Vol. 612: 29–42, 2019
https://doi.org/10.3354/meps12879

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 7

Inhibition of coral settlement at multiple spatial scales by a pervasive algal competitor

Nicolas R. Evensen[1,*], Christopher Doropoulos[2], Kathleen M. Morrow[3], Cherie A. Motti[4], Peter J. Mumby[1]

[1]Marine Spatial Ecology Lab, ARC Centre of Excellence for Coral Reef Studies and School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

[2]CSIRO Oceans and Atmosphere, Queensland Biosciences Precinct, St Lucia, QLD 4067, Australia

[3]Department of Molecular, Cellular, and Biomedical Sciences, University of New Hampshire, Durham, NH 03824, USA

[4]Australian Institute of Marine Science, Townsville, QLD 4810, Australia

ABSTRACT: Larval settlement to the benthos can be influenced by physical and chemical cues. On coral reefs, the macroalga *Lobophora* is known to negatively impact coral recruitment, though the scales at which it affects coral larvae is unclear. We used aquarium experiments to mechanistically assess the response of larvae from 3 *Acropora* species to *Lobophora* at multiple spatial scales, and complemented these experiments with an analysis of the effects of *Lobophora* on *Acropora* spp. field recruitment patterns. The smallest scale (0–10 cm) focused on the effects of the distribution of *Lobophora* across an experimental tile, with settlement declining 60% for 2 of the species when a 15 cm^2 piece of *Lobophora* was distributed throughout a 100 cm^2 tile, compared to the control. The intermediate scale (5–15 cm) focused on the effects of increasing algal biomass on settlement, with settlement for all species negatively associated with algal biomass. Settlement decreased almost 50% in the highest treatment (6.2 g of *Lobophora* in the tanks), compared to the control. The mechanism of settlement inhibition was also tested at this scale, with waterborne compounds highlighted as a key settlement inhibitor. *Lobophora* also impaired overall settlement at the largest scale (0–100 cm), decreasing settlement by 40–50%, regardless of its location relative to the settlement substrate. Finally, *Acropora* field recruitment patterns also demonstrated a negative effect of *Lobophora* on coral recruitment *in situ*. Our results reveal the ability of *Lobophora* to inhibit coral settlement at multiple spatial scales, which may contribute to large-scale recruitment failure on coral reefs following disturbances.

KEY WORDS: Recruitment · Allelochemicals · *Acropora* · Macroalgae · *Lobophora*

1. INTRODUCTION

Organisms are most vulnerable during early life-history stages, and thus develop physiological and/or behavioural traits that attempt to maximise the likelihood of survival to reach adulthood (Walters & Wethey 1996, Harrington et al. 2004). Larvae are the earliest life-history stage for the vast majority of marine animals and their behaviour influences processes at multiple scales. At the macro scale, swimming ability influences geographic dispersal, while at micro scales, larvae rely on innate traits to locate ideal settlement locations (Mundy & Babcock 2000, Raimondi & Morse 2000, Montgomery et al. 2006). Once near suitable settlement habitats, larvae exhibit behavioural responses to biotic and abiotic cues that facilitate optimal settlement and early post-settlement survival (Pawlik 1992, Hay 2009, Vermeij et al. 2010, Beatty et al. 2018). These cues, positive and negative, include light, microhabitat complexity, and chemicals released by other benthic organisms (Rittschof et al. 1985, Patzkowsky 1988, Hay 2009). Ultimately,

*Corresponding author: nicolas.r.evensen@gmail.com

determining the relative influence of positive and negative settlement cues on larval behaviour remains complex, particularly as the cues on which larvae rely to choose a settlement location can vary depending on the spatial scale in question. For example, barnacle larvae rely on biological cues at a large scale to find a broad settlement zone, before focusing on habitat micro-heterogeneity at the scale of microns to find a final settlement location (Le Tourneux & Bourget 1988).

The complexity of settlement cues is likely to be greatest in taxonomically diverse ecosystems like coral reefs. Here, larvae may be exposed to a number of positive and negative biotic settlement cues prior to recruitment to the substratum (Arnold et al. 2010). Coral larvae have developed clear responses to physical and chemical cues, favouring settlement into cryptic habitats and onto particular species of crustose coralline algae (CCA), presumably to maximise post-settlement survival (Heyward & Negri 1999, Harrington et al. 2004, Ritson-Williams et al. 2009, Tebben et al. 2015). Despite the demographic benefits of these adaptations, they likely evolved in a different ecological setting to that of many contemporary reefs, where the cover of turf algae and fleshy seaweeds has tended to increase and/or the cover and diversity of CCA has declined (Steneck 1994, 1997). Thus, the sources of settlement cues on reefs dominated by algae may have shifted strongly in favour of inhibition at the expense of attraction, with evidence that coral larvae display a clear preference towards water from coral-dominated reefs over water from algal-dominated reefs (Dixson et al. 2014). Indeed, reefs that have shifted to macroalgal dominance are often found to exhibit coral recruitment failure, even when suitable settlement substrate is present, suggesting a waterborne chemical effect of macroalgae on coral settlement success (Chong-Seng et al. 2014, Dixson et al. 2014, Doropoulos et al. 2014). This is supported by evidence from experimental studies that show that small quantities of macroalgae can impair settlement to suitable settlement substrates a few centimetres away from the alga itself (Kuffner et al. 2006, Diaz-Pulido et al. 2010).

The brown macroalga *Lobophora* is highly competitive (Jompa & McCook 2002, Slattery & Lesser 2014) and contains allelochemicals that have been shown to impair coral settlement (Kuffner et al. 2006, Diaz-Pulido et al. 2010; though see Birrell et al. 2008) and overall recruitment (Mumby et al. 2016, Doropoulos et al. 2017a). Recent research has indicated that *Lobophora* can inhibit settlement and cause larval mortality through the release of both waterborne and lipid-soluble allelochemicals (Morrow et al. 2017), and can continue to affect coral growth and survival after recruitment by releasing lipid-soluble compounds that induce coral bleaching on adult fragments (Rasher & Hay 2010). Due to the contrasting solubility of these chemicals, it is likely that their effectiveness varies as a function of spatial scale, though the scale at which larvae exhibit sensitivity to these allelochemicals remains untested. Further, it remains uncertain how effectively larvae detect and discriminate between positive settlement cues, associated with CCAs or biofilm surfaces (Webster et al. 2004, Sneed et al. 2014), and negative cues, released by macroalgae, depending on the spatial distribution or relative abundance of each cue. Here, we use experimental tanks and flumes to assess the response and sensitivity of coral larvae to a variety of waterborne and surface-associated chemical cues from *Lobophora* across a variety of spatial scales, and propose a mechanistic explanation for how *Lobophora* reduce coral recruitment rates on coral reefs. At a small scale (0–10 cm), we assessed (1) the influence of the spatial distribution of *Lobophora* on larval settlement. At an intermediate scale (5–15 cm), we assessed (2) the effect of increasing *Lobophora* biomass on larval settlement success, and (3) the mechanisms by which *Lobophora* can inhibit settlement beyond the space it physically occupies. At larger spatial scales (0–100 cm), we focused on (4) the effect of *Lobophora* on the ability of larvae to detect and swim toward optimal settlement habitats (i.e. those containing positive settlement cues). Finally, (5) we complemented our experimental results with a field study to determine the effects of *Lobophora* on coral recruitment patterns *in situ*.

2. MATERIALS AND METHODS

2.1. Specimen collection, coral spawning, and experimental overview

This study was conducted at the Palau International Coral Reef Center (PICRC), Koror, Palau from March to May 2017. The study took place over 2 mass spawning events, using *Acropora hyacinthus* in March, and *A. gemmifera* and *A. aspera* in April. The study focused on the response of *Acropora* larvae, due to the importance of *Acropora* for reef resilience (Ortiz et al. 2014), while also being a genus that is particularly sensitivity to macroalgae (Rasher et al. 2011) and commonly interacts with *Lobophora* on shallow coral reefs (Vieira et al. 2016). Additionally,

the 3 species of *Acropora* were used to test whether any effects of *Lobophora* on settlement are generalisable across species of this genus. Eight gravid colonies of *A. hyacinthus* were collected from ~3 m depth from an outer reef site on the eastern coastline of Palau (East Sheltered [ES]; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m612p029_supp.pdf) in March, while 6 gravid *A. gemmifera* colonies were collected from ~3 m depth from an outer reef site on the eastern coastline (Airai Reef [AR]; Fig. S1) and 6 gravid *A. aspera* colonies were collected at ~5 m depth from an outer reef on the western coast (West Pass [WP]; Fig. S1) in April. After collection, colonies were placed in 1300 l tubs with flow-through seawater, with corals monitored regularly each evening until spawning. The *A. hyacinthus* colonies spawned on March 15 and 16 from 20:30 to 21:30 h, 3 and 4 d after the full moon, while *A. gemmifera* and *A. aspera* colonies spawned on April 13 and 16 from 21:00 to 22:00 h, 2 and 5 d after the full moon, respectively. Larvae then were reared using standard practice (e.g. Heyward & Negri 1999, Harrington et al. 2004, Doropoulos et al. 2017b). Larval competency was achieved after 7–10 d for all 3 coral species.

