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Vermetid gastropods modify physical and chemical conditions above coral–algal interactions

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Abstract

Interaction modifications can arise when a third species alters the physical and chemical environment within which two other species interact. On coral reefs, corals and algae commonly interact amid a suite of other species that may modify their interaction. Massive *Porites* coral and algal turfs often are covered by mucus nets cast by the vermetid gastropod, *Ceraesignum maximum*. Previously, vermetid mucus nets have been shown to have deleterious effects on corals. Here, we hypothesized that vermetids not only have direct effects on coral, but they also change the local physical and chemical environment establishing the potential for interaction modifications by intensifying the effects of algae on corals. To test this, we examined the effect of vermetids on physical and chemical aspects of the environments. We quantified light penetration, water flow, diffusive boundary layer (DBL) thickness, and oxygen concentrations in the presence and absence of vermetid nets. Vermetid nets did not affect light levels. Because we observed reduced water flow and increased DBL thickness in the presence of nets, we also expected to observe high oxygen concentration over coral surfaces. Instead, we observed no difference in oxygen concentrations in the presence of mucus nets. To explain the lower than expected oxygen concentrations, we hypothesize that nets decreased photosynthesis and/or increased respiration of corals and algae and their associated microbiota. This is the first study to explore mechanisms underlying the deleterious effects of vermetids on corals, and shows that vermetid mucus nets may modify coral–algal interactions by intensifying physical and chemical conditions.

Keywords *Ceraesignum maximum* · Coral reefs · Competition · Interaction modification · Physical and chemical conditions

Introduction

Interaction modifications (or higher order interactions: Vandermeer 1969) arise when a third species alters the strength and/or direction of a pairwise interaction. For example, the presence of a non-lethal predator can decrease the intensity of competition between a potential prey and its competitor if the predator reduces the feeding activity of its prey (Peacor and Werner 2001). Predators also can induce changes in prey morphology, thus modifying the prey's interactions with its resources, competitors, or other predators (e.g., Relyea and Yurewicz 2002). In other cases, the strength of a predator–prey interaction can be modified by a biogenic habitat, which can alter the search ability of the predator. For example, the presence of large seaweeds can increase survival of mussels by decreasing their visibility to their crab predators (Bertness et al. 1999).

Interaction modifications can also arise when a species ameliorates harsh environmental conditions. For example, in the stress gradient hypothesis, one species modifies the physical environment, and thereby alleviates stress in another species, which may, therefore, affect interactions with other species in fundamentally different ways (Callaway 1997). The presence of a third species may also confer other changes in the physical environment. For example, increased shading by canopy trees intensifies competition among understory plants (Pagès et al. 2003). Similarly, the litter of *Pinus ponderosa* (pine) changes the soil chemical environment, thereby modifying the strength of competition between a grass and a shrub (Metlen et al. 2013; Metland

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and Callaway 2015). The importance of environmental modification by a third species and its effect on interactions between two other species emphasizes how species-driven changes to the physical and chemical environment can lead to complex ecological effects.

The influence of the physical and chemical environment on species interactions likely occurs in a diversity of systems. Here, we examine effects in a coral reef, where previous work has demonstrated that coral growth and survival is sensitive to changes in the physical–chemical environment. For example, reduced light availability can inhibit photosynthesis of the coral's symbiotic algae, *Symbiodinium*, and may lead to decreased coral growth (Chalker and Taylor 1975; Marubini et al. 2001). Reduced water flow increases boundary layers, and thicker boundary layers can lead to the build-up of harmful metabolic by-products and thus can decrease coral growth (Dennison and Barnes 1988; Kühl et al. 1995; Finelli et al. 2007).

Corals also are affected by interactions with other species. For example, algae are fast-growing sessile competitors that can overgrow or shade corals (Box and Mumby 2007), transfer harmful microbes to corals (Nugues et al. 2004; Barott et al. 2011, 2012), or exude allelopathic chemicals that harm corals (Rasher and Hay 2010). Algae can also facilitate the growth of heterotrophic bacteria via the production of bioavailable dissolved organic carbon (DOC, Kline et al. 2006; Smith et al. 2006; Nelson et al. 2013). Increased microbial growth leads to higher microbial respiration, which can result in hypoxic conditions at coral surfaces when corals are in close proximity to algae (Smith et al. 2006). Furthermore, algae likely mediate their deleterious effects, in part, by altering water flow. For example, algal turf (small, < 5 mm in height, multispecific filaments) can reduce water flow just above the coral surface, leading to greater retention of solutes (Brown and Carpenter 2015), thicker boundary layers (Wangpraseurt 2012; Brown and Carpenter 2013; Stocking et al. 2016), and increased concentrations of bacteria (Brown and Carpenter 2015). Importantly, the strength of the interaction between coral and algae (Wangpraseurt et al. 2012; Brown and Carpenter 2013; Jorissen et al. 2016) is affected by water flow. For example, reduced water flow increases exposure of corals to metabolic waste products released by the algae, which can enhance deleterious effects and produce hypoxia or hyperoxia (Hauri et al. 2010; Brown and Carpenter 2013, 2015; Haas et al. 2013a).

