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REPORT

Utilisation of macroalgal habitats by juvenile rabbitfishes on an inshore reef

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Abstract Macroalgal beds are increasingly recognised as nursery habitats for coral reef fish; however, the extent to which they are used as a source of food and/or a refuge from predation remains largely unexplored. Here, we investigate the distribution, feeding behaviour, diet, and predation risk for juvenile rabbitfish in macroalgal habitats on Orpheus Island, Great Barrier Reef. Visual surveys revealed that juvenile and adult *Siganus doliatus* had different among-habitat distributions with juveniles being largely restricted to the reef flat and positively associated with macroalgal cover, while adults were abundant on the reef crest. Focal feeding observations show that within macroalgal habitats, juvenile *S. doliatus* targeted epiphytes on *Sargassum* (80% of bites), with relatively few bites taken on turfs or the *Sargassum* itself (27% and 8%, respectively). These observations were supported by stomach content analyses with filamentous algae being the dominant item in the stomach content of both small (< 4 cm total length, TL; 58%) and large juvenile *S. doliatus* (> 4 cm TL; 47%). The stomach content of juvenile *S. doliatus, S. canaliculatus,* and *S. spinus* collected from macroalgal habitats was similar, consisting primarily of filamentous algae and detritus. We found no relationship between the abundance of potential predators and juvenile rabbitfishes across the study sites. Collectively, our results suggest that juvenile rabbitfishes are using macroalgal habitats on this, and potentially other, inshore reefs as a food source and add to a growing body of literature highlighting the importance of these habitats for the early life stages of reef fish.

Keywords Nursery habitat · *Siganus doliatus* · Diet · Coral reef · Ontogenetic shift

Introduction

Macroalgae are an important component of tropical seascapes yet are often depicted as a sign of degradation on coral reefs. This negative association has developed because under certain conditions (e.g. reduced herbivory and elevated nutrients) macroalgae can proliferate in places where they once did not occur (i.e. phase shift; Hughes 1994; Cheal et al. 2010; Graham et al. 2015) and negatively impact the recruitment (Webster et al. 2015; Smith et al. 2022), fecundity (Foster et al. 2008; Monteil et al. 2020), growth (Hughes et al. 2007; Fong and Todd 2021), and survival of corals (Box and Mumby 2007; van Woesik et al. 2018). Nevertheless, macroalgae are a prominent and important component of healthy reef systems (Vroom and Braun 2010; Hoey and Bellwood 2011; Fulton et al. 2019; Sievers et al. 2020), providing a source of food and/or habitat for a diversity of marine organisms (Burkepile and Hay 2008; Tano et al. 2016). Furthermore, an increasing body of literature has reported that beds of canopy-forming macroalgae, such as *Sargassum*, support high abundances of juvenile fish (e.g. Tang et al. 2020; Webber et al. 2024). Many of these juvenile fish species are found almost exclusively in macroalgal beds with adult conspecifics found in other habitats (e.g. coral-dominated habitats), leading to

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suggestions these areas may function as a nursery habitat (Wilson et al. 2010; Evans et al. 2014; Sambrook et al. 2019). Despite the potential importance of tropical canopy-forming macroalgae beds as a nursery habitat, their role in providing dietary resources and/or reducing predation risk on juvenile fishes is limited and context specific. For example, Chaves et al. (2013) found fewer predators within *Sargassum* beds compared to adjacent reef habitats, while Hoey and Bellwood (2011) found that densities of predators within *Sargassum* beds were positively related to thallus density. While some studies have shown that there is a greater abundance of invertebrates or epiphytes within *Sargassum* beds (Martin-Smith 1993; Buzá-Jacobucci and Pereira-Leite 2014; Chen et al. 2020), few have directly linked this to the feeding of juvenile fishes.

For recently settled and juvenile reef fishes, survival rates are generally low (e.g. McCormick and Hoey 2004) as smaller individuals are more vulnerable to predation (Millet et al. 1988; Anderson 1988), and naïve to reef-based predators. As such, juvenile fishes often seek habitats which optimise growth and/or reduce predation risk (McIvor and Odum 1988). These "nursery habitats" are broadly defined by their larger-than-average contribution of recruits into a spatially separate adult population through increased fitness benefits (Beck et al. 2001). Typically, areas of increased structural complexity are thought to provide conditions suitable as nursery areas through the provision of refugia from predation (Robertson and Blaber 1992; Beukers and Jones 1998) and/or increased surface area for prey to inhabit and hence prey-increased food availability (Beck et al. 2001; Heck et al. 2003).

Within tropical macrophyte (macroalgae and seagrass) habitats, areas of increased structural complexity typically harbour increased abundances of juvenile fish with this generally being related to the greater surface area of the macrophytes and the higher abundances of epiphytes and epifauna they support (Attrill et al. 2000; Viega et al. 2014; Tano et al. 2016). Indeed, large complex canopy-forming macroalgae such as *Sargassum* (Phaeophyceae) have been shown to support high abundances of microinvertebrates (crustaceans: Chen et al. 2020; Martin-Smith 1993; gastropods: Leite and Turra 2003; Martin-Smith 1993). Within macroalgal beds, the high abundances of small invertebrates and epiphytes along with the macroalgae itself may provide abundant dietary resources for juvenile fishes. Indeed, in littoral rocky reef systems, juvenile fish have been found in higher abundances within macroalgal beds, with their abundances related to the morphology and/or complexity of the algae (Chiminee et al. 2013, 2017; Hinz et al. 2023); however, few studies have directly related this to the diet of individuals (but see Hinz et al. 2019). Despite this, most studies to date within tropical macroalgal beds have focused on the distribution of juvenile fishes and how they relate to the composition and/or physical structure of the macroalgae, and few, if any, have investigated the diet or feeding behaviour of juvenile fishes in these habitats.

Rabbitfishes (f. Siganidae) are a group of herbivorous fishes that are abundant on nearshore reefs across the Indo-Pacific (Woodland 1990), with high abundances of juvenile rabbitfish typically being found in association with beds of canopy-forming macroalgae (e.g. Evans et al. 2014; Sambrook et al. 2019; Tang et al. 2020). Despite their similar morphology, interspecific differences in foraging behaviour (Fox et al. 2009; Fox and Bellwood 2013) and diet (Hoey et al. 2013; Ebrahim et al. 2020) have been reported for adult rabbitfishes. For example, comparisons of the diet of 11 species of co-occurring rabbitfish in the northern Great Barrier Reef revealed four distinct groups: macroalgal browsers, algal croppers, spongivores, and mixed algal and sessile invertebrate feeders (Hoey et al. 2013). However, the diet and feeding behaviour of juvenile rabbitfishes, especially within tropical macroalgal habitats, is poorly understood. The aim of this study was to examine the feeding behaviour and diet of juvenile rabbitfishes in macroalgal habitats on an inshore reef of the Great Barrier Reef. Using a combination of focal behavioural observations and stomach content analyses, we investigated the feeding substrata of juvenile rabbitfishes within macroalgal habitats, and how the diet of rabbitfishes varies among species and life stages. Using surveys of fish and benthos from three reef habitats, we also investigated whether the abundance of potential predators or cover of macroalgae influence the distribution of juvenile rabbitfish.

