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ORIGINAL PAPER

Water flow influences the mechanisms and outcomes of interactions between massive *Porites* and coral reef algae

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Abstract Negative interactions between corals and algae often are implicated in preventing the recovery of coral-depauperate reefs. However, few studies have explored the effects of environmental conditions on the mechanisms underlying the outcomes of coral–algal interactions. We examined the influence of water flow, a pervasive feature of reefs that is known to affect both coral and algal physiology, on massive *Porites*–algal interactions at different spatial and temporal scales with two types of algal competitors. Outcomes of coral–algal interactions were influenced by both water flow and algal type. Algal turfs outcompeted corals more frequently in low flow conditions, where microbial concentrations were higher, than in higher flow areas. *Turbinaria ornata* outcompeted massive *Porites* more often in higher flow and consistently was associated with lower microbial concentrations. This study highlights that outcomes of coral–algal interactions are microhabitat dependent and that water flow limits the effectiveness of some mechanisms of coral–algal competition.

Introduction

Coral reefs are complex ecosystems composed of a diverse assemblage of interacting organisms that vary in abundance over space and time (Hughes 1994). Coral reef diversity and ecosystem function are related significantly to the abundance of live corals (Moberg and Folke 1999). Declines in coral abundance lead to increased space availability and the potential for shifts in the dominant space-holders on the reef from coral to other benthic taxa like macroalgae. Increased macroalgal abundances have been suggested to prevent the reversal of these phase shifts by inhibiting the settlement, establishment, and growth of corals (Birrell et al. 2005; Quan-Young and Espinoza-Avalos 2006; Bellwood et al. 2004).

Algae can negatively affect corals via a suite of different mechanisms, which often are inferred from the algal morphology or functional group affiliation (McCook 2001). The common macroalga, *Turbinaria ornata*, for example, likely competes with corals via physically mediated mechanisms due to their large canopy height and thick blades which make them more likely to shade and/or abrade corals (McCook et al. 2001; River and Edmunds 2001). Small, fleshy, or filamentous algae likely compete with corals chemically due to their short canopy heights and thin blades/filaments (McCook et al. 2001), although recent studies (Rasher and Hay 2010) suggest that allelopathy may be common among different algal morphologies. Chemically mediated mechanisms can affect corals negatively via an alteration of the chemical microenvironment, from allelopathy (Rasher and Hay 2010), microbially mediated disease (Nugues et al. 2004), or localized hypoxia (Barott et al. 2009; Smith et al. 2006). Algal turfs, for example, may compete through a microbially mediated pathway that alters the chemical microenvironment between the coral and alga (Smith et al. 2006).

Algae and corals coexist on reefs, and thus, outcomes of interactions between competing corals and algae likely are not determined only by the coral and alga involved in the

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interaction. In addition to herbivory, which is well known to control algal abundance (Bellwood et al. 2004), we propose that outcomes of coral–algal interactions are regulated by the effectiveness of the underlying mechanisms that govern the relative success of corals and algae. Physically and chemically mediated mechanisms of competition likely are modulated by the physical microenvironment that corals and algae experience, for example light and water flow. Water flow is a pervasive physical feature on coral reefs that influences key benthic processes, including organismal physiology (Atkinson and Bilger 1992; Helmuth et al. 1997; Carpenter and Williams 2007; Mass et al. 2010), settlement, nutrient delivery and uptake (Denny 1988), and coral–coral competition (Genin et al. 1994). Increased water flow results in a decreased diffusive boundary layer (DBL), the small (≪1 mm) water layer above organisms across which mass exchange occurs by diffusion (Patterson et al. 1991). Thinner DBLs promote the exchange of dissolved gases and nutrients for metabolic processes and removal of wastes in both corals and algae (Kühl et al. 1995; Mass et al. 2010).

The role of water flow on the mechanisms underlying coral–algal interactions is not well understood. Physically mediated mechanisms likely are more effective in higher flow environments where abrasion by macroalgae may occur more frequently. Competitors whose interactions with corals are dependent on chemical mediation of the zone of interaction likely are more successful in low flow environments, where DBLs above the zone of interaction potentially are thicker and can retain higher densities of bacteria and may to lead to localized alterations in oxygen concentrations (Azam et al. 1983; Smith et al. 2006).

The flow experienced by sessile organisms is affected both by wave- and wind-driven currents, the rugosity of the substratum, and the morphology of the organism (Denny 1988). Flow velocities at the surface of stationary structures approach zero due to friction (Denny 1988; Reidenbach et al. 2006; Monismith 2007). In both laminar and turbulent flows, as distance from a stationary surface increases, flow velocity increases. Thus, the flow that corals and algae experience as sessile organisms may differ from the bulk water flow. At the point of contact between corals and algae (the zone of interaction), flow not only is affected by the overall water flow, but also by the morphologies of the alga and coral (Shashar et al. 1996; Hauri et al. 2010).

