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High CO_2 reduces the settlement of a spawning coral on three common species of crustose coralline algae

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ABSTRACT: Concern about the impacts of ocean acidification (OA) on ecosystem function has prompted many studies to focus on larval recruitment, demonstrating declines in settlement and early growth at elevated CO_2 concentrations. Since larval settlement is often driven by particular cues governed by crustose coralline algae (CCA), it is important to determine whether OA reduces larval recruitment with specific CCA and the generality of any effects. We tested the effect of elevated CO_2 on the survival and settlement of larvae from the common spawning coral *Acropora selago* with 3 ecologically important species of CCA, *Porolithon onkodes*, *Sporolithon* sp., and *Titanoderma* sp. After 3 d in no-choice laboratory assays at 447, 705, and 1214 µatm pCO_2, the rates of coral settlement declined as pCO_2 increased with all CCA taxa. The magnitude of the effect was highest with *Titanoderma* sp., decreasing by 87% from the ambient to highest CO_2 treatment. In general, there were high rates of larval mortality, which were greater with the *P. onkodes* and *Sporolithon* sp. treatments (~80%) compared to the *Titanoderma* sp. treatment (65%). There was an increase in larval mortality as pCO_2 increased, but this was variable among the CCA species. It appears that OA reduces coral settlement by rapidly altering the chemical cues associated with the CCA thalli and microbial community, and potentially by directly affecting larval viability.

KEY WORDS: Climate change · Ocean acidification · Recruitment · Metamorphosis · *Acropora* · Crustose coralline algae

INTRODUCTION

Larval settlement success and microhabitat selectivity are critical to the recruitment of marine invertebrates. Planula survivorship is important for the dispersal of pelagic larvae, and the attachment and metamorphosis of coral larvae to the benthos is commonly induced by crustose coralline algae (CCA) and their microbial communities (Heyward & Negri 1999, Negri et al. 2001, Ritson-Williams et al. 2010). The choice of specific CCA is important to the post-settlement survival of coral recruits (Harrington et al. 2004, Arnold et al. 2010, Price 2010), so disturbances that alter the settlement substrate and patterns of larval settlement have the potential to change population maintenance and recovery.

Ocean acidification (OA) is caused by the uptake of atmospheric carbon dioxide (CO_2) by the oceans. It decreases seawater pH and carbonate saturation state (Kleypas et al. 1999), reducing the calcification of many calcifying organisms (Hall-Spencer et al. 2008), including CCA (Anthony et al. 2008, Russell et al. 2009, Diaz-Pulido et al. 2012) and coral recruits (Cohen et al. 2009, Albright et al. 2010, Suwa et al.

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2010, Doropoulos et al. 2012b). The early life-history of many calcifying invertebrates is negatively affected by OA, through reduced fertilisation, larval survival and settlement, and early growth (Havenhand et al. 2008, Kurihara 2008, Byrne 2011). For the pre-settlement phase of broadcast spawning corals, OA can reduce gamete fertilisation (Albright et al. 2010), but it often has negligible effects on larval metabolism and survival (Suwa et al. 2010, Nakamura et al. 2011). Coral settlement is often reduced by OA (Albright et al. 2010, Nakamura et al. 2011), and recent investigations in the Caribbean (Albright & Langdon 2011) and Great Barrier Reef (Doropoulos et al. 2012a) demonstrated that settlement is disrupted by the altered composition of the settlement substrata.

Coralline algae are a highly important functional group for coral reef ecosystems, acting as framework organisms by cementing carbonate fragments into massive reef structures (Littler & Doty 1975). *Porolithon*, *Sporolithon*, and *Titanoderma* are 3 genera of CCA common to coral reefs, but exhibit different abundances and occupy different microhabitats. For example, *Porolithon onkodes* is one of the most abundant CCA found on the topsides of reef crests and slopes (Littler & Doty 1975, Price 2010); both *Sporolithon* spp. and *Titanoderma* spp. are also common, yet are generally found in cryptic microhabitats (Littler & Littler 2003, Price 2010). Typically, CCA are recognised as the optimal settlement substrate for corals (Birrell et al. 2008), but different rates of settlement induction are associated with different genera from this algal group. For instance, the live tissue of *Titanoderma* spp. are often the most inductive substrate for coral larvae (Harrington et al. 2004, Ritson-Williams et al. 2010), but both *P. onkodes* (Heyward & Negri 1999, Harrington et al. 2004, Diaz-Pulido et al. 2010) and *Sporolithon durum* (Daume et al. 1999) also induce larval settlement in corals and abalone, respectively.

