



Let the fish do the cropping: identifying fish grazers to improve coral aquaculture

Rachel C. Neil^{1,2,3} · Andrew Heyward⁴ ·
David G. Bourne^{1,2} · Craig Humphrey²

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Abstract Controlling the growth of fouling organisms in coral aquaculture is a recognised approach to enhance survival during grow-out of recruits. Herbivorous fish can reduce algae growth, though indiscriminate grazing by the fish pose a risk to the early life stages of corals. To identify a suitable age or size to introduce fish to coral recruit culture, settlement tiles with 1-week-old, single-polyp and 1-month-old, multi-polyp *Acropora millepora*, *Acropora kenti* and *Goniastrea retiformis* were exposed to “brusher”, “cropper” and “concealed cropper” fish grazers for 24 h, in addition to a manual aquarist cleaned treatment and a control uncleaned treatment for comparison. In general, acroporid recruits displayed lower mortality than *Goniastrea* recruits across all types of grazing, and younger, smaller recruits were more vulnerable to grazing, with the “brusher” fish functional group more likely to cause mortality. Mortality was low in the uncleaned controls for all corals, whilst single-polyp recruits generally saw slightly elevated mortality under manual aquarist cleaning. Grazing by the “brusher” *Ctenochaetus binotatus* resulted in the highest mortality

across all treatments with week old, single-polyp recruits experiencing 2.5% and 8.6% mortality for *A. millepora* and *A. kenti*, respectively, and as high as 88.9% mortality for *G. retiformis*. In contrast, month old acroporids that were 2–7 polyps in size displayed < 1% probability of mortality when exposed to the same *C. binotatus* grazing. Grazing intensity of the fish also played a role, as fish belonging to the same functional group with higher bite rates caused higher recruit mortality. Overall, “cropper” *Acanthurus nigrofuscus* represented the best trade-off between minimising recruit mortality whilst reducing algae coverage on the settlement tiles. Based on our results and knowledge of coral recruit growth, coral grow-out operations would gain the most benefit by introducing fish grazers once corals reach the multi-polyp stage at > 1 month old for acroporids and other fast growing species, and later for smaller, slower growing species such as *G. retiformis*.

Keywords Coral recruits · Fish · Grazing · Aquaculture · Herbivory

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✉ Rachel C. Neil
rachel.neil@my.jcu.edu.au

- ¹ College of Science and Engineering, James Cook University, 1 Angus Smith Drive, Douglas, QLD 4814, Australia
- ² Australian Institute of Marine Science, Cape Cleveland, Townsville, QLD 4811, Australia
- ³ AIMS@JCU, James Cook University, Townsville, QLD DB17-1484811, Australia
- ⁴ Australian Institute of Marine Science, Indian Ocean Marine Research Centre, University of Western Australia, 39 Fairway Street, Crawley, WA 6009, Australia

Introduction

The demand for sustainably produced sexually propagated coral recruits is growing, due to a burgeoning ornamental trade and the need to supply reef restoration efforts globally (Barton et al. 2017; Ferse et al. 2021). Ex situ sexual production and nursery rearing of corals require a higher initial investment but maintain higher genetic diversity, allow for selective breeding and have been shown to be more cost-effective due to increased survival rates compared to asexual transplants (Baria-Rodriguez et al., 2019; Guest et al. 2023; van Oppen et al. 2015). However, the production of corals remains hampered by critical

bottlenecks, including high mortality in the post-settlement grow-out phase (Randall et al. 2020). Growth of fouling organisms around recruits can be problematic in the early stages of culture, interfering with growth and increasing mortality (Birrell et al. 2008; Jompa and McCook 2003; Jorissen et al. 2020; Tebben et al. 2014). Crustose coralline algae (CCA), a common settlement inducer, can quickly overgrow recruits (Buenau et al. 2012; Craggs et al. 2019; Jorissen et al. 2020), and filamentous algae can colonise aquaria systems, causing reductions in coral settlement and potential overgrowth of recruits (Birkeland 1977; Birrell 2003). Other more persistent fouling algae species such as macroalgae *Bryopsis* sp. or *Dictyota* sp. can have allelopathic effects on different coral life stages and potentially cause tissue loss or reduced growth via abrasion or shading (Fong et al. 2019; McCook et al. 2001; Neil et al. 2024; Paul et al. 2011). Control of fouling can be achieved via labour intensive approaches such as coating plugs in anti-fouling material (Roepke et al. 2022; Tebben et al. 2014) or removal by aquarists (Serafy et al. 2013) or by less-intensive biological solutions such as co-culture of corals with herbivores (Ladd & Shantz 2020). In the early stages of grow-out, microherbivores such as juvenile sea urchins and small gastropods (< 1 cm) have been shown to be effective at controlling successional filamentous algae and CCA; however, other algae species often still require manual removal (Guest et al. 2023; Henry et al. 2019; Neil et al. 2024).

Herbivorous fish can control algal species that are resistant to smaller grazers, both in natural and aquaria systems (Brawley and Adey 1981; Burkepille and Hay 2008; Hughes et al. 2007). For example, in mid-water nurseries, coral fragments benefited from the recruitment of herbivorous fish, which reduce cleaning requirements (Frias-Torres et al. 2015; Frias-Torres and van de Geer, 2015; Knoester et al. 2023). Importantly however, incidental predation by herbivores can also be a driver of mortality in young recruits (Baria et al. 2010; Penin et al. 2010; Trapon et al. 2013; Whitman et al. 2024). Guest et al. (2013) noted that caging of in situ nurseries was beneficial as it excluded herbivorous fish in the early stages of grow-out, but once a suitable size was reached, cages could be removed to allow fish to feed on deleterious fouling algae (Knoester et al. 2019). This size-escape threshold is critical, with Doropoulos et al. (2012) demonstrating that the survival of 2-month *Acropora millepora* corals subjected to grazing was inversely proportional to size. Similarly, 1-week-old, single-polyp recruits of *Pocillopora damicornis* experienced high mortality when exposed to grazing by *Salarias fasciatus* (combt toothed blenny); however, once they reached 5 weeks of age with multiple polyps, recruit survival was high with only minor damage observed (Christiansen et al. 2009). From these studies, it follows that the multi-polyp stage, which is reached approximately

1-month post-settlement, represents a critical size-escape threshold in faster-growing, branching species.

Size-escape thresholds for coral recruits may be reached relatively quickly for many species, though these thresholds can vary depending on the feeding method of grazers. Herbivorous fish common in aquaria typically belongs to defined functional groups including “brushers”, “croppers” or “concealed croppers” (Tebbett et al. 2022). Brushers, sometimes called “combers”, target detritus in the algal matrix by using long, comb-like teeth to brush through algal filaments and the substrate (Purcell and Bellwood 1993; Wilson 2000; Wilson et al. 2003). Brushers are considered more nominal herbivores since their gut-contents are dominated by detritus material and sediment, whilst any algae removal is likely incidental (Christiansen et al. 2010; Marshall and Mumby 2012; Tebbett et al. 2017b). Croppers primarily target turf algae by using their shorter teeth to nip off strands above the substrate (Purcell and Bellwood 1993; Tebbett et al. 2017b). Concealed croppers function in a similar fashion to croppers, but their long narrow snouts allow them to harvest algae from small crevices unavailable to other grazers (Tebbett et al. 2022). Survival has been demonstrated to be higher for coral recruits subjected to *Salarias fasciatus* and *Acanthurus nigrofuscus* grazing, which use brushing and cropping grazing methods, respectively, but decreased when exposed to juvenile parrot fish grazing (*Scarus* spp.), which employ a scraping feeding method that effectively scrapes and remove the top layer of material from the substratum, and are not typically used in aquaria (Bellwood and Choat 1990; Christiansen et al. 2010; Doropoulos et al. 2012; Tebbett et al. 2017b). This evidence indicates that fish with grazing strategies that bring them into closer contact with coral recruits on the substrate will have a larger negative effect on their survival.

Whilst it has been established that grazers with scraping feeding strategies pose a threat to coral recruits, questions remain around how grazers with less disruptive feeding methods will affect corals of different species and ages. In *ex-situ* coral culture, control of fouling growth in grow-out systems with grazing fish is a low-effort alternative to time-consuming manual cleaning, thus identifying size-escape thresholds of coral recruits under various feeding strategies could offer practitioners a guideline for when fish grazers may be introduced to cultures. To this end, this study compared the survival of *Acropora millepora*, *Acropora kenti* and *Goniastrea retiformis* recruits at one-week and one-month post-settlement when exposed to a variety of different fish grazing strategies (brushing, cropping and concealed croppers), and the percentage of algae removed by each of the fish species during the exposure. Based on past studies, we hypothesised that one-month old recruits would be less likely to suffer mortality than one-week old recruits exposed to the same grazing pressures, and that fish of the

less disruptive concealed cropper functional group would be the least likely to cause coral recruit mortality.

Materials and methods

Coral and fish preparation

Fifty 20 × 20 cm (400 cm²) concrete tiles were conditioned prior to coral spawning in established aquaria at the Australian Institute of Marine Science's National Sea Simulator to develop a ~ 10% coverage of crustose coralline algae (CCA). Tiles were then frozen and stored at – 20 °C to kill CCA and biofilm to prevent competition between the coral recruits and the encrusting algae.

Gravid colonies of *Acropora millepora*, *Acropora kenti* (formerly *A. tenuis*, see Bridge et al. (2023)) and *Goniastrea retiformis* were collected from Falcon Reef (-18.767116, 146.534248) and Esk Reef (-18.766080, 146.520822) in the Great Barrier Reef Marine Park in November and December 2023, then returned to the Australian Institute of Marine Science's National Sea Simulator. On spawning nights, colonies were monitored and gametes collected, fertilised, then cultured until competent to settle as per Nordborg et al. (2024). Competent larvae were settled onto the pre-conditioned concrete settlement tiles at a concentration of 1000 larvae per tile. During settlement, larvae were provided with Symbiodiniaceae (*Cladocopium* sp. C1) at a concentration of 10,000 cells mL⁻¹ to initiate symbiont inoculation. Tiles were first settled during November, then corals grown-out for 1 month in mesocosm systems to allow the settlement tiles to develop a fouling community. These tiles were then settled again with new recruits from the December spawning, to ensure all tiles contained both month old (November) and week old (December) recruits. The exception was the *G. retiformis* settlement tiles, which had been left to develop a fouling community the same as the other tiles, but were only settled in December due to a lack of gravid broodstock in November. The settlement tiles were then fragmented into smaller 5 × 5 cm (25 cm²) sections and left for a further 5 days in the mesocosm tanks, until the younger recruits were approximately 1 week old.

Fish species commonly used in coral aquaculture and representing a range of grazing strategies as identified in Tebbett et al. (2022) and Wilson et al. (2003) were selected, including *Ctenochaetus binotatus* (brusher), *Acanthurus nigrofuscus* (cropper), *Zebriasoma scopas* (concealed cropper) and *Salarias fasciatus* (brusher). Fish was sourced from ornamental suppliers and introduced to clean 60L fibre-glass tanks 4 days prior to the start of the experiment for acclimation, with one fish per tank and four replicate tanks per fish species. Tanks contained shelters of appropriate size for the different fish species and were covered with a shade-cloth

to help reduce stress and prevent jumping by fish. Each tank was supplied with 0.875 L min⁻¹ of 0.1 µm filtered seawater (FSW) at 27 °C and sufficient light across a daily photoperiod of 12 h, with light intensity being 100 µmol cm⁻² s⁻¹ at the bottom of the tank with the shade-cloth on. Fish was fed to satiation twice daily, once in the morning and once in the afternoon, with a mixture of commercial pellets and dried nori. During the 24-h experimental exposures, fish was not supplied with food to encourage feeding on the coral tiles.

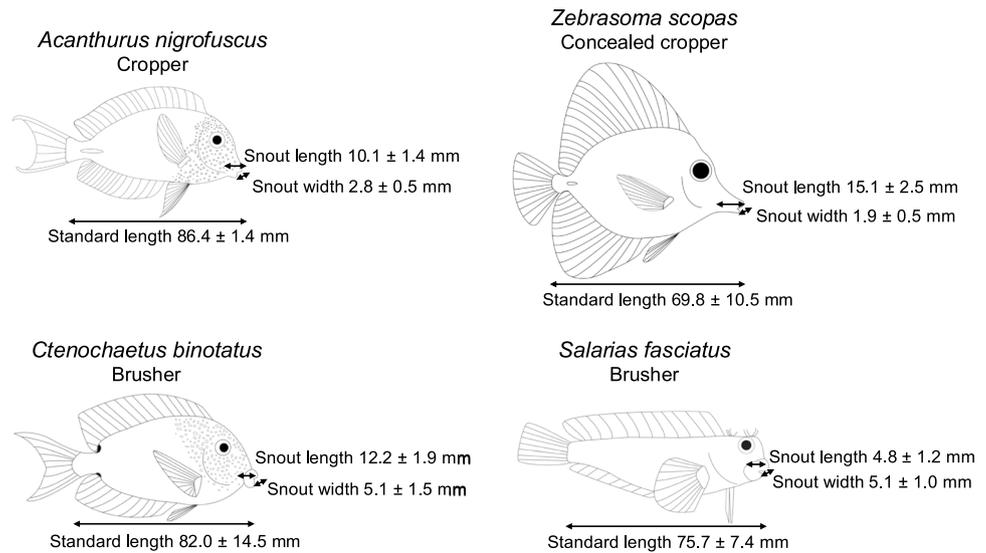
Data collection

Each 25 cm² tile section was photographed using a high-resolution camera (Nikon® DSLR D810) then randomly assigned to tanks, with four *A. millepora*, three *A. kenti* and one *G. retiformis* tile per tank. Alongside the fish, two control treatments were conducted; an uncleaned control where tiles were simply placed in the tanks then left undisturbed, and a manual cleaning control, where algae was cleaned from the tiles by an aquarist using a small brush. These treatments each had four replicate tanks to match the replicates for the fish treatments. Tiles were placed in the tanks in the morning then left for 24 h, during which fishes were filmed using GoPros during daylight hours to monitor their activity. After 24 h, tiles were removed and rephotographed.

At the conclusion of the experiment, fish were anaesthetised with Aqui-S® (540 mg mL⁻¹ isoeugenol) then photographed, and body and snout width measured using callipers. Other body measurements were taken from photographs, with snout length measured as per Brandl and Bellwood (2013) (Fig. 1). Bite-scar measurements were taken where possible by photographing visible scars with a scale-bar and their total surface area determined via ImageJ (Schneider et al. 2012). Only bite-scars with distinct edges, separate from any other bite-scars or disturbance to the algae, were used for analysis, and for *S. fasciatus*, the area of the top and bottom of the scar was summed for a total bite-scar measurement. Fish was then transferred to larger coral-holding tanks to live-out their natural lifespan.

For each fish, six random 5-min video segments were analysed to determine bite rate and substrate of bite-scar (tank walls or outside of shelters vs. coral tiles) during the coral exposure, for a total of 30 min per fish. Videos were selected using a random number generator, and before inclusion in the analysis were assessed for any signs of disturbance of the fish (e.g. by aquarists conducting checks). If a fish appeared disturbed (e.g. retreating to hides for > 1 min), the video was excluded from the analysis and a new clip randomly selected. All the fish species included in the experiment are diurnal feeders who are active throughout daylight hours, when the videos were taken. Bite rate was converted to bites per minute, which was used as a measurement of grazing intensity for the different fishes. ImageJ was used to measure

Fig. 1 Summary of standard length, snout length and snout width measurements for each fish species, presented as mean \pm standard deviation ($n=4$ for all species)



the size of recruits and track their survival post-exposure. Coral point count with CPE (Kohler and Gill 2006) was used to estimate coverage of different types of algae and other organisms (bare tile, algal turf, filamentous algae, detritus, dead and alive coral recruits and fouling worms) using 50 random points per tile for both pre- and post-exposure. Turf algae and filamentous algae were differentiated by their attachment, morphology and species composition. Briefly, ‘turfs’ were short (< 1 cm), firmly attached to the substrate, multi-species assemblages of filamentous and foliose algae, whilst ‘filamentous’ was unattached, typically monospecific, filamentous algae. Detritus was included in general fouling estimates, as the build-up of detritus and sedimentation can have negative effects on recruits, and has been shown to disproportionately affect younger recruits (Brunner et al. 2021; Moeller et al. 2016).

Data analysis

Data were analysed using *R* version 4.3.1 (R Core Team 2023) and *RStudio* version 2023.06.1 (Posit team 2023), using the *brms* package (Bürkner 2021) and *rstan* (Stan Development Team 2024). Bayesian hierarchical models were used to compare the bite rates of the fish species, the change in coverage of fouling and mortality of the different coral species at the two ages under the different treatments, using a range of binomial, negative binomial and zero-inflated negative binomial models with tank ID as a blocking factor. For all Bayesian models, weakly informative priors were used, and MCMC sampling diagnostics were performed by checking for well-mixed trace-plots, \hat{r} (< 1.01), autocorrelation (< 0.25) and effective sample size (> 1000). Density plots of the posterior and DHARMA residuals were used to check goodness of fit. Modelled median and 95% credibility intervals (Bayesian version of a

confidence interval, calculated as highest posterior density interval) were then calculated. Bayesian probabilities were also calculated to determine likelihood of true differences between treatments, i.e. a 95% probability means we are 95% certain there is a true difference between the treatments. Code with details of priors and models can be found on GitHub, and an overview of the model parameters including priors and outputs (median and 95% CI) is included in the supplementary materials.

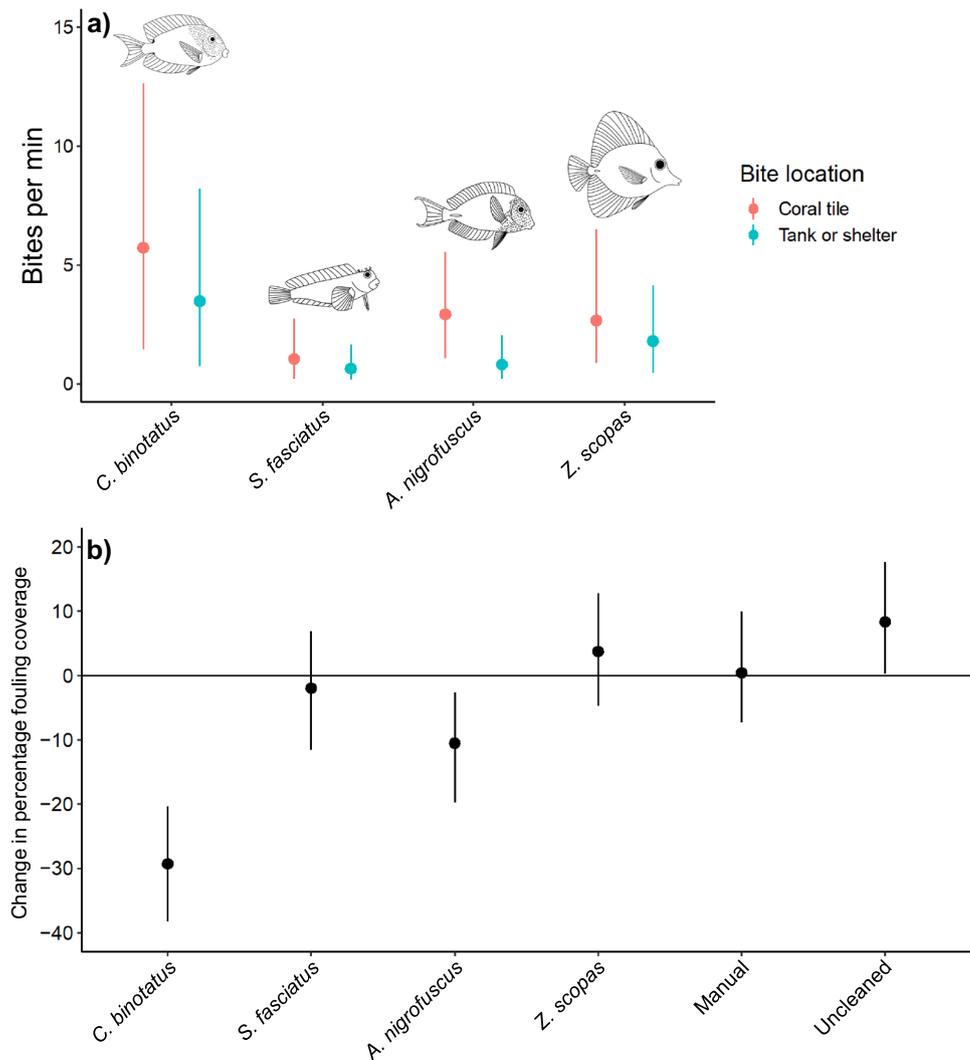
Results

Fish grazing behaviour and changes to algae coverage

All fishes had similar standard lengths (Fig. 1), though their jaw widths varied from ~ 2 mm in *Zebrasoma scopas* to ~ 5 mm in *Ctenochaetus binotatus* and *Salaria fasciatus*. The area of bite-scar produced by the fish was measured in *C. binotatus*, *S. fasciatus* and from one individual of *Acanthurus nigrofuscus*, though bite-scars in the *Z. scopas* and remaining *A. nigrofuscus* were not observed, likely due to their small mouth size. *C. binotatus* and *S. fasciatus* both had similar mean snout widths (~ 5.1 mm), though the mean bite-scar area of *C. binotatus* was much smaller (31.4 ± 11.4 mm²) than that of *S. fasciatus* (73.2 ± 18.7 mm²) (mean \pm sd). For both species, individuals with larger fish snout width had a larger bite-scar area. The single *A. nigrofuscus* that was able to be measured had much smaller bite-scars than either of the other species, at 1.0 ± 0.4 mm².

Overall median grazing intensity (measured as the sum of bites per minute on coral tiles, tank walls and shelters) varied between fish species (Fig. 2a), with *C. binotatus* having the highest (Bayesian $P > 89\%$) and *S. fasciatus* the lowest ($P > 86\%$) bite rates. *C. binotatus* also had a greater grazing

Fig. 2 a Grazing intensity of the different fish species, measured as number of bites per minute. **b** Absolute change in percentage fouling coverage on tiles after exposure to the different treatments. Dots and bars represent modelled medians and 95% credibility intervals



intensity on coral tiles (measured as bites per minute on just the coral tiles) than all other species ($P > 87\%$) and *S. fasciatus* had a lower rate than all others ($P > 89\%$). Though all fish species had higher rates of grazing on the coral tiles than the tank walls or shelter, only *A. nigrofuscus* showed evidence for a higher bite rate on the tiles than on the shelters or walls of the tank ($P = 99.5\%$). In the videos, all fishes were observed grazing adjacent or directly over recruits whilst biting coral tiles.

Median percentage coverage of fouling (i.e. the sum of turf algae, filamentous algae and detritus) ranged from ~27–42% on the coral recruit tiles prior to the start of the experiment. After the 24-h exposure to fish, only *A. nigrofuscus* and *C. binotatus* tanks saw reductions in total fouling coverage, of 10.5% and 29.3%, respectively ($P > 99\%$, Fig. 2b), which resulted in median fouling coverages of 31.5% and 6.5%. The uncleaned tanks saw a median increase of 8.3% in fouling ($P = 97.6\%$), whilst the *Z. scopas*, *S. fasciatus* and manual tanks had no evidence for a change

in fouling coverage (Fig. 2b). The average time required for an aquarist clean all the tiles in a manual cleaning tank was 9.1 ± 1.5 min (mean \pm sd). In *C. binotatus* and the uncleaned tanks, the majority of change in fouling could likely be attributed to changes in filamentous algae coverage, which dropped from a median of 27.5 to 6.1% coverage in *C. binotatus* tanks and grew from 17.5 to 30.5% in the uncleaned tanks pre- and post-fish exposure. In *A. nigrofuscus* tanks, filamentous algae coverage remained at 25.0% both pre- and post-exposure, but turf algae coverage decreased from 10.7 to 5.1%. Turf algae coverage was also reduced in *C. binotatus* tanks, from a median of 9.0% pre-exposure to 2.7% post-exposure.

Coral mortality across species and age

Mean *Acropora millepora* recruit density was similar for week old, single-polyp and month old multi-polyp recruits, though density varied between different tiles, at

$2.1 \pm 0.2 \text{ cm}^{-2}$ of settlement tile (mean \pm se) for both. *A. kenti* density was also consistent between week old and month old recruits, though lower on average, at 1.1 ± 0.1 recruits per cm^2 . Week old, single-polyp *Acropora millepora* and *A. kenti* recruits were similar in size, with non-chimera individuals having mean basal areas of $1.43 \pm 0.31 \text{ mm}^2$ and $1.45 \pm 0.30 \text{ mm}^2$, respectively (mean \pm sd). One-month-old *A. millepora* recruits displayed a small increase in mean basal area to $1.49 \pm 0.30 \text{ mm}^2$, whilst *A. kenti* recruits had a smaller area at $1.32 \pm 0.26 \text{ mm}^2$ (likely due to growth being directed upwards rather than basally), with both having $\sim 2\text{--}7$ polyps per recruit. Both *A. millepora* and *A. kenti* recruits had low mortality rates under all the tested grazing treatments (Fig. 3a, b), with strong evidence that the highest probability of mortality occurred in single-polyp, 1-week-old recruits under the *Ctenochaetus binotatus* treatment for both species (*A. millepora*: 2.5% median chance of mortality, $P > 92\%$; *A. kenti*: 8.6% mortality, $P > 91\%$). In general, single-polyp recruits were more likely to die than their month-old counterparts when exposed to grazing treatments. Uncleaned recruits (both week old, single and month old, multi-polyp) had the lowest mortality for *A. millepora* ($P > 87\%$). *A. kenti* saw its lowest modelled mortality under *Z. scopas* grazing, though similar mortality rates were found in the other treatments (barring *C. binotatus* for the single-polyp recruits and manual cleaning for the multi-polyp). The majority of acroporid recruits that experienced mortality had a skