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Seeing red: Coral larvae are attracted to healthy-looking reefs

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ABSTRACT: Settlement cues play an essential role in larval habitat selection and influence post-settlement survival. Recent studies have investigated the impacts of elevated temperature and partial pressure of carbon dioxide (pCO_2) on the ability of marine larvae to locate the reef. In coral larvae, there has been a focus on chemical settlement cues, which are critical to successful habitat selection, but less is known about the role of spectral cues. In this study, we provided larvae with crustose coralline algae (CCA), their preferred settlement surface (and chemical cue), and either a white or a red synthetic settlement surface that simulated the wavelengths emitted by bleached and unbleached CCA, respectively. We performed these experiments under 4 temperature–pCO_2 regimes to determine whether elevated temperature (+3°C) or pCO_2 (900 µatm) affected how larvae respond to settlement cues. Settlement rates increased by ~85% on the synthetic surface if the background colour was red compared to white. Larvae preferentially settled on the CCA chips, since these provided both a chemical and a spectral cue. However, when most of the CCA was occupied, particularly the preferred spaces along edges and in depressions, larval settlement on the synthetic surface only occurred if it appeared red. Neither elevated temperature nor elevated pCO_2 directly affected settlement rates or substrate preference, but our findings indicate that larvae could be indirectly affected by these stressors. Elevated temperatures and acidification are already known to disrupt chemical cues but may also disrupt spectral cues by causing CCA bleaching, thereby inhibiting the ability of larvae to either 'smell' or 'see' the reef.

KEY WORDS: Coral larvae · Settlement · Red · Spectral cues · Temperature · pCO_2

INTRODUCTION

Many coral reef organisms have a pelagic stage in their life history during which they disperse for hours to months before recruiting to a suitable reef habitat. Once thought to be passive particles, it is now known that coral larvae actively distinguish and select habitat types (Babcock & Mundy 1996, Raimondi & Morse 2000, Baird et al. 2003, Harrington et al. 2004). Habitat selection affects early post-recruitment survival (Harrington et al. 2004) and also influences the likelihood of surviving to the adult (reproductive) stages, as once the coral larva has metamorphosed, it will usually remain attached to the substrate for the duration of its life, able to alter its habitat conditions only through asexual growth and propagation. Thus, it is not surprising that the larvae of corals and other sessile organisms have well-developed sensory abilities (Vandermeulen 1974, Hadfield et al. 2000).

Once coral larvae are competent to settle, they begin to actively seek a suitable settlement substrate (Harrison & Wallace 1990). The surface irregularity and angle of the substrate have been shown to affect settlement (Carleton & Sammarco 1987, Doropoulos et al. 2016). In addition to these physical attributes, chemical cues associated with reef substrata, such as

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crustose coralline algae (CCA) and microbial biofilms, are known to induce settlement (Morse et al. 1988, 1996, Heyward & Negri 1999, Negri et al. 2001). The ability to detect favoured settlement surfaces suggests that coral larvae have a relatively advanced chemical sensory system. Coral larvae investigate the substrate with their aboral ends and then attach aboral end first. Unlike other marine invertebrate larvae, coral larvae do not have an apical sensory organ (Hadfield et al. 2000, Nedved & Hadfield 2009) but do have sensory cells concentrated in the aboral epidermis (Vandermeulen 1974). These sensory cells have been shown to detect chemical settlement cues associated with the substrate (Tran & Hadfield 2013); however, there is still little known about the internal signaling involved in metamorphosis. Some coral larvae have settlement preferences that are specific to certain CCA species (Morse et al. 1988, Raimondi & Morse 2000), while others have been shown to prefer substrate communities specific to the depth occupied by adult corals of the same species (Baird et al. 2003). Larvae have also been shown to detect chemical signals associated with healthy coral reef substrates in preference to those associated with degraded, seaweed-dominated substrates (Kuffner et al. 2006, Dixson et al. 2014). This has led to concerns about the potential for recovery in overfished and locally degraded areas, where recruitment is inhibited by chemical signals (Dixson et al. 2014). In addition to local stressors, global changes in oceanic carbonate chemistry and temperature can also impede coral larval settlement by driving shifts in the microbial communities associated with CCA (Webster et al. 2011, 2013a,b).

