Coral-algal interactions at Weizhou Island in the northern South China Sea: variations by taxa and the exacerbating impact of sediments trapped in turf algae

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Competitive interactions between corals and benthic algae are increasingly frequent on degrading coral reefs, but the processes and mechanisms surrounding the interactions, as well as the exacerbating effects of sediments trapped in turf algae, are poorly described. We surveyed the frequency, proportion, and outcomes of interactions between benthic algae (turf algae and macroalgae) and 631 corals (genera: Porites, Favites, Favia, Platygyra, and Pavona) on a degenerating reef in the northern South China Sea, with a specific focus on the negative effects of algal contact on corals. Our data indicated that turf algae were the main algal competitors for each surveyed coral genus and the proportion of algal contact along the coral edges varied significantly among the coral genera and the algal types. The proportions of algal wins between corals and turf algae or macroalgae differed significantly among coral genera. Compared to macroalgae, turf algae consistently yielded more algal wins and fewer coral wins on all coral genera. Amongst the coral genera, Porites was the most easily damaged by algal competition. The proportions of turf algal wins on the coral genera increased 1.1–1.9 times in the presence of sediments. Furthermore, the proportions of algal wins on massive and encrusting corals significantly increased with the combination of sediments and turf algae as the algal type. However, the variation in proportions of algal wins between massive and encrusting corals disappeared as sediments became trapped in turf algae. Sediments bound within turf algae further induced damage to corals and reduced the competitive advantage of the different coral growth forms in their competitive interactions with adjacent turf algae.
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Abstract

Background. Competitive interactions between corals and benthic algae are increasingly frequent on degrading coral reefs, but the processes and mechanisms surrounding the interactions, as well as the exacerbating effects of sediments trapped in turf algae, are poorly described.

Methods. We surveyed the frequency, proportion, and outcomes of interactions between benthic algae (turf algae and macroalgae) and 631 corals (genera: Porites, Favites, Favia, Platygyra, and Pavona) on a degenerating reef in the northern South China Sea, with a specific focus on the negative effects of algal contact on corals.

Results. Our data indicated that turf algae were the main algal competitors for each surveyed coral genus and the proportion of algal contact along the coral edges varied significantly among the coral genera and the algal types. The proportions of algal wins between corals and turf algae or macroalgae differed significantly among coral genera. Compared to macroalgae, turf algae consistently yielded more algal wins and fewer coral wins on all coral genera. Amongst the coral genera, Porites was the most easily damaged by algal competition. The proportions of turf algal wins on the coral genera increased 1.1–1.9 times in the presence of sediments. Furthermore, the proportions of algal wins on massive and encrusting corals significantly increased with the combination of sediments and turf algae as the algal type. However, the variation in proportions of algal wins between massive and encrusting corals disappeared as sediments became trapped in turf algae.
Discussion. Sediments bound within turf algae further induced damage to corals and reduced the competitive advantage of the different coral growth forms in their competitive interactions with adjacent turf algae.
Introduction

Coral reefs around the world, including those of the South China Sea, have been undergoing rapid degradation due to anthropogenic stressors and changes in their natural environment (Yu, 2012). Macroalgae and turf algae generally tend to increase in abundance in degraded reefs (Nugues and Bak, 2006; Haas et al., 2010) and develop intense competitive interactions with the remaining corals (Hughes, 1994; McCook et al., 2001; Bellwood et al., 2004). This is particularly pronounced in reefs that experience frequent human activity (Barott et al., 2012; Brown et al., 2017). Indeed, phase shifts from coral to algal domination in reefs have been observed with increasing frequency as a result of overfishing (Hughes, 1994), eutrophication (Littler et al., 2006), sediment deposition (Goatley and Bellwood, 2013; Goatley et al., 2016), and global climate change (Hoegh-Guldberg et al., 2007).

The interaction between benthic algae and scleractinian corals can be a major determinant of reef community structure and composition, particularly in degrading reefs that are dominated by macroalgae (McCook et al., 2001). The outcomes of such interactions mainly depend on the species involved (McCook et al., 2001; Nugues and Bak, 2006), as the competitive mechanisms and strengths of algae and the resistance abilities of corals varies among species (Jompa and McCook, 2003; Nugues and Bak, 2006; Bonaldo and Hay, 2014). Moreover, polyp size (hypothesized by McCook et al., 2001), coral colony size (Barott et al., 2012; Ferrari et al., 2012; Brown et al., 2017), coral growth form (Swierts and Vermeij, 2016), and environmental factors (Vermeij et al., 2010) are also important determinants of the outcomes of coral-algal
competitions. Barott et al. (2012) found that large and small coral colonies were more successful in competing against algae than mid-sized corals because they were able to allocate more energy to the competition. Different coral growth forms can also influence the nature of competitive interactions between coral and algae (Swierts and Vermeij, 2016). Different growth forms use either one of two, or both, strategies to compete against algae: the ‘escape in height’ strategy, in which corals invest energy in vertical growth to escape algal competition, and the ‘direct confrontation’ strategy, in which corals directly fight off algal invasion (Meesters and Wesseling et al., 1996; McCook et al., 2001; Swierts and Vermeij, 2016). In addition to these strategies, McCook et al. (2001) suggested that coral species-specificity can affect the outcomes of their interactions with algae. This interactive process depends more on the properties (e.g., species, functional groups, etc.) of the algae than of the coral (McCook et al., 2001; Jompa and McCook, 2003).

