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Evidence for water-mediated mechanisms in coral–algal interactions

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Although many coral reefs have shifted from coral-to-algal dominance, the consequence of such a transition for coral–algal interactions and their underlying mechanisms remain poorly understood. At the microscale, it is unclear how diffusive boundary layers (DBLs) and surface oxygen concentrations at the coral–algal interface vary with algal competitors and competitiveness. Using field observations and microsensor measurements in a flow chamber, we show that coral (massive *Porites*) interfaces with thick turf algae, macroalgae, and cyanobacteria, which are successful competitors against coral in the field, are characterized by a thick DBL and hypoxia at night. In contrast, coral interfaces with crustose coralline algae, conspecifics, and thin turf algae, which are poorer competitors, have a thin DBL and low hypoxia at night. Furthermore, DBL thickness and hypoxia at the interface with turf decreased with increasing flow speed, but not when thick turf was upstream. Our results support the importance of water-mediated transport mechanisms in coral–algal interactions. Shifts towards algal dominance, particularly dense assemblages, may lead to thicker DBLs, higher hypoxia, and higher concentrations of harmful metabolites and pathogens along coral borders, which in turn may facilitate algal overgrowth of live corals. These effects may be mediated by flow speed and orientation.

1. Introduction

Competition for space plays a major role in structuring networks of interacting species [1]. On coral reefs, intense competition occurs between sessile benthic organisms, particularly corals and algae that can be two major components of the benthos [2]. During recent decades, many tropical reefs have transitioned from coral-to-macroalgal dominance [3]. This community shift increases the frequency and diversity of coral–algal interactions and frequently results in coral competitive loss that can drive coral into further decline [4]. Algal overgrowth is facilitated by the combined effects of local (e.g. nutrients, overfishing of herbivorous fish) and global (e.g. climate-induced coral bleaching) stresses [3–7]. These stresses alter existing coral–algal interactions and create new interactions with different algal groups through a concomitant shift in algal composition from low biomass crustose coralline algae (CCA) and short turfs towards dense turfs, fleshy macroalgae, and cyanobacterial mats [4,8–9]. Despite being a well-documented phenomenon, the consequence of such a shift for coral–algal interactions and their underlying mechanisms remain poorly understood.

Interactions between corals and algae typically involve a range of physical, microbial, and chemical mechanisms [2,10]. Direct, physical effects include

shading, abrasion, and smothering [11,12]. However, plastic algal mimics, used to simulate physical effects, often produce fewer effects on corals than live organisms, supporting the role of chemistry and metabolic activity [13–15]. Chemicals and microbes can be transmitted by contact- or water-mediated mechanisms. However, the relative importance of contact- versus water-mediated mechanisms on the competition between corals and algae is unclear [10]. Direct contact can facilitate the transfer of hydrophobic allelochemicals and pathogens which are present on algal surfaces [8,15,16]. For example, direct contact with some species of macroalgae, as well as their hydrophobic extracts, has been shown to cause bleaching, tissue necrosis, and/or disease of some corals [13,14,17]. Algae also produce or harbour a number of potentially harmful hydrophilic compounds, including dissolved organic matter (DOM), free-living microbes, and exosomes, which are mobile in the water column [10,18]. These compounds will be elevated within the diffusive boundary layer (DBL) downstream of the algae and spread on to downstream neighbouring corals [10,19,20].

Water-mediated interactions are likely to depend on several physical (e.g. light, flow, topography) and biological (e.g. metabolic activities) processes. In the field, seaweeds placed 3 cm away from corals had no impact on the severity and dynamics of a microbe-generated coral disease [21]. More recently, a two-dimensional diffusion model based on oxygen measurements in the field estimated that the transport of a low molecular weight substance produced continuously at a fixed rate by algae is mainly restricted to the DBL and extends only 1 mm across the border to a neighbouring coral [22]. These studies suggest that hydrodynamics limit the impact of algal exudates in the natural environment and that water-mediated interactions between corals and algae largely operate at the mm-to-µm scale within the DBL. The benthic DBL is a thin film of stagnant, diffusion-limited water surrounding the benthos, whose thickness is determined by flow and microtopography [23,24]. Thinner DBLs promote the exchange of dissolved gases and nutrients for metabolic processes and the removal of wastes [25,26]. Conversely, thicker DBLs may lead to the accumulation of harmful substances and bacteria and localized alterations in oxygen concentrations [22,27]. The chemical microenvironment within the DBL of the coral–algal interface is also likely to depend on the rates of release of chemical and microbial compounds from each competitor, which are species specific. For example, under similar environmental conditions, turf algae produce almost twice as much dissolved organic carbon (DOC) per unit surface area compared with other fleshy macroalgae [18]. This could lead to high concentrations of DOC within the DBL at the coral–turf interface and cause enhanced microbial growth and respiration, particularly that of opportunistic pathogens [28], and subsequently coral mortality [29,30].

Here, we describe field observations and laboratory microsensor measurements used to assess the importance of water-mediated interactions between corals and algae. We characterized the oxygen conditions and DBL thickness at interaction zones between the massive coral *Porites* and different benthic competitors using oxygen microsensors in a flow chamber and compared our results with competitive outcomes in the field in Moorea, French Polynesia. A flow chamber with recirculating natural seawater was preferred over *in situ* measurements to minimize the effect of macro-scale (cm-to-m) variations in ambient flow, light, and topography. Interactions between massive *Porites* and the following six benthic competitors were studied: (i) massive *Porites* (i.e. conspecific), (ii) the CCA species *Porolithon onkodes*, (iii) thin turf algae (less than 5 mm canopy height), (iv) thick turf algae (5–20 mm canopy height), (v) the red macroalga *Amansia rhodantha* (Rhodophyta), and (vi) the cyanobacterium *Hydrocoleum majus*. These competitors belong to functional groups which are known to vary in their competitiveness against corals [10,31] and they can be used in a space for time comparison to examine transitions from coral to fleshy algal dominance.

