually represent samples in at least two dimensions and aid interpretation of the dissimilarities in diversity. The many zeros in the data meant that Bray–Curtis similarities were undefined between some samples. This was corrected using the zero-adjusted Bray–Curtis coefficient, which involved adding a dummy species with value 1 for all samples (Clarke et al. 2006).

To determine whether grazing density per functional group varied with cleaner presence, bite counts per species

were combined per group and analysed separately for tiles and natural benthos. Since video duration varied slightly among recordings, bite counts were adjusted to an hourly rate, and rounded to a whole number (bites h^{-1}). Many of the tile recordings had zero bites h^{-1} [tiles: *Ct. striatus* (67%, percent of all tiles), extensive farmers (93%), intensive (93%), indeterminate (17%); natural benthos: *Ct. striatus* (23%), other grazers (56%)]. Attempts to address zero-inflation and overdispersion in these count data using generalised linear mixed models (GLMM) and various distributions (poisson, negative binomial distribution without and with zero-inflation), including adding a random effect with one level for each observation, were not successful (Brooks et al. 2017; Zuur et al. 2009).

Due to the high proportion of zero values, we could only test the effect of time of day (morning/afternoon) on grazing density, and whether time of day interacted with cleaner presence, for indeterminate farmers (tiles, bites $\text{tile}^{-1} \text{h}^{-1}$) and *Ct. striatus* (natural benthos, bites $\text{field of view}^{-1} \text{h}^{-1}$). For both functional groups, time of day was not significant (tiles: GLMM, $X^2_1 = 2.338$, $P = 0.1268$, Table S3b, natural benthos: GLMM, $X^2_1 = 0.3924$, $P = 0.5311$, Table S3f), nor did it interact significantly with cleaner presence (Table S3a, e).

Therefore, the rate per reef was computed by pooling samples across the reef and time of day (tiles: $n = 2$ to 4; bites $\text{tile}^{-1} \text{h}^{-1} \text{reef}^{-1}$; natural benthos: $n = 4$, bites $\text{field of view}^{-1} \text{h}^{-1} \text{reef}^{-1}$, rounded to a whole number). This increased sampling duration and reduced the number of zeros in the data. The above generalised linear mixed models were re-run, with cleaner presence, site, and functional group as fixed effects and reef as a random effect. Models with a negative binomial distribution (and without zero-inflation) were selected for tile and natural bites rates per reef. The best fit model was selected using the Akaike Information Criterion (AIC). We analysed the bite rates on tiles grouped into bites by *Ct. striatus* (a detritivore and sediment-remover) or indeterminate farmers. We analysed the bite rates on the natural benthos grouped into bites by *Ct. striatus* or other relatively rare roving grazers combined (species from various functional groups: turf removing and/or sediment removing/crevice cleaning/bioeroding/spongivores, hereafter called “other grazers”; Fig. S4a). We used R software v. 4.0.2 (R Core Team 2020) to test models using the packages “glmmTMB” and “car” with the function “Anova” (Bates et al. 2015). Residual diagnostic tests and least square means (LSM) were calculated with the packages “DHARMa” and “emmeans”, respectively (Hartig 2021; Lenth 2020). An effect plot was used to interpret a significant interaction, using the packages “effects” and “lattice” (Fox and Weisberg 2019; Sarkar 2008).

In all univariate models, a full model was initially fitted, then any non-significant ($P > 0.20$) interaction terms

omitted, one by one, to obtain a simplified model following Quinn and Keough (2002); main effects, were always retained, even if not significant. The final model was selected using AIC. Both the full and final simplified models are presented in the online supplementary tables. 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. For linear mixed effect models, as the sample sizes were unequal, Type III (marginal) sums of squares were used as they are based on unweighted marginal means and so are not influenced by the sample size (Quinn and Keough 2002). All statistical analyses, unless otherwise stated, were carried out in R version 3.2.3 (R Core Team 2015).

Fouling material on tiles

To test whether cleaner removals had an indirect effect on benthic community structure on the reef, percent cover of eight benthic substrate types [calcareous, fleshy, *Halimeda*, and turf algae, live coral, sediment, detritus, and other invertebrates (consisting of sponge, other large invertebrates, and tube worms combined)], we used the same multivariate approach and model as for grazing density. The response was the percent of intersects out of 25 points per quadrat, for each substrate type.

To examine the effect of cleaner presence on the organic weight of fouling material on tiles, we used a linear mixed effect (LME) model fit, with a random effect (reef identity), and restricted maximum likelihood estimation (REML). With R software, we used the package “nlme” and the function “lme” (Pinheiro et al. 2012), with cleaner presence and site as fixed effects, and reef area and initial dry weight of sample as covariates. The latter covariate was included because initial plots indicated that organic weight and dry weight were positively related, and because we wanted to address the possibility that the proportion of organic weight might vary differently according to dry weight and the other factors in the model. We also conducted the same model without dry weight. These weights were log₁₀ transformed to normalise, homogenise, and linearise the data. The same model was used for inorganic weight, but without dry weight. As the sample sizes were unequal, Type III (marginal) sums of squares were used. For other models considered, see Supplementary methods.

Grazing on tiles relative to fouling material and fish per reef

To determine whether, within a grazer species, mean grazing density $\text{tile}^{-1} \text{h}^{-1}$ was correlated with the percent cover of any the most abundant fouling material types (sediment, *Halimeda* spp., detritus, and turf algae) and fish abundance

reef⁻¹, we used two species (*P. adelus* and *Ct. striatus*). As data were not homoscedastic, Spearman's correlation analyses were used, using JMP® v.14.1.0 (SAS Institute Inc. 2018). These fishes were selected as they were ubiquitous on reefs, grazed on tiles on most reefs, and had high grazing densities. *P. adelus* abundance of fish reef⁻¹ is from Waldie et al. (2011). The results for the abundance of *Ct. striatus* are from Grutter et al. (2020b). To determine whether cleaner presence had an effect on the abundance of grazers (and thus possibly ultimately their grazing density), whether *P. adelus* abundance reef⁻¹ was affected by cleaner treatment and reef area was tested; a full generalised linear model with a Poisson distribution and maximum likelihood test was used using the packages “lme4” and function “glm” the package “car” with the function “Anova” (Bates et al. 2015; Fox and Weisberg 2019) in R version 4.0.2 (R Core Team 2020).