On coral reefs, macroalgae and turf algae are the main competitors against corals for space (McCook et al., 2001; Vermeij et al., 2010). With regard to coral-algal interactions, macroalgae are the most frequently researched and have been shown to inhibit nearby coral growth (Jompa and McCook, 2003; Titlyanov et al., 2007), recruitment (Birrell et al., 2008; Vermeij et al., 2009) and fecundity (Foster et al., 2008). Crustose coralline algae (CCA) are generally thought to have positive or minimal negative effects on corals (Negri et al., 2001; Harrington et al., 2008; Vermeij and Sandin, 2008). Compared to macroalgae and CCA, turf algae grow quickly and can pre-emptively colonize available space (McCook et al., 2001; Littler et al., 2006). Turf algae
interact most frequently with corals on degraded reefs (Littler et al., 2006; Haas et al., 2010) and
can cause hypoxia (Smith et al., 2006; Wangpraseurt et al., 2012; Gregg et al., 2013; Haas et al.,
2013; Roach et al., 2017), physical damage (McCook et al., 2001), bleaching (Titlyanov, et al.,
2007; Rasher and Hay, 2010; Rasher et al., 2011), and disease (Barott and Rohwer, 2012) in
adjacent corals. Turf algae have also been seen to have critical negative effects on the settlement
and recruitment of coral larvae (Birrell et al., 2005; Birrell et al., 2008). In addition, algal turfs
often accumulate a variety of sediments on the reef substrate (Purcell, 2000; Birrell et al., 2005),
which exacerbate the stress and mortality that they cause in underlying corals and CCA (Steneck,
1997; Nugues and Roberts, 2003; Cetz-Navarro et al., 2013). The harmful effects of sediments
are influenced by water flow, e.g., low flow rates can increase the rates of sediment
accumulation (Gowan et al., 2014). When sediments are bound within turf algae, grazing by
herbivores may also be inhibited (Wilson and Bellwood, 1997; Bellwood and Fulton, 2008;
Goatley and Bellwood, 2011), which further enables the growth of algal turfs and hinders the
settlement of coral larvae (Birrell et al., 2005; Goatley et al., 2016).

Although various researchers have conducted sound investigations into the influences of
different algae on corals, their field surveys often do not consider the diversity of traits
associated with the competitors or the environmental factors that could influence the outcome of
coral-algal interactions. Field surveys on the influence of coral traits (e.g., genus, growth form,
polyp size, etc.) and sediments on coral-algal interactions may help to improve our
understanding of the complex processes involved in these competitive interactions. Such insights
may be helpful in the selection of corals for use as coral transplants in the restoration of degraded
coral reefs that have become dominated by algae.

In the present study, we conducted field surveys to investigate the influence of turf algae
and macroalgae (*Lobophora variegata* and *Bryopsis pennata*) on five common coral genera
(*Pavona*, *Porites*, *Favites*, *Favia*, and *Platygyra*) on the coral reef of Weizhou Island, northern
South China Sea. The study objectives were: (1) to survey the frequency of coral-algal contact,
as well as the composition and proportion of contiguous algae along the coral edges; (2) to
determine the outcomes of the competitive interactions between the common corals and
dominant algae; and (3) to determine the impact of accumulated sediments on the negative
effects of turf algae (i.e., algal wins) on corals. Our central hypothesis was that sediment
deposition would increase the competitiveness of turf algae in coral-algal interactions, enable
them to overgrow corals, and reduce the competitive advantage of the coral growth forms.

**Materials and methods**

**Study site**

The survey was conducted in October 2015 (autumn) at Weizhou Island (21°03′N, 109°07′E);
the largest and youngest volcanic island in the Chinese coastal areas, located 48 km from the
mainland coastline in the Beibu Gulf in the northern South China Sea (Fig. 1A). Weizhou Island
has experienced a dramatic decline in its coral reefs since the 1990s: from 80 % coral cover to an
estimated current live coral cover of less than 10 % (Wang et al., 2016). The rapid development
of tourism, fishing, aquaculture, and other human activities in recent years have likely had
detrimental effects on the coral reef ecosystem. In addition, long-term investigations have
indicated that fish populations have been at low levels for a long time (Chen et al., 2015).
However, no recent surveys have been conducted on the benthic algae of the Weizhou coral reef.

**Benthic cover**

Field research was conducted with permission from the School of Marine Sciences, Guangxi
University. Coverage of hard corals and benthic algae and coral-algal interactions were surveyed
along transects at four sites on the reef flat of Weizhou Island. The distance between sites was
greater than 1 km (Fig. 1B). Two 100 m parallel transects, separated by over 100 m, were
installed at each of the four sites at a depth of 3–7 m; i.e., a total of eight transects were surveyed.
For each transect, a 100 m fiberglass measuring tape was fixed to the reef flat and sampling
quadrats (0.5 × 0.5 m) were placed every 10 m along the transect.

An OLYMPUS TG-4 camera (effective pixel density: 12 million pixels) was used to
photograph each quadrat. Benthic cover and composition were analyzed using Coral Point Count
with Excel extensions (CPCe) software that used 50 randomly-placed points within each frame
(Preskitt et al., 2004; Kohler and Gill, 2006). Reef benthic cover was calculated from 11 quadrats
along each of the 8 transects, i.e., n = 88 quadrats. Hard corals were identified to the genus level,
macroalgae were identified to the species or genus level, and CCA and turf algae were classified
as individual functional groups. We also identified other benthic organisms, such as soft corals
and sponges. Non-biological substrates were classified as sand, rock, rubble, and dead coral.
Frequency of contact, proportion, and outcomes of coral-algal interactions

Videos were also recorded along each transect (as previously described) using an OLYMPUS TG-4 camera, held 15–25 cm above the benthos by a SCUBA diver at a swimming speed of 4 m min\(^{-1}\). The frequency and proportion of coral-algal interactions (i.e., algal contacts along coral edges) were assessed based on screenshots of the transect videos. We derived top-view photographs (screenshots) of the common corals (\textit{Porites}, \textit{Favites}, \textit{Favia}, \textit{Platygyra}, and \textit{Pavona} genera). We ensured that these photographs clearly reflected information regarding the coral genus, algal type, and algal contacts along the coral edge (Fig. 2), and that the coral colony photographs revealed over half of the coral edge. We also ensured that part of the tape measure was visible alongside or above the measured corals in these photographs for the accurate quantification of coral edge perimeters and identification of the outcomes of coral-algal interactions (Fig. 2E). Using these photographs, we carefully investigated and recorded features of the coral colonies, i.e., coral genus, growth form, and perimeter; we visually examined the edges of the corals for the presence or absence of turf algae and macroalgae; and we quantified the proportion of coral-algal interactions. CCA were ignored as they had minimal interactions with the corals. Using the software ImageJ 1.50i (Abramoff et al., 2004), we determined the type and proportion of coral-algal interactions, and we recorded the contact length of each species and functional group of algae at each coral edge (Fig. 2E). The percentage of contact of each algal species around the coral was calculated by dividing the contact length of each algal taxon by the total perimeter of the coral. The outcomes of coral-algal interactions were visually evaluated
from the interface (e.g., Figs. 2A and 2B) and classified as coral win, algal win, or neutral outcome. An outcome was scored as ‘coral win’ if the coral had grown taller than the contiguous algae or had damaged the adjoining algal tissue. An outcome was scored as ‘algal win’ if the coral edge showed signs of tissue necrosis, discoloration, bleaching, or if the algae had overgrown the coral colony (Barott et al., 2012; Swierts and Vermeij, 2016). An outcome was scored as ‘neutral’ if neither the coral nor the algae caused damage or overgrowth at their interaction interface (see Barott et al., 2012, Fig. 2). The proportions of algal wins were calculated for each coral by dividing the length of damage from the algae by the total length of contact of each type of algae along the coral edge. The proportions of coral wins and neutral outcomes were calculated using the same equation with respective substitutes. Outcomes were grouped by coral genera and colony growth forms, i.e., coral colonies were classified as one of three growth forms: encrusting (colonies encrusting the substrate without upward growth), massive (solid colonies with similar size in all directions), and upright (colonies growing upward with a small base fixed to the substrate) based on the growth morphology of the dominant surveyed coral genera. Some coral genera, including Porites, Favites, Favia, and Platygyra, were found in both encrusting and massive growth forms, while the Pavona genus was found only in the upright growth form. The polyp sizes of each coral genera were classified as being smaller than 2 mm (i.e., Porites and Pavona genera) or larger than 5 mm (i.e., Favites, Favia, and Platygyra genera).
Determining the effects of accumulated sediments

