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Canopy macroalgae influence understorey corallines' metabolic control of near-surface pH and oxygen concentration

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ABSTRACT: Understorey macroalgae can alter pH at their surface via metabolic activity within the concentration boundary layer (CBL), but it is unknown to what degree the presence of larger macroalgal canopies can modify the pH micro-environment of understorey species. We examined whether flow reduction by a canopy-forming macroalga could alter the thickness of the CBL at the surface of understorey crustose coralline macroalgae (CCA). This could lead to a greater metabolic influence of macroalgae on the pH and oxygen environment at the coralline's surface. Three experimental treatments were examined in a re-circulating flume: (1) a full canopy (consisting of *Carpophyllum maschalocarpum*) and understorey (*Corallina officinalis* and CCA), (2) a mimic (plastic/silk) canopy plus understorey, and (3) an understorey only. Profiles of seawater velocity and pH/O_2 concentration gradients were measured at 3 bulk seawater velocities (2, 4 and 8 cm s^{-1}) above the CCA in both the light and dark. Canopy macroalgae altered the pH and O_2 environment encountered by understorey coralline algae via their physical presence rather than by directly altering bulk seawater chemistry through their metabolism. Reduced seawater velocities beneath *Carpophyllum* and mimic canopies resulted in increased CBL thicknesses, higher pH (up to 8.9) and O_2 concentrations in the light, and lower pH (down to 7.74) and O_2 concentrations in the dark. The ability of canopies to facilitate greater metabolic changes in pH at the surface of understorey species highlights a previously unrecorded species interaction that could play an important role in influencing the physiology and ecology of understorey assemblages.

KEY WORDS: Hydrodynamics · Understorey–canopy interactions · Seawater pH · Coralline algae · Boundary layers · Ocean acidification

INTRODUCTION

Large canopy-forming brown macroalgae (e.g. members of the Laminariales and Fucales) are a ubiquitous component of temperate rocky reefs, acting as ecosystem engineers (sensu Jones et al. 1994) by reducing seawater velocity (Gaylord et al. 2007), light levels (Reed & Foster 1984), and altering seawater carbonate chemistry through their metabolism (Delille et al. 2000, Cornwall et al. 2013a). Coralline algae often form understoreys beneath larger macroalgal canopies, as either upright articulated or flat

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crustose forms (Reed & Foster 1984, Irving et al. 2004), and are important in their role as foundation species, creating new regions of biogenic reef, and providing a settlement substrate for a variety of invertebrate species (Roberts 2001). Coralline algae are sensitive to changes in seawater carbonate chemistry, such as those predicted to occur due to ocean acidification, exhibiting lower rates of growth and net calcification as pH/carbonate ion concentration declines and pCO_2/dissolved inorganic carbon (DIC) increases (Semesi et al. 2009a,b). Ocean acidification could therefore have large negative impacts on temperate rocky reef ecosystems where coralline algae play an important ecological role.

While ocean acidification is predicted to be a threat to calcareous marine species (Kroeker et al. 2013), some may possess the ability to alter carbonate chemistry at the site of calcification/dissolution (Borowitzka 1987, Hurd et al. 2011). Photosynthetic organisms are also able to modify the carbonate chemistry of the surrounding bulk seawater via their metabolic activity (Delille et al. 2000, Cornwall et al. 2013a). Photosynthetic uptake of CO_2 during the day increases pH and decreases DIC concentrations within the bulk seawater in macroalgal beds (Kleypas et al. 2011, Cornwall et al. 2013a). At night, macroalgal respiration releases CO_2, thereby decreasing pH and increasing DIC (Anthony et al. 2011). Similar changes in pH also occur at the surface of photosynthesising macroalgae at slow rates of flow (Hurd et al. 2011, Cornwall et al. 2013b). At both scales, diel changes in carbonate chemistry influence the net calcification of coralline algae (Cornwall et al. 2013a, 2014), where net calcification increases during the day and decreases at night (Semesi et al. 2009a). However, the role of canopy-forming brown macroalgae in modifying the seawater carbonate chemistry encountered by understorey calcifying macroalgae on the micro-scale has not been explored, and may have implications for the responses of calcifying species to ocean acidification.

Canopy-forming brown macroalgae could modify the pH encountered by understorey coralline algae by (1) metabolic modification of pH near and within the macroalgal canopy via photosynthesis and respiration as described above, and (2) by attenuating seawater flow (Gaylord et al. 2007, Kregting et al. 2011), resulting in thicker velocity (momentum) and concentration (diffusion) boundary layers at the surface of the coralline algae. A thicker concentration boundary layer (CBL) results in a greater difference in solute concentrations between the surface of the alga and the overlying bulk seawater. The concentrations of the metabolic solutes that combine to influence pH at the organism's surface are largely governed by the interplay between water velocity and the organism's metabolic activity (de Beer & Larkum 2001, Hurd et al. 2011, Cornwall et al. 2013b). Thick boundary layers around photosynthesizing coralline algae create a region with higher pH at their surface, which is conducive to higher rates of net calcification even under lower bulk seawater pH (Cornwall et al. 2014). Therefore, the hydrodynamic and chemical environment encountered by understorey calcifying macroalgae within macroalgal beds is likely to be very different than that of the bulk seawater outside the beds. It is recognised that turfing macroalgae generally have thicker CBLs than crustose forms (Cornwall et al. 2013b), likely due to flow attenuation. However, the effect of larger canopy macroalgae on the CBL of understorey macroalgae has not been quantified to date.

The brown fucoid macroalga *Carpophyllum maschalocarpum* (hereafter *Carpophyllum*) forms dense beds on subtidal rocky reefs in northern New Zealand (Schiel 1988, Shears & Babcock 2007). In New Zealand, the densities of fucoid canopies can reach 115 ind. m^{-2} but are often around 10 to 40 m^{-2} (Choat & Schiel 1982). Beneath the canopy of *Carpophyllum* is often an understorey of *Corallina officinalis* (hereafter *Corallina*), which can form dense assemblages of thousands of ind. m^{-2} (C. E. Cornwall unpubl. data). Beneath *Corallina*, at the rock surface, are crustose coralline algae (hereafter CCA) that can cover >80% of the rock surface (Hepburn et al. 2011). These types of communities, with several canopy layers, are ubiquitous to temperate rocky reefs throughout the world (Reed & Foster 1984, Irving et al. 2004). While modification of the bulk seawater pH by macroalgae in large beds has been previously documented (Delille et al. 2000, Cornwall et al. 2013a), it is unknown whether discrete, smaller patches of canopy-forming brown macroalgae influence the pH microenvironment encountered by understorey species.

The aim of this study was to determine whether the presence of the canopy-forming macroalga *Carpophyllum* could alter the pH environment encountered by understorey *Corallina* and CCA, due to their physical effect of attenuating seawater velocity within the canopy (which would alter the CBL thickness around understorey organisms). This was done over a short time period (30 to 60 min) to avoid acclimation to the laboratory setting. To achieve this, profiles of pH, O_2 concentration and seawater velocity were measured at the surface of the CCA and through the *Corallina*

understorey at different seawater velocities within a laboratory flume using 3 treatments: (1) a full canopy and understorey, (2) a mimic (plastic/silk) canopy plus understorey, and (3) an understorey only. Mimic canopies were included to separate the influence of *Carpophyllum* metabolism and flow reductions on the pH and O_2 environment encountered by the understorey. pH and O_2 profiles were measured both in the light and dark to determine the effect of photosynthesis and respiration on these variables. We chose these 2 variables because they are regulated by, and influence, metabolic processes (Axelsson 1988, Kübler et al. 1999), and can be measured accurately within the CBL of macroalgae with commercially sold sensors (de Beer & Larkum 2001, Hurd et al. 2011, Cornwall et al. 2013b).

