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Coral early life history dynamics: conspecific facilitation or limitation are dependent on distinct life stage interactions

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ABSTRACT: Replenishment of species within a community is largely determined by early life history dynamics, yet the relative contributions of settlement versus post-settlement processes in establishing coral community structure are not well understood. Here, we examined the effect of larval density, number of settlers and presence of conspecific adults on settlement and post-settlement success for 3 broadcast-spawning scleractinian corals under aquarium conditions. We found that settlement and post-settlement survival are dependent on larval or settler densities but with contrasting effects among the studied coral species. Settlement of *Anacropora spinosa* larvae was inversely density-dependent, while settlement of *Acropora gemmifera* and *Acropora digitifera* larvae was density-independent. *A. spinosa* had high post-settlement survivorship, while *A. digitifera* underwent significant density-dependent post-settlement mortality within 14 d after settlement. *A. gemmifera* showed no significant trend in post-settlement survival by number of initial settlers, but had higher mortality in the second week than the first week, as did *A. digitifera*. For all species, settler spatial patterns were under-dispersed; the probability of contact between settlers positively correlated to initial settler numbers, and the extent of under-dispersion showed little change over time. The presence of conspecific adults led to a decrease in larval settlement of *A. spinosa* and *A. gemmifera* but had only a weak influence on settler survival for *A. spinosa*. These data indicate, in an experimental setting, that settlement success of larvae can be reduced when in close proximity to a conspecific adult and may be mediated by a waterborne agent. Overall, our results demonstrate the potential for self-limitation via conspecific larval–adult interactions and facilitation among early life stages of a cohort.

KEY WORDS: Coral larvae · Settlement · Post-settlement survival · Density dependence · Spatial patterns

1. INTRODUCTION

Changes in biodiversity are increasingly common across the globe due to widespread anthropogenic local impacts which are also compounded by the effects of climate change (Magurran & Dornelas 2010, Hughes et al. 2018, Arneth et al. 2020). These changes impose critical effects on ecosystem functioning, productivity, and stability (Tilman 1999, Duffy et al. 2017, McWilliam et al. 2018, Clements & Hay 2019). Understanding the processes that structure ecological communities and maintain species diversity are thus of immediate importance to predicting and anticipating shifts in biodiversity from local to global scales (Van Woesik 2000, Pandolfi 2015, Valladares et al. 2015). In hyper-diverse communities of sessile foundational

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species (Ellison 2019), such as rainforests and coral reefs, ecological differences that cause organisms to limit the propagation of conspecifics more strongly than that of other species are proposed to promote species coexistence (Chesson 2000, Levine & HilleRisLambers 2009). Such intra-specific interactions are often discussed in terms of density-dependence (sensu stricto Hixon & Johnson 2009) that acts to regulate population numbers. For example, as the population density of a particular species increases locally, the resources to sustain that population may decrease and intra-specific competition increases, followed by down-regulation of population density. Density-dependent population regulation has important implications for population replenishment and resilience, and scales up to community-level processes and dynamics (Hixon et al. 2002).

The sessile foundational species of hyper-diverse communities are generally restricted in their movement to early life stages (e.g. seeds for plants, eggs and larvae for marine invertebrates, including reef-building corals). Theory and evidence from terrestrial and marine systems persistently points to ecological processes occurring during the dispersal and establishment stages as key periods for establishing patterns of species coexistence (Janzen 1970, Connell 1971, Roughgarden et al. 1985, Chesson 2000, Hubbell 2001, Wisz et al. 2013). For corals, the early life stages represent the greatest demographic bottleneck and are the period when density-dependent interactions are expected to be most pronounced, thus having the greatest potential to promote or inhibit species coexistence (Gosselin & Qian 1997, Hunt & Scheibling 1997, Vermeij & Sandin 2008, Doropoulos et al. 2017, Álvarez-Noriega et al. 2018). Despite knowledge on when key bottlenecks occur for corals, the mechanisms underlying mortality at the settlement and post-settlement stages remain unclear for many coral species as does the relative importance of mortality at each stage in driving coral population establishment and community dynamics (Adjeroud et al. 2017).

Coral settlement is not a passive phenomenon, but is influenced by active larval behaviours (Lewis 1974, Babcock & Mundy 1996). Settlement substrate selection is achieved through sensory adaptations (Morse et al. 1996, Foster & Gilmour 2016) that enable coral larvae to respond to abiotic and biotic cues (Babcock & Mundy 1996, Mundy & Babcock 1998, Gilmour 1999, Webster et al. 2004, Doropoulos et al. 2016). The presence of such cues and adaptive responses of coral larvae influence the success and extent of settlement, and the selection of suitable habitats has been linked to increased post-settlement survival (Raimondi & Morse 2000, Harrington et al. 2004). Coral larvae, like many marine invertebrates, exhibit behavioural modifications in response to individuals of a cohort and established colonies. Some of these interactions can enhance initial settlement, with larvae forming conspecific clusters (Lewis 1974, Harrison & Wallace 1990, Vermeij 2005, Sampayo et al. 2020, Huffmyer et al. 2021, Sims et al. 2021) and conspecific settlement trends indicating either density-independence or inverse density-dependence (Edwards et al. 2015, Doropoulos et al. 2017, 2018, Cameron & Harrison 2020, Sims et al. 2021). Yet, proximity to a conspecific adult colony (Vermeij 2005) or water collected near conspecific adult colonies (Marhaver et al. 2013, Sims et al. 2021) were found to reduce coral settlement and post-settlement survival, and these effects may be magnified with increases in densities of conspecific adults (Vermeij & Sandin 2008).

Several studies provide evidence for density-dependent settler survival in corals (Suzuki et al. 2012, Edwards et al. 2015, Doropoulos et al. 2017, Cameron & Harrison 2020), yet these field-based studies make it difficult to parse out the effects of density dependence versus environmental or stochastic processes and often census early survival on settlement tiles after long time frames (1–2 mo). High mortality is commonly seen in the first few weeks to months for many marine invertebrates (Harrington et al. 2004, Gosselin & Qian 1997, Marhaver et al. 2013), and inferences regarding the influence of early life stage processes on population dynamics that skip initial bottlenecks will likely be incomplete (Keough & Downes 1982). As demographic patterns among older individuals may reflect interactions that occurred at earlier stages (Chesson 1998), experiments in aquaria provide direct observation of early life stage processes while controlling for confounding factors and capturing settlement and early post-settlement survival stages. Overall, intra- and inter-specific interactions at larval, settler, and adult life-history stages require further quantification. Particularly, the influence of established communities that form the habitat for incoming settlers, ('settlement neighborhood') are likely a key component of early life stage bottlenecks for corals (Vermeij & Sandin 2008, Marhaver et al. 2013, Edmunds et al. 2018) but few data exist on how settlement and post-settlement rates respond to species identity, species diversity, and population density within the settlement neighborhood.

Here, we address the question of whether larval settlement and post-settlement survival are influenced by larval density or number of settlers, respectively, and the presence of conspecific adults. While similar in its approach and overall aim, the current study complements previous findings (Sims et al. 2021) by examining distinct coral species in a new location, assessing a greater range of larval densities, and censusing early survivorship weekly. Extending studies across various species as well as locations is a crucial step towards understanding whether observed responses are consistent across species, regions, or key characteristics. We conducted controlled aquarium experiments on 3 common Indo-Pacific scleractinian coral species: *Acropora digitifera*, *A. gemmifera*, and *Anacropora spinosa*. We tested whether (1) settlement success is dependent on larval density and altered by the presence of conspecific adults, and (2) post-settlement survival is dependent on number of settlers and affected by the presence of conspecific adults. We follow Hixon & Johnson (2009) and report results in reference to gain rates (i.e. settlement success or settler survival), with inverse density-dependence indicating a positive correlation between density and gain and density-dependence indicating a negative relationship. We hypothesized that settlement success would be either inversely density-dependent or not associated with larval density, because conspecific larvae tend to aggregate (Sampayo et al. 2020, Sims et al. 2021), yet that post-settlement survival would be reduced within dense conspecific settler aggregations (Doropoulos et al. 2017, 2018). We also hypothesized that the presence of adult conspecifics would reduce larval settlement and post-settlement survival (Fearon & Cameron 1997, Marhaver et al. 2013). Using settlement and survival data from (1) and (2), we (3) conducted spatial analyses of settlement patterns over time in relation to settler density and presence of adult conspecifics to gain insights into ecological processes (e.g. competition, facilitation) that structure early life stage spatial patterns (Hart & Marshall 2009, Aguirre et al. 2013). We expected larvae to be under-dispersed at settlement because gregarious settlement is a common phenomenon among coral species in experimental settings and may be beneficial to early life stage survival (Harrison & Wallace 1990, Rinkevich 2004, Puill-Stephan et al. 2012, Sampayo et al. 2020).