Coral larvae were used in 3 aquarium experiments (described in detail in subsections 2.2 to 2.4) that contrasted the presence of a settlement inducer, a 10 × 10 cm chequered tile (see Fig. S2 in the Supplement for details) conditioned in the field for 3–4 wk to allow the development of a biofilm, and a known settlement inhibitor, *Lobophora*. All experiments were run as 24 h assays, and larvae were scored as either dead, swimming, or settled at the end of each assay. Larvae were considered dead when they were not moving after 5 s of observation or showed signs of degradation, whereas larvae actively moving through the water column were classified as swimming. 'Settled' was defined as larvae that had firmly attached to the tile or tank, and undergone transformation into the coral primary polyp stage. Seawater used during the experiments was filtered using a 4-stage canister stack and UV sterilisation (Odyssea CFS-1000) to minimise the presence of microbes from local reef water and isolate the effects of the experimental treatments. Additionally, water was flushed from the aquaria between assays, and the treatments were randomised each day to avoid any aquaria-specific effects.

For each set of experiments, thalli from a cohort of morphologically similar *Lobophora* spp. were collected from an inshore reef close to the research station (Malakal Bay [MB]; Fig. S1), and kept for no more than 2 d in a large flow-through seawater tank before use in the experiments. This is referred to henceforth as *Lobophora*, as reliable identification to species level for each macroalgal thallus would require extensive genetic investigation based on the existence of over 80 species of *Lobophora* (Vieira 2015).

2.2. Expt 1: Small-scale effects of *Lobophora* on settlement (0–10 cm)

The first experiment explored how the distribution of *Lobophora* affected coral settlement at a small scale (within a 10 × 10 cm tile), using 2 spatial arrangements of *Lobophora*: (1) 'clustered' (LC): a 15 cm^2 piece of *Lobophora* thallus in a corner of the tile; and (2) 'dispersed' (LD): fifteen 1 cm^2 pieces cut from *Lobophora* thalli dispersed randomly across the tile (Fig. 1). Cut pieces of *Lobophora* were left in flow-through seawater for ~48 h following manipulation to minimise possible enhanced leakage of compounds from cut edges. Plastic controls (black plastic soaked in seawater for 24 h prior to use) were used for each of the spatial arrangements (control clustered [CC], and control dispersed [CD]), as well as a control with no algae or plastic (control). *Lobophora* and plastic pieces were held in place using rubber bands, with rubber bands also included on the control tiles. This yielded 5 treatments, with 6 replicate assays conducted for each treatment, for each coral species. Additionally, the settlement locations of larvae on the tiles in the 'clustered' treatments (LC and CC) were recorded to determine any difference in mean settlement distance from the *Lobophora* thallus and from the single piece of plastic. Twenty larvae were used in each assay for this experiment. Assays were conducted in 12 l flow-through tanks, supplied with seawater at ~45 ml min^{-1}, with 50 µm mesh covering the outflow to ensure larvae did not escape. Tanks were maintained in an air-conditioned room at 28–30°C, which is representative of temperatures recorded *in situ* (i.e. ~28–31°C; van Woesik et al. 2012, Barkley & Cohen 2016), and received indirect sunlight (~200 photons µmol m^{-2} s^{-1}).

2.3. Expt 2: Intermediate-scale effects of *Lobophora* and mechanisms of settlement inhibition (5–15 cm)

The second experiment assessed the effect of *Lobophora* on coral settlement at a local scale (5–15 cm) and the mechanism by which it deters settlement beyond direct space occupation (Fig. 1). To assess this, larvae from each coral species were placed into tanks with treatments of 0, 1.55, 3.1, 4.65, and 6.2 g

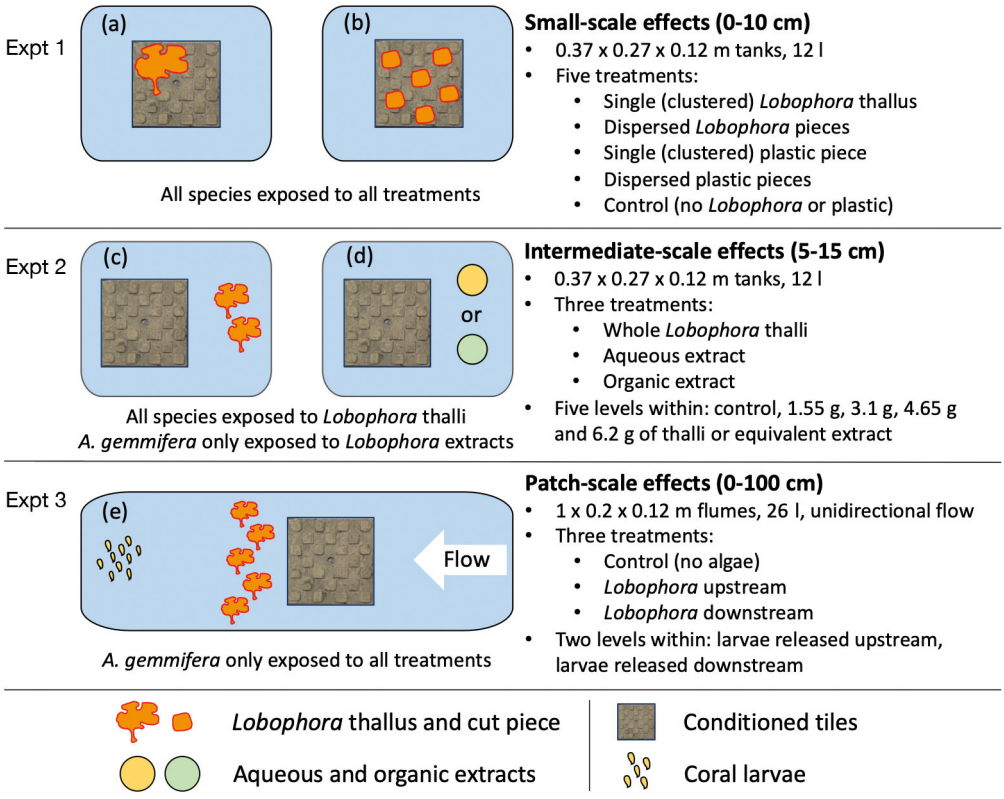

Fig. 1. Schematic representation of aquarium-based experiments conducted with coral larvae *Acropora hyacinthus*, *A. aspera*, and *A. gemmifera*. Competent coral larvae were exposed in Expt 1 to (a) a single *Lobophora* thallus ('clustered' treatment), and (b) randomly spaced *Lobophora* pieces (dispersed treatment) placed on conditioned tiles; in Expt 2 to (c) *Lobophora* thalli, and (d) *Lobophora* extracts (aqueous or organic) in the presence of conditioned tiles; and in Expt 3 to (e) *Lobophora* thalli placed downstream of the conditioned tile, with larvae released downstream of water flow. For Expts 1 and 2, plastic containers served as mesocosms, while Expt 3 was conducted in handmade plexiglass flumes

(all ± 0.1 g, based on spun wet weights) of *Lobophora* thalli, termed control, low, medium, high, and very high treatments, respectively. Assessing the natural biomass of *Lobophora* on the reefs of Palau remains difficult due to the microhabitats in which the alga grows, such as at the dead basal parts of branching coral colonies (sensu Vieira et al. 2016) or encrusting in and around cryptic microhabitats (Doropoulos et al. 2017a), with abundance also appearing to be highly variable across reefs (Roff et al. 2015). Thus, the treatment levels were arbitrarily selected to represent a range of biomasses that may be present on the reefs, while also assessing the nature of the relationship between coral settlement success and *Lobophora* biomass. In turn, the aforementioned treatment levels were equivalent to 0, 4, 8, 12, and 16% cover of *Lobophora* in the tanks, respectively. Six replicate assays were conducted for each treatment level, for each coral species.