Competition between coral and algae, and the importance of physical factors (such as light and water flow), set the stage for other species to affect corals if they alter the physical environment. For example, sessile vermetid gastropods may alter the ecological context in which corals and algae interact by changing light and/or water flow. The largest vermetid, *Ceraesignum* (formerly *Dendropoma*) *maximum*, inhabits shallow coral reefs in the Pacific and Indian Oceans and the Red Sea. This worm-like snail casts a mucus net over the substrate to capture small particles, including plankton. Frequently, their nets cover corals and have deleterious effects on adult coral growth, survival, and photophysiology (Shima et al. 2010, 2013, 2015). The putative mechanisms underlying this negative effect likely involve the mucus net, although the mechanism(s) has not yet been identified. Here we hypothesize that the net alters the physical and chemical conditions around corals, leading not only to potential direct effects on corals but also to modification of coral–algal interactions. We, therefore, predict that vermetid nets: (1) reduce light availability and (2) decrease water flow. (3) We also predict that vermetid nets will have greater effects on physical conditions in the presence of turf algae because vermetids will reduce water flow and thus exacerbate effects of algal turf on the microenvironment. In particular, we expect that vermetid nets alter the physical and chemical conditions on coral surfaces by increasing the thickness of the diffusive boundary layer (DBL) over corals, which should lead to enhanced hyperoxic conditions at the coral surface in light due to the production of oxygen by turf algae (and similarly enhanced hypoxia in the dark due to respiration, although in our study we focused on daytime responses).

Methods

We conducted our studies in Mo'orea, French Polynesia at the UC Berkeley Richard B. Gump Marine Station, where massive *Porites* corals dominate the shallow back reefs and frequently interact with a myriad of algal species, especially algal turf (Brown and Carpenter 2015). The vermetid gastropod, *C. maximum*, is common in shallow water where *Porites* and turf algae also are common (Shima et al. 2010; but see Brown et al. 2016). To feed, this vermetid casts a mucus net, which collects particles in the water column before the net is retracted and the net and its contents are consumed by the snail (Kappner et al. 2000). Thus, microsites in which massive *Porites* and algal turfs interact are frequently covered by vermetid mucus nets (ESM Fig. 1). Our studies were designed to evaluate how vermetids modify the physical microenvironment (with respect to light, flow, and boundary layers) and alter the context in which corals and turf algae interact.

Light levels

To determine how vermetids influence the light environment, we used DEFI-L 2pi light meters to measure light levels in the presence and absence of mucus nets. We drilled holes onto dead areas of coral colonies where vermetids were present and placed a light sensor into the drilled hole, which served to hold the sensor upright, with the sensor surface

just protruding above the top of the reef. The sensor was approximately flush with the coral surface and, therefore, measured light levels a coral would experience. We placed a second sensor 2–5 m away from the primary sensor, in an area without vermetids nearby, and at a comparable water depth. The second sensor was secured in a weighted frame to ensure that it was upright and stable. Sensors recorded light levels (μmol photon m^{-2} s^{-1}) every second. To determine when the primary sensor was covered by vermetid mucus nets, we placed a GoPro camera in front of the primary sensor and photographed the sensor every 30 s. At the end of a 4-h period, the sensors and camera were collected. This procedure was repeated on 6 days in 2013: June 7, 9, 10, 26, 30 and July 17. Light sensors were randomly assigned to a different treatment and new location each day.

Using the time series for each deployment, light levels were averaged every 30 s to align with the photographic time series. Each photograph from the primary sensor was then scored as either having a net present or not. We then calculated the log ratio [ln(Primary sensor/Second sensor)] to control for ambient fluctuations in light levels, and averaged these log ratios during all times when the nets were present and during all times when they were absent. Thus, each deployment (i.e., a temporal block) generated two log ratios (i.e., differences on a log-scale). If vermetids reduced light levels, then the log ratio between the two sensors should have been reduced (e.g., become more negative) when nets were present. These data were analyzed using a paired *t* test ($n = 6$ pairs) to quantify the effect of vermetids on light levels and test the null hypothesis that the presence of nets did not affect light levels. Additional information, including justification for this design and additional analyses, is included in the electronic supplementary materials.

Retention time of water

We tested if the presence of vermetid nets and algae influenced the retention of water near corals. Changes in retention times of fluorescein dye have previously been used as a proxy for changes in water flow and diffusive boundary layers (Brown and Carpenter 2015). We recorded the retention time of fluorescein dye in the presence vs. absence of a vermetid net in microsites at which only coral was present or in sites at which algal turf also was present. After identifying an area of coral (or coral and algal turf) covered by a mucus net, we inserted 2 ml of fluorescein dye (40 mg ml^{-1}) underneath the mucus net using a 5-ml syringe with a needle attached, and recorded (to the nearest second) the elapsed time until the dye had visually dissipated from a 1×1 cm^2 area. The net was then removed and, after 10 s, another 2 ml of dye was released in the same spot and the dissipation time re-measured. To check our methods, we also assessed dissipation using a fluorometer. All methods were identical to the previous approach, except that we sampled the water with a clean syringe 2 s after releasing the dye and determined the residual concentration of dye using a fluorometer. We analyzed the data using a two-way ANOVA (net presence vs. absence crossed with algae presence vs. absence) with a random effect for site (since the same site was measured in the presence and absence of a net) using the lme4 package with Satterthwaite approximation for degrees of freedom (Bates et al. 2015; Kuznetsova 2016).

Oxygen concentration profiles

We quantified oxygen concentrations under two flow regimes (low flow at 7.7 cm s^{-1} and high flow at 14.5 cm s^{-1}) using a laboratory flume, and used these data to estimate diffusive boundary layer (DBL) thickness at microsites above coral, above algae, and above the coral where it was directly interacting with algae (hereafter the "coral–algal interface"). We conducted our study with field-collected cores, the tops of which were comprised by half living massive *Porites* coral and half algal turf. We identified interfaces in the field and used a pneumatic drill with a hole saw attachment (6.35 cm diameter, 3.81 cm cutting depth; McMaster Carr) to remove the core. Cores were brought back to the lab and placed in aquaria with constant flow of seawater until they were used in the flume (always within a week of collection). On the day that a core was to be placed in the flume, we first took it into the field and draped a vermetid mucus net over the top to simulate the typical field condition in the presence of vermetids. The core (with the overlaying net) was enclosed in a small plastic container, brought back to the lab and returned to the seawater table until placed in the flume 1–4 h later. A core (with an intact net) was placed in the center of a ramp in the working section ($160 \times 10 \times 12$ cm) of the flume to ensure smooth flows, and then acclimated to the flume for 5 min at low flow (7.7 cm s^{-1}) in light (800 μmol photon m^{-2} s^{-1}; Hubbell 1000 W metal halide light). Although this handling and transport may stress corals and algae and, therefore, affect the absolute oxygen concentrations we measured, we expected the relative differences among the treatments to reflect relative responses measured under more natural conditions.