2. MATERIALS AND METHODS

2.1. Study site, coral spawning, and larval rearing

Experiments were conducted in Palau, Micronesia (07° 30′ N, 134° 30′ E), in the northwest Pacific, where corals spawn on several occasions throughout the year from February to April and August to September (Penland et al. 2004). We collected 3 regionally common branching coral species, *Acropora digitifera*, *A. gemmifera*, and *Anacropora spinosa*, in the state of Airai prior to the April 2017 full moon. In total, 9 *A. digitifera* and 8 *A. gemmifera* colonies were collected from the inner reef flat of the south Airai fringing reef in waters 2–5 m deep. Multiple *A. spinosa* branches were collected from large thickets of colonies in a lagoonal area, north-east of the Koror-Babeldaob Channel, at 3 m depth. Colonies of each species were placed together in flow-through aquaria at Biota, an aquaculture facility located in Airai, Palau. Colonies of *A. digitifera* spawned 1 d (12 April) and *A. gemmifera* and *A. spinosa* spawned 2 d (13 April) following the full moon, between 19:00 and 21:30 h. The egg–sperm bundles of the 2 *Acropora* species were positively buoyant, while those of *A. spinosa* were neutrally buoyant and considerably smaller than those of the *Acropora* species. The gamete bundles of each species were collected in bowls and agitated gently to release eggs and sperm and to allow cross-fertilization. Fertilization success was monitored using a dissecting microscope. Following observation of initial division stages or after a maximum of 2 h, the eggs were washed in a 63 µm mesh filter using 0.45 µm filtered seawater to reduce polyspermy. The eggs were left to develop in 3 l bowls, where seawater temperatures ranged between 26 and 29°C over 24 h periods; the seawater was changed twice a day using filtered seawater. Once the majority of larvae of each species displayed signs of competency (e.g. active swimming behaviour, searching the bottom surfaces), they were transferred to the experimental treatments (i.e. 6 d post spawning for *A. digitifera* and *A. gemmifera*, 5 d post spawning for *A. spinosa*).

2.2. Experimental procedures and analyses

2.2.1. General experimental setup

For *A. gemmifera* and *A. spinosa*, 3 replicate aquaria per adult treatment (2 levels: absent or present) were established, each with 3 replicate containers per stocking larval density treatment (4 levels: 10, 50, 100 and 200; Fig. 1). For *A. digitifera*, 3 replicate aquaria were established, each with 3 replicate containers per stocking larval density treatment. We did not include an adult treatment for *A. digitifera*, because the adult colonies showed visible signs of stress, including tissue pigmentation change or some

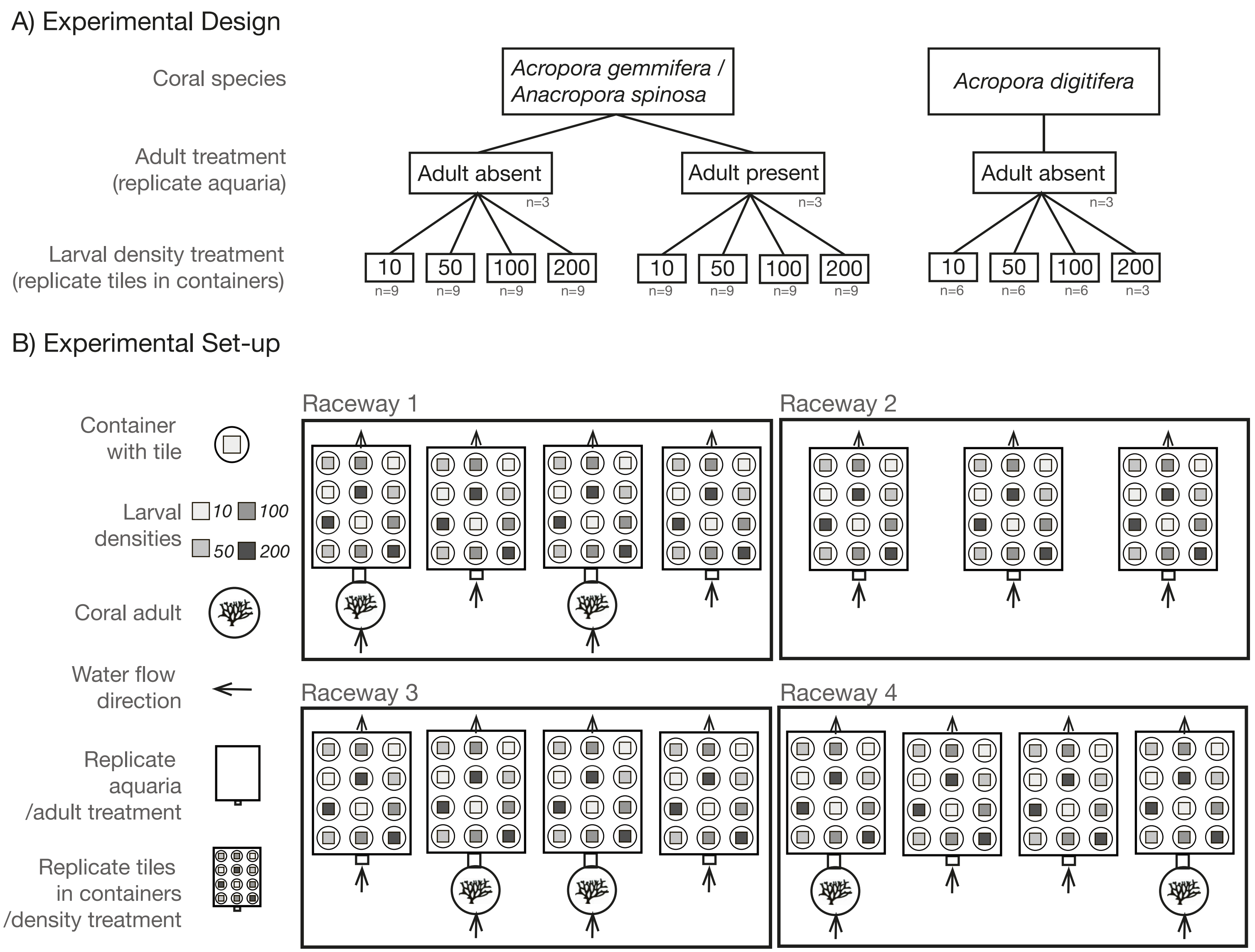

Fig. 1. (A) Experimental design. For *Acropora gemmifera* and *Anacropora spinosa*, 3 replicate aquaria per adult treatment were randomly allocated to one of 4 outdoor raceways. Three replicate containers with tiles for each of the 4 density treatment levels were randomly positioned within each replicate aquarium. For *Acropora digitifera*, 3 replicate aquaria were randomly allocated to one of 4 outdoor raceways and 3 replicate containers with tiles for each of the 4 density treatment levels were randomly positioned within each replicate aquarium. (B) Experimental set-up: flow-through seawater entered each aquarium at one end and out the other (adult absent treatment) or first flowed through a bucket containing an adult conspecific colony then to the aquarium (adult-present treatment). Legend on the left depicts a circle with square as the replicate container with tile; grey shading of squares (tiles) in containers indicates the different density treatment levels of coral larvae; coral graphic depicts a coral adult colony was present; and arrow indicates water flow direction (depiction does not show exact randomization of densities; see Section 2.2 for further information on treatments and replication for each coral species)