To determine potential mechanism(s) by which *Lobophora* inhibits larval settlement at this scale, additional experiments were conducted using waterborne (aqueous) and lipid-soluble (organic) allelochemicals extracted from *Lobophora*. To test for the effects of these allelochemicals, larvae were placed in tanks with either aqueous or organic extracts of *Lobophora*, matching the corresponding treatment levels of the *Lobophora* thalli. Chemical extracts were obtained from *Lobophora* thalli (210 g, spun wet weight) collected from the same site in MB as the *Lobophora* thalli used in all other experiments (Fig. S1) and brought back to PICRC where the samples were rinsed quickly in freshwater and frozen (–80°C) until transportation to Australia. Chemical extracts from the *Lobophora* thalli were obtained using a slight modification of the protocol described in Morrow et al. (2011, 2017). Briefly, freeze-dried thalli were extracted in 1:1 ethyl acetate:methanol with sonication for ~20 min. This was repeated twice more and the 3 extractions combined, concentrated under rotary evaporation at 35°C and freeze-dried overnight to obtain a dry weight. This yielded a lipid-rich non-polar extract (referred to as the organic crude extract [OC]). The remaining thalli tissue was

subsequently extracted with 1:1 ethanol:distilled water (3× with sonication for ~20 min) to yield a lipid-depleted polar extract (referred to as the aqueous crude extract [AC]), which was also freeze-dried and weighed. Extract treatments then were prepared in Palau by dissolving the dried extracts in 97.5% ethanol, before being incorporated into molten Phytagel (Sigma-Aldrich). The extract-gel mixture was allowed to set in Petri dishes for 1–2 h. The concentration of the 2 types of extract in the gel discs were prepared such that they were equivalent to the *Lobophora* thalli biomass treatment levels, based on the yield of OC and AC obtained from the algal wet weights. Yet, it is unlikely that the release rate of the extracts from the gel matches that of the release of compounds from the metabolising algae or that the chemical concentrations in the treatments matched the concentrations on the reef. Thus, the experiment did not assess the absolute impact of waterborne allelochemicals on larval behaviour in nature or the relative importance of waterborne versus lipid-soluble compounds in shaping larval behaviour on the reef. Nonetheless, the experiment aimed to identify the mechanisms by which the alga might inhibit settlement at a distance, while also contrasting the solubility of each extract type in seawater at various spatial scales, with lipid-soluble extracts less likely to disperse from the gel, given its lower solubility in seawater. Solvent controls were prepared using ethanol and Phytagel only to account for any possible effect of the carrier. This yielded 10 treatments (control, solvent control, and 4 levels for both lipid-soluble and waterborne extracts), with 6 replicate assays conducted for each treatment. Due to logistic constraints, experiments using the chemical extracts utilised *A. gemmifera* larvae only (Fig. 1). Experimental conditions for Expt 2 were the same as those detailed in Expt 1.

2.4. Expt 3: Patch-scale settlement effects of *Lobophora* on settlement (0–100 cm)

At the largest spatial scale, we tested how position of a settlement inhibitor, *Lobophora*, and position of the larvae relative to water flow direction affects the ability of larvae to detect and swim towards suitable settlement substrate. The experiment used twelve 100 × 20 × 15 cm plexiglass 26 l flumes that received seawater from 1 of 3 header tanks, flowing into the flumes at ~65 ml min^{-1} to create a flow rate of 2–3 mm s^{-1} across the flume. Flume assays were conducted with 40 larvae, with 50 µm mesh covering the outflow of the flumes to ensure larvae did not escape. The experiments were set up to contrast 3 levels within the *Lobophora* treatment with thalli placed (1) upstream of a tile, (2) downstream of a tile, or (3) absent (control), and 2 levels nested within each of the 3 *Lobophora* treatments with larvae released at the (a) upstream or (b) downstream end of the flumes, in a fully orthogonal design. This yielded 6 treatments, with 6 replicate assays conducted for each treatment, focusing on *A. gemmifera* larvae only due to logistic constraints (Fig. 1). *Lobophora* thalli, weighing 13.8 g (± 0.1 g, based on spun wet weights) were placed in a line running across the width of the flumes along a piece of twisted cotton rope, 3–4 cm upstream or downstream of the conditioned tiles depending on the aforementioned treatments, while control treatments contained the piece of rope only.

Flumes were single-pass to prevent a build-up of chemicals during the assays. While seawater was constantly flowing into the flume at the upstream end and out of the flumes at the downstream end, the small outflow may have resulted in some water mixing in the flume over the course of the assays. Flumes were placed outside, receiving indirect natural lighting (~600 photons µmol m^{-2} s^{-1} at 12:00 h on a clear day) and experiencing temperatures ranging from 28 to 31°C.

2.5. Data analysis for Expts 1 to 3

For Expt 1, settlement success was analysed using a mixed-effect ANOVA, with coral species and treatment type as fixed effects, and tanks as random effects. Tukey's honestly significant difference (HSD) post hoc tests then were conducted to test for significant differences within treatments. Differences in settlement distance from the 'clustered' *Lobophora* treatment and the 'clustered' plastic control treatment were analysed using separate mixed-effect ANOVAs for each species, with treatment as a fixed factor and tiles nested within each treatment.

For Expt 2, settlement success and mortality in response to the presence of *Lobophora* thalli were analysed using 2-way ANOVAs, with coral species and *Lobophora* treatment level as fixed factors, and tanks as individual replicates. When main effects were significant, differences among level within treatments were tested using a Tukey's HSD post hoc. To assess the effects of algal extracts (OC and AC), total rates of settlement and mortality were analysed using 1-way ANOVAs. Post hoc analysis of the extracts was conducted using Dunnett's test, as the analysis

required the extract treatments to be compared to a specific control, the solvent control, rather than a consideration of all pairwise comparisons.

For Expt 3, overall settlement success in the flumes and settlement onto the tiles were analysed using separate mixed-effects ANOVAs, with position of the *Lobophora* thallus relative to the tile (downstream, upstream, or absent) and swimming direction of the larvae (with or against the incoming water flow) as fixed factors, and flume runs incorporated as a random effect to incorporate temporal pseudo-replication.

Data conformed to the assumptions of ANOVA for all analyses, with distribution of the residuals plotted to ensure they fit a normal distribution and residuals plotted against fitted values to confirm that the errors had constant variance. Data analyses were performed using R (v.3.3.1) (R Development Core Team 2015), with the 'multcomp' package (Hothorn et al. 2008), and using Prism (v.7.0; GraphPad Software).

2.6. Field recruitment patterns

To assess the effect of *Lobophora* on *Acropora* spp. recruitment patterns in the field, we analysed data taken of 29 flat 5 × 5 cm ceramic tiles that had been deployed at 3 sites on the eastern coastline of Palau (9 at Beluu Lukes [BL], 10 each at ES and Short Drop Off [SDO]; Fig. S1) during the major *Acropora* recruitment period for ~6 wk, from mid-March to the end of April 2013 (Doropoulos et al. 2016). Initial scoring of the tiles was conducted under a dissecting microscope, during which time recruits were identified following Babcock et al. (2003), measured to 10 µm using a micrometer, and their location on the tile mapped. A high-resolution image was then taken, onto which the information relating to the coral recruits transposed, and subsequent outlining of other groups was conducted (e.g. *Lobophora*, other invertebrates) (Doropoulos et al. 2016). The distribution of suitable (CCA, spiral worms, and biofilm) and unsuitable (macroalgae, thick turf, sponges/ascidians, and bryozoans) settlement substrata (Arnold et al. 2010), as well as *Lobophora* patches and *Acropora* recruits, was mapped for each tile using superimposed 20 × 20 grids (Fig. S3a in the Supplement). *Lobophora* patches were scored if 0.04 cm^2 or larger because they could be positively identified, and were more likely to have pre-dated coral settlement. First, we measured the distance from each patch of substrate on the grid to the closest patch of *Lobophora* on the tile. We then measured the distance between each coral recruit and the nearest patch of *Lobophora* (Fig. S3b). This allowed us to express the observed proximity of corals to *Lobophora* as a percentile of the possible proximities on that tile (Fig. S3c). Percentiles were used as a means to standardise across all tiles, each of which had a different cover and pattern of *Lobophora*. When pooled across all tiles, this produced a distribution of the observed percentile classes in which *Acropora* larvae recruited onto individual tiles (i.e. in the closest 10% [0–10th percentile] of available space to the farthest 10% [90th–100th percentile]), with each recruit allocated to a 10% bin of percentile values. If corals tended to avoid *Lobophora* during settlement, or if *Lobophora* overgrew recruits immediately following settlement, they would rarely fall into the percentile bins that constituted high proximity to the alga (i.e. the 1–10%, 11–20% bins). To test for this, we performed a linear regression between the frequency of observed recruits per class (response) and the percentile class (predictor). Given the complexity of the dataset, with tiles each having different combinations of *Lobophora* cover, recruit densities, and available settlement space, we tested over a null model whether the observed regression was significantly greater than would have been expected by chance—i.e. if corals recruited randomly with respect to the proximity of *Lobophora*. To do this, we recreated identical datasets in MATLAB (v.9.1 R2016b; MathWorks), but substituted the observed position of each recruit with a random location from the available settlement space. Each null dataset was used to repeat the regression described above and the process was repeated for 1000 Monte Carlo simulations. Finally, we calculated the probability that the observed regression coefficient could have been obtained by chance by evaluating its percentile among the null simulations. The same analysis was conducted to assess the effects of CCA, 'other macroalgae', and bryozoan and sponge/ascidian cover on *Acropora* spp. recruitment patterns in the field.

