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REPORT

The influence of *Sargassum* biomass and thallus density on the recruitment of coral reef fishes

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Abstract A habitat's structural complexity is a key determinant of the recruitment and composition of associated communities. While the influence of the physical structure of corals on coral reef fish recruitment is well studied, the significance of other benthic components, like macroalgae, remains unclear. We used experimental patches of the canopy-forming macroalga *Sargassum* to assess the influence of macroalgal complexity, which was manipulated by altering thallus density and biomass, on coral reef fish recruitment. We established twenty-five 75 × 75 cm patches on the reef flat of Orpheus Island, (inshore, central Great Barrier Reef) during austral summer. Patches were randomly divided into five treatments of varying *Sargassum* thallus density (3–9 thalli) and/or biomass (177–779 g per patch) and surveyed daily for recruiting fishes for 18 d. We recorded 35 fish species recruiting to our patches, with *Sargassum* biomass having the greatest influence on fish recruits' abundance and species richness. Comparisons between treatments with equal thallus density but varying biomass revealed a positive association between *Sargassum* biomass and fish species richness and abundance (up to ~ 2.5-fold differences). Additionally, treatments with similar total *Sargassum* biomass but different density revealed a negative relationship between density and fish species richness and abundance (20–30% reduction). These positive associations with *Sargassum* thallus biomass suggest that recruiting fishes favour the fine-scale complexity of intra-thallus spaces, rather than the larger, inter-thallus gaps. This study highlights that fine-scales of complexity within tropical macroalgal beds may influence the reef fish recruitment value of these often-underappreciated areas.

Keywords Macroalgae · Structural complexity · Juvenile fish · Habitat quality · Macroalgal canopy

Introduction

Habitat structural complexity has been recognised as a key driver of species distributions across a range of habitats and spatial scales (MacArthur and MacArthur 1961; Hixon and Beets 1993; Downes et al. 1998). On local scales, habitats of higher structural complexity are generally associated with greater numbers of species (e.g., MacArthur and MacArthur 1961; McCoy et al. 1991; Downes et al. 1998). On tropical reefs, fish diversity (Roberts and Ormond 1987; Darling et al. 2017), abundance (Graham and Nash 2013; Darling et al. 2017), assemblage composition (Agudo-Adriani et al. 2016; Darling et al. 2017) and size distributions (Wilson et al. 2010b, 2022; Nagelkerken et al. 2015) have each been linked to measures of structural complexity. However, the majority of studies have focussed on the rigid complexity provided by coral skeletons, with fewer studies investigating the complexity of other habitat-forming taxa, such as soft corals (Rilov et al. 2007; Moynihan et al. 2022), sponges

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(Coppock et al. 2022) and macroalgae (Fulton et al. 2020), whose structure can also influence fish assemblages.

Fishes living within tropical, shallow-water seascapes persist in spatially and temporally dynamic complex mosaics with a diverse array of habitats available at any given time (Chong-Seng et al. 2012; Guest et al. 2016; Sambrook et al. 2019). For larval and recently-settled fish that are vulnerable to predation (e.g., Jones 1990; Webster 2002; Hoey and McCormick 2004), selection of suitable habitat is critical for survival to juvenile and adult life stages (Nemeth 1998; Aburto-Oropeza et al. 2007). Fish population sizes, and the ecosystem services they provide (e.g., fisheries production; Wilson et al. 2022), can therefore be linked to the availability of suitable recruitment habitats (Doherty 2002; Aburto-Oropeza et al. 2007; Nagelkerken et al. 2015; Wilson et al. 2016). Within tropical seascapes, suitable habitats may include the solid structures of corals (e.g., Coker et al. 2014) or mangroves (Faunce and Serafy 2006), or the flexible structure of seagrasses (Dorenbosch et al. 2005) or macroalgae (Eggertsen et al. 2017; Tano et al. 2017; Fulton et al. 2020). Positive relationships between recruiting fishes and macroalgae are long established in the temperate reef literature (e.g., Russell 1977; Jones 1984; Levin 1994), and now increasingly also in tropical marine ecosystems (e.g., Fulton et al. 2020; Tang et al. 2020). However, much remains to be understood about the characteristics of macrophytes, such as tropical macroalgae, that attract fishes in their vulnerable juvenile stages.

Beds of canopy-forming macroalgae provide a productive and unique habitat for an array of reef organisms, and recognition for their role in the provision of habitat for fishes, particularly juvenile fishes, has recently grown (Eggertsen et al. 2017; Tano et al. 2017; Fulton et al. 2020). For example, data from six Indo-Pacific locations demonstrated that up to 49% of tropical reef fish species associated with macroalgal canopy habitats in their juvenile life stage (Fulton et al. 2020). In temperate reef systems, where most juvenile fish—macroalgal habitat association studies have been conducted, the structural complexity of these habitats is widely viewed as a key component of such relationships (Carr 1994; Levin and Hay 1996). In contrast to corals, upright macroalgae typically provide a visual, but not physical barrier, which has been suggested to reduce use of these habitats by some species due to increased risk of predation (Hoey and Bellwood 2011). However, in seagrass beds, another flexible macrophyte habitat, structural characteristics such as macrophyte density, biomass and surface area have been shown to be positively related to the abundance and composition of fish assemblages by moderating predation (Heck and Orth 2006). In addition to provision of shelter, macroalgal beds, like seagrass, may support abundant prey, including epiphytic algae (Ceccarelli et al. 2005; Bittick et al. 2019) and invertebrates (Carvalho et al. 2018; Wenger et al. 2018; Chen et al. 2022). While some studies have associated epibiotic and nektonic assemblages with various features of macroalgae (Wenger et al. 2018; Chen et al. 2020; Tang et al. 2020), relatively few have directly investigated the influence of macroalgal structural complexity on the recruitment of coral reef fish. In particular, relationships between fine-scale, intra-thallus structural characteristics of tropical macroalgae (i.e., the foliage and branch structures of canopy-forming algae) and fishes are difficult to infer from the literature, as studies typically focus on coarse macroalgal structural metrics such as per cent cover (Eggleston 1995; Chaves et al. 2013; Sievers et al. 2020b), or less commonly thallus density (Wilson et al. 2017; Wenger et al. 2018; Bittick et al. 2019; Tang et al. 2020) and/or canopy height (Evans et al. 2014; Wilson et al. 2014; Lim et al. 2016; van Lier et al. 2018; Tang et al. 2020). As an organism's perception and use of its environment depends on its body size (Levin 1992; Gee and Warwick 1994), intra-thallus complexity may be particularly relevant to small and juvenile macroalgal-associated fishes.