tissue loss, from being kept in aquaria. Our stocking larval density treatments, 0.05–0.2 larvae ml^{-1}, were chosen to reflect a range of coral larvae densities reported in spawning slicks either at the center of the slick or a few meters away (roughly 0.230–0.009 larvae ml^{-1}; Oliver & Willis 1987). While the densities used here are comparable to those in slicks, it is unlikely that these densities are maintained as larvae disperse towards the substrate. Yet such realistic estimates are currently unknown. Replicate containers were assigned to 1 of 12 positions in each aquarium following an incomplete Latin squares randomized block experimental design (Cochran & Cox 1992); each aquarium was then randomly assigned to 1 of 4 large outdoor raceways (Fig. 1). Each aquarium received constant flow-through seawater at a rate of approximately 5–7 l min^{-1}, except for short periods (1–2 h) during the new moon afternoon spring low tides from 26–30 April. However, 2 aeration lines per aquaria provided some water movement and oxygen exchange during these periods. The replicate containers were 1 l cylindrical plastic bottles (180 mm height × 85 mm diameter) with two 40 mm diameter holes cut out at approximately mid-height with a 63 µm mesh cover to allow water exchange. Each container held approximately 900 ml of seawater, and when placed in the aquaria, seawater could move in and out of the containers through the 63 µm mesh holes. A single limestone settlement tile (dimensions: 5 × 5 × 1.2 cm) with a 1 cm hole drilled into the center was haphazardly sampled from holding raceways and placed in each of the settlement containers, elevated slightly off the bottom by a cable tie placed through the center hole. All limestone settlement tiles had been conditioned on a local reef for 2 mo to acquire crustose coralline algae (CCA) and microbial films that act as larval settlement cues (Hadfield & Paul 2001). Both the tile conditioning site (10 km south from the adult collection site) and adult collection site were back-reef zones adjacent to a barrier, outer reef and had similar coral assemblages (both *A. digitifera* and *A. gemmifera* abundant). Prior to use, large benthic organisms (e.g. sponges, bryozoans) and excess filamentous or macro-algae were removed from the settlement tiles using gentle scrubbing or tweezers. The final substrate of conditioned settlement tiles included a mixture of CCA, biofilms, and bare substrate; some tiles had small branches of filamentous algae and encrusting bryozoans. Settlement tiles were haphazardly allocated to treatments among species. Replicate containers, each with a single settlement tile, were placed into their respective aquaria and left in running flow-through seawater adult treatments (described below) for 12 h prior to starting the experiment, at which point they were stocked with one of the 4 larval densities (10, 50, 100, 200).

For the adult treatments, water flowed either past an adult colony into the experimental aquaria holding containers, or not. In the 'adult-absent' treatment, flow-through seawater entered aquaria from one end and exited the other, ensuring constant exchange of seawater. For aquaria with the 'adult-present' treatment, flow-through seawater first ran through a 15 l bucket with an aeration stone containing the conspecific adult (Fig. 1) and then flowed into the aquaria holding the containers. All inlet tubes were covered with a 125 µm mesh bag to stop sediment and other debris and were cleaned daily. The adult-present treatment represents species interactions between adults and early life stages, mediated by adult-induced microbes, metabolites, or allelochemicals in the water (Fearon & Cameron 1997, Brown & Bythell 2005, Ochsenkühn et al. 2018, Dunphy et al. 2019). A small colony of approximately 15–20 cm diameter or 2 fragments from the same colony each of approximately 10 cm diameter were used in the *A. gemmifera* adult treatments. For the *A. spinosa* adult treatment, several branches were collected since the collection of whole colonies was not possible due to their morphology (forming large, interconnected stands) and fragility. Multiple 10–15 cm long branches were affixed to a cement disc using marine epoxy and left to recover in flow-through aquaria for 3 d prior to experiments. Two clusters of *A. spinosa* of approximately 10 cm diameter each were placed into each adult treatment bucket. Adults were put in the buckets with flow-through seawater 24 h prior to the start of the experiment.

To account for possible spatial variability in environmental factors for each aquarium within and across raceways, 'aquaria' was included as a random effect in each model (see full model terms below). However, seawater temperature and light intensity were monitored with HOBO data loggers for 4 d in 6 haphazardly selected aquaria (so loggers were not randomly clustered in the same location) across raceways at the end of the experiment. We used daily average seawater temperatures for analysis and maximum midday seawater temperature values for visualization. Seawater temperatures in aquaria averaged (±SE) 29.6 ± 0.19°C and did not vary significantly among aquaria (Kruskal-Wallis ANOVA, $\chi^2 = 0.37$, df = 5, p = 0.99; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m720p039_supp.pdf). The seawater temperatures recorded here reflected local Airai reef sea surface temperatures during the month of April 2017 (29.1 ± 0.09; Chao et al. 2009) and the ranges were also within those reported from field sensors on Palauan eastern outer fringing reefs during the same period (Gouezo et al. 2020). The outdoor raceway area was covered by a large, elevated shade cloth. Furthermore, each raceway was covered with a strip of elevated tarpaulin (the same width as the raceway) to protect aquaria from direct rainfall inundation during frequently occurring tropical storms. Only daylight hours were kept in the light data for analysis (hours after sunset and before sunrise were removed), and maximum midday light values were extracted for visualization. Over 4 d and across all aquaria, the loggers recorded a daily average (±SE) of 1733 ± 104 lux. These low light levels were due to persistently high cloud cover across the monitored days. There was a significant difference in light lux between aquaria (ANOVA, $F = 3.5$, df = 5, p = 0.02); however, this was only between aquarium 22 (highest lux value) and aquaria 6 and 12 (lowest lux values). The average maximum midday light intensity was 2750.49 ± 328 lux, and among aquaria, significant differences in lux values seem to be evident at this time of day (see Fig. S1). While the light (lux) differences measured by the HOBO loggers varied consistently for 4 d across these 3 aquaria (and possibly others) during the experiment, the experiment had a fully randomized and crossed set of larval densities within each tub, and replicates were randomized across raceways.

2.2.2. Settlement analyses

Potential settler spatial bias of coral larvae to a specific tile orientation (top, bottom, sides) was assessed prior to modelling spatial patterns across the entire tile surface by running species-level linear regressions with log density (number settled/tile orientation area) as the response variable and tile orientation as the predictor variable. All 4 side orientations were grouped together. Data from both adult treatments were included for *A. spinosa* and *A. gemmifera* (not for *A. digitifera*). We used diagnostic plots to distinguish the distribution of the tile orientation data set the 'vcd' package (Meyer et al. 2017) and checked to confirm the data met the assumptions for a Gaussian linear regression.

We tested whether larval density influenced settlement success for the 3 coral species and whether the presence of a conspecific adult altered settlement success for *A. gemmifera* and *A. spinosa*. The adult-absent treatment served as the control for adult-present treatment. For *A. spinosa*, we had insufficient larvae for a fully replicated experimental design, so the number of replicate containers per larval density were reduced for the adult-present treatment and evenly spread across the 3 aquaria (replication of containers across aquaria: 2 for 10, 50 and 100 [total: 6 for each density]; 1 for 200 [total: 3]). A coral larva was considered a 'settler' as soon as it had attached to the settlement substrate and metamorphosed into the primary polyp stage. Settlement was scored (number of successful settlers versus number unsettled) 4 d after larvae were added to the containers. Settlers were counted visually on all tile orientations (top, bottom and sides) using a dissection microscope and mapped onto a photographic image of each tile surface using Adobe Illustrator version 19.0 (Adobe Systems Incorporated 2015).

For *A. gemmifera* and *A. spinosa*, the effect of larval density and adult presence on the probability of settlement success was examined with species-level binomial generalised linear mixed effects models (GLMMs, 'lme4' package; Bates et al. 2015). Probability of settlement (success: 1; failure: 0; per tile) was tested against categorical predictors larval density (4 levels: 10, 50, 100 and 200) and adult presence (2 levels: absent or present). To avoid fitting overly complex models (Matuschek et al. 2017), we compared various levels of random effect structures between models using Akaike information criterion scores corrected for small sample sizes (AICc), using a minimum threshold of 2 ('MuMIn' package; Bartoń 2018). However, we accounted for the non-independence of the experimental design by maintaining the minimum random effect structure, with tile replicate nested in aquaria. As a result, the model for *A. spinosa* and *A. gemmifera* was fit with tile nested in aquaria as a random effect (raceway did not explain any variance and thus was not included as a model term). For *A. digitifera*, the effect of larval density (no adult treatment) on the probability of settlement was evaluated using a binomial GLMM with tile nested in aquaria, and aquaria nested in raceway as the random intercept. Additive and interactive models were compared and the best-fit model was selected using AICc (Bartoń 2018). Model overdispersion and normality of residuals were checked to meet assumptions, and the variance explained by the model was estimated using conditional R-squared (cR^2) values ('DHARMa' package; Hartig 2019). ANOVA tables were produced to check main effects ('car' package; Fox & Sanford 2011). For significant main effects, Tukey pairwise comparisons were run ('emmeans' package; Lenth 2020), and for significant interaction effects, we used Bonferroni-adjusted post hoc tests ('lsmeans' package; Lenth 2016). Main effects are presented here, with further model summary tables and pairwise comparisons provided in the Supplement. All data analyses were conducted in R (R Core Team 2017) and graphs were produced using the package 'ggplot2' (Wickham 2016).

