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Settlement patterns of the coral *Acropora millepora* on sediment-laden surfaces

Gerard F. Ricardo [a,b,c,*], Ross J. Jones [b,c], Mikaela Nordborg [b], Andrew P. Negri [b,c]

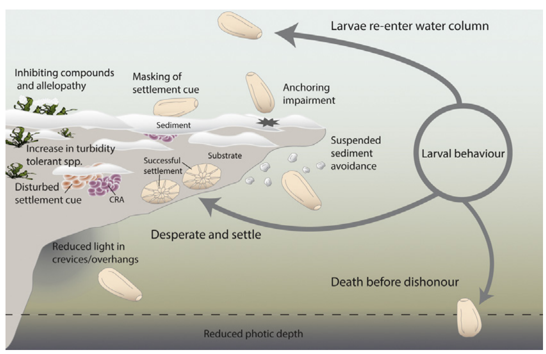
[a] *Centre for Microscopy, Characterisation and Analysis, and UWA Oceans Institute, The University of Western Australia, Perth, Western Australia 6009, Australia*
[b] *Australian Institute of Marine Science, Townsville 4810, Queensland, Australia*
[c] *Western Australian Marine Science Institution, Perth 6009, Western Australia, Australia*

HIGHLIGHTS

- Very low levels of deposited sediment impact coral settlement behaviour.
- Larvae avoid sediment-covered substrates, but will settle nearby (e.g. downward facing surfaces).
- Deposited sediment also decreases the effectiveness of crustose red algae to induce settlement.
- There was no evidence of light intensity impacting settlement under realistic conditions.
- These results have implications for natural and anthropogenic sediment deposition events.

GRAPHICAL ABSTRACT

A conceptual diagram showing possible coral settlement behaviour and cause–effect pathways in response to sediment stressors, such as suspended sediments, deposited sediment and reduced light.



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ABSTRACT

Successful recruitment in corals is important for the sustenance of coral reefs, and is considered a demographic bottleneck in the recovery of reef populations following disturbance events. Yet several factors influence larval settlement behaviour, and here we quantified thresholds associated with light attenuation and accumulated sediments on settlement substrates. Sediments deposited on calcareous red algae (CRA) directly and indirectly impacted coral settlement patterns. Although not avoiding direct contact, *Acropora millepora* larvae were very reluctant to settle on surfaces layered with sediments, progressively shifting their settlement preference from upward to downward facing (sediment-free) surfaces under increasing levels of deposited sediment. When only upward-facing surfaces were presented, 10% of settlement was inhibited at thresholds from 0.9 to 16 mg cm^{-2} (EC_{10}), regardless of sediment type (carbonate and siliciclastic) or particle size (fine and coarse silt). These levels equate to a very thin (<150 μm) veneer of sediment that occurs within background levels on reefs. Grooves within settlement surfaces slightly improved options for settlement on sediment-coated surfaces (EC_{10}: 29 mg cm^{-2}), but were quickly infilled at higher deposited sediment levels. CRA that was temporarily smothered by sediment for 6 d became bleached (53% surface area), and inhibited settlement at ~7 mg cm^{-2} (EC_{10}). A minor decrease in settlement was observed at high and very low light intensities when using suboptimal concentrations of a settlement inducer (CRA extract); however, no inhibition was observed when natural CRA surfaces along with more realistic diel-light patterns were applied. The low deposited sediment thresholds indicate that even a thin veneer of sediment can have consequences for larval settlement due to a reduction of optimal substrate. And while grooves and overhangs provide more settlement options in high deposition

* Corresponding author at: Australian Institute of Marine Science, 1526 Cape Cleveland Road, Cape Cleveland 4810, Queensland, Australia.
E-mail address: g.ricardo@aims.gov.au (G.F. Ricardo).

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areas, recruits settling at these locations may be subject to ongoing stress from shading, competition, and sediment infilling.

1. Introduction

1.1. Sedimentation on coral reefs

Sedimentation in tropical ecosystems poses a threat to the persistence of coral reefs through direct impacts on existing populations and by reducing recovery following disturbance events (Hodgson, 1990; Weber et al., 2012). Sediments can be released into the water column by terrestrial run-off (Kroon et al., 2012; Fabricius et al., 2016), natural resuspension events (Orpin and Ridd, 2012), and a range of anthropogenic activities including dredging and dredge spoil disposal (Jones et al., 2016). Once released into the water column, fine sediments can remain in suspension for extended periods and travel considerable distances via advection (Wolanski and Spagnol, 2000; Bainbridge et al., 2012; Fisher et al., 2015). Sediments will also settle out of suspension depending on suspended sediment concentration (SSC), grain size, density, ability to flocculate, and hydrodynamics of the water column (Smith and Friedrichs, 2011). Compaction and consolidation of recently settled sediments takes days to weeks (Wolanski et al., 1992), and until consolidated, sediments are prone to successive resuspension and deposition and further lateral dispersion. While the impact of sediment deposition on adult corals has been reasonably well studied (see reviews Erftemeijer et al., 2012, and Jones et al. (2016)), comparatively less is known about how sediment accumulating onto substrates may interfere with coral settlement, and the recolonisation of local populations in turbid environments.