We point out that where we state ‘no effect’ from our statistical analyses ($P < 0.05$), we specifically mean ‘no measurable effect’. Thus, we mean that either the effect size was too small or the variability too large (or both) to resolve a statistically meaningful difference despite using fairly high replication.

Results

Grazer bites on tiles

A broad range of grazer fishes, including territorial farming damselfishes and roving grazers (for species, Figure S2), and carnivorous fishes (for species, see Supplementary results, section non-grazer species) were recorded grazing on tiles. Grazers were grouped into narrower grazing functional groups (Figure S2, Table S1). Bites by carnivorous species were rarely observed (6%, of total bites h⁻¹); fish occasionally chased other fish (carnivore, conspecific, other farmer) away from the tile (see Supplementary results, section non-grazing interactions with tiles).

Territorial farmers

The species of extensive farmers observed taking bites off tiles were *Dischistodus prosopotaenia* and *Hemiglyphidodon plagiometopon* (Fig. S2). The species of indeterminate farmers were *P. adelus*, *P. bankanensis*, *P. chrysurus*, *P. grammorhynchus*, and *P. wardi*. Almost no feeding bites per tile by intensive (*Stegastes nigricans*, 4%) nor extensive (3%) farmers were observed (Fig. S2), therefore, except for the multivariate analysis, these were not considered further. *Pomacentrus adelus* and *Ct. striatus* (a roving grazer) had the most consistent and highest grazing densities (Fig. S2).

When the grazing density of all eight different farmer species per tile was compared using a multivariate approach,

there was no effect of cleaner presence on the farmers' grazing density on tiles (PERMANOVA: pseudo- $F_1 = 0.8874$, $P = 0.4390$; Table S2). There was also no effect of site on the farmers' grazing density (pseudo- $F_1 = 0.4259$, $P = 0.8161$). The first two axes of the PCO captured a reasonable representation of the general overall structure (61%) of the variability in the grazing density among species (Fig. S3). The PCO showed no apparent differences in the composition of farmer species between reefs with and without cleaner fish at both sites (Fig. S3). Two farmer species, *P. adelus* and *P. wardi*, contributed the most to the dissimilarity among species (species with Pearson's correlations > 0.5).

All (non-farming) grazers

The sediment-remover (detritivore) *Ct. striatus* was the most common grazer species observed feeding on tiles (25%, of all bites, Fig. S2). Other roving and site-attached species, including partly or wholly grazing species (Randall et al. 1997) occasionally were observed feeding off tiles, but were not considered further. These included roving grazers [4.6%; “turf remover and crevice cleaner” (*Zebrasoma scopas*, 3%), “turf and sediment remover” (*Scarus altipinnis*, 0.6%), other Acanthuridae spp. (1%)] and site-attached grazers [14%; Blennidae (12%) and Pomacentridae (2%; i.e., *Acanthochromis polyacanthus*, *Chrysiptera rex*; *Chr. rollandi*, *Pomacentrus amboinensis*, and *P. moluccensis*)].

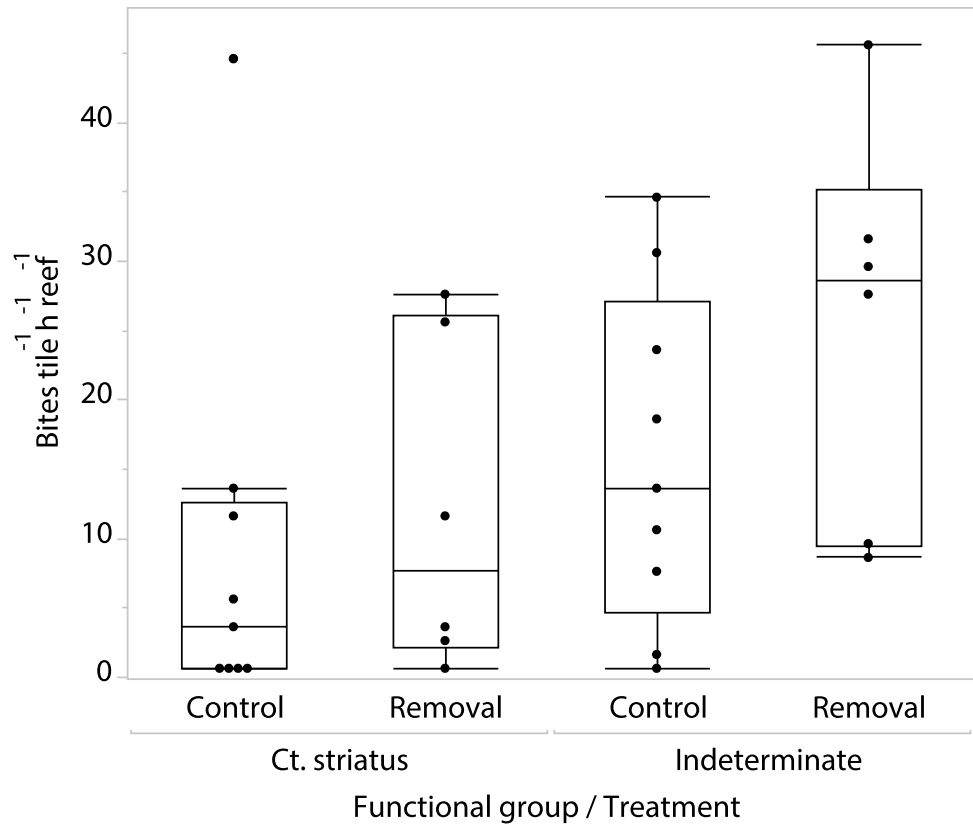
Comparison among all common grazer functional groups

The bite rates for the most common grazing functional groups were compared (i.e., sediment-remover *Ct. striatus* and indeterminate farmers). Bites tile⁻¹ h⁻¹ reef⁻¹ did not differ with cleaner presence (GLMM, $X^2_1 = 1.5138$, $P = 0.2186$; least square mean (LSM), control: 8, 2/3; removal: 14, 5/7; back-transformed LSM, -SE/+SE), and site (GLMM, $X^2_1 = 0.0444$, $P = 0.8332$, Table S3d). However, they differed for functional group, being twice as high in indeterminate farmers compared with *Ct. striatus* (GLMM, $X^2_1 = 8.154$, $P = 0.0043$; Fig. 1, Table S3d, *Ct. striatus*: 7, 2/3; indeterminate: 16, 4/6; back-transformed LSM, -SE/+SE).