2.2.3. Post-settlement survival analyses

We investigated the effect of initial number of settlers on post-settlement survival for all 3 species. While experiments were planned to test the combined effects of settler densities and adult treatments on settler survival, this could only be examined for *A. spinosa*, as settlement success for *A. gemmifera* with the adult-present treatment was too low for further survival analysis. After settlement was scored, the tiles were placed back into their respective aquaria on elevated plastic crates with at least 1 cm between each tile, again elevated off the bottom by the cable tie in the center hole. Survival was scored weekly for 2 time points: 7 d and 14 d post settlement; settlement represented Day 0. At each time point, survived settlers were annotated with colored dots on the photographic image overlays produced at settlement, with a unique color assigned for each time point. In a few instances, new settlers were found at 7 d, after which the image from scoring settlement was reviewed, and only if the settler could be observed in the image was it post-corrected for settlement and included in the survival scoring. For *A. digitifera* and *A. gemmifera*, the effect of number of settlers (continuous predictor) on the probability of survival (to 14 d) was assessed with a binomial GLMM, with random intercept tile nested in aquaria. For *A. spinosa*, a binomial GLMM was used to evaluate the probability of survival against the number of settlers (continuous) and adult presence (absent or present) as fixed predictors, with random intercepts fitted for tile nested in aquaria.

Survival over time was evaluated with species-level binomial GLMMs. Survivorship between time points was recorded relative to the previous time step (e.g. 7 d from settlement). For both *Acropora* species, the response variable was survival (success versus failure), the fixed effect was time point (7 and 14 d), and random intercepts were fitted for tile nested in aquaria. For *A. spinosa*, a binomial GLMM was used to test probability of survival against time point (7 and 14 d) and adult presence (absent or present) as fixed effects, and random intercepts were fit for tile nested in aquaria. For all survival analyses, the best-fit model was identified, overdispersion and normality of residuals checked, variance explained by the model estimated, ANOVA tables produced, and post-hoc comparisons for significant interactions run as described in the settlement analyses.

2.2.4. Spatial analyses

Settler spatial patterns were analysed considering the whole 3-dimensional surface of the tile. Each tile had a total surface area of 67.72 cm^2 (excluding the 1 cm center hole). The nearest neighbor distance (NND) was calculated between settlers across the entire 3-dimensional tile surface, allowing for distances to travel through the central hole of the tile (R scripts; Sims & Staples 2020). The Clarke and Evans (CE) index (Clark & Evans 1954) was then used to determine spatial patterns of settler distributions on each of the tiles. The CE index accounts for differences in settler density (Aguirre et al. 2013), thus allowing comparisons between tiles with varying settler densities. The CE index ranges between $R = 0$ (maximum under-dispersion), where all settlers would overlap at the same position, and $R = 2.15$ (maximum inhibition), where all settlers are evenly distributed at their maximal distance from one another, whereas $R = 1$ indicates a random distribution (Clark & Evans 1954). Tiles with less than 5 recruits at 14 d were removed from analyses to avoid biased significance tests (Donnelly 1978, Sinclair 1985) and to ensure reliable spatial pattern estimates, since a single settler's location has a high power to change the spatial patterns with a limited number of recruits.

For the adult-absent data set (*A. digitifera*, *A. gemmifera* and *A. spinosa*), the settler spatial patterns of all species were examined using a linear regression (histogram and *Q–Q* norm plots indicated normality of the data), with the CE index values as the response variable (continuous); fixed effects included number of settlers (continuous) and species. In addition, temporal changes in settler spatial patterns were examined with a linear mixed effects model (LMM, 'lme4' package; Bates et al. 2015). The CE index values were included as the response variable (continuous), experimental time point (settlement, 7 and 14 d) and species were added as fixed effects, and random intercepts were fit for tile nested in aquaria. For *A. spinosa*, additional, separate models were run as above, with the addition of adult (absent or present) as a fixed effect and tile nested in aquaria as random effect.

Even though the CE index gives an indication of dispersion, it does not provide an estimate of settler aggregations (i.e. whether settlers are in direct contact with each other). Therefore, we also ran species-level binomial GLMMs with the probability of forming aggregates (1: settler touching; 0: settler not touching) against the number of settlers (continuous) and time (7 and 14 d) as fixed effects with tile nested in aquaria as a random intercept. The influence of adult presence was tested by including this as a categorical predictor (absent or present) in a model for *A. spinosa* only. A settler was considered touching another settler when at least tissue margins were touching. For all spatial analyses, the best-fit model was selected, assumptions were checked, ANOVA tables produced, and Tukey pairwise comparisons run as detailed above for the settlement analyses.

3. RESULTS

3.1. Settlement

For all 3 species, larvae had a significant preference for tile surface orientation (*Anacropora spinosa*: $F_{2,182} = 16.36$, $p < 0.001$; *Acropora gemmifera*: $F_{2,141} = 12.13$, $p < 0.001$; *Acropora digitifera*: $F_{2,151} = 15.76$, $p < 0.001$). Larval settlement was highest on the top and bottom orientations of tiles and was lowest on the sides for *A. spinosa* and *A. gemmifera*, while *A. digitifera* showed a preference for the top, then bottom, and lastly side orientations (Fig. 2A–C). As settlement was common on both the top and bottom orientations, and not just to one orientation, this outcome provided support for using the whole 3-dimensional surface of the tile to examine spatial patterns (see Section 3.3).

Larval settlement in the presence of a conspecific adult was significantly reduced for both *A. spinosa*

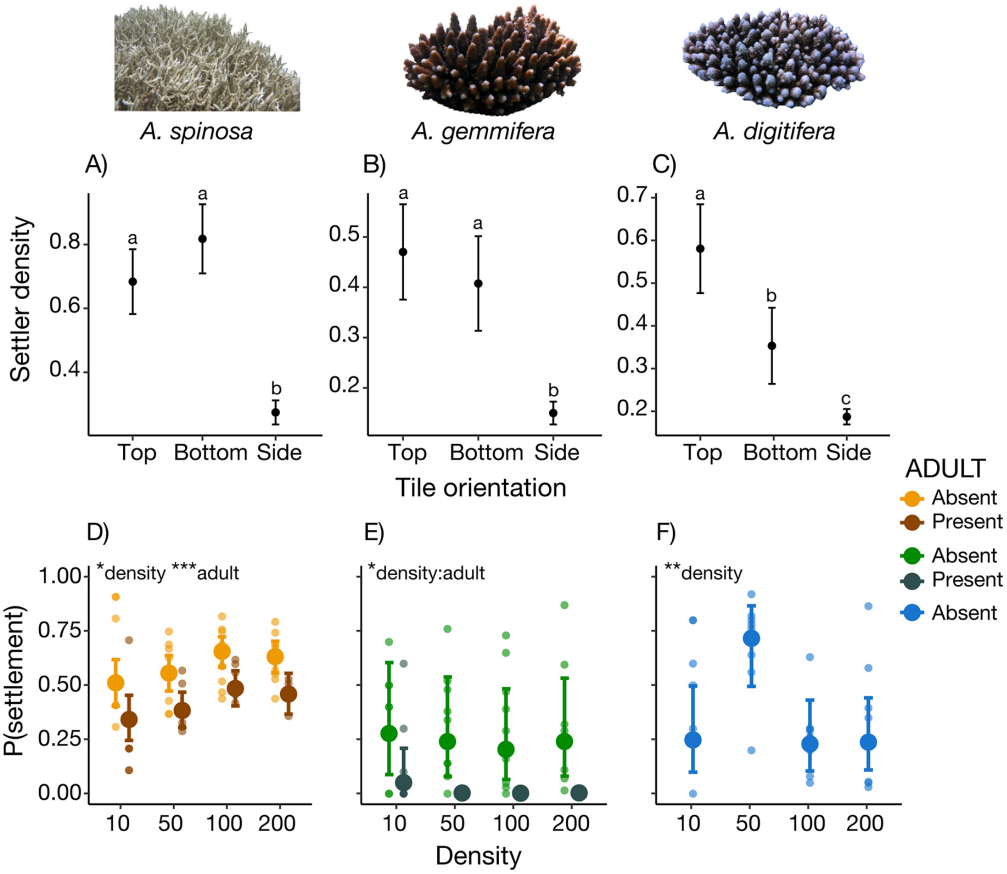

Fig. 2. Mean (±SE) density of coral settlers (number/orientation area) by tile orientation for (A) *Anacropora spinosa*, (B) *Acropora gemmifera* and (C) *Acropora digitifera* (different lowercase letters denote significant differences between groups). All 4 side orientations were grouped together. Probability of settlement (mean ± 95% CI) of coral larvae by stocking density and adult treatments (absent or present) for (D) *A. spinosa* and (E) *A. gemmifera*, and by stocking density for (F) *A. digitifera*. Individual data points are raw proportions of settlement success. $^{*}p < 0.05$; $^{**}p < 0.001$; $^{***}p < 0.0001$

