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RESEARCH

The structure and composition of macroalgal communities influence coral recruitment on an inshore reef of the Great Barrier Reef

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Abstract On inshore coral reefs, coral cover declines from disturbances are often accompanied by increases in macroalgal cover. Thus, coral recovery often occurs against a backdrop of elevated macroalgae cover. While 'macroalgae' are generally assumed to reduce coral recruitment, their taxonomic composition and structure vary considerably. Here, we test whether different macroalgal assemblages affect coral recruitment on an inshore reef by experimentally manipulating macroalgal assemblages within forty 1 m^2 plots on the shallow reef crest in Florence Bay, Magnetic Island (central inshore Great Barrier Reef). Specifically, we investigated the effect of canopy-forming macroalgae (e.g. *Sargassum*, *Turbinaria*, *Sirophysalis*), understorey macroalgae (e.g. *Hypnea*, *Lobophora*, *Padina*), mixed macroalgal assemblages (both canopy- and understorey macroalgae) and plots cleared of macroalgae on rates of coral recruitment to tiles. We also quantified coral size frequency distribution in Florence Bay to investigate its relationship with macroalgal structure and composition. The presence of canopy-forming macroalgae was the most important factor affecting coral recruitment, with coral recruitment being ~ fivefold greater in plots with no canopy-forming macroalgae compared to those with canopy-forming macroalgae. Moreover, the presence of two macroalgal taxa, *Sargassum* and *Lobophora*, within the plots was associated with lower coral recruitment to the tiles. Coral size frequency distribution in Florence Bay showed similar trends, with smaller corals (< 20 cm diameter) only present in areas with low density and height of canopy-forming macroalgae and, in particular, low abundance of *Sargassum*. We thus suggest that both the structure and composition of the macroalgal community drive, at some point, coral replenishment dynamics.

Keywords Coral recruitment · Macroalgae · Competition · Coral reef · Coral size frequency distribution · *Sargassum*

Introduction

Climate change and local anthropogenic disturbances have led to widespread loss of coral cover on coral reefs globally (GCRMN 2021; Graham et al. 2015; Hughes et al. 2017). The dead coral skeletons are colonised by opportunistic and fast-growing species that rapidly occupy the available substratum, such as turfs (algae and cyanobacteria) or macroalgae (Ceccarelli et al. 2020; Diaz-Pulido & McCook 2002; Hughes 1994). Indeed, current estimates indicate that algal cover on coral reefs globally has increased by 25% between 2011 and 2019 (GCRMN 2021). Therefore, any recovery of coral populations is likely to occur against a backdrop of elevated algal cover. Quantifying the outcomes of coral–algal interactions and how they vary among taxa and life stages is important to predict the potential recovery of coral assemblages and future reef configurations (Diaz-Pulido et al. 2009; Ritson-Williams et al. 2009).

Benthic algae can affect corals throughout their life cycle, especially when in close proximity or direct contact with the coral (Birrell et al. 2008; Ritson-Williams et al.

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2009). For adult corals, most studies have reported sublethal physiological responses when in direct contact with macroalgae (reviewed by Burgo & Hoey 2024), including reduced growth (Clements et al. 2018, 2020; River & Edmunds 2001), tissue loss or partial mortality (Rasher et al. 2011; Rasher & Hay 2010; Thinesh et al. 2019), increased incidence of disease (Barott & Rohwer 2012), and reduced fecundity (Monteil et al. 2020). The effect of macroalgae on the early life stages of corals is generally more pronounced (Burgo & Hoey 2024). Macroalgae have been shown to decrease the settlement of coral larvae (Evensen et al. 2019a, b; Fong et al. 2019) and reduce the survival (Chong-Seng et al. 2014; Smith et al. 2022) and growth of recently settled and juvenile corals (Olsen et al. 2014; Venera-Ponton et al. 2011; Webster et al. 2015). However, studies have reported considerable variation in the response of corals to macroalgae across small spatial scales (Johns et al. 2018; Smith et al. 2022). This variation may be related to the presence and/or proximity of particular algal taxa rather than the presence of macroalgae sensu lato (McCook 2001). For example, differences in coral recruitment within a reef have been related to the surrounding algal community (Johns et al. 2018), and the removal of macroalgae at small scales has been shown to boost coral recruitment (Smith et al. 2022). While laboratory experiments generally isolate specific macroalgal taxa, field studies that examine the influence of macroalgal communities on coral recruitment often do not isolate the specific properties of these habitats, such as composition and structure (Chong-Seng et al. 2014). Instead, macroalgae are often treated as a homogeneous group ‘macroalgae’ (Beatty et al. 2018) or described in terms of the dominant taxon (e.g., *Sargassum,* Webster et al. 2015).

Macroalgae are taxonomically, morphologically and ecologically diverse and may influence coral recruitment in a variety of ways. For example, canopy-forming macroalgae, such as *Sargassum*, can create a flexible barrier that alters water flow, shades the substratum and has been suggested to prevent coral planulae from reaching the benthos (McCook 2001). Other macroalgae, such as the understorey macroalga *Lobophora,* while not creating a tall barrier, produce chemical compounds that have been shown to inhibit metamorphosis in coral larvae in aquaria (Baird & Morse 2004), and inhibit the settlement of other organisms, such as sea urchins (Agatsuma et al. 2008; Cano et al. 2024; Vieira et al. 2017). Consequently, the response of coral settlement will likely vary depending on the structure (i.e. height and density) and composition of the surrounding algal community. The aim of this study, therefore, was to investigate the effects of the structure and composition of macroalgal assemblages on coral recruitment. Specifically, we manipulated macroalgal communities on the shallow reef crest of an inshore reef on the Great Barrier Reef to investigate the differential effects of canopy-forming macroalgae (e.g. *Sargassum*, *Turbinaria*, *Sirophysalis*) and /or understorey macroalgae (e.g. *Hypnea*, *Lobophora*, *Padina*) on rates of coral recruitment.