Methods

Study site and species

This study was conducted on Orpheus Island (18.6161°S, 146.4972°E), an inshore continental island located in the Palm Island group of the central Great Barrier Reef (GBR), Australia. Orpheus Island has well-developed fringing reefs on its leeward (western) margin (Fig. 1). Data were collected from three sites on the leeward side of the island: Pioneer Bay, Hazard Bay, and Harrier Point between 27 February and 23 April 2023. This sampling period was selected to coincide with the predicted peak in rabbitfish settlement following the last full moon of summer (Takemura et al. 2004).

Benthic cover and fish distributions

A series of visual transects were used to quantify benthic and fish communities within each of three habitats (reef slope, reef crest, and reef flat) within each of the three sites over two time periods that spanned the time of the feeding

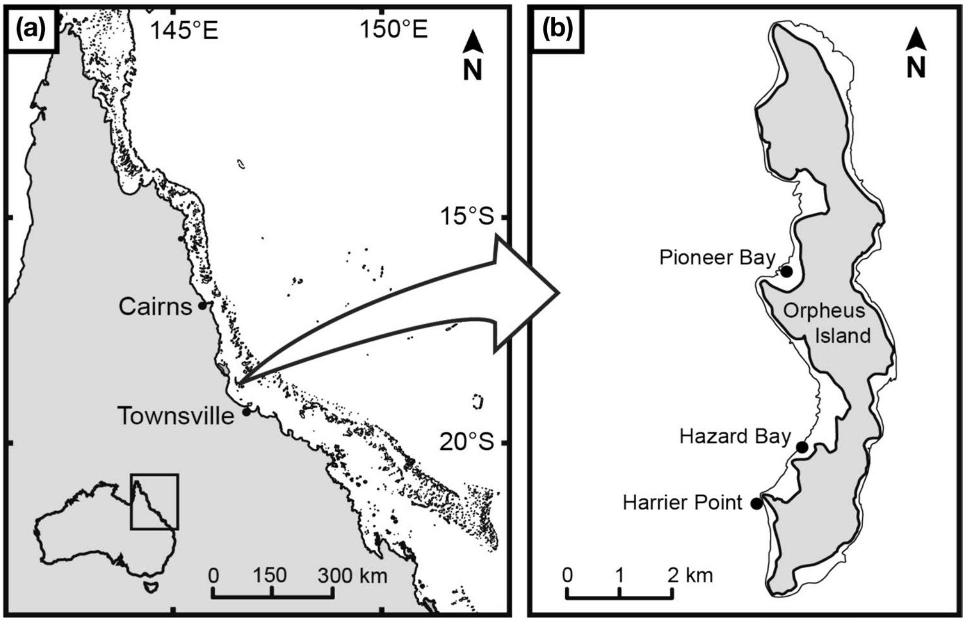


Fig. 1 Map showing location of three study sites at Orpheus Island, GBR: **a** map of the north-east coast of Australia showing the location of Orpheus Island in the Palm Islands of central Great Barrier Reef and **b** map of Orpheus Island showing the location of the three study sites: Harrier Point, Hazard Bay, and Pioneer Bay

observations and fish collections (27 February–5 March and 18–23 April 2023). The shoreline at each site is fringed with mangroves, primarily *Rhizophora*. The reef slope (4–6 m depth) was defined as the steeply inclined section of the reef, on the seaward side of the reef crest and was characterised by massive *Porites* colonies and a low cover of macroalgae in Pioneer Bay (Fox and Bellwood 2007; Oakley-Cogan et al. 2020), and by 'other' coral in Hazard Bay and Harrier Point (Loffler et al. 2015). The reef crest (1–3 m depth) was the region that marked the transition between the steeply inclined reef slope and the extensive shallow region of the reef and was characterised by massive *Porites* colonies (Loffler et al. 2015; Oakley-Cogan et al. 2020). The reef flat (1–2 m depth) was approximately midway between the crest and the shoreline and has previously been described by the presence of *Sargassum* beds and other canopy-forming algae (Fox and Bellwood 2007; Loffler et al. 2015; Loffler and Hoey 2018) or the foliose alga *Padina* (Oakley-Cogan et al. 2020). These differences among studies likely reflect seasonal variation in algal communities (Lefevre and Bellwood 2010). At the time of our study (February–April), *Sargassum* was the most abundant alga on the reef flat.

Fish assemblages within each habitat at each site at each time period were surveyed using three replicate 30-m belt transects. Briefly, a diver (always KW) swam slowly within the defined habitat recording all large (> 10 cm total length, TL) fishes observed 2.5 m on either side of the transect (forming a 30 m × 5 m belt), while simultaneously deploying the transect tape (following Hoey and Bellwood 2011). All fishes > 10 cm TL within the 5-m belt were identified to species and their total length estimated to the nearest 1 cm. The same diver then swam back along the transect recording all small (< 10 cm TL) fish to species, and estimating size to the nearest 1 cm, within 1 m on either side of the transect (forming a 30 m × 2 m belt). Each transect was laid parallel to the reef crest with 5–10 m between adjacent transects within each habitat.

Benthic communities were quantified using the point-intercept method along the same transects used to quantify the fish communities. The substratum directly under 60 evenly spaced points along each transect (0.5 m apart) was recorded. All macroalgae and hard (scleractinian) corals were identified to genus, and all other substrata were placed into broad categories (i.e. sand, rubble, turf, crustose coralline algae, and soft coral).

Behavioural feeding observations

The bluelined rabbitfish, *Siganus doliatus*, was selected for this study as it is abundant on inshore reefs of the GBR (Cheal et al. 2012; Hoey et al. 2013), including reefs around Orpheus Island (Fox and Bellwood 2007). Recently settled and juvenile *S. doliatus* have also been reported to associate with areas of high cover of *Sargassum* and other canopy-forming macroalgae on Orpheus Island (Tang et al. 2020; Webber et al. 2024).