3. RESULTS

3.1. Expt 1: Small-scale effects of *Lobophora* on settlement (0–10 cm)

The spatial arrangement of *Lobophora* thalli on the tiles had a significant effect on settlement for *Acropora hyacinthus* (Fig. 2a) and *A. gemmifera* (Fig. 2b; both $p \leq 0.02$), but not *A. aspera* ($p = 0.38$, Fig. 2c). For *A. hyacinthus*, post hoc comparisons revealed a significant difference between the control and 'clus-

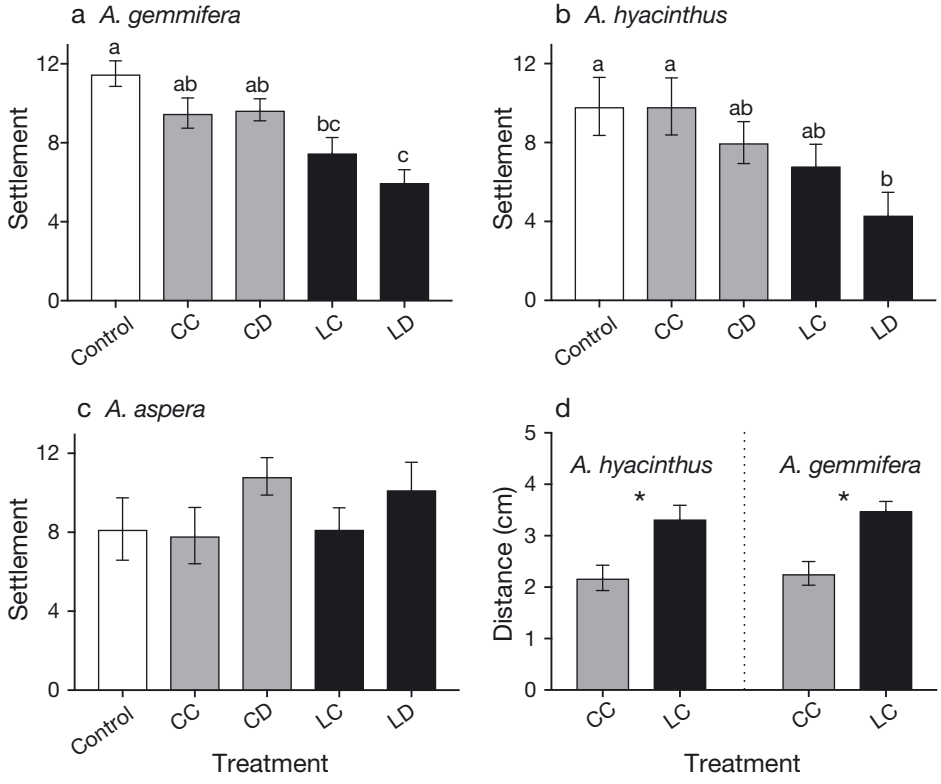

Fig. 2. Expt 1. Small-scale (0–10 cm) effects of *Lobophora* on larval settlement rates (20 larvae per tank) for (a) *Acropora hyacinthus*, (b) *A. gemmifera*, and (c) *A. aspera*. Control = nothing on tile; CC = control clustered, and LC = *Lobophora* clustered, i.e. a 15 cm^2 piece of black plastic or thallus of *Lobophora* in the top left-hand corner of the tile; CD = control dispersed, and LD = *Lobophora* dispersed, i.e. fifteen 1 cm^2 pieces of black plastic or *Lobophora* (all n = 6). (d) Average distance of *A. hyacinthus* and *A. gemmifera* larvae to *Lobophora* and to plastic in the LC and CC treatments, respectively (n = 63–82 settlers per treatment). Letters and asterisks above bars indicate significant differences among treatments (α = 0.05), based on (Tukey's HSD post hoc tests). Each bar represents mean ± SEM

tered' control (CC) treatments, and the dispersed *Lobophora* treatment (LD; both p = 0.03). For *A. gemmifera*, post hoc comparisons revealed a significant difference between the 3 control treatments (control, CC, and CD) and the dispersed *Lobophora* treatment (LD; all $p \leq 0.01$). Additionally, there was a significant difference between the control and the dispersed *Lobophora* treatment (LD; $p < 0.01$). For *A. hyacinthus* and *A. gemmifera* larvae, there was a 30% decline when *Lobophora* was 'clustered' (single thallus on tile) compared to the control, and a 60% decline when *Lobophora* pieces were dispersed throughout the tile compared to the control.

Larvae from *A. hyacinthus* and *A. gemmifera* settled farther away from patches of *Lobophora* than plastic controls ($p \leq 0.003$), with no difference between tiles within treatments ($p \geq 0.22$). Larvae settled 2.2 ± 0.3 (mean ± SEM) and 2.3 ± 0.2 cm from the plastic control on average (CC treatment), and 3.3 ± 0.3 and 3.5 ± 0.2 cm from the *Lobophora* thallus on average (Fig. 2d), for *A. hyacinthus* and *A. gemmifera*, respectively, with no difference in settlement distances for *A. aspera* larvae (p = 0.916).

3.2. Expt 2: Intermediate-scale effects of *Lobophora* and mechanisms of settlement inhibition (5–15 cm)

There was no interactive effect of *Lobophora* treatment by species on settlement (Treatment × Species, p = 0.513), with increasing amounts of *Lobophora* biomass consistently decreasing rates of settlement across the 3 species ($p < 0.001$; Fig. 3a). Settlement rates declined from an average of 9.0 larvae (± 0.9 SEM) in the control, to 6.8 (± 0.8) in the medium treatment (3.1 g of *Lobophora*) and 4.7 (± 0.8) in the highest treatment (6.2 g of *Lobophora*). While the effect of *Lobophora* biomass was consistent across the 3 species, overall rates of settlement differed ($p < 0.001$; Fig. 3b), being highest for *A. aspera* (9.7 ± 0.6) compared to *A. gemmifera* and *A. hyacinthus* (5.3 ± 0.5 and 4.6 ± 0.4, respectively).