Rover grazer bites on natural benthos

Twenty different roving fishes, belonging to the Acanthuridae, Labridae (tribe Scarini), and Siganidae were recorded grazing on the natural benthos (for list, see Table S1). These species were grouped into two grazing functional groups (sediment-remover *Ct. striatus*, and ‘other grazers’). For number of bites according to species and cleaner treatment, see Fig. S4a.

Fig. 1 Grazing density on tiles, according to functional group, and cleaner treatment. *Ct. striatus* = sediment-remover *Ctenochaetus striatus*; extensive and indeterminate represent farming groups. Boxplots: center line = median, box = inner interquartiles, and error bars = 90th and 10th percentiles, circles = outliers



The sediment-remover (detritivore) *Ct. striatus* was the most common species observed feeding on the natural benthos (62%, % of all bites). The remainder consisted of turf removing and/or sediment removing/crevice cleaning/bioeroding/spongivores (38%) combined into “other grazers” (Table S1). The “macroalgal remover” *Naso unicornis* accounted for 0.04% of all bites and so was not considered further.

When bites were summed within the two common grazing functional groups, the bites field of view⁻¹ h⁻¹ reef⁻¹ did not differ with cleaner presence (GLMM, $X^2_1 = 0.1771$, $P = 0.6739$; control: 65, 27/45; removal: 47, 22/41; back-transformed LSM, -SE/+ SE); there was a significant interaction between site and functional group, due to less (90%) bites by other grazers at Casuarina Beach (CB) than the Lagoon (GLMM, $X^2_1 = 7.2187$, $P = 0.0072$, Fig. 2, S4b, Table S3h; other grazers: CB, 8, 5/13, Lagoon, 87, 33/52; *Ct. striatus*: CB, 107, 53/104, Lagoon, 122, 45/72).

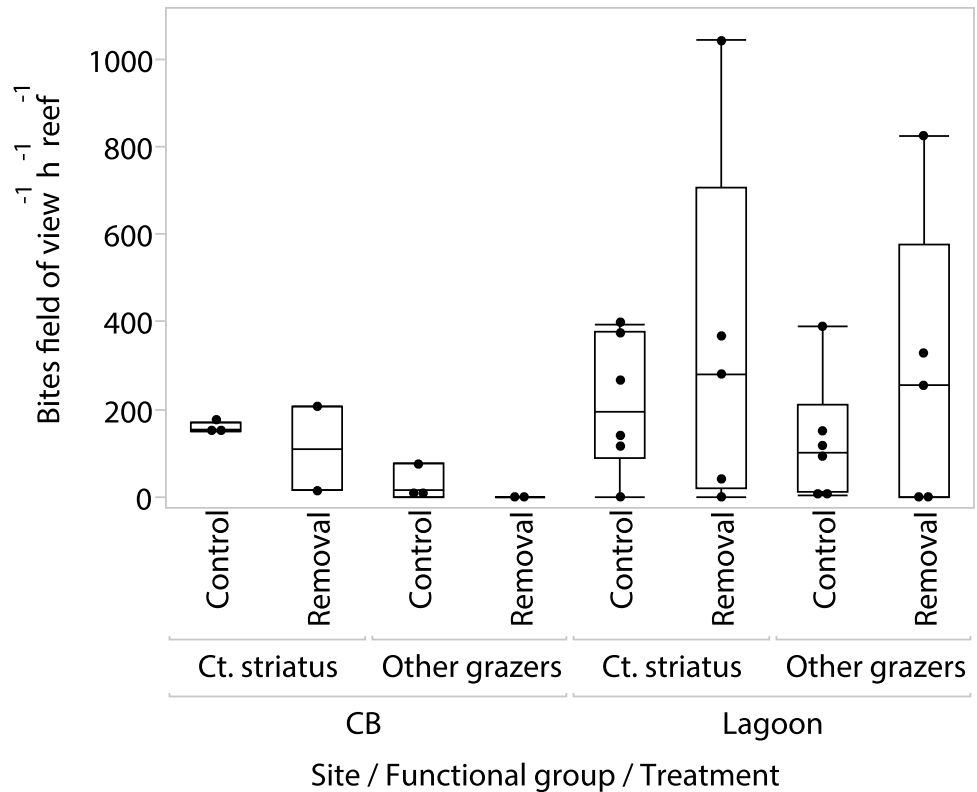
Fouling material on settlement tiles

Composition

After 10 months, the accumulation of fouling material on tiles generally consisted of a thick mat; after its removal

from tiles and subsequent drying, then rehydration for quantification, the percent cover of the reconstituted material consisted of detritus (46%, median), followed by turf algae (20%), sediment (10%), *Halimeda* spp. (2%), fleshy, calcareous algae, and relatively rarely, hard coral, sponge, other large invertebrates, and tube worms were also present (Fig. 3). After 10 years of manipulating the presence of cleaner fish, there was no effect of cleaner presence on the composition of the fouling material on tiles, when measured using the percent cover of the 8 (out of 10) fouling material types (PERMANOVA: pseudo- $F_1 = 0.252$, $P = 0.8685$; Table S4). There was also no effect of site on the benthic composition (pseudo- $F_1 = 0.6988$, $P = 0.5635$; Table S4). A PCO found that the total variation inherent in the resemblance matrix that was explained by the first two PCO axes provided a reasonable representation of the general overall structure (77.1%, Fig. 4a). The PCO plot showed that the composition of fouling material generally overlapped on reefs with cleaner fish present and absent, at both sites (Fig. 4). Three benthic substrates, turf algae, detritus, and sediment contributed the most to the dissimilarity (substrates with Pearson’s correlations > 0.5, Fig. 4b). There was much variation in the composition per tile within a reef (Fig. S5).