Methods

Study site and experimental setup

This study was conducted on a fringing reef surrounding Magnetic Island (Yunbenun; 19.1385° S, 146.8339° E), an inshore island in the central Great Barrier Reef (GBR). Located approximately 8 km north of Townsville, the coast of Magnetic Island consists of many small bays and rocky headlands where fringing reefs have formed. The waters around Magnetic Island are typically turbid due to seasonal inputs of sediments and nutrients from a coastal river catchment (Browne et al. 2013; Fabricius et al. 2014) and the resuspension of sediments through currents, waves, boat traffic and maintenance dredge materials from the Port of Townsville. Over the past two decades, the reefs around Magnetic Island have also been affected by numerous acute disturbances, such as cyclones (notably Cyclone Yasi in 2011) and repeated bleaching events (Thompson et al. 2024). These disturbances have resulted in a shift from high coral (~40%) and low macroalgal cover (~15%) in 2004 to high macroalgal (~40%) and relatively low coral cover (20%) in 2016 (Ceccarelli et al. 2020). Although recent monitoring surveys have observed an increase in coral cover and the density of juvenile corals, the reefs on Magnetic Island have still not recovered from the impacts of Cyclone Yasi (Thompson et al. 2024). Due to its relatively high macroalgal cover, the fringing reefs of Magnetic Island offer ideal study sites to investigate the effects of macroalgal assemblages on coral recruitment.

This study was conducted on the shallow reef crest (~3 m depth) of Florence Bay, on the northeastern aspect of Magnetic Island (Fig. 1a and b). Florence Bay was selected as it has high macroalgal cover (40%) with moderate coral cover (30%; mostly *Montipora* and *Acropora*). The canopy-forming genus *Sargassum* is the dominant algal taxon, which shows strong seasonal patterns, reaching its maximum height in summer (November–January, up to 2 m). After reaching its peak, *Sargassum* senesces and remains at 10–40 cm height for the rest of the year (Supplementary Fig. 1). *Turbinaria* and *Sirophysalis* are other, less common canopy-forming macroalgae present in Florence Bay. In the understorey, common macroalgal taxa include *Hypnea*, *Padina*, and *Lobophora*. Ephemeral macroalgae such as *Hydroclathrus* and *Colpomenia* are frequently found in the cooler months (July–September). Finally, other algal taxa such as *Halymenia*, *Galaxaura*, *Bornetella*, *Caulerpa,* and *Neomeris* are present but generally infrequent throughout the year. Cover of crustose coralline algae (CCA) is low (< 2%;

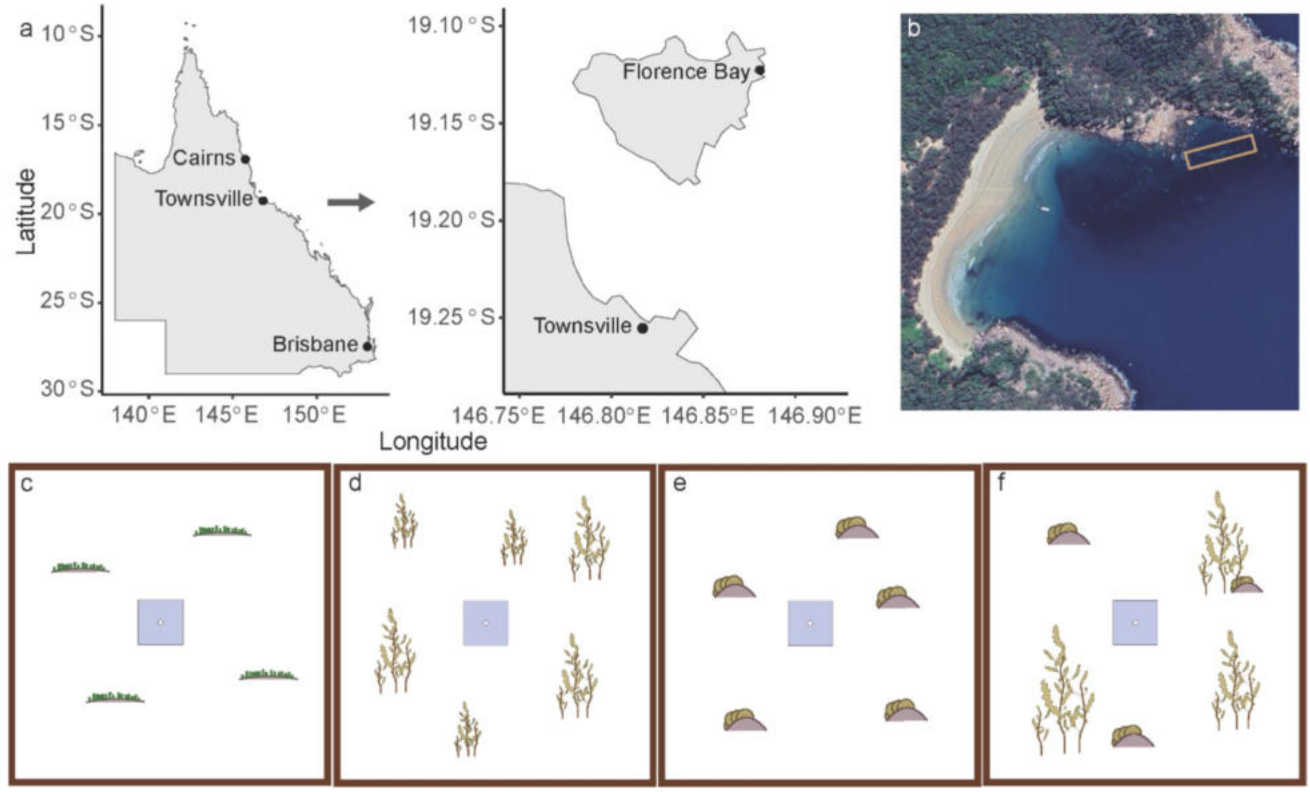


Fig. 1 **a** Map of the Queensland coast showing the location of Florence Bay (Magnetic Island); **b** the approximate location of the experimental study site within Florence Bay; **c**–**f** diagrams of each treatment: no macroalgae (**c**); canopy-forming macroalgae (**d**); understorey macroalgae (**e**); and mixed-algae (both canopy-forming and understorey) community (**f**). The icons in each image represent the respective treatments

Australian Institute of Marine Science 2015; Hermanto et al. 2023).