Even a small amount of turf algae can collect a large quantity of sediment on near-shore reef substrata (Figs. 2C and 2D). Sediments were identified using magnified (1–2 times) photographs. Gray sediments sharply contrasted the colors (red, green, and brown) of the turf algae, and their presence or absence in the turf algae was recorded non-quantitatively. Turf algae that interacted with corals were divided into two categories, namely ‘turf algae with sediment’ (Turf + S) and ‘turf algae without sediment’ (Turf – S). We compared the proportions of algal wins that resulted from encounters between the coral colonies and ‘Turf + S’, and between coral colonies and ‘Turf – S’.

Statistical analyses

Homogeneity of variances was tested on all data using Levene’s test. Parametric and non-parametric analyses were applied to data that were homoscedastic and non-homoscedastic, respectively. The proportions of algal contacts (i.e., coral-algal interactions) were analyzed for differences between coral genera and algal types (e.g., macroalgae, ‘Turf + S’, and ‘Turf – S’) using a two-way ANOVA, with the coral genus and algal type as fixed factors. Differences in the proportions of a specific competitive outcome (e.g., coral win, algal win, or neutral) among coral genera were quantified using a Kruskal-Wallis test followed by a Student-Newman-Keuls (SNK) post-hoc comparison. To assess the differences in the proportions of algal wins, a two-way ANOVA was used (with the type of turf algae or macroalgae genus and coral genus as fixed factors), followed by an SNK test. To assess the differences in the proportions of algal wins and
the similarity among interaction groups (including: massive corals vs. ‘Turf – S’, massive corals vs. ‘Turf + S’, encrusting corals vs. ‘Turf – S’, and encrusting corals vs. ‘Turf + S’), a two-way ANOVA (with the type of turf algae and coral growth form as fixed factors) was used, followed by an SNK test. All statistical analyses were conducted using IBM SPSS Statistics 19 software and \( p < 0.05 \) were considered statistically significant.

**Results**

**Benthic cover**

The benthos of Weizhou Island consisted of 7 % hard coral, 31 % benthic algae, 5 % other biological substrates, and the residual 57 % consisted of non-biological substrates (Fig. 1B). The five common coral genera, *Pavona*, *Porites*, *Favites*, *Favia*, and *Platygyra* accounted for 31 %, 23 %, 13 %, 11 %, and 4 % of the total hard coral cover, respectively (Fig. 3A). The major algal functional group was turf algae, which made up 23 % of the total benthic cover. Macroalgae contributed relatively little to the benthic coverage, at 4 % *L. variegata* and 2 % *B. pennata*. Other algae contributed ~2 % to the total benthic coverage (Fig. 3B).

**Algal composition, contact frequency, and proportion around the coral edges**

In total, 631 coral colonies with a combined perimeter of 25,716 cm were measured in the surveyed transects. Amongst all genera, *Porites* was the most frequently in contact with algae (86 ± 2.4 % of colonies; mean ± SE), followed by *Favia* (85 ± 2.7 %) and *Favites* (80 ± 5.5 %; Table 1). The proportions of algal contacts varied significantly with coral genera and with algal
types, and a significant interaction was found between coral genus and algal type (two-way
ANOVA, coral genera: $F = 11.99$, df = 4, 1889, $p < 0.0001$; algal types: $F = 55.22$, df = 2, 1889,
$p < 0.0001$; interaction: $F = 11.36$, df = 8, 1889, $p < 0.0001$; Table 2). The mean percentage of
coral edges in contact with algae was higher for turf algae (38 ± 1.0 %, which consisted of 19 ±
0.9 % ‘Turf – S’ and 19 ± 1.0 % ‘Turf + S’) than for macroalgae (6 ± 0.5 %, n = 631; Table 1).
The *Porites* genus was the most frequently engaged in algal contact (n = 211, 53 ± 1.9 %), while
the *Pavona* genus was the least frequently engaged in algal contact (n = 113, 27 ± 2.2 %; Table
1).

**Interactions between corals and algae**

The proportions of algal wins between the corals and turf algae were significantly higher in
interactions with the *Porites* genus (which have a small polyp size), i.e., 76 ± 1.7 % (mean ± SE)
of the interaction outcomes (65 % algal overgrowth and 11 % coral bleaching), than with any
other coral genera with large polyp sizes (Kruskal-Wallis, $X^2 = 147.65$, df = 4, $p < 0.0001$; Fig.
4B). Proportions of turf algal wins in interactions with *Platygyra*, *Favites*, and *Favia* genera
(which have large polyp sizes) ranged from 40 ± 5.7 % to 51 ± 3.1 % but did not significantly
differ among these genera (Fig. 4B). In these genera, algal overgrowth was the major contributor
to algal wins, with few instances of coral bleaching occurring. Proportions of neutral outcomes
differed significantly among coral genera, with this outcome being significantly less occurred in
the *Porites* genus than in any other coral genera (Kruskal-Wallis, $X^2 = 68.27$, df = 4, $p < 0.0001$;
Fig. 4B). There were significant differences in the proportions of coral wins in coral-turf algal
interactions among the coral genera (Kruskal-Wallis, $X^2 = 15.43$, df = 4, $p = 0.0039$; Fig. 4B).