Fig. 2 Grazing density on the natural benthos, according to site, functional group, and cleaner treatment. *Ct. striatus* = sediment-remover *Ctenochaetus striatus*. For boxplot details, see Fig. 1



Organic and inorganic content

There was much variation in the weight of dried samples. After 10 months, organic weight (\log_{10}) of fouling material on settlement tiles was not affected by cleaner presence (LME, $F(1,12) = 0.6129$, $P = 0.4489$) and differed according to an interaction between site and the covariate initial dry weight (\log_{10}) of the sample (LME, $F(1,183) = 5.2328$, $P = 0.0233$; Fig. 5); the effect of reef area was not significant (LME, $F(1,12) = 0.1921$, $P = 0.6690$; Table S5b). When sites were examined separately to investigate the site \times dry weight interaction, a positive association between \log_{10} organic weight and covariate \log_{10} dry weight occurred at the Lagoon (LME, \log_{10} dry weight: $P < 0.0001$, Fig. 5a) but no significant association was found at Casuarina Beach (LME, \log_{10} dry weight: $P = 0.0786$, Fig. 5b). A second model for organic weight (\log_{10}), but without dry weight, also found no effect of cleaner presence (LME, $F(1,12) = 0.5730$, $P = 0.4637$; Table S5d), site (LME, $F(1,12) = 0.0060$, $P = 0.9395$), or reef area (LME, $F(1,12) = 1.8408$, $P = 0.1998$); control: 0.0491 ± 0.0851 , g; removal: 0.1423 ± 0.0968 , g; LSM \pm SE).

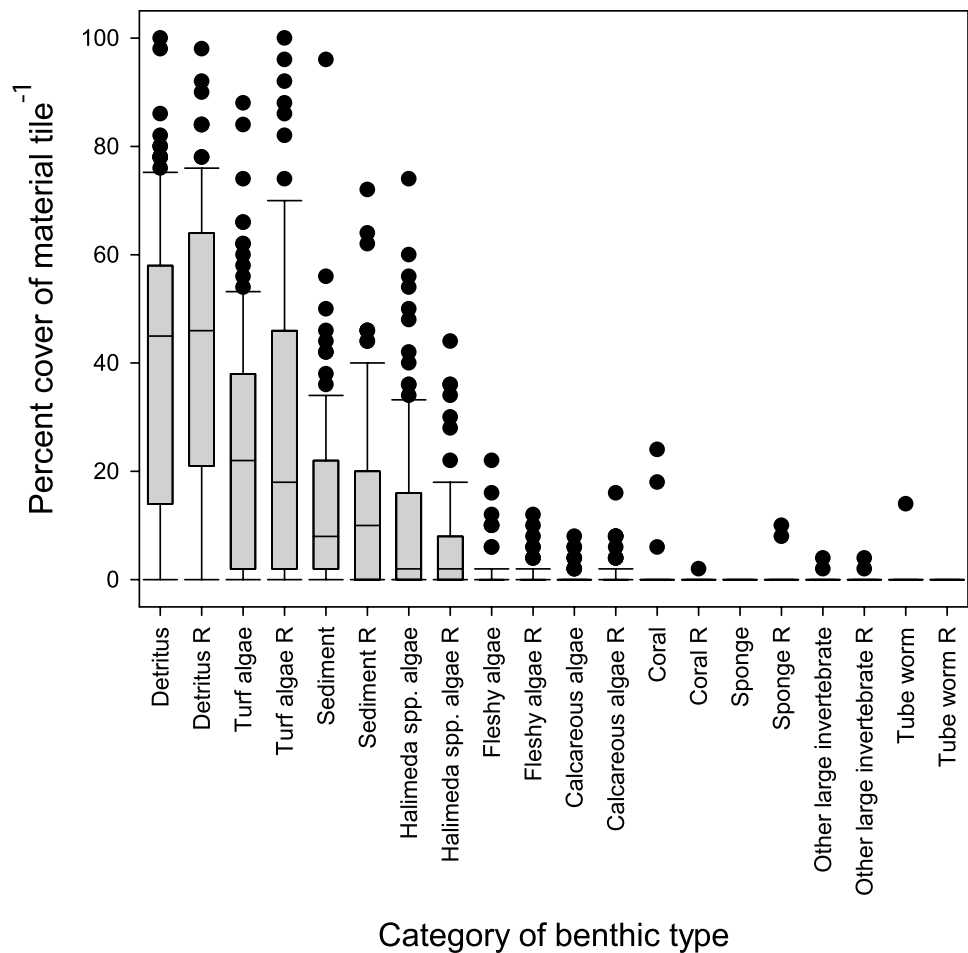
Inorganic weight (\log_{10}) of fouling material on tiles also did not differ with cleaner presence (LME, $F(1,12) = 0.0734$, $P = 0.7911$, Table S5f; control: 1.0063 ± 0.0865 ; removal: 1.0402 ± 0.0983 ; LSM \pm SE) and differed between sites (LME, $F(1,12) = 6.9856$, $P = 0.0215$) due to a higher load

at Casuarina Beach (1.2066 ± 0.1155 , g) compared with the Lagoon (0.8399 ± 0.0751 , g). The effect of reef area was not significant (LME, $F(1,12) = 3.7643$, $P = 0.0762$).

Grazing on tiles relative to fouling material and fish per reef

Abundance of *P. adelus* per reef varied according to an interaction between cleaner treatment and reef area, due to an increase in fish abundance with reef area on reefs with cleaners but no association on reefs without cleaners (GLM, Likelihood ratio $\chi^2_1 = 11.874$, $P = 0.0006$; Fig. S6; Table S6). There was no effect of cleaner treatment on *Ct. striatus* abundance per reef, but there was a positive effect of reef area (Grutter et al. 2020b). Hence, grazing rates were pooled across cleaner treatments, whereas fish abundance was adjusted for reef area (i.e., fish density) in the correlation analyses below. Grazing density on tiles was not correlated with the four most common fouling material types (Fig. S7), nor with fish density, for both *P. adelus* and *Ct. striatus* (Fig. S8a, b; Spearman's correlations, all $P < 0.05$, $N = 11$).