We hypothesized that the interface between *Porites* and superior benthic competitors is characterized by thick DBL and high diel oxygen fluctuations, including hypoxic conditions at night. We then tested the effect of flow speed and direction on interactions between *Porites* and two benthic competitors (thin and thick turf algae), with the assumption that DBL thickness and oxygen fluctuations are reduced with increasing flow speed and when the coral is upstream of the algae. Finally, we estimated the importance of bacterial respiration in generating hypoxic conditions during the night by adding antibiotics, with the hypothesis that microbes cause highly hypoxic conditions at the coral–algal interface.

2. Material and methods

(a) Field study

Field data were collected between October 2013 and February 2014 across the back reef habitat at water depths of less than 3 m between Opunohu and Cook's Bays on the island of Moorea, French Polynesia (17°28.864′ S, 149°50.726′ O). This zone supports dense patches of live and dead coral, including large (1–4 m in diameter) bommies of *Porites lobata*, *P. australiensis*, and *P. lutea*. These three species are difficult to differentiate in the field, and we therefore refer to this complex of three species as massive *Porites*. The composition of major benthic functional groups across this habitat was determined using 10 randomly placed 30 m long line intercept transects orientated parallel to the shoreline. We distinguished thin and thick turf algae as dense filamentous algae of heights less than 5 mm and 5–20 mm, respectively, owing to the importance of algal turf height for corals, especially coral recruits [32], and boundary layers [10]. In order to quantify the abundance of coral–algal interactions, benthic organisms in contact with the perimeter of 16 haphazardly chosen massive *Porites* colonies were identified to species and/or functional groups. The length of the coral colony's edge in contact with each species and/or functional group (hereafter referred to as 'interface', see also electronic supplementary material, figure S1*a*) was measured to the nearest centimetre using a dressmaker's tape.

The movement of the interface between massive *Porites* and each of the six benthic competitors listed above was estimated using photographic time series ($n = 4$–10). Approximately every four weeks over a 90 day period, photos were taken of a 10×10 cm area that included an interaction, a quadrat for scale, and four permanently installed stainless-steel nails at each corner. Changes in the position of the interface were analysed in Adobe Photoshop (CS3, Adobe Systems Inc.) using distinctive polyp structures as lines of reference to redraw the final (day 90) interface next to the initial interface (day 0). The rate of overgrowth was calculated by subtracting the surface area of retreat from advance and dividing it by the initial length of interaction. For the *Porites*–*Porites* interactions, the reference

colony was the larger sized colony dominating the bommie which is comparable to the colonies used in other interactions.

Temperature and light were recorded in 30 s intervals for a 7 day period in October 2013 at a water depth of 1 m using a HOBO Pendant® temperature/light 64 K data logger to set environmental parameters for the experiments. Temperature averaged 27.36 ± 0.77°C with a diurnal variation of 1.24 ± 0.64°C. Day-time (06.00–18.00 h) photosynthetically active radiation (PAR) availability averaged 550 µmol quanta m^{-2} s^{-1} (measured in lux and converted using the approximation of Valiela [33]).

(b) Flow chamber experiments

(i) Sample collection

Core samples of interactions were collected on the back reef platform using an air-powered drill with a diamond coated drill bit of 42 mm diameter (electronic supplementary material, figure S1*a*). Drilling was done perpendicular to the surface and leaving the interaction boundary crossing the middle of the core. Back in the laboratory, cores were adjusted to a height of 3 cm by sawing or filing and kept in an outdoor tank with running filtered seawater at the CRIOBE research station. They were acclimated for at least 6 h and used within 48 h.

(ii) Experimental set-up

To characterize the oxygen microenvironment of the interactions, a flow chamber (8 l) with controllable flow speeds and recirculating natural seawater from the outdoor tank, where the cores were acclimated, was used in combination with oxygen microsensors (electronic supplementary material, figure S1*b*). A unidirectional flow was created in the chamber by a built-in paddle wheel and flow straighteners built into the upstream and downstream ends of the working section. By controlling the rotation speed of the paddle wheel, the ambient flow could be adjusted within a range of 1–30 cm s^{-1} (see calibration procedure in electronic supplementary material, text S1). The temperature in the chamber was regulated (26.5–27.5°C) by a separate closed circuit warming/cooling system to match *in situ* conditions. During the day, additional artificial light was provided by 4 JAD Aquarium Co. Ltd. lights, each containing 3 T5–14 W bulbs, resulting in photosynthetic active radiation of 446 µmol quanta m^{-2} s^{-1} on the core as measured by a LI-COR LI-193 spherical quantum sensor. The chamber had an opening on the top side to enable measurements with a needle-type fibre-optical oxygen microsensor (OXR50-OI) to be taken on the core surface. All microsensor equipment was from Pyro-Science GmbH. The microsensor had an outer tip diameter of 50 µm and a 90% response time of less than 3 s. It was connected to an optical oxygen meter (FireStingO2), a dual channel reader (DCR16), and a PC and was mounted on a PC-interfaced, motorized micromanipulator (MU-1) controlled by dedicated data acquisition and positioning software (ProFix). A stereomicroscope rotated horizontally was used to visualize the core surface and to help position the sensor tip.