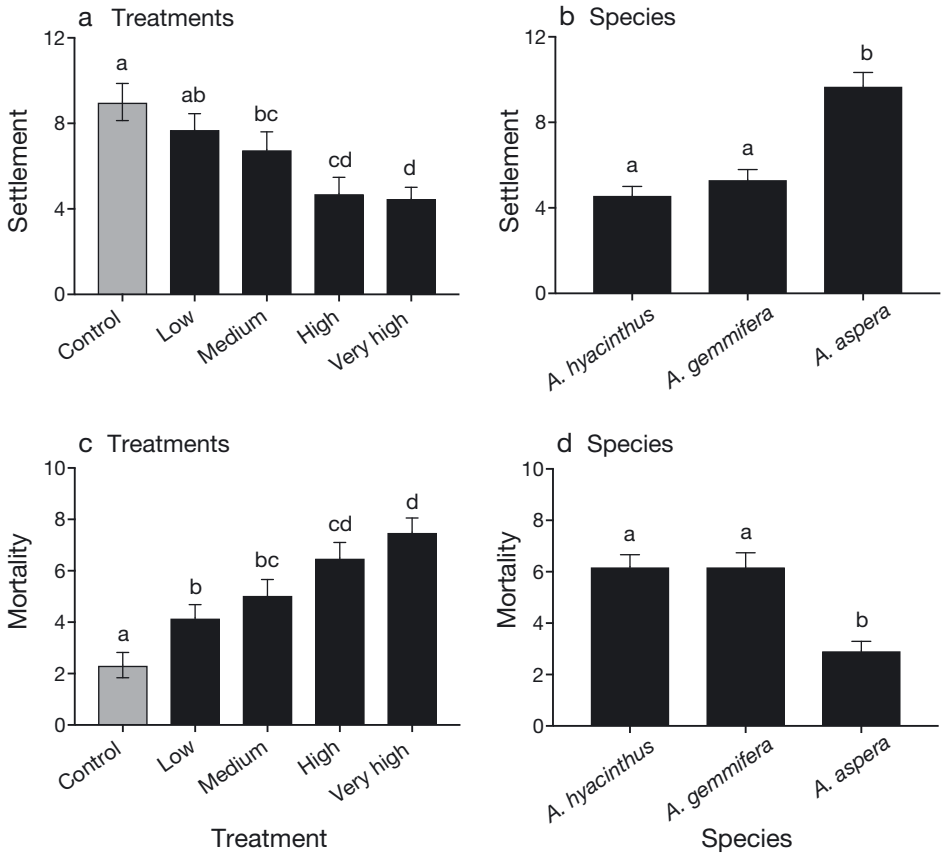

Fig. 3. Expt 2: (a,b) settlement and (c,d) mortality. Intermediate-scale effects of increasing *Lobophora* biomass on (a) coral (*Acropora* spp.) larval settlement and (c) mortality, and overall rates of (b) settlement and (d) mortality for each coral species (20 larvae per tank). Control, low, medium, high, and very high treatments refer to 0, 1.55, 3.1, 4.65, and 6.2 g (all ± 0.1 g) of *Lobophora* in each tank, respectively. Letters above bars indicate significant differences among treatments ($\alpha = 0.05$), based on Tukey's HSD post hoc tests. Each bar represents mean ± SEM (n = 18 for bars grouped by treatment, and n = 30 for bars grouped by species)

Larval mortality showed the inverse pattern to larval settlement. There was no interactive effect of treatment by species ($p = 0.375$), with mortality consistently increasing as *Lobophora* biomass increased for all 3 species ($p < 0.001$; Fig. 3c). Overall rates of mortality also differed among species ($p < 0.001$; Fig. 3d), with rates of mortality lowest for *A. aspera* compared to *A. gemmifera* and *A. hyacinthus*.

Chemical extracts from the *Lobophora* had a significant effect on *A. gemmifera* settlement ($p = 0.007$); this effect was only evident for the aqueous crude extracts ($p < 0.001$) and not the organic crude extracts ($p = 0.133$, Fig. 4a). For the aqueous crude extracts, planned comparisons revealed that medium, high, and very high levels all significantly reduced settlement rates ($p \leq 0.03$), by 55% on average. Similarly, extracts had a significant effect on larval mortality ($p < 0.001$), which was again due to the aqueous crude extracts ($p < 0.001$) and not the organic crude extracts ($p = 0.723$, Fig. 4b). Comparisons revealed that all the aqueous crude extracts significantly increased mortality rates ($p \leq 0.03$). All treatments were compared against the solvent control to test for any effects of the extract treatments, even though there was no significant difference between the control and solvent control for settlement and mortality ($p > 0.25$).

3.3. Expt 3: Patch-scale settlement effects of *Lobophora* on settlement (0–100 cm)

In the flume experiments, the presence of *Lobophora* thalli reduced total settlement by 40–50% ($p < 0.001$), from 10.3 ± 0.7 settlers in the control treatment without *Lobophora* to 5.8 ± 0.5 and 6.5 ± 0.8 settlers in the upstream and downstream treatments, respectively (Fig. 5a). *Lobophora* position in relation to the water flow did not affect settlement. There was no effect of swimming direction on overall settlement rates, nor an interaction between treatments (Fig. 5a,

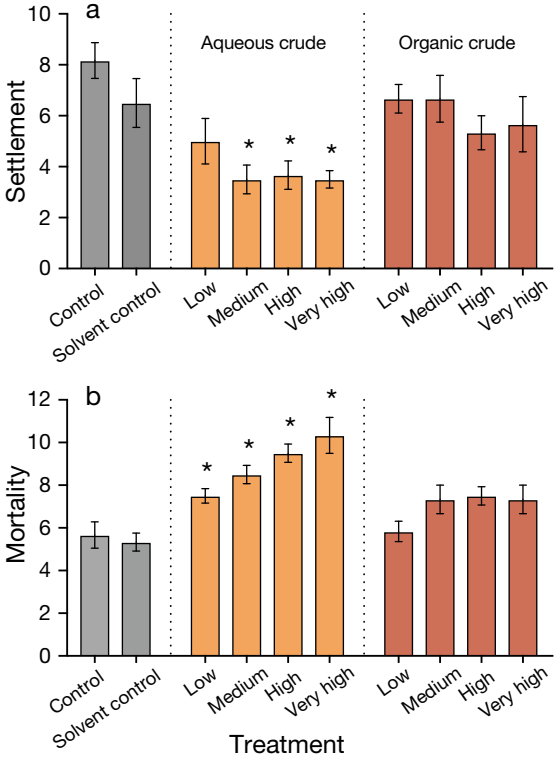

Fig. 4. Expt 2. Effect of *Lobophora* aqueous crude and organic crude extracts on *Acropora gemmifera* (a) settlement and (b) mortality (20 larvae per tank). The amount of extract used for each treatment level was obtained from the equivalent wet weight of alga (refer to Fig. 1). *Significant differences between treatments and the solvent control (α = 0.05), based on Dunnett's test. Each bar represents mean ± SEM (n = 6)

$p \geq 0.754$). For settlement rates onto the tiles, there was no effect of *Lobophora* position or swimming direction, or an interaction between the 2 main effects ($p \geq 0.774$). Settlement rates across all treatments ranged from 3.5 ± 0.8 settlers to 4.2 ± 0.5 settlers per tile (Fig. 5b).

3.4. Field recruitment patterns

Acropora spp. recruitment rates on the conditioned tiles varied from 1 to 21 recruits per tile, with a total of 233 recruits recorded. Analysis of recruitment patterns in the field revealed that *Acropora* larvae had recruited farther from *Lobophora* patches than by chance (p = 0.002), even at such a small spatial scale of 5 × 5 cm tiles, with the positive slope of the observed data (Fig. 6) being greater than that of 99.8% of simulations. Repeating the analysis for CCA and 'other macroalgae' found no effect on recruit proximity vs. a null model (p = 0.16 and p = 0.19, respectively). Conversely, *Acropora* recruits were located closer to bryozoan and sponge/ascidian covered substrate than would be expected by chance, with the observed slope stronger than 95% and 95.2% of simulations, respectively (p = 0.05 and 0.048).

4. DISCUSSION

There is growing evidence that macroalgae use allelochemicals to deter coral settlement (Kuffner et al. 2006, Diaz-Pulido et al. 2010, Dixson et al. 2014, Morrow et al. 2017) and impair the health of corals post-recruitment (Rasher & Hay 2010, Paul et al. 2011, Rasher et al. 2011, Morrow et al. 2012, Vieira et al. 2016), thereby impeding the recovery of coral