In September 2022, forty 1 m^2 plots were established in Florence Bay at ~ 3 m depth by divers on SCUBA. The plots were established along a 50-m transect tape marked at each end by GPS points. Each plot was laid parallel to the transect, and its position along the transect and its distance away from the transect (0–5 m) were recorded to ensure that the same plots could be revisited. Each plot was randomly selected and was at least 1 m away from adjacent plots. To manipulate the structure and composition of the macroalgal communities, plots were randomly assigned to one of four treatments: 'no macroalgae' (T1), 'canopy-forming macroalgae' (T2), 'understorey macroalgae' (T3); 'mixed-macroalgae community' (T4), with 10 plots per treatment (Fig. 1c–d). Plots assigned to 'mixed macroalgal community' (T4) were left untouched, while all macroalgae were removed by hand from the 'no macroalgae' plots (T1), leaving only short turfs. For the 'canopy-forming macroalgae' plots (T2), all understorey macroalgae were removed by hand, leaving algae that can form tall canopies (> 20 cm height), e.g. *Sargassum*, *Turbinaria*, and *Sirophysalis*. For the 'understorey macroalgae' plots (T3), all canopy-forming macroalgae were removed to leave the taxa that form the macroalgal understorey, i.e. *Lobophora*, *Padina*, and *Hypnea* (Supplementary Table 1).

Settlement tiles

Polyvinyl chloride (PVC) tiles were used to quantify coral recruitment (Price 2010; Randall et al. 2021). PVC tiles have been shown to promote CCA recruitment (Kennedy et al. 2017), which in turn can enhance coral settlement (Harrington et al. 2004). One 10 cm × 10 cm × 0.5 cm PVC settlement tile was deployed in the centre of each plot. To do so, a stainless steel base plate was secured to the substratum using two nylon expansion plugs inserted through two holes in the plate (Mundy 2000). The PVC tile was attached to the base plate using a stainless steel bolt that passed through the centre of the tile and was secured with a wingnut. A 1 cm gap was created between the tile and the base plate using two stainless steel nuts and a ~ 1 cm piece of plastic tube. This setup ensured the tile was positioned above the substratum, providing a refugium for coral larvae. Each tile was individually numbered using a stainless steel tag attached with a cable tie to a hole in one corner of the PVC tile. Individually numbering each tile allowed us to assign a specific treatment to each tile. Tiles were deployed on 20th September 2022, ~ 4 weeks before the predicted spawning on Magnetic Island (13th–18th October 2022), to allow the tiles to condition and a biofilm to form before coral settlement.

Tiles were revisited on 15th February 2023, and a photo of the upper surface of each tile was taken in situ from a distance of ~ 50 cm directly above the tile. Each tile was retrieved by divers on SCUBA, carefully placed on a stainless steel rod with ~ 1 cm plastic spacers between adjacent tiles to avoid abrasion, and transported in bins of seawater to the Australian Institute of Marine Science. Tiles were soaked in a weak bleach solution (5% sodium hypochlorite) for 24h to remove organic material, then soaked in seawater for a further 24h and dried.

Since turfs have been shown to inhibit coral recruitment (Arnold et al. 2010) and grazing can cause incidental mortality of coral recruits (Trapon et al. 2013), turf height (‘No turf’, ‘Low’, ‘Medium’, ‘High’) and grazing (‘No grazing’, ‘Light’, ‘Medium’, ‘Heavy’) were qualitatively assessed using in situ photos (15th February 2023). To ensure that turf height and grazing intensity were objectively estimated, the photos were assessed twice with the observer (MB) ‘blind’ to the tile number.

The upper and lower sides and edges of each tile were then thoroughly searched under a dissecting microscope to quantify the number of corals that had settled on the tiles. All tiles were surveyed by a single observer (MB), and the observer was blind to the treatment and tile number to avoid biases when searching for coral recruits. Very few coral recruits were recorded on the upper surface and edge of the tiles, so the number of coral recruits from the different surfaces of the tile was combined, and recruitment was expressed as the total number of recruits per tile.

Benthic surveys in the plots

To investigate the effect of the composition and structure of the benthic communities on coral recruitment, benthic surveys were conducted by divers on SCUBA on 20th September 2022, immediately following the manipulation of macroalgal assemblages. To examine the relative importance of the nearby macroalgal community versus the community in direct contact with the tiles, the benthic community within each 1 m^2 plot (“nearby”) and around the perimeter of each tile (“contact”) was quantified.

Coverage of benthic taxa was visually estimated. For the “nearby” benthic community, the per cent cover of major benthic groups within each 1 m^2 plot was recorded to the nearest 5% (Fig. 1c–d). For the benthic community in “contact”, the per cent of the edges of each tile in contact with each group was recorded (Fig. 1e–f). The benthos was classified into macroalgae, hard corals, crustose coralline algae (CCA), rubble, sand, turfs, and other benthic taxa. Macroalgae and hard corals were identified to genus.

To ensure that the treatments differed, the macroalgal community composition within each plot (nearby community) was examined using nonmetric multidimensional scaling (nMDS) based on a Bray–Curtis dissimilarity matrix of the taxa per cent cover data (Table 1; Supplementary Fig. 2) and tested via permutational multivariate analysis of variance (PERMANOVA). This analysis confirmed that the macroalgal communities in our manipulated plots differed among treatments (PERMANOVA *p* value < 0.01). These analyses were performed using the *vegan* package in R (Oksanen et al. 2020).

To quantify the structure of the macroalgal community, we recorded the height and density of the macroalgal canopy in each plot (i.e. “nearby”) and the height of the canopy in

Table 1 Per cent cover of macroalgal taxa (means and SE across the 10 plots per treatment), turf, and CCA

Treatment	Macroalgal genus, turf, CCA
T1—‘No macroalgae’ (0%)	Turf (63% ± 13 SE)
T2—‘Canopy-forming’ (69.3%)	*Sargassum* (69.3% ± 11.2 SE) Turf (0.9% ± 1 SE)
T3—‘Understorey’ (34.1%)	*Colpomenia* (10.7% ± 6.3 SE), *Hypnea* (10.2% ± 4.1 SE), *Lobophora* (7.9% ± 3 SE), *Gelidiopsis* (2% ± 1.3 SE), *Asparagopsis* (1.2% ± 1.2 SE), *Galaxaura* (1% ± 0.8 SE), *Halimeda* (0.6% ± 0. 5 SE), *Padina* (0.4% ± 0.3 SE), *Dictyota* (0.1% ± 0.1 SE) Turf (47.6% ± 7 SE), CCA (6.6% ± 3 SE)
T4—‘Mixed-algae community’ (78.7%)	*Sargassum* (62.7% ± 7.2 se), *Colpomenia* (6.4% ± 2.1 SE), *Hypnea* (3.1% ± 1.8 SE), *Halymenia* (3% ± 3 SE), *Asparagopsis* (1% ± 1 SE), *Galaxaura* (1% ± 1 SE), *Lobophora* (0.6% ± 0.4 SE), *Dictyota* (0.5% ± 0.3 SE), *Padina* (0.4% ± 0.3 SE) Turf (2% ± 2 SE), CCA (0.2% ± 0.2 SE)