Here, we empirically tested relationships between recruitment of coral reef fishes and macroalgal patch complexity at a fine, intra-thallus scale (thallus biomass), and a coarser inter-thallus scale (thallus density). This was achieved using a field experiment which manipulated the thallus biomass and density of the macroalga *Sargassum* in experimental patches. Based on the small size of recruiting fishes we expect that manipulation of fine, intra-thallus complexity, i.e., thallus biomass, would have a greater influence on fish recruitment than manipulation of thallus density. More specifically, we predicted the following:

Prediction 1 Recruit abundance and species richness will be positively related to *Sargassum* biomass when density is constant.

Prediction 2 Recruit abundance and species richness will not vary with *Sargassum* density when biomass is similar.

Methods

This study was conducted in Pioneer Bay, Orpheus Island (18.606° S, 146.487° E), an inshore island in the central Great Barrier Reef (GBR), during November–December 2022. The timing of the study was selected to coincide with the peak in the settlement of reef fish (i.e., following a new moon during the austral Spring–Summer; Williams and Sale 1981; Meekan et al. 1993), and to ensure the *Sargassum* hadn't started to senesce (Lefèvre and Bellwood 2010).*Sargassum* thalli to be used in the experiment were collected from the reef flat of Pioneer Bay, and Hazard Bay, approximately 1 km to the south of Pioneer Bay. Thalli of approximately equal height were removed from the substratum using a paint scraper including as much of the holdfast as possible. Collected thalli were placed in a mesh bag and transported immediately to a raceway with fresh flow-through seawater at Orpheus Island Research Station, where thalli from the two collection sites were mixed. Each thallus was rinsed in filtered seawater to remove any sediments and particulates, spun in a salad spinner for 10 s, and the fresh weight and maximum height recorded. Each thallus was then randomly assigned to a patch in one of five treatments that differed in *Sargassum* biomass and/or thallus density: high density-high biomass (D9BH); high density-medium biomass (D9BM); high density-low biomass (D9BL); medium density-high biomass (D5BH); and low density-high biomass (D3BH, Table 1). The high, medium and low density treatments consisted of nine, five and three *Sargassum* thalli, respectively, positioned evenly throughout the patches. The biomass treatment relates to the biomass of the individual *Sargassum* thalli, with the high biomass being unmanipulated (86.5–103.0 g thallus^{-1}), and the medium (43.1 g thallus^{-1}) and low (18.6 g thallus^{-1}) being approximately 50 and 25% of the unmanipulated biomass (Table 1). Biomass manipulations were achieved by removing primary and/or lateral branches with scissors. Thallus heights were similar (29.2 ± 2.4 cm; mean length ± SE; Table 1) among treatments after this manipulation. Individual thalli were then attached to a small, numbered lead weight (*ca.* 110 g) for deployment into patches.

Twenty-five patches (five per treatment, each 75 cm × 75 cm) were established on areas of rubble that were relatively free of live coral or canopy-forming algae on the mid-reef flat (approximately 60 m from the reef crest, and at a depth of *ca.* 0.1 m below Mean Low Water Spring). The tidal regime at the time of study was such that this habitat was exposed on 12 occasions after deployment for up to 3 h between 23:00 and 05:00, i.e., never during daylight hours. This habitat was chosen as it coincides with the natural distribution of *Sargassum* at the study location (Fox and Bellwood 2007), while also ensuring patches were at least 10 m from naturally occurring *Sargassum* stands. Patches were positioned within a 5-m wide band parallel to the reef crest following a random sequence of treatments, with a minimum of 5 m between adjacent patches. The patches were established on the reef flat on the 20th November 2022, several days prior to the new moon to pre-empt the predicted peak in settlement of reef fishes (e.g., Shima et al. 2018, Takemura et al. 2004).

Patches were first surveyed on the morning of the 25th November (immediately following the new moon) and each morning for 18 d (until 12th December). A diver (always KW) thoroughly and systematically searched each patch for any fish that had recruited to the patches. Each patch was approached slowly, and visually conspicuous fishes surveyed from a distance of ~ 1 m, before examining each *Sargassum* thallus and then gently moving each thallus to facilitate detection of any fishes that were sheltering within its fronds (following Tang et al. 2020). The species identity of all observed fishes was recorded, and their total length (TL) estimated to the nearest 0.25 cm for those fishes ≤ 5 cm, and to the nearest cm for fishes > 5 cm TL. A fish was recorded if it was observed within the boundary (i.e., 75 × 75 cm area) of the patch and/or within 5 cm of an experimental algal thallus. Each day, the order in which patches were visited was randomised. Patch integrity was maintained daily, and any damaged thalli (presumably due to herbivory) was replaced with a similarly sized *Sargassum* thallus collected from Pioneer Bay (23 replacements).