(iii) Microsensor measurements

Following transfer to the flow chamber, individual cores were placed at distances of greater than 4 cm from the chamber walls and the water surface, and were allowed to acclimate for 30 min before the measurements started. Ambient flow was set at a speed of 3 cm s^{-1} (except for Exp. 2) based on averaged values that can be found *in situ* in the back reef habitat in Moorea [34,35]. Ambient oxygen concentrations were maintained at 181.41 ± 1.8 µM during the day and 173.09 ± 1.7 µM at night by re-filling the flow chamber with seawater twice daily. Oxygen profiles were run at three positions in a random order along an axis perpendicular to the interaction boundary (i) apparently healthy *Porites* tissue 1 cm away from the interaction boundary ('coral'), (ii) the interface between *Porites* and the competitor ('interface'), and (iii) apparently healthy tissue of the competitor 1 cm away from the interface ('competitor'; electronic supplementary material, figure S1*a*). Measurements on coral tissue were exclusively conducted on the coenosarc (tissue between polyps) in order to minimize the influence of tissue movement [36] and the spatial heterogeneity of coral photosynthesis [25]. The microsensor was oriented vertically. Shading from the sensor was minimal as artificial light sources were spread on either side. The sensor tip was moved as close as possible to the hard surface of the core (defined as 0 µm depth) and then moved upwards into the overlying water column in 50–500 µm steps. Note that, for the algal or cyanobacterial measuring positions, measurements were taken starting at the hard surface of the core underneath the algal canopy or cyanobacterial mat and not at the top of the canopy or mat. The microsensor was allowed 20 s resting time between each measurement. Prior to running the measurements on each core, the sensor was linearly calibrated, at experimental temperature and salinity, from measurements in air-saturated seawater and oxygen-free seawater (made anoxic by the addition to saturation of sodium sulfite).

(iv) Experiment 1: effects of benthic competitors

To determine whether the coral microenvironment depends on benthic competitors, we performed microsensor measurements on core samples of interactions between massive *Porites* and each of the six benthic competitors listed above ($n = 5$). One replicate of each interaction type was measured in a random order before starting with the next set of replicates. Measurements were conducted with the competitor portion of the core placed upstream of *Porites* during day- (08.00–15.00) and night- (21.00–02.00) times.

(v) Experiment 2: effects of turf height, ambient flow speed, and direction

This experiment was designed to determine whether the coral microenvironment depended on flow speed and direction. Day- and night-time microsensor measurements were made on core samples of *Porites* versus thin turf and *Porites* versus thick turf interactions ($n = 4$). Each core was subjected to four increasing ambient flow speeds (1, 3, 5, and 10 cm s^{-1}) at each of two orientations (algae upstream from coral versus coral upstream from algae). Measurements were performed after an acclimation period of 15 min following each speed/orientation change. As for Exp. 1, one replicate of each interaction type was measured in a random order before starting with the next set of replicates. Measurements on each core were run with algae upstream from coral first starting with the slowest velocities and then moving on to the fastest velocities before switching orientation.

(vi) Experiment 3: effects of microbes

The final experiment tested whether night-time hypoxia caused by algae could be prevented with the addition of antibiotics. Core samples of *Porites* versus thin turf and *Porites* versus thick turf interactions were placed in 12 individual aerated 1 l containers for 24 h. Half of the containers were filled with seawater alone and the other half were filled with seawater plus the broad-spectrum antibiotic ampicillin (concentration of 100 µg ml^{-1}). This exposure time and concentration are sufficient to dramatically reduce the density of microbes without impacting coral health in small-volume containers [27,37,38]. All water and antibiotic treatments were changed after 12 h. Microsensor measurements were performed at night starting with the untreated cores. The seawater of the flow chamber was then replaced by ampicillin-treated seawater to conduct night-time measurements on the treated cores.