Fig. 3 Percent cover of ten different benthic fouling material types of fouling material removed per settlement tile, for reefs with cleaners and without cleaners (R). For boxplot details, see Fig. 1



Discussion

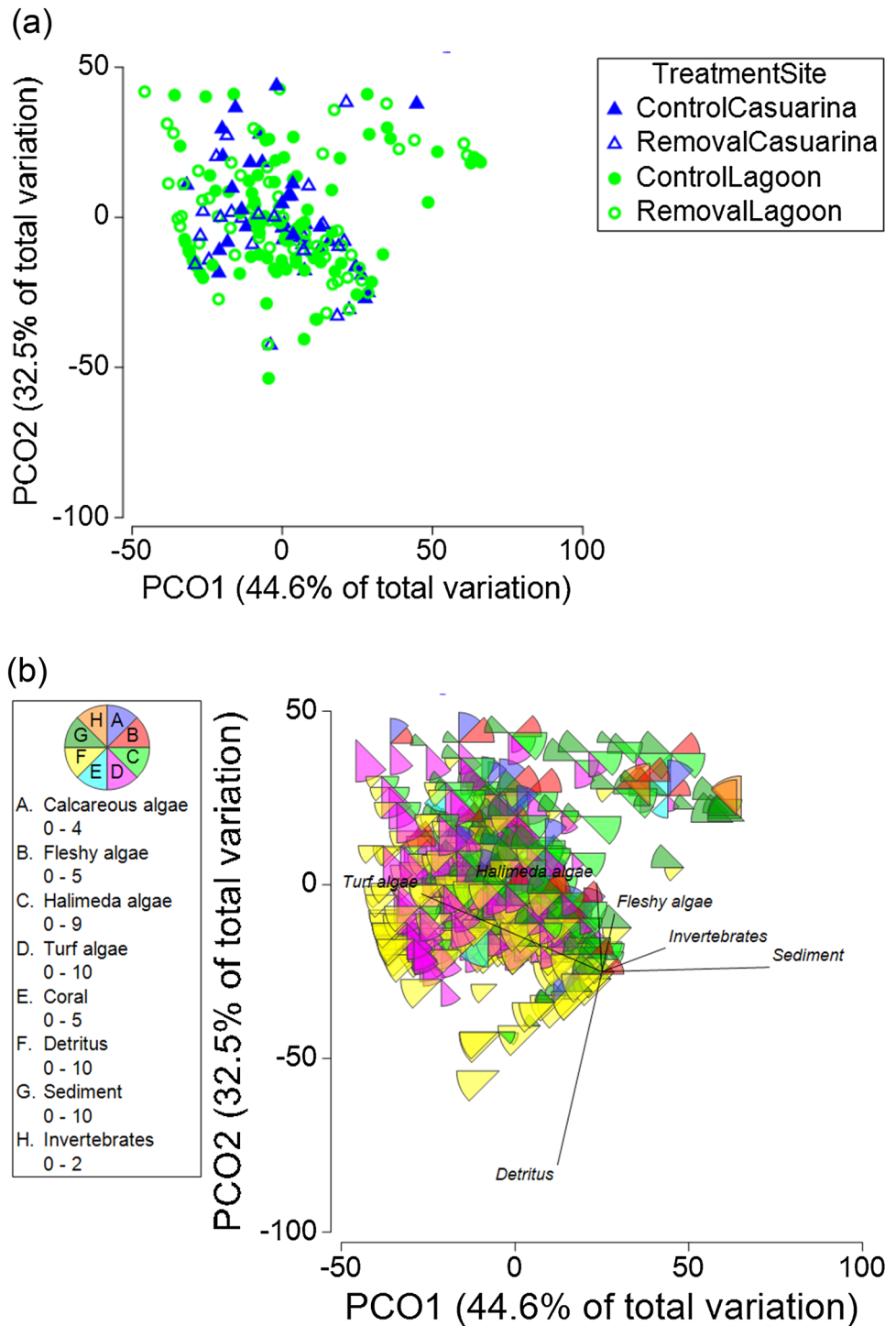
Summary

We tested whether there are indirect interactions between a cleaning behaviour mutualism and the coral reef benthic community. These interactions are ones that may result from cleaners' numerous beneficial effects on their fish clients, one effect being a higher abundance of some territorial algal farming and roving grazing fish functional groups (Grutter et al. 2020b). Fish grazing enhances certain algae and reduces other algae, detritus, and sediment (Ceccarelli 2007; Clements et al. 2009; Eurich et al. 2018; Goatley and Bellwood 2010; Mantyka and Bellwood 2007; Mumby et al. 2006). We hypothesized a higher abundance of grazers, due to cleaners' presence, would result in a higher grazing density (bites area⁻¹) with consequences for the benthos (i.e., fouling material on tiles). However, we found no support for our hypothesis, with no indirect effect of cleaner presence on grazing density nor the benthos.

We found that grazing density on tiles and the natural benthos was sustained primarily by fish functional

groups known to affect the benthos, specifically, territorial indeterminate farmers and the roving sediment-remover (detritivore), *Ctenochaetus striatus* (Ceccarelli 2007; Clements et al. 2009; Eurich et al. 2018; Goatley and Bellwood 2010; Mantyka and Bellwood 2007; Marshall and Mumby 2015). Yet, grazing density was not affected by the presence of the cleaner fish *Labroides dimidiatus* that had been manipulated for 10 years. The fouling material community that accumulated on tiles after 10 months was dominated by detritus, followed by turf algae, and sediment—all substrates the common grazers are known to interact with. The composition of this material, and its total organic and inorganic dry weight tile⁻¹ were also not affected by cleaner presence. Hence, the benthos (i.e., fouling material on tiles and natural benthos) sampled here experienced similar levels of grazing density regardless of cleaner presence treatment. This occurred despite higher grazer abundances of some grazer functional groups (i.e., extensive and intensive farmers and roving grazer parrotfishes and *Acanthurus* spp. surgeonfishes; Grutter et al. 2020b) on reefs with cleaners.

