



Cost-effective coral settlement substrates for restoration, exports and research

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Abstract The sexual production of corals in aquaculture could increase the sustainability of coral restoration and export industries, particularly in developing countries where these industries predominantly rely on wild coral collections. Development of low-cost aquaculture facilities and coral settlement substrates is essential to encourage the uptake of these methods. Clay is widely available, easy and safe to use, and provides a low-cost option for coral settlement. The inclusion of non-toxic waste materials as additives in substrates to reduce costs may also promote coral settlement, given their combustion during firing creates pores and some coral taxa prefer to settle in crevices. Additives may also indirectly influence settlement via changes to the development of settlement-inducing biofilms during substrate conditioning. Here, we demonstrated the successful settlement of *Acropora millepora* larvae to substrates handmade from local clay (Kalimantan, Indonesia), to which three widely available cheap or free waste products were

added [(1) coconut charcoal, (2) grog (fired clay ground into a granular form), and (3) breadcrumbs] at three concentrations (5, 15, and 25%). No differences in coral settlement to substrates containing the three additives were detected, nor were there differences among substrates with different additive concentrations. Also, crustose coralline algae cover, a common coral settlement inducer, did not vary among substrates containing different additives or additive concentrations after 28 days conditioning. Further testing of these and other additives across a broader suite of coral species should be explored, given their potential to reduce substrate costs while maintaining coral settlement.

Keywords Coral larvae · Early life history stages · Aquarium trade · Coral collection · Export · Waste · Recycling

Introduction

Reef restoration by local communities and tourism operators, and the export of corals by the aquarium industry, are important sources of income for many developing countries with coral reefs (Razak et al. 2022; Bruckner and Borneman 2006). Reef tourism is worth US\$35.8 million globally and increasingly includes participation in restoration activities, particularly “coral gardening” (the collection or generation of coral fragments for out-planting to reefs) (Razak et al. 2022). In Indonesia alone, 533 restoration projects were initiated prior to 2022, generating over 1 million out-planted coral fragments, while one community-led coral gardening programme in Bali Province employed over 10,000 locals (Razak et al. 2022). Southeast Asia is also a world leader in coral exports, an industry valued at US\$10.70 million in 2016 (Bruckner and Borneman 2006). Bans on wild coral

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collections and exports, such as those previously implemented in Fiji and Indonesia that aimed at reducing impacts on increasingly degraded coral populations (Sosnowski et al. 2020), threaten the livelihoods of coral restoration and tourism operations, as well as coral collectors and exporters in these regions (Intyas et al. 2023). The potential for future coral collection and export bans highlights the importance of improving the sustainability of coral restoration and export industries, for the benefit of local reefs and communities (Rhyne et al. 2014).

The sexual production of corals in aquaculture facilities could supply both the coral restoration and export industries and reduce their reliance on wild coral collections, thus increasing their sustainability (Burke et al. 2011; Barton et al. 2017). Also, it is increasingly recognized that the maintenance of genetically diverse and resilient coral populations via restoration will require the use of sexual propagules, rather than the historically popular asexually produced fragments (Randall et al. 2020). The uptake of coral aquaculture in developing countries requires the establishment of low-cost infrastructure and methods, including cheap substrates to which sexually produced larvae are seeded. Clay substrates are inexpensive to produce from local clays and are currently being used by coral exporters in Bali, Indonesia, for the grow-out of attached coral fragments (pers. comm. Widiastuti). These same substrates are likely to be suitable for the settlement of sexually produced coral larvae, given previous studies have found a wide variety of substrates, including clay tiles, suitable for coral settlement (Harriott and Fisk 1987; Babcock and Mundy 1996; Pollock et al. 2017; Fong et al. 2024b).

The inclusion of combustible non-toxic waste products (e.g., charcoal, breadcrumbs, waste ceramics (grog), coconut husks, sawdust, etc.) as additives prior to firing is common practice in brick and ceramic filter manufacturing, to enhance mechanical and thermal insulating properties, but importantly to reduce costs and agricultural, industrial or manufacturing waste streams (Gitis and Rothenberg 2016; Dele-Afolabi et al. 2017; Mocciano et al. 2017; Moujoud et al. 2023). The combustion of additives during firing results in pores of varying sizes, shapes, and abundances in the fired clay, depending on the composition and concentration of the additive (Gitis and Rothenberg 2016; Mocciano et al. 2017). Charcoal, grog, and breadcrumbs have historically been used in water filtration ceramics to produce pores (Gitis and Rothenberg 2016; Dele-Afolabi et al. 2017; Mocciano et al. 2017) and are available cheaply or for free in Indonesia and many other developing nations that are home to coral reef ecosystems (pers. comm. Widiastuti). The use of cheap or free waste materials commonly produced in many developing countries in clay coral settlement substrates could reduce the cost of substrates, while also contributing to reductions in local waste streams. Substrate

porosity may also facilitate coral larval settlement, given the preference of many taxa to settle in micro-crevices and refugia (Whalan et al. 2015; Randall et al. 2021). Care must be taken to ensure that additives do not inhibit coral settlement directly or via changes to biofilm development and the recruitment of crustose coralline algae (CCA) during substrate conditioning (Levenstein et al. 2022; Fong et al. 2024b), given their importance as coral settlement cues (Heyward and Negri 1999).