Analysis

All analyses were conducted using R version 4.2.3 (R Core Team 2023). The abundance and species richness of fish assemblages that recruited to the patch reefs, and the abundance of the six most common species (*Halichoeres miniatus*, *Petroscirtes* sp., *Pomacentrus tripunctatus*, *Siganus doliatus*, *Lethrinus atkinsoni*, *Siganus fuscescens*) were modelled using Bayesian Poisson linear mixed models using the package "brms" (Bürkner 2017). The size (TL) of all fishes that had recruited to the patches was modelled using a Bayesian hurdle-Gamma linear mixed model using "brms". Treatment was incorporated into the models as a population level effect, while an individual patch identifier was incorporated as a group level, variance effect. Temporal autocorrelation was included in models as a first-order autoregressive (with Date as the time variable and individual

Table 1 Details of experimental *Sargassum* patch treatments

Treatment	Density patch^{-1}	*Sargassum* biomass thallus^{-1} (g, mean ± SE)	*Sargassum* biomass patch^{-1} (g, mean ± SE)	*Sargassum* thallus length (cm, mean ± SE)
D9BH	9	High—86.5 ± 3.6	High—778.8 ± 38.5	31.7 ± 0.8
D9BM	9	Medium—43.1 ± 1.0	Medium—387.6 ± 7.4	28.4 ± 0.6
D9BL	9	Low—18.6 ± 0.8	Low—167.7 ± 6.5	27.3 ± 0.5
D5BH	5	High—90.9 ± 4.4	Medium—454.5 ± 22.5	29.2 ± 0.8
D3BH	3	High—103 ± 5.4	Medium–Low—310.3 ± 15.4	29.5 ± 1.1

patch as the grouping variable) where there was evidence of autocorrelation of the residuals (all models except *Halichoeres miniatus* and *Siganus fuscescens* abundance and overall fish length models). These model specification details are also summarised along with R^2 values in Table S2. Bayesian models were fit with weakly informative priors (confirmed by comparing the prior and posterior distributions), with 10,000 iterations, a warmup of 2000 and a thinning factor of 10. Markov Chain Monte Carlo (MCMC) diagnostics were performed using the package "rstan" (Stan Development Team 2023) to ensure all chains were well mixed and converged (all 'Rhat' values < 1.05) with no autocorrelation. "DHARMa" (Hartig 2022) was used for residual diagnostics. Routines for generating simulations from "brms" models with "DHARMa" do not yet account for autocorrelation, leading to more conservative residual tests. These tests indicated underdispersion in several models (all except *Lethrinus atkinsoni* and *Siganus fuscescens* abundance and overall fish length), which may have led to wider credibility intervals for effect estimates and more conservative comparisons between treatments. Among treatment 'Key Contrasts' relating to Prediction 1 and 2 are displayed visually in Results (Figs. 1, 2). These are contrasts among the three treatments of equal density but varying biomass (D9BH, D9BM and D9BL), and between the treatments with varying density but approximately equal patch biomass (D9BM and D5BH), respectively.

Fish assemblage composition on the final day of observation was compared among treatments using Permutational Multivariate Analysis of Variance (PERMANOVA), using the function "adonis2" in the package "vegan" (Oksanen et al. 2022), and visualised using non-metric multidimensional scaling (nMDS). Analyses were based on a Bray–Curtis dissimilarity matrix of 4th-root transformed, Wisconsin double-standardised fish abundance data. This dissimilarity matrix was also tested for multivariate homogeneity of variance among groups, also using the package "vegan", to assess whether significant differences found using PERMANOVA could have been confounded by differences in multivariate dispersion (Anderson 2006). Species vectors were fitted onto the nMDS ordination using the function "envfit", also in "vegan", with 999 permutations. Vectors where the probability of a higher correlation ($P > r$) with nMDS axes was < 0.1 were displayed on the nMDS.