MATERIALS AND METHODS

Sample collection and pre-treatment

Three large cobbles (L × W × H = ~200 × 150 × 50 mm) with ~100% cover of *Corallina* and CCA, and 15 *Carpophyllum* individuals were each removed from the shallow (1 to 1.5 m) subtidal near Raglan, North Island, New Zealand (37° 82′ 49″ S, 174° 80′ 07″ E) 4 times between July and August 2011. The average height (mean ± SE) of the *Corallina* understorey was 22.8 ± 0.3 mm (n = 60). All macroalgae were collected 1 to 3 d prior to the experiments, cleaned of all visible epiphytes and kept together in 4 glass tanks (600 × 300 × 300 mm) under natural irradiance and temperature (~13 to 15°C). The glass aquaria were filled with artificial seawater at the same salinity as the collection site in the field (~30.2; see Table 1 for seawater chemistry) and aerated vigorously. Water in the aquaria was re-circulated to and from a 10 m^3 storage tank.

Prior to experiments, the photosystem II 'health' of the macroalgae was assessed using a Pulse Amplitude Modulated (PAM) chlorophyll fluorescence meter (Diving PAM, Walz) to measure F_v/F_m (photosystem II efficiency) on dark adapted (15 min) individuals. This model PAM had a red light-emitting diode, and both gain and dampening were set to 2. On all occasions, F_0 was >130 before measurements were made. Five random individuals were selected each day for measurement; F_v/F_m was always >0.55 for CCA and *Corallina* and >0.70 for *Carpophyllum* — values that are indicative of a healthy photosystem II (Maxwell & Johnson 2000, Harrington et al. 2005).

Experimental protocol

Experiments were conducted in a recirculating, unidirectional flume (L × W × D = 7.23 × 0.5 × 0.5 m). The flume is described in Miller et al. (2002), but briefly, it consisted of an impeller in a return pipe that controls seawater velocity via a variable-speed AC motor. Two flow straighteners (1 cm^2 square mesh size) were positioned 400 and 600 mm downstream from the flume entrance. The flume was filled with 1500 l of 5 µm filtered artificial seawater to a depth of 35 cm. For each replicate run (n = 8), 3 cobbles covered with *Corallina* and CCA were placed in a recessed Perspex box insert (0.9 × 0.5 × 0.05 m) in the working section of flume (located 5.41 to 6.31 m downstream of the entrance) approximately 0.15 m from each other, and the remaining space filled with abiotic, smooth cobbles of a similar size. All cobbles were arranged randomly throughout the working section of the flume, but so that their top surfaces were at approximately the same height as the flume floor in an effort to simulate the rough bottom of the cobble habitat in the field (Fig. 1). Light (190 µmol photons m^{-2} s^{-1} at the water's surface and 126 µmol photons m^{-2} s^{-1} at the base of the CCA) was provided via an overhead high pressure sodium (tubular) Agro 400 light. Irradiance was measured with a 4π LI-COR® Quantum Sensor (LI-190, LI-COR).

The 8 replicates were subjected to all possible combinations of the following factors: unidirectional water velocity (3 levels: 2, 4 and 8 cm s^{-1}), irradiance (2 levels: light [190 µmol photons m^{-2} s^{-1}] and dark), and 3 canopy treatments. The canopy treatments (Fig. 1) were (1) a large macroalgal canopy of *Carpophyllum*, (2) a large mimic canopy, and (3) the absence of a large canopy (i.e. only *Corallina* + CCA). Hereafter, these 3 treatments will be referred to as '*Carpophyllum*', 'mimic' and '*Corallina* only' respectively. For both the *Carpophyllum* and mimic treatments, there was a density of 15 individuals in the working section, equating to 33 ind. m^{-2}. Individual *Carpophyllum* and mimics were ~205 × 200 × 180 mm.

The mimic macroalgae were made by SeaGarden® aquarium décor from silk and plastic and were styled on the macroalga *Dictyota verde*. This mimic was used because it was the most morphologically similar that was available commercially. Mimic and *Carpophyllum* individuals were attached to plastic pegs and 200 g lead sinkers, and were randomly placed throughout the working section of the flume. Their locations for 1 replicate profile of each velocity and light level were identical. This was done to reduce potential artefacts introduced by small-scale differences in sea-