Fig. 4 Benthic composition. Principal coordinate analysis (PCO) ordering settlement tiles based on their composition and percent cover of eight fouling material types. Each tile is labelled by **a** cleaner fish treatment (control: reefs with cleaners; removal: reefs with no cleaners) and site and **b** by benthic type using segmented balloons representing the percent cover of each benthic type per sample; key shows minimum and maximum proportions (square root) per benthic type plotted. Vector overlays correspond to the correlations between that variable and each of PCO axis 1 and 2 (only vectors with Pearson's correlations > 0.2 are shown). Data were square root transformed and a Bray–Curtis similarity was calculated for the PCO

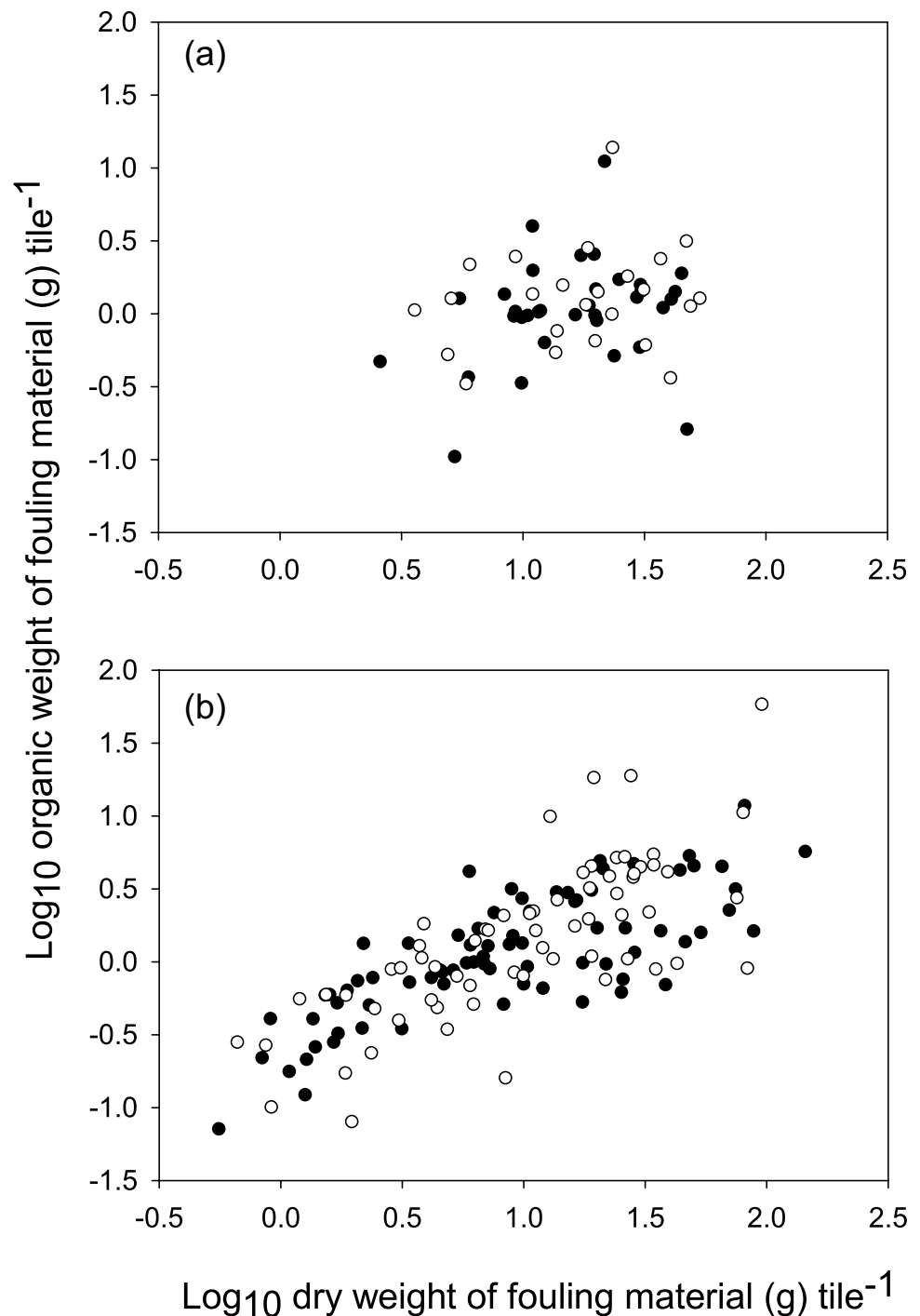


Grazer bites on tiles and natural benthos

Grazing density on tiles was dominated by indeterminate farmers followed by the roving sediment-remover *Ct. striatus*, with twice as many bites by the former, and was not affected by cleaner presence on the reef. Extensive farmers produce a large mixed culture of algae over a large area and harvest a smaller yield per unit area than do intensive

farmers, but rarely were observed grazing on tiles; whereas the territories of indeterminate farmers, while not obvious, have more palatable filamentous algae and negatively affect coral settlement (Hata and Ceccarelli 2016). Grazing density on the natural benthos was dominated by *Ct. striatus*, with other grazers foraging on tiles to a lesser degree and was also not affected by cleaner presence. Farmers’

Fig. 5 The \log_{10} organic weight, relative to the dry weight, of fouling material per settlement tile at **a** Casuarina Beach and **b** Lagoon. Solid and open circles denote tiles from reefs with and without cleaner fish present, respectively



grazing density on the natural benthos, however, could not be reliably recorded.

The composition of the common eight farmer species observed grazing on tiles (50%, percent of all bites) did not differ with cleaner presence. Two species, *P. adelus* and *P. wardi* (both indeterminate farmers), contributed the most to the dissimilarity in species composition and had the highest grazing densities. Since the diet and behaviour of farmers varies greatly among species, with most species feeding on

specific algal taxa (Ceccarelli 2007; Hata and Ceccarelli 2016), their effect on the benthic community should also vary according to the farmers' species composition. Note that bites involved in harvesting algae could not be distinguished here from ones that may have involved weeding and cropping, behaviours which influence composition and productivity of algae (Hata and Ceccarelli 2016).

While grazing by rovers on tiles and the natural benthos was dominated by *Ct. striatus*, the 'other grazers' group

played a relatively larger role in the natural benthos than on tiles. Of the rovers that grazed upon tiles, *Ct. striatus* (25% of all bites) took 5.4 times more bites, compared with the other grazers combined (4.6%, turf removing and sediment removing/crevice cleaning and unidentified Acanthuridae grazers). Whereas, of the rovers that grazed on the natural benthos, where farmers were not recorded, *Ct. striatus* (62%) also took the most bites, but this ratio (1.6 times) relative to the other grazers combined (38%, turf removing and/or sediment removing/crevice cleaning/bioeroding/spongivores) was less, compared with that on tiles. This relative difference is most likely due to the greater variety of food sources in the natural benthos attracting other grazers compared with that of tiles.