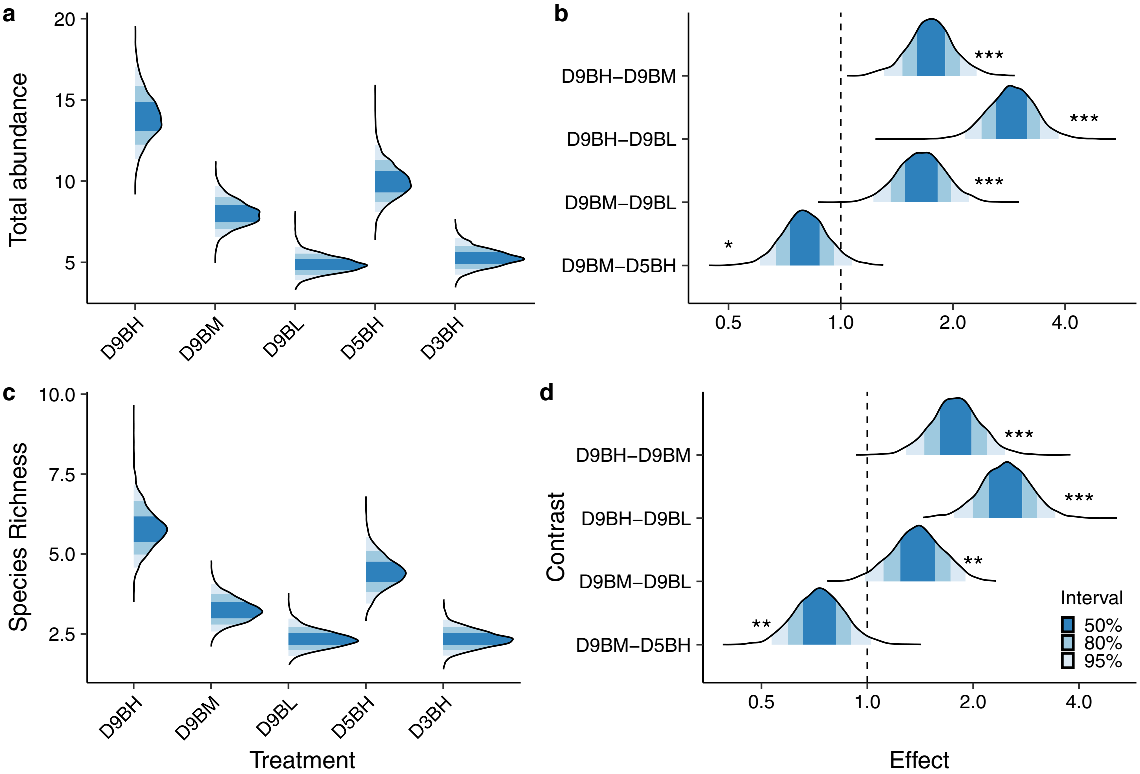


Fig. 1 Bayesian Generalised Linear Mixed Model (GLMM) estimated marginal means (EMMs) distributions of total abundance (**a**) and species richness (**c**) $\text{patch}^{-1}\text{day}^{-1}$ for each treatment and the distributions of EMMs of the four 'key' contrasts (note x axis is on the $\log_2$ scale) for total abundance (**b**) and species richness (**d**). Abbreviations in treatment names are as follows: "D9", "D5", "D3 = thallus densities of 9, 5 and 3 thalli per patch, respectively; "BH", "BM", "BL" = high, medium and low thallus biomass, respectively. Asterisks represent the strength of evidence of a difference: "***" = very strong evidence, ≥ 99% of draws; "**" = strong evidence, ≥ 95% of draws; "*" = evidence, ≥ 90% of draws. For EMM distribution plots of all Treatment contrasts, see Fig. S2

Results

A total of 3942 observations of 35 fish species were recorded over the 18-d study period. The species recorded most frequently were: *Halichoeres miniatus* (Labridae, 1862 observations), *Petroscirtes* sp. (Blenniidae, 587 obs.), *Pomacentrus tripunctatus* (Pomacentridae, 476 obs.), *Siganus doliatus* (*Siganidae*, 381 obs.), *Lethrinus atkinsoni* (Lethrinidae, 133 obs.) and *Siganus fuscescens* (*Siganidae*, 101 obs.) (Table S1). Each of these species were recorded on at least one patch on every survey day.

Based on our Bayesian modelling, total fish abundance (mean per patch, per day) was highest in high density, high biomass (D9BH) patches (predicted 13.94 individuals per patch, 95% Highest Posterior Density Interval [HPDI] 11.35–16.98; Fig. 1a), and lowest in high density, low biomass (D9BL) and low density, high biomass (D3BH) treatments where total abundance was approximately 2.5 times fewer (predicted: 4.85 and 5.26 individuals per patch, HPDI: 3.90–5.89, 4.23–6.48, respectively). High density, medium biomass (D9BM) and medium density, high biomass (D5BH) treatments had intermediate total fish abundance (predicted: 7.98 and 9.95 individuals per patch, HPDI: 6.57–9.69, and 8.07–12.17, respectively). Similarly, mean fish species richness (per patch, per day) was greatest in high density, high biomass (D9BH) patches (predicted 5.77 species per patch, 95% HPDI 4.53–7.05: Fig. 1c), while the high density, low biomass (D9BL) and low density, high biomass (D3BH) treatments had the lowest species richness with approximately 2.5 times fewer species (predicted: 2.33 and 2.34 species per patch, HPDI: 1.83–2.98, 1.79–2.91, respectively). The final Bayesian mixed effects models described the patterns in total abundance and species richness reasonably well, explaining approximately 64 and 54% of variance on average, respectively (Table S2).

Modelled mean abundance per patch, per day, of the six most common fish species was greatest on the high density, high biomass (D9BH) patches, however, high biomass (D5BH) patches had similarly high abundances in all except *Petroscirtes* sp. (Fig. 2). D5BH patches had intermediate abundances of *Petroscirtes.* sp. The treatment on which abundances were lowest varied among species: lowest abundances were recorded either on high density, low biomass patches (D9BL) (*H. miniatus*), low density, high biomass (D3BH) patches (*Petroscirtes* sp.), or were shared between D9BL, D3BH and high density, medium biomass (D9BM) patches (*P. tripunctatus*, *S. doliatus*, *L. atkinsoni*, *S. fuscescens*). Linear mixed effects models of the abundance of each species varied in the proportion of variance explained (R^2), ranging from approximately 55% (*Petroscirtes* sp.) to approximately 16% (*H. miniatus*) (Table S2).

Key contrast 1: varying biomass, constant density (D9BH—D9BM—D9BL)