1.2. Coral recruitment

The coral recruitment process is a complex sequence that involves larval supply, settlement behaviour, successful attachment and metamorphosis, and post-settlement survival (Harrison and Wallace, 1990). Successful recruitment is dependent on a suite of physical and biological factors (Ritson-Williams et al., 2009; Doropoulos et al., 2016), and referred to by Gleason and Hofmann (2011) as a '…dizzying array of abiotic and biotic factors, both positive and negative, that can determine whether a coral larva ultimately ends up on the reef…'. The larvae are weak swimmers predominantly relying on currents for dispersal (Baird et al., 2014). When they reach developmental competence (the ability to settle), they descend in the water column and temporarily enter a demersal phase, when they actively and repeatedly test, probe and explore the substrate presumably searching for some characteristic properties to indicate a favourable settlement location (Müller and Leitz, 2002). Settlement for many species is induced by chemical cues, often associated with calcareous red algae (CRA — which includes crustose coralline algae (CCA) and non-coralline red algae) (Heyward and Negri, 1999; Tebben et al., 2015), and/or microbial biofilms (Webster et al., 2004). For most larvae of broadcast spawning corals, competency occurs after only a few days development (Connolly and Baird, 2010), with settlement peaking between 4 and 10 d after spawning (Jones et al., 2015). Observations of attachment through mucous production and firing of spirocysts or nematocysts have been reported (Paruntu et al., 2000; Harii and Kayanne, 2002; Okubo et al., 2008; Larsson et al., 2014), and once attached the larvae metamorphose by flattening into disc-shaped structures with septal mesenteries radiating from the central mouth region (Heyward and Negri, 1999). Early recruits are small, initially <1 mm in diameter, and vulnerable to grazing, overgrowth and smothering from sediment for the ensuing 12 months (Rogers, 1990; McCook et al., 2001; Jones et al., 2015; Moeller et al., 2016).

1.3. Cause-effect pathways

Many studies have shown correlations between low recruitment success and sediment in situ although the specific mechanism(s) or cause-effect pathway(s) underlying this correlation is not known (Wittenberg and Hunte, 1992; Dikou and Van Woesik, 2006; Salinas-de-León et al., 2013; Jokiel et al., 2014; Bauman et al., 2015). A range of established and also biologically plausible mechanisms (i.e. where there is a credible or reasonable biological and/or toxicological basis linking the proposed cause and effect) has recently been described in Jones et al. (2015). These mechanisms, which are based on larval behaviour, chemotaxis, and physical characteristics of the substrate have been expanded upon in Fig. 1, and include: 1) avoidance of small non-consolidated grains that prevent attachment or access to suitable underlying substrates (Harrigan, 1972; Perez et al., 2014); 2) masking, obscuring or deterioration of chemical settlement cues by sediment (Harrington et al., 2005); 3) the production of inhibitory chemicals from sediment-tolerant organisms (Quéré and Nugues, 2015; Morrow et al., 2017); and 4) changes in the quality and quantity of light (Mundy and Babcock, 1998; Fabricius et al., 2016).

In the presence of these inhibitory factors, or absence of cues to stimulate settlement, coral larvae may either continue to seek a more suitable substrate until lipid reserves become depleted and death occurs (colloquially referred to as '*death before dishonour*' – see Fig. 1) (Raimondi and Morse, 2000; Bishop et al., 2006), or possibly re-enter the plankton to seek a more suitable reef. The larvae may also settle onto sub-optimal microhabitats (colloquially referred to as '*desperate larva hypothesis*'), which may have subsequent consequences for the recruits, juveniles and/or adult stages, including increased competition, light-limitation or sediment smothering (Baird and Hughes, 2000; Doropoulos et al., 2016; Moeller et al., 2016).

1.4. Concentration–response thresholds

The effects of sediments on coral settlement have been investigated in several different ways, including examining responses to suspended sediment i.e. sediments kept in suspension expressed as mg L^{-1} (Te, 1992; Gilmour, 1999), accumulating sediments i.e. to a continual downward flux (deposition) of sediment expressed in mg cm^{-2} d^{-1} (Babcock and Davies, 1991; Babcock and Smith, 2002), or accumulated sediment i.e. sediments that have settled on surfaces and expressed as mg cm^{-2} (Hodgson, 1985; Perez et al., 2014). Often only one of these measurements is reported when several cause–effect pathways could be co-occurring, complicating the interpretation of the reported thresholds (Jones et al., 2015). Despite this, there is clear evidence that SSCs have a limited impact larval settlement (Babcock and Davies, 1991; Te, 1992; Humanes et al., 2017), indicating that sediment depositing and accumulating on surfaces may represent more significant cause–effect pathways (Babcock and Davies, 1991).

The aim of the present study was to experimentally determine and quantify the effects of accumulated sediment that result directly and indirectly (via impact to the CRA) in changes to larval settlement patterns, and whether these thresholds were influenced by additional factors such as light intensity, surface structure and surface aspect. These thresholds may assist regulatory agencies assign improved guideline