We measured oxygen concentration profiles using a PreSens needle microsensor oxygen probe (diameter: < 50 μm) attached to a PreSens Microx TX3 system (PreSens Precision Sensing GmbH). The probe was attached to a micromanipulator, which allowed fine-scale, precise motion to measure oxygen concentration profiles. The probe was lowered through the net to the coral surface. From the surface (distance = 0 μm), the probe was then raised in incremental steps of 100 μm until reaching a height of 2500 μm. At each step (every 100 μm) the probe was paused for 1 s and the oxygen concentration was recorded. See Brown and

Carpenter (2013) for more information about probe calibration, flume measurements, and description of the flume set up.

Oxygen profiles were obtained directly above the live coral ($n = 6$–7), above the coral–algal interface ($n = 8$), and above the algal turf ($n = 6$–8). The net was then removed and the profiles were obtained in all three locations again. All six profiles were obtained under low (7.7 cm s^{-1}) and high (14.5 cm s^{-1}) flow for each coral core with the net present, and again after nets were removed. Light levels were saturating (Carpenter 1985; Chalker 1981) and similar to those experienced in the field. Flow speeds also were chosen based on conditions experienced in the field (Brown and Carpenter 2015) and were calibrated in the flume with an acoustic Doppler velocimeter (Nortek AS Vectrino).

The thickness of the diffusive boundary layer (DBL) was determined by the height (above the substrate) at which oxygen concentrations reached 99% of the bulk oxygen concentration (Jorgensen and Revsbech 1985) based upon graphical representations of the profiles (concentrations by distance), and finding the distance at which oxygen concentrations reach 99% of the bulk oxygen concentration (see Kühl et al. 1995; Brown and Carpenter 2013). Oxygen profiles are provided in the electronic supplementary materials. Surface oxygen concentrations (i.e., measurements at distance 0) were compared to determine if mucus nets exacerbated hyperoxic conditions at the coral surface, indicative of retention of oxygen due to the presence of a mucus net.

DBL thicknesses and surface oxygen concentrations were compared using mixed model ANOVA, in which core was treated as a random effect. All data analyses were conducted using the programming language R (R Core Team 2015, version 3.2.3); ANOVA was performed with the lme4 package (Bates et al. 2015) with the degrees of freedom approximated using the Sattherwaite approximation (Kuznetsova et al. 2016). Tukey HSD post hoc tests were completed on the model using the lsmeans and multcompView packages in R (Graves et al. 2015; Lenth 2016).

Results

Light levels

Light levels at the field sites were typically between 600 and 850 µmol photons m^{-2} s^{-1}, although 1 day (9 June 2013) had consistent cloud cover so light levels averaged only 182–245 µmol photons m^{-2} s^{-1} and the sensor located away from vermetids measured consistently higher light levels. The average log ratio between the two sensors was typically small and near 0 (0.035 ± 0.005, mean ± 95% Confidence Interval), and ratio did not vary consistently due to the presence versus absence of a vermetid net (difference in log ratio = 0.0081 ± 0.0393, mean ± 95% confidence interval; $t_5 = 0.529$, $P = 0.620$, ESM Table 1, Fig. 1), which resulted in a less than 1% decrease in light. The most extreme difference in light levels (30-June-2013) corresponded to only a 6% reduction in light in the presence of nets. On five of the six dates, light levels were likely saturating (Chalker et al. 1981; Marubini et al. 2001). We, therefore, concluded that vermetid nets do not appreciably affect corals via reductions in light levels.

Retention time of water

Fluorescein dye was retained for significantly longer in the presence of vermetid mucus nets compared to when the nets were absent ($F_{1,32} = 13.79$, $P = 0.0008$, Fig. 2a). Additionally, we observed longer retention times when algae were present ($F_{1,32} = 6.9$, $P = 0.0131$, Fig. 2a). On average, dye was retained nearly twice as long in the presence of nets (1.7 × for the coral alone, and 1.9 × when corals were interacting with algae: see ESM Table 2). Results using a fluorometer to measure fluorescein concentrations after 2 s revealed similar patterns (Fig. 2b).