Our overall aim was to quantify how the outcomes of coral–algal interactions were related to the water flow conditions in which they occurred and to quantify water flow at different spatial scales from millimeters to meters. We addressed four goals in this study. The first was to quantify differences in water flow on the upstream and downstream sides of coral bommies (large mounding coral colonies on which corals and algae are located on dead portions) on three spatial scales. Water flow was quantified in the overall water column (scale of meters), on the surface of bommies (scale of centimeters) and within the zones of interaction (scale of millimeters) between massive *Porites* and either algal turf (a likely chemical competitor) or *T. ornata* (a likely physical competitor). Algal turfs are a very common multi-specific assemblage of densely packed small filaments with canopy heights <10 mm. *Turbinaria* is a common fucoid phaeophyte with a tough thallus reaching 25 cm in canopy height. A second goal was to determine whether water flow modulates the potential for microbially mediated competition between corals and algae as a mechanism that determines the outcomes of coral–algal interactions. A third goal was to evaluate whether water flow and retention of microbes influenced the outcome of interactions, and how this was related to the mechanism underlying competition. This was tested by quantifying the frequency of coral–algal contacts, the proportion of the perimeter of *Porites* spp. in contact with other organisms (the extent of an interaction), and outcomes of *Porites* spp.–algal interactions on the upstream and downstream sides of coral bommies. Lastly, the fourth goal was to quantify the effects of prolonged algal contact on *Porites* spp. abundance to determine how water flow and algal contact affect massive *Porites* over longer time scales.

Methods

This study was conducted on the north shore of Moorea, French Polynesia (17°52′S, 149°56′W) at the Richard B. Gump South Pacific Research Station between January 2010 and May 2011 in back reef habitats. The back reef on the north shore of Moorea is a heterogeneous mixture of large coral bommies mainly formed by massive *Porites* spp. The surfaces of partially dead bommies (heights range from 0.5 to 2.0 m) are a mosaic of live corals, algae, and other invertebrates.

Wave-driven water flow in the back reef moves primarily unidirectionally from the fore reef, over the reef crest toward shore, decreasing in velocity across the back reef (Hench et al. 2008). Flow velocities change seasonally on the north shore due to differences in oceanic swells, with higher water flow during the austral summer (January) than during the austral winter (May).

Water flow measurements

Flow was measured on the upstream (direction of the incoming flow) and downstream sides of coral bommies in May of 2010 and January 2011 across three spatial scales using different methods to capture flow differences among the scales. Coral bommies divert water around their semicircular shape

and create a lower flow wake downstream (Denny 1988; Hench and Rosman 2013). Thus, these structures provide a natural system where the influence of water flow on coral–algal interactions can be addressed.

Flow at the largest scale was measured on the upstream and downstream sides of bommies using a pair of acoustic Doppler profilers (ADP, Aquadopp, Nortek, USA). The ADPs were placed simultaneously ≥1 m upstream and downstream of bommies (1–1.5 m in height, $n = 6$ per season) that were ~50 m downstream of the reef crest. Bommies were >1 m away from other structures that could disrupt flow. Flow velocities were measured from 25 cm above the seafloor to the top of the water column in 10-cm bins at a frequency of 1 Hz. Flow speeds were averaged over time (6–7 h) and water column depth bins to calculate average water flow on the upstream and downstream sides of the coral bommies. Similar methods were employed in both May and January on different bommies within the back reef. Flow from the upstream and downstream replicates was compared using a paired t test using for both May 2010 and January 2011 separately.

At a smaller spatial scale, relative flow differences were quantified on the surface of a coral bommie as an estimate of the flow experienced by corals and algae. Measurements were made using clod card dissolution as a proxy for relative differences in flow rates (Doty 1971, Thompson and Glenn 1994). Clod cards were made from Plaster of Paris (Dap©) molded in ice cube trays (4.7 × 2.7 × 2.2 cm). Replicates ($n = 2$ clod cards) were placed in the middle of a bommie, either on the side facing the dominant flow (upstream) or the side opposite the dominant flow (downstream) in May ($n = 5$ bommies) and January ($n = 7$ bommies). Clod cards were left in the field for 19 h (May) and 7 h (January) and reweighed after drying for 7 days in the laboratory. Controls were placed in still water for the same amount of time as the clod cards in the field. Controls were used to correct for dissolution in still water (seawater in a bucket in the laboratory) by multiplying the proportion of still water dissolution by the initial mass of the clod cards that were placed in the field. The final mass after deployment in the field was subtracted from the corrected initial mass normalized to the time in the field and was expressed as a rate of dissolution (g h^{-1}). The average dissolution rates for upstream and downstream sides of bommies were compared using a paired t test for both May and January.

At the smallest spatial scale, the flow experienced by coral–algal interactions was estimated by quantifying the retention times of fluorescein dye within coral–algal interactions. Retention time of dye is a proxy for boundary layer thickness with the assumption that longer retention times indicate thicker DBLs (Patterson et al. 1991). Two milliliters of fluorescein dye (0.1 g 200 ml^{-1}) was injected using a 15-ml syringe into the zone of interaction between algal turf and massive *Porites* or *T. ornata* and massive *Porites* on both the upstream and downstream sides of coral bommies (Fig. 1). Retention times were recorded to the point at which the dye no longer was visually detectable within a 1-cm^2 area of the zone of interaction. Separate analyses were conducted for measurements completed in May 2010 ($n = 20$ $side^{-1}$ of coral bommie for algal turf–massive *Porites*, $n = 10$ $side^{-1}$ of coral bommie for *Turbinaria*–massive *Porites*) and January 2011 ($n = 10$ $side^{-1}$ of bommie for both).