Behavioural feeding observations were conducted to assess primary dietary targets of juvenile *S. doliatus* within macroalgal habitats. A minimum of 50 focal observations were conducted within macroalgal habitats on the reef flat at each of the three sites, with all feeding observations being conducted between 0900 and 1600 h. The reef flat was selected as this habitat supported the highest abundance of juvenile *S. doliatus* and macroalgae; juvenile rabbitfish were rare or absent within the reef crest and reef slope habitats. After locating a juvenile *S. doliatus* (i.e. between 10 and 50 mm TL), a diver would estimate the total length (TL) of the individual to the nearest 0.1 cm then wait 30 s to ensure the fish had acclimated to the diver presence prior to commencing the observation period. Each individual would then be followed for an additional 1–2 min (mean = 1.3 min) during which the number of bites, and the substratum of each bite was recorded. Longer observations were not possible as the fish would often disappear into the dense areas of *Sargassum.* The feeding substratum was categorised as either turfs (filamentous algae and/or cyanobacteria on dead coral or reef pavement), macroalgae (identified to genus), or epiphytes on macroalgae. After a juvenile *S. doliatus* was observed feeding on a macroalga or epiphytes (on macroalgae), the blade of the macroalgae at the location of the bite was carefully examined for the presence of any damage consistent with a potential bite. If no damage was evident on the blade, it was recorded as epiphytes.

Fish collections and stomach content analysis

To supplement the behavioural feeding observations, a total of 16 juvenile *S. doliatus* between 23 and 45 mm TL were collected from the reef flat using a hand net, barrier net, and a dilute clove oil solution (1:10 clove oil to ethanol). Additionally, 16 juvenile *S. canaliculatus* and two juvenile *S. spinus* between 23 and 55 mm TL were collected opportunistically using a hand net, barrier net, and a dilute clove oil solution. Fish collections took place between 0900 and 1630. Individual fish were euthanised immediately following capture using a seawater ice slurry. Fish were transported to the Orpheus Island Research Station within 60 min of capture and preserved in an 80% ethanol solution for transport back to James Cook University (JCU) Townsville, QLD. Capture and handling protocols were in accordance with JCU Animal Ethics Approval A2802.

The standard and total length of each juvenile fish collected was measured to the nearest 0.1 cm using callipers. Using a dissection microscope, the entire alimentary tract of each individual was removed and carefully uncoiled, and the content of the stomach removed and placed into a small petri dish. The stomach content was then carefully spread across the petri dish and a photo was taken of the stomach content at 7–14 × magnification. A series of random points were then overlaid on each photo with a minimum of 20 points overlaying dietary content. The dietary item found directly under each point was identified to the lowest taxonomic level. Algal material was identified to genus (where possible) or algal functional group (following Steneck and Dethier 1994). Consequently, dietary items were placed into one of six categories: *Sargassum,* foliose algae, corticated terete algae, filamentous algae, unidentified algae, and detritus. Proportion of diet was then calculated by dividing the count of each category by the total count of all categories.

Statistical analysis

Spatial variation in the abundance of juvenile and adult *S. doliatus*, potential predators, macroalgae, and turf was modelled separately using generalised linear mixed models (GLMMs) with habitat as a fixed effect and site as a random effect (Table S1). Macroalgal cover, turf cover, and the abundance of juvenile *S. doliatus* and potential predators did not differ between the two time periods (ESM) and were subsequently pooled. The response of juvenile *S. doliatus* abundance and potential predator abundance (i.e. sum of lethrinids, lutjanids, and serranids > 10 cm TL per 150 m^2) were modelled separately with a negative binomial (log-link) distribution. Total macroalgal cover (summed across all genera per transect) and total turf cover were both modelled with a tweedie (log-link) distribution.

To investigate relationships between the abundance of juvenile *S. doliatus* and the availability of macroalgae and potential predation risk, the abundance of juvenile *S. doliatus* was modelled against percent cover of macroalgae and visual estimates of the abundance of potential predators. These analyses were restricted to the reef flat due to juvenile *S. doliatus* and macroalgae being rare or absent on the reef crest and reef slope. Each model was run separately using a GLMM with site as a random effect. The response of juvenile *S. doliatus* abundance per 60 m^2 to macroalgal percent cover (continuous fixed effect) was modelled with a negative binomial (log-link) distribution. The response of juvenile *S. doliatus* abundance to predatory fish abundance was modelled with a negative binomial (log-link) distribution, with the abundance of juvenile *S. doliatus* and the abundance of potential predators standardised to individuals per 150 m^2.

To investigate whether the bite rate of juvenile *S. doliatus* differed with body size, total bites taken by juvenile *S. doliatus* was modelled against body size as a categorical fixed effect (three levels: < 3 cm, 3–4 cm, > and 4 cm) with observation period as an offset, using a zero-inflated negative binomial (log-link) generalised linear mixed model (GLMM) with site as a random effect. To evaluate whether the proportion of bites by juvenile *S. doliatus* on epiphytes and turfs was influenced by fish body size (logged continuous fixed effect), separate-ordered beta regression (Kubinec 2022) GLMMs (probit-link) were fit, with site as a random effect.

All GLMMs were run using the package ‘glmmTMB’ (Brooks and Kristensen 2017). All models were validated and checked for goodness-of-fit using the ‘DHARMa’ and ‘performance’ packages, specifically assessing collinearity, normality of residuals and random effects, Levene's test for homogeneity of variance, zero-inflation, and overdispersion. Estimated means, slopes, and their associated 95% confidence intervals were computed using the functions *emmeans* and *emtrends* within the 'emmeans' package. Significant differences among levels of fixed factors for GLMMs were assessed using TukeyHSD tests via the *pairs* function in 'emmeans'. Statistical analyses were conducted and figures produced in R using version 4.3.3 (R Core Team 2024).

Non-metric multidimensional scaling analyses (nMDS) based on a Bray–Curtis dissimilarity matrix were used to investigate variation in benthic composition among sites and habitats and the dietary variation among collected juvenile *S. doliatus* of different sizes (< 3 cm, 3–4 cm, > 4 cm) and species (*S. canaliculatus, S. doliatus, S. spinus*). To assess differences in benthic composition among reef habitats (flat, crest, and slope), all macroalgae and hard scleractinian corals were placed into broad morphological categories. To assess differences among stomach content of juveniles, the proportion of each of the six algal categories identified was calculated. nMDS were run using the *metaMDS* function in the 'vegan' package. Gut content proportions underwent Double Wisconsin standardisation to account for highly abundant taxa that would otherwise be overly influential, and to ensure rare taxa were not underrepresented. To investigate differences between groupings for all nMDS, a PERMANOVA was run using the *adonis2* function from the 'vegan' package and the *pairwiseAdonis2* function from the 'pairwiseAdonis' package (Martinez Arbizu 2020).