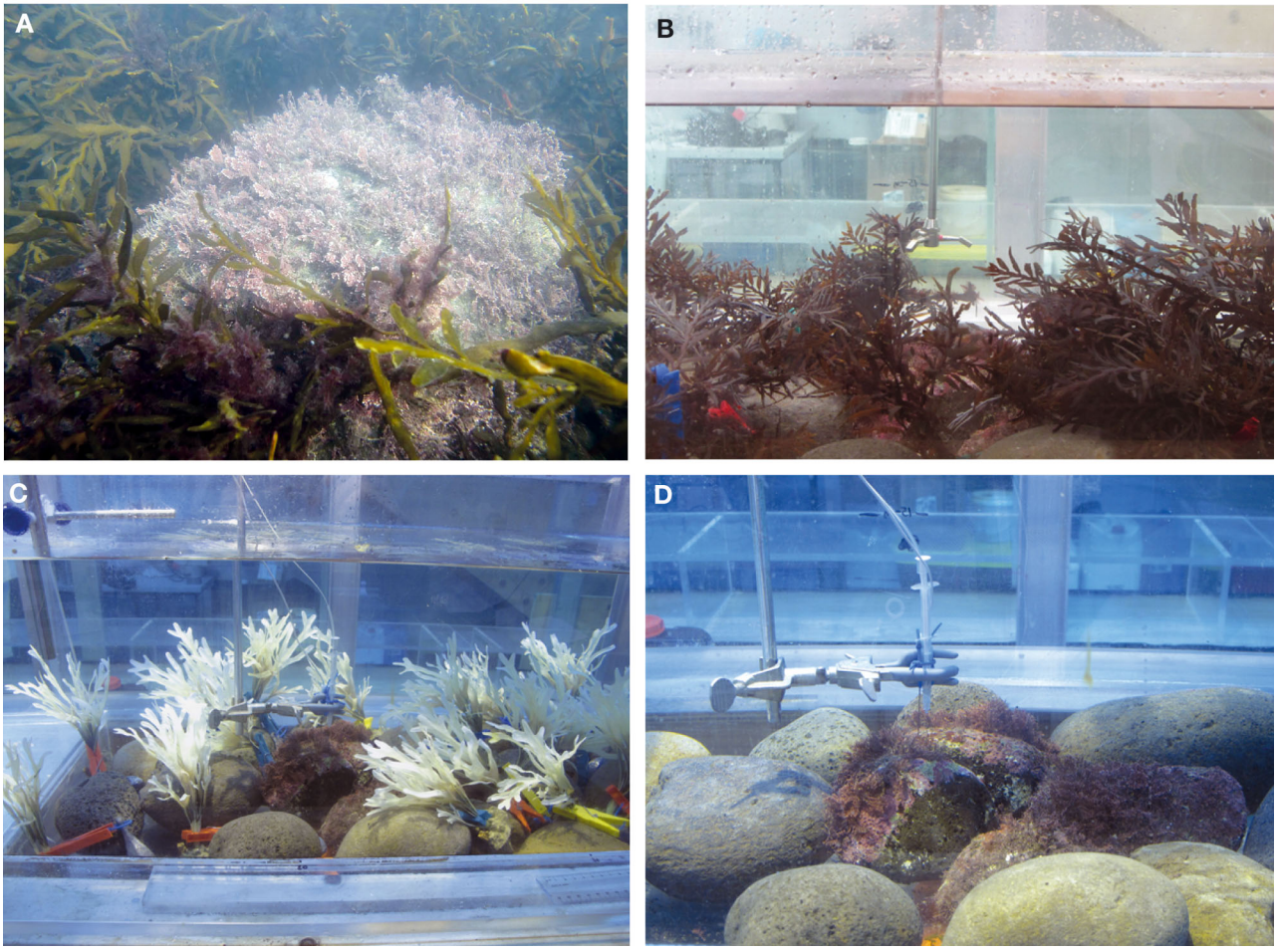

Fig. 1. (A) Macroalgal assemblage at the collection site. In the background and foreground is *Carpophyllum maschalocarpum* and in the centre is *Corallina officinalis* above the crustose coralline macroalgae (CCA). Also pictured are the 3 canopy treatments within the working section of the flume: (B) *Carpophyllum*, (C) Mimic, and (D) *Corallina* only. All treatment types had an understorey of *Corallina* and CCA

water velocity. A 5 × 5 cm section of *Carpophyllum* canopy and the *Corallina* understorey was removed before each set of measurements (i.e. velocity, pH and O_2 profiles) were taken to prevent interference with the sensors, following Kregting et al. (2011).

The mean pH measured in the bulk seawater at the start and end of each experimental run is given in Table 1. pH was measured with a semi-micro electrode (1.5 mm tip diameter; Micro-electrodes®) and a reference electrode (Micro-electrodes®) attached to a Unisense pH meter (Aarhus). A Presens 50 µm microoptode was used to measure O_2 concentrations. A minimum period of 30 min acclimation to each treatment (after which pH and O_2 concentration at the surface of the CCA had stabilised) occurred prior to starting vertical profiles.

Table 1. Mean (SE) carbonate parameters, temperature and salinity of seawater used during the experiment. Total pH (pH_T), total alkalinity (A_T), temperature and salinity (S_A) were measured, while other dissolved inorganic carbon (DIC) species were calculated from measured parameters (n = 8)

Parameter	Mean
pH_T	8.04 (0.01)
pCO_2 (µmol)	363 (4)
A_T (µmol kg^{-1})	1971 (11)
DIC (µmol kg^{-1})	1806 (2)
Temperature (°C)	14.09 (0.06)
[CO_2] (µmol kg^{-1})	14 (1)
[HCO_3^-] (µmol kg^{-1})	1674 (3)
[CO_3^{2-}] (µmol kg^{-1})	118 (1)
S_A	30.24 (0.16)

Profiles of O_2 concentration and pH were taken by placing the O_2 microoptodes and pH electrodes simultaneously at the surface (0 mm) of the CCA under the *Corallina* and (if present) macroalgae canopy. Due to differences in probe sampling frequency, a mean of 60 pH measurements were collected over 1 min, while for O_2 a mean of 30 readings were collected over the same time period. pH and O_2 measurements were then made at 0.2, 0.4, 0.6, 0.8, 1, 2, 3, 5, 7, 11, 15, 19, 23, 27, 31, 35 and 40 mm above the CCA surface. These distances were chosen to most accurately measure the thickness of the CBL when it was relatively thin (<1 mm) and thick (>11 mm) (Hurd et al. 2011, Cornwall et al. 2013b). These measurements are hereafter referred to as replicate 'profiles', and each one was conducted in <1 h. One replicate profile was conducted at the same position on each *Corallina* + CCA cobble replicate for each combination of irradiance, velocity and canopy treatment level. This approach avoided uncontrollable variation among treatments due to assemblage composition and morphology, and followed that recommended by Hurlbert (1984, p. 196), where any confounding effects would influence all treatments equally. Replicate identity was therefore treated as a random variable in the statistical design (see 'Data analyses' below). For each replicate cobble, the order of profiles for all canopy treatment, irradiance level and flow velocity combinations were randomised, with the exception of irradiance level, which alternated between light and dark to reduce any possible effects of photoinhibition. Two replicate profiles were measured with the same canopy assemblage arrangement on 2 different cobbles (out of the 3 present) within the flume. These 4 different cobble and canopy assemblages are referred to as 'arrays'. For logistical reasons, the coralline cobbles were replaced every second replicate. See Table S1 in the Supplement at www.int-res.com/articles/suppl/m525p081_supp.pdf for a detailed explanation of the measurement sequence.

The O_2 microoptode and the semi-micro pH electrode were attached to a World Precision Instruments M3301R manual micro-manipulator with the semi pH electrode positioned 8 mm downstream of the oxygen microoptode and at a 120° angle relative to the microoptode. pH was measured on the total scale, then standardized to 12°C using TRIS and 2-aminopyridine buffers. Buffers were prepared as directed by Dickson et al. (2007). TRIS buffers were standardized against a seawater buffer provided by A. Dickson (Scripps Institution of Oceanography).

During all profile measurements, temperature was recorded using a Precision Multi digital thermometer. The salinity of the seawater was measured using an YSI salinity probe. Total alkalinity (A_T) was determined via closed cell titration using methods described by Dickson et al. (2007). A_T samples were taken in the bulk seawater outside the working section. The accuracy of the method was estimated to be 3.7 µmol kg^{-1} based on reference material provided by A. Dickson (Scripps Institution of Oceanography). Average carbonate chemistry parameters for the bulk seawater at pH 8.03 are given in Table 1. A_T, pH on the total scale (pH_T), salinity measurements (S_A) and temperature were used to calculate DIC. Using these values, concentrations of CO_2, CO_3^{2-} and HCO_3^- were calculated using the constants of Mehrbach et al. (1973) refitted by Dickson & Millero (1987).

After the O_2 and pH profiles had been completed for a particular replicate of all experimental treatment levels, the microsensors were removed and velocity profiles were measured at the same location using a Sontek acoustic Doppler velocimeter (ADV). The bottom of the ADV sampling volume (17 to 19 mm volume, 56 to 58 mm above the substrate, which had been previously mapped; Finelli et al. 1999) was placed at the surface of the CCA and velocity was measured at 23 heights to a distance 68 mm above the surface. At each height, velocity was recorded for 60 s at 16 Hz. The ADV measures velocity in 3 directions, but for the purposes of this analysis we considered only horizontal velocity (u). Hereafter, all mention of seawater velocity is referring to horizontal velocity. To control for the effects of drag from the macroalgae canopy on bulk seawater velocity in the flume, we also measured one velocity profile upstream of the full *Carpophyllum* canopy treatment and another without biotic cobbles (i.e. with no macroalgae/cobbles of any type present).

CBL thickness was calculated for each O_2 and pH profile, and was defined as the greatest height above the surface of the alga at which the concentration of O_2 or H^+ was >99% of the mainstream value, essentially similar to methods used previously (Hurd et al. 2011, Cornwall et al. 2013b). In order to calculate this, O_2 concentrations and pH were standardised to bulk values to account for small variations among replicates (<5% variation in concentrations). pH was standardised to H^+ concentration, as it is a logarithmic scale, using the conversion of $[H^+] = 10^{-pH}$ (Riebesell et al. 2010). O_2 and H^+ were then standardised by dividing the concentration at any given profile location by the mean of the bulk seawater con-

centration measured at the start and end of the profile (Hurd et al. 2011, Cornwall et al. 2013b), then multiplying it by the mean O_2 concentration or pH (respectively) of the bulk seawater for all 8 profiles. These methods were employed rather than using the linear (Jørgensen & Revsbech 1985) or hyperbolic tangent methods (derived from Nishihara & Ackerman 2007) because the linear fit overestimates CBL thickness for pH, while the hyperbolic tangent method was not appropriate because O_2 concentration increased above the canopies in some light treatments.