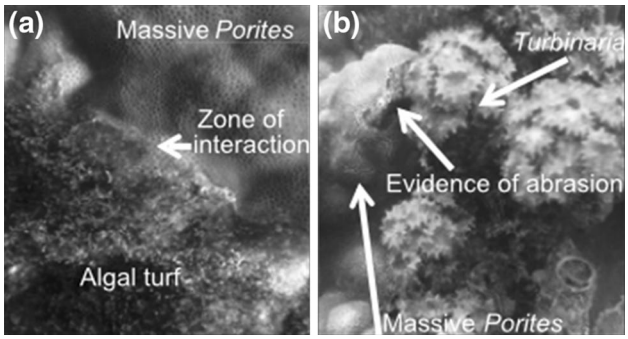

Fig. 1 Evidence of algal winners for, **a** algal turf–massive *Porites* interactions, and **b** *Turbinaria*–massive *Porites* interactions. *Arrows* are pointing to evidence of an algal "win"

Microbial concentrations

To address the potential importance of microbially mediated competition in different flow environments, microbial concentrations (cells ml^{-1}) were compared at the surface of massive *Porites*, in the zone of interaction of algal turf–*Porites*, *Turbinaria–Porites*, and in the water column on both the upstream and downstream sides of bommies. Samples were collected with a 5-ml syringe with 2 cm of plastic aquarium tubing attached to the tip (diameter 1 cm). A hole made with a dissecting needle 0.5 mm from the end of the tube allowed entry of water containing both surface microbes and microbes from above the surfaces sampled (Patten et al. 2006). Coral microbial samples were collected 5 cm away from either an algal turf–*Porites* or *Turbinaria–Porites* interaction. Microbe samples from the zone of interaction were obtained by placing the end of the tube at the point of contact between an algal turf–*Porites* interaction, or near the holdfast of a *Turbinaria–Porites* interaction. The water column samples were collected by placing a syringe either 30 cm behind or in front of the bommie surface. Samples around both types of interactions (algal turf–*Porites*, *Turbinaria–Porites*) were collected on the same bommies ($n = 16$) in January 2011 and May 2011.

Samples were fixed with 10 % paraformaldehyde (PFA) and frozen at −80 °C for analysis. Coral and algal

turf-massive *Porites* interaction samples were diluted by 50 %. Cell counts were estimated with a flow cytometer using methods from Nelson et al. (2011) and log-transformed for analysis. Each sampling location (zone of interaction, coral, water column) was analyzed with separate 2-way ANOVAs, blocked by bommie. Algal type (*Turbinaria* or algal turf) and Location (upstream/downstream) were treated as fixed factors, and the blocking factor (bommie) was treated as a random factor on JMP 5.1.

Extent, frequency, and outcome of interactions

The extent and frequency of interactions between corals and algae were surveyed on the upstream and downstream sides of coral bommies. Coral bommies (1–2 m high, 1–3 m wide) were selected haphazardly for sampling in January 2010. On each bommie, the length of all organisms (i.e., algae, invertebrates) surrounding the perimeter of each massive *Porites* coral patch that came into contact with the transect ($n = 2$ transects bommie^{-1}) was measured using dressmaker's tape. Transects were placed from the top to the bottom (each were 1–2 m), in the middle of the downstream or upstream sides of coral bommies to avoid the sides. The extent of the interaction was considered the proportion of the total interaction perimeter of the coral patch in contact with other organisms. The extent of interactions between *Porites* and each benthic component (algal turf, crustose coralline algae, macroalgae, and other coral) was normalized to bommie height and averaged across the two transects. Separate one-way ANOVAs were used to compare the extent of interactions between the upstream ($n = 10$) and downstream sides of bommies ($n = 10$). Frequency of contact was estimated by counting each occurrence that an alga or another coral was in contact with each coral patch, regardless of location on a coral bommie, across all coral bommies. Macroalgae first were recorded by genera, but for analyses, were combined into a single macroalgae category to estimate frequency of coral–algal contact. Species of algal turf and CCA were not identified in the field and so were characterized as functional groups (Steneck and Dethier 1994) to estimate the frequency of contact.