Results

Benthic composition

There were statistically significant differences in benthic composition among the three reef habitats (PERMANOVA,

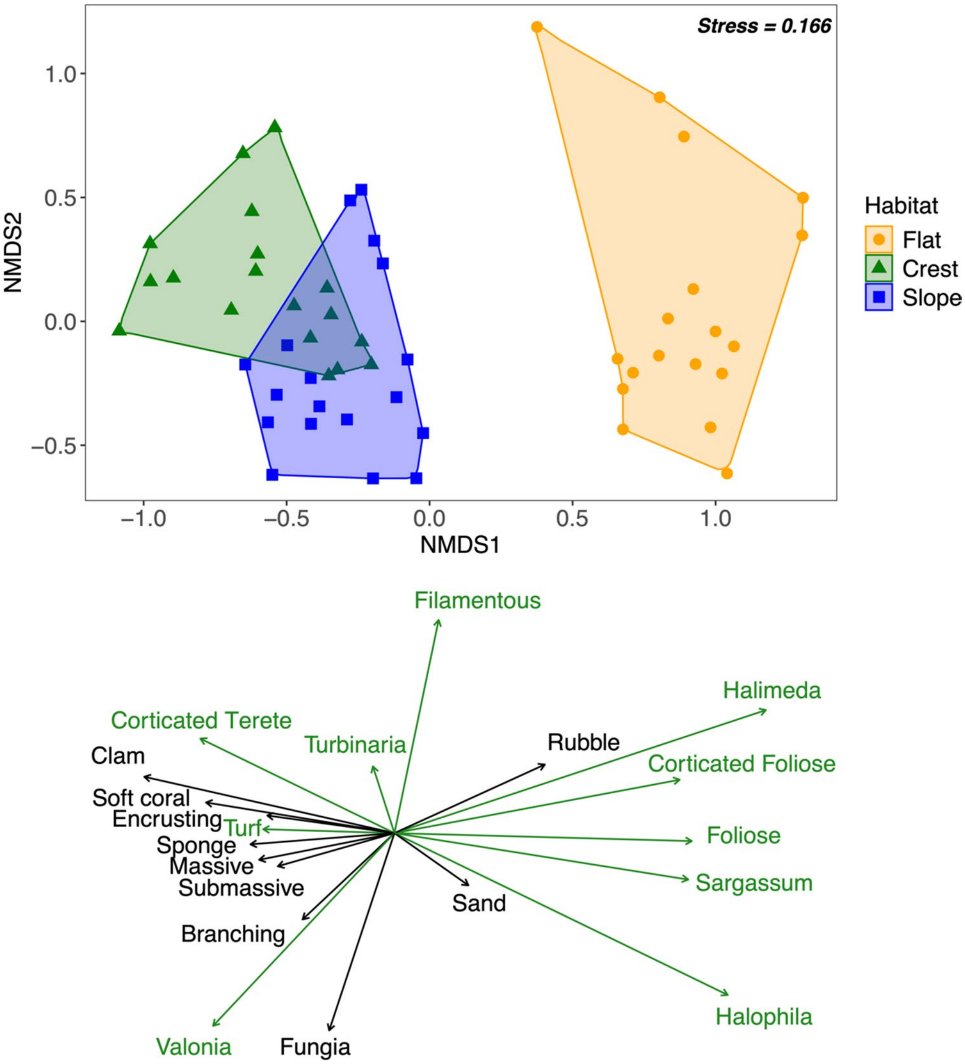


Fig. 2 Non-metric multidimensional scaling (nMDS) analysis showing variation in benthic composition across three reef habitats (reef flat: orange circles, reef crest: green triangles, and reef slope: blue squares) on Orpheus Island, central Great Barrier Reef. Vectors in green represent macrophytes and vectors in black represent non-algal benthos. Analysis was based on Bray–Curtis dissimilarity matrix of cover data along 30 m transects ($n = 18$ per habitat). Convex hulls drawn on for visual clustering of groups

$F_{(2,24)} = 18.2$, $p < 0.001$), with the reef flat being distinct from the reef slope and reef crest (Fig. 2). Macroalgal cover was significantly higher on the reef flat (mean = 39.7%, 95% CI 30.3–49.0) compared to minimal cover on the crest (0.3%, 95% CI −0.11 to 0.7) and slope (0.8%, 95% CI 0.1–1.4) (Fig. 3a). In contrast, turf cover was highest on the reef crest (mean = 40.8%, 95% CI 34.9–46.6), compared to the reef slope (17.8%, 95% CI 14.2–21.4) and reef flat (6.0%, 95% CI 4.1–7.9; Fig. 3b).

Spatial variation

The abundance of juvenile *S. doliatus* was greatest on the reef flat (2.1 ± 0.6 ind/60 m^2), followed by the reef crest (1.2 ± 0.4 ind/60 m^2), and lowest on the reef slope (0.08 ± 0.1 ind/60 m^2; Fig. 4a), coinciding with the highest cover of macroalgae (Figs. 2, 3). There was a positive trend between macroalgal cover (%) and abundance of juvenile *S. doliatus;* however, this relationship was not significant (GLMM, $p > 0.05$, Fig. 4c, Table S2). In contrast, no adult *S. doliatus* were observed on the reef flat, and although variable, the abundance was greatest on the reef crest (1.7 ± 0.7 ind/150 m^2) (Fig. 4b, Table S3). There was no relationship between abundance of potential predators and abundance of juvenile *S. doliatus* (GLMM, $p = 0.312$, Fig. S2).

Feeding substrata

Juvenile *S. doliatus* took between 0 and 90 bites (per min) irrespective of body size, equating to a mean of 12.4 bites per minute. The bite rate was relatively consistent among size classes of *S. doliatus*, ranging from 16.4 bites (95% CI 13.3–19.5), 17.0 bites (95% CI 13.2–20.8), and 19.0 bites (95% CI 12.5–25.4) per min for individuals < 3 cm, 3–4 cm, and > 4 cm TL, respectively (Fig. S3). Juvenile *S. doliatus* took a significantly larger proportion of bites on epiphytes on *Sargassum* (mean = 0.80, 95% CI 0.75–0.85) compared to turf (0.28, 95% CI 0.21–0.34) or the *Sargassum* itself (0.08, 95% CI −0.04 to 0.11; Fig. 5).