Corals with small polyp sizes ($< 2$ mm), such as the *Porites* and *Pavona* genera, were least successful in turf algal interactions and accounted for $4 \pm 1.0\%$ and $7 \pm 2.8\%$ of the coral wins, respectively (Fig. 4B).

Proportions of macroalgal wins varied significantly among coral genera (Kruskal-Wallis, $X^2 = 22.93$, df = 4, $p = 0.0001$; Fig. 5B). Of the five coral genera, *Porites* was the most susceptible to damage by macroalgae, with macroalgal wins accounting for $64 \pm 5.5\%$ (mean $\pm$ SE) of their interaction outcomes (Fig. 5B). The proportions of macroalgal wins in the *Favia*, *Pavona*, *Platygyra*, and *Favites* genera ranged from $22 \pm 4.0\%$ to $51 \pm 10.4\%$ (Fig. 5B). The proportions of neutral outcomes in coral-macroalgal interactions did not significantly differ among coral genera (Kruskal-Wallis, $X^2 = 6.80$, df = 4, $p = 0.147$; Fig. 5B). Corals were more successful in outcompeting macroalgae, with proportions of coral wins ranging from $9 \pm 3.5\%$ to $55 \pm 6.4\%$ (Kruskal-Wallis, $X^2 = 37.65$, df = 4, $p < 0.0001$; Fig. 5B).

**Negative effects of macroalgae and turf algae in contact with corals**

Proportions of turf algal wins varied among the types of turf algae and the coral genera, but there were no interactions between the type of turf algae and coral genus (two-way ANOVA, types of turf algae: $F = 30.15$, df = 1, 655, $p < 0.0001$; coral genera: $F = 57.70$, df = 4, 655, $p < 0.0001$; interaction: $F = 1.57$, df = 4, 655, $p = 0.1810$; Fig. 6A). The *Porites* genus showed significantly higher proportions of turf algal wins than other coral genera, regardless of whether the turf algae contained sediments (Fig. 6A). In all coral genera, proportions of algal wins in ‘Turf + S’
competitions were 1.1 to 1.9 times higher than in ‘Turf – S’ competitions (Fig. 6A).

In contrast, macroalgae had fewer proportions of algal wins than turf algae. Similar to turf algae, their proportions of algal wins varied with macroalgae and coral taxa, but no interactions were found between macroalgal species and coral genus (two-way ANOVA, macroalgae genera: $F = 40.48$, df = 1, 181, $p < 0.0001$; coral genera: $F = 9.35$, df = 4, 181, $p < 0.0001$; interaction: $F = 1.14$, df = 4, 181, $p = 0.3399$; Fig. 6B). Within the coral genera, algal wins of brown algae *L. variegata* were 2.5 to 5.7 times more frequent than those of green algae *B. pennata*. Both species caused the most harm to the *Porites* genus (93 ± 2.4 % for *L. variegata* and 37 ± 7.6 % for *B. pennata*; mean ± SE; Fig. 6B).

**Negative effects of turf algae on massive and encrusting corals**

The effects of the coral growth form and the sediment on the outcomes of coral and turf algae interactions were analyzed for the *Porites, Favites, Favia*, and *Platygyra* genera. The proportions of algal wins varied significantly between the two types of turf algae, but did not vary significantly between the two coral growth forms (massive and encrusting), and a significant interaction was found between the types of turf algae and coral growth forms (two-way ANOVA, types of turf algae: $F = 28.42$, df = 1, 585, $p < 0.0001$; coral growth forms: $F = 1.26$, df = 1, 585, $p = 0.2625$; interaction: $F = 4.23$, df = 1, 585, $p = 0.0401$; Fig. 7). For the same coral growth forms, the proportions of turf algal wins increased significantly when sediments were trapped in the turf algae (Fig. 7). The proportions of algal wins of ‘Turf – S’ were significantly higher on massive corals than on encrusting corals (Fig. 7). However, the proportions of algal wins caused...
by ‘Turf + S’ did not differ significantly between these two coral growth forms (Fig. 7).

Discussion

Coral-algal interactions varied with algal taxa

The majority of coral colonies competed with benthic algae, with interaction outcomes mostly being in favor of the algae rather than the corals. The interactions of the algae and corals varied among species and algal functional groups. Interactions between turf algae and corals were most frequent, with the proportions of algal wins and the proportion of algal contacts being considerably greater in turf algae than macroalgae (Table 1, Figs. 4 and 5). These findings have previously been observed on degraded coral reefs, where contact with turf algae resulted in algal overgrowth and caused bleaching or damage to adjacent corals (Haas et al., 2010; Wild et al., 2014; Swierts and Vermeij, 2016). Some of our study findings were consistent with the results of these previous studies, i.e., corals were frequently observed to suffer overgrowth by turf algae; however, in the present study, coral bleaching was rarely observed. Although the causes of the observed algal overgrowth and coral bleaching were not surveyed in this study, previous studies have confirmed that turf algae can negatively influence corals by hypoxia and microbial growth (Smith et al., 2006; Wangpraseurt et al., 2012; Gregg et al., 2013; Haas et al., 2013; Roach et al., 2017). Turf algae may also influence corals via potential algal allelopathy (Jompa and McCook, 2003). Moreover, turf algae can rapidly increase in length and occur in both creeping and upright growth forms (Hay, 1981; Connell et al., 2014), which allow it to rapidly and densely overgrow adjacent corals.
Macroalgae caused relatively less damage than turf algae (Figs. 4B and 5B). Comparatively, *L. variegata* exhibited a greater damaging effect on corals than *B. pennata* (Fig. 6B). On degraded reefs, *L. variegata* is often widespread and competes with hard coral (Hughes, 1994). Because of its creeping growth pattern and thallus which can attach tightly to the coral surface, it is possible for *L. variegata* to smother and overgrow the subsurface of coral tissue (McCook et al., 2001; Nugues and Bak, 2006; Longo and Hay, 2015). Meanwhile, bleaching on neighboring corals may be associated with allelopathic or microbial mechanisms during the overgrowth of *Lobophora* spp. (Rasher and Hay, 2010; Vieira et al., 2016). In contrast, *B. pennata* is characterized by a prostrate rhizoid and erect pinnule, which possibly account for its lower frequency of damage to corals in this study. The soft and short erect pinnules of *B. pennata* may have limited shading effects on adjacent corals. Other rhizophytic algae (e.g., *Caulerpa* spp.) in the Bryopsidales tend to bury their rhizoids in sand and sediment substrates for nutrient absorption (Williams, 1984; Friedlander et al., 2006), suggesting that hard coral may not be a suitable substrate for the growth of rhizophytic algae. Other investigators have reported that competition with *Bryopsis* sp. resulted in coral bleaching or tissue necrosis (Barott et al., 2009), but this was not recorded in our study. The effects of macroalgae on corals have been demonstrated, with a high variance in the potency of different algae and in the susceptibility of different corals (Rasher and Hay, 2010; Rasher et al., 2011). The interactions between macroalgae and corals varied among the different algal species, and these differences may be explained by algal growth patterns.
Resistance to algal contact: driven by coral traits and growth forms