Table 1. ANOVA summary of species-level generalised linear mixed effect models (GLMM) testing the influence of larval stocking density and adult conspecific presence on larval settlement (Type II Wald test). Significant p-values ($p < 0.05$) are in *italics*

Model	Fixed effect	χ^2	df	p
Anacropora spinosa	Density	8.884	3	*0.0309*
	Adult	20.439	1	*<0.0001*
Acropora gemmifera	Density	8.5276	3	*0.0363*
	Adult	21.304	1	*<0.0001*
	Density × Adult	9.2558	3	*0.0261*
Acropora digitifera	Density	15.990	3	*0.0011*

($cR^2 = 0.89$; Table 1) and *A. gemmifera* ($cR^2 = 0.99$; Table 1). For *A. spinosa*, larvae had a 33% lower chance of settling when an adult was present (averaged over all tested densities). While the probability of settlement for *A. spinosa* showed a positive trend with larval density (Fig. 2D), no significant pairwise comparisons (averaged over adult treatments) were identified. For *A. gemmifera*, a significant interaction between adult treatment and larval density was observed at 3 (50, 100, 200) of the 4 stocking levels (Fig. 2E, Table 1). For *A. digitifera*, with no adult treatments, there was a significant difference in settlement probability by larval density ($cR^2 = 0.98$; Table 1). Optimal settlement was identified at a stocking density of 50 larvae (0.717 ± 95%, CI = 0.50–0.87), where larvae had a greater than 2-fold increased chance of settling compared to the average settlement probability (0.24 ± 95%, CI = 0.10–0.46) of the other 3 densities (Fig. 2F).

3.2. Post-settlement survival

Survival up to 14 d post-settlement was high for *A. spinosa* settlers (Fig. 3A), both in the adult-absent (0.91 ± 95%, CI = 0.87–0.93) and adult-present (0.87 ± 95%, CI = 0.80–0.91) treatments. There was no significant difference in survival probability

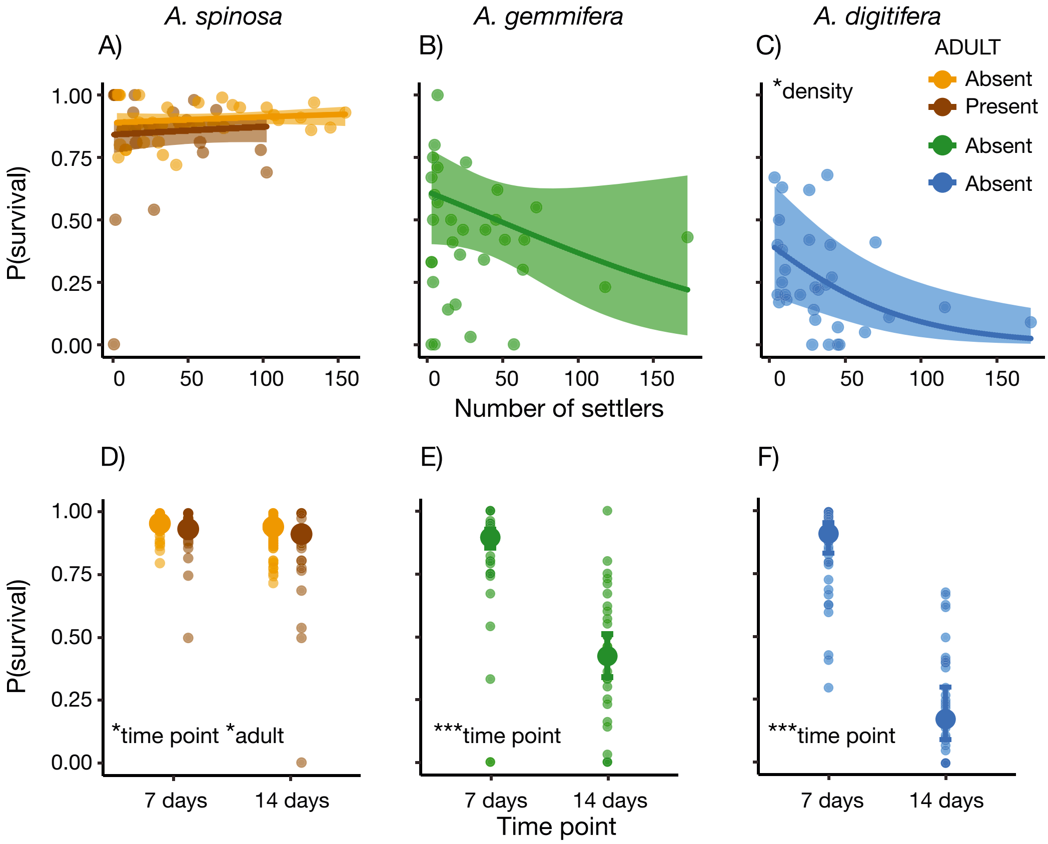

Fig. 3. Probability of post-settlement survival to 14 d (mean ± 95% CI) by the number of settlers and adult treatments for (A) *Anacropora spinosa*, and number of settlers for (B) *Acropora gemmifera* and (C) *Acropora digitifera*. Probability of settled survivors (mean ± 95% CI) over experimental time point and adult treatments (absent or present) for (D) *A. spinosa*, and over experimental time point for (E) *A. gemmifera* and (F) *A. digitifera*. Individual data points are raw proportions of survival success. *$p < 0.05$; **$p < 0.001$; ***$p < 0.0001$

Table 2. ANOVA summary of species-level generalised linear mixed effect models testing settler survival in relation to the number of initial settlers and survival over time points (Type II Wald test). Significant p-values ($p < 0.05$) are in *italics*. All analyses were run in the absence of a conspecific adult with the exception of *Anacropora spinosa*, which had an adult-absent and adult-present treatment

Model		Fixed effect	χ^2	df	p
Survival	*Anacropora spinosa*	Number settlers	0.8743	1	0.3497
		Adult	2.9241	1	0.0873
	Acropora gemmifera	Number settlers	0.5496	1	0.4585
	Acropora digitifera	Number settlers	8.2122	1	*0.0042*
Survival	*Anacropora spinosa*	Time point	6.5343	1	*0.01058*
		Adult	4.0198	1	*0.04497*
	Acropora gemmifera	Time point	360.77	1	*<0.0001*
	Acropora digitifera	Time point	674.65	1	*<0.0001*

across adult treatments and no relationship between the number of settlers and survival for *A. spinosa* ($cR^2 = 0.68$; Table 2). The average survival probability of *A. gemmifera* was 0.34 ± 95% (CI = 0.20–0.54), and survival was also independent of settler number ($cR^2 = 0.89$; Table 2, Fig. 3B). By contrast, *A. digitifera* settlers (no adult treatment) displayed significant density-dependent survival ($cR^2 = 0.90$; Table 2), with higher survival probability when lower numbers of initial settlers were present (Fig. 3C).

All species showed significant differences in the probability of survival over time (Table 2). Survival over time for *A. spinosa* was relatively high compared to the 2 *Acropora* species (Fig. 3D–F). For *A. spinosa*, survival reduced over time and was influenced by adult presence, but the effects were small ($cR^2 = 0.53$; Fig. 3D), with survival probability decreasing from 7 to 14 d by 1.4% for the adult-absent treatment (0.96 ± 95%, CI = 0.95–0.97 and 0.95 ± 95%, CI = 0.93–0.96, respectively) and by 2.2% for the adult-present treatment (0.94 ± 95%, CI = 0.90–0.96 and 0.92 ± 95%, CI = 0.88–0.94, respectively). For both *A. gemmifera* and *A. digitifera*, the probability of survival decreased significantly with time (no data for adult treatment; Fig. 3E,F). Overall, the absolute percent decrease in survival probability from Day 7 to 14 was 52.9% for *A. gemmifera* (0.89 ± 95%, CI = 0.85–0.92 and 0.42 ± 95%, CI = 0.34–0.51, respectively) and 80.9% for *A. digitifera* (0.91 ± 95%, CI = 0.84–0.96 and 0.18 ± 95%, CI = 0.09–0.30, respectively).