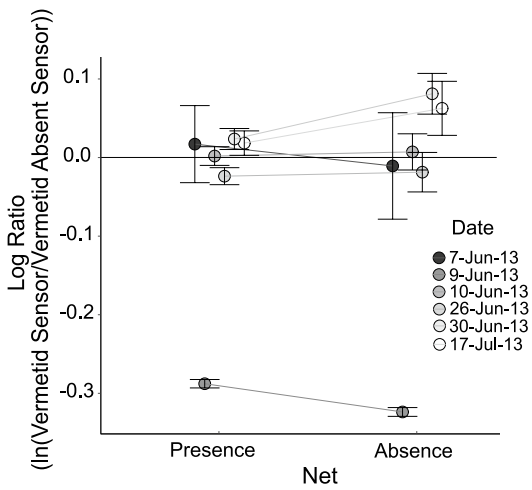

Fig. 1 Mean log ratio (± 95% confidence intervals) in light levels between sensors that were either close to (primary sensor), or isolated from (secondary), vermetids during periods when the sensor close to vermetids was covered by a mucus net (net present) or not covered by a mucus net (net absent) for each date sampled (circles represent the different dates: June 7, 9, 10, 26, 30 and July 17). The second sensor provided a standard to adjust for temporal fluctuations in light intensity. Mean log ratio and confidence intervals are based upon observations of light levels (taken every second but averaged over 30-s periods) on the sensors near vs. isolated from vermetids. Departures of the log ratio from 0 in the absence of the net simply indicate that one sensor was in a location or orientation that received slightly more (or less) light on average. If vermetids reduced light levels, then the log ratio should be reduced (e.g., become more negative) when nets were deployed (i.e., the mean log ratio when nets were present should consistently lie below the log ratios when nets were absent)

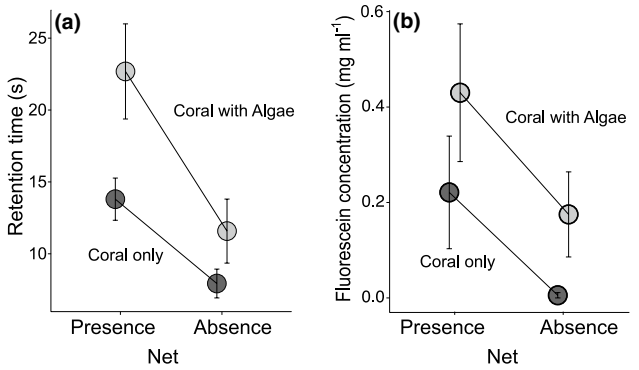

Fig. 2 Mean (± SE; $n = 15$ for algae absent and 19 for algae present) **a** retention time of fluorescein dye, and **b** fluorescein dye concentrations (after 2 s), over corals when algae are absent and when algae are present at the coral–algal interface, and when vermetid snail mucus nets are absent (no net) or present (net). Both algal presence and mucus nets led to significant increases in fluorescein dye retention times ($P = 0.0131$ and $P = 0.0008$, respectively). Nets also led to higher concentrations of fluorescein dye ($P = 0.045$)

Oxygen concentration profiles

There were significant complex interactions among the factors (surface × net presence and a nearly significant three-way interaction), in part because there was little effect of flow or net presence on DBL thickness over algal turf (Table 1, Fig. 3). Over the coral and coral–algal interface, in general, we observed thicker boundary layers in the presence of mucus nets (Table 1, Fig. 3), although because of the complex interactions, we cautiously interpret this main effect. Increasing flow had no effect on DBL thickness over the coral–algal interface (or over algae), although higher flow did reduce the DBL thickness over coral when mucus nets were present (Fig. 3a,b; Table 1). Thus, it appears that flow reduced DBL thickness except in the presence of algae (i.e., algae alone or at the coral–algal interface) and nets, suggesting that nets reduce the mixing effects of flow over complex three-dimensional surfaces (e.g., algal turf) but not over relatively simple surfaces (e.g., coral).

All surface oxygen concentrations were hyperoxic, as expected given that profiles were obtained in light when algal turf and *Symbiodinium* would be photosynthesizing. High flow decreased surface oxygen concentrations (as expected from greater mixing, Fig. 4). However, there was a nearly significant complex three-way interaction between flow, substrate and nets (Table 2). For coral surfaces, in low flow, surface oxygen concentrations were elevated in the presence of nets, but there were no differences between low and high flow in the absence of a net (Fig. 4a). At the coral–algal interface, the presence of a net had little effect on surface oxygen concentration (Fig. 4b, Table 2). For algal surfaces, nets appeared to depress surface oxygen concentrations especially compared to low-flow conditions (Fig. 4c, Table 2).

Discussion

Our study is one of the first to evaluate possible mechanisms that underlie the deleterious effect of vermetids on corals (as documented by Shima et al. 2010; Stier et al. 2010; and Shima et al. 2013). Vermetids change the physical and chemical microenvironment below their mucus nets by reducing water flow, increasing retention times, and increasing boundary layer thickness, but not by reducing light levels. These effects, however, depended on the substrate over which the measurements were made. When corals and algae abut, the presence of vermetid mucus nets increases retention times. However, the effects of mucus nets and flow were dependent on surface type. Notably, when algae were present near corals, increased water flow did not decrease DBL thickness, indicating that the presence of algae and mucus nets combine to create conditions that lower flow. As a result, algae and nets create more homogeneous conditions near coral surfaces that are independent of the overlying water flow regime.

These modified physical and chemical conditions induced by vermetids may intensify the interactions between coral

Table 1 Results of mixed model ANOVA on the thickness of the diffusive boundary layer (DBL)

	Numerator DF	Denominator DF	*F*	*P*
Net presence	**1**	**76.57**	**14.82**	**0.0002**
Flow	**1**	**77.16**	**11.59**	**0.001**
Surface	**2**	**82.47**	**3.46**	**0.036**
Net presence × flow	1	76.57	0.54	0.466
Net presence × surface	**2**	**76.57**	**5.52**	**0.006**
Flow × surface	2	78.64	0.33	0.716
Net presence × flow × surface	*2*	*76.57*	*2.81*	*0.066*

Surface refers to the location of the profile (over the coral, coral–algal interface, or algae), flow is either low or high, and net presence is either present or absent. Significant terms ($P < 0.05$) are indicated in bold and nearly significant terms are italicized ($0.05 < P < 0.10$)