The percentage next to the treatment name is the total macroalgal cover for that treatment contact with the edges of each tile (i.e. "contact") at the time of tile deployment (September). Canopy height was measured by averaging the height of five randomly chosen thalli of canopy-forming macroalgae (i.e. *Sargassum*, *Turbinaria*, and *Sirophysalis*). If < 5 thalli were present, the height of all thalli was measured and averaged. The density of the macroalgal community was estimated by counting the number of canopy-forming thalli within each 1 m^2 plot.

Natural coral size frequency distribution in Florence Bay

To investigate the effect of the macroalgal structure and canopy height on the density of juvenile and small corals on natural substrata in Florence Bay, benthic surveys were conducted by divers on SCUBA at six-week intervals between September 2022 and August 2023. Benthic surveys were carried out across Florence Bay at three depths: reef flat (0–1 m), reef crest (2–3 m), and reef slope (4–5 m) (relative to mean tide). At each depth, three 30-m transects were placed parallel to the reef crest with a minimum of 5 m between adjacent transects. The beginning and end of each transect were marked using GPS coordinates. Five 1 m × 1 m quadrats were placed along each transect at 6-m intervals on the landward side to ensure that the same area was surveyed at each visit. Within these plots, macroalgae were identified to the genus, and their per cent cover was recorded. The height and density of canopy-forming macroalgae were also measured in each quadrat at 6-week intervals during the tile deployment (i.e. September 2022 to February 2023), as described above. The density and size of corals within each plot were quantified in August 2023. The timing of these coral surveys was selected to coincide with a low cover and height of canopy-forming macroalgae, enhancing the detection of small corals. In each quadrat, the diameter of every coral was measured and later grouped into three class sizes: 1–20 cm, 21–40 cm, and > 40 cm. Each coral was identified to the genus level.

Statistical analysis

All statistical analyses were performed in the R (version 4.3.0) Statistical and Graphical Environment (R Core Team 2024). All plots were produced using the *ggplot2* package.

The relationship between the number of coral recruits on each tile and the potential predictor variables was explored in a Bayesian framework using the *brms* package (Bürkner 2021) fitted in STAN (Stan Development Team 2024). The number of recruits was modelled against predictor variables in separate models to avoid collinearity (i.e. treatment, turf height–ordered factor, canopy height, canopy density, and macroalgal taxa) with a zero-inflated Poisson family and weakly informative priors (see below). All models used the grazing level (ordered) on each tile as a varying effect (random effect in frequentist analysis). All Bayesian models included three No-U-Turn (Markov chain Monte Carlo, MCMC) chains, each of 5000 iterations, thinned to a ratio of 5, and excluded the first 1000 iterations (warmup). MCMC were found to be well mixed and converged ($\text{Rhat} < 1.01$) on a stable posterior using trace plots, autocorrelation plots, Rhat and effective sample size diagnostics. Models were validated via DHARMa simulated residuals (Hartig 2021) and posterior probability checks.

Five models were fitted: one for the treatment and turf, three for the community structure, and one for the community composition. To examine the effect of the benthic community structure and composition at two spatial scales ("nearby" versus "in contact") on coral recruitment, we modelled the number of recruits against canopy height at the two spatial scales using two separate models due to collinearity between the two community structure variables. Coral recruitment was modelled against canopy density (only in the "nearby") in a separate model to avoid collinearity with canopy height. Finally, coral recruitment was modelled against the most common macroalgal genera in the plots (i.e. *Sargassum, Lobophora, Hypnea,* and *Colpomenia*). Model comparison was conducted using the leave-one-out information criterion (LOOIC) using Pareto smoothed importance sampling via the *loo* package (Vehtari et al. 2017).

The *emmeans* package was used to interrogate all model outputs (Lenth 2023). The relative effect of all predictors was inferred from Bayesian credibility intervals (CIs) based on the median highest density continuous interval (HDCI) as a measurement of uncertainty and exceedance *P*. Exceedance *P* is the probability that a certain value will be exceeded in a predefined situation a and was used as a metric of occurrence of a given event. To further investigate the models, the proportion of the HDCI of the posterior distribution that lies within the region of practical equivalence (ROPE) was computed to test similarities between treatments based on a 10% interval (Makowski et al. 2019).

To assess whether the density of coral class sizes on natural substrata was related to the macroalgae community in Florence Bay, the number of coral colonies per transect grouped into class sizes (1–20 cm; 21–40 cm; > 40 cm) was modelled against *Sargassum* height, canopy density, and cover of common macroalgal taxa using Bayesian Cumulative Link Mixed Models (CLMM). CLMMs were selected as they allow an ordinal response variable (i.e. class sizes) and the inclusion of varying effects (i.e. coral genus). The models (one for community height and density and one for community composition) were built via the *brms* package (Bürkner 2021) fitted in STAN (Stan Development Team 2024) using weakly informative priors. The model included three chains, each of 5000 iterations, thinned to a ratio of 5, and excluded the first 1000 iterations (warmup). The model was checked and validated using trace plots, autocorrelation plots, Rhat, effective sample size diagnostics, DHARMa simulated residuals (Hartig 2021) and posterior probability checks as explained above. The *emmeans* (Lenth 2023) and *tidybayes* (Kay 2023) packages were used to interrogate model outputs.