3.3. Spatial distribution patterns

A total of 3881 settlers across 88 tiles were used for spatial analyses at settlement (adult-absent only; Table S1). The number of tiles excluded for each species (<5 settlers) for settlement spatial analyses was 4 (adult absent) for *A. spinosa*, 11 for *A. gemmifera* and 5 for *A. digitifera*. For the adult-absent treatment, all species showed a significant negative correlation between the CE index and the number of settlers (adjusted $R^2 = 0.37$; Table 3), with settlers becoming more under-dispersed (closer together than expected) as settler numbers increased (Fig. 4A). Settlers of *A. spinosa* were significantly more under-dispersed compared to those of both *Acropora* species (Table S2). Furthermore, 72% of the settlement tiles assessed across all 3 species indicated that larvae settled in under-dispersed spatial patterns (Table S1).

Across 62 tiles, a total of 2176 (7 d) and 2174 (14 d) settlers were analysed for post-settlement spatial pattern analyses over time (Table S3). The number of tiles excluded from spatial analyses at survival (<5 survivors), were 1 (adult absent) for *A. spinosa*, 7 for *A. gemmifera* and 17 for *A. digitifera*. Hence, this is a smaller data set than the full data set used for the survival over time analyses. There was a significant effect of both time and species on settler spatial patterns ($cR^2 = 0.86$; Table 4). We observed a significant decrease in the CE index values between settlement and Day 7, and between settlement and Day 14, but there was no difference between Days 7 and 14 (Table S4). These findings indicated that mortality within 1 wk post settlement led to increased under-dispersion of settlers (Fig. 4B). The percentage of tiles showing under-dispersed spatial patterns of

Table 3. ANOVA summary of linear model regressions for spatial pattern analyses of settlement trials that excluded an adult ('adult absent') and included all species (Fig. 3A), with species identity as a predictor. Additionally, the influence of adult presence was tested for *Anacropora spinosa* independently (Type II test). Significant p-values ($p < 0.05$) are in *italics*

Model	Fixed effect	SS	df	*F*	p
Adult absent	Number settled	0.4224	1	12.569	*0.0006*
	Species	1.0040	2	14.939	*<0.0001*
Adult presence (absent or present)	Number settled	0.1078	1	8.1493	*0.0065*
	Adult	0.0058	1	0.4368	0.5120

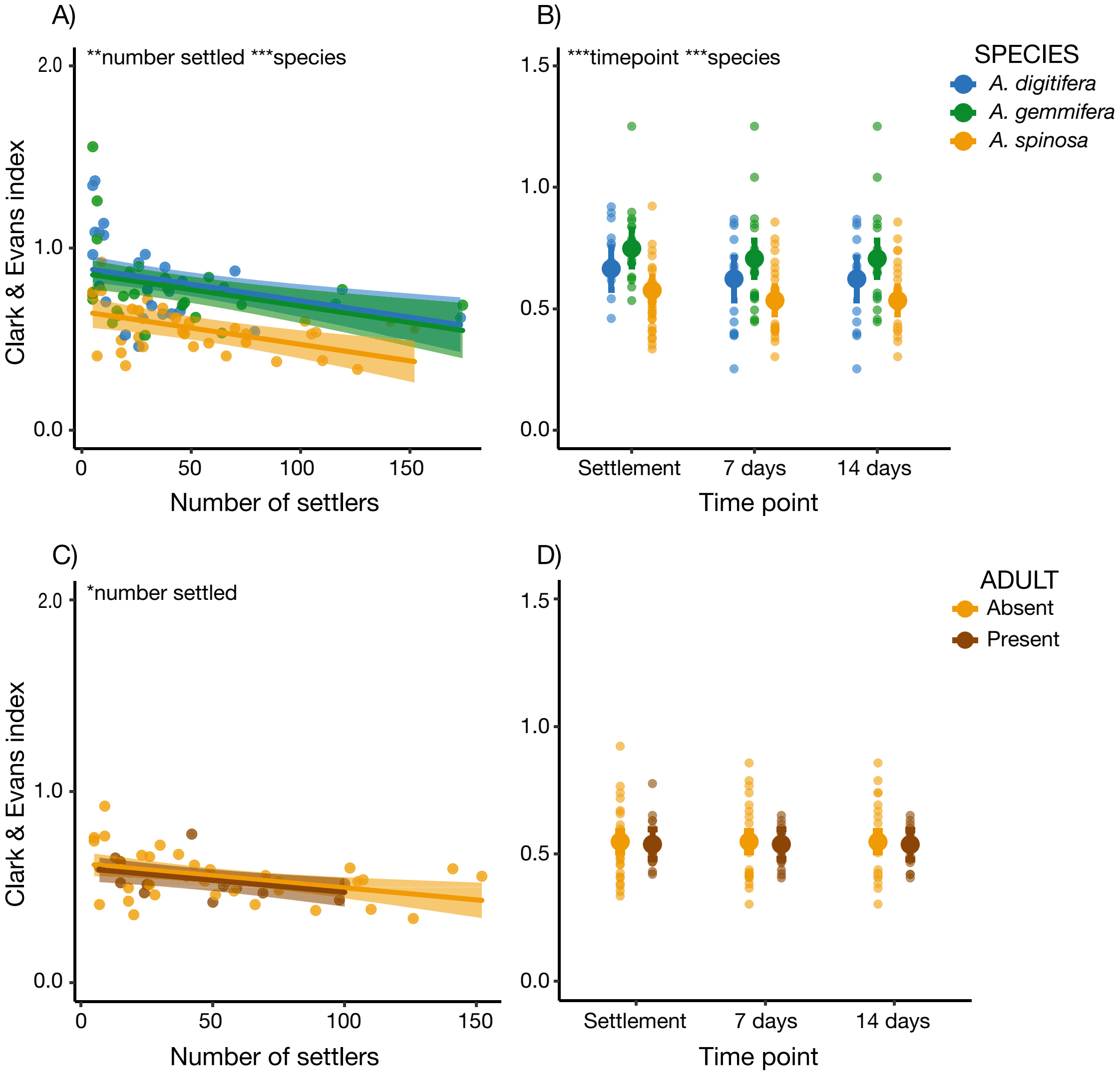

Fig. 4. Settler spatial patterns at settlement and post-settlement survival (7 and 14 d). Linear regression of Clark and Evans (CE) index by number of settlers for (A) all 3 species (*Anacropora spinosa*, *Acropora gemmifera* and *Acropora digitifera*) and (C) *A. spinosa* by adult treatments at settlement. Linear mixed effects model of CE index over experimental time points for (B) all 3 species and (D) *A. spinosa* by adult treatments. Individual data points represent raw CE index values (0.0 = maximum under-dispersion; 1.0 = random; 2.15 = maximum inhibition). *p < 0.05; **p < 0.001; ***p < 0.0001

settlers was 74 % for both Day 7 and Day 14 across all 3 species (Table S3).

Table 4. Linear mixed effect models for spatial pattern analyses at survival over time points for adult absent (included all species) and adult present (only *Anacropora spinosa* included) (Type II Wald test). Significant p-values ($p < 0.05$) are in *italics*

Model	Fixed effect	χ^2	df	p
Adult absent	Time point	15.806	2	*0.0004*
	Species	14.047	2	*0.0009*
Adult presence (absent or present)	Time point	0.0131	2	0.9935
	Adult	0.0890	1	0.7654

To test whether adult presence influenced spatial patterns, a total of 47 tiles of *A. spinosa* were used (only species with data for this treatment test), with 5 tiles removed because they each had less than 5 settlers on them (adult-present only tiles; Tables S5 & S6). No differences were seen in settler spatial patterns between adult treatments (adjusted $R^2 = 0.12$; Fig. 4C, Table 3). Additionally, the spatial patterns analysed over the time points showed consistent CE index values over time (Fig. 4D) and no effect of adult treatment ($cR^2 = 0.90$; Table 4). All adult-present settlement tiles had under-dispersed settler spatial patterns at every time point (Tables S5 & S6).

Finally, we tested the degree to which settlers were in direct contact with other settlers, thereby forming an aggregation. We found that settlers were more frequently found in aggregations as the number of settlers increased for *A. spinosa* (cR^2 = 0.88, χ^2 = 33.97, n =114, $p < 0.0001$) and *A. digitifera* (cR^2 = 0.71, χ^2 = 11.09, n = 72, $p < 0.001$), with a similar but marginally non-significant trend for *A. gemmifera* (cR^2 = 0.54, χ^2 = 3.24, n = 72, p = 0.07; Table S7, Fig. 5). The level of aggregation did not change over time for all 3 species, nor did adult presence for *A. spinosa* have an effect (Table S7).