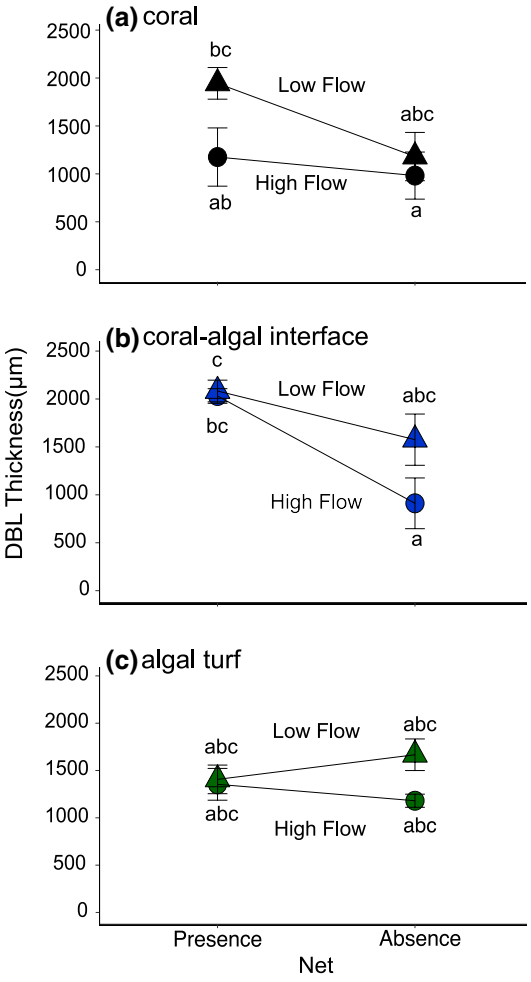

Fig. 3 Mean (± 1 SE; *n* ranges from 6 to 8) diffusive boundary layer thickness (DBL) over: **a** coral, **b** the coral–algal interface, and **c** algae, at two flow speeds (low: triangles; and high: circles) in the presence and absence of a vermetid net. DBLs were thicker in the presence of nets over coral and the coral–algal interface, but not over the algae. Under most conditions, increased flow reduced thickness of the DBL, except over the coral–algal interface and over algae, in the presence of nets. See Table 1 for statistical analyses. Letters refer to Tukey HSD post hoc analyses, where the same letters indicate no significant difference where groups with different letters indicate significant differences at a $P < 0.05$

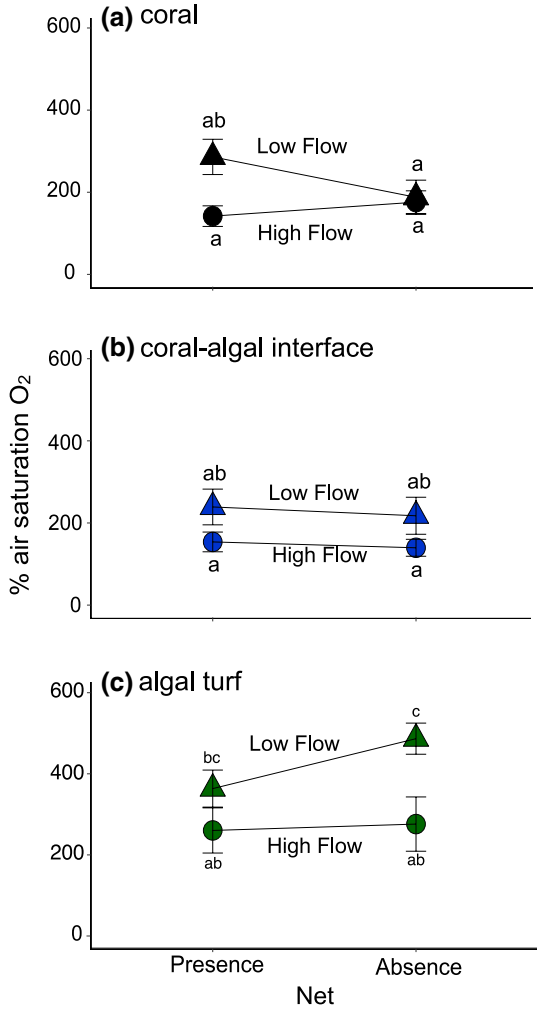

Fig. 4 Mean (± 1 SE; *n* ranges from 6 to 8) surface oxygen concentrations in light over **a** coral, **b** the coral–algal interface, and **c** the algae, at two flow speeds (low: triangles; high: circles). The effects of mucus are influenced by the flow regime and the surface type (Table 2). Letters refer to Tukey HSD post hoc analyses, where different letters indicate significant differences at a $P < 0.05$

and algae. For example, Smith et al. (2006) hypothesized that algae indirectly affect coral by releasing DOC and increasing heterotrophic microbial growth, leading to hypoxic conditions and coral mortality. Others have suggested that this process depends on water flow, and can only occur in low-flow conditions (Wangprasseurt 2012; Brown and Carpenter 2013; Haas 2013a; Jorissen 2016). Additionally, long retention times, lowered flow, and/or thicker diffusive boundary layers can lead to the build-up of noxious conditions, for example, by maintaining harmful waste products near the surface of corals (Hauri et al. 2010). Thus, the presence of mucus nets, by lowering flow and increasing boundary layer thickness, can exacerbate the mechanisms underlying coral–algal competition. This is especially evident at the surface of coral–algal interactions, where increasing water flow, which usually decreases boundary layer thickness, has little effect on DBL thickness when nets are present (Fig. 3).

Interestingly, we did not observe an accumulation of oxygen concentration in the presence of mucus nets (Fig. 4). This result is curious, as previous work has shown a positive relationship between diffusive boundary layer thickness and oxygen concentrations at coral and algal surfaces during daylight (Brown and Carpenter 2013; Jorissen et al. 2016). The lack of increase in surface oxygen concentrations in the presence of nets and algae suggests that nets not only increased the DBL but also led to lower net production of oxygen (although the overall condition remained hyperoxic).