Outcomes of coral–algal interactions were estimated to quantify the association of water flow with the outcomes of coral–algal competition. Surveys of the outcomes of interactions were conducted over two seasons to examine whether patterns were consistent, as they only evaluate interactions in a snapshot in time (Lang 1973). Surveys were conducted using a point-intercept method, where a transect was placed on either the upstream or downstream side of a coral bommie from the top to the base of the bommie. Every 5 cm, if a coral was in contact with either *Turbinaria* or algal turf, the outcome of the interaction was scored as either an algal win or a neutral interaction. Algal turf wins were indicated by overgrowth of coral tissue or bleached coral at the zone of interaction between algal turf and massive *Porites* (Fig. 1). *Turbinaria* wins were characterized by a lesion of dead tissue or a patch occupied by algal turf where the macroalgal thallus hit the coral surface (Fig. 1). Neutral interactions for both algal turf–*Porites* and *Turbinaria–Porites* were indicated if there was no clear overgrowth by either algae or coral. Coral overgrowth of algae was not observed. Outcomes of algal turf–*Porites* ($n = 86$ downstream, 94 upstream in May; $n = 37$ downstream, 62 upstream in January) and *Turbinaria–Porites* ($n = 17$ downstream and 13 upstream in May; $n = 11$ downstream and 11 upstream in January) interactions were analyzed separately using a contingency analysis, and a Chi-square test was used to test for significance for May 2010 and January 2011 surveys separately.

Change in percentage cover of massive *Porites* in contact with algae over time

To estimate the effects of algal contact on coral cover over time, massive *Porites* that were surrounded by algae (algal turf, *Amansia rhodantha* and/or *T. ornata*) were selected on the upstream and downstream sides of coral bommies that were ≤50 % covered by live coral. A 0.2-m^2 plot was marked with two nails above the coral patch that was tracked over time. Photographs of the plots ($n = 9$ downstream, $n = 7$ upstream) were taken with a Canon SD 1000 camera attached to a 0.2-m^2 photoquadrat during the austral Winter 2010, the austral Summer 2011, and the austral Winter 2011. Percentage cover of massive *Porites* was estimated using coral point count (CPCe) with 200 dots projected onto the photoquadrat (Kohler and Gill 2006). Results comparing differences in percentage cover of coral over time between upstream and downstream sides of coral bommies were analyzed using a repeated measures ANOVA on a MANOVA platform in JMP 5.1, where time is treated as multiple dependent variables (Cole and Grizzle 1966).

Results

Water flow

Water flow at the largest spatial scale was significantly higher on the upstream sides of coral bommies in both May ($t_{1,5} = 2.98$, $p = 0.03$) and January ($t_{1,5} = -3.9$, $p = 0.01$, Fig. 2). Mean upstream flow speeds in May were 0.18 ± 0.02 m s^{-1} ($n = 6$) and 0.11 ± 0.01 m s^{-1} ($n = 6$) downstream. In January, mean flow was higher than May both upstream (0.36 ± 0.06 m s^{-1}) and downstream (0.26 ± 0.04 m s^{-1}, $n = 6$ for both). At the scale of organisms

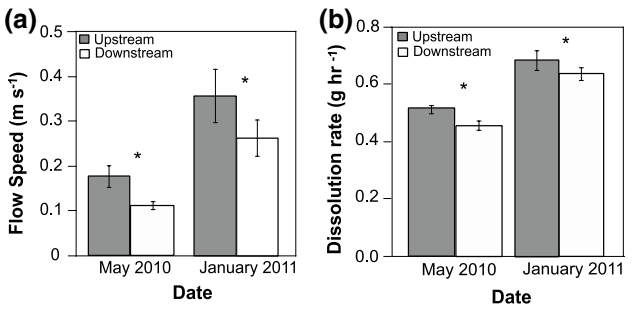

Fig. 2 **a** Mean (±SE) flow speeds as measured by ADPs on the upstream and downstream sides of coral bommies for the austral winter 2010 ($n = 6$) and austral summer 2011 ($n = 6$). There was a significant decrease in water flow from the upstream to downstream sides of the coral bommies. **b** Mean (±SE) clod card dissolution rate on the upstream to downstream sides of 1-m-high coral bommies from the austral winter 2010 ($n = 5$) and the austral summer 2011 ($n = 8$). There was a significant decrease in dissolution rates between upstream and downstream sides of coral bommies. *Asterisks* indicate significance between locations ($p < 0.05$)

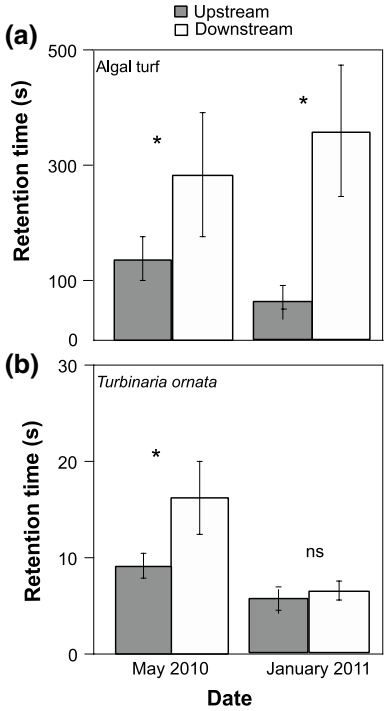

Fig. 3 Mean (±SE) retention times of fluorescein dye in seconds between interactions of massive *Porites* and, **a** algal turf, and **b** *Turbinaria* in May 2010 ($n = 10$, 11 side^{-1}, respectively) and January 2011 ($n = 7$ side^{-1}, for both types of interactions). Downstream interactions retained significantly more dye than upstream interactions. Retention times in algal turf–massive *Porites* interactions are much longer than *Porites–Turbinaria* interactions. *Asterisks* indicate significance; *one asterisk* indicates $p < 0.05$, *ns* indicates not significant

on the surfaces of bommies, similar to flow measured by the ADP, mean clod card dissolution rates were higher on the upstream sides of coral bommies in May ($t_{1,4} = 7.92$, $p < 0.001$) and January ($t_{1,7} = 2.73$, $p = 0.03$, Fig. 2). Dissolution rates in January were 0.78 ± 0.06 g h^{-1} ($n = 7$) upstream and 0.69 ± 0.05 g h^{-1} ($n = 5$) downstream. In May, mean dissolution rates upstream were 0.51 ± 0.01 g h^{-1} ($n = 5$) and 0.45 ± 0.02 g h^{-1} ($n = 5$) downstream.

At the scale of coral–algal interactions, retention times of fluorescein dye were longer within algal turf–*Porites* interactions (108–330 s) than *Turbinaria–Porites* interactions (7–14 s). Mean retention times were three times longer within downstream algal turf–massive *Porites* interactions (330 ± 81 s, $n = 17$) than upstream interactions (109 ± 27 s, $n = 17$) in both May ($t_{1,9} = -1.9$, $p = 0.04$, Fig. 3) and January ($t_{1,6} = 2.6$, $p = 0.04$, Fig. 3). *Turbinaria*–massive *Porites* interactions retained dye significantly longer in downstream (12 ± 3 s, $n = 11$) than in upstream (8 ± 1.0 s, $n = 11$) only in May 2010 ($t_{1,10} = -2.616$, $p = 0.03$, Fig. 3). In January, retention times within *Turbinaria–massive Porites* did not differ between the upstream to downstream sides of coral bommies.

Microbial concentrations

Microbial concentrations ranged from 9 to 10 × 10^5 cells ml^{-1} in the water column to 2 × 10^7 cells ml^{-1} above the surfaces of corals in samples collected from both upstream and downstream sides of coral bommies. Differences in microbial concentrations within zones of interaction were consistent with patterns of dye retention times. Mean cell concentrations within zones of interaction of massive *Porites*–algal turf (1 × 10^7 ± 3 × 10^6 cells ml^{-1}, $n = 16$) were significantly higher than concentrations within massive *Porites–T. ornata* interactions (2 × 10^6 ± 5 × 10^5 cells ml^{-1}, $n = 16$; ANOVA, $F_{1,30} = 55.7$, $p < 0.001$, Fig. 4). Upstream microbial concentrations within zones of interactions between massive *Porites* and both algal types were significantly lower (6 × 10^6 ± 2 × 10^6 cells ml^{-1}, $n = 16$) than downstream (9 × 10^6 ± 3 × 10^6 cells ml^{-1}, $n = 16$; ANOVA, $F_{1,30} = 4.9$, $p = 0.03$, Fig. 4). There was a significant difference among the bommies sampled ($F_{15,30} = 6.8$, $p < 0.001$) and a significant interaction between bommie and algal type ($F_{1,15} = 3.5$, $p < 0.05$).

There were no significant differences in microbial concentrations due to proximity to algal turf or *Turbinaria* (coral samples collected 5 cm away from the zone of interaction). Additionally, there were no differences in microbial concentrations over corals between upstream and downstream sides of coral bommies, but there was an effect of the blocking factor, bommie (ANOVA, $F_{15,30} = 47.2$, $p < 0.001$). Water column samples collected away from algal turf–massive *Porites* interactions yielded significantly greater microbial concentrations than those collected adjacent to *Turbinaria*–massive *Porites* interactions

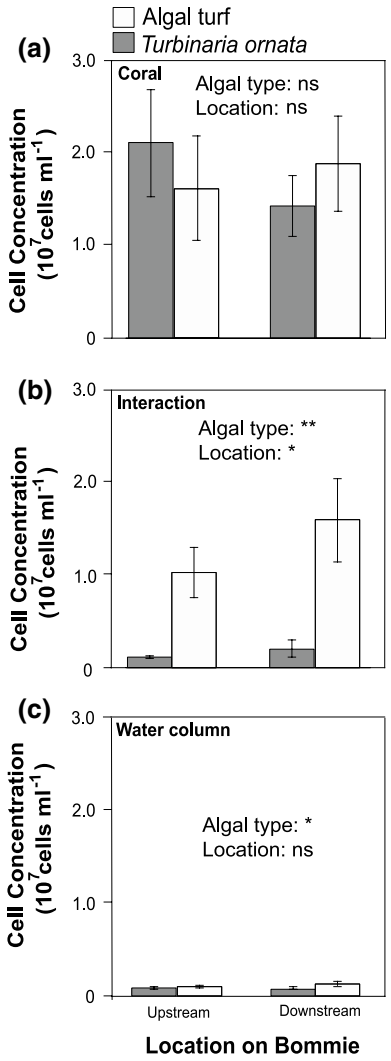

Fig. 4 Mean (±SE) microbial densities in water samples from the back reef **a** on the surface of coral, **b** within zones of interaction, and **c** in the water column. *Bars* indicate samples from algal turf versus massive *Porites* spp. and *T. ornata* versus massive *Porites* spp. ($n = 16$ samples per measurement). Downstream algal turf–massive *Porites* interactions contained higher microbial densities than upstream algal turf and all *Turbinaria*–massive *Porites* interactions. *Asterisks* indicate level of significance; *two asterisks* indicate $p < 0.01$, *one asterisk* indicates $p < 0.05$, *ns* indicates not significant

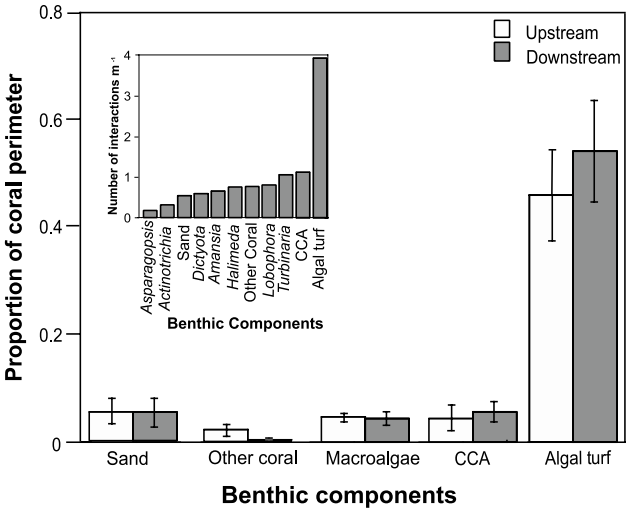

Fig. 5 Mean ± SE of interaction types around the perimeter of *Porites* sp. on the upstream and downstream sides of coral bommies ($n = 10$ bommie^{-1}). There were no significant differences ($p > 0.05$) between the upstream and downstream sides of coral bommies for any of the benthic components. *Inset* total number of interactions between *Porites* sp. and major organisms surrounding colonies normalized to the height of the coral bommie ($n = 20$ bommies)

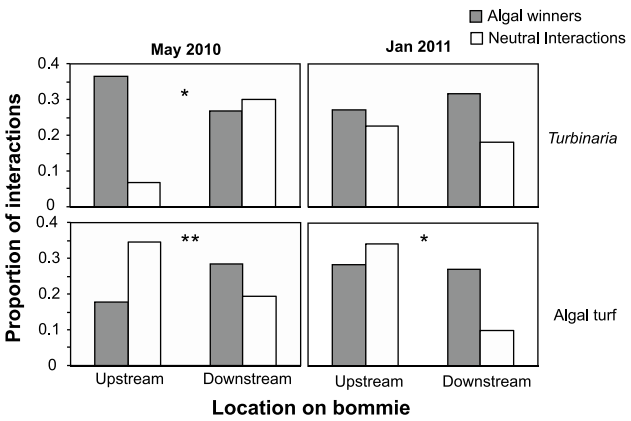

Fig. 6 Proportions of neutral versus algal winners between the upstream and downstream sides of bommies for *T. ornata*–massive *Porites* spp. in May 2010 and January 2011 (*top* graphs) and Algal turf–massive *Porites* spp. in May 2010 and January 2011 (*bottom* two graphs). *Asterisks* indicate level of significance; *two asterisks* indicate $p < 0.01$, *one asterisk* indicates $p < 0.05$, *ns* indicates not significant

($2 \times 10^6 \pm 1 \times 10^5$ and $8 \times 10^5 \pm 8 \times 10^4$ cells ml^{-1}, $n = 16$, respectively; ANOVA $F_{1,30}$, $p = 0.02$, Fig. 4). There also was a significant difference between bommies ($F_{15,30} = 14.4$, $p < 0.001$).

Extent, frequency, and outcome of interactions

The most abundant algal functional group in contact with massive *Porites* spp. was algal turf; macroalgal species also were present, and they included *T. ornata*, which was the most frequent macroalgal competitor with *Porites* spp., *Halimeda* spp., *A. rhodantha*, *Lobophora variegata*, *Dictyota* spp., and *Actinotrichia fragilis* (Fig. 5). Algal turf communities occupied 50 % of the interaction perimeter of massive *Porites* spp. colonies, while macroalgae collectively, only, accounted for an average of 5 % of the interacting perimeter of coral colonies (Fig. 5). There were no significant differences in the proportion of massive *Porites* perimeters in contact with algal turf (ANOVA, $F_{1,18} = 0.426$, $p = 0.912$), macroalgae ($F_{1,18} = 0.013$,

$p = 0.912$), CCA ($F_{1,18} = 0.137$, $p = 0.716$), or other corals ($F_{1,18} = 1.582$, $p = 0.225$) on the upstream or downstream sides of coral bommies.

The proportion of algal turf wins and neutral interactions differed between the upstream and downstream sides of coral bommies. There were significantly more algal turf wins on downstream sides (28–40 %) than on the upstream sides of coral bommies (18–22 %) in May ($\chi^2_{179} = 11.7$, $p < 0.01$) and January ($\chi^2_{70} = 5.6$, $p = 0.02$, Fig. 6). *Turbinaria* wins were higher on the upstream sides of coral bommies (36 %) compared to the downstream (26 %) in May ($\chi^2_{29} = 4.76$, $p = 0.03$). There were no differences in *Turbinaria* wins on the upstream and downstream sides of bommies when flow was higher in January (Fig. 6).

Changes in percentage cover of corals over time

The mean percentage cover of corals within 0.2-m^2 quadrats surrounded by algae decreased over time (from 49 ± 3.7 to 37 ± 4.6 %, $n = 23$; RM ANOVA, $F_{2,12} = 5.5$, $p = 0.02$, Fig. 7), but there was no difference in percentage cover between the upstream and downstream sides of coral bommies (RM ANOVA, $F_{1,20} = 1.124$, $p = 0.71$).

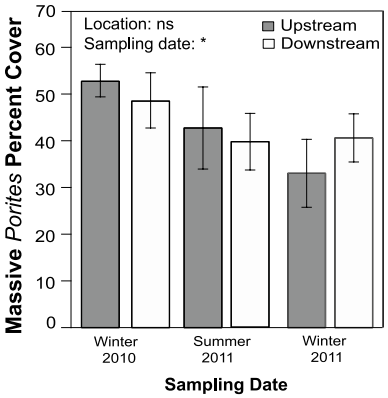

Fig. 7 Mean (±SE) percentage of live coral cover in contact with algae from the austral winter 2010 to austral winter 2011 within photoquadrats ($n = 15$) decreased significantly. *Asterisks* indicate significance ($p < 0.05$), *ns* indicates no significance

Discussion

Coral–algal interactions are pervasive on coral reefs (Barott et al. 2012). Coral–macroalgal and coral–algal turf interactions often are considered negative (River and Edmunds 2001; Jompa and McCook 2002); however, few studies have explored variation in the outcomes of interactions relative to the physical environment. This study showed that the results of coral–algal interactions are dynamic with outcomes modulated by the flow environment.

Coral reefs are structurally complex, and as a result, corals and algae experience different environmental conditions depending on their microhabitats. Microhabitats with differing flows are common on reefs as flow speeds can vary according to heights of structures (i.e., bommies), distances from the reef crest, as well as within cracks and crevices (Hench et al. 2008; Lenihan et al. 2008; Hench and Rosman 2013). We observed that flow over the upstream and downstream sides of coral bommies differed across three spatial scales. On the back reef, differences in the flow environment were associated with the effectiveness of different hypothesized mechanisms underlying coral–algal interactions.

Our results suggest that microbially mediated hypoxia (Smith et al. 2006) may only occur and be effective in promoting overgrowth under conditions of low flow. Short retention times of fluorescein dye suggest thin DBL thicknesses, conditions under which hypoxia cannot develop and cannot result in coral tissue death (Kühl et al. 1995; Smith et al. 2006; Barott et al. 2009, 2011; see Wangpraseurt et al. 2012; Brown and Carpenter 2013). Algal turf–massive *Porites* interactions in high flow and *Turbinaria*–massive *Porites* interactions in both low flow and high flow had shorter dye retention times and lower microbial concentrations than algal turf–massive *Porites* in low flow (downstream side of bommies), indicating that algal competitive success under these conditions likely is not microbially mediated through hypoxia (Wangpraseurt et al. 2012; Brown and Carpenter 2013; but see Haas et al. 2013). Furthermore, upstream *Turbinaria*–massive *Porites* interactions contained microbial concentrations similar to concentrations observed in the water column ($2 \times 10^6 \pm 5 \times 10^5$ cells ml^{-1}), suggesting the algae do not stimulate microbial growth/activity within the DBL (Azam et al. 1983; Kline et al. 2006). Downstream *Turbinaria*–massive *Porites* interactions showed slightly higher microbial concentrations than water column concentrations, suggesting that despite short retention times, there is potential for microbially mediated competition via creating a reservoir of microbes. These results combined with the generally shorter retention times of fluorescein dye within *Turbinaria*–massive *Porites* interactions (7–14 s) indicate that algal turf communities could provide conditions that would support microbially mediated hypoxia (Barott et al. 2009, 2011; Haas et al. 2011, 2013; but see Brown and Carpenter 2013), but the effects are dependent on the flow environment. There are other mechanisms that may be environment specific, including transfer of pathogenic microbes or changes in coral microbial community composition, but these were not tested in this study. However, it is likely that there are more complex interactions at play as microbial concentrations are only one metric by which to assess potential microbial activity. Because there were differences in water column

concentrations based on proximity to interactions, this indicates a potential feedback between interactions and the water column as has been observed in other studies (Dinsdale et al. 2008; Barott and Rohwer 2012).