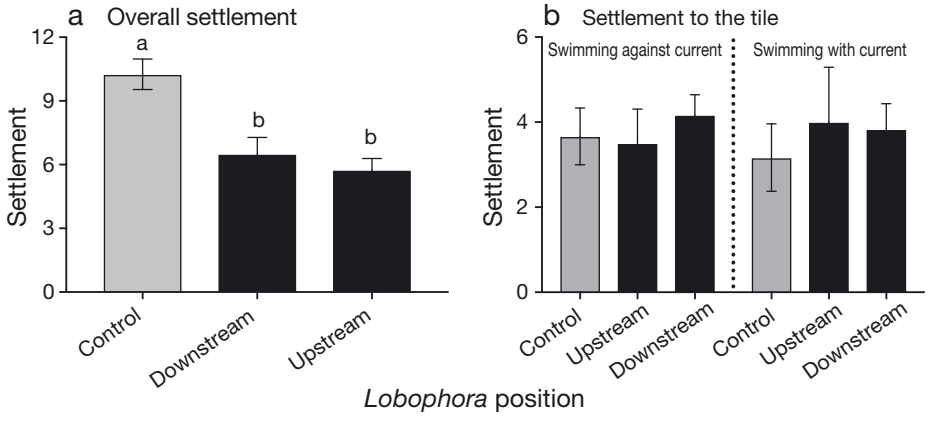

Fig. 5. Expt 3. Patch-scale effects of *Lobophora* on (a) *Acropora gemmifera* overall settlement rates in the experimental flumes and (b) to the conditioned tiles in the flumes (40 larvae per flume). Letters above bars indicate significant differences among treatments (α = 0.05), based on Tukey's HSD post hoc tests. Each bar represents mean ± SEM (n = 6). *Lobophora* thalli were positioned 3–4 cm upstream or downstream of a conditioned tile along a piece of rope, with control assays just containing the rope. Coral larvae then were pipetted in at either end of the flumes depending on the swimming treatment, thus navigating with or against the water current, created by water flowing into the flumes from header tanks

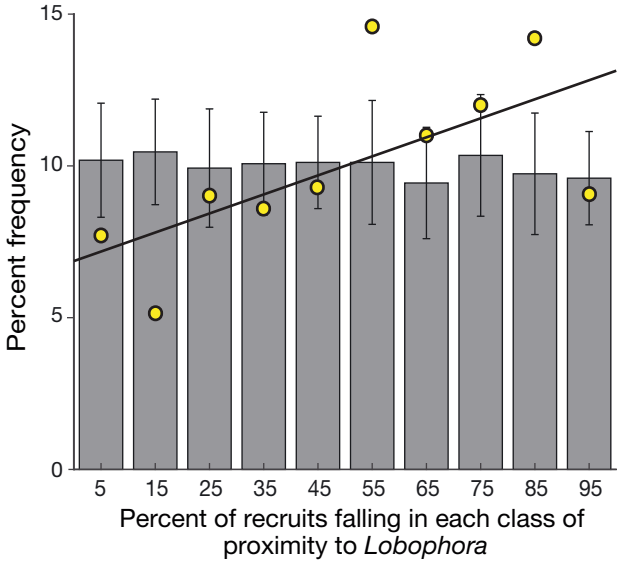

Fig. 6. Comparing the slope (black line) produced by the observed data of *Acropora* field recruitment patterns (yellow circles) to the null model of recruitment (grey bars) where *Lobophora* has no effect on settlement patterns. The null model was obtained from 1000 Monte Carlo simulations with recruits randomly placed in cells containing suitable substrata to demonstrate that corals recruited further from *Lobophora* than by chance (p = 0.002)

communities following disturbances. Here, we demonstrate that *Lobophora* thalli can deter settlement far beyond just the physical space it occupies, releasing waterborne allelochemicals that inhibit coral settlement at a variety of spatial scales, up to 1 m. Moreover, *Lobophora* can limit coral recruitment success by significantly increasing larval mortality and may also affect larval recruitment patterns through altered larval settlement behaviour, with experimental observations demonstrating that larvae avoided settlement in proximity to the alga. Contrary to expectations (e.g. Arnold & Steneck 2011, Doropoulos et al. 2012), field settlement patterns also indicated that corals did not recruit closer to CCA than by chance, suggesting a stronger inhibitive effect of *Lobophora* on recruitment than a facilitative effect of CCA. These findings reinforce the severity and complexity by which *Lobophora* detrimentally impact coral recruitment, by altering larval behaviour at low macroalgal biomasses, and also reducing settlement rates and increasing larval mortality at higher biomasses.

At the smallest spatial scale, *Lobophora* has the ability to deter settlement, consistent with previous studies (Kuffner et al. 2006, Morrow et al. 2017), with larvae seemingly avoiding settlement in close proximity (<3 cm) to the macroalga. Indeed, Kuffner et al. (2006) indicated that larval settlement onto tiles where *Lobophora* thalli were placed decreased compared to controls, while settlement to the walls of the experimental chambers did not change, indicating an unwillingness to settle close to the alga. Analysis of field recruitment patterns also indicate possible avoidance of *Lobophora*, even at such a low cover of 4% on the tiles, though the recruitment patterns also may be caused by overgrowth of the recruits by *Lobophora in situ*. While studies by Doropoulos et al. (2014) and Mumby et al. (2016) could not ascertain the relative effects of *Lobophora* on settlement inhibition versus early post-settlement mortality in Mo'orea and Palau, respectively, the present study implies that inhibition at the settlement stage is likely a key factor. Though the allelopathic effects of *Lobophora* on early post-settlement survival is yet to be tested, we recognise that mortality immediately following settlement may have contributed to the field recruitment patterns observed on the tiles, as *Lobophora* is capable of overgrowing and killing juvenile and adult corals (Jompa & McCook 2002, Box & Mumby 2007, Rasher & Hay 2010, Vieira et al. 2015) and thus can likely overgrow recently settled corals. Still, analysis of field recruitment patterns indicated that any possible avoidance behaviour of *Lobophora* could have led to larvae being in closer proximity to a different post-settlement competitor (bryozoans; Doropoulos et al. 2016), resulting in an indirect mechanism by which *Lobophora* would further impede coral recruitment on disturbed reefs.

The negative effects of *Lobophora* were strengthened in proportion to increases in algal biomass, with settlement proportionally decreasing with increasing algal biomass across the first 3 treatment levels before plateauing, and little difference between the 2 highest treatments. Similar patterns have been reported for studies investigating the effects of turf algae on coral recruitment, with coral recruitment initially decreasing with an increase in turf algal biomass before plateauing as turf algal biomass increased further (Arnold et al. 2010). Conversely, larval mortality in the present study increased proportionally with *Lobophora* biomass across all treatments, indicating a stronger effect of *Lobophora* on mortality than on settlement. Studies investigating the effects of *Sargassum* on coral growth reported a similar linear relationship, with coral growth decreasing proportionally as the density of *Sargassum* thalli surrounding corals increased (Clements & Hay 2015, Clements et al. 2018), but no effect of the alga on overall coral mortality (Clements et al. 2018). The lack of a threshold effect of *Lobophora* on settlement and mortality meant the larvae still settled in the highest *Lobophora*

biomass treatment, albeit at reduced rates. Still, our results indicate that *Lobophora* can impact coral recruitment considerably by causing higher rates of larval mortality, as well as lowering rates of settlement. The negative effects of *Lobophora* at high biomasses (i.e. to about 0.6 g l^{-1}) was evident even at larger spatial scales, with overall settlement in the experimental flumes (Expt 3) almost halved in treatments containing *Lobophora* compared to controls.

Due to the logistical constraints of working with coral larvae under experimental conditions, rates of water flow through the experimental tanks and flumes would have resulted in longer residence times than on most reefs (Black et al. 1990), yielding elevated allelochemical concentrations compared to those that would normally occur. This is particularly likely in the experiments using chemical extracts, where dissolution of the gels would release chemical compounds at greater rates than live algae. Yet, water collected from reefs with high macroalgal cover often contains elevated concentrations of chemical compounds that negatively impact the behaviour and survival of coral larvae (Dixson et al. 2014, Beatty et al. 2018). Such has been postulated on recently impacted reefs in Palau, where *Lobophora* cover reached 40% following an algal bloom (Roff et al. 2015). At impacted sites, coral recruitment was virtually absent and, based on the sensitivity of coral larvae to *Lobophora* in the present study, the high cover of *Lobophora* was likely partially responsible for the large-scale recruitment failure on these reefs (Doropoulos et al. 2014, 2017a). Additionally, while larvae in the present study and other similar experimental studies (Golbuu & Richmond 2007, Gleason et al. 2009, Dixson et al. 2014) displayed a clear ability to search and swim towards positive cues or away from negative cues due to the reduce flow rates, recent research has indicated that coral larvae are often not strong enough to swim against currents on the reef (Hata et al. 2017). However, if *Lobophora* is able to deter settlement within the benthic boundary layer, where water flow is greatly reduced and larvae are more readily able to search for appropriate settlement space (Koehl et al. 2007), then it is likely that *Lobophora* could strongly reduce settlement rates on reefs containing large amounts of the alga.