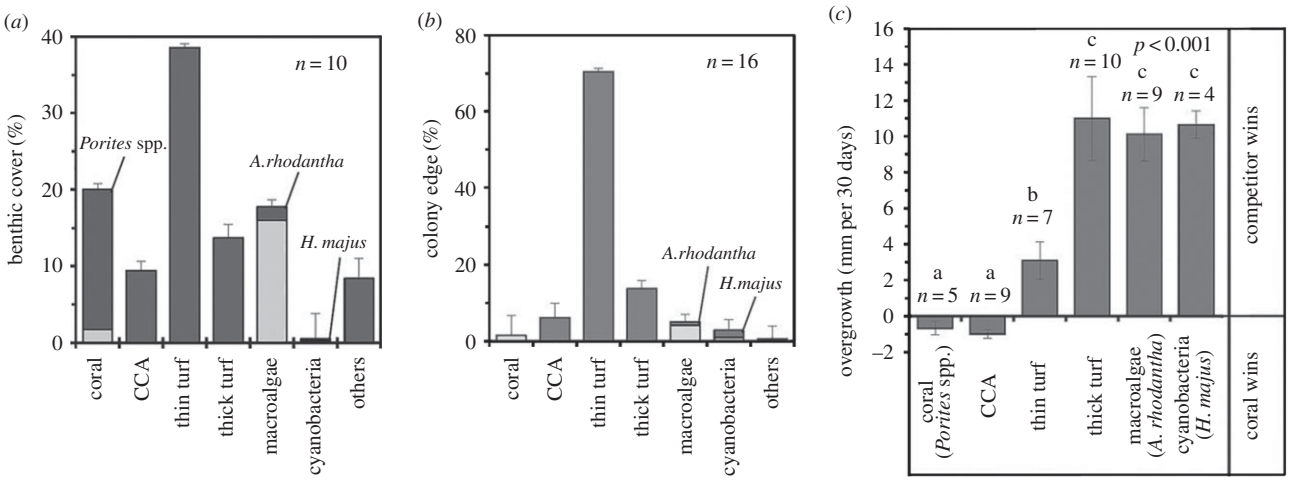

Figure 1. (*a*) Composition of the reef benthos (hard substratum). (*b*) Proportion of massive *Porites* colony edge interacting with major benthic functional groups. (*c*) Rates of overgrowth of the benthic competitors over massive *Porites* spp. The dark grey colour indicates the benthic competitors used in the experiments. Rates of overgrowth were analysed by a one-way ranked based ANOVA ($F_{5,13} = 34.201$, $p < 0.001$). Letters indicate homogeneous subgroups by Tukey post hoc tests. Data points are mean $\pm$ s.e.m.

(c) Statistical analyses

To characterize the microenvironment, two variables were used: (i) the oxygen concentration at depth = 0 µm (hereafter referred to as surface oxygen) and (ii) the thickness of the DBL, which was calculated from each oxygen profile from the intercept between the linear extrapolation of the oxygen curve at the benthic surface and the bulk concentration in the water column [22,39]. In cases when profiles were not linear (e.g. owing to low oxygen concentrations within the algal canopy followed by high oxygen concentrations at the canopy surface), only the linear section of the oxygen curve reaching the bulk oxygen was used for the calculation of the DBL thickness. Field (overgrowth) and microsensor data (surface oxygen and DBL thickness) were normally distributed (Shapiro–Wilk's test) but not equal in variance (Levene's test). To account for the unequal variances, data were rank transformed prior to analysis. Field data were analysed using a one-way ANOVA with benthic competitors as a fixed factor. Differences in oxygen concentrations and DBL were analysed day and night separately except for Exp. 3 which was run only at night. Data from Exp. 1 were examined using ANOVAs, with measuring position (coral, interface, and benthic competitor) as a fixed factor and core as a random factor. To examine variables influencing coral damage (overgrowth), we ran Spearman's rank-order correlations between the rates of overgrowth and four metrics characterizing the microenvironment at the interface using mean values for each benthic competitor ($n = 6$): (i) surface oxygen concentrations during the day and (ii) night, (iii) diel oxygen fluctuations (i.e. difference in mean oxygen concentrations between day and night), and (iv) DBL thickness. Data from Exp. 2 were analysed separately for each flow orientation $\times$ turf category (thin versus thick turf) combination using ANOVAs, with measuring position as a fixed discrete factor, flow as a continuous fixed factor, and core as a random factor. Finally, surface oxygen data from Exp. 3 were evaluated using an ANOVA, with turf category, measuring position, and antibiotic treatment as fixed factors and core as a random factor. Differences among subgroups were analysed using Tukey post hoc tests. Statistical analyses were performed using SPSS Statistics v. 20 (IBM, Armonk, NY).

3. Results

(a) Field study

The dominant benthos on the reef hard substratum was thin turf, followed by corals, macroalgae, and thick turf (figure 1*a*). Massive *Porites* was the dominant coral. Colonies interacted mostly with thin turf, followed by thick turf, CCA, and macroalgae (figure 1*b*). Photographic time series demonstrated that *H. majus*, *A. rhodantha*, and thick turf algae rapidly gained space at the interaction zone with *Porites* (figure 1*c*). Thin turf overgrew *Porites* but at a significantly lower rate than thick turf, *H. majus*, and *A. rhodantha*. In contrast, *Porites* gained space when competing against CCA and conspecifics, albeit at very slow rates.

(b) Experiment 1

The oxygen microenvironment at the interaction interface varied widely between competitors (figure 2; oxygen profiles and complete ANOVA results in electronic supplementary material, figure S2 and table S1). During the day, the interfaces with thin and particularly thick turf were hyperoxic (surface oxygen of approx. 300 and approx. 600 µM, respectively) relative to ambient seawater (approx. 180 µM) and to oxygen concentrations on the coral tissue (approx. 210 µM; figure 2*a*). Day-time surface oxygen concentrations at interfaces with conspecifics, CCA, *A. rhodantha*, and *H. majus* did not differ from the coral tissue. During the night, the interfaces with *H. majus*, *A. rhodantha*, and thick turf algae were hypoxic (approx. 50 µM) relative to ambient seawater (approx. 170 µM) and to oxygen concentrations on the coral tissue or at the interfaces with thin turf, CCA, and conspecifics (approx. 110 µM) (figure 2*b*). Surface oxygen concentrations on apparently healthy *Porites* tissue (i.e. coral measuring position) during day or night did not vary with benthic competitors.