Here we compared the settlement of *Acropora millepora* larvae to low-cost substrates made by hand from local clay (Kalimantan, Indonesia) with one of three widely available and low-cost or free additives (coconut charcoal, grog, and breadcrumbs). We also examined the influence of substrate properties on CCA recruitment and coral settlement. The aims of this study were to confirm the suitability of low-cost handmade clay substrates for the settlement of sexually produced corals and to test the effect of clay additives on settlement and biofilm development. Such low-cost coral settlement substrates could be used by live coral exporters, restoration practitioners, and researchers alike, particularly in developing countries where price is often a barrier to the uptake of novel techniques (Barton et al. 2017).

Methods

Substrate production, qualities and conditioning

Replicate substrates (3 × 3 × 0.5 cm) were handmade using the pressure die casting method and were comprised predominantly of Kalimantan clay (code BL1) (40% Kalimantan clay, 20% quartz, 13.50% kaolin, 13.50% feldspar, 10% ball clay, 2% talc, and 1% bentonite). One of three additives was included in each substrate: (1) coconut charcoal, (2) grog (fired clay ground into a granular form), and (3) breadcrumbs, at one of three concentrations (5%, 15%, and 25%). In water filter ceramics, additives are typically included up to concentrations of ~30%, which effectively reduces costs while maintaining the integrity of the ceramic (Moujoud et al. 2023; Saleh et al. 2023). Hence, three concentrations lower than 30% were chosen for this study (5%, 15%, and 25%) to ensure additives did not impact substrate integrity. Coconut charcoal and breadcrumbs were purchased commercially from a local store and traditional market in Bali, Indonesia, while grog was provided free by a local ceramic workshop from their fired clay waste. Additives were crushed and ground to a similar consistency before being combined with the clay using a pugmill at each of the three concentrations. 72 substrates were made in total, resulting in 8 replicate tiles per additive and concentration combination. Substrates were fired in an electric furnace that took 8 h to reach 1050 °C and then maintained this temperature

for 2 h prior to cooling. The concentration and composition of additives, which combust during firing creating cavities or pores in the clay matrix, influence pore size, shape, and abundance, as well as substrate integrity (Mocciaro et al. 2017).

On the 9th of October 2023, substrates were placed horizontally in indoor aquaria with flow-through ambient 0.4 µm filtered seawater (FSW) at 27.5 °C under ambient lighting at the Australian Institute of Marine Science National Sea Simulator (SeaSim), Cape Cleveland, to develop a biofilm and recruit CCA for 6 weeks to the top surface of substrates, ahead of coral larval settlement. A 4–6-week conditioning period has previously been identified as suitable for substrates to recruit sufficient CCA and biofilm to induce coral settlement (Fong et al. 2024b; Randall et al. 2024).

Substrate cost and properties

The cost of producing substrates was calculated in local currency (Indonesian Rupiahs, IDR) and converted to U.S. dollars using the contemporary (2024) exchange rate of 1 USD = 15,906.8 IDR (calculated on 2nd December 2024). The cost of each substrate type and additive concentration was calculated using the cost of BL1 clay (0.94 USD per kg) and additives (coconut charcoal = 0.75 USD per kg, grog = free, breadcrumbs = 1.13 USD per kg) and firing costs (0.047 USD per tile), but excluding 4 h of labour required to produce the 72 substrates (excluding substrate firing time).

The chemical composition, porosity, and water absorption were determined from one substrate of each of the substrate types and concentrations (Table 1). Chemical composition was determined by scanning electron microscope-energy dispersive X-ray. Substrate porosity was calculated using the weight (Dry Weight, g) and volume (v, ml) of the tile after firing, and the weight of the fired substrate after 24 h submerged in water (Wet Weight, g) (Eq. 1). Substrate water absorption was calculated using the substrate weight after firing (Dry Weight) and the weight of substrate (Wet Weight) (Eq. 2).

$$\text{Porosity (\%)} = \left(\frac{\text{Wet Weight} - \text{Dry Weight}}{v} \right) \times 100 \quad (1)$$

$$\text{Water absorption (\%)} = \left(\frac{\text{Wet Weight} - \text{Dry Weight}}{\text{Dry Weight}} \right) \times 100 \quad (2)$$

Coral spawning, culturing, settlement and censusing

Eleven gravid partial or whole colonies of *Acropora millepora* were collected from Falcon Reef, inshore central Great Barrier Reef, ~one week prior to the predicted dates of spawning. Colonies were transported via vessel to SeaSim and maintained in outdoor aquaria under ambient lighting and at 27.5 °C. Colonies spawned on the 31st October 2023 and gametes were collected and pooled to allow bulk

Table 1 Generalized linear mixed model summary statistics predicting settlement of *Acropora millepora* larvae to upward conditioned surfaces of substrates based on the additive included (Substrate

Type = Coconut Charcoal, Grog, Breadcrumbs), cover of crustose coralline algae (%) (CCACover) and the additive concentration (Concentration = 5, 15 or 25%)