While chemical cues clearly influence coral larval settlement, less is known about the other sensory capabilities larvae utilize to identify a suitable settlement substrate. Both coral and fish larvae respond to acoustic cues and are attracted to reef sounds produced by fish and crustaceans (Simpson et al. 2005, Vermeij et al. 2010). Coral larvae are also sensitive to light, displaying positive phototaxis (Szmant & Meadows 2006) and preferences for certain light intensities at settlement (Mundy & Babcock 1998). More recently, larvae have been found to exhibit colour preferences during settlement, with a remarkable preference for red settlement substrates (Mason et al. 2011). In those experiments, coral larvae were offered a variety of different-coloured unconditioned plastic surfaces as settlement substrates, with no chemical settlement cue (such as CCA) present. Regardless of species or shape of the plastic settlement surface, larvae consistently preferred red settlement substrates, which the authors suggested was an adaptation for identifying coralline algae (Mason et al. 2011). Further investigation into their physiology indicated that coral larvae sense spectral cues via light-sensitive proteins called acropsins, some of which are able to form photoreceptors and could allow colour preference during settlement (Mason et al. 2012). We tested the importance of photosensory and chemosensory cues in influencing settlement rates under 4 temperature–pCO_2 scenarios. In particular, our study further investigates the preference coral larvae have for red settlement substrates and determines whether this colour preference is altered under elevated temperature and pCO_2.

MATERIALS AND METHODS

For more detail on the experimental set-up and maintenance of experimental conditions, see Foster et al. (2015). Gravid adult colonies of the abundant plate coral *Acropora spicifera* were collected from a depth of ~1 to 3 m at the sub-tropical Houtman Abrolhos Islands in Western Australia. Colonies were maintained in natural light conditions prior to spawning. Corals spawned on 6 March 2013 at ~21:00 h (9 d after the full moon in February). Eggs were cross-fertilized from 6 spawning colonies (representing equal contributions from 6 genotypes) and were then maintained indoors, under ambient conditions (~24°C and ~pH 8.1), until they reached the planulae stage of development. Once larvae reached the planulae stage, they were transferred into the temperature–pCO_2 treatment aquaria (Table 1). Seawater was treated in 4 separate sump tanks (1 sump per temper-

Table 1. Physical and chemical conditions for the duration of the experiment (mean ± SD). Table from Foster et al. (2015). pH_T: pH on the total scale; TA: total alkalinity; pCO_2: partial pressure of carbon dioxide; Ω_{ar}: aragonite saturation state; High T: elevated temperature; High pCO_2: elevated pCO_2; High T + pCO_2: elevated temperature and pCO_2

Treatment	Temperature (°C)	pH_T	TA (µmol kg^{-1})	pCO_2 (µatm)	Ω_{ar}
Control	24.4 ± 0.5	8.22 ± 0.05	2308 ± 40	242 ± 22	4.51 ± 0.14
High T	27.6 ± 0.8	8.18 ± 0.05	2312 ± 26	275 ± 24	4.68 ± 0.17
High pCO_2	24.1 ± 0.6	7.77 ± 0.06	2307 ±30	872 ± 58	1.93 ± 0.08
High T + pCO_2	27.4 ± 0.9	7.75 ± 0.08	2309 ± 32	976 ± 103	2.03 ± 0.12

ature–pCO_2 treatment) that flowed into replicate tanks (4 per temperature–pCO_2 treatment) every 3 h for a ~90% water change. Water temperature was monitored continuously for the duration of the experiment using Hobo Pendant temperature loggers and found to vary between only 0.5 and 0.9°C. There was also little variation in the carbonate chemistry, with pH deviating from set values by between 0.05 and 0.08 pH unit. For more information on the carbonate chemistry variability with time of day and for the duration of the experiment, see Foster et al. (2016, their Figs. S1 & S2). Light levels were maintained at a 12 h light:12 h dark cycle, with a mean (± SE) light intensity of 212 ± 8 µmol photons m^{-2} s^{-1} (Biospherical Instruments, QSL-2100). Light intensity and spectra data were not obtained from the collection site of the parent colonies.

Forty larvae were added to 50 ml clear acrylic tubes lined with transparency paper (washed and soaked in filtered seawater), with 100 µm mesh on either end to allow for water exchange and 3 chips (~0.5–1 cm^2) of *Hydrolithon* CCA added to each tube. CCA was collected from the same site as the parent colonies. To preserve their chemical cues, CCA chips were maintained in filtered seawater in outdoor aquaria under ambient conditions until the commencement of the experiment. The clear settlement tubes had either a white or a red background, which simulated the wavelengths emitted by healthy (red) and bleached (white) CCA; however, no bleached CCA were provided in this experiment. Transparent tubes and the transparency paper lining allowed for accurate counting of settlement in the tubes (i.e. including the underside of the CCA chips). Settlement was counted daily from when the larvae were introduced into the treatment tanks (6 d post-fertilisation) until 10 d post-fertilisation, when all competent larvae had settled. This assay aimed to investigate settlement surface preference based on the chemosensory (synthetic vs. natural CCA substrate) and photosensory (red vs. white background colour) abilities of larvae and the effects of elevated temperature and/or pCO_2 conditions on these sensory systems.

To determine whether the red and white synthetic backgrounds simulated the spectral emission of healthy and bleached CCA, respectively, fluorescent emission spectra were obtained for the red and white plastic backgrounds as well as for bleached and unbleached CCA. These spectra were measured using a Leica TCS SP2 multiphoton confocal microscope. Samples were scanned in multiphoton mode using an excitation wavelength of 488 nm. Scans were from 490 to 720 nm, using $xy\lambda$ mode with 10 nm windows. Spectra were peak normalized (the peak emission value was set to 100) to compare peak locations between samples. Reflectance data were not collected for the substrates, nor were analyses conducted on CCA biofilms.

To avoid nesting, when there was more than 1 tube per tank, percent settlement data from different tubes were pooled within each tank, so that there were 4 replicates per group. A 2-way MANOVA was used to compare the effect of background colour, seawater treatment and their interaction on percent settlement on the CCA and on the synthetic transparency paper. Data were tested for normality using the Shapiro-Wilk test. Settlement data for the synthetic substrate were log transformed to meet this assumption. Box's test of equality of covariance matrices showed that the assumption of homogeneity of variance–covariance matrices was also met. Pillai's Trace was used as the multivariate test of significance. All statistical analyses were conducted in SPSS version 21.

RESULTS

Fluorescence emission spectra

The fluorescence emission spectra of the red and white synthetic surfaces had similar spectral properties to unbleached and bleached CCA, respectively (Fig. 1). The red synthetic surface peaked at 600 nm, while the unbleached CCA peaked at 580 nm. The white synthetic surface had higher relative fluorescence than the bleached CCA, but both followed

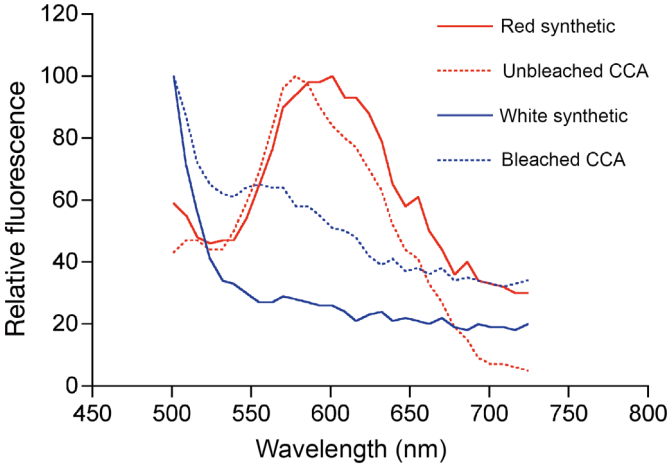

Fig. 1. Fluorescence emission spectra of the synthetic settlement surfaces (red and white) and bleached and unbleached crustose coralline algae (CCA)

similar spectral trends, peaking at the UV end of the spectrum (<400 nm) and both clearly differing from the spectra emitted by the red surfaces.

Settlement

The temperature–pCO_2 seawater treatments did not significantly affect larval settlement, and there was also no interactive effect with background colour (Table 2). In contrast, larval settlement varied considerably with the background colour alone (Table 2, Fig. 2). There was significantly higher settlement overall when the background colour was red (21%) compared to white (11%). Settlement on the CCA was ~12 to 20% regardless of background colour, but settlement on the synthetic substrate was ~25 to 30% when the background appeared red and ~3 to 5% when it appeared white (Fig. 2). However, larvae had more available space on the synthetic surfaces than on the CCA chips. Thus, larvae probably preferred to settle on the CCA, with much of the surface area of the small CCA chips occupied by recruits in all treatments (Fig. 3). Settlement on the synthetic substrate then occurred at much higher rates if the substrate appeared red. Settlement on the red synthetic substrate also occurred adjacent to the CCA chips, generally forming a ring or cluster of settled larvae around the CCA (Fig. 3).

Table 2. Two-way MANOVA comparing coral larval settlement on crustose coralline algae (CCA) and synthetic transparency paper with 2 background colour and 4 temperature–pCO_2 seawater treatments. **Bold**: significantly different ($p < 0.05$)

	df	*F*	p
Multivariate tests (Pillai's trace)			
Colour	2, 23	23.869	**<0.001**
Seawater treatment	6, 48	0.734	0.624
Seawater treatment × Colour	6, 48	0.288	0.940
Between-subject effects (CCA)			
Colour	1	1.108	0.303
Seawater treatment	3	0.907	0.452
Seawater treatment × Colour	3	0.257	0.855
Between-subject effects (synthetic)			
Colour	1	44.434	**<0.001**
Seawater treatment	3	0.977	0.420
Seawater treatment × Colour	3	0.147	0.851

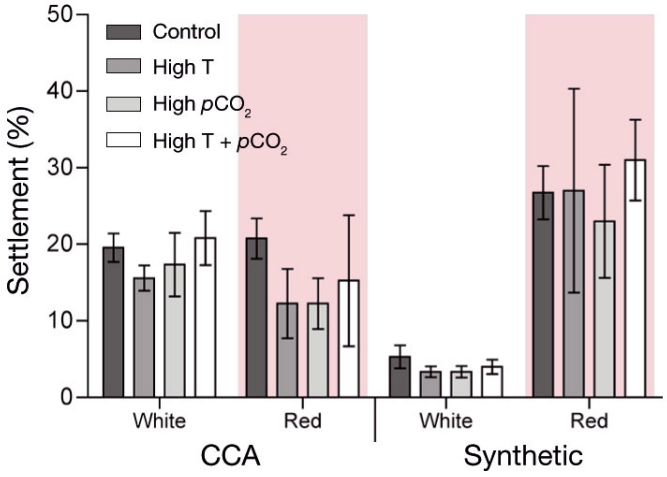

Fig. 2. Coral settlement (% mean ± SE) on healthy crustose coralline algae (CCA) versus the synthetic substrate when the background colour was either red or white under control, elevated temperature (High T), elevated partial pressure of carbon dioxide (High pCO_2) and elevated temperature and pCO_2 (High T + pCO_2) conditions

DISCUSSION

Background colour had a remarkable effect on the settlement of coral larvae regardless of temperature–pCO_2 treatment. When the background colour was red, there was an increase in overall settlement, particularly due to much higher settlement rates on the red synthetic surface. These observations suggest that settlement and selectivity are influenced by more than just chemical cues and certainly indicate that larvae display photosensitivity. These findings are consistent with those of Mason et al. (2011), who suggested that coral larvae use spectral cues for habitat selection during settlement, with a strong preference for red settlement surfaces. We used a different species, from a different location and maintained under different laboratory conditions (including elevated temperature and pCO_2 treatments), and additionally offered CCA as a settlement substrate, yet we still observed this striking preference for red on the synthetic settlement substrates. The fluorescent emission spectra of CCA and the red plastic cable ties in Mason et al. (2011) were shown to peak at 580 and 590 nm, respectively, suggesting that the red preference may be an adaptation to aid in the location of CCA for settlement. Subsequent work has shown that coral larvae show photosensitivity to long wavelengths (Mason & Cohen 2012) and may have photoreceptor-like cells at the aboral end of the larvae to allow light sensing during settlement (Mason et al. 2012). Similarly, in the present study, the red synthetic substrate and unbleached CCA had spectral peaks at 600 and 580 nm, respectively, highlighting that the red synthetic substrate simulated the spectral properties of healthy CCA.

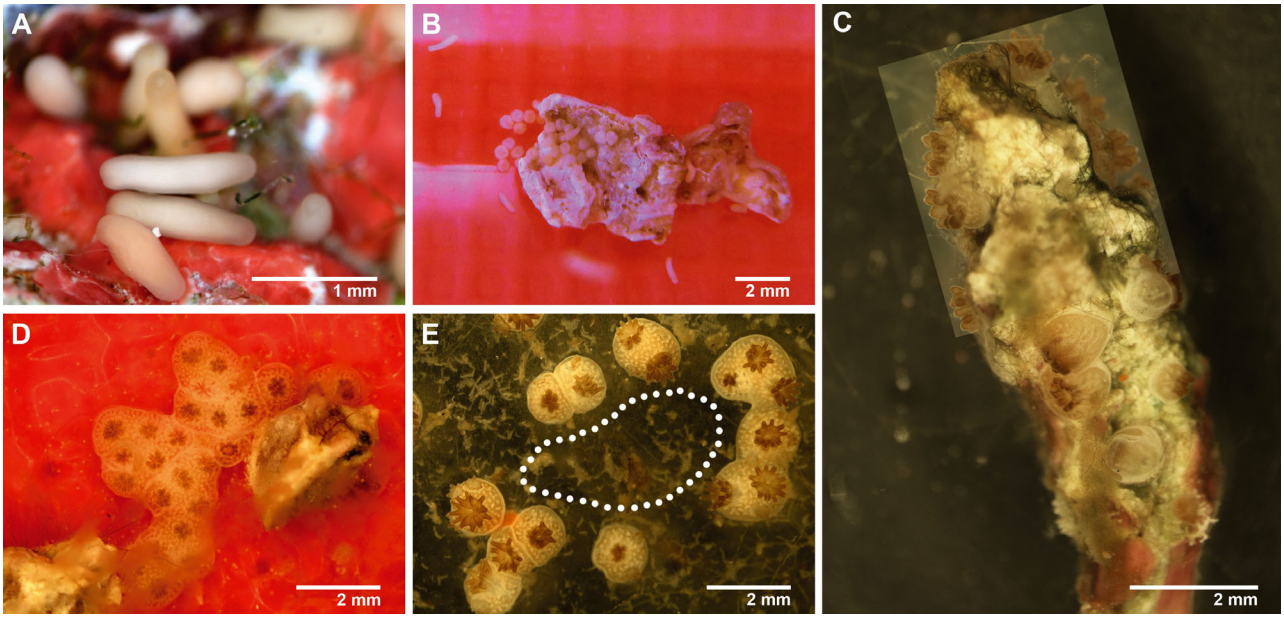

Fig. 3. Settlement on the red synthetic surface, which typically occurred near or surrounding the crustose coralline algae (CCA) chip. (A) Planulae 'searching' the surface of a CCA chip; (B) settlement in the red background treatment, with newly settled larvae on and adjacent to the CCA chip; (C) CCA chip with much of the surface occupied by 1 mo old recruits (red background removed for imaging); (D) coral recruits settled around CCA chips on the synthetic substrate when it appeared red; (E) CCA chip and background colour have been removed to show a typical ring formation of recruits surrounding the CCA chip when the background colour was red (dotted line indicates where the CCA used to be)

In our study, the small CCA chip size (and therefore limited availability of settlement space) as well as the similar settlement rates on the CCA (~12–20%), regardless of background colour, suggests that larvae did not prefer the red synthetic surfaces to the CCA but would settle on them if better options (i.e. CCA) were not available. That is, providing a red background appeared to facilitate settlement on the synthetic surface when much of the preferred settlement surface (CCA) was already occupied. This was further highlighted by the tendency to settle in a ring around the CCA chip. These findings indicate that coral larvae respond to both spectral and chemical settlement cues but ultimately prefer substrata that satisfy both criteria.

CCA and associated microbial communities are clearly the preferred settlement substrata for coral larvae, but with differences among species (Harrington et al. 2004). A high cover of consolidated CCA, as opposed to other substrate types (e.g. sediment and coral rubble; Sheppard et al. 2002, Schuhmacher et al. 2005) or benthic organisms more typical of degraded reefs (e.g. macroalgae and sponges; Aronson et al. 2002, Dixson et al. 2014, Doropoulos et al. 2014), may be fundamental to the resilience of the reef following severe disturbances (Sheppard et al. 2008, Gilmour et al. 2013). High CCA cover may also distinguish optimal settlement substrates from those with a high abundance of coral competitors. When distinguishing optimal substrata for settlement and metamorphosis, larvae probably respond to a complex combination of chemical, spectral and textural cues. Surface texture and structure are important, as larvae routinely settle in cryptic microhabitats (Harrison & Wallace 1990, Edmunds et al. 2004, Vermeij 2005). This is likely another reason they were attracted to the structure provided by the CCA. Microcrevices and ledges help to protect recruits and maximize survival in the smallest and most vulnerable size classes by minimizing interactions with large competitive dominants (Vermeij 2006, Doropoulos et al. 2016). However, as corals grow into larger and less vulnerable size classes, exposure to light for autotrophic nutrition becomes a more important requirement. Therefore, larvae must discern conditions that are not only suitable for initial attachment but also for later growth and survival.

Climate change has the potential to detrimentally alter the important cues on which coral larvae rely to find a suitable settlement substrate. Warmer water temperatures and acidification change microbial biofilms on the CCA surface, thereby disrupting chemical settlement cues and inhibiting larval settlement (Albright & Langdon 2011, Webster et al. 2011, 2013a,b,

Doropoulos et al. 2012). Furthermore, elevated temperature and pCO_2 can also cause bleaching in CCA (Anthony et al. 2008, Webster et al. 2011), changing the colour of CCA from red or dark pink to pale pink or white. In our study, the CCA chips were not pretreated in manipulated temperature–pCO_2 tanks; therefore, the chemical settlement cues presumably remained intact, and the CCA were not bleached while larval substrate selection and settlement was occurring. Thus, the larvae settled preferentially on the healthy CCA chips provided. However, once the CCA chips were occupied, larvae deemed the synthetic substrate adequate for settlement only if they perceived it as red, i.e. larvae only settled on the synthetic substrate with spectral properties similar to that of healthy CCA. The white synthetic substrate provided neither a chemical nor a spectral cue; consequently, settlement was severely reduced, with larvae tending to continue to swim and search, using up their lipid reserves, until they eventually died. Consequently, the effects of increased water temperature and pCO_2 could be additive, with the disruption of settlement by inhibiting both chemical and spectral cues. An interesting area for future studies would be to test the effects of ocean acidification and elevated temperature on the spectral settlement cues of CCA by providing CCA substrates ranging in colour from bleached white to healthy red as well as a similar range of coloured synthetic substrates. Although these impacts of warmer water temperature and acidification on settlement are indirect, if larvae can neither 'smell' nor 'see' the reef, they may be unable to locate it, which could in turn lead to significant reductions in recruitment success.

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