Results

Coral recruitment on tiles

Coral recruitment to the tiles was low (range: 0–3 coral recruits per tile). The number of recruits varied among treatments, with the highest number of recruits found on tiles in the understorey treatment (median: 1 recruit/tile; CI 0–3 recruits/tile; Fig. 2a), while the lowest number of recruits was recorded on tiles in canopy-forming algae and mixed-algae community treatments (median: 0 recruit/tile; CI 0–1 recruits/tile; Fig. 2a). There was strong evidence that the

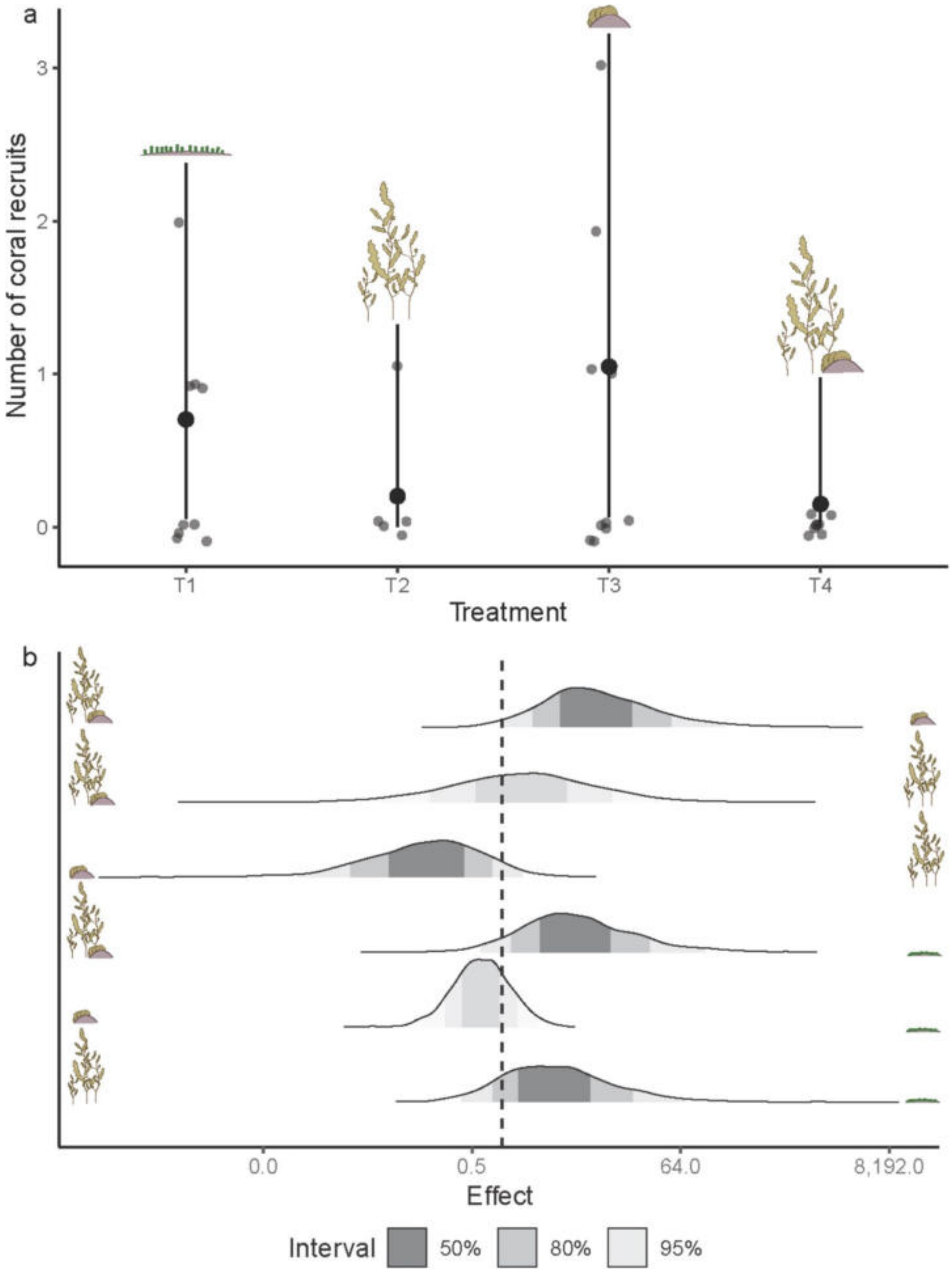


Fig. 2 Coral recruitment on PVC tiles. **a** Marginal effects plots showing the effect of different macroalgal treatments on coral recruitment in Florence Bay. Coral recruitment was modelled against treatment and turf height using Bayesian hierarchical generalised models, and the estimated means were marginalised for macroalgal treatment. The bars indicate the 95% credibility interval based on the highest posterior density interval (HDI). The grey points are the observed number of recruits. **b** Pairwise contrasts among the four macroalgal treatments showing the posterior HDI. The vertical dashed line represents the cutoff above which more recruits were found in the treatment depicted with the symbol on the right side of the vertical line. **a** and **b** The icons represent each treatment: ‘no macroalgae’ (T1), ‘canopy-forming’ (T2), ‘understorey’ (T3), and ‘mixed-algae community’ (T4)

presence of canopy-forming algae (T2/T4 vs T1/T3) reduced the recruitment of coral to the tiles by 84%. However, there was no evidence that understorey algae alone reduced coral recruitment relative to the no macroalgae treatment (T3 vs T1; Fig. 2b). The height of turfs on each tile did not affect coral recruitment.

When comparing the models with the canopy height of the nearby versus in-contact macroalgal community, the LOOIC of both models were similar (nearby community model LOOIC: 59.4 ± 11.8 SE; in contact community model LOOIC: 59.1 ± 11.6 SE). For consistency, we used the model with the nearby macroalgal community for the rest of the analysis, as this approach allowed us to incorporate canopy density, which was only estimated for the nearby community. We found strong evidence that canopy height and thallus density were negatively related to coral recruitment (Fig. 3). However, neither model (number of coral recruits ~ *Sargassum* height and number of coral recruits ~ *Sargassum* density) performed better than the other with similar LOOIC values.

The most common macroalgal taxa in our plots were *Sargassum* (T2 and T4)*, Colpomenia* (T3 and T4)*, Lobophora* (T3)*,* and *Hypnea* (T3 and T4) (Table 1). When investigating the specific effect of individual macroalgal genera, we found strong evidence that higher *Sargassum* and *Lobophora* cover were both associated with lower recruitment, but the effect size of *Sargassum* was greater than that of *Lobophora* (Fig. 4a-b). Other common genera, such as *Hypnea* and *Colpomenia,* had no discernible effect on coral recruitment (Fig. 4c-d).