Data analyses

Separate repeated measures analysis of variance (ANOVA) were used to determine the effect of the fixed categorical factors irradiance (light, dark), canopy type (*Carpophyllum*, mimic, *Corallina* only), bulk seawater velocity (2, 4, 8 cm s^{-1}), and their interaction on near-surface O_2 and H^+ concentrations and derived CBL thicknesses. Because of the overwhelming effect of irradiance, which influenced the direction of the response and was highly significant in most models ($p < 0.001$; see Table S2 & S3 in the Supplement), the analysis was conducted separately for the light and dark treatments to examine flow and canopy effects. Replicate number (i.e. which of the 8 cobble and canopy replicates were used) was treated as a random variable. The effect of canopy treatments and bulk velocity on the velocity nearest to the surface of the CCA was also examined in this way, except irradiance was not a factor in this model. pH and O_2 concentration was standardised as described above, and surface O_2 concentrations and CBL thicknesses were log (x +1) transformed to satisfy test assumptions (normality and homogeneity of variances). This analysis was repeated using readings from the furthest distance from the CCA (i.e. the end of the profile) and with bulk seawater pH measurements to determine whether the *Carpophyllum* treatment significantly modified seawater chemistry. When statistical differences were found in the main effects or the interactions in any model, a Tukey's post hoc test was conducted for that model with the random factor removed.

To further investigate the role of velocity on pH, O_2 concentration and CBL thickness, a model was constructed with the same factors as above, except with bulk velocity replaced by near-surface velocity, which was treated as a continuous variable. Near-surface velocity was treated as a positive integer regardless of the direction of flow, which occasionally reversed close the surface of the CCA or *Corallina*. Post hoc multiple comparison tests were performed using the package 'phia' in R v.2.7.0 (R Development Core Team 2008) when statistical differences were found in main effects or in interactions. All statistics were performed in R©.

RESULTS

Effects of canopy treatments on flow

Seawater velocity was reduced by the presence of *Carpophyllum* and mimic macroalgal canopies at all measured heights above the CCA and understorey *Corallina* (Fig. 2). This was especially the case closer to the surface of the CCA, where the presence of *Carpophyllum* and the mimic treatments significantly lowered seawater velocity more than the *Corallina* treatment at all 3 bulk seawater velocities (post hoc tests, $p < 0.04$; Table 2, Fig. 2). This equated to a 91 to 100% attenuation of the bulk seawater velocity at the surface of the CCA under *Carpophyllum* canopies, an 82 to 100% attenuation under mimic canopies, and 62 to 79% attenuation under sub-canopies of *Corallina* only (Fig. 2). The amount of attenuation was dependent on bulk seawater velocity, with significantly greater proportions of the bulk seawater velocity being attenuated under faster flows (Table 2). For the *Carpophyllum* and mimic canopies, this attenuation occurred throughout the measurement range (up to 6 cm above the cobbles), whereas for the *Corallina* only treatment, this attenuation occurred only at distances <4 cm above the surface of the CCA (Fig. 2), which was the greatest height of the *Corallina* sub-canopy. The slowest mean velocity at the surface of the CCA was under the *Carpophyllum* treatments at the bulk seawater velocity of 2 cm s^{-1} (mean ± SE = 0.24 ± 0.08 cm s^{-1}), while the fastest was in *Corallina* only treatments at 8 m s^{-1} (2.92 ± 0.87 cm s^{-1}).

pH and O_2 concentration

The artificial seawater used for the experiments had a stable bulk pH (mean = 8.04, SE < 0.01) and the variability in the associated carbonate parameters during the course of individual profiles and between individual profiles was low: the calculated SE of the concentrations of the 3 DIC species was below that of measurement uncertainty (<1 for CO_2 and CO_3^{2-},

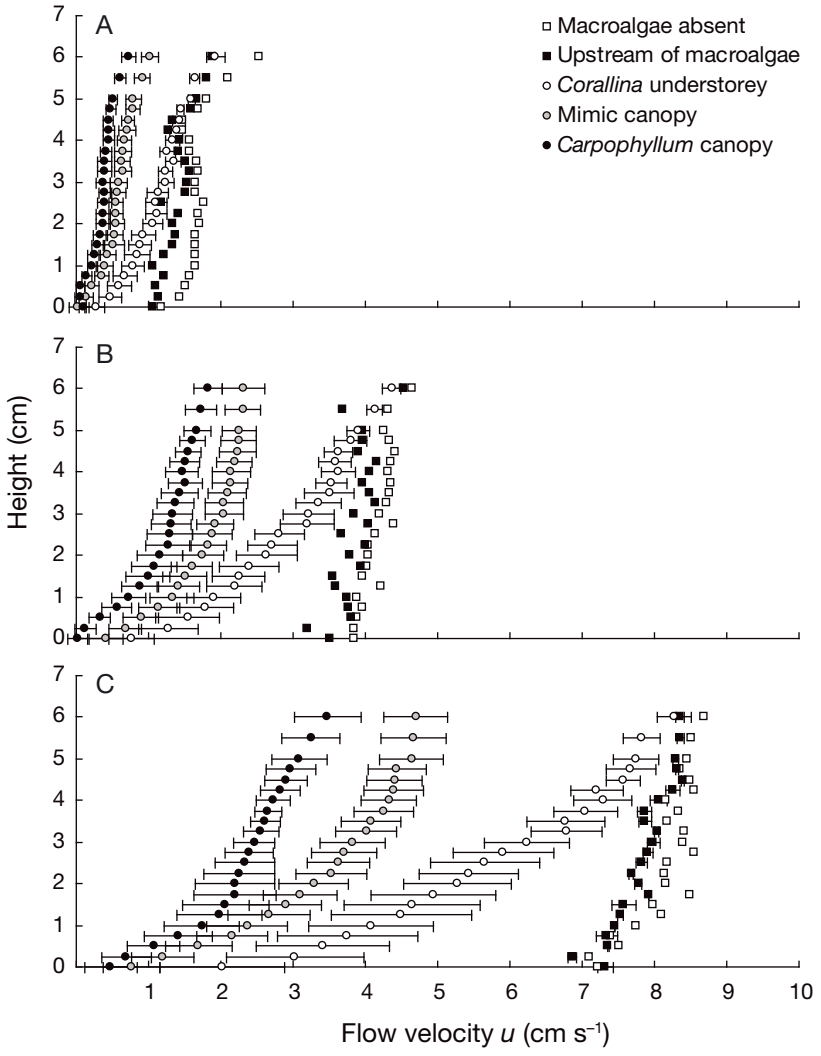

Fig. 2. Seawater velocity as function of (standardised) height (6.6 to 0.6 cm) from the boundary. Measurements were made with 1 of 3 experimental canopy treatments above the crustose coralline macroalgae (CCA): *Carpophyllum* canopy with *Corallina* understorey, mimic canopy with *Corallina* understorey, and *Corallina* only. Measurements were made at treatment bulk seawater velocities of (A) 2 cm s^{-1}, (B) 4 cm s^{-1}, and (C) 8 cm s^{-1}. Also shown are velocity profiles with no macroalgae (i.e. no canopy, *Corallina*, or CCA), and upstream of the macroalgae. Data represent the mean (±SE) of 8 replicate assemblages, except for the no macroalgae and upstream measurements where n = 1 to 2

and <3 for HCO_3^-) throughout the course of the experiment. There was no difference between seawater O_2 concentrations and pH at the greatest distance from the CCA surface among any of the canopy treatments used, nor were there any differences in measured bulk seawater pH between canopy treatments ($p > 0.25$ on all occasions).

Seawater chemistry at the surface of the CCA was significantly modified by biological activity. pH and O_2 concentration within the CBL at the surface of CCA was altered by irradiance level, bulk seawater velocity, and the canopy treatment (Table 2 & S2, Figs. 3, 4 & 5). pH within the CBL decreased due to respiration by *Corallina* and CCA in the dark (Fig. 3A,C,E), and increased due to photosynthesis in the light in all treatments (Fig. 3B,D,F). Changes in pH compared to the bulk seawater pH were greatest under low bulk seawater velocities (2 cm s^{-1}) and beneath *Carpophyllum* canopies (max. mean pH in the light = 8.90; min. mean pH in the dark = 7.74). Changes in pH were lowest at 8 cm s^{-1} and in *Corallina* only treatments (min. mean pH in the light = 8.03; max. mean pH in the dark = 7.98). O_2 concentration closely mimicked pH and followed the same trends described above, where the maximum mean O_2 concentrations at the surface of the CCA were 3.1 times higher than the bulk seawater in the light, and 0.8 times lower than the bulk seawater in the dark (both recorded at 2 cm s^{-1} under *Carpophyllum* canopies; Fig. 5).

The effect of canopy treatment was not significant when the measured near-surface seawater velocity was added as a continuous factor to the analysis of near-surface pH and O_2 concentration (Table 3, Fig. 5), as canopy treatments differentially reduced near-surface velocity (Table 2, Fig. 5). There was a significant interaction between near-surface seawater velocity and canopy treatment in the light for pH and O_2 concentration (Table 3), where comparisons between canopy treatments revealed that concentrations were higher under *Carpophyllum* and mimic canopies as near-surface velocity decreased ($p < 0.05$ on all occasions).

CBL thickness

The thickest mean CBLs measured using O_2 and pH were 22.5 ± 5.83 (O_2) and 12.6 ± 4.83 mm (pH) under a *Carpophyllum* canopy at 2 cm s^{-1} bulk seawater velocity in the light. The thinnest mean CBLs measured using O_2 and pH, respectively, were 0.22 ±

Table 2. Repeated measures ANOVA examining the effect of bulk seawater velocity and canopy treatment type ('Canopy') on the flow velocity and pH/O_2 concentration in the light and dark near the surface of the crustose coralline macroalgae (CCA). Effects of replicate identity are not presented in the output (but were included in the analysis) as they were not significant in any model. Post hoc results indicate significant differences between canopy treatments (*Carpophyllum* = *Ca*, mimic = M, *Corallina* only = *Co*) and velocity treatments (2, 4 and 8 cm s^{-1})

	Factor	df	*F*-value	p-value	Post hoc results
Seawater velocity	Canopy	2	4.74	0.01	*Ca* = M > *Co*
	Bulk velocity	2	13.78	<0.01	2 = 4 > 8
	Canopy × Bulk velocity	4	1.67	0.18	
	Residuals	33			
pH [H^+] — light	Canopy	2	3.40	0.04	*Ca* = M > *Co*
	Bulk velocity	2	24.59	<0.01	2 > 4 > 8
	Canopy × Bulk velocity	4	0.53	0.71	
	Residuals	33			
pH [H^+] — dark	Canopy	2	0.96	0.39	
	Bulk velocity	2	7.37	<0.01	2 < 4 = 8
	Canopy × Bulk velocity	4	0.58	0.68	
	Residuals	33			
[O_2] — light	Canopy	2	3.79	0.03	*Ca* > M > *Co*
	Bulk velocity	2	6.39	<0.01	2 > 4 = 8
	Canopy × Bulk velocity	4	0.65	0.63	
	Residuals	33			
[O_2] — dark	Canopy	2	3.45	0.04	*Ca* = M < *Co*
	Bulk velocity	2	13.15	<0.01	
	Canopy × Bulk velocity	4	0.71	0.59	2 < 4 = 8
	Residuals	33			

0.10 and 0.7 ± 0.23 mm under *Corallina* only treatments at 8 cm s^{-1} in the dark. The conditions where the CBLs were thickest corresponded to the slowest measured seawater velocity near the surface of the CCA (Figs. 5 & 6; mean ± SE = 0.24 ± 0.04 cm s^{-1}), whereas the conditions where the thinnest CBLs were measured corresponded to the same treatment in which the highest mean seawater velocities near the surface of the CCA were measured (Figs. 5 & 6; 2.92 ± 0.90 cm s^{-1}).

Table 3. Mixed effects model examining the effect of near-surface seawater velocity and canopy treatment type ('Canopy') on the pH/O_2 concentration in the light and dark near the surface of the crustose coralline macroalgae (CCA). Effects of replicate identity are not presented in the output (but were included in the analysis) as they were not significant in any model

	Factor	df	*F*-value	p-value
pH [H^+] — light	Near-surface velocity	1	13.71	<0.01
	Canopy treatment	2	0.87	0.42
	Near-surface velocity × Canopy treatment	2	5.59	<0.01
	Residuals	60		
pH [H^+] — dark	Near-surface velocity	1	3.05	0.09
	Canopy treatment	2	0.34	0.71
	Near-surface velocity × Canopy treatment	2	1.24	0.29
	Residuals	60		
[O_2] — light	Near-surface velocity	1	9.90	<0.01
	Canopy treatment	2	3.17	0.04
	Near-surface velocity × Canopy treatment	2	4.55	0.01
	Residuals	60		
[O_2] — dark	Near-surface velocity	1	6.61	0.01
	Canopy treatment	2	1.31	0.28
	Near-surface velocity × Canopy treatment	2	2.38	0.10
	Residuals	60		

For both pH and O_2 concentration, CBLs tended to be thicker at slower bulk seawater velocities (Fig. 6), though only CBLs at 2 cm s^{-1} were statistically different from other velocity treatments ($p < 0.01$; Table 4). O_2 CBLs were significantly thicker in the light compared to the dark (Tables 4 & S3). Both O_2 and pH CBLs were significantly thicker under the *Carpophyllum* canopies than the mimic or *Corallina* only treatments (Tables 4 & S3, Fig. 6; $p < 0.04$ on all occasions). When the canopy treatments were compared with each other, CBLs measured under *Carpophyllum* canopies were significantly thicker than those in *Corallina* only treatments when measured using O_2 ($p < 0.01$; Table 4), but were only marginally significant when using

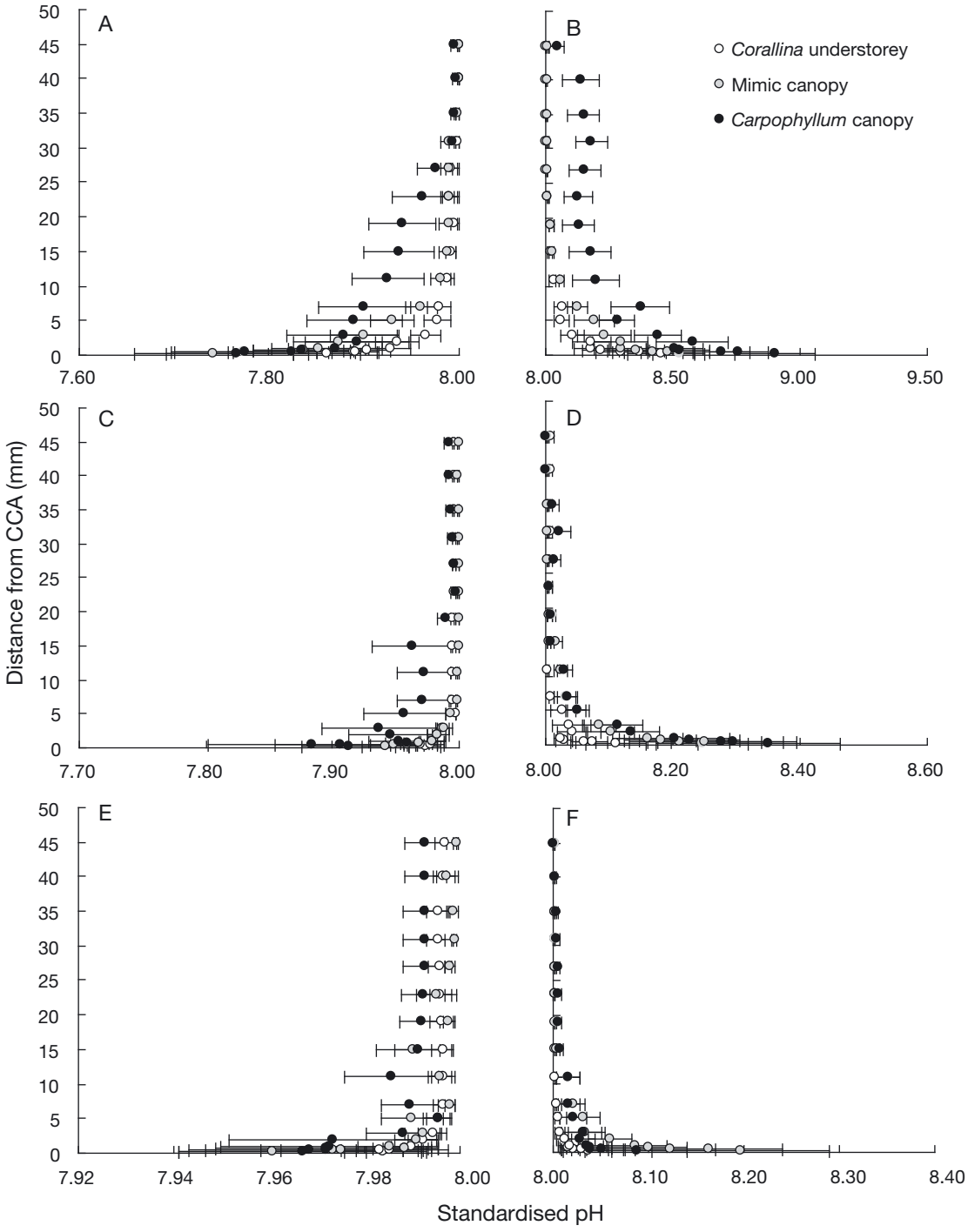

Fig. 3. Mean (±SE) standardised pH above the surface of crustose coralline macroalgae (CCA) in the dark at (A) 2, (C) 4, and (E) 8 cm s^{-1} bulk seawater velocity, and in the light at (B) 2, (D) 4, and (F) 8 cm s^{-1} bulk seawater velocity. pH was measured in the presence of a *Corallina* understorey, a mimic canopy and a *Carpophyllum* canopy (n = 8 replicate assemblages)

pH ($p = 0.08$; Table 4). This was especially the case under slower bulk seawater velocities, as in the model there was a significant interaction between the effect of treatments and bulk velocity, which was revealed in post hoc tests to be due to the effects of increasing differences between *Carpophyllum* and *Corallina* only treatments at 2 cm s^{-1} velocity ($p < 0.05$ for both pH and O_2).

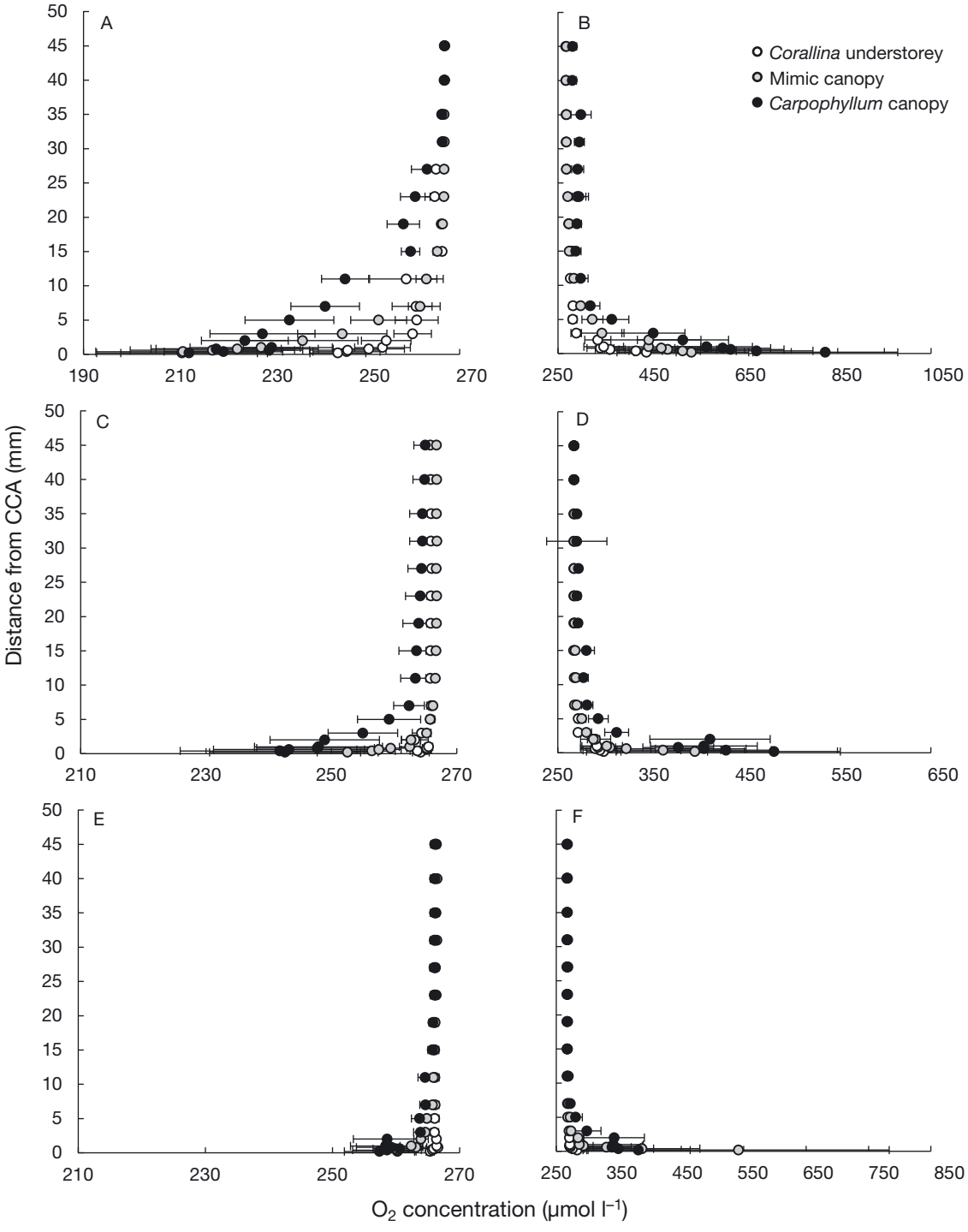

Fig. 4. O_2 concentration standardised to the mean (±SE) bulk seawater concentration, above the surface of crustose coralline macroalgae (CCA). Other details are as in Fig. 3

DISCUSSION

Canopy macroalgae altered the pH and O_2 environment of understorey coralline algae via their physical presence. This ability of macroalgal canopies to increase the degree of metabolic changes in pH within the CBL of understorey organisms has not been previously documented. The largest extent that the CBL can physically form is dependent on water velocity throughout the CBL (Denny & Wethey 2000,

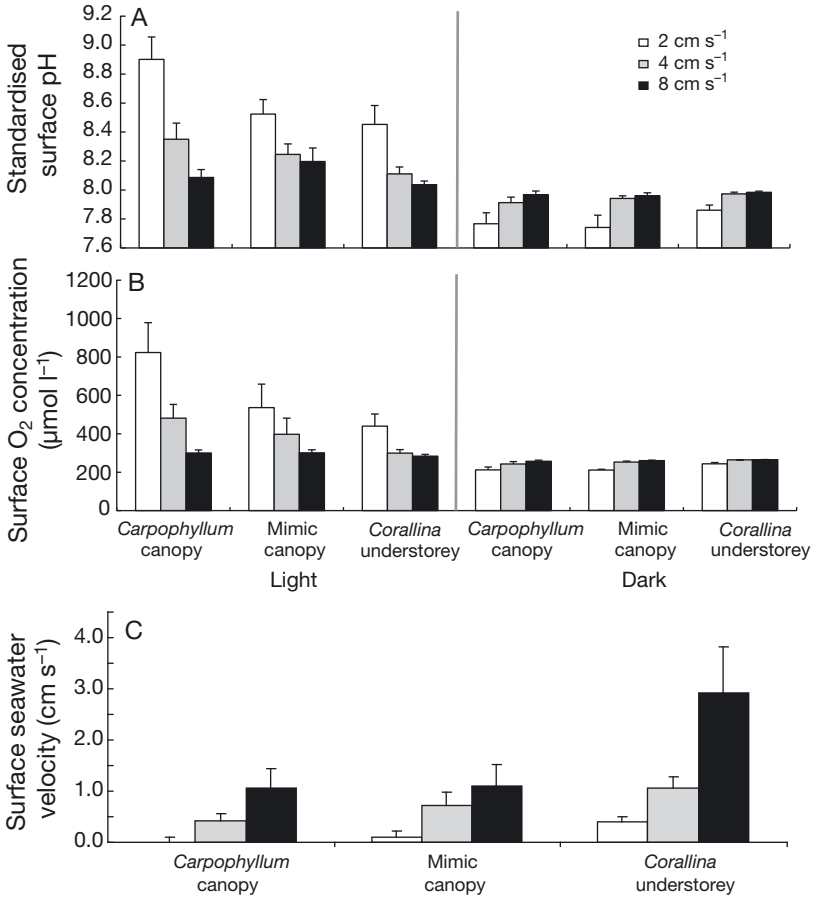

Fig. 5. Mean (±SE) standardised (A) pH, (B) O_2 concentration, and (C) seawater velocity at or near the surface of the crustose coralline macroalgae (CCA) in the light and dark (A,B); parameters were measured in the presence of a *Corallina* understorey, a mimic canopy and a *Carpophyllum* canopy (n = 8 replicate assemblages) and at 2, 4 and 8 cm s^{-1} bulk seawater velocities

Hurd 2000). In this study, the thickness of the CBL was controlled by the amount of velocity attenuated by the 3 canopy treatments as well as the bulk seawater velocity. Flow attenuation therefore determined the degree of biological modification of seawater that the CCA encountered within each canopy treatment, when combined with factors such as the metabolic rates at the surface of the CCA (Nishihara & Ackerman 2007), CCA surface topography (Hurd et al. 2011), and the influence of the *Corallina* subcanopy (Cornwall et al. 2013b). In this experiment it is likely that the CBL around the CCA merged with that of the above *Corallina* (Cornwall et al. 2013b), but did not merge with that of the *Carpophyllum* above them. It is likely that the distance between the *Carpophyllum* and *Corallina* CBLs was too great (>60 mm) here for them to merge, though if smaller *Carpophyllum* individuals were used or the *Corallina* CBL was thicker (due to larger individuals or greater metabolic activity), they might have formed a continuous CBL. Sessile organisms possess a wide variety of morphologies in rocky reef communities. It is probable that the morphology and composition of species — or of abiotic substrates — above and around understorey species will determine their CBL thickness. In addition, flow is rarely unidirectional in the field as a result of wave action and reflectance off surfaces. The varied nature of rocky shore communities makes testing any generalities about the thickness of compound CBLs in the field very difficult; however, it is probable the CBLs of shorter canopies of macroalgae (e.g. non calcareous turf-forming species) could merge to form even larger CBLs than those measured here under unidirectional flow. Conversely, CBLs will likely be thinner under canopies in areas with higher turbulence and wave action. Both considerations require further research.

The physical and metabolic effects of the *Carpophyllum* canopy could be separated by examining the effects of the mimics on pH and O_2 profiles. Treatments containing canopies of *Carpophyllum* or mimics attenuated a greater amount of seawater velocity than treatments containing an understorey of *Corallina* alone; this in turn created a thicker CBL, resulting in greater metabolic alteration of pH/O_2 concentration within the CBL by understorey coralline algae in those treatments. Differences observed in pH/O_2 profiles between the *Corallina* and the *Carpophyllum* treatments were not due to the biological activity of the *Carpophyllum* canopy. This is because the difference in pH/O_2 concentration at the furthest distance from the CCA was not different between *Carpophyllum* and mimic canopy treatments, and because there were no significant changes in seawater pH between different canopy treatments. This result was likely caused by the small biomass of macroalgae to seawater ratio purposely used in the flume. This biomass to water ratio was chosen to enable us to measure the indirect effects of canopies on understorey macroalgal pH conditions without it being masked by the direct effects of

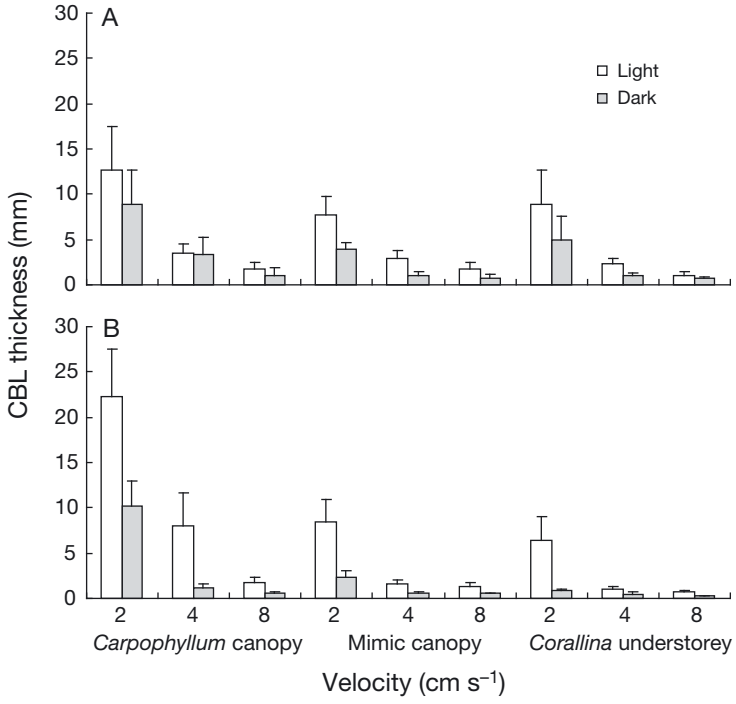

Fig. 6. Concentration boundary layer (CBL) thicknesses above assemblages of the *Corallina* and crustose coralline macroalgae (CCA) measured using (A) pH and (B) O_2 concentration under 3 different canopy types (*Carpophyllum* canopy, mimic canopy, and an understorey of *Corallina* only) and 3 different bulk seawater velocities (2, 4 and 8 cm s^{-1}). White bars: CBLs in the light; grey bars: CBLs in the dark. Data represent the mean ± SE (n = 8 replicate assemblages)