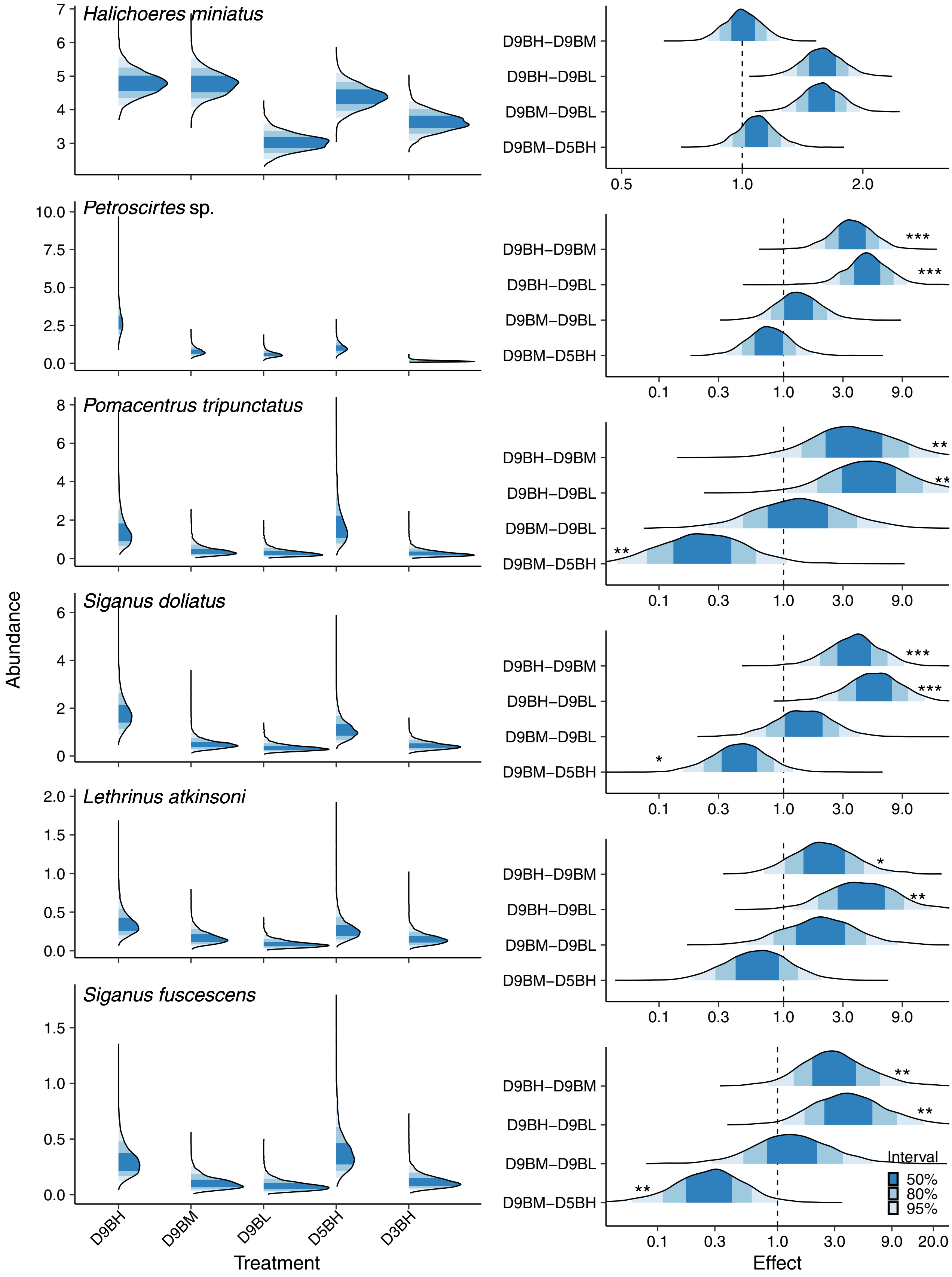
When comparing Bayesian model estimates for treatments D9BH, D9BM and D9BL, there was very strong evidence ($\geq$ 99% of model draws) that total fish abundance increased when *Sargassum* biomass increased independently of density (D9BH—D9BM, D9BH—D9BL and D9BM—D9BL contrasts, Fig. 1b). Average effect sizes of these contrasts ranged from 1.65 (D9BM—D9BL) to 2.53 (D9BH—D9BL). Similarly, there was strong ($\geq$ 95% of model draws) or very strong evidence of increased fish species richness with increased *Sargassum* biomass across the three constant density treatment comparisons (D9BH, D9BM, D9BL, Fig. 1d), with average effect sizes ranging from 1.39 (D9BM—D9BL) to 2.48 (D9BH—D9BL).

For each of the six most common species, there was always strong or very strong evidence to support greater abundance in the highest biomass patches compared to the lowest biomass patches at the same high density (contrast D9BH—D9BL Fig. 2, righthand column). For *H. miniatus*, there was also very strong evidence that the lowest biomass treatment (D9BL) had fewer individuals than treatments D9BM, but there was no evidence ($<$ 90% of model draws) that the highest biomass treatment (D9BH) had more individuals than the medium biomass treatment (D9BM). There was evidence ($\geq$ 90% of model draws) for each of the remaining modelled species that treatment D9BH had more individuals than D9BM, but no evidence of a difference when medium and low biomass was compared (D9BM–D9BL Fig. 2, righthand column).

Key contrast 2: varying density, similar patch biomass (D9BM–D5BH)

When comparing model estimates for treatments D9BM and D5BH, there was strong evidence that modelled total fish abundance was reduced when *Sargassum* density increased at similar patch biomass– on average, 20% fewer fishes overall were predicted on high density, medium biomass D9BM patches compared with medium density, high biomass D5BH patches (Fig. 1b). There was also strong evidence that D9BM patches contained fewer species compared to D5BH patches, with an average reduction of 27% (Fig. 1d).

There was evidence that the lower density patches (D5BH) had more individuals than D9BM in three of the six most common species (*P. tripunctatus*, strong evidence; *S. doliatus*, evidence; *S. fuscescens*, strong evidence, Fig. 2). For the other three of the most common species (*H. miniatus*, *Petroscirtes* sp., and *L. atkinsoni*), there was no evidence of a difference in abundance between D9BM and D5BH.


Halichoeres miniatus
Petroscirtes sp.
Pomacentrus tripunctatus
Siganus doliatus
Lethrinus atkinsoni
Siganus fuscescens
Abundance
Treatment
D9BH
D9BM
D9BL
D5BH
D3BH
D9BH–D9BM
D9BH–D9BL
D9BM–D9BL
D9BM–D5BH
Effect
0.5
1.0
2.0
0.1
0.3
1.0
3.0
9.0
20.0
***
**
*
Interval
50%
80%
95%

◂**Fig. 2** Bayesian Generalised Linear Mixed Model (GLMM) estimated marginal means (EMMs) distributions of the abundance of the six most common fish species (lefthand column) and the distributions of EMMs of the four 'key' contrasts for each species (righthand column, $\log_2$ scale). Asterisk s represent the strength of evidence of a difference: "***" = very strong evidence, $\geq$ 99% of draws; "**" = strong evidence, $\geq$ 95% of draws; "*" = evidence, $\geq$ 90% of draws. For EMM distribution plots of all Treatment contrasts, see Figure S2. *Note*: For ease of presentation, entire posteriors are not shown for all species

Assemblage composition

The composition of fish assemblages on the *Sargassum* patches at the end of the experimental period (day 18) differed among treatments (PERMANOVA $F = 2.571$, $P = 0.002$). The nMDS displays a separation of high density, high biomass (D9BH) patches from the other treatments (Fig. 3). D9BH patches were characterised by a higher abundance of several species, especially *S. fuscescens*, *Stethojulis interrupta* and *Stethojulis strigiventer*, while the other treatments were not typified by higher abundances of any particular species. There was no evidence that multivariate dispersion on day 18 differed among treatments (ANOVA $F = 0.987$, $P = 0.437$), indicating that the PERMANOVA result was unlikely to be confounded by dispersion differences (dispersion among Treatments presented graphically in Fig S3). However, visual inspection of the NMDS plot suggests a trend of higher similarity among D9BH patches compared to the other treatments, potentially due to fewer species with low but variable abundances in treatments with fewer or smaller *Sargassum* thalli (Fig. 3).