Long dye retention times within algal turf–massive *Porites* interactions were due to both algal morphology and reduced overall water flow (Carpenter and Williams 1993). Microbial concentrations within algal turf–massive *Porites* interactions both upstream and downstream were closer to concentrations observed on and above the surface of corals ($1 \times 10^7 \pm 3 \times 10^6$ cells ml^{-1}) than in the water column, suggesting the potential for high microbial activity via increased growth (Azam et al. 1983; Garren and Azam 2010). These results suggest that densely packed algal turf canopies retain water soluble substances (i.e., labile DOC) and provide conditions that could lead to increased microbial respiration, the creation and retention of low oxygen conditions, and ultimately coral tissue death (Kline et al. 2006; Smith et al. 2006). Additionally, other chemical alterations (i.e., increased pathogenic microbes, increased pCO_2, and accumulation of chemotactic cues) may also be maintained (Ducklow and Mitchell 1979; Kline et al. 2006; Garren et al. 2014) and lead to increased incidence of disease/decreased coral health, which can have cascading effects on the outcomes of coral–algal interactions. However, these environmental conditions may only develop under reduced flow and thus likely are limited in coral reef habitats that are characterized by higher water flow.

Coral–*Turbinaria* contact increases in areas of higher flow. Increased coral–algal contact also may lead to greater allelochemical transfer (Rasher et al. 2011), but this was not tested here, and the algae that were tested either are not allelopathic (*T. ornata*) or have not been tested for allelopathy (algal turf). *Turbinaria* tended to outcompete corals more frequently in upstream locations than in downstream locations. However, there was no difference in outcomes in the higher flow month, January, likely because the algae are located closer to the tops of coral bommies, where turbulence is higher because it is closer to the water surface (Denny 1988; Hench and Rosman 2013). Thus, in austral summer, *Turbinaria*–massive *Porites* interactions, may regularly experience higher flow regardless of the side of the coral bommie where they are located.

Although algal turf consistently outcompeted massive *Porites* on downstream sides of coral bommies across the seasons sampled, this pattern did not lead to differences in the extent (proportion of coral perimeter) of algal turf around the interacting perimeter of coral, or coral percentage cover over time between the upstream and downstream sides of coral bommies. The proportion of coral perimeter in contact with algal turf was similar on the upstream and downstream sides of coral bommies as was the proportion of perimeter involved in macroalgal interactions. Thus, algae that are "better" at competing in high flow environments may have the advantage upstream and those with advantage in low flow were likely more effective in downstream microhabitats. Additionally, corals lost two-dimensional space when surrounded by algae regardless of whether they were located on the upstream or downstream of a coral bommie. Together, these results demonstrate that coral margins shrink in response to contact with multiple algal types. We suggest that the absence of a difference in coral percentage cover between the upstream and downstream sides of coral bommies is due to the algal diversity and abundance surrounding the coral, which were not statistically different between upstream to downstream habitats. Corals surrounded by a diverse algal assemblage likely are affected by multiple competitive encounters, some of which involve mechanisms that are differentially effective in different flow environments. This suggests that the outcomes of coral–algal competitive interactions likely are not deterministic but are context dependent and will vary across several spatial scales, determined at least in part, by the local flow environment.

Water flow is only one of the factors that affect corals and algae. Algal abundance and growth often are regulated by top-down (herbivory) and bottom-up (nutrients) processes (Jompa and McCook 2003; Rasher and Hay 2010). Scarids and acanthurids are abundant on the back reef of Moorea resulting in consistently high levels of herbivory on these reefs (Adam et al. 2011). Herbivory limits the frequency and strength of competitive interactions between corals and algae (Hughes 1994; Bellwood et al. 2004; Rasher and Hay 2010). Cropping of the algal canopy by herbivores decreases the canopy height and the thickness of the DBL created by the algal canopy (Carpenter and Williams 1993). Thus, herbivores in low flow areas can mitigate the effects of chemically mediated competition between corals and algae by decreasing DBLs, preventing or shortening retention times of hypoxic conditions, decreasing microbial concentrations between coral–algal interactions as well as decreasing coral–algal contact. Additionally, algal encroachment on live coral tissue can be a slow process (months to years, Box and Mumby 2007), especially if algal growth is regulated by other factors such as herbivory (Hughes 1994).

On small scales and at discrete times, flow influences the effectiveness of some chemically and physically mediated mechanisms underlying massive *Porites*–algal interactions. Microbially mediated competitive interactions leading to hypoxic conditions are likely only possible in low flow areas, where longer retention times could facilitate the maintenance of hypoxic micro-zones. We suggest that the algal morphology and flow operate in concert to influence the outcomes of interactions between corals and algae. On a larger spatial and longer temporal scale, the effects of

flow likely are masked by the effects of herbivory, which control algal abundance and canopy heights. Together, these results demonstrate that the outcomes of coral–algal interactions are dynamic and context dependent and can be influenced by the complex flow environments created by a spatially complex reef habitat.

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