Macroalgae have long been identified as important inhibitors of coral recovery on degraded reefs, through a reduction in available settlement space (Hughes 1985) and direct competition with established corals (McCook et al. 2001). However, recent studies have highlighted the importance of allelopathic interactions between corals and algae, with some macroalgae releasing allelochemicals that are toxic to adult corals and their larvae (e.g. Morrow et al. 2011, 2012, 2017, Vega Thurber et al. 2012). Studies on the allelopathic effects of *Lobophora* to date have focused largely on the effects of lipid-soluble compounds on corals through direct contact (Rasher & Hay 2010, Rasher et al. 2011, Andras et al. 2012, Slattery & Lesser 2014, Vieira et al. 2016, Longo & Hay 2017). Yet, recent work has indicated the potential for macroalgae to release allelochemicals that impact coral larvae at larger spatial scales, with both lipid-soluble and waterborne extracts obtained from *Lobophora* samples from the Great Barrier Reef deterring coral settlement at a small scale (using 10 ml well plates; Morrow et al. 2017). Our results implicate the importance of waterborne extracts from *Lobophora* samples from the reefs of Palau at larger spatial scales, with these extracts reducing settlement rates of *Acropora* larvae to conditioned tiles located >5 cm from the extracts. As per Morrow et al. (2017), when compared to lipid-soluble extracts, our results also indicate a stronger toxic effect of waterborne extracts on larvae, with an inverse trend between settlement and mortality, and mortality exceeding 50% in the highest treatment. Unlike the present study, Morrow et al. (2017) found a threshold effect of waterborne extracts, with no settlement at concentrations ≥0.1 mg ml^{-1}, as well as a strong effect of lipid-soluble extracts, with no settlement at concentrations ≥0.3 mg ml^{-1}. Lipid-soluble extracts did not impact settlement at the scale tested in the present study (5–15 cm), likely due to the lipophilic nature of the compounds limiting their dissolution in the tanks. Yet, Vieira et al. (2016) indicated that the strength of allelopathy of compounds isolated from *Lobophora* against coral correlates with the polarity of the compounds, with less polar (i.e. lipid-soluble) compounds displaying the highest allelopathic activity against adult corals. However, lipid-soluble compounds are deployed through direct contact with surfaces (Rasher et al. 2011, Andras et al. 2012). Indeed, Dixson et al. (2014) indicated that rubbing settlement tiles with allelopathic algae such as *Galaxaura* decreased settlement rates to those tiles, a process that was not tested with *Lobophora* in the present study. Thus, the potential effects of lipid-soluble compounds may have been underrepresented in the present study. Nonetheless, our results, together with the results from previous studies (Rasher & Hay 2010, Morrow et al. 2012, 2017, Slattery & Lesser 2014, Vieira et al. 2016), suggest that *Lobophora* produce a variety of chemical defences that can act across a variety of spatial scales to impact corals across multiple life-history stages.

Though the effects of *Lobophora* at the intermediate scale (5–15 cm) were consistent across coral taxa, the response to *Lobophora* at the local scale (0–10 cm) varied among species. *Acropora aspera* settlement was unaffected by *Lobophora*, whereas *A. hyacinthus* and *A. gemmifera* were negatively impacted. It is possible that the differences are attributed to different sensitivities of *A. aspera* to chemicals that may have been present at the smallest spatial scale (Expt 1), with previous studies indicating that the extent to which corals are sensitive to macroalgal allelopathy and the extent to which macroalgae can affect corals is species-specific (Rasher et al. 2011, Vieira et al. 2016). *Lobophora* has been observed growing on the dead portions of lower branches of *A. aspera* colonies (N. R. Evensen pers. obs.) and may explain the lack of sensitivity of *A. aspera* compared to the 2 other species. This also supports findings from a previous study, which found only minor effects of *Lobophora* on the tissue recovery of adult *A. aspera* following disturbance (Bender et al. 2012). Our results further indicate that the effects of *Lobophora* can be species-specific and could contribute to the transformation of benthic assemblages if certain corals are less sensitive to the chemical effects of *Lobophora* during recruitment.

Overall, our results demonstrate the potential for a pervasive macroalga (de Ruyter van Steveninck & Bak 1986, Done et al. 2007, Cheal et al. 2010, Slattery & Lesser 2014, Roff et al. 2015) to impair coral settlement, and the subsequent recruitment and recovery of impacted coral populations, at much higher rates than through the direct occupation of settlement space alone. Notably, the ability of *Lobophora* to inhibit settlement at multiple spatial scales further highlights the negative impact of this alga on coral reef resilience (Mumby et al. 2016, Doropoulos et al. 2017a). Although shifts to algal-dominated states remain unlikely for Indo-Pacific reefs (although see Graham et al. 2015), these results demonstrate that the larvae of important reef-building corals can exhibit strong sensitivities to certain algal taxa, with *Lobophora* appearing to have a big impact on settlement even at low coverage. The ability of macroalgae such as *Lobophora* to impede settlement through the release of waterborne allelochemicals can result in considerable reductions in coral recruitment and subsequent population growth, despite the presence of ample suitable settlement substrate (Doropoulos et al. 2014, Mumby et al. 2016). Thus, it is important to consider the type of macroalgae and coral present, rather than macroalgal cover and coral cover alone, when considering the health or recovery potential of a coral reef.

Acknowledgements. We are grateful to the Palau International Coral Reef Center for hosting this study. We thank Carrie Sims for providing us with *A. gemmifera* larvae, L. Puk, M. Gouezo, D. Olsudong, A. Tredennick, K. Miller, K. Wong, S. Smith, and L. Rehm for help with field work, J. Werminghausen for mapping biota on the field tiles, and G. Roff and S. Ward for advice that improved the quality of the work. Y.-M. Bozec, R. Dwyer, J.-C. Ortiz, and C. J. Brown provided advice for statistical analyses and figures. We also thank 4 anonymous reviewers for providing valuable feedback that substantially improved the manuscript. This work was funded by ARC grants awarded to P.J.M. and an Australian Endeavour Award to C.D.

LITERATURE CITED

Andras TD, Alexander TS, Gahlena A, Parry RM and others (2012) Seaweed allelopathy against coral: surface distribution of a seaweed secondary metabolite by imaging mass spectrometry. J Chem Ecol 38:1203–1214

Arnold SN, Steneck RS (2011) Settling into an increasingly hostile world: the rapidly closing 'recruitment window' for corals. PLOS ONE 6:e28681

Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105

Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool Stud 42:211–226

Barkley HC, Cohen AL (2016) Skeletal records of community-level bleaching in *Porites* corals from Palau. Coral Reefs 35:1407–1417

Beatty DS, Clements CS, Stewart FJ, Hay ME (2018) Intergenerational effects of macroalgae on a reef coral: major declines in larval survival but subtle changes in microbiomes. Mar Ecol Prog Ser 589:97–114

Bender D, Diaz-Pulido G, Dove S (2012) Effects of macroalgae on corals recovering from disturbance. J Exp Mar Biol Ecol 429:15–19

Birrell CL, McCook LJ, Willis BL, Harrington L (2008) Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora.* Mar Ecol Prog Ser 362:129–137

Black KP, Gay SL, Andrews JC (1990) Residence times of neutrally-buoyant matter such as larvae, sewage or nutrients on coral reefs. Coral Reefs 9:105–114

Box SJ, Mumby PJ (2007) Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Mar Ecol Prog Ser 342:139–149

Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, Sweatman H (2010) Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs 29:1005–1015

Chong-Seng KM, Graham NAJ, Pratchett MS (2014) Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33: 449–461

Clements CS, Hay ME (2015) Competitors as accomplices: Seaweed competitors hide corals from predatory sea stars. Proc R Soc B 282:20150714

Clements CS, Rasher DB, Hoey AS, Bonito VE, Hay ME (2018) Spatial and temporal limits of coral-macroalgal competition: the negative impacts of macroalgal density, proximity, and history of contact. Mar Ecol Prog Ser 586:11–20

de Ruyter van Steveninck ED, Bak RPM (1986) Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum.* Mar Ecol Prog Ser 34:87–94

Diaz-Pulido G, Harii S, McCook LJ, Hoegh-Guldberg O (2010) The impact of benthic algae on the settlement of a reef-building coral. Coral Reefs 29:203–208

Dixson DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. Science 345:892–897

Done TJ, Turak E, Wakeford M, DeVantier L, McDonald A, Fisk D (2007) Decadal changes in turbid-water coral communities at Pandora Reef: loss of resilience or too soon to tell? Coral Reefs 26:789–805

Doropoulos C, Ward S, Diaz-Pulido G, Hoegh-Guldberg O, Mumby PJ (2012) Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. Ecol Lett 15:338–346