Discussion

Our results highlight the importance of intra-thallus features in influencing the recruitment of reef fish to macroalgae. Manipulation of *Sargassum* biomass to create differences in structural complexity at a fine spatial scale was a much better predictor of fish abundance and diversity than complexity measured at the coarser scale of thallus density. Species richness, total abundance and the abundance of all six of the most common species increased with the biomass of individual *Sargassum* thalli, supporting Prediction 1. However, contrary to expectation (Prediction 2), the comparison of two treatments with similar total patch *Sargassum* biomass (D9BM and D5BH), revealed that fish species richness, total abundance and the abundance of three of the six most common species were higher in the lower density treatment patches (D5BH), suggesting that patches with fewer, larger thalli with higher intra-thallus complexity were more attractive to fishes than those with more abundant, less complex thalli. *Sargassum* biomass and density manipulations also produced differences in assemblage composition among treatments, with high biomass, high density patches supporting fish assemblages with increased abundances of more species compared to the other treatments. These results invite comparison with studies from the coral reef literature, where corals with high intra-colony complexity (e.g. large colonies with many spaces between branches) can be especially beneficial for fish diversity and abundance (e.g., Kerry and Bellwood 2015; Pereira and Munday 2016; Fisher 2023) and studies in seagrass that show architectural complexity of seagrass taxa can influence the composition and size distribution of associated fishes (e.g., Hyndes et al. 2003). Differences in richness, composition and abundance of reef fish among treatments may be explained by differences in the size distribution of algal complexity offered by algal patches, with higher availability of fine-scale, intra-thallus spaces found on higher biomass *Sargassum* thalli. Again, similar fish–habitat relationships have been measured in coral systems, where the size of inter-branch gaps may determine fish abundance (Pereira and Munday 2016). In *Sargassum*, increased complexity at this fine-scale may offer more suitable refugia, prey, or a combination of both, to recruiting macroalgal-associated fishes.

Structural complexity may be measured at different spatial scales, and the relevance of these measures to fish will depend on fish body size, shape and behaviour (McCormick 1994). Notably, most fish use refuge space that closely aligns with their body dimensions (Friedlander et al. 2007; Wilson et al. 2013). Fine-scale architectural features are therefore likely to have a positive effect on small-bodied fishes, including juveniles and new recruits, while larger features may benefit larger fishes, indirectly disadvantaging small fishes due to predation risk (Nemeth 1998). In the present study, diversity and abundance of the predominantly small (~ 3 cm) recruiting fishes responded positively to higher *Sargassum* intra-thallus complexity at a fine (0–5 cm) scale, as opposed to the larger (> 10 cm) inter-thallus scale. Similarly, albeit with larger organisms, kelp frond biomass was found by Carr (1994) to have a consistently positive relationship with fish recruit abundance, while recruitment increased to an asymptote with kelp stipe densities. Additionally, the smallest size classes of several fish species in this study (e.g., *Halichoeres* and *Siganus* species) were observed to maintain closer proximity to experimental *Sargassum* thalli than larger conspecifics (KW pers. obs.). With a high availability of complexity at a fine-scale, high biomass *Sargassum* may be ideal for small, macroalgal-associated fishes that can easily shelter among branching algal structure.

While predation events on recruiting fishes were not observed in this study, several potential predators of recently-settled and small-bodied fishes (e.g. > 30 cm *Lethrinus* spp., *Symphorus nematophorus, Carangoides fulvoguttatus*) were observed within the study site. Therefore,