There was also some evidence of a shift in the feeding substrata with body size of juvenile *S. doliatus*, with the proportion of bites taken on epiphytes tending to decline, and the proportion of bites on turf algae increasing with body length (Fig. 6, $p < 0.05$, Table S4).

Stomach content analyses

The stomach content of juvenile *S. doliatus* was dominated by filamentous algae (52%). There was, however, a significant difference in the stomach content composition among the two size classes of juvenile *S. doliatus* (PERMANOVA, $F_{(1,14)} = 3.6$, $p < 0.05$; Fig. 7a), with larger (> 4 cm TL) individuals having a lower proportion of filamentous algae and a greater proportion of *Sargassum*, terete corticated, and foliose algae than smaller (3–4 cm TL) conspecifics (pairwise adonis, $F_{(1,14)} = 3.6$, $p < 0.05$; Table S5). The stomach contents of all three juvenile rabbitfish species were predominantly composed of filamentous algae (19.4–64.4%) and detritus (10.5–22.0%). There were however differences in the composition between *S. doliatus* and *S. canaliculatus,* with *S. canaliculatus* containing a higher proportion of

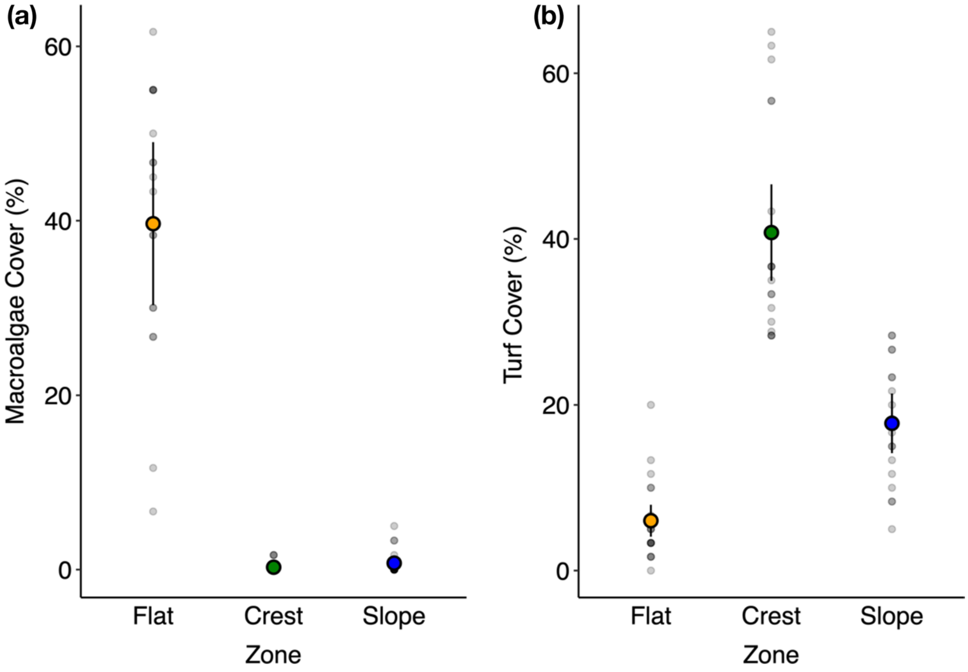
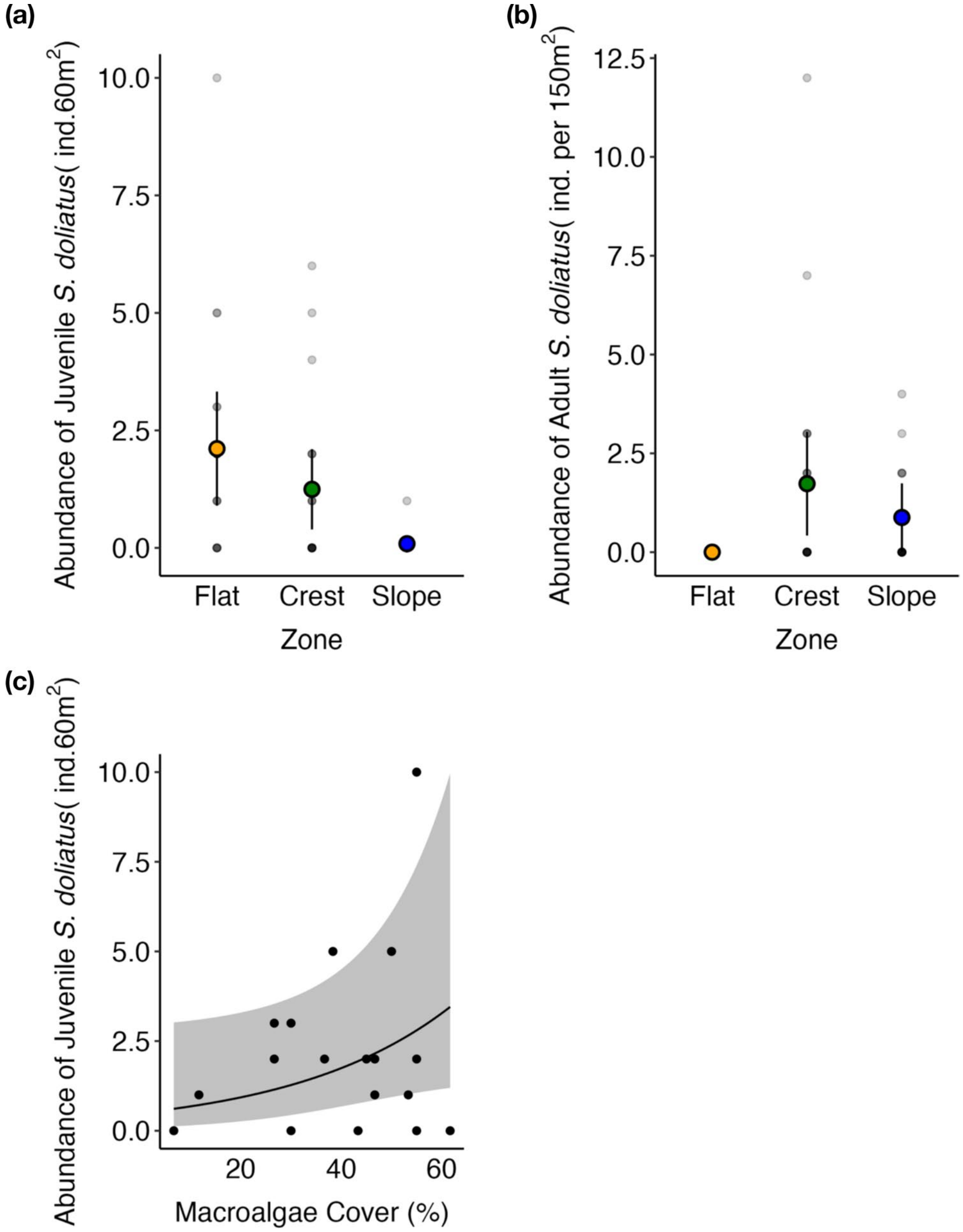


Fig. 3 Variation in the cover of **A** macroalgae and **B** turfs among habitats on Orpheus Island, central Great Barrier Reef. Coloured symbols are the modelled mean from tweedie Genralised Linear Mixed Model (GLMMs) and the error bars show 95% confidence limits. Grey dots are raw data. $n = 18$ transects per habitat

Fig. 4 Variation in the abundance of **A** juvenile *Siganus doliatus* and **B** adult *Siganus doliatus* among habitats on Orpheus Island, central Great Barrier Reef. Coloured symbols are the modelled mean from negative binomial genralised linear mixed model (GLMM) and the error bars the 95% confidence limits. Grey circles are the raw data. **C** The relationship between macroalgal cover and the abundance of juvenile *S. doliatus* in the reef flat at Orpheus Island. The solid line is the mean model fit from a zero-inflated poisson GLMM and the shaded area indicates 95% CIs. The analyses were based on three replicate transects within each of three habitats (reef flat, crest, and slope) at each site ($n = 18$)



filamentous algae and detritus, while *S. doliatus* consumed a greater diversity of algae (PERMANOVA, $F_{(1,30)} = 21.1$, $p < 0.001$, Fig. 7b).

Discussion

Tropical macroalgal habitats harbour unique assemblages of juvenile fish that have led to suggestions they are important nursery habitats (Evans et al. 2014; Fulton et al. 2020); yet, few have directly examined the diet of juvenile fishes within this habitat. This study found that juvenile and adult *Siganus doliatus* had different among-habitat distributions on Orpheus Island. Specifically, juveniles were largely present in the reef flat and positively associated with macroalgal cover, while adults were absent from the reef flat and most abundant on the reef crest. Focal feeding observations revealed the vast majority (80%) of bites by juvenile *S. doliatus* within macroalgal habitats were targeting epibiota on *Sargassum*, rather than turfs or large thallate macroalgae. This finding, combined with the stomach content analysis of *S. doliatus*, suggests that individuals were feeding on filamentous epiphytic algae. Moreover, the stomach content of juvenile *S. doliatus, S. canaliculatus,* and *S. spinus* collected from macroalgae habitats was composed predominantly of filamentous algae and detritus. This similarity in diet among juvenile rabbitfishes contrasts with that of adult conspecifics from the northern Great Barrier Reef (GBR) in which there

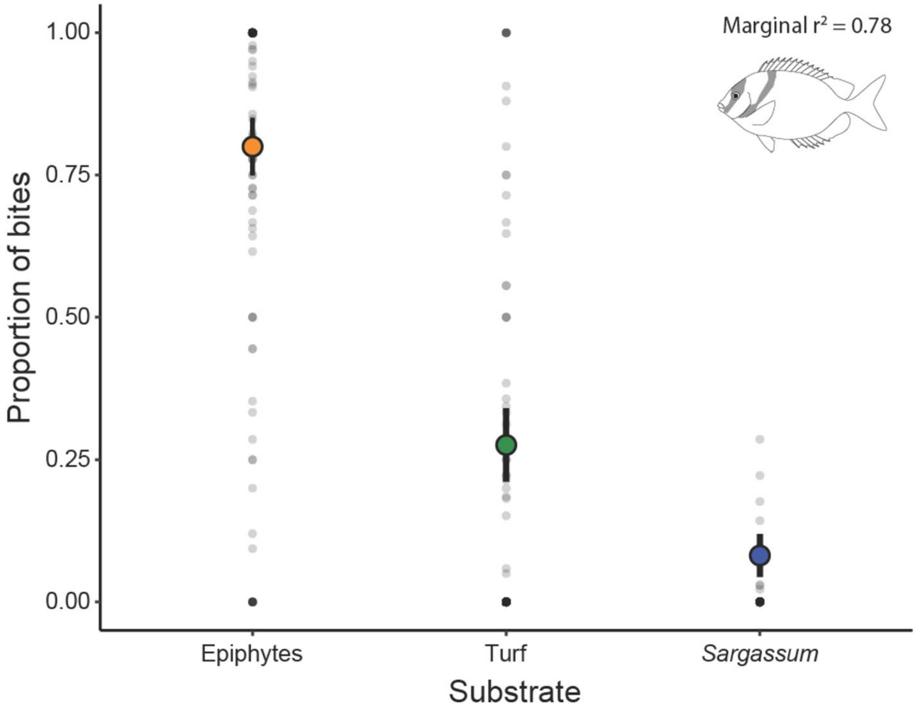


Fig. 5 Variation in the feeding substrata of juvenile *Siganus doliatus* within macroalgae habitats on Orpheus Island, Great Barrier Reef. Coloured circles are estimated marginal mean bites from an ordered beta GLMM. Error bars represent 95% confidence limits. Grey circles are raw data ($n = 184$)