In the present study, we aimed to explore whether the acute exposure to OA altered the direction (positive or negative) and magnitude of larval settlement with different CCA taxa. Since these algae have different ecologies and induce different rates of larval settlement, we used *Porolithon onkodes*, *Sporolithon* sp., and *Titanoderma* sp. to test specific responses of the coral larvae to elevated pCO_2. On this occasion, we used no-choice settlement experiments with larvae of the common broadcast spawning coral, *Acropora selago*.

MATERIALS AND METHODS

The study was conducted at Heron Island Research Station (HIRS), southern Great Barrier Reef, Australia. Five gravid colonies of *Acropora selago* (Fig. 1a) were collected from a shallow reef slope and placed in individual 60 l flow-through

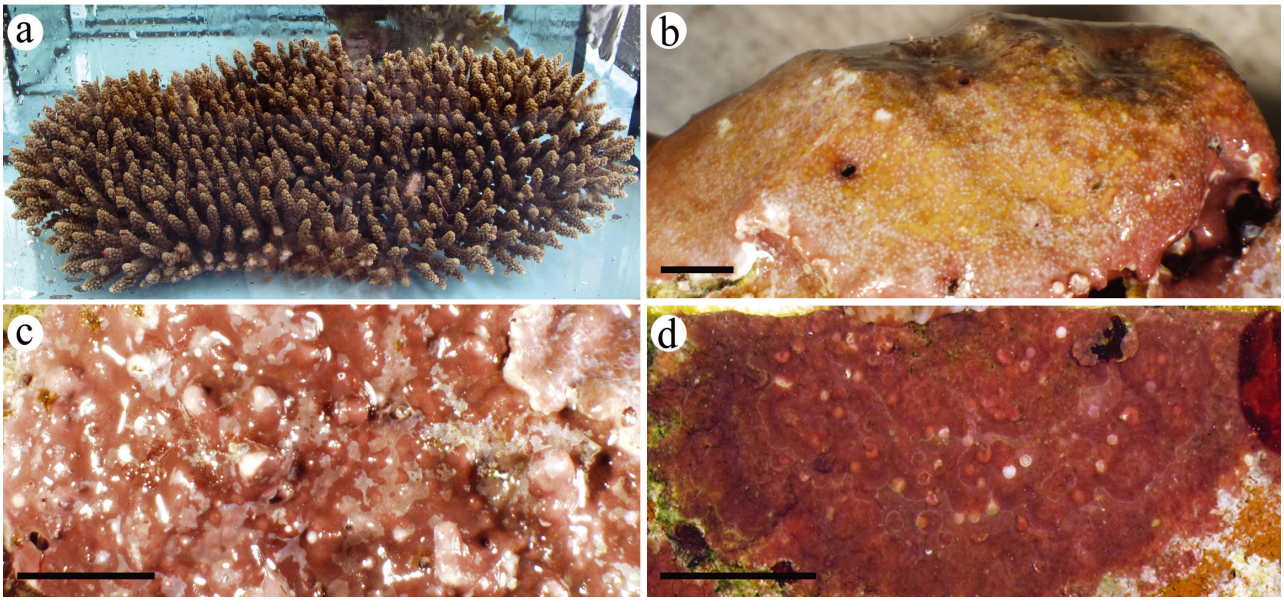

Fig. 1. (a) Adult *Acropora selago* colony, and fragments of (b) *Porolithon onkodes*, (c) *Sporolithon* sp., and (d) *Titanoderma* sp. Scale bars = 5 mm (b,c,d)

outdoor aquaria until they spawned (22:00 h, 1 December 2010). Upon gamete release, the egg–sperm bundles were gently mixed and cross-fertilised among the 5 colonies. Larvae were then transported to a laboratory, maintained at 25°C, and reared in 200 l sumps with light aeration using standard techniques described in Doropoulos et al. (2012a). After rearing for 4 d, the larvae had developed cilia and were actively searching for settlement substrata.