Fouling material on settlement tiles

The composition, and organic and inorganic weight of the fouling material did not differ with cleaner presence. Fouling material consisted of a thick mat, and comprised largely detritus, turf algae, and sediment. This 10-month old community was clearly more complex than an earlier shorter younger one (3.5. month), where tiles only had a mat of sediment and detritus (Grutter et al. 2020b).

The organic and inorganic content of fouling material also did not differ with cleaner presence. This result is consistent with the earlier shorter study (Grutter et al. 2020a, b). The inorganic weight of fouling material on tiles was higher at Casuarina Beach compared with the Lagoon site, an effect not detected in the earlier shorter study. The overall organic weight of samples was higher compared to the shorter study (Grutter et al. 2020b), likely due to the longer colonization period allowing more material to accumulate, as well the increase in complexity of habitat, particularly the algal turf matrix which is known to trap other material such as detritus and sediment (Tebbett et al. 2017a). It should be noted that the earlier study used ash-free dried samples to obtain organic weight, which may underestimate organic content (Purcell 1997), whereas here we used sodium hypochlorite.

Link between grazing and fouling material

How farmers might influence the fouling community on tiles remains an open question. Farmers largely interacted with tiles with bites, though occasionally they appeared to defend the tile from carnivorous fish, conspecifics, and other farmers. Many factors interact to determine the area that fish can cultivate and defend, including variation among farmer species and reef habitat in algal composition and size of territories, and in the identity and abundance of potential competitors, food, and space (Hata and Kato 2004, Ceccarelli 2007). These factors may have contributed to the high variation within a reef in tile composition.

There was no relationship between grazing density and the percent cover of fouling material, when examined separately for the two abundant and ubiquitous grazers, *P. adelus* and *Ct. striatus*, and the four most common fouling types of benthos (sediment, detritus, and *Halimeda* spp. and turf algae). While *P. adelus* feed largely on corticated red algae and filamentous algae and their territories are characterised by thin turfs (Ceccarelli, 2007), they did not graze more on tiles with more turf algae. *Ctenochaetus striatus*, an important grazer on both tiles and the natural benthos, targets detritus in algal turfs in the natural benthos and their grazing on tiles were not related to turf algae or detritus.

Ctenochaetus striatus transports sediment off the reef, via its feeding behaviour involving specialized teeth that sift and retain the sediment and associated detritus living within the algal turf matrix, then defecating the indigestible sediment off the reef (Goatley and Bellwood 2010; Tebbett et al. 2017a). That the grazing density by *Ct. striatus* on tiles was not affected by cleaner presence could, in part, explain why no effect of cleaners was detected on the inorganic component on tiles—an important component of the material *Ct. striatus* removes and transports off the reef. All fishes on reefs with cleaners, including *Ct. striatus* and other roving grazers, have the option to engage in cleaning interactions, yet, cleaning duration does not come at a cost to individual rovers' grazing rates (bites individual⁻¹ min⁻¹) on the natural benthos nor does cleaner presence affect their grazing rate (Grutter et al. 2020b). Thus, both from the point of view of the individual grazing rate of *Ct. striatus* on the natural benthos, as well from their grazing density (bites tile⁻¹ h⁻¹), there was no effect of cleaners' presence. This suggests inorganic sediment loads on reefs, which play an important role in reef ecology, including affecting grazer foraging rates (Tebbett et al. 2017b), are resilient to changes in cleaner fish presence at the temporal scale sampled.

Lack of an effect of cleaners

There are several explanations for why no indirect effect of cleaner fish presence on the benthos (i.e., fouling material on tiles) was detected here. First, there was no density dependent effect of fish density on grazing rates. Density-dependent grazing rates are commonly observed in herbivorous coral reef fishes (Bonaldo and Bellwood 2011; Lewis and Wainwright 1985). Hence, we assumed the positive effect of cleaners on the abundance of intensive and extensive farmers and roving parrotfish and *Acanthurus* spp. detected in 2009 on the same reef (Grutter et al. 2020b) would translate into higher grazing rates in cleaners' presence. However, grazing density in relation to conspecific density (obtained from other studies, Grutter et al. 2020b; Waldie et al. 2011), when examined for two common species at the reef level (*P. adelus*

and *Ct. striatus*, surveyed in 2009 and 2012, respectively), were not correlated.

Second, there may not have been a positive effect of cleaners on fish density during the present study. As fish counts were not conducted during this study period (2010), we had assumed the previous year's enhanced effect of cleaners on fish populations remained. However, cleaners' effect on fish density varies temporally, but also between rovers and site-attached fishes. For example, for all rovers combined, cleaners enhanced their abundance in 2002 and 2009, but not in 2012; for all site-attached fishes, cleaners did not enhance their diversity in 2002 but did in 2009 (Clague et al. 2011; Grutter et al. 2020b, 2019, 2003). An explanation for this variability is that rovers, due to their greater mobility, may respond to changes in cleaner access more quickly than site-attached fishes can (Grutter et al. 2003). Hence, an alternative explanation, is that mobile roving grazers can seek cleaning elsewhere, without reducing their grazing rates on cleaner-absent reefs (but see Adam 2012; Grutter et al. 2020b, 2002) whereas site-attached fishes cannot. An exception may be *Ct. striatus*, whose abundance was not affected by cleaners in 2012, probably because they are long-lived (maximum 37 years; Trip et al. 2008), have small home ranges (12 m², Krone et al. 2008), and their local density is better explained by physical habitat than cleaner presence (Adam 2011; Grutter et al. 2020b). For example, they do not increase their visitation rates to other reefs following cleaner additions (Adam 2011). Nevertheless, the body condition index of *Ct. striatus* is lower on reefs with a natural absence of cleaners (Ros et al. 2011). Our experiment, however, does not preclude the possibility of deleterious impacts on roving species if the reef-wide population of cleaners declined (i.e., if there were few opportunities to be cleaned within reasonable home ranges).