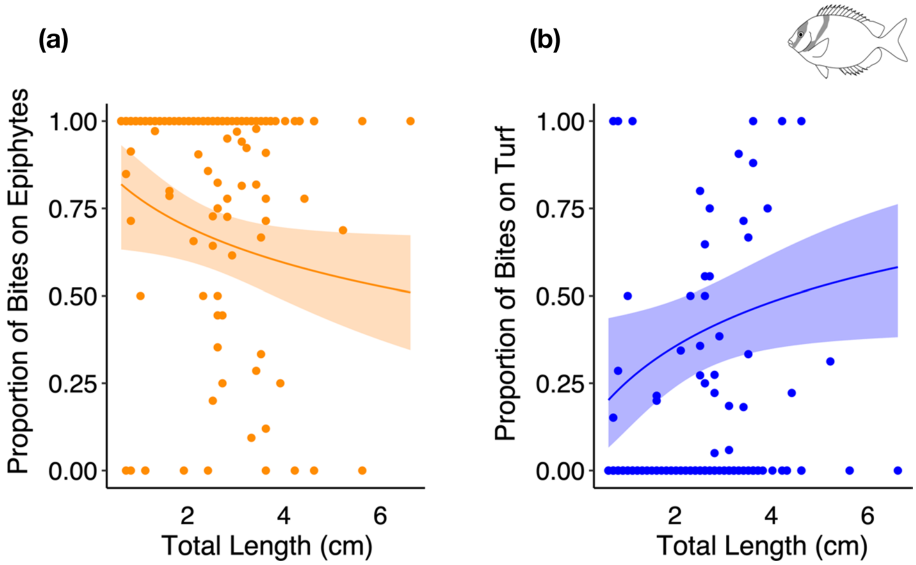


Fig. 6 Changes in the feeding substrata with total length of juvenile *Siganus doliatus* within macroalgae habitats at Orpheus Island, Great Barrier Reef; **A** epiphytes, and **B** turfs. Solid lines are the mean model fits from ordered beta GLMMs and the shaded colours indicate 95% confidence limits. Total length was log-transformed for analyses and back-transformed for visual presentation. Coloured points are raw data ($n = 184$)

is considerable interspecific variation among the dominant macroalgae in the stomachs of these three species; *S. spinus*: corticated algae, *S. canaliculatus*: leathery brown algae, *S. doliatus*: filamentous and corticated algae (Hoey et al. 2013). The importance of epiphytes as a food source for juvenile fishes is supported by studies within other vegetated habitats (e.g. seagrass beds) in which stable isotope analyses have indicated that epiphytes are a key source of carbon for juvenile fishes (Whitfield 2017; Igulu et al. 2013). These findings indicate that juvenile rabbitfishes on Orpheus Island are using beds of canopy-forming macroalgae for feeding and are consistent with the idea that macroalgal beds function as nursery habitats for these species.

The high abundance of juvenile *S. doliatus* on the reef flat coupled with the positive association with the cover of macroalgae on the reef flat, the predominance of bites on epiphytes, and filamentous algae in the stomach content of juvenile *S. doliatus* indicates that they are most likely using macroalgal beds for food resources. Abundances of juvenile lethrinids, siganids, and labrids have been positively associated with the cover, composition, and complexity of macroalgal beds on nearshore coral reefs (Wilson et al.

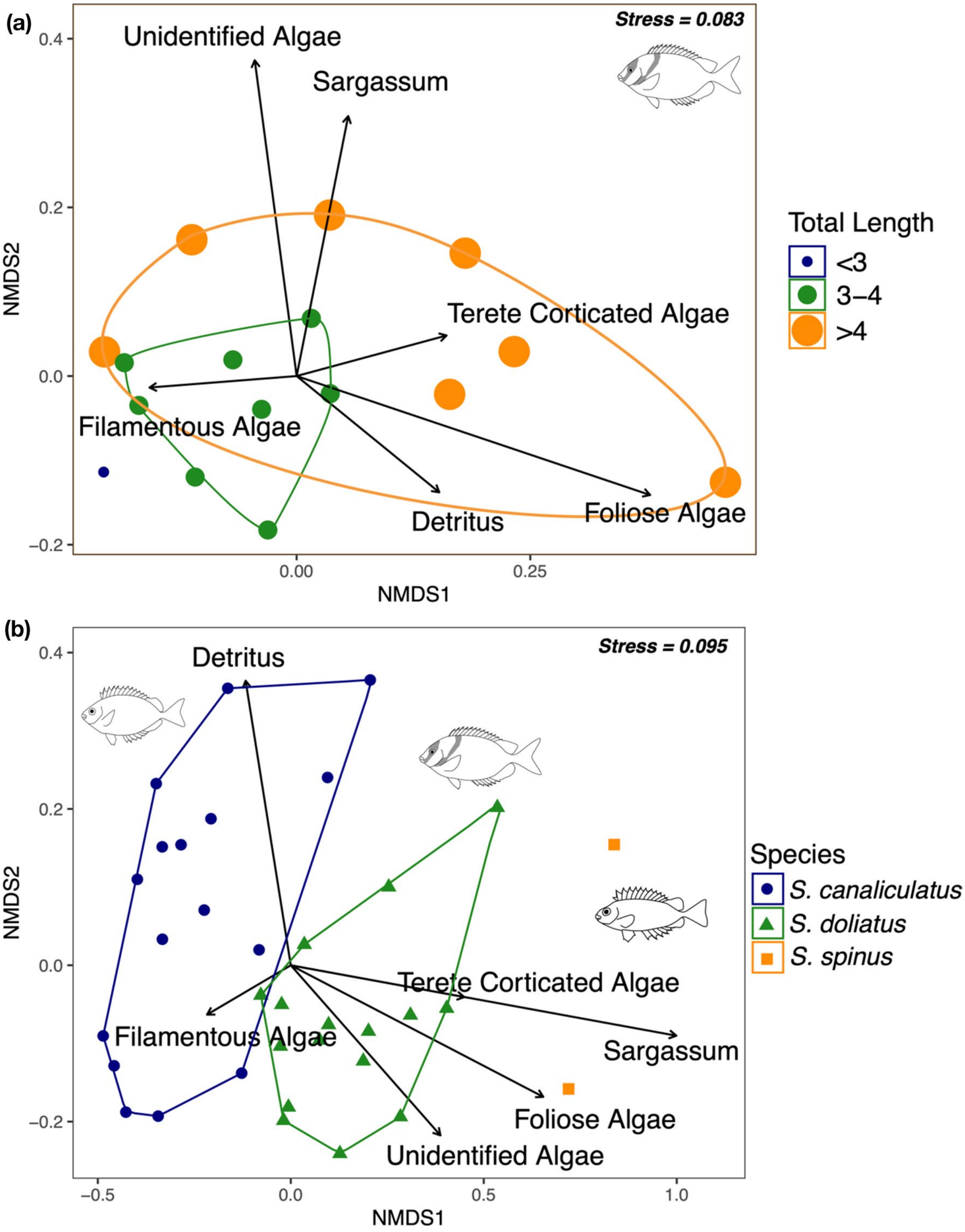


Fig. 7 Non-metric multidimensional scaling showing the variation in the composition of stomach content of **A** three size classes of juvenile *Siganus doliatus*: < 3 cm TL (blue; *n* = 1) (excluded from analyses), 3–4 cm TL (green; *n* = 8), > 4 cm TL (orange; *n* = 7) and **B** three species of juveniles rabbitfishes. *S. canaliculatus* in blue (*n* = 16), *S. doliatus* in green (*n* = 16), *S. spinus* in orange (*n* = 2) collected from macroalgae habitat on Orpheus Island, Great Barrier Reef. *S. spinus* were excluded from analyses. Analysis was based on Bray–Curtis dissimilarity matrix of proportions of total stomach content. Vectors represent algal categories. Convex hulls drawn on for visual clustering of groups