The 3 species of CCA used in the assays, *Porolithon onkodes* (Fig. 1b), *Sporolithon* sp. (Fig. 1c), and *Titanoderma* sp. (Fig. 1d), were collected from the shallow reef slope and reef flat (3 to 4 m depth at a spring high tide). The reef slope is exposed to wave energy, has high water flow, and is characterised by high CCA and coral cover, while the reef flat is found on the leeward side of the slope and protected from wave energy, has low water flow, and relatively low CCA and coral cover. Sections of reef matrix were brought to the laboratory, visually inspected for CCA, and identified using a light microscope. Samples of specimens were decalcified, stained, and the reproductive structures, cell fusions and secondary pit connections observed under a compound microscope for taxonomic verification (see Doropoulos et al. 2012a for further information). The samples were sectioned into 1 × 1 cm chips of live algal tissue with a dead algal skeleton ~0.5 cm thick, cleaned with forceps and a toothbrush under a dissecting microscope, and placed in filtered (0.45 µm) seawater prior to use in the assays.

The settlement assays were conducted using 3 OA treatments, based on the worst case scenarios predicted by the Intergovernmental Panel on Climate Change (Meehl et al. 2007). These treatments used ambient (pH 7.98, 447 µatm) and 2 elevated (Mid: pH 7.81, 705 µatm; High: pH 7.60, 1214 µatm) levels of CO_2 (Table 1). The ambient and elevated pCO_2 seawater was controlled with a flow-through, outdoor aquarium system (see Doropoulos et al. 2012b for full system details), using standard protocols for OA research (Gattuso et al. 2010). Briefly, the seawater was continually pumped from the reef flat and was subjected to natural changes in temperature and alkalinity. The total pH of the seawater was adjusted with slow injection of analytical grade CO_2 into 3 continuously flowing 200 l sumps and measured every 10 s by temperature-compensated pH electrodes (Mettler-Toledo, InPro4501VP). The pH electrodes were connected to a control unit (Aquatronica, AEB Technologies) and monitored daily for calibration validity, and recalibrated with Mettler-Toledo calibration buffers to 0.01 pH units when necessary (Dickson 2010).

The settlement assays were conducted using 200 ml containers, which were sealed with screw-on lids to eliminate gas exchange (following Albright et al. 2010). Each container included a single chip of CCA placed at the bottom of the container and 4 d old randomly sampled coral larvae (n = 20), and there were 6 replicate containers per treatment combination. The experiment was conducted at 25°C with a 12 h light cycle at 30 µmol m^{-2} s^{-1}. The treatment seawater was filtered with nylon syringe filters (0.45 µm), added to each container and changed every 24 h, during which time any dead larvae were removed, minimising changes in water chemistry. The temperature, pH, and alkalinity were measured in the filtered seawater samples at the beginning of the experiment and at each subsequent water exchange (i.e. 0, 24, and 48 h; n = 3 per CO_2 treatment). Total alkalinity was measured in replicates (between 2 and 4) within a sample collected in each of the 3 CO_2 treatments using Gran titration with a T50 Titrator (Mettler-Toledo) until <2% error was met. The carbonate chemistry parameters of the seawater were calculated using CO2SYS (Lewis & Wallace 2006), with temperature, total pH, total alkalinity, and salinity (35 ppt) as inputs (Table 1).

Table 1. Summary of the physical and chemical seawater values (mean ± SD) for the 3 levels of ocean acidification treatments. Temperature (26.6 ± 1.4°C), total pH (pH_T), and total alkalinity (TA) were measured in filtered seawater samples taken at the beginning of the settlement assays and at each water exchange. pCO_2, HCO_3^-, CO_3^{2-}, $\Omega_{Calcite}$, and $\Omega_{Aragonite}$ were calculated using CO2SYS (Lewis & Wallace 2006), with the temperature input from the sump measurements displayed in the table and an output temperature of 25°C according to the laboratory conditions