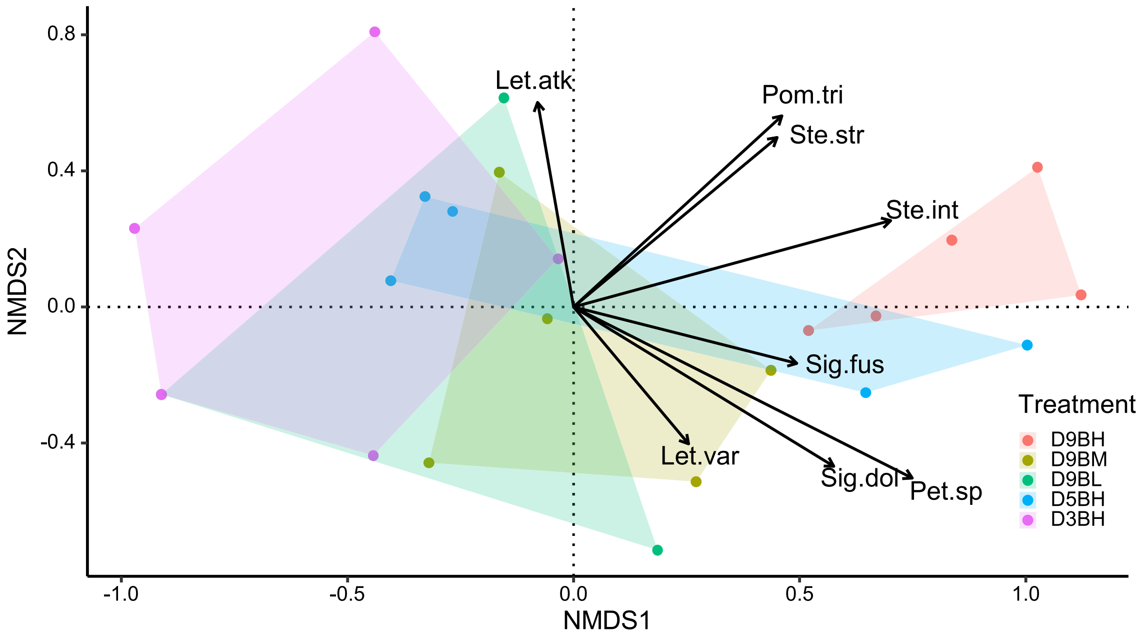


Fig. 3 NMDS of fish assemblage composition on day 18 (Bray–Curtis dissimilarity on Wisconsin double standardised, 4th root transformed abundance data). Each point represents a single patch. Envfit species vectors (black arrows) displayed are for those species where $P > \mathrm{r}$ was < 0.1: (clockwise from top) “Let.atk” = Lethrinus atkinsoni, “Pom.tri” = Pomacentrus tripunctatus, “Ste.str” = Stethojulis strigiventer, “Ste.int” = Stethojulis interrupta, “Sig.fus” = Siganus fuscescens, “Pet.sp” = Petroscirtes sp., “Sig.dol” = Siganus doliatus, “Let.var” = Lethrinus variegatus. Stress = 0.14

predation avoidance through refugia seeking may help to explain the patterns observed here. The habitat used by an organism often reflects behavioural decision-making relating to predator avoidance, foraging and reproductive demands (Sutherland 1996), decisions which may optimise the predation risk/growth optimisation trade-off at that organism’s ontogenetic stage (Dahlgren and Eggleston 2000; Grol et al. 2011). Though some species of herbivorous fish have been shown to avoid feeding within dense macroalgal stands, presumably due to elevated risk of predation (Hoey and Bellwood 2011), the reverse may be true for other species and/or ontogenetic stages. For example, the Nassau grouper (*Epinephelus striatus*) recruits to stands of the macroalga *Laurencia*, before undergoing an ontogenetic habitat shift to more open rubble-dominated areas as a larger juvenile (Eggleston 1995). Such ontogenetic habitat shifts may represent a trade-off between early survival and enhanced growth in larger sized individuals. This was confirmed by experiments in which different life stages of *E. striatus* were tethered in different habitats with settlement habitats exhibiting lower predation risk, but habitats used at larger, less predation-prone size classes allowing greater foraging opportunities, and thus faster growth (Dahlgren and Eggleston 2000). Similarly, a tethering study on the French grunt (*Haemulon flavolineatum*) showed lower predation risk in settlement habitats, but better foraging opportunities, and faster growth and reproductive potential in subsequent habitats (Grol et al. 2011). Recruitment site selection by fishes observed in the present study is likely determined by similar predation avoidance/growth optimisation processes, and patches containing high biomass macroalgal thalli with more intra-thallus complexity may offer protection and/or concealment from predators which better matches recruit fish body size than those with low *Sargassum* biomass. Though few other studies have explored the influence of macroalgal complexity on predation for coral reef fishes, studies of temperate marine macroalgae (Moksnes et al. 1998; Perez-Matus et al. 2016), seagrass (Heck and Orth 2006), and freshwater algae (Warfe and Barmuta 2004) generally show that complex macrophytes can moderate predation rates and the distributions of associated fauna, although the nature of this relationship may depend on the behavioural strategies of predator and prey species (e.g. Horinouchi et al. 2009). In addition to offering suitable shelter, however, the high biomass treatment in our study likely provided ample prey for foraging, given macroalgal biomass is typically correlated with invertebrate biomass and productivity (Chen et al. 2021).

Epibiota (algae and invertebrates) which inhabit macroalgae (Leite and Turra 2003; Bittick et al. 2019; Chen et al. 2020, 2022) may be attractive dietary resources to macroalgal-associated fishes (Levin 1994; Chen et al. 2022; Nieder et al. 2022) and may explain some of the variation in recruitment observed here. Indeed, Levin (1994) provided evidence that the small-scale recruitment distribution of a temperate macroalgal-associated fish was a response to the patchiness of its preferred prey (small crustaceans). In the present study, both herbivorous (e.g., juvenile *Siganus* spp.; Hoey et al. 2013) and invertivorous (e.g., adult and juvenile *Halichoeres miniatus*, *Stethojulis* spp.; Bellwood et al. 2005, and *Petroscirtes* sp.; Gilby et al. 2016) fishes were observed foraging on *Sargassum* thalli. Though the actual targets of bites were not identified, these observations suggest that prey availability may have influenced fish recruitment to experimental patches in both feeding guilds. Epiphyte density has been shown to increase with thallus density in some tropical macroalgae (Bittick et al. 2019), and evidence suggests that invertebrate abundances increase with macroalgal size, and thus, surface area (Fong et al. 2018; Wenger et al. 2018; Chen et al. 2020, 2021). Although not quantified in the present study, epibiota abundance and secondary production is therefore likely to have been elevated on patches with more, larger *Sargassum* thalli due to their higher surface area for epibiota to colonise and/or their higher primary production enabling greater individual size of epifauna (Chen et al. 2021). The diversity and abundance of invertivores (e.g., *H. miniatus, Petroscirtes* sp., *L. atkinsoni;* Kulbicki et al. 2005) and herbivores (e.g., *Siganus* spp., *P. tripunctatus;* Ceccarelli 2007), which were elevated on higher biomass experimental patches, could therefore have been influenced by this elevated prey availability. *Sargassum* tissues themselves, particularly the potentially more palatable secondary and tertiary laterals (Streit et al. 2015; Loffler and Hoey 2018), which were most abundant on high biomass patches, may also have been sought by *S. doliatus* and *S. fuscescens*, although rhodophytes and invertebrates appear to be more highly preferred prey items for juveniles of these species (Pitt 1997).