Surface oxygen concentrations on thin and thick turf algae were hyperoxic (more than 500 µM) during the day and anoxic (less than 2 µM) during the night. Surface oxygen concentrations on *A. rhodantha* and *H. majus* were hypoxic or anoxic during both day- and night-time. Although these results may appear unexpected during day-time for these photosynthesizing organisms, surface measurements refer to measurements taken at a depth of 0 µm, which is the hard (skeletal) surface of the core, and not from the surface of the algae/mat itself (see Material and methods). Thus, these measurements were taken underneath the algal canopy or cyanobacterial mat where hypoxic conditions

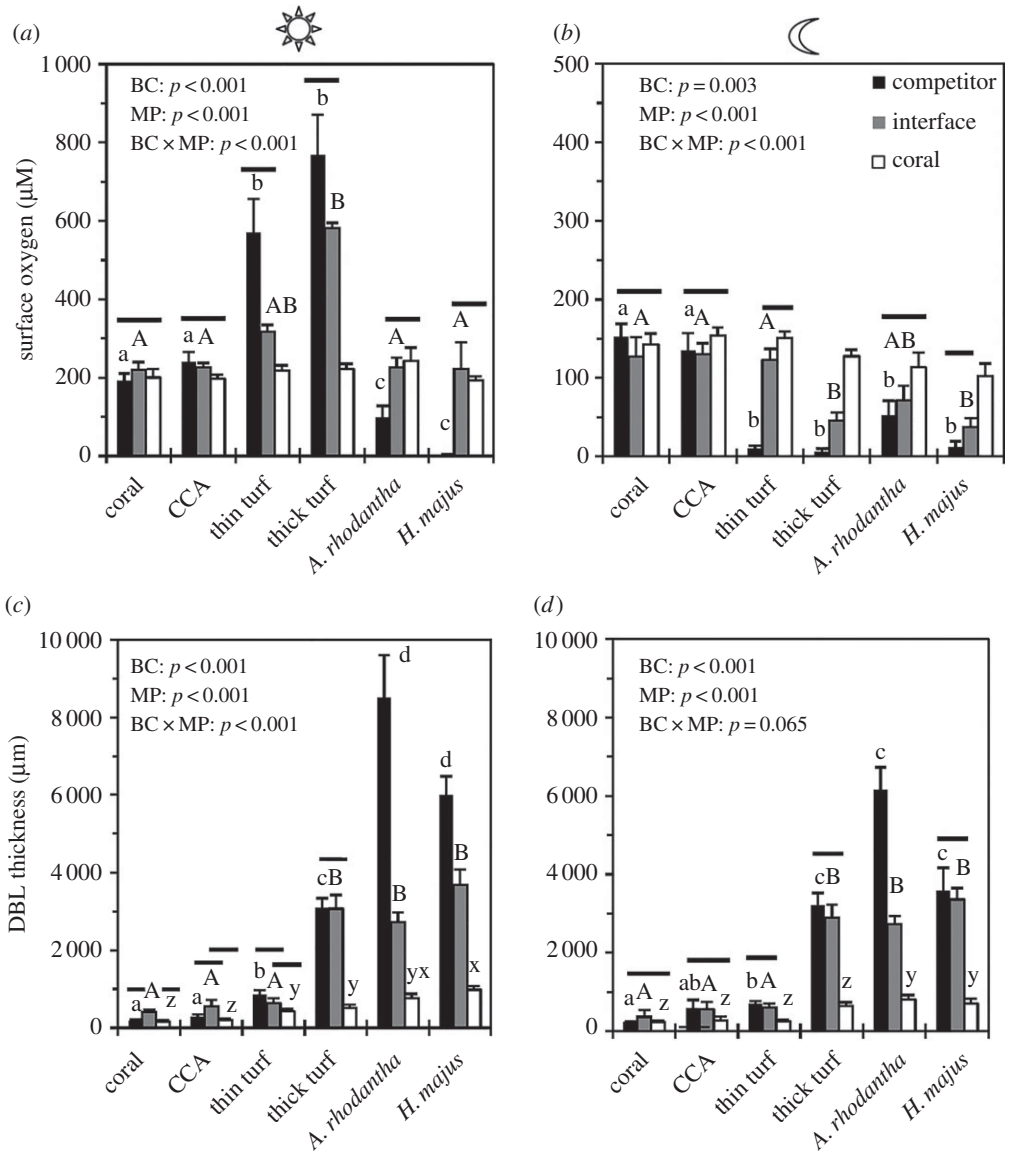

Figure 2. Day and night surface oxygen concentrations (*a*,*b*) and DBL thicknesses (*c*,*d*) in interactions between massive *Porites* spp. and different benthic competitors. Competitors were placed upstream of *Porites*. Data points are mean ± s.e.m. ($n = 5$). *p*-values are from rank-based ANOVAs. See electronic supplementary material, table S1 for complete ANOVA results. Letters indicate significant groupings of benthic competitors (BC) for each of the three measuring positions (MP) by Tukey multiple comparisons tests. Horizontal bars indicate significant groupings of measuring positions for each benthic competitor. Note scale differences on the *y*-axis for day and night surface oxygen concentrations.

could occur throughout the day and the night. In contrast, surface oxygen concentrations on conspecific coral and CCA remained above 100 µM at night.

DBL thickness remained similar between day and night for each benthic competitor × sampling position combination (figure 2*c*,*d*). The interfaces with *H. majus*, *A. rhodantha*, and thick turf algae showed a thick DBL (approx. 3 000 µm). In contrast, the interfaces with thin turf, CCA, and conspecifics showed a thin DBL (approx. 500 µm). DBLs on competitor surfaces were thickest for *H. majus*, *A. rhodantha*, and thick turf algae and thinnest for conspecifics, CCA, and thin turf. DBL thickness on apparently healthy *Porites* tissue was always less than 1 000 µm. It was higher in interactions with *A. rhodantha* and *H. majus*, probably owing to the effect of their high canopies affecting flow regime downstream beyond the 1 cm distance separating the interface (i.e. edge of the canopies) and coral measuring positions.