Third, a diel temporal decoupling of herbivory from cleaning, where a higher grazing density due to cleaners' presence, is counteracted by time spent cleaning at a different time, could explain the lack of an effect of cleaner presence on grazing density. Foraging rates in farming and grazing fishes has been widely shown to be higher during the afternoon than the morning (Khait et al. 2013; Polunin et al. 1995; Zemke-White et al. 2002). In contrast, cleaning in some client fishes peaks in the morning (Côté and Molloy 2003; Sikkell et al. 2004, 2000, 2005). However, we detected no effect of time of day on grazing density on tiles and natural benthos for indeterminate farmers and *Ct. striatus*, respectively, nor an interaction with cleaner presence. This is supported by other studies. For example, at our experimental site, foraging rates of individual *Ct. striatus* and roving grazers (*Acanthurus* spp., *Scarus globiceps*, *S. rivulatus*, *Siganus doliatus*) are unaffected by cleaner presence, or for *Ct. striatus* and *Acanthurus* spp., by cleaning duration (Grutter et al. 2020b). The latter indicates no cost

to foraging from cleaning, a behaviour that was also only 6 to 7% of their total time budgets, respectively, and often occurred during foraging. Furthermore, individual clients from 11 species, including *Ct. striatus*, show no diel variation (0700 to 1800 h) in their cleaning rates (Grutter 1995), despite cleaning frequency of individual *L. dimidiatus* being highest around dawn (0600 h, Grutter 1996). Nevertheless, our sample size per time of time day ($N=2$), and thus our ability to detect an effect of time of day, may be low.

Finally, multiple species that perform similar ecosystem functions (Table S1) and their foraging and trophic plasticity, including by *Ct. striatus* (Tebbett et al. 2018; Wolfe et al. 2021), may have increased resilience to cleaners' effects. Variation in the importance of positive and negative effects in space and time likely influence the outcomes of many interactions, including cleaning behaviour. Processes other than grazing, such as biological interactions, environmental effects, physical structure, and reef hydrodynamics are known to influence benthic composition and sedimentation rates (Goatley and Bellwood 2012; Hata and Ceccarelli 2016; Kench 1998). These are highly likely to have contributed variation, over spatial and temporal scales, to this study which could have swamped any potential effect of cleaner presence/absence.

Conclusions

We found no support for the hypothesis that the experimental removal of cleaner fish *L. dimidiatus*, although shown to negatively influence the abundance of many grazers at the same site at various times, indirectly affects fish grazing density and subsequently the sessile benthic community. While algal farming fishes enhance algal growth and the associated material found within the algal turf matrix, such as detritus and sediment, roving grazer species remove this material from the natural benthos (Ceccarelli 2007; Clements et al. 2009; Eurich et al. 2018; Goatley and Bellwood 2010; Mantyka and Bellwood 2007; Mumby et al. 2016). Thus, both groups may counteract each other. That there is no cost of engaging in cleaning on individual grazing rates for common roving grazer fishes, but that there is for a micro invertebrate predator and a corallivore (Adam 2012; Grutter et al. 2020b, 2002) also adds another level of complexity to this system. The likely complex interactions between cleaner fish presence, a highly diverse client fish fauna, and the opposite effects some fish have on the natural benthos emphasize the difficulty in determining indirect effects of cleaner fish on sessile benthic communities. For example, cleaner fish presence can indirectly affect the local coral community near cleaning stations by influencing both the demography (density-dependant indirect interactions) and behaviour (i.e., trait-mediated indirect interactions) of clients (Adam 2012). More information is needed on trade-offs between cleaning

and other activities, including feeding, defending territories, and predator avoidance of client fishes to understand their interactions with the natural benthos.

Yet, there is much support to emphasize the considerable extent to which cleaning behaviour influences the reef community. By promoting fish diversity combined with a high client diversity, *L. dimidiatus* are part of a diverse network of fishes (Bshary 2003; Grutter et al. 2003; Quimbayo et al. 2018; Wagner et al. 2015; Waldie et al. 2011). The number of links among cleaners and other reef organisms are, therefore, likely to be much greater than those considered to date. These links include ones revealed using cleaner exclusion experiments, reviewed above. The also include potential links associated with cleaners' diet of diverse parasites (Grutter 1997), and cleaners' roles in reducing predator aggression in bystander fish (Cheney et al. 2008) and client stress (Soares et al. 2011), influencing juvenile fish habitat selection (Sun et al. 2016), and a possible reduction of fish blood parasite transmission—by controlling vectors (Curtis et al. 2013). Indirect effects are more likely to be detected in complex mutualisms where third-party species tend to generate feedbacks to communities (Bronstein 2015). In cleaning interactions, ectoparasites are likely important third-party antagonist candidates. The potential for greater community-wide effects of cleaning behaviour on coral reef organisms, therefore, remains an open question.

This study adds to the increasing evidence that more grazers do not necessarily lead to more grazing pressure on the reef (Bellwood et al. 2019; Grutter et al. 2020b; Tebbett et al. 2020). A decrease in grazing fishes in this study did not translate into less grazing, nor an impact on both the fouling community on tiles and natural benthos indicating the link between grazer abundance, grazing behaviour, and influence on the benthos is unsupported at this location. Our study indicates a certain level of resilience of the marine benthic community to the experimental reduction of a key species at the patch-reef scale.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-022-04122-y>.

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Author contributions ASG, PJM, and SB designed the study. SB and DS collected the data. ASG analysed the data and wrote the paper. All authors contributed to drafting and editing. All authors provide consent for publication.

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Availability of data and materials The datasets analysed during the current study are available from the corresponding author on reasonable request.

Code availability All software and packages and their sources are provided. Code is not supplied.

Declarations

Conflict of interest The authors declare that they have no conflict of Interest.

Ethics approval The authors declare that all applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed and all necessary approvals have been obtained. The research was approved by The University of Queensland Animal Ethics Committee (permit numbers 560 ZOO/ENT/017/00, 171/01, 320/03, 335/04, 265/05, SIB/269/06, 837/07, 604/08, 821/08).

Consent to participate All the authors have provided their consent to participate in this study.

Consent for publication All listed authors have approved the manuscript before submission.

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