Model	Fixed effects	Estimate	Standard error	Z value	Pr (> Z)
1. Settlement ~ SubstrateType + CCACover + (1 SubstrateType/Concentration) + (1 Container)	Intercept (Coconut charcoal)	0.020	1.101	0.019	0.985
	Grog	0.533	1.440	0.370	0.711
	Breadcrumbs	−0.268	1.451	−0.185	0.853
	CCA Cover	0.025	0.021	1.152	0.249
2. Charcoal: Settlement ~ Concentration + CCACover + (1 Container)	Intercept (Substrate 5%)	0.353	0.754	0.469	0.639
	Substrate 15%	−0.595	0.371	−1.604	0.109
	Substrate 25%	−0.677	0.392	−1.722	0.085
	CCA Cover	0.031	0.040	0.782	0.434
3. Grog: Settlement ~ Concentration + CCACover + (1 Container)	Intercept (Substrate 5%)	−0.456	0.541	−0.843	0.399
	Substrate 15%	−0.202	0.333	0.606	0.544
	Substrate 25%	0.439	0.318	1.379	0.168
	CCA Cover	0.089	0.034	2.574	0.010
4. Breadcrumbs: Settlement ~ Concentration + CCACover + (1 Container)	Intercept (Substrate 5%)	0.696	0.645	1.079	0.281
	Substrate 15%	−0.568	0.469	−1.209	0.227
	Substrate 25%	−0.474	0.471	−1.006	0.314
	CCA Cover	−0.041	0.051	−0.789	0.430

P values in bold indicate statistical significance at $p < 0.05$

cross-fertilization of gametes from the eleven colonies. Larvae were cultured in a single 500L tank at a density of 1 larva mL⁻¹. Larval competency for settlement was tested daily until six-day-old larvae demonstrated $\geq 65\%$ settlement competency in the presence of CCA chips (*Porolithon* cf. *onkodes*).

On the 6th November 2023, 28 days after substrate conditioning was initiated, one substrate of each additive type and concentration (total of 9 substrate types) was haphazardly arranged in each of eight replicate 2L plastic containers with the CCA-conditioned surface facing upward. Larvae therefore had the choice to settle on their preferred substrate type and additive concentration. Containers were placed into aquaria with low flow FSW at 27.25 °C. Plastic containers had mesh windows (180 µm) to allow water exchange but no loss of larvae. Each container was illuminated by an Aquarium LED light scheduled with a 12-h light and 12-h dark cycle, reaching a peak of 100 PAR. Approximately 300 6-day-old *A. millepora* larvae were carefully loaded into a 50 ml-syringe and injected into the centre of each container via a self-sealing pore. After ~48 h the numbers of larvae that had settled, defined as the metamorphosis and successful attachment to a substrate, on each surface (upward-facing, side-facing, downward-facing tile surface) of each of the substrates, were counted by one of two observers under magnification using a dissecting microscope. The upward-facing surface of each substrate was photographed using an Olympus Tough TG5 camera. Substrates were then moved to an indoor aquarium until 7th February 2024 for a 90-day grow-out period. CCA cover on the upward-facing surface of each substrate was analysed from photographs using ImageJ (Schneider et al. 2012). Pixels corresponding to CCA were selected and summed using the area measurement tool. This was achieved by initially identifying approximately 20 representative CCA patches via manual freehand selection, and then adjusting the selection using the colour threshold tool (hue, saturation, and brightness).

Data analysis

All statistical analyses were completed in R (R Core Team 2022), and all data were visualized using the “ggplot2” package (Wickham 2016). Most larvae settled to upward-facing surfaces (~97%); therefore, only settlement densities on upward-facing surfaces were statistically analysed. To investigate differences in coral settlement to substrates containing different additives, herein referred to as substrate types, we modelled the density of settled spat against substrate type using a generalized linear mixed effect model (GLMM) with a Poisson distribution, using the “glmmTMB” function from the glmmTMB package (Brooks et al. 2017). To account for variation in CCA cover on substrates, percent CCA cover was included as a fixed effect. The additive concentration

nested in substrate type and the container number were included as random factors. Model diagnostics, including overdispersion and zero inflation, were checked using the “DHARMA” package (Hartig 2020), and assumptions validated. For significant factors, pairwise comparisons were undertaken by calculating least squares means with a Tukey adjustment using the “emmeans” package (Lenth 2021).

To investigate differences in coral settlement among the three additive concentrations, we modelled the density of settled spat against additive concentration using a GLMM as above, for each substrate type separately. CCA cover (%) was again included as a fixed factor and container number as a random factor. Model diagnostics were validated and pairwise comparisons completed as above. Differences in CCA cover (%) among the three additive concentrations were modelled against additive concentration using a GLMM with a Poisson distribution as above, for each substrate type separately. The container number was included as a random factor. Model diagnostics were validated and pairwise comparisons completed as above.

Differences in the chemical composition and physical properties of substrates were visualized using principal component analysis (PCA) with vector plots. PCAs were generated using “PCA” from the FactoMineR package (Josse and Husson 2008) and visualized using “fviz_pca_biplot” from the factoextra package (Kassambara and Mundt 2020). Relationships between chemical (C, O, Mg, Fe, Al, Si, K, Ti) and physical properties (porosity and water absorption) of substrates and both coral settlement and cover of CCA were examined using generalized linear models (GLMs) with a negative binomial and beta distribution respectively, using the glm.nb and betareg functions, respectively. Physical and chemical properties were determined from one substrate of each of the substrate types and additive concentrations, therefore, these results are interpreted with caution.