Natural coral size frequency distribution in Florence Bay

A total of 96 coral colonies were recorded across the three transects and three habitat zones in Florence Bay, with only five of these colonies being < 5 cm in diameter (i.e. juveniles). The probability of occurrence of each coral class size varied depending on the density and height of the surrounding canopy-forming macroalgae (Fig. 5a-b). The probability of observing small corals (1–20 cm) decreased as the canopy height increased. Specifically, the probability of observing corals < 20 cm decreased to < 0.1 when the height of canopy-forming algae (primarily *Sargassum*) reached ~ 50 cm. In comparison, larger corals (> 40 cm) were more likely to be found in quadrats with a high canopy. Similarly, there was some evidence that the probability of observing smaller corals decreased as *Sargassum* density increased.

In terms of macroalgal community composition, we specifically tested whether the natural occurrence of coral class sizes was related to the abundance of key taxa identified in our experiment. Specifically, we investigated the effect of *Sargassum* and *Lobophora*, as these two genera reduced coral recruitment (Fig. 4a-b). There was strong evidence that higher cover of *Sargassum* reduced the probability of observing small (1-20cm diameter) corals (Fig. 5c). There was no evidence of a similar pattern with the cover of *Lobophora,* and this taxon had no effect on the frequency of coral class sizes (Fig. 5d).

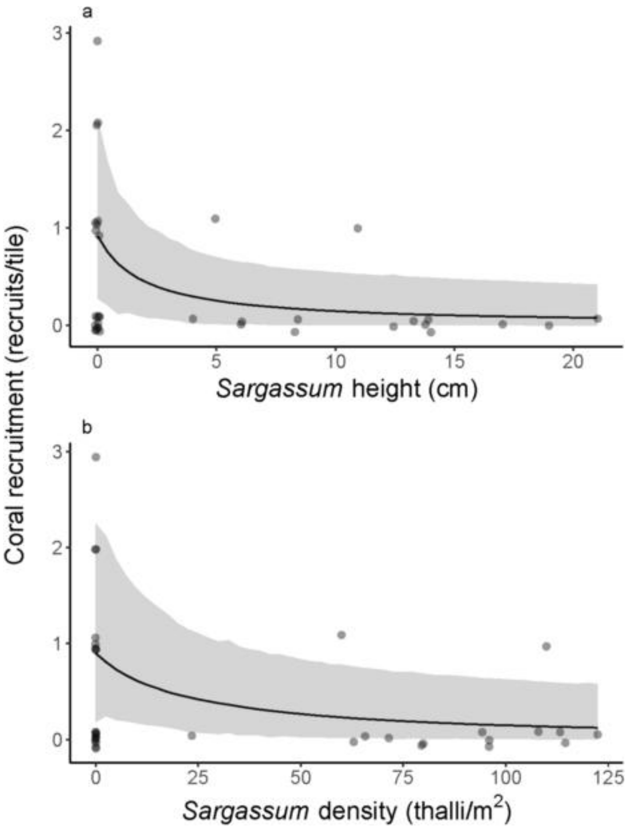
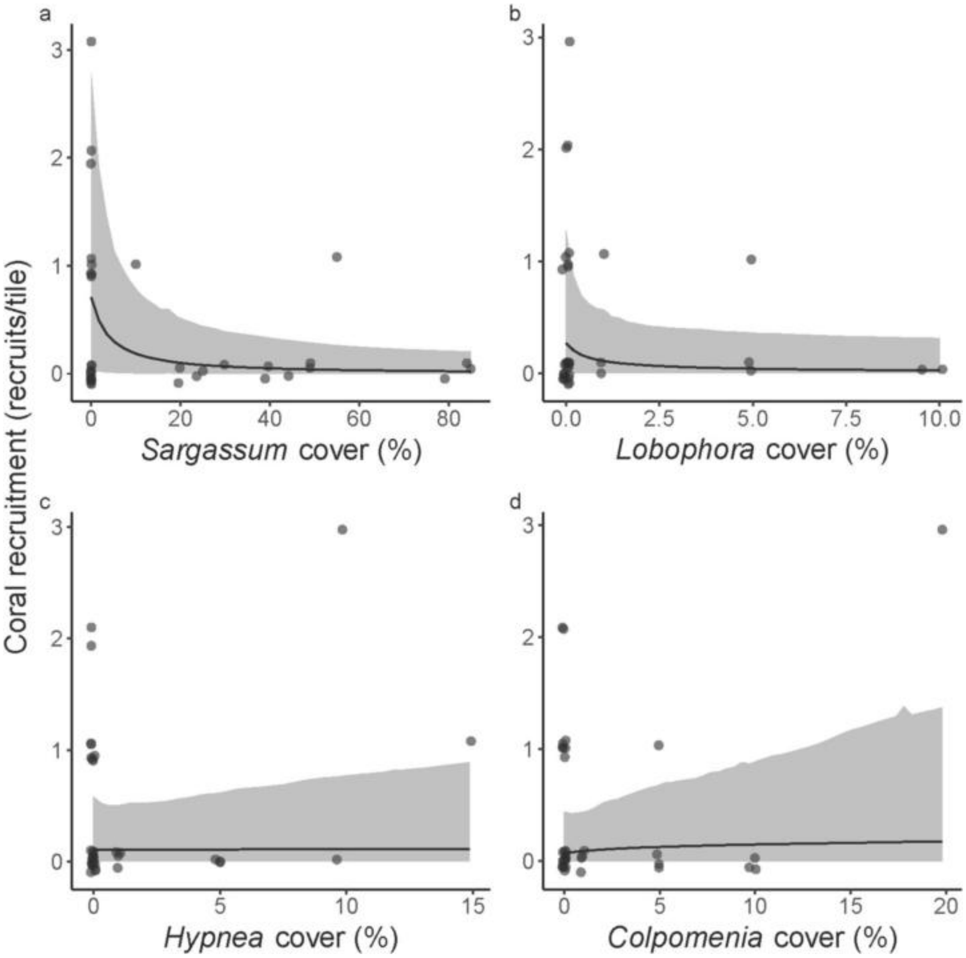