Differences in fish assemblage composition with varying structural complexity are often documented in coral habitats (e.g., Hixon and Beets 1993; Friedlander and Parrish 1998; Chong-Seng et al. 2012), though variation in fish assemblages within tropical macroalgal habitats is less well established (although see Wilson et al. 2014; van Lier et al. 2018; Robinson et al. 2019). The present experiment demonstrated that macroalgal resources provided by high density, high biomass *Sargassum* patches attracted a distinct, more diverse assemblage of fishes compared to patches of lower *Sargassum* density and/or biomass. This recruit assemblage bore some resemblance to recruit assemblages observed in tropical macroalgal habitats of other Indo-Pacific locations, with siganids and lethrinids also prominent among macroalgal meadows in Western Australia (WA) (Wilson et al. 2010a; Evans et al. 2014), and labrids being prominent in macroalgal habitats in both WA and Tanzania (Wilson et al. 2010a; Evans et al. 2014; Tano et al. 2017). Our findings therefore corroborate the importance of macroalgal canopies, in particular those with high algal complexity, as recruitment habitats in these groups. In contrast, a relative scarcity ($<0.01\%$ observations) of juvenile parrotfishes (Labridae: Scarinae) was observed in the present study compared to previous work in WA, Tanzania and the Philippines (Wilson et al. 2010a; Evans et al. 2014; Lim et al. 2016; Tano et al. 2017; Sievers et al. 2020a), although very different approaches (experimental vs observational) and scales (0.56 m^2 patches vs 30–78.5m^2 survey areas) were used here. Juvenile parrotfish species with affinities for macroalgal habitats (Green 1998; Wilson et al. 2014; Lim et al. 2016; Sievers et al. 2020a) may therefore have habitat requirements (e.g. larger patches, taller thalli) beyond what was on offer on our small experimental patches, needs that may be met in the more extensive natural macroalgal beds available nearby (Fox and Bellwood 2007) in which they are commonly observed (Tang et al. 2020; KW pers. obs.). The nursery value of macroalgal habitats may then be highly influenced by surrounding seascape (Nagelkerken et al. 2015). Previous studies demonstrate that proximity and/or quality of other viable habitats in the ecosystem can affect the structure of juvenile fish assemblages in tropical macroalgal habitats (van Lier et al. 2018).

Although each of the six common fish species in this study displayed positive relationships with intra-thallus complexity, there were some subtle differences in the nature of these relationships among species that may reflect interspecific differences in behaviour, morphology and biology. For instance, *Petroscirtes* sp. exhibited the clearest preference for the high density, high biomass patches (D9BH). Adults of this species are likely highly site attached (Gilby et al. 2016) which may make recruitment to sites that provide adequate shelter and prey more critical than for the other common species. In contrast, *H. miniatus* roams large areas at Orpheus Island (McCormick et al. 2010) and has also been observed using habitats dominated by many substrata, including corals, macroalgae, mangroves and bare sand (McCormick et al. 2010; Barnes et al. 2012; Espadero et al. 2021). Recruitment habitat selection is therefore unlikely to be tightly constrained in *H. miniatus*, as reflected in this study, where similarly high abundances were observed in three of the five treatments (D9BH, D9BM and D5BH).

Canopy forming macroalgae such as *Sargassum* display marked seasonality in height and biomass (e.g., Lefèvre and Bellwood 2010; Fulton et al. 2014; Hoang et al. 2016), likely driven by seasonality in plant ontogeny and climatic variables, including rainfall, nutrient concentrations and temperature (Hoang et al. 2016), which the present short-term study could not capture. Some macroalgal-associated fish species may shift their behaviour and utilise non-canopy macroalgae during low biomass periods, making them somewhat resilient to such changes (Wenger et al. 2018). Alternatively, patches of macroalgal habitat that retain structure year-round may be especially important for persistence of fishes through low biomass periods, as demonstrated in Ningaloo Reef, Western Australia (Lim et al. 2016; Wilson et al. 2017). However, the mechanisms and extent of resilience to temporal variation in macroalgal habitats for most macroalgal-associated fishes remain underexplored. On the GBR, peaks in reef fish spawning (Russell, et al. 1977) and *Sargassum* biomass (Lefèvre and Bellwood 2010) co-occur during the warmer months. Inter-annual variation in the availability and quality of macroalgal canopies, caused for instance by climate change (McCourt 1984; Hwang et al. 2004; Ateweberhan et al. 2006), during this critical recruitment period, may have strong impacts on macroalgal-recruiting fish populations and the ecosystem functions (e.g., herbivory, invertivory) they carry out.

The results of this study demonstrated that increases in *Sargassum* biomass, particularly when distributed at the fine, intra-thallus scale, can positively influence recruit fish diversity and abundance on tropical reefs and result in distinct assemblages. We suggest that this relationship may be driven by increased shelter and prey availability with high thallus biomass that provides refugia for juvenile fishes closely matching their body size, although further work is required to determine the relative importance of these drivers. While not commonly implemented at present, including measures of algal complexity, such as biomass (or some well validated proxy), density and height in more studies could enhance understanding of factors that influence juvenile survival and improve predictions of population sizes for macroalgal-associated fishes (e.g., Aburto-Oropeza et al. 2007). This information could then be used for fisheries stock assessments and gaining a deeper insight into the ecosystem services provided by macroalgae-recruiting fish (e.g., Wilson et al. 2022). When combined with data on juvenile fish survival, growth and connectivity to adult habitats, an understanding of habitats that support high juvenile fish diversity and abundance may also identify fish nurseries (Nagelkerken et al. 2015; Wilson et al. 2016). Such valuable data could inform spatial planning and management decisions aimed at preserving habitats with substantial fish recruitment potential.

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Data availability Data and code used for this this study are available from ResearchData, James Cook University: [doi.org/10.25903/fhsy-8163].

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Ethics approval This work was conducted with the approval of the JCU Animal Ethics Committee (protocol A2831) and conducted in accordance with GBRMPA permit G22/47285.1

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