Treatment	pH_T	TA (µmol kg^{-1})	pCO_2 (µatm)	HCO_3^- (µmol kg^{-1})	CO_3^{2-} (µmol kg^{-1})	$\Omega_{Calcite}$	$\Omega_{Aragonite}$
Ambient	7.98 ± 0.08	2266.2 ± 52.1	447.0 ± 131.0	1779.9 ± 111.0	197.3 ± 32.1	4.7 ± 0.8	3.1 ± 0.5
Mid	7.81 ± 0.03	2269.8 ± 54.7	705.3 ± 88.0	1921.5 ± 72.1	141.6 ± 7.2	3.4 ± 0.2	2.2 ± 0.1
High	7.60 ± 0.03	2266.6 ± 51.2	1214.1 ± 89.6	2039.2 ± 42.1	92.6 ± 7.6	2.2 ± 0.2	1.5 ± 0.1

After 72 h of addition of larvae to the experimental containers, the numbers of swimming, dead, and settled (i.e. attached and metamorphosed; Heyward & Negri 1999) larvae in the sealed containers were counted using a dissecting microscope. Percentage data were analysed using 2-way ANOVAs, with CCA taxa (3 levels) and pCO_2 (3 levels) as fixed factors. Significant main effects were examined using Student-Newman-Keuls tests (SNK). The percentage of dead larvae and swimming larvae were ln(x + 1) transformed prior to analysis to meet the requirements of homogeneity (Cochran's C), while larval settlement analysis was conducted on the raw percentage data that met homogeneity assumptions. All ANOVAs were performed using the statistical package GMAV5 (coded by A. J. Underwood & M. G. Chapman, University of Sydney, Australia).

RESULTS

At the end of the 3 d assays, larval mortality was generally high across all treatments (Fig. 2a). Larvae in the containers with *Porolithon onkodes* and *Sporolithon* sp. had ~80% mortality, significantly higher than the 65% larval mortality in the *Titanoderma* sp. treatment (Table 2a). There was an increase in larval mortality with increasing pCO_2, with significant differences between the ambient and highest pCO_2 (Table 2a). Increased mortality only occurred in *Sporolithon* sp. and *Titanoderma* sp. at elevated pCO_2 (Fig. 2a), and the magnitude of the effect was greatest with *Titanoderma* sp., where larval mortality increased by 25% at 1205 µatm compared to ambient conditions. CCA taxa had a significant effect on the number of swimming larvae at the end of the experiment, whereas pCO_2 had no significant effect (Table 2b). There were twice the number of swimming larvae in the *Titanoderma* sp. treatment compared to the *P. onkodes* and *Sporolithon* sp. treatments (Fig. 2b).

Coral settlement declined as the CO_2 concentration increased, and this result was consistent among the 3 CCA species (Fig. 2c). Differences in coral settlement were significant between the ambient and 2 elevated CO_2 treatments, whilst there was no significant effect between the 2 elevated CO_2 treatments (Table 2c). The magnitude of the effect among CO_2 treatments was greatest when *Titanoderma* sp. was the settlement inducer, as coral settlement decreased by 56 and 87% at 722 and 1205 µatm, respectively, compared to the ambient treatment. Settlement declined by 50% at the highest CO_2 concentration compared to the ambient treatments with *Porolithon onkodes* and *Sporolithon* sp. (Fig. 2b).