4. DISCUSSION

An underlying theme in ecology is to identify patterns through the study of ecological processes across species. Only by expanding studies across taxa and biogeographical space are we able to discover which components of early life stage processes and interactions are driven by inherited traits, local environments, and communities. Few studies have specifically investigated conspecific density dependence during the early life stages in corals (main studies we are aware of are Vermeij & Sandin 2008, Marhaver et al. 2013, Edwards et al. 2015, Doropoulos et al. 2017, 2018, Cameron & Harrison 2020, Sims et al. 2021). Data from these studies represent 11 coral species spread across few locations (Florida Keys, Curacao, Palau, Coral Bay, Philippines, and Great Barrier Reef) and ocean basins (Caribbean Sea, Indian Ocean, and Pacific Ocean). These coral species not only have very distinct lifestyles and traits but are also characterized by markedly different geological and evolutionary histories. With several hundred coral species in existence, this clearly indicates a paucity of global data. Our data provides information on 2 new coral species (*Acropora gemmifera* and *Anacropora spinosa*), and 1 that was previously studied (*Acropora digitifera*), at the same location (Palau; Edwards et al. 2015) and elsewhere (Coral Bay; Doropoulos et al. 2018).

Here, we found species-specific settlement and survival patterns. Larval settlement was either positively correlated with larval densities (*A. spinosa*), unaffected by larval densities (*A. gemmifera*), or showed an optimal larval density for settlement (*A. digitifera*). Higher settler numbers also led to reduced survivorship for *A. digitifera* but had no influence on survival of the other 2 species. Despite the differences in density-dependent settlement and survival between species, all coral species displayed similar settler spatial patterns, with settlers becoming more under-dispersed and the probability of aggregates forming increasing as settler number increased. These findings suggest that facilitation among larvae and recent settlers may be occurring. Yet the coral species examined here were limited at settlement by conspecific adult water treatments. Within cohorts, the *Acropora* displayed self-limiting post-settlement survival (decreased survival at higher settler densities), while *A. spinosa* settlers were predominantly self-facilitative, with high settlement and survival as well as a higher degree of under-dispersion at higher settlement densities.

4.1. Settlement patterns

Coral larval settlement success has the propensity to be highly stochastic both across and within species. Repeated experiments on the same species have yielded contrasting results of inverse density-dependence versus density-independent settlement over consecutive years (Doropoulos et al. 2017, 2018). A recent investigation revealed density-independent settlement for 6 broadcast-spawning, scleractinian coral species from the southern Great Barrier Reef (Sims et al. 2021). Here, we found the influence of

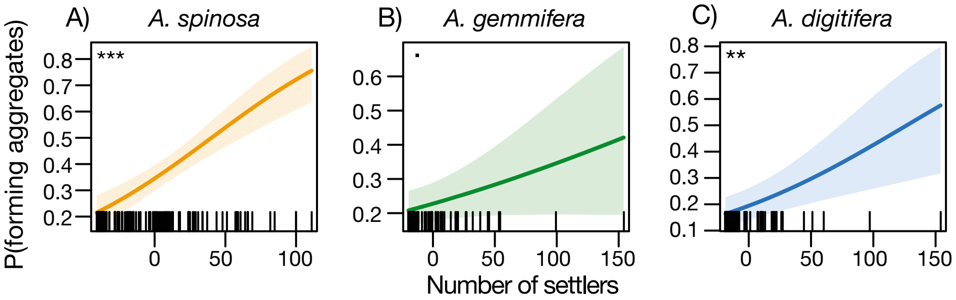

Fig. 5. Predictor effect plots (predicted means ± 95% CI) from the aggregation generalised linear mixed effects models of the probability of settlers touching by number of settlers for (A) *Anacropora spinosa*, (B) *Acropora gemmifera* and (C) *Acropora digitifera*. **$p < 0.001$; ***$p < 0.0001$; (·) marginally non-significant (0.07)

density on settlement success to be distinct across the 3 species examined. While larval density did not lead to a linear increase in settlement success, *A. digitifera* larvae showed a 2-fold increase in the probability of settlement success at a mid-level stocking density (50 larvae) compared to the average settlement probability across the other 3 density treatment levels. This may be an optimal larval stocking density for this species, as another study using *A. digitifera* found a high probability of settlement success at a similar stocking density compared to lower densities (Doropoulos et al. 2018). The positive settlement trend with increasing larval density found in *A. spinosa* is a common pattern noted in other coral species (Doropoulos et al. 2017, 2018). *A. spinosa* larvae also had an overall higher settlement success than both *Acropora* species (Fig. 2D–F). The gamete bundles of *A. spinosa* were neutrally buoyant, which favors reduced dispersal distances (Black 1993) relative to positively buoyant bundles as found in both *Acropora* species. Additionally, the relatively small and rapidly developing larvae of *A. spinosa* (~2 d) reach competency (i.e. ability to settle) faster than species with larger larvae (Figueiredo et al. 2013). Both neutral buoyancy and small size are likely linked to a higher degree of local larval retention and promote high-density settlement of conspecifics close to natal sources in this species, promoting the formation of dense thickets.

Cues from conspecific early life stages are likely important drivers of settlement site selection, and this is consistent with recent experimental studies that found aggregated patterns of conspecific settlers (Doropoulos et al. 2017, Sampayo et al. 2020, Sims et al. 2021) and 2 recent field studies identifying co-recruitment of siblings (Barfield et al. preprint https://doi.org/10.1101/2020.02.26.956680, Dubé et al. 2020). Here, we also found that settlers of all 3 examined coral species were closer to each other than expected from random settlement, and this response was strongest in *A. spinosa* (Fig. 4A,B). A rich literature for a variety of other marine sessile invertebrates indicates that conspecific chemical cues are likely candidates underlying larval settlement preferences and success (Pawlik 1992, Hadfield & Paul 2001). Certain species of CCA are known to induce settlement and metamorphosis of specific coral species, and larvae actively seek out particular species of CCA (Heyward & Negri 1999, Harrington et al. 2004). However, the spatial heterogeneity of CCA on surfaces, such as our tiles, does not necessarily drive settler aggregation, as we observed that individuals and aggregates of coral larvae settled on, near, and away from CCA, a result consistent with findings from other studies (Szmant & Miller 2006, Elmer et al. 2018, Davidson et al. 2019, Sampayo et al. 2020). Repeated findings of gregarious settlement behaviour, irrespective of coral species, suggests that larval or metamorphosing stages might act as strong attractants to conspecific larva. Cascading effects might occur as higher settler densities are related to increased formation of aggregates (Fig. 5). At lower settler densities, reduction in settler under-dispersion (more random spatial patterns) and probability of forming an aggregate (not touching) suggests that cues to settle gregariously may be diluted. Density-dependent social cues that influence settlement have been illustrated in other species such as birds (Fletcher 2007) and crabs (Donahue 2006). Social cues derived from other settlers, or juveniles, highlight that there are likely benefits associated with positive interactions amongst conspecifics, such as Allee effects or signaling of suitable habitat (Bertness & Callaway 1994, Stachowicz 2001, Donahue 2006). Therefore, settling in conspecific groups must provide some fitness gain that outweighs costs (e.g. competition for resources) at this life stage (Bruno et al. 2003, Donahue 2006, Doropoulos et al. 2012, Rinkevich 2019).

Given the behavioural capabilities of coral larvae, their responses to diverse cues (e.g. chemical or physical) lead to strong substrate preferences and influence settlement processes (Harrison & Wallace 1990). In our study, settlement probability was significantly reduced when a conspecific adult was present for 2 of the study species in which this was examined (*A. gemmifera*, *A. spinosa*; Fig. 2D,E). Such larval–adult effects could be mediated by a waterborne agent that is of adult origin and acts to suppress settlement success. While we did not attempt to define the source of adult waterborne factors, several other studies have also found that cues from established corals influence settlement success (Pawlik 1992, Fearon & Cameron 1997, Marhaver et al. 2013). For example, highly diverse and typically species-specific (Littman et al. 2009) coral adult microbial communities, along with their mucous coating, can be shed into the surrounding water column (Brown & Bythell 2005) and are able to negatively affect recent coral settlers (Marhaver et al. 2013). Adult corals also possess strong allelochemicals (Gunthorpe & Cameron 1990) that can be fatal to early life history stages (Fearon & Cameron 1997). Adult waterborne effects may deter and ultimately reduce conspecific larvae from settling near established colonies to reduce competition (Jackson & Buss 1975) or exposure to natural enemies, such as predators or pathogens (Janzen 1970, Connell 1971).