Table 2 Results of mixed model ANOVA on surface oxygen concentration in light

	Numerator DF	Denominator DF	*F* value	*P* value
Net presence	1	74.657	0.105	0.7463
Flow	**1**	**75.147**	**26.19**	**2.3×10^{-6}**
Surface	**2**	**81.15**	**29.05**	**3.06×10^{-10}**
Net presence × flow	1	74.657	0.071	0.7901
Net presence × surface	*2*	*74.657*	*2.463*	*0.0921*
Flow × surface	2	76.202	0.823	0.4428
Net presence × flow × surface	*2*	74.657	*2.836*	*0.0650*

Surface refers to the location of the profile (over the coral, coral–algal interface, or algae), flow is either low or high, and net presence is either present or absent. Significant terms ($P < 0.05$) are indicated in bold and nearly significant terms are italicized ($0.05 < P < 0.10$)

We propose and discuss two hypotheses: (1) lowered photosynthesis in the presence of vermetid mucus nets; (2) increased oxygen consumption (i.e., respiration), potentially by the microbial community.

If photosynthesis of *Symbiodinium* and/or algal turf was reduced by the presence of nets, oxygen production would have been reduced, which may have prevented the accumulation of oxygen despite increased DBL thickness. This reduction in photosynthesis must involve a mechanism other than light (Fig. 1) since vermetid nets did not appreciably reduce light intensity. For algal turf, the physical barrier the net creates may lead to difficulty acquiring DIC (dissolved inorganic carbon) needed to maintain high rates of photosynthesis (Carpenter and Williams 2007). Corals may also exhibit reduced photosynthetic efficiency under low flow (Finelli et al. 2007; Mass et al. 2010), a condition created by vermetids (Fig. 2), possibly because hyperoxic conditions can damage *Symbiodinium* photosynthetic apparatuses (Mass et al. 2010). Effects on surface oxygen concentrations of algal turfs are likely to be even more pronounced than effects on *Symbiodinium* (as observed, see Fig. 4). For example, algal turfs in low flows are mass transfer limited, but generally have high rates of photosynthesis (0.3–3.2 µmol O_2 cm^{-2} h^{-1}, Carpenter and Williams 2007) compared to photosynthetic rates of *Symbiodinium*/massive *Porites* (0.21 µmol O_2 cm^{-2} h^{-1}; Anthony et al. 2008). Thus, a reduction in the photosynthetic rate of algal turfs would likely have a more demonstrable effect on oxygen concentrations than a reduction in photosynthesis by *Symbiodinium*.

Alternatively, the presence of the nets may lead to an increase in respiration, e.g., by increasing the activity of heterotrophic microbes or through photorespiration of *Symbiodinium* (Mass and Genin 2010). Heterotrophic microbes can reduce oxygen concentrations at the interface between corals and algae (Smith et al. 2006; Barott et al. 2011; Jorrisen et al. 2016; but see Brown and Carpenter 2013), putatively due to excess DOC produced by leaky algae (Kline et al. 2006). For example, in no flow, the interface between coral (*Favia* sp.) and algae (*Chaetomorpha* sp.) can approach hypoxia due to microbial respiration, even in light (Haas et al. 2013a). Evidence for increased microbial activity due to algal by-products has been found in Moorea, French Polynesia where DOC produced by algal turf leads to increased growth and respiration of heterotrophic microbes (Haas et al. 2013b). If algal-derived DOC or coral metabolic by-products used by heterotrophic microbes are trapped under the net, microbial activity might increase, leading to increased respiration, and thus preventing the accumulation of oxygen when nets are present. Additionally, mucosal products of corals and other mucus-producing organisms have been previously found to fuel microbial growth (Wild et al. 2004, 2010). Similarly, it is possible that the mucus net from vermetids may provide a food source for the heterotrophic microbial communities on corals, leading to increased respiration in the presence of mucus nets. However, vermetid nets also contain bioactive compounds, which may have antibacterial properties (Kloppel et al. 2013), suggesting that nets could instead reduce microbial growth and respiration.

These hypotheses are not mutually exclusive, and may act in concert to influence the chemical conditions around coral–algal interactions when vermetid nets are present. Indeed, previous studies have shown that vermetids decrease the photosynthetic efficiency of corals (Shima et al. 2015), indicating vermetids may reduce coral photosynthesis. Alternatively, mucus nets, by affecting coral microbial communities, indirectly could affect the efficiency of photosynthesis (e.g., chemical effects of algae on corals decrease photosynthetic efficiency, Rasher and Hay 2010). Thus, nets, by lowering flow, preventing mixing and exacerbating deleterious chemical conditions may lead to a combination of decreased photosynthesis and increased respiration, which would depress oxygen concentration below that expected from thicker DBLs.

Although our short-term, mechanistic studies do not directly quantify the effects of vermetids on coral–algal competition, many past studies demonstrate that the effects on the physical environment will alter the interaction between corals and algae. For example, reduced flow (and

increased DBL thickness) intensifies the deleterious effects of algae on corals (Brown and Carpenter 2015; Gowan et al. 2014). Because coral–algal dynamics are critical to the understanding of coral reef resilience, we suggest that vermetid gastropods, through their modification of the environment, could play an important role in coral reef community dynamics in areas where corals, algae and vermetids co-occur (e.g., South Pacific and Red Sea). Previous studies have demonstrated the dominant role that higher order interactions can have on species interactions (Werner and Peacor 2003; Schmitz et al. 2004). Often, interaction modifications are characterized by phenotypic or behavioral responses to the presence of another organisms (e.g., a predator: Werner and Peacor 2003), or by the effects of another organism on the physical structure of the environment (Bertness et al. 1999; Pagès et al. 2003). Our study is the first to demonstrate how a gastropod (in this case, *C. maximum*) acts as an interaction modifier by changing the physical and chemical environment in which competitors, corals and algae, interact.