Results

The majority (~97%) of *A. millepora* larvae settled on upward-facing conditioned surfaces, compared to side- and downward-facing surfaces that were relatively free of visible biofilms and CCA. The density of settlement to upward-facing surfaces averaged 1.88 ± 0.2 spat cm⁻². Settlement did not vary statistically among the three substrate types, although settlement was two-fold higher on grog (2.77 ± 0.5 spat cm⁻²) than on breadcrumb substrates (1.13 ± 0.3 spat cm⁻²) ($p > 0.7$, Fig. 1b, Table 1). Within a substrate type, settlement did not vary significantly across the three additive concentrations ($p > 0.05$, model 2, 3, and 4, Table 1); however, trends in settlement densities with additive concentrations differed among substrate types (Fig. 1c). On coconut charcoal and breadcrumb substrates, settlement was

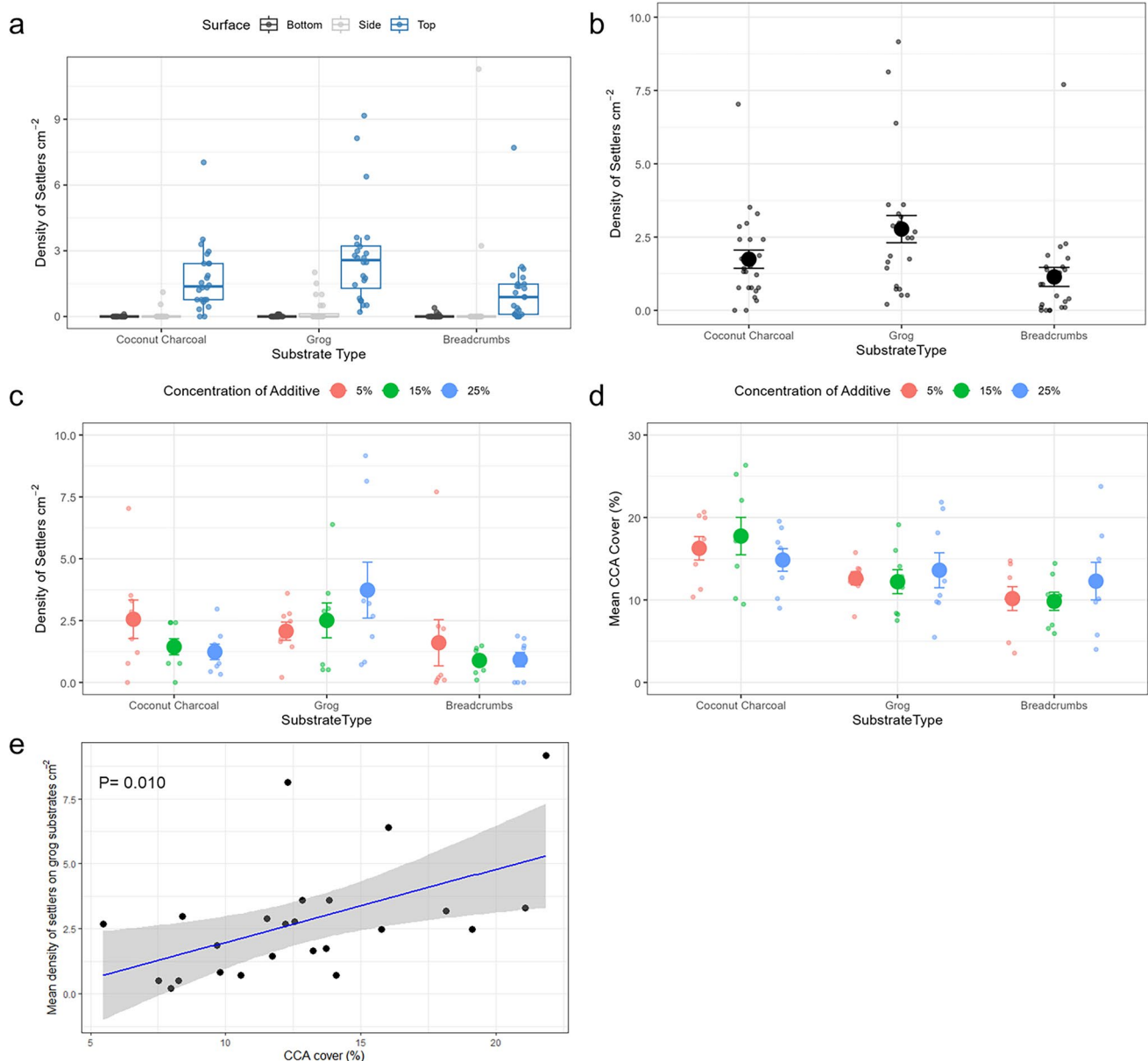


Fig. 1 **a** Mean density of *Acropora millepora* settlers per cm² per substrate type and surface orientation. **b** Mean density of *Acropora millepora* settlers per cm² per substrate type, on upward-facing surfaces only. **c** Mean density of settlers of *Acropora millepora* per cm² per substrate type and additive concentration (5, 15, and 25%), on upward-facing surfaces only. **d** Mean per cent cover of crustose coral-