Fig. 3 The relationship between *Sargassum* height (**a**) and density (**b**) and coral recruitment. *Sargassum* height is the average canopy height in the 1 m^2 quadrats surrounding each tile. The number of coral recruits on each tile was modelled against *Sargassum* height and density using Bayesian hierarchical generalised models. The grey ribbons indicate the 95% credibility interval based on the highest posterior density interval. The points indicate the observed number of coral recruits per tile. *Sargassum* height and density were recorded at the time of tile deployment in September 2022

Discussion

Numerous studies have reported negative effects of macroalgae on the recruitment of corals; however, few, if any, have considered the relative effects of canopy-forming versus understorey macroalgae on coral recruitment. We show that coral recruitment varies at fine spatial scales depending on the nearby macroalgal community on a turbid inshore reef in the central GBR. We found that canopy-forming macroalgae reduced coral recruitment on tiles by 80%, whereas the

Fig. 4 The relationship between coral recruitment and cover of *Sargassum* (**a**), *Lobophora* (**b**), *Hypnea* (**c**), and *Colpomenia* (**d**). The number of corals on each tile was modelled against the macroalgal taxa using a Bayesian hierarchical generalised model. The grey ribbons indicate the 95% credibility interval based on the highest posterior density interval. The points indicate the observed number of coral recruits



presence of understorey macroalgae had no detectable effect on coral recruitment compared to plots free of all macroalgae. Interestingly, the density and height of canopy-forming macroalgae had a similar effect on coral recruitment. Finally, two macroalgal taxa, *Sargassum* and *Lobophora*, reduced coral recruitment. Trends similar to our experimental study were observed in the natural size frequency distribution of corals in Florence Bay, suggesting that both the flexible barrier created by macroalgal canopies and their composition are important mechanisms limiting coral recruitment on reefs with high macroalgal cover.

The observed variation in coral recruitment on tiles was primarily driven by the presence of *Sargassum* in the plots. In fact, the greatest difference in recruit number was found when plots with canopy-forming macroalgae (canopy and mixed-algal communities dominated by *Sargassum*) were compared to those without (no macroalgae and understorey macroalgae). Similarly, previous studies have reported that upright canopy-forming macroalgae such as *Sargassum* limit coral settlement and recruitment. Specifically, Webster et al. (2015) found a 93% reduction in coral settlement under the *Sargassum*-dominated canopy in caged treatments on Ningaloo Reef (central Western Australian Coast) after 9 months. Hughes et al. (2007) found lower recruitment of coral to natural substrata within large (25 m^2) herbivore exclusion cages that had a dense canopy of *Sargassum* (5–8 kg/m^2) compared to control plots that were largely free of macroalgae over a 3-year experiment on Orpheus Island (inshore central GBR). Similarly, *Sargassum* has been shown to reduce the settlement of coral planulae to only 0.6% in a 2-week lab experiment (Vermeij et al. 2009) and to reduce coral settlement by ~ 60% in a 24-h lab experiment (Leong et al. 2018), although the mechanisms driving these changes were not explored.

These interactions between coral larvae and canopy-forming macroalgae may be related to the physical properties of *Sargassum*. Specifically, *Sargassum* and other canopy-forming macroalgae form flexible barriers that may alter water flow and/or drive mechanical abrasion, inhibiting coral larvae from reaching the substratum. For example, Diaz-Pulido et al. (2010) found that aquarium plastic mimics (8 cm height, resembling *Halimeda* spp.) strongly reduced settlement of *Platygyra daedalea* compared to other macroalgae such as *Hypnea*, with only 3% of corals settled after

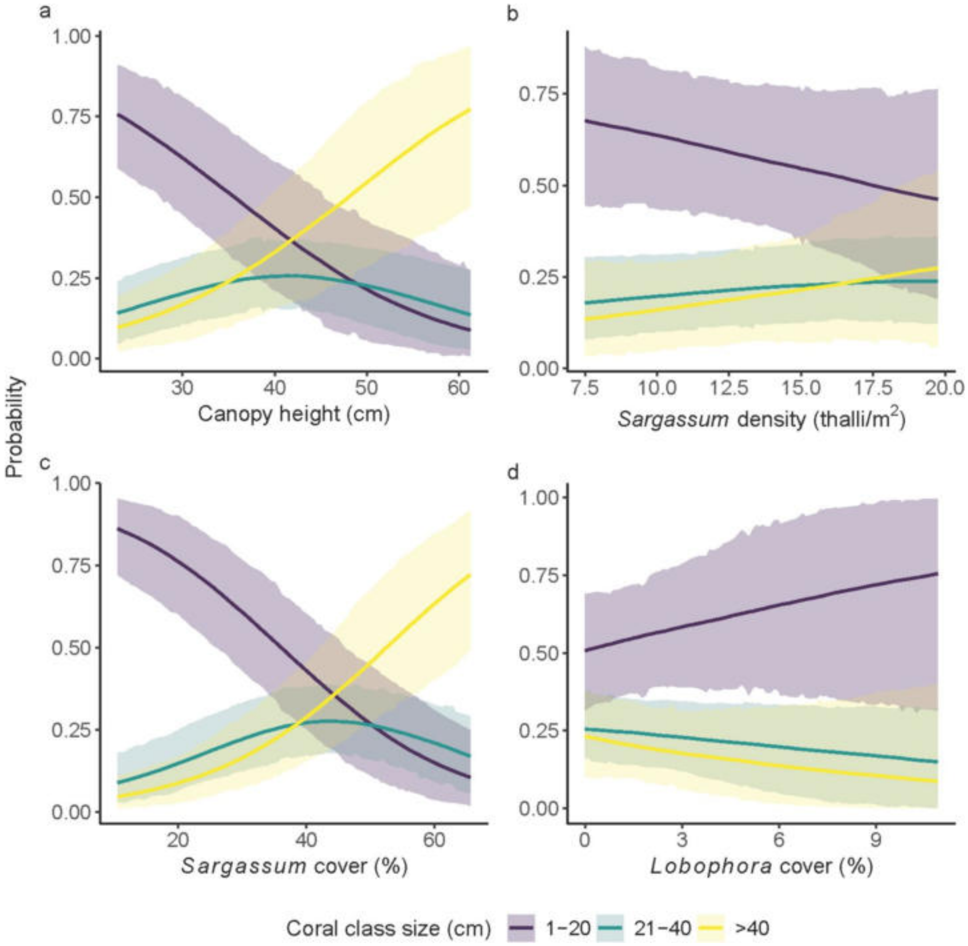


Fig. 5 The probability of occurrence of coral class sizes in relation to canopy height (**a**), *Sargassum* density (**b**), *Sargassum* cover (**c**), and *Lobophora* cover (**d**). The density of coral class sizes was modelled against the predictors using a Bayesian Cumulative Link Mixed Model. Colours represent coral class sizes, and the shaded ribbon indicates the 95% credibility interval based on the highest posterior density interval. Canopy height is the average canopy height in summer (6-weekly surveys from September 2022 until February 2023) in Florence Bay for the 1 m^2 quadrat in which each coral was recorded, while the cover of *Sargassum* and *Lobophora* is the average per cent cover of that genus in summer in each quadrat

8 days post-spawning compared to 30% in the treatment with the CCA *Porolithon onkodes* or mixed turf, with the authors suggesting this was related to the physical structure of the mimic. On the contrary, Kuffner et al. (2006) found that algal mimics (seawater-conditioned plastic aquarium plants) did not affect the settlement of *Porites astreoides* in aquaria. Moreover, our study showed that it was not simply the presence of *Sargassum* that affected coral recruitment but rather the height and density of canopy-forming algae. Similarly, another recent study in Florence Bay observed a negative relationship between *Sargassum* biomass and the number of coral recruits on the reef slope (Smith et al. 2022).

Interestingly, we found that understorey algae had little effect on coral recruitment. The most abundant algae in the ‘understorey’ treatments were *Colpomenia*, *Hypnea* and *Lobophora*, with a total of ~ 30% cover. While *Colpomenia* and *Hypnea* had no detectable effect on coral recruitment, *Lobophora* was negatively associated with the number of recruits on tiles despite its relatively low abundance in our plots (mean ~ 8% cover). In fact, *Lobophora* is considered a highly allelopathic alga (Morrow et al. 2017; Rasher & Hay 2010; Slattery & Lesser 2014; Vieira et al. 2016), and dense beds of *Lobophora* have been related to reduced recruitment of corals to terracotta tiles on Havannah Reef, approximately 45 km north of our study site (Johns et al. 2018). Similarly, *Acropora palmata* and *Pseudodiploria strigosa* larvae experienced reduced survival but no effect of settlement or metamorphosis when exposed to *Lobophora* in a field study in the Caribbean (Ritson-Williams et al. 2020). In laboratory studies, *Lobophora* sp. has been shown to inhibit the metamorphosis of larvae of *Stylophora pistillata* and *Acropora palifera* (Baird & Morse 2004), while settlement and survival of multiple *Acropora* species were reduced when exposed to *Lobophora* (Evensen et al. 2019a, b). Despite its negative effect on coral recruitment, we found that *Lobophora* had no effect on the natural occurrence of small corals (up to 20 cm) on Florence Bay. Similarly, Johns et al. (2018) found no difference in the density of juvenile corals between *Lobophora*-dominated habitats and areas free of *Lobophora* on Havannah Island (inshore central GBR), suggesting that the negative effect of this macroalga is stronger on coral larvae than on settled corals.

Many other understorey macroalgae have been shown to cause partial mortality of adult corals (Rasher & Hay 2014). However, evidence for their effects on coral recruitment is taxon-specific. Previous experiments isolating *Hypnea* suggest that this taxon does not have a strong effect on coral settlement (Diaz-Pulido et al. 2010; using algal extracts: Fong et al. 2019), and only one laboratory study observed a slight reduction in settlement rates in treatments with *Hypnea* compared to controls without macroalgae (Leong et al. 2018). We are unaware of any studies that have investigated the effect of *Colpomenia* on coral recruitment. *Dictyota*, a widespread understorey macroalgae that was rare in our study site (< 1%), has been shown to inhibit coral recruitment (Kuffner et al. 2006; Paul et al. 2011).

The negative effect of high *Sargassum* cover as well as tall and dense macroalgal canopy on coral recruitment was also found in the natural occurrence in coral class sizes in Florence Bay. While this result confirms our experimental study, it is important to point out that our data on coral size-frequency distribution in Florence Bay are based on surveys carried out between 0 and 5 m. As shallow reef areas typically present fewer recruits (Turner et al. 2018) and macroalgal canopy is highest between 0 and 3 m on Florence Bay, the negative effect of canopy height on the density of small coral juveniles on natural substrata may also be due to depth-related patterns in coral recruitment. Low recruitment on shallow reef areas could also explain the low number of recruits found on our tiles (up to 3 recruits/tile) as the tiles were deployed at ~ 3 m depth. Recruitment is also generally lower on inshore reefs on the GBR. For example, another study found a maximum of 9 recruit/tile after two years of deployment in the central GBR (Drake et al. 2025). Moreover, high sedimentation in the bay could have masked settlement cues and/or directly impacted coral recruits (Birrell et al. 2005; Drake et al. 2025), thus contributing to the overall low recruitment observed in our study.

While our study did not directly test the effect of macroalgal communities on coral post-settlement and early-life stage survival, it does suggest that the presence of tall and dense macroalgal canopies, as well as the presence of *Sargassum* and/or *Lobophora*, is negatively associated with coral recruitment. Moreover, these patterns were also observed in the natural coral size frequency distribution of smaller corals in Florence Bay, suggesting that the processes identified in our study drive, at some point, coral replenishment dynamics. We suggest that further studies isolating the physical properties of macroalgal canopies and tracking newly settled corals over longer periods could be useful in identifying key mechanisms underlying low coral replenishment on macroalgal-dominated reefs.

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Author contributions All authors conceived the study and contributed to the development and design. MB led the field sampling, statistical analysis and writing. All authors contributed to the reviewing and editing of the manuscript.

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Data availability Data used for this this study is available from ResearchData, James Cook University: https://research.jcu.edu.au/data. The code is available at https://github.com/martinaburgo/coral-settlement-algal-habitats.

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Declarations

Conflict of interest The authors declare no known competing financial or personal conflicts that are relevant to the information discussed in this manuscript.

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