Rates of overgrowth correlated significantly with night-time surface oxygen concentrations and DBL thickness (Spearman's rank-order correlations, $r^2 = 0.889$ and 0.785, respectively, $p < 0.05$) and not with day-time surface oxygen concentrations or diel oxygen fluctuations.

(c) Experiment 2

Day-time hyperoxia and night-time hypoxia at the interface were alleviated by increasing ambient flow, except for when thick turf was upstream (figure 3*a*,*b*, complete ANOVA results in electronic supplementary material, tables S2 and S3). Increased flow also reduced day-time surface oxygen concentrations on the turf algae, regardless of flow orientation. At night, thick turf remained anoxic, regardless of flow speed. Concentrations on apparently healthy *Porites* tissue during day or night remained stable, regardless of flow speed and direction.

DBL thickness showed similar trends between day and night, so only day-time values are presented (figure 3*c*, night values in electronic supplementary material, figure S3). DBL thickness at the interface decreased with increasing flow, except for when thick turf was upstream. When the

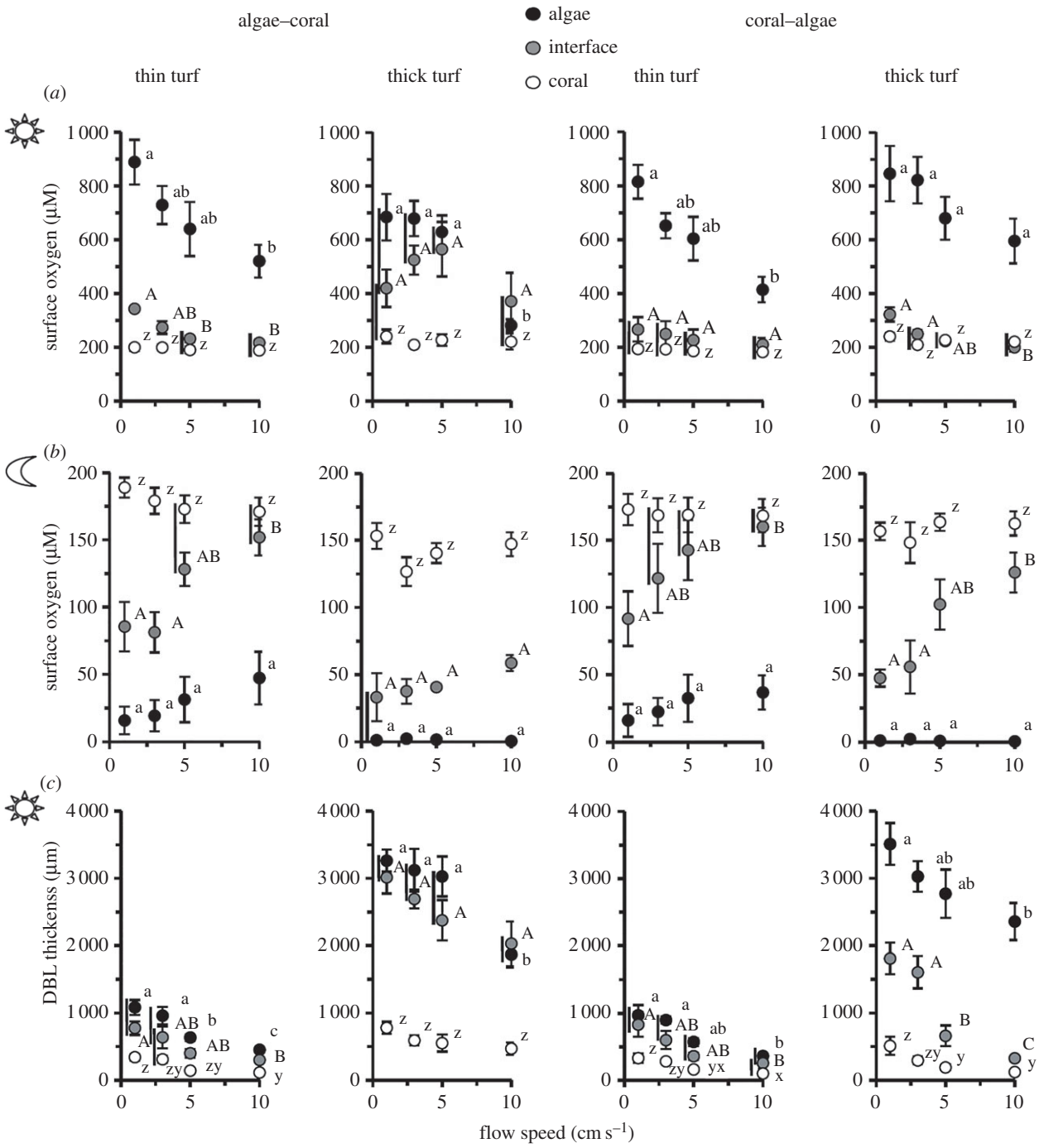

Figure 3. (*a*) Day- and (*b*) night-time surface oxygen concentrations, and (*c*) day-time DBL thickness as a function of flow speed (FS) and direction (D) in interactions between massive *Porites* spp., with thin and thick turf algae. Data points are mean ± s.e.m. ($n = 4$). See electronic supplementary material, tables S2 and S3 for complete statistical results. Letters indicate significant groupings of flow speeds for each of the three measuring positions (MP) by Tukey multiple comparison tests. Vertical lines indicate significant groupings of measuring positions within each flow speed. Algae–coral: algae upstream; coral–algae: coral upstream. Note scale differences on the *y*-axis for day and night.

coral was upstream, DBL thickness at the interface between coral and thick turf became rapidly similar to the DBL thickness on the coral surface with increasing flow. In contrast, when thick turf was upstream, values at the interface remained close to those present on the algae.