In our study, the proportions of algal wins of different algal interactions varied among coral genera (Fig. 6). We found that the *Porites* genus was more susceptible to damage by algal contact. Other studies have also demonstrated the sensitivity of *Porites* spp. to algal contact and showed that they often suffered algal overgrowth, tissue bleaching, or even mortality (Titlyanov et al., 2007; Rasher and Hay, 2010). The harmful influences of a specific macroalgae on corals may be associated with specific coral traits, including taxonomy, growth form, and colony and polyp size. McCook et al. (2001) hypothesized that size classes of the coral colonies and polyps may be associated with the ability of corals to compete against algae. It seems that corals with large polyps possess a higher tissue expansion potential than those with small polyps (Erftemeijer et al., 2012), which enables them to perform better in resisting foreign matter invasion (e.g., algae, and sediments). This phenomenon may account for our observation of the *Porites* genus suffering greater damage from algal turf contact than the *Favites*, *Favia*, and *Platygyra* genera, all of which have larger polyp sizes.

Meanwhile, the coral growth form has also been found to be an important determinant of the outcomes of interactions between corals and turf algae (Lirman, 2001; Haas et al., 2010; Swierts and Vermeij, 2016). Previous research found that encrusting corals suffered the least harm from turf algae and that they had a higher percent of wins against turf algae than other coral growth forms (Swierts and Vermeij, 2016). The combination of sediments on turf algae appears to potentially alter the ability of the turf algae to damage different growth forms of coral (Fig. 7).
The explanation for this may be that the combination of turf algae and sediments often exacerbates their damaging effects on adjacent corals (Steneck, 1997; Erftemeijer et al., 2012; Goatley and Bellwood, 2013). The proportions of algal wins of these combinations on massive and encrusting corals were extremely similar. In such cases, the morphology of colonies did not affect the coral-turf algal interactions. Thus, we hypothesized that the competitive advantage of the encrusting coral disappeared in the interactions between coral and turf algae when turf algae were combined with sediments.

Sediments bound within turf algae can further affect the reef ecosystem

Our results suggested that the proportions of turf algal wins were augmented when sediments were trapped by turf algae (Figs. 6A and 7). Inshore coral reefs are usually exposed to high levels of suspended sediments (Gilmour, 1999), and turf algae can trap considerable quantities of sediments and reduce sediment resuspension (Purcell, 2000; Gowan et al., 2014). Water flow is the key driver of sediments that influence the interactions between corals and turf algae (Gowan et al., 2014). The water flow rate at Weizhou Island reef is low, with a seasonal range of 2.7–6.2 cm s\(^{-1}\) (Wei et al., 2017). High sedimentation rates have also been recorded on the reef flat of Weizhou Island, with an average deposition rate of 2157.9 g m\(^{-2}\) d\(^{-1}\) (Wang, 2009).

In addition, sediments in reefs contain an abundance of organic matter, and turf algae and sediment combinations have been shown to promote the growth of turf algae and inhibit grazing by herbivores (Wilson and Bellwood, 1997; Bellwood and Fulton, 2008; Goatley and Bellwood, 2011; Goatley et al., 2016). Herbivorous fish are a critical factor in coral reef environments,
where grazing controls the abundance of benthic algae and coral-algal interactions (Rasher and Hay, 2010; Bonaldo and Hay, 2014; Wild et al., 2014). The Reef Check on Weizhou Island reef showed that the average density of reef fish was only 0.03 ind m\(^{-2}\) in the past few years (Chen et al., 2016), which is lower compared to that of the Luhuitou fringing reef (0.51 ind m\(^{-2}\)) 300 km from Weizhou Island (Sun et al., 2018). Thus, we speculated that the high frequency of coral-algal interactions and negative effects of turf algae on corals may be attributed to the increase in sediments trapped in the turf algae and the decrease in the abundance of herbivorous fish.

Conclusions

The present study aimed to demonstrate the influence of species-specificity and sediment deposition on the outcomes of coral-algal interactions. We found that the outcomes of their interactions were related to biotic (i.e., taxa and growth patterns of algae, genus, polyp size, and coral growth forms) and abiotic factors (i.e., sediments). In the competition between corals and turf algae, sediments can exacerbate the ability of the turf algae to attack corals and weaken the ability of corals to resist algal invasion. Our data on the interactions between coral and algae were collected during a snapshot in time, and long-term field surveys and experiments need to be conducted to further understand the impact of sediments, their release of nutrients and housing of pathogens on coral-algal interactions as well as to determine the underlying mechanisms.

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References

Abramoff MD, Magalhaes PJ, Ram SJ. 2004. Image processing with ImageJ. *Biophotonics International* 11:36-42.

Barott KL, Rohwer FL. 2012. Unseen players shape benthic competition on coral reefs. *Trends in Microbiology* 20:621-628 DOI 10.1016/j.tim.2012.08.004.

Barott K, Smith J, Dinsdale E, Hatay M, Sandin S, Rohwer F. 2009. Hyperspectral and physiological analyses of coral-algal interactions. *PLoS One* 4:e8043 DOI 10.1371/journal.pone.0008043.