Doropoulos C, Roff G, Zupan M, Nestor V, Isechal AL, Mumby PJ (2014) Reef-scale failure of coral settlement following typhoon disturbance and macroalgal bloom in Palau, Western Pacific. Coral Reefs 33:613–623

Doropoulos C, Roff G, Bozec YM, Zupan M, Werminghausen J, Mumby PJ (2016) Characterising the ecological trade-offs throughout the early ontogeny of coral recruitment. Ecol Monogr 86:20–44

Doropoulos C, Roff G, Visser MS, Mumby PJ (2017a) Sensitivity of coral recruitment to subtle shifts in early community succession. Ecology 98:304–314

Doropoulos C, Evensen NR, Gómez-Lemos LA, Babcock RC (2017b) Density-dependent coral recruitment displays divergent responses during distinct early life-history stages. R Soc Open Sci 4:170082

Gleason DF, Danilowicz BS, Nolan CJ (2009) Reef waters stimulate substratum exploration in planulae from brooding Caribbean corals. Coral Reefs 28:549–554

Golbuu Y, Richmond RH (2007) Substratum preferences in planula larvae of two species of scleractinian corals, *Goniastrea retiformis* and *Stylaraea punctata.* Mar Biol 152:639–644

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97

Harrington L, Fabricius K, De'ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. Ecology 85: 3428–3437

Hata T, Madin JS, Cumbo VR, Denny M and others (2017) Coral larvae are poor swimmers and require fine-scale reef structure to settle. Sci Rep 7:2249

Hay ME (2009) Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystems. Annu Rev Mar Sci 1:193–212

Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. Coral Reefs 18:273–279

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363

Hughes TP (1985) Life histories and population dynamics of early successional corals. In: Gabrie C, Salvat B (eds) Proc 5th Int Coral Reef Symp, Vol 4. Attenne Museum – EPHE, Moorea, French Polynesia, p 101–105

Jompa J, McCook LJ (2002) Effects of competition and herbivory on interactions between a hard coral and a brown alga. J Exp Mar Biol Ecol 271:25–39

Koehl MAR, Strother JA, Reidenbach MA, Koseff JR, Hadfield MG (2007) Individual-based model of larval transport to coral reefs in turbulent, wave-driven flow: behavioral responses to dissolved settlement inducer. Mar Ecol Prog Ser 335:1–18

Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar Ecol Prog Ser 323:107–117

Le Tourneux F, Bourget E (1988) Importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides.* Mar Biol 97: 57–66

Longo GO, Hay ME (2017) Seaweed allelopathy to corals: Are active compounds on, or in, seaweeds? Coral Reefs 36:247–253

McCook L, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400–417

Montgomery JC, Jeffs A, Simpson SD, Meekan M, Tindle C (2006) Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. Adv Mar Biol 51: 143–196

Morrow KM, Paul VJ, Liles MR, Chadwick NE (2011) Allelochemicals produced by Caribbean macroalgae and cyanobacteria have species-specific effects on reef coral microorganisms. Coral Reefs 30:309–320

Morrow KM, Ritson-Williams R, Ross C, Liles MR, Paul VJ (2012) Macroalgal extracts induce bacterial assemblage shifts and sublethal tissue stress in Caribbean corals. PLOS ONE 7:e44859

Morrow KM, Bromhall K, Motti CA, Munn CB, Bourne DG (2017) Allelochemicals produced by the brown macroalga, *Lobophora* sp., are active against coral larvae and associated bacteria, supporting pathogenic shifts to *Vibrio*-dominance. Appl Environ Microbiol 83:e02391-16

Mumby PJ, Steneck RS, Adjeroud M, Arnold SN (2016) High resilience masks underlying sensitivity to algal phase shifts of Pacific coral reefs. Oikos 125:644–655

Mundy C, Babcock R (2000) Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? A case study of three contrasting species. Mar Ecol Prog Ser 198:109–119

Ortiz JC, Bozec YM, Wolff NH, Doropoulos C, Mumby PJ (2014) Global disparity in the ecological benefits of reducing carbon emissions for coral reefs. Nat Clim Change 4:1090–1094

Patzkowsky ME (1988) Differential response of settling larvae to resident colony density in two species of *Bugula* (Bryozoa: Cheilostomata). J Exp Mar Biol Ecol 124:57–63

Paul VJ, Kuffner IB, Walters LJ, Ritson-Williams R, Beach KS, Becerro MA (2011) Chemically mediated interactions between macroalgae *Dictyota* spp. and multiple life-history stages of the coral *Porites astreoides.* Mar Ecol Prog Ser 426:161–170

Pawlik JR (1992) Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr Mar Biol Annu Rev 30:273–335

R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Raimondi PT, Morse ANC (2000) The consequences of complex larval behavior in a coral. Ecology 81:3193–3211

Rasher DB, Hay ME (2010) Chemically rich seaweeds poison corals when not controlled by herbivores. Proc Natl Acad Sci USA 107:9683–9688

Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME (2011) Macroalgal terpenes function as allelopathic agents against reef corals. Proc Natl Acad Sci USA 108:17726–17731

Ritson-Williams R, Arnold S, Fogarty N, Steneck RS, Vermeij M, Paul VJ (2009) New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithson Contrib Mar Sci 38:437–457

Rittschof D, Hooper IR, Branscomb ES, Costlow JD (1985) Inhibition of barnacle settlement and behavior by natural products from whip corals, *Leptogorgia virgulata* (Lamarck, 1815). J Chem Ecol 11:551–563

Roff G, Doropoulos C, Zupan M, Rogers A, Steneck RS, Golbuu Y, Mumby PJ (2015) Phase shift facilitation following cyclone disturbance on coral reefs. Oecologia 178:1193–1203

Slattery M, Lesser MP (2014) Allelopathy in the tropical alga *Lobophora variegata* (Phaeophyceae): mechanistic basis for a phase shift on mesophotic coral reefs? J Phycol 50: 493–505

Sneed JM, Sharp KH, Ritchie KB, Paul VJ (2014) The chemical cue tetrabromopyrrole from a biofilm bacterium induces settlement of multiple Caribbean corals. Proc R Soc B 281:20133086

Steneck RS (1994) Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978-1988). In: Ginsburg RN (ed) Global aspects of coral reefs: health, hazards, and history. University of Miami Press, Miami, FL, p 220–225

Steneck RS (1997) Crustose corallines, other algal functional groups, herbivores and sediments: complex interactions along reef productivity gradients. In: Lessios HA, Macintyre IG (eds) Proc 8th Int Coral Reef Symp, Vol 1. University of Panama and Smithsonian Tropical Research Institute, Panama City, p 695–700

Tebben J, Motti CA, Siboni N, Tapiolas DM and others (2015) Chemical mediation of coral larval settlement by crustose coralline algae. Sci Rep 5:10803

van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012) Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. Ecol Evol 2: 2474–2484

Vega Thurber R, Burkepile DE, Correa AMS, Thurber AR and others (2012) Macroalgae decrease growth and alter microbial community structure of the reef-building coral, *Porites astreoides*. PLOS ONE 7:e44246

Vermeij MJA, Marhaver KL, Huijbers CM, Nagelkerken I, Simpson SD (2010) Coral larvae move toward reef sounds. PLOS ONE 5:e10660

Vieira C (2015) *Lobophora*: biotic interactions and diversification. PhD thesis, Ghent University

Vieira C, Payri C, De Clerck O (2015) Overgrowth and killing of corals by the brown alga *Lobophora hederacea* (Dictyotales, Phaeophyceae) on healthy reefs in New Caledonia: a new case of the epizoism syndrome. Phycol Res 63:152–153

Vieira C, Thomas OP, Culioli G, Genta-Jouve G and others (2016) Allelopathic interactions between the brown algal genus *Lobophora* (Dictyotales, Phaeophyceae) and scleractinian corals. Sci Rep 6:18637

Walters LJ, Wethey DS (1996) Settlement and early post-settlement survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. Mar Ecol Prog Ser 137:161–171

Webster NS, Smith LD, Heyward AJ, Watts JEM, Webb RI, Blackall LL, Negri AP (2004) Metamorphosis of a scleractinian coral in response to microbial biofilms. Appl Environ Microbiol 70:1213–1221

Editorial responsibility: Joseph Pawlik, Wilmington, North Carolina, USA

Submitted: September 27, 2018; Accepted: January 29, 2019
Proofs received from author(s): February 24, 2019