line algae (CCA) per substrate type and additive concentration (5, 15, and 25%), on upward-facing surfaces only. **e** Statistically significant correlation between CCA cover (%) and mean density of *Acropora millepora* settlers per cm² on grog substrates only. Error bars in panels b, c and d represent standard errors

highest at the lowest additive concentration (5%), while on grog substrates settlement was highest at the highest additive concentration (25%), noting that these differences were not statistically significant (Fig. 1c, Table 1). The highest overall settlement of *A. millepora* larvae was recorded on substrates comprised of 25% grog (Fig. 1c), while not quantified or statistically compared, live corals were present on all substrate types and all additive concentrations after 90 days maintained in flow-through aquaria, indicating the

longer-term suitability of all tested substrates for use in coral aquaculture.

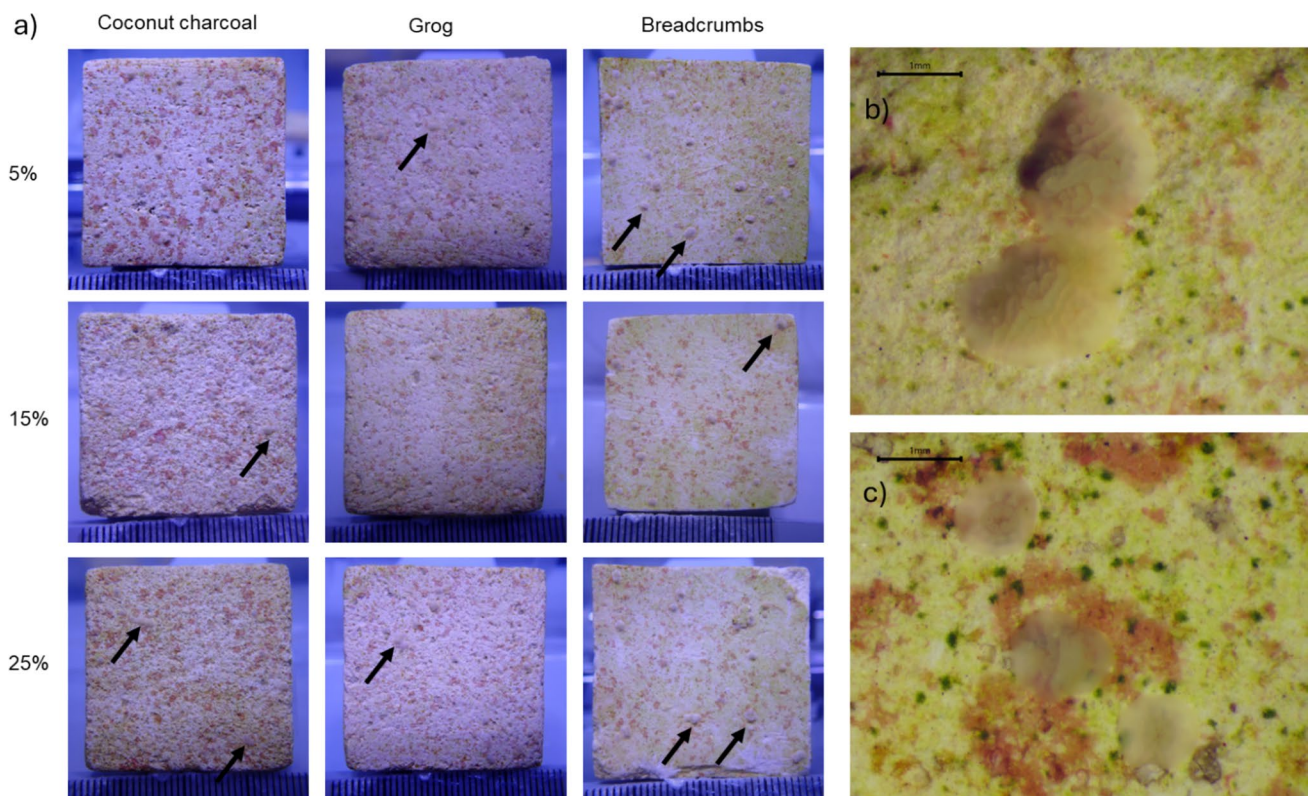
At the time of coral settlement, after 28 days conditioning, CCA cover on substrates averaged $13.29 \pm 0.6\%$ and did not significantly differ amongst substrate types (Table 2, Fig. 1d). Within a substrate type, CCA cover did not vary with additive concentration ($p > 0.05$ models 5, 6, and 7 Table 2, Figs. 1d, 2) and settlement did not correlate with CCA cover on substrates overall ($p = 0.2$, Table 2); however,

Table 2 Generalized linear mixed model summary statistics predicting cover of crustose coralline algae (% CCAcover) on upward conditioned surfaces of substrates based on the additive included (Sub-

strate Type = Coconut Charcoal, Grog, Breadcrumbs) and the additive concentration (Concentration = 5, 15 or 25%)