Barott KL, Williams GJ, Vermeij MJ, Harris J, Smith JE, Rohwer FL, Sandin SA. 2012. Natural history of coral-algae competition across a gradient of human activity in the Line Islands. *Marine Ecology Progress Series* 460:1-12 DOI 10.3354/meps09874.

Bellwood DR, Fulton CJ. 2008. Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea levels and climate change? *Limnology and Oceanography* 53:2695-2701 DOI 10.4319/lo.2008.53.6.2695.

Bellwood DR, Hughes TP, Folke C, Nyström M. 2004. Confronting the coral reef crisis. *Nature* 429:827-833 DOI 10.1038/nature02691.

Birrell CL, McCook LJ, Willis BL. 2005. Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* 51:408-414 DOI 10.1016/j.marpolbul.2004.10.022.
Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanography and Marine Biology* 46:25-63 DOI 10.1201/9781420065756.ch2.

Bonaldo RM, Hay ME. 2014. Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PLoS One* 9:e85786 DOI 10.1371/journal.pone.0085786.

Brown K T, Bender-Champ D, Bryant D E P, Dove S, Hoegh-Guldberg O. 2017. Human activities influence benthic community structure and the composition of the coral-algal interactions in the central Maldives. *Journal of Experimental Marine Biology and Ecology* 497: 33-40 DOI 10.1016/j.jembe.2017.09.006.

Cetz-Navarro NP, Espinoza-Avalos J, Hernández-Arana HA, Carricart-Ganivet JP. 2013. Biological responses of the coral *Montastraea annularis* to the removal of filamentous turf algae. *PLoS One* 8:e54810 DOI 10.1371/journal.pone.0054810.

Chen G, Zhao MX, Bin L, Zhang CH, Liang Q. 2016. Ecological situation of coral reefs in the Weizhou Island based on reef check. *Tropical Geography* 36:66-71 DOI 10.13284/j.cnki.rddl.002807.

Connell SD, Foster MS, Airoldi L. 2014. What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series* 495:299-307 DOI 10.3354/meps10513.
Erftemeijer PLA, Riegl B, Hoeksema BW, Todd PA. 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. *Marine Pollution Bulletin* 64:1737-1765 DOI 10.1016/j.marpolbul.2012.05.008.

Ferrari R, Gonzalez-Rivero M, Mumby, PJ. 2012. Size matters in competition between corals and macroalgae. *Marine Ecology Progress Series* 467:77-88 DOI 10.3354/meps09953.

Foster NL, Box SJ, Mumby PJ. 2008. Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastraea annularis*. *Marine Ecology Progress Series* 367:143–152 DOI 10.3354/meps07594.

Friedlander M, Kosov Y, Keret G, Dawes C. 2006. Production of rhizoids by *Caulerpa prolifera* in culture. *Aquatic Botany* 85(3):263-266 DOI 10.1016/j.aquabot.2006.06.004

Gilmour J. 1999. Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. *Marine Biology* 135:451-462 DOI 10.1007/s002270050645.

Goatley CHR, Bellwood DR. 2011. Sediment suppresses herbivory across a coral reef depth gradient. *Biology Letters* 8:1016-1018 DOI 10.1098/rsbl.2012.0770.

Goatley CHR, Bellwood DR. 2013. Ecological consequences of sediment on high-energy coral reefs. *PLoS One* 8:e77737 DOI 10.1371/journal.pone.0077737.

Goatley CHR, Bonaldo RM, Fox RJ, Bellwood DR. 2016. Sediments and herbivory as sensitive
indicators of coral reef degradation. *Ecology Society* 21:29 DOI 10.5751/ES-08334-210129.

Gowan JC, Tootell JS, Carpenter, RC. 2014. The effects of water flow and sedimentation on interactions between massive *Porites* and algal turf. *Coral Reefs* 33:651-663 DOI 10.1007/s00338-014-1154-1

Gregg AK, Hatay M, Haas AF, Robinett NL, Barott K, Vermeij MJA, Marhaver KL, Meirelles P, Thompson F, Rohwer F. 2013. Biological oxygen demand optode analysis of coral reef-associated microbial communities exposed to algal exudates. *PeerJ* 1: e107 DOI 10.7717/peerj.107.

Haas AF, el-Zibdah M, Wild C. 2010. Seasonal monitoring of coral-algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. *Coral Reefs* 29:93-103 DOI 10.1007/s00338-009-0556-y.

Haas AF, Gregg AK, Smith JE, Abieri ML, Hatay M, Rohwer F. 2013. Visualization of oxygen distribution patterns caused by coral and algae. *PeerJ* 1: e106 DOI 10.7717/peerj.106.

Harrington L, Fabricius K, De’ath G, Negri A. 2008. Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:3428-3437 DOI 10.1890/04-0298.

Hay ME. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62:739-750 DOI 10.2307/1937742.
Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737-1742 DOI 10.1126/science.1152509.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1551 DOI 10.1126/science.265.5178.1547.

Jompa J, McCook LJ. 2003. Coral-algal competition: macroalgae with different properties have different effects on corals. *Marine Ecology Progress Series* 258:87-95 DOI 10.3354/meps258087.

Kohler KE, Gill SM. 2006. Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computer and Geosciences* 32:1259-1269 DOI 10.1016/j.cageo.2005.11.009.

Lirman D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19:392-399 DOI 10.1007/s003380000125.

Littler MM, Littler DS, Brooks BL. 2006. Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory. *Harmful algae* 5:565-585 DOI 10.1016/j.hal.2005.11.003.
Longo GO, Hay ME. 2015. Does seaweed-coral competition make seaweeds more palatable? *Coral Reefs* 34:87-96 DOI 10.1007/s00338-014-1230-6.

McCook LJ. 2001. Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. *Coral reefs* 19:419-425 DOI 10.1007/s003380000119.

McCook LJ, Jompa J, Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400-417 DOI 10.1007/s003380000129.

Meesters EH, Wesseling I, Bak RPM. 1996. Partial mortality in three species of reef-building corals and the relation with colony morphology. *Bulletin of Marine Science* 58:838-852.

Negri AP, Webster NS, Hill RT, Heyward1 AJ. 2001. Metamorphosis of broadcast spawning corals in response to bacteria isolated from crustose algae. *Marine Ecology Progress Series* 223:121-131 DOI 10.3354/meps223121.

Nugues MM, Roberts CM. 2003. Coral mortality and interaction with algae in relation to sedimentation. *Coral Reefs* 22:507-516 DOI 10.1007/s00338-003-0338-x.