Table 4. Repeated measures ANOVAs examining the effect of bulk seawater velocity ('Velocity'), canopy treatment type ('Canopy'), and irradiance on the pH and O_2 concentration boundary layer (CBL) thickness measured around assemblages of crustose coralline macroalgae and *Corallina officinalis*. Effects of replicate identity are not included in the output as they were not significant in any model. Post hoc results indicate significant differences between canopy treatments (*Carpophyllum* = *Ca*, mimic = M, *Corallina* only = *Co*) and velocity treatments (2, 4 and 8 cm s^{-1})

	Factor	df	*F*-value	p-value	Post hoc results
$[O_2]$	Canopy	2	15.87	<0.01	*Ca* = M > *Co*
	Velocity	2	28.46	<0.01	2 > 4 = 8
	Irradiance	1	19.86	<0.01	
	Canopy × Velocity	4	6.34	<0.01	
	Canopy × Irradiance	2	2.53	0.08	
	Velocity × Irradiance	2	5.84	<0.01	
	Canopy × Velocity × Irradiance	4	0.51	0.73	
	Residuals	103			
pH $[H^+]$	Canopy	2	5.14	<0.01	*Ca* > M = *Co*
	Velocity	2	18.14	<0.01	2 > 4 = 8
	Irradiance	1	2.98	0.09	
	Canopy × Velocity	4	3.66	<0.01	
	Canopy × Irradiance	2	0.11	0.89	
	Velocity × Irradiance	2	0.77	0.46	
	Canopy × Velocity × Irradiance	4	0.05	0.99	
	Residuals	103			

macroalgal biomass that can occur in the shallow subtidal within dense macroalgal beds (Cornwall et al. 2013a). Our experimental setup represents conditions that would be more common in deeper subtidal habitats (Frieder et al. 2012), habitats that are more wave-exposed and therefore have lower seawater retention times (Pelejero et al. 2010), or in macroalgal beds that possess lower densities.

The role of larger canopy-forming species in altering the pH micro-environment has important implications for the functioning of understorey species assemblages beneath them. Both O_2 and pH (and carbonate parameters related to pH: CO_2, HCO_3^-, CO_3^{2-}) all play a complex physiological role for many marine organisms. For calcareous macroalgae, seawater pH plays an important role in influencing rates of net calcification and photosynthesis (Semesi et al. 2009b). Also, small-scale changes in the density of canopy-forming macroalgae in a particular habitat could alter growth rates of understorey macroalgae by reducing the supply of DIC at their surface. CO_2 has traditionally not been considered to limit the productivity of macroalgae (including coralline macroalgae) due to the presence of energetically expensive carbon concentrating mechanisms (CCMs), which increase the concentration of CO_2 relative to O_2 for photosynthesis at the site of RuBisCO by activity transporting HCO_3^-/CO_2 across the plasma membrane and/or plastid (Raven 1997, Raven et al. 2002). However, different species of macroalgae possess CCMs with varying efficiencies, and some do not possess CCMs at all (Kübler et al. 1999, Hepburn et al. 2011, Cornwall et al. 2015). In addition, some species may be able to regulate the use of the CCM, where at higher CO_2 concentrations its activity could be reduced to some degree, resulting in possible energetic benefits (Raven 1991, Cornwall et al. 2012). This means that CO_2 concentrations

could be considered a limiting resource for some macroalgae, where the supply of CO_2 can limit the growth of some species with inefficient or no CCMs (Connell et al. 2013). Therefore, changes in DIC (and O_2) at the surface of understorey macroalgae due to canopy cover could result in spatial differences in productivity between individuals of the same species over even a few meters.

The role that canopy-forming macroalgae play in altering light levels (Gerard 1984, Reed & Foster 1984), and how this interacts with understorey species growth and assemblage compositions, is well documented (Kennelly & Underwood 1993, Edwards 1998, Connell 2005). However, variations in canopy cover above understorey macroalgae could reduce their growth rates through reducing light, by canopy macroalgae altering the understorey CBL thickness, and through the effects of macroalgal metabolism on bulk seawater pH within a habitat (Anthony et al. 2011, Hofmann et al. 2011, Cornwall et al. 2013a). The effects of canopy macroalgae on understorey species is likely context dependent, and could vary by density. At extremely high densities, shading could also cause net respiration of understorey species. It is currently unknown how these 3 processes interact to influence understorey species. Our experiment measured the short-term capacity of understorey algal metabolism to modify pH and O_2 concentration under a range of flow, light and canopy conditions. There is now a need to quantify the multiple, interactive effects of canopies on understorey calcareous macroalgae in long-term growth experiments.

Enhancement of metabolic changes in pH around understorey species by canopy-forming macroalgae likely has important implications for the current and future functioning of macroalgal-dominated habitats. Predicting how ocean acidification and other anthropogenic impacts will affect temperate rocky reefs is difficult, as the role canopy species play is inherently intertwined with both the chemical and physical processes that could both potentially have strong effects on the physiology of nearby species. Not only that, complex changes in species interactions could occur between canopy-forming species and other understorey species under one set of conditions but not others (e.g. light, nutrients; Russell et al. 2009, 2011). Future research examining the effects of ocean acidification on temperate rocky reef macroalgae should acknowledge that the responses of a single species in isolation could be different than the same species in natural assemblages. Effects due to differences in light, O_2 concentrations and, importantly, pH/CO_2 at the surface of an individual could nullify, dampen or even amplify the effects of CO_2 treatments.

Future ocean acidification could have negative consequences for macroalgal-based ecosystems (Caldeira & Wickett 2003, Hall-Spencer et al. 2008). However, the presence of thicker boundary layers around coralline macroalgae can create areas of seawater carbonate chemistry that are conducive to higher net calcification rates (Cornwall et al. 2014). Water motion modulates this process; increasing seawater velocity results in smaller CBLs and smaller changes in pH in systems (Hurd et al. 2011, Cornwall et al. 2013b). The potential for photosynthesis by calcareous autotrophs to modify the magnitude of the effects of ocean acidification could be further enhanced by the presence of larger macroalgae canopies that reduce flow and increase the CBL thickness of understorey species (as in this study). Variability in bulk seawater pH can be ±1 unit or more over diel cycles in macroalgal beds (Cornwall et al. 2013b, Delille et al. 2000); within dense canopies that slow flow, understorey species could see an even wider envelope of pH and O_2 variability in the field than that measured previously. Understorey species may be more robust to ocean acidification compared to species that do not live under macroalgal canopies if exposure to higher pH during the day decreases that particular organism's susceptibility to ocean acidification. These hypotheses remain untested, but if true, it is likely that the removal of canopy species through disturbance (such as increases in temperature or direct harvesting) could exacerbate any potential influence of ocean acidification on the calcareous organisms that live beneath them.

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