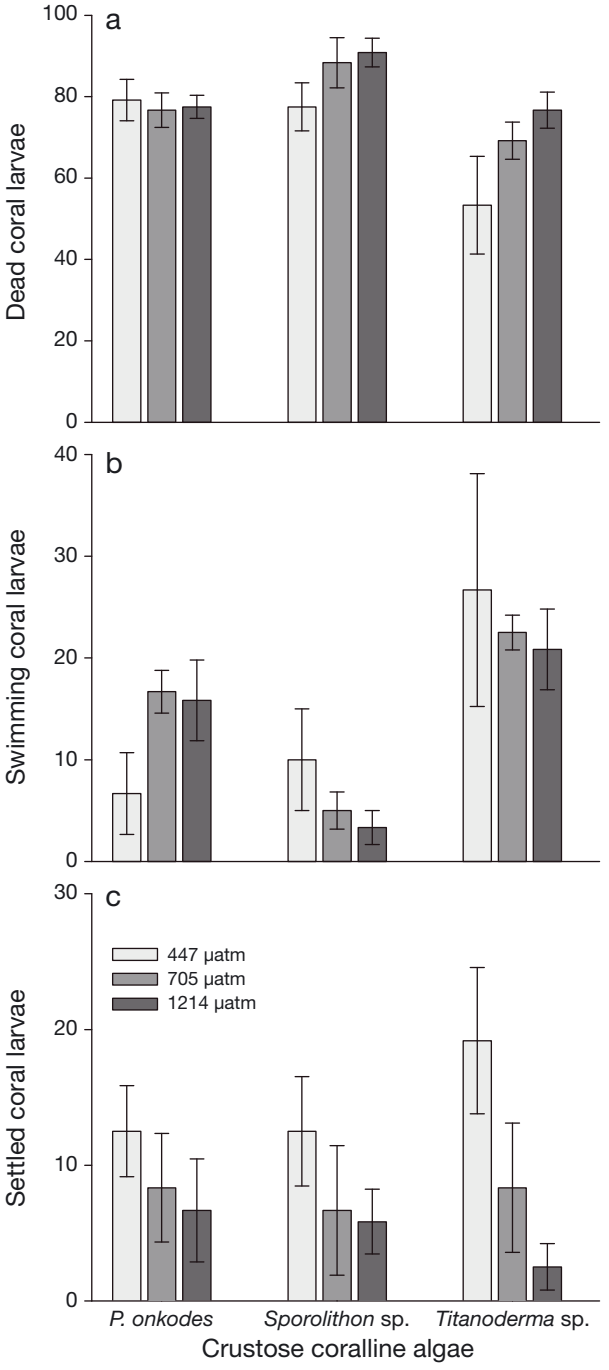

Fig. 2. Percentage (mean ± SE) of coral *Acropora selago* larvae (a) dead, (b) swimming, and (c) settled at ambient (447 µatm) and elevated (705 and 1214 µatm) pCO_2, with 3 species of crustose coralline algae (*Porolithon onkodes*, *Sporolithon* sp., *Titanoderma* sp.) (n = 6). Note the different scales on the y-axes

Table 2. ANOVA results comparing the percentages of (a) dead, (b) swimming, and (c) settled coral *Acropora selago* larvae at 3 CO_2 (447, 705, and 1214 µatm) concentrations, with 3 crustose coralline algae (CCA) species (*Porolithon onkodes*, *Sporolithon* sp., *Titanoderma* sp.). Only significant ($p < 0.05$) post-hoc tests (Student-Newman-Keuls) are displayed

Source of variation	df	MS	*F*	p	Conclusion: Student-Newman-Keuls
(a) Dead larvae					
pCO_2	2	0.2335	3.50	0.0385	447 < 1214
CCA	2	0.4449	6.68	0.0029	*Titanoderma* sp. < *P. onkodes* and *Sporolithon* sp.
pCO_2 × CCA	4	0.1162	1.74	0.1569	
Residual	45	0.0666			
(b) Swimming larvae					
pCO_2	2	1.3691	1.25	0.2965	
CCA	2	11.9287	10.88	0.0001	*Titanoderma* sp. > *P. onkodes* > *Sporolithon* sp.
pCO_2 × CCA	4	1.8328	1.67	0.1731	
Residual	45	1.0960			
(c) Settled larvae					
pCO_2	2	451.3889	4.79	0.0130	447 > 705 and 1214
CCA	2	12.5000	0.13	0.8769	
pCO_2 × CCA	4	55.556	0.59	0.6716	
Residual	45	94.1667			

DISCUSSION

This was the first study to isolate the effects of OA on coral settlement with single species of CCA. Previous work demonstrated that elevated pCO_2 alters settlement substrates (by shifting benthic community structure and composition) to reduce coral settlement (Albright & Langdon 2011, Doropoulos et al. 2012a), and our study provided direct evidence that rates of coral settlement were consistently reduced from OA with 3 common CCA species, without changing CCA abundance. Even though there was generally high larval mortality in our experiment, the negative settlement response to elevated CO_2 was consistent among treatments. Our findings are important as they suggest that the decline in coral settlement at elevated pCO_2 is likely caused by rapid changes to the (1) microbial community associated with the CCA, and/or (2) chemical cues associated directly with the algal tissue.