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Author contribution statement ALB and CWO conceived the ideas and experiments. ALB conducted the experiments for the lab and field water retention and oxygen studies. ALB and CWO did the fieldwork for the light experiment. ALB analyzed the data. ALB and CWO wrote the manuscript.

Compliance with ethical standards

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

Conflict of interest We declare no conflicts of interest.

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Electronic Supplemental Material

Vermetid gastropods modify physical and chemical conditions above coral-algal interactions

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SI.1 Table: Results of Mixed Effects Model evaluating the effect of net cover on the log-ratio of light levels with random effects of date and time. Results were analyzed using the lme4 packages (Bates et al. 2015). This test ignores temporal autocorrelation in the time series and thus likely inflates the error degrees of freedom. We prefer the analysis provided in the main text; however, we include this analysis for completeness. Because neither analysis provides evidence for a consistent effect of vermetid nets on light, we conclude that our interpretation that effects of vermetids on light are small (or non-existent) is robust to the specific approach take to analyze the data.

	Estimate	SE	df	t value	P
(Intercept)	-0.034	0.049	6	-0.69	0.52
Net Cover	-0.01	0.006	3180	-1.48	0.14

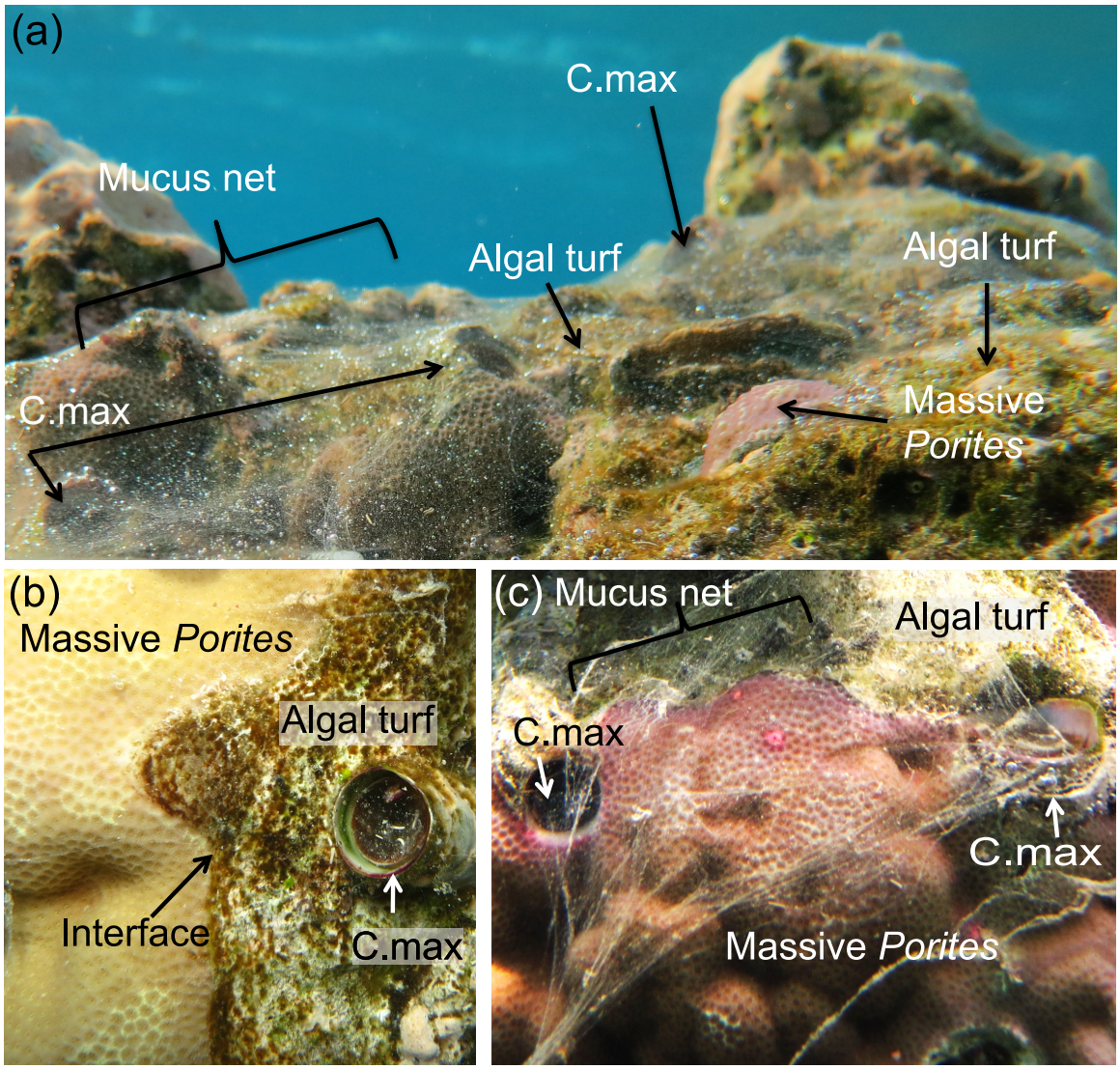
SI.2 Table: Mean ± SE (sample size) of retention times of fluorescein dye over corals and the coral-algal interfaces.