Reduced settlement may be attributed to behavioural responses of larvae that actively move away from surfaces or corals that exude particular allelochemicals (Hadfield & Paul 2001) or contain microbial components (e.g. bacteria and pathogens; Brown & Bythell 2005). Whether such adult-induced effects are species-specific or a general response of early life stages and whether potential species-specific water-mediated mechanisms occur remain intriguing questions deserving further investigation.

Some indications exist that the response differs between con- and hetero-specific larval–adult interactions. Marhaver et al. (2013) found that survival of *Orbicella faveolata* (previously *Montastrea*) larvae decreased when they were exposed to water collected next to a conspecific adult compared to water near heterospecific adults or open water. In the same body of work, larval survivorship was improved when conspecific adult water was treated with antibiotics or filter-sterilized, suggesting that adult pathogens were the primary mechanism. However, the vast majority of studies have examined conspecifics only. Larvae of a brooding coral species, *Siderastrea radians*, were found to increase settlement near adult conspecifics, with settlement choice linked to habitat suitability and adult proximity and density (Vermeij 2005, Vermeij & Sandin 2008). Brooding coral species release competent larvae that are ready to settle (Harrison & Wallace 1990) and typically have higher local retention compared to corals that spawn their gametes into the water column (Ayre & Hughes 2000). Interestingly, the survival of the brooded settlers increased with the distance from conspecific adults, indicating that adults subsequently had a negative influence on settler survival (Vermeij 2005). Similarly, the presence of conspecific adults reduced post-settlement survival, but not settlement, in 6 broadcast-spawning coral species (across 4 genera) from the southern Great Barrier Reef (Sims et al. 2021). Thus, while negative effects on settlement or survival from nearby conspecific adults seem pervasive across species, the life history stage at which the influence occurs may differ, with the direction or intensity of these early life history dynamics changing over life stages (as observed here from settlement to post-settlement survival).

4.2. Post-settlement survival patterns

Long-term studies examining settler survival in the field provide some evidence for density-dependent post-settlement survival in corals over months (Suzuki et al. 2012, Edwards et al. 2015, Doropoulos et al. 2017, Cameron & Harrison 2020). There is need, however, for shorter-term observations to capture survivorship and bottlenecks that occur immediately post settlement. Despite being in an experimental setting, we identified that immediate post-settlement survival was density-independent for both *A. spinosa* and *A. gemmifera* (Fig. 3A,B). *A. spinosa* settlers had a higher probability of survival (Fig. 3A) and were more under-dispersed (Fig. 4A) than those of both *Acropora* species, and the effect of adult presence on survival or spatial settler patterns was minimal (Figs. 3D & 4C,D). *A. spinosa* is one of few broadcast-spawning coral species that vertically transmits zooxanthellae in their eggs (Baird et al. 2009), with both larvae and recent settlers observed as visibly pigmented in this study. Vertical transmission has been linked to increased larval survival, settlement and post-settlement survival (Harii et al. 2002, 2010, Ritson-Williams et al. 2016). However, defining whether survival is linked to larval size or symbiont presence is problematic. Larvae containing zooxanthellae from broadcast spawners have fewer maternally provisioned resources and are relatively small (Gutierrez-Isaza et al. 2023), as is the case with *A. spinosa*. In contrast, brooding species with vertical transmission generally produce larger larvae with high energy stores (Harii et al. 2010). Our findings here, of small broadcast-spawned larvae with high settlement and post-settlement survival, suggests a role of the symbionts in early life stage success. Nonetheless, high settlement densities will likely lead to strong density-dependence at later stages (Doropoulos et al. 2017, Cameron & Harrison 2020).

Density-dependent post-settlement survival of *A. digitifera* settlers was previously found in a Palau-based field study examining mass larval seeding techniques for restoration (Edwards et al. 2015). Even with the exclusion of external factors that drive recruit mortality, such as predation or competition with macroalgae (Penin et al. 2010, Doropoulos et al. 2016, 2017), we also found that in contrast to the other 2 species, *A. digitifera* settlers showed density-dependent post-settlement survival within a 2 wk period (Fig. 3C). The finding of density-dependent survival in *A. digitifera* was unlikely the result of intra-specific competition, since spatial analyses for both *Acropora* species indicated that mortality led to slightly greater under-dispersion of conspecific settlers (Fig. 4B). A similar relationship was also found in *A. millepora*, whereby gregarious settlement led to doubled survivorship compared to solitary settlers (Doropoulos et al. 2017). In these first few weeks of life, positive interactions amongst gregarious settlers may increase survivorship via benefits from space pre-emption, reduction of competition with other benthic fauna, or facilitation amongst individuals in colonial animals (Rinkevich 2004, Ritson-Williams et al. 2009, Edwards & Stachowicz 2011). Yet the spatial scale at which these events occurred was very small (mm to cm), and some aspects of the extent of clustering (e.g. large versus small clusters, distance between clusters and single settlers) cannot be determined from the spatial metrics applied (Clark & Evans 1954). Therefore, it may be that intraspecific competition does occur but at scales of 10s–100s of mm (between clusters and single settlers), and co-operation occurs at scales of <10s of mm (within clusters), leading to increased under-dispersed spatial patterns.

Post-settlement mortality was significantly greater in the second week (14 d) than the first week (7 d) for both *Acropora* species (Fig. 3E,F). Field studies of settlement and survival in a range of sessile benthic marine invertebrates (e.g. polychaetes, bivalves and ascidians) have found that mortality typically increases after the first week (Hurlbut 1991). Field-based studies aiming to estimate recruitment (cumulative outcome of settlement and post-settlement) leave settlement tiles out over several months (Price et al. 2019). Unfortunately, these timescales do not allow us to distinguish between settlement and post-settlement processes that lead to mortality. Furthermore, early life stage mortality may be driven by a multitude of direct and indirect factors or even be delayed to later stages due to latent effects. For example, stressors experienced by larvae during the dispersal stage may manifest at later stages and can lead to increased post-settlement mortality (Ross et al. 2013). Overall, studies on multiple species examining mortality patterns during these earlier life stages of corals will benefit our understanding of the drivers of recruitment limitation. At present, the timescales of most field studies are incompatible with determining whether shifts in recruitment are due to changes in reproductive output, habitat suitability/unsuitability, or shifts in signaling (e.g. allelochemicals or microbes) from the surrounding environment. Based on our results (Fig. 3D–F), if settlement tiles placed in the field are examined 1–2 wk after local spawning events (accounting for larval development and competency periods), we may be able to collate more relevant data on the drivers of settlement success prior to significant post-settlement mortality.

4.3. Conclusion

Determining the contribution of settlement and post-settlement processes that influence early life history demographic processes can improve our understanding of the ecological drivers of community dynamics. We found that early life history dynamics varied (facilitative or limiting) depending on the life history stage (settlement versus post-settlement survival) being investigated, highlighting the importance of examining interactions across multiple life stages (Figs. 2 & 3). Intra-cohort facilitation was evident amongst larvae and early settlers, and, for some species, the formation of aggregates may facilitate short-term survival by increasing the probability of settler survival. Our findings suggest that conspecific cueing amongst settling larval cohorts could be an important adaptive larval behaviour (Rinkevich 2004, Donahue 2006). As such, declines in coral recruitment in disturbed areas due to reductions in fecundity, fertilization success and, thus, sizes of larval cohorts (Hughes et al. 2019) may suffer further depensation effects due to a lack of conspecific or social cues (Figs. 2D–F, 4 & 5).

Adult coral colonies often exhibit spatial distribution patterns that are random to inhibited (even), which is indicative of self-limitation (Stimson 1974, Abel et al. 1983, Reichelt & Bradbury 1984, Endean et al. 1997, Edmunds et al. 2018, Pedersen et al. 2019). Therefore, density-dependent processes leading to mortality of individuals in aggregates may occur over longer time frames than investigated here, eventually leading to even distributions between more established colonies. However, larvae may also preferentially move and settle away from established conspecific colonies, developing spatial distribution patterns instead at the settlement period. In our experimental setting, larval settlement was consistently limited by conspecific adults (Fig. 2D,E), a finding supported by further *ex situ* and *in situ* experimental studies on a number of diverse coral species (Vermeij & Sandin 2008, Marhaver et al. 2013, Sims et al. 2021). These findings indicate that local coral population sizes may be reduced via conspecific density-dependent larval–adult effects, a process well known to be important for warranting further exploration of species coexistence mechanisms (Chesson 2000). Whether these processes indeed lead to increased diversity in the local community needs to be further examined by experiments that verify that negative conspecific interactions, as found here, are stronger than heterospecific interactions.

Data availability. Data for this paper are available at https://doi.org/10.5281/zenodo.8169392.

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