Model	Fixed effects	Estimate	Standard error	Z value	Pr(> Z)
5. Charcoal: CCAcover ~ Concentration + (1 Container)	Intercept (Substrate 5%)	− 1.629	0.128	− 12.75	< 2e-16
	Substrate 15%	0.087	0.155	0.561	0.575
	Substrate 25%	− 0.106	0.160	− 0.667	0.505
6. Grog: CCAcover ~ Concentration + (1 Container)	Intercept (Substrate 5%)	− 1.90	0.138	− 13.816	< 2e-16
	Substrate 15%	− 0.054	0.179	− 0.304	0.761
	Substrate 25%	0.032	0.178	0.184	0.854
7. Breadcrumbs: CCAcover ~ Concentration + (1 Container)	Intercept (Substrate 5%)	− 2.16	0.176	− 12.276	< 2e-16
	Substrate 15%	0.013	0.244	0.056	0.955
	Substrate 25%	0.160	0.239	0.670	0.503

P values in bold indicate statistical significance at $p < 0.05$

**Fig. 2** a Representative surface texture and cover of crustose coralline algae and biofilm on substrates containing 5%, 15% and 25% coconut charcoal, grog, and breadcrumbs. Obvious examples of set-

tled *Acropora millepora* larvae are indicated with a black arrow. Scale bars indicate mm. b and c settled *Acropora millepora* spat on substrates under magnification

on grog substrates, settlement increased significantly with increasing CCA cover ($p = 0.01$, Fig. 1e, Table 2).

Analysis of the physical and chemical properties of substrates revealed that substrate porosity and water absorption were both significantly negatively correlated with *A. millepora* settlement (Table 4). Water absorption and porosity were highest in 25% breadcrumb and 25% coconut charcoal

substrates (Table 3); however, increasing concentrations of all three additives increased the water absorption and porosity of substrates (Table 1, Supplementary Fig. 1). *A. millepora* settlement also showed a significant and positive relationship with the concentration of iron (Fe) and aluminium (Al), despite very little variation in these elements across substrates (Table 4). The cover of CCA on substrates was

Table 3 Properties and production cost (in Indonesian Rupiah (IDR) and United States Dollars USD)) of each of the three substrate types (coconut charcoal, grog, breadcrumbs) per additive concentration (5, 15 and 25%). Elemental make up for C-Ti is shown as a percentage

Tile additive/ Substrate type	Additive concentration (%)	Cost per tile (IDR)	Cost per tile (USD)	Water absorption (%)	Porosity (%)	C	O	Mg	Fe	Al	Si	K	Ti
Coconut Charcoal	5	390	\$0.025	13.2	33.1	23.8	40.7	1.9	0.8	9.5	21.2	1.4	0.7
	15	382.5	\$0.024	21.7	43.4	20.9	42.4	1.8	0.9	10	22	1.4	0.6
	25	375	\$0.024	30.3	55.9	25.7	38.3	0.8	0.8	10.2	22.2	1.4	0.5
Grog	5	375	\$0.024	11.6	30.7	28	38	0.9	0.9	10.5	20.4	1.3	0
	15	337.5	\$0.021	13	39	22.5	42.4	1.2	0.9	10.1	20.9	1.3	0.5
	25	300	\$0.019	14.2	41	19.2	41.9	1.2	1.1	11.6	22.9	1.4	0.7
Bread-crumbs	5	397.5	\$0.025	15.4	36.3	26.4	38.3	0.8	0.8	10.2	21.4	1.3	0.8
	15	405	\$0.025	25.1	44.6	27.7	40.5	1.4	0.8	9.3	18.9	1	0.4
	25	412.5	\$0.026	34.7	49.1	21.8	40.7	1.2	0.8	10	23.4	1.5	0.6

C= Carbon, O= oxygen, Mg= Magnesium, Fe= Iron, Al= Aluminium, Si= Silicon, K= Potassium, Ti= Titanium

Table 4 Generalized linear model summary statistics predicting settlement and cover of crustose coralline algae (% CCAcover) on upward conditioned surfaces of substrates based on physical (water absorption and porosity) and chemical properties (C, O, Mg, Fe, Al, Si, K, Ti) of substrates

Response Variable	Fixed effect	Estimate	Standard error	Z value	Pr (> Z)	Relationship if significant
Settlement	Water absorption	− 0.049	0.014	− 3.333	0.001	Negative
	Porosity	− 0.036	0.016	− 2.270	0.023	Negative
	C	0.067	0.041	− 1.643	0.1	
	O	0.081	0.073	1.187	0.235	
	Mg	0.076	0.324	0.233	0.816	
	Fe	3.222	1.223	2.635	0.008	Positive
	Al	0.415	0.190	2.180	0.029	Positive
	Si	0.083	0.095	0.872	0.383	
	K	1.108	0.919	1.206	0.228	
CCA cover (%)	Ti	0.288	0.554	0.520	0.603	
	Water absorption	− 0.002	0.006	− 0.346	0.730	
	Porosity	0.001	0.006	0.155	0.877	
	C	− 0.028	0.017	− 1.64	0.101	
	O	0.035	0.030	1.144	0.252	
	Mg	0.320	0.129	2.483	0.013	Positive
	Fe	0.381	0.532	0.717	0.474	
	Al	0.016	0.082	0.198	0.842	
	Si	0.047	0.040	1.195	0.232	
	K	0.822	0.394	2.085	0.037	Positive
	Ti	0.029	0.232	0.126	0.899	

P values in bold indicate statistical significance at $p < 0.05$

also significant and positively correlated with concentrations of magnesium (Mg) and potassium (K) (Table 4).