	Retention time (s)		
Surface	Net Present	Net Absent	Net Present – Net Absent
Coral	13.8±1.5 (15)	7.9±3.9(15)	5.9±1.2 (15)
Interface	22.7±14.4 (19)	11.6±9.7 (19)	11.1±4.7 (19)

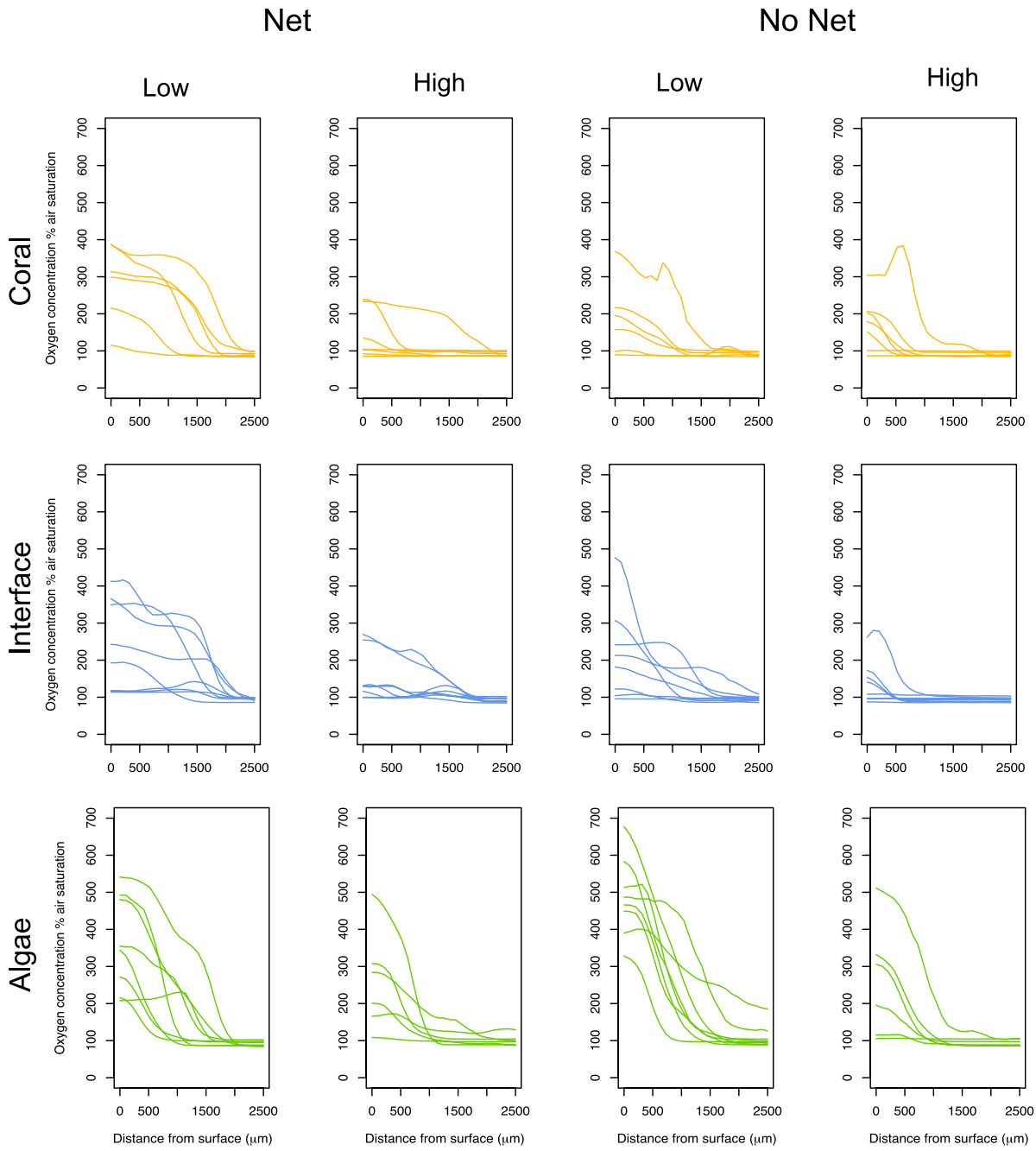
SI.3. Mean±SE (sample size) thickness of the diffusive boundary layer (DBL) over the coral, the coral-algal interface, and over the algae (algal turf).

Surface	Flow	Net (μm)	No Net (μm)
Coral	Low	1944.4±165.1 (6)	1180.6± 251.8 (6)
	High	1175.6± 303.9 (7)	982.1±245.7 (7)
Interface	Low	2083.3±113.1 (8)	1575.5±267.4 (8)
	High	1966.1±69.4 (8)	494.8±167.9 (8)
Algae	Low	1406.2±151.2 (8)	1666.6±167.0 (8)
	High	1354.1±168.0 (6)	1180.5±69.4 (6)

SI Figure 1. (a) Photograph of the top of a coral bommie, showing the vermetid (*C. maximum*: C.max), live coral (massive *Porites*), algal turf, and mucus nets (the opaque, spider-web like material covering the algae and coral with bubbles forming underneath the net). (b) Image of massive *Porites* coral, algal turf and the interface between them, near a vermetid that has not yet exuded a net. (c) Image of massive *Porites* coral, algal turf and vermetids with mucus nets deployed (the nets are the opaque spider-web like material).



SI Figure 2. Raw data for oxygen concentration profiles in the light. Measurements were taken in 100µm steps from the surface of the coral, the interface or the algal turf. Rows give results for different surfaces (Coral in orange; coral-algal interface in blue; algae in green). Columns give results in the presence vs. absence of nets and under low vs. high water flow. DBL thickness and initial oxygen concentrations were extracted from these data.



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