Exposure to elevated pCO_2 seawater may have altered the signals associated with the CCA, which are active inducers for invertebrate settlement (Rodriguez et al. 1993). CCA are often the most preferred settlement substrata of spawning corals due to the morphogen content of the algal tissue (Morse et al. 1988, Heyward & Negri 1999, Harrington et al. 2004) and associated bacterial communities that live in the algal epithelium (Negri et al. 2001, Webster et al. 2004). The exposure of CCA to elevated pCO_2 may have affected the quantities/qualities of algal morphogens and/or the bacterial communities associated with the thalli (as suggested by Webster et al. 2012), with potential subsequent effects on larval settlement. OA increases the susceptibility of coralline algae to tissue necrosis and bleaching, and reduced calcification (Anthony et al. 2008, Gao & Zheng 2010, Diaz-Pulido et al. 2012), although this was not observed in our experiment due to the short exposure to OA conditions. It has also recently been demonstrated that OA altered the microbial community associated with *Acropora eurystoma* mucus (Meron et al. 2011), as well as biofilms grown on glass slides (Witt et al. 2011) and CCAs (Webster et al. 2012). Whether OA affects the morphogen content or microbial communities associated with CCA remains unknown, and future research should elucidate whether it is shifts in the bacterial communities and/or the morphogens associated with CCA, or a combination of both that reduces larval settlement under scenarios of elevated CO_2.

We found that the magnitude of the effect of OA to reduce coral settlement was the greatest with *Titanoderma* sp. compared to the other CCA taxa, in which settlement was reduced 4-fold from the ambient to highest CO_2 treatment. Harrington et al. (2004) demonstrated that coral larvae respond to much lower morphogen concentrations in *Titanoderma* sp. compared to *Porolithon onkodes* and other species of CCA, and our data suggest that the chemical signals associated with *Titanoderma* sp. were the most rapidly affected by elevated pCO_2. In addition, the numbers of surviving larvae and swimming larvae were both highest in the *Titanoderma* sp. treatments, compared to the *P. onkodes* and *Sporolithon* sp. treatments. The cover of *Titanoderma* sp. and the prefer-

ential settlement of coral larvae on this algae were both recently demonstrated to decline under similar levels of pCO_2 (Doropoulos et al. 2012a), and the data from the present study demonstrated additional negative effects of OA to the ecological interactions between coral larvae and *Titanoderma* sp. *Titanoderma* sp. is known to be a highly inductive CCA for coral metamorphosis (Harrington et al. 2004, Ritson-Williams et al. 2010), with the highest rates of post-settlement survival (Harrington et al. 2004, Arnold et al. 2010, Price 2010), and the results in this study suggest that the relationship between *Titanoderma* sp. and coral larvae is the most rapid to breakdown from acute OA exposure.

Based on our results and those from the literature, the direct effects of OA on coral larval survivorship remain quite variable. In our experiment, we found overall high mortality rates of the larvae, but that number consistently increased at elevated CO_2 levels in chambers with the algae *Sporolithon* sp. and *Titanoderma* sp., but not in chambers with *Porolithon onkodes*. A recent study using 2 species of *Acropora* exposed the larvae to experimental treatments for 7 d and found that the survival of *A. digitifera* larvae was significantly reduced from 60% at pH 8.0 to 33% at pH 7.6, whereas there was no effect on the survivorship of *A. tenuis* larvae (Suwa et al. 2010). Another recent study with *A. digitifera* larvae demonstrated that survivorship was not affected by exposure to seawater of pH 7.3 after 3 or 7 d (Nakamura et al. 2011). The effect of OA on the survival and swimming capabilities of pelagic larvae warrants further investigation to predict how dispersal potential and reef connectivity may be altered with continually rising pCO_2. It is also possible that chemical changes occurred to the CCA during the experimental assays, which use allelopathic chemicals as defence mechanisms against fouling organisms (Suzuki et al. 1998). The concentration of any allelopathic chemicals could have been exacerbated by the sealed containers, causing the generally high mortality of coral larvae in our study.

Our study has added to the growing body of literature demonstrating the negative effects of anthropogenic-induced OA on the recruitment of marine invertebrates. We demonstrated that rates of coral settlement decrease with increasing OA, with 3 common species of CCA important to coral reef ecology. However, the direct effects of elevated CO_2 on the viability of coral larvae and the chemical and microbial ecology of CCA require further investigation to fully understand the mechanics of how OA disrupts patterns of coral recruitment.

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