(d) Experiment 3

When ampicillin was added, night-time hypoxia was alleviated both at the interface and on the algae (figure 4, complete ANOVA results in electronic supplementary material, table S4). The reduction of hypoxia at the interface matched the reduction at the algal surface for both thin and thick turf. Surface oxygen concentrations on apparently healthy *Porites* tissue declined slightly with antibiotic addition.

4. Discussion

Benthic algae are commonly grouped into functional groups, including CCA, turf algae, and fleshy macroalgae [2,10]. CCA are typically poor competitors against corals and are even used as controls in studies of coral–algal interactions [31,40]. They are often associated with healthy reefs [8] as they facilitate the settlement and survival of recruiting corals [41] and prevent the colonization of macroalgae [42].

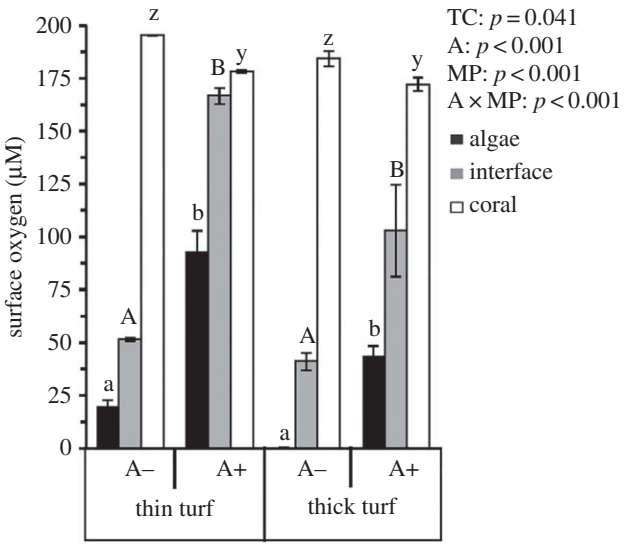

Figure 4. Night-time surface oxygen concentrations for thin and thick turf in the presence and absence of antibiotic treatment (A−, without ampicillin; A+, with ampicillin, respectively). Turf algae were placed upstream of *Porites*. Data points are mean ± s.e.m. ($n = 3$). *p*-values are from rank-based ANOVAs. See electronic supplementary material, table S4 for complete ANOVA results. Letters indicate significant groupings for each of the three measuring positions (MP) by Tukey multiple comparison tests. Horizontal bars indicate significant groupings of measuring positions for each antibiotic (A) and turf category (TC) treatment combination.

In contrast, fleshy macroalgae are frequently superior competitors against corals, inhibiting coral growth, reproduction, and recruitment [43–46]. Turf algae and benthic cyanobacteria have been less studied but they have also been shown to negatively affect corals at all life stages [12,32,47]. Our study confirms this ranking of competitiveness among algal functional groups against the massive coral *Porites*. In addition, we found that thin turf algae (less than 5 mm in height) did not overgrow corals as rapidly as thick turf algae (5–20 mm), highlighting the importance of turf height in coral–algal interactions. Elevated turf algae have been negatively associated with coral cover [48] and are known to be deleterious to coral settlement and survival [32,47].

Importantly, we show that the competitive abilities of the different functional groups, expressed as rate of overgrowth, matched patterns of hypoxia during the night and DBL thickness at the coral–algae interface, supporting (but not demonstrating) a causal link between the physiological processes occurring at the coral–algal interface and the competitive dynamics in the field. Coral interfaces with thick turf algae, macroalgae, and cyanobacteria were characterized by a thick DBL and strong hypoxia at night, whereas coral edges bordered by conspecifics, CCA, and thin turf had thin DBLs and less reduced oxygen concentrations at night. These results support the importance of water-mediated mechanisms in coral–algal interactions, in particular in interactions between corals and dense algal and cyanobacterial assemblages which are commonly encountered in degraded reefs. To date, a number of studies support the importance of allelochemical interactions among corals and algae. Seaweed extracts experimentally induce coral mortality in direct contact, with the extent of damage matching that caused by intact, live seaweeds [13,14]. Allelochemicals produced by algae are frequently hydrophobic and rely on transfer via direct contact. They are present on algal surfaces with highest concentrations found on basal portions of blades [15]. However, contact- and water-mediated mechanisms are not mutually exclusive and might act in synergy. It is plausible that allelochemicals transferred from algae to corals by direct contact initiate coral damage and subsequently facilitate the action of hydrophilic compounds.

Our results suggest that DBL thickness and/or hypoxia during the night at the coral–algal interface are important variables influencing coral tissue loss. A thick DBL at the coral–algal interface is likely to alter several physical, chemical, and microbial properties of the microenvironment. For example, mat-forming algal species, which severely restrict water exchange, decrease light and oxygen, and increase concentrations of DOC and soluble reactive phosphorus above understorey corals, and corals exposed to these conditions (i.e. pre-incubated seawater with macroalgae and shading) show significant physiological stress [49]. Likewise, a thick DBL is likely to facilitate the development of night-time hypoxia by impeding oxygen diffusion, limiting the removal of metabolic waste products, and enhancing the water-mediated transport of hydrophilic compounds (e.g. DOC) and microbes at the coral–algal interface [10]. Hypoxia, especially at night, limits coral respiration [25] and reduces the metabolism of coral symbionts [50]. Hypoxia has been measured in experimentally initiated and naturally occurring interactions between corals and turf or macroalgae [8,22,27,31,37]. Stressful pH levels are also likely to develop during the night in conjunction with hypoxia as a result of net respiration of turf or macroalgae [51]. A combination of locally reduced pH and oxygen can rapidly kill coral tissue [52], and a decrease in ambient pH values can facilitate coral overgrowth by algae [53].

In our study, high oxygen concentrations were measured at the coral–turf interface during daytime. Such hyperoxia has also been shown to create oxidative stress and bleaching in corals [26,54]. Hence, it cannot be ruled out as a stressor contributing to coral tissue loss, particularly in coral–turf interactions. However, we did not find a significant correlation between competitive gain/loss against the coral and day-time oxygen concentrations or diel oxygen fluctuations.

Alternatively, thick DBLs ameliorate the negative effects of ocean acidification by providing a biologically controlled buffer between the calcifying organism's external structure and the outer bulk seawater, potentially reducing rates of dissolution [55–57]. Dense algal canopies can decrease the susceptibility of understorey species to ocean acidification by providing regions of slow flow and higher day-time pH [57,58]. For example, reduced seawater velocities beneath the canopy-forming macroalga *Carpophyllum maschalocarpum* resulted in increased DBL thicknesses, higher pH (up to 8.9) and oxygen concentrations in the light, and lower pH (down to 7.74) and oxygen concentrations in the dark in understorey crustose coralline macroalgae [58]. Subsequent investigations should test the hypothesis that certain coral–algal interfaces could act as buffer zones against the corrosive effects of ocean acidification.

The oxygen concentrations at the coral–competitor interface largely matched those occurring on the algae, suggesting that algal-associated metabolites and microbes can spread to neighbouring corals, particularly when the algae are located upstream of the dominant current. When testing for the effect of flow speed on the coral–turf interactions, we found that increased flow reduces DBL thickness and

oxygen extremes at the coral–algae interface. Increased flow commonly results in thinner DBLs [56,59]. Previous studies showed that high flow reduces algal competitiveness over corals and bacterial concentrations at the coral–algal interaction zone [60,61]. Furthermore, our study shows that thick turf oriented upstream retains the hyper- and hypoxic conditions at the coral–algal interface more strongly compared to thin turf, supporting the importance of algal canopy height, flow speed, and orientation in water-mediated interactions between corals and algae. Elevated turf algae are known to create thick DBLs [23]. They might create a thick DBL at the downstream interface with corals by acting as a physical barrier, especially in low flow conditions. In turn, this could facilitate the accumulation of water-soluble leachates and microbes from algae over downstream neighbouring corals. Here, we studied unidirectional flow. However, *in situ* interactions are likely to be influenced by oscillatory or bidirectional flows that reverse according to the wave phase, although there may be net flow created by waves of similar wavelengths travelling in the same direction [62]. More research is needed to investigate precisely to what extent such flows disrupt the DBL and alleviate diffusion limitation at the interaction zones.

Hypoxia at the interaction zones between corals and algae has been suggested to be the result of bacterial respiration, with the hypothesis that microbes cause highly hypoxic conditions at the coral–algal interface owing to tissue degradation [31]. In our study, antibiotics reduced the hypoxic conditions at the coral–turf interface, suggesting that hypoxia during night-time is partially due to bacterial respiration. Antibiotics also suppressed the hypoxic conditions on the turf. The microbial biofilm at the interface could be fed by DOM from the algae leaching downstream during the day and resulting in high rates of microbial metabolism during the night. In such a case, oxygen depletion as a result of coral tissue degradation may be relatively minor. In a similar flume experiment, Brown & Carpenter [27] found no evidence of hypoxia caused by bacteria at the interface between massive *Porites* and turf. Possible explanations include different species composition of the turf assemblage and lower antibiotic concentrations.

As reefs transition towards macroalgal dominance, their algal assemblages commonly change from coralline algae and thin turf to thick turf, macroalgae, and cyanobacterial mats. Our results provide evidence for the importance of water-mediated mechanisms in coral–algal interactions and suggest that these mechanisms will increase as reefs shift towards fleshy algal domination. Denser algal assemblages may lead to thicker DBLs at coral–algal interfaces. In turn, this may lead to higher frequencies of hypoxia and higher concentrations of harmful metabolites and pathogens along coral borders, which would ultimately facilitate algal overgrowth of live corals and produce a positive feedback loop for coral reef decline [4]. High water flow could alleviate these conditions, as well as other factors (e.g. herbivores, nutrients) that control algal abundance. For example, in low flow areas, grazing by herbivores could help decrease the height and density of turfs and the abundance of macroalgae [3,4,46,48], which in turn could mitigate the effects of water-mediated interactions between corals and algae by decreasing DBLs and preventing hypoxic conditions along coral edges.

Data accessibility. The datasets supporting this article can be found on Dryad doi:10.5061/dryad.t8j15.

Authors' contributions. H.J. collected and analysed the data and drafted the manuscript; C.S. collected the data; R.O. and D.B. participated in the design of the study and provided materials; M.N. designed the study, provided materials, and drafted the manuscript. All authors contributed to writing of the manuscript and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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