Substrates containing 25% breadcrumbs were most costly to produce given that breadcrumbs were more expensive than clay (thus their inclusion increased substrates costs); nonetheless, 25% breadcrumb substrates cost only 2.6 cents per substrate (USD)(Table 3). Grog was available for free, and coconut charcoal was cheaper than clay; therefore, increasing concentrations of grog and coconut charcoal in substrates decreased costs (Table 3). Grog substrates were

cheapest to produce, costing 1.9 cents (USD) per 25% grog substrate (Table 3).

Discussion

Reef restoration and coral exports form an important part of the economies of many developing countries with coral reefs (Burke et al. 2011; Razak et al. 2024). The collection of wild corals by these industries may be adding to the

increasing impacts of growing populations, overexploitation, and climate warming on coral reefs in these regions (Selig and Bruno 2010; Intyas et al. 2023; Bruckner and Borneman 2006), highlighting the importance of the development of a sustainable coral aquaculture industry. The use of sexually propagated corals is one step towards increasing the sustainability of coral export and restoration industries (Randall et al. 2020); however, cost is a common barrier to the uptake of new methods in developing countries (Barton et al. 2017). Results of this study indicate that substrates handmade from local clays and made cheaper using widely available, free, or affordable additives (breadcrumbs, coconut charcoal, and grog) provide an inexpensive (< 3 cents (USD)) and suitable substrate for the settlement and grow-out of *Acropora millepora* spat. The use of waste materials as additives in these settlement substrates (coconut charcoal, breadcrumbs, and grog), while contributing to the reduction of agricultural and industrial waste streams, may also assist with the development of a sustainable local coral aquaculture industry and the transition to the use of sexually produced corals in research, exports, and restoration in developing countries.

The inclusion of additives in settlement substrates in this study (grog, coconut charcoal, and breadcrumbs) did not change the settlement of *A. millepora* larvae. Spat also survived on all substrate types 90 days after settlement, indicating the suitability of these substrates for longer-term coral holding and grow-out. This result highlights the suitability of these substrates, made cheaper by the inclusion of additives, for the settlement of *A. millepora* larvae. Although no ‘control substrate’ was tested in this study to allow direct comparison of biofilm development and coral settlement on clay substrates with and without additives, settlement (~ 2.8 spat cm^{-2}) was similar to *A. millepora* settlement to aragonite plugs (~ 3.8 spat cm^{-2}) (Page et al. 2024) and concrete tiles ($\sim 2\text{--}3$ spat cm^{-2}) (Neil et al. 2025) in previous studies, demonstrating the general suitability of these substrates and additives for coral settlement and grow-out. The addition of a “control” substrate in the future trials is encouraged to ensure additives do not negatively impact biofilm development and coral settlement. Corals exhibit taxa-specific settlement preferences, including for composition and texture (Abdul Wahab et al. 2023; Randall et al. 2024); therefore, trials across a wider range of coral taxa are also recommended to ensure the utility of these clay-based substrates across a broader suite of coral taxa.

Coral larvae often preferentially settle in microrefugia, and substrate heterogeneity has been the focus of several studies of coral settlement (Nozawa 2008; Whalan et al. 2015; Levenstein et al. 2022; Fong et al. 2024b). We expected that increased concentrations of additives, their combustion during firing to increase substrate porosity and water absorption (Dele-Afolabi et al. 2017; Moujoud et al. 2023), would also increase coral settlement, as found

in previous studies (Whalan et al. 2015). However, within each substrate type, we found no increase in coral settlement with increasing additive concentrations and corresponding substrate porosity and water absorption. Instead, we unexpectedly detected declines in coral settlement with increasing substrate porosity and water absorption. Substrate properties were determined from one tile per substrate type and additive combination in this study; therefore, correlations between settlement and substrate properties should be interpreted with caution. Whalan et al. (2015) found increased settlement of *A. millepora* and *Ctenactis crassa* larvae to porous substrates that closely matched the width of the coral larvae, consistent with Attachment Point Theory (Scardino and De Nys 2011). Attachment Point Theory proposes that marine fouling organisms preferentially settle to surfaces with microrefugia similar in size to their own body width (Scardino and De Nys 2011). The influence of substrate porosity, and specifically pore size, on the settlement of corals is therefore worthy of further investigation to optimize coral settlement to artificial substrates, as previously suggested (Spieler et al. 2001; Whalan et al. 2015; Levenstein et al. 2022; Fong et al. 2024b).

Substrate rugosity and porosity can also influence the recruitment of CCA and other biofilm elements (Fong et al. 2024b), known to be important biochemical inducers of settlement and metamorphosis of coral larvae (Heyward and Negri 1999; Webster et al. 2004). Substrate porosity can therefore indirectly influence coral settlement and is an important consideration in coral settlement substrate design (Levenstein et al. 2022; Fong et al. 2024b). Overall, the additives investigated in this study did not result in significant differences in CCA cover on the substrates tested after 28 days of conditioning. In addition, settlement overall did not reflect differences in CCA cover on substrates. Nonetheless, *A. millepora* settlement increased with increasing CCA cover on grog substrates only, and CCA cover and coral settlement were highest on substrates with the highest concentration of grog (25%). Trials using even higher concentrations of grog, to further reduce costs of substrates, while also increasing CCA cover and coral settlement are encouraged, particularly given that 25% grog substrates were the cheapest substrates to produce (1.9 cents (USD)). Grog was obtained free of charge and is a widely available waste product arising from brick production (Zawrah et al. 2016). There is the risk that high CCA cover will outcompete and overgrow settled spat during grow-out (Page et al. 2024; Ramsby et al. 2024). However, recent experiments suggest that negative CCA and coral interactions could be managed via manipulation of grow-out lighting and temperature (Fong et al. 2024b, 2024a; Ramsby et al. 2024). Given positive correlations between both magnesium and potassium and CCA cover in this study, experiments using substrates with reduced concentrations of these elements are warranted, to

determine if they can be utilized to reduce negative impacts of CCA on coral growth post-settlement. The inclusion of additives that do not reduce coral settlement and growth but discourage the recruitment or growth of biofilms that may later outcompete or kill settled spat (Page et al. 2024; Ramsby et al. 2024) should also be explored.

We found *A. millepora* settlement was positively correlated with concentrations of iron and aluminium. A wide variety of materials have been found to be suitable for the settlement of coral larvae, including plastic, glass, ceramic, dead coral skeleton, cement, etc. (Harriott and Fisk 1987; Fitzhardinge and Bailey-Brock 1989; Babcock and Mundy 1996; Spieler et al. 2001; Randall et al. 2021); however, the role of specific chemical elements in inducing or encouraging coral settlement is poorly understood. Settlement of *Acropora palmata* and *Diplora labrinthiformis* increased in the presence of quartz-rich sand particles, and *D. labrinthiformis* settlement also increased in the presence of strontianite (SrCO_3) (Levenstein et al. 2022). Detection and navigation of coral larvae towards water-soluble ions released from the substrates are proposed as the mechanism driving these associations (Levenstein et al. 2022). Further experimentation using substrates of different compositions and, in particular, elevated concentrations of iron, aluminium, strontianite, and quartz-rich sand particles may help elucidate the optimal substrate chemical composition to maximize coral settlement and survival. Given possible taxa-specific preferences for substrate composition (Levenstein et al. 2022; Randall et al. 2024), testing across as wide a range of coral taxa as possible is advised.

Importantly, the inclusion of grog and coconut charcoal reduced the cost of substrates, given both are widely available and cheaper than local clays. The inclusion of breadcrumbs slightly increased substrate costs in this study, as they cost more than local clays; however, given the short shelf life and high wastage of bread, free sources of bread are likely available in many developing countries (Narisetty et al. 2021). Given the importance of keeping costs low to maximize uptake of coral aquaculture, particularly in developing countries, where cost is a significant barrier to the uptake of novel techniques (Barton et al. 2017), we encourage further experimentation with widely available, cheap or free additives to minimize substrate costs while ensuring coral settlement and survival are not compromised. Noting non-significant but negative trends in coral settlement with increasing concentrations of breadcrumbs and coconut charcoal, we suggest additional trials to determine if increased concentrations of these additives significantly reduce coral settlement and survival. Potential trade-offs between substrate porosity, cost, and fragility should also be considered (Mocciaro et al. 2017). Reduced costs achieved from increased additive concentrations that increase substrate

porosity may increase the likelihood of substrate breakage, negating the benefit of cost reductions, and should be tested over longer-term studies.

In conclusion, we demonstrated the suitability of low-cost coral settlement substrates made from local Indonesian clay, combined with cheap or free pore-forming additives, for the settlement of sexually produced *Acropora millepora* corals. Given these substrates are cheap and easy to make by hand, we encourage testing across a broader suite of coral taxa ahead of larger-scale trials to test their suitability for upscaled manufacturing and long-term field or aquarium deployments. The next steps for the development of a coral aquaculture industry in many developing countries include the identification of coral spawning windows and the development of coral aquaculture skills and infrastructure, to enable the production of sexually propagated corals for use in restoration and the aquarium trade. Coral restoration is inherently costly (Bayraktarov et al. 2016); however, the development and implementation of low-cost, low technology methods should be prioritized, particularly in developing countries, to accelerate the uptake of coral aquaculture and support the more sustainable use of coral reef ecosystems.

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Author contributions WK, AANAIW, CAP, and CJR designed the study; AANAIW made the substrates; WK, CAP, CG, KA, VJ, and AANAIW collected the data. VJ and CAP analysed the data. WK, VJ, and CAP wrote the manuscript with input from all authors.

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Data availability Data will be provided via an online AIMS record.

Declarations

Competing Interests The authors declare no competing interests.

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