2010, 2014; Tang et al. 2020; Fulton et al. 2020; Webber et al. 2024). While the selection of structurally complex habitats by small and/or juvenile fishes is often related to the availability of refugia from predation (Robertson and Blaber 1992; Beukers and Jones 1998), they also offer greater surface area and hence greater food availability than less complex habitats. Indeed, recently settled rabbitfishes (*S. doliatus* and *S. lineatus*) have been recorded in greatest abundances within areas of moderate *Sargassum* densities (20–30 holdfasts/m^2), with the authors suggesting this was likely related to increased refugia from predators or increased food availability (Tang et al. 2020). In mangroves and other highly complex, vegetated nursery seascapes juvenile fishes have been shown to actively select habitats irrespective of predator presence (Welch et al. 2023), and in some instances have left areas of enhanced refugia to forage in habitats of higher epiphyte abundances but fewer refugia (Nagelkerken et al. 2000; Whitfield 2017). It is likely that canopy-forming algae, such as *Sargassum*, provide a greater surface area for the settlement and growth of epibiota (Martin-Smith 1993; Carvalho et al. 2018), therefore increasing prey available to juvenile fish within macroalgal habitats (Hammerschlag et al. 2010).

The distribution of juvenile *S. doliatus* within macroalgal beds on the reef flat was distinct from that of adult *S. doliatus*, which were recorded only on the reef crest and reef slope. This distribution of both juvenile and adult *S. doliatus* is consistent with previous studies at Orpheus Island (juvenile: Waldeland 2017; Tang et al. 2020; adult: Fox and Bellwood 2007; Loffler et al. 2015; Oakley-Cogan et al. 2020) and supports the idea that macroalgal beds on inshore reefs function as a nursery habitat for rabbitfishes (Wilson et al. 2010; Evans et al. 2014). This spatial separation may reflect differences in the distribution and availability of nutritional resources and/or predation risk among habitats. Indeed, Oakley-Cogan et al. (2020) found that the availability of the epilithic algal matrix (or turfs) was a better predictor of grazing fish distributions (including *S. doliatus*) among habitats in Pioneer Bay, Orpheus Island, than habitat complexity.

Comparisons of the stomach content of juvenile rabbitfish (this study) with adult conspecifics from the northern GBR (Hoey et al. 2013) revealed that while the diets of juvenile *S. canaliculatus*, *S. doliatus*, and *S. spinus* were broadly similar and dominated by filamentous algae and detritus, the diets of adult conspecifics were more distinct and dominated by a variety of larger thallate algae (Fig. S6). These comparisons of the diet of juvenile and adult rabbitfish are, however, spatially and temporally confounded, with diet data of adult rabbitfish being from individuals collected from inner-shelf reefs in the northern GBR some 10 years previous (Hoey et al. 2013). While a recent study has shown that the taxonomic composition of the diet of adult rabbitfish (including *S. doliatus*) varies spatially (Zarco-Perello et al. 2024), the functional composition of algae in the diet is largely consistent among locations and studies (e.g. Pitt 1997; Fox et al. 2009; Hoey et al. 2013; Zarco-Perello et al. 2024).

The lack of animal material in the stomach content of juvenile rabbitfishes in the present study indicates that they had already transitioned to an herbivorous diet. This is in marked contrast to juvenile *S. canaliculatus* (2.6–5.7 cm standard length) collected from seagrass habitats around Magnetic Island (approximately 70 km south of Orpheus Island) whose stomach content was exclusively animal material (87.4% crustacean, 12.6% polychaetes; Kwak et al. 2015). The reason for this difference in the diet of juvenile *S. canaliculatus* among studies is unknown and warrants further investigation. It should be noted that our sample size was relatively small for *S. canaliculatus* and *S. doliatus* ($n = 16$ per species) and extremely small for *S. spinus* ($n = 2$), and as such, caution should be applied in generalising from our findings. As the gut and alimentary track of juvenile rabbitfishes is less developed compared to adults (Pitt 1997), it is likely to be beneficial, in terms of growth, for juveniles to target smaller and more easily digestible filamentous algae or detritus that is rich in protein (Wilson et al. 2003).

Together with the acquisition of dietary resources, risk of predation has also been hypothesised as an important process in habitat selection by juvenile reef fish (Grol et al. 2014). Although there was no relationship between the abundance of potential predators and the abundance of juvenile *S. doliatus* in the present study, the role of predation in influencing habitat use cannot be discounted. Predator abundance may be a poor predictor of predation pressure (Streit et al. 2019), and the cryptic colouration and general tendency of juvenile *S. doliatus* to hide among blades of *Sargassum* has been suggested as a means of reducing predation (Pitt 1997). Blending in with their environment potentially decreases the likelihood of being detected by visual predators and ultimately their risk of predation. Additionally, structural features of macroalgae can be highly variable among species and assemblages (Wilson et al. 2017), and as such may affect the foraging tactics and success of predators (Horinouchi et al. 2009). Future studies are required to elucidate the potential importance of predators in shaping patterns of habitat use in juvenile rabbitfish and other juvenile reef fish species that use macrophyte habitats.

Our results indicate that juvenile *S. doliatus* primarily occupy reef flat habitats that are spatially distinct from those of adult conspecifics, and they appear to use these habitats to access dietary resources (primarily filamentous, epiphytic algae). Macroalgal beds harbour unique assemblages of juvenile fishes, many of which are targeted by fishers as adults, or ecologically significant species such as rabbitfishes

(Sambrook et al. 2019; Wilson et al. 2022). While macroalgal habitats are becoming increasingly recognised as nurseries for a diversity of reef fish species, past studies have fallen short in assessing the drivers that influence habitat use by juvenile fish. Our study offers new insights into the feeding behaviour and diet of juvenile rabbitfishes within an inshore reef on the Great Barrier Reef. However, further research is required to fully understand the importance of these habitats to adult reef fish populations and the ecology of the broader seascape. Despite growing evidence of the benefits of macroalgae on reefs, the prevailing perception remains negative. Evidently, a shift in perspective is needed, one that emphasises the advantages of these habitats, as without these systems, we risk losing the many benefits they provide.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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