Nugues MM, Bak R. 2006. Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. *Marine Ecology Progress Series* 315:75-86 DOI 10.3354/meps315075.
Preskitt LB, Vroom PS, Smith CM. 2004. A rapid ecological assessment (REA) quantitative survey method for benthic algae using photoquadrats with scuba. *Pacific Science* 58:201-209 DOI 10.1353/psc.2004.0021.

Purcell SW. 2000. Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. *Bulletin of Marine Science* 66:199-214.

Rasher DB, Hay ME. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. *Proceedings of the National Academy of Sciences* 107:9683-9688 DOI 10.1073/pnas.0912095107.

Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME. 2011. Macroalgal terpenes function as allelopathic agents against reef corals. *Proceedings of the National Academy of Sciences* 108:17726-17731 DOI 10.1073/pnas.1108628108.

Roach TNF, Abieri ML, George EE, Knowles B, Naliboff DS, Smurthwaite CA, Kelly LW, Haas AF, Rohwer FL. 2017. Microbial bioenergetics of coral-algal interactions. *PeerJ* 5: e3423 DOI 10.7717/peerj.3423.

Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M, Rohwer FL. 2006. Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecology Letters* 9:835-845 DOI 10.1111/j.1461-0248.2006.00937.x.

Steneck RS. 1997. Crustose corallines, other algal functional groups, herbivores and sediments:
complex interactions along reef productivity gradients. *Proceedings of the Eighth International Coral Reef Symposium* 1:695-700.

Sun Y, Lei X, Lian J, Yang J, Wu Y, Huang H. 2018. Ecosystem status and health assessment of Sanya Coral Reef National Nature Reserve. *Biodiversity science* 26(3):258-265 DOI 10.17520/biods.2017312

Swierts T, Vermeij MJA. 2016. Competitive interactions between corals and turf algae depend on coral colony form. *PeerJ* 4:e1984 DOI 10.7717/peerj.1984.

Titlyanov EA, Yakovleva IM, Titlyanova TV. 2007. Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. *Journal of Experimental Marine Biology and Ecology* 342:282-291 DOI 10.1016/j.jembe.2006.11.007.

Vermeij MJA, Sandin SA. 2008. Density-dependent settlement and mortality structure the earliest life phases of a coral population. *Ecology* 89:1994-2004 DOI 10.1890/07-1296.1.

Vermeij MJA, Smith JE, Smith CM, Vega Thurber R, Sandin SA. 2009. Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. *Coral reefs* 159:325-336 DOI 10.1007/s00442-008-1223-7.

Vermeij MJA, van Moorselaar I, Engelhard S, Hörnlein C, Vonk SM, Visser PM. 2010. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to
overgrow coral in the Caribbean. *PLoS One* 5:e14312 DOI 10.1371/journal.pone.0014312.

Vieira C, Engelen AH, Guentas L, Aires T, Houbreque F, Gaubert J, Serrão EA, De Clerck O, Payri CE. 2016. Species specificity of bacteria associated to the brown seaweeds *Lobophora* (Dictyotales, Phaeophyceae) and their potential for induction of rapid coral bleaching in *Acropora muricata*. *Frontiers Microbiology* 7:316 DOI 10.3389/fmicb.2016.00316.

Wang WH, Yu KF, Wang YH. 2016. A review on the research of coral reefs in the Weizhou Island, Beibu Gulf. *Tropical Geography* 36:72-79 DOI 10.13284/j.cnki.rddl.002806.

Wang X. 2009. Research of the relationship between the deposit of suspended and the growth of coral reef in Weizhou Island, Beibu Bay. M. Sc. Thesis, *Guangxi University*.

Wangpraseurt D, Weber M, Røy H, Polerecky L, de Beer D, Suharsono, Nugues MM. 2012. In situ oxygen dynamics in coral-algal interactions. *PLoS One* 7:e31192 DOI 10.1371/journal.pone.0031192.

Wei CL, Gao JS, Cao X F, Ya HZ, Chen B, Shi MC. 2017. Observational analysis of the surface current characteristics and mechanisms off the southern coast of Weizhou Island, Guangxi. *Periodical of Ocean University of China* 47(4):7-13 DOI 10.16441/j.cnki.hdxb.20160137.

Wild C, Jantzen C, Kremb SG. 2014. Turf algae-mediated coral damage in coastal reefs of Belize, Central America. *PeerJ* 2:e571 DOI 10.7717/peerj.571.

Williams SL. 1984. Uptake of sediment ammonium and translocation in a marine
green macroalga *Caulerpa cupressoides*. *Limnology and Oceanography* 29 (2), 374-379.

DOI 10.4319/lo.1984.29.2.0374.

Wilson S, Bellwood DR. 1997. Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidei). *Marine Ecology Progress Series* 153:299-310.

DOI 10.3354/meps153299.

Yu KF. 2012. Coral reefs in the South China Sea: their response to and records on past environmental changes. *Science China Earth Sciences*, 55(8):1217-1229.

DOI 10.1007/s11430-012-4449-5.
Figure 1

Maps of Weizhou Island, Beibu Gulf, and study sites.

(A) Map of Weizhou Island in the Beibu Gulf of the South China Sea. (B) The eight transects are marked with red dots; the table inset shows the cover of biological and non-biological substrates and the number of surveyed coral colonies at each site.
Figure 2

Examples of coral-algal interactions and the effects of sediments bound within turf algae.

(A, B) Typical interaction interfaces of the *Favites* and *Porites* genera and algae (turf algae and *L. variegata*). (C) *Porites* colony surrounded by turf algae with massive sediments trapped in sparse turf algae, a widespread phenomenon at surveyed reef; (D) the same *Porites* colony showing bleached tissue after sediments were removed using a burst of air. (E) An example of the interaction outcomes between the genus *Favites* and turf algae. ‘Turf + S’ indicates turf algae with sediment; ‘Turf – S’ indicates turf algae without sediment. Photo credit: Zhiheng Liao.
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A B C D E

1cm 1cm 1cm 1cm

- No algal contact
- Neutral
- ‘Turf - S’ win *Favites*
- ‘Turf + S’ win *Favites*
Figure 3

Percentage of coral and algae cover on the coral reef of Weizhou Island.

The bar within each box represents the median; the two bars above and below each box represent the upper and lower 25% quartiles, respectively; the whiskers represent the minimum and maximum values; ‘●’ represents the mean value; ‘○’ indicates the data > the 1.5 interquartile range; ‘△’ indicates the data > the 3.0 interquartile range. CCA: crustose coralline algae.
A. Benthic cover (%) for different coral genera:
- **Pavona**
- **Porites**
- **Favites**
- **Favia**
- **Platygyra**
- **Others**

B. Benthic cover (%) for different algal taxa:
- **Turf algae**
- **Lobophora variegata**
- **Bryopsis pennata**
- **CCA**
- **Others**

Both sections were measured across **n = 8 transects**.
Figure 4

Competitive outcomes between corals and turf algae.

(A) Proportions of coral edges in contact with turf algae. (B) Competitive outcomes between coral and turf algae, where green (algal overgrowth) and purple (coral bleaching) indicate the proportions of algal wins, yellow indicates the proportions of neutral outcomes, and orange indicates the proportions of coral wins. The numbers indicate the number of coral colonies included in the analyses. Similar letters (uppercase or lowercase) above each set of bars indicate significant differences (assessed by a Kruskal-Wallis test) in post-hoc comparisons for a specific competitive outcome among coral genera (SNK test, $p < 0.05$).
### A
Coral edge in contact with turf algae (%)

- **Porites**: 211
- **Pavona**: 113
- **Favia**: 70
- **Favites**: 192
- **Platygyra**: 45

### B
Turf algal competition outcomes (%)

- **Porites**: A
- **Pavona**: B
- **Favia**: B
- **Favites**: B
- **Platygyra**: B

- **Coral bleaching**
- **Algal overgrowth**
- **Neutral**
- **Coral win**

Coral genera
Figure 5

Competitive outcomes between corals and macroalgae.

(A) Proportions of coral edges in contact with macroalgae. (B) Competitive outcomes between corals and macroalgae, where green (algal overgrowth) and purple (coral bleaching) indicate the proportions of algal wins, yellow indicates the proportions of neutral outcomes, and orange indicates the proportions of coral wins. The numbers indicate the number of coral colonies included in the analyses. Similar letters (uppercase or lowercase) above each set of bars indicate significant differences (assessed by a Kruskal-Wallis test) in post-hoc comparisons for a specific competitive outcome among coral genera (SNK test, $p < 0.05$).
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A.

B.

Coral genera

Coral bleaching
Algal overgrowth
Neutral
Coral win

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Figure 6

Proportions of algal wins observed along edges of different coral genera.

(A) Proportions of turf algal wins on coral genera, with turf algae grouped into ‘Turf + S’ (turf algae with sediments) and ‘Turf – S’ (turf algae without sediments). (B) Proportions of macroalgal wins on coral genera. The *numbers* indicate the number of coral colonies included in the analyses. Similar *letters* (*uppercase* or *lowercase*) indicate significant differences (assessed by a two-way ANOVA) in *post-hoc* comparisons for proportions of algal wins among coral genera (SNK test, *p* < 0.05).
Figure 7

Proportions of turf algal wins observed along massive and encrusting coral edges.

Measured interaction groups were massive corals vs. ‘Turf – S’, massive corals vs. ‘Turf + S’, encrusting corals vs. ‘Turf – S’, and encrusting corals vs. ‘Turf + S’. ‘Turf + S’ indicates turf algae with sediments and ‘Turf – S’ indicates turf algae without sediments. The numbers indicate the number of coral colonies included in the analyses. Similar letters (uppercase or lowercase) indicate significant differences (assessed by a two-way ANOVA) in post-hoc comparisons for proportions of algal wins among interaction groups (SNK test, $p < 0.05$).
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![Graph showing proportions of turf algal wins (Mean % ± SE) for different interaction groups.](image)

- **Massive corals vs. ‘Turf - S’**
- **Massive corals vs. ‘Turf + S’**
- **Encrusting corals vs. ‘Turf - S’**
- **Encrusting corals vs. ‘Turf + S’**

| Interaction groups | Massive | Encrusting |
|--------------------|---------|------------|
|                     | 169     | 136        |
|                     | 141     | 142        |

**Notes:**
- a, b, c indicate significant differences.
Table 1 (on next page)

Frequency of coral-algal contact, and composition and proportion of algae along the coral edges.

Turf algae were divided into ‘Turf + S’ (turf algae with sediments) and ‘Turf – S’ (turf algae without sediments).
| Genus   | Surveyed colonies (n) | Polyp size (mm) | % Colonies in contact with algae | % No algal contact | % Turf algal contact | % Macroalgal contact |
|---------|-----------------------|----------------|---------------------------------|--------------------|---------------------|---------------------|
|         |                       |                |                                 |                    | Turf – S            | Turf + S            |                     |
| Porites | 211                   | 2 <            | 86 ± 2.4                         | 47 ± 1.9           | 24 ± 1.7            | 23 ± 1.9            | 6 ± 0.8             |
| Favites | 192                   | > 5            | 80 ± 5.5                         | 53 ± 1.5           | 17 ± 1.5            | 25 ± 1.8            | 5 ± 0.7             |
| Favia   | 70                    | > 5            | 85 ± 2.7                         | 59 ± 2.8           | 18 ± 2.5            | 20 ± 3.1            | 3 ± 0.9             |
| Platygyra | 45               | > 5            | 64 ± 7.8                         | 67 ± 4.1           | 19 ± 3.3            | 10 ± 3.2            | 4 ± 1.2             |
| Pavona  | 113                   | 2 <            | 61 ± 3.1                         | 73 ± 2.2           | 15 ± 1.5            | 3 ± 0.9             | 10 ± 1.8            |
| Mean value |                   |                | 56 ± 1.0                         | 19 ± 0.9           | 19 ± 1.0            | 6 ± 0.5             |                     |
Table 2 (on next page)

Results of the two-way ANOVA test for the effects of coral genera and algal types on the proportions of algal contacts along coral edges.
| Source of variation | df | MS  | F    | p      |
|---------------------|----|-----|------|--------|
| Proportion of algal contact |   |     |      |        |
| Coral genus         | 4  | 0.47| 11.99| < 0.0001 |
| Algal type          | 2  | 2.18| 55.22| < 0.0001 |
| Coral genus × Algal type | 8  | 0.45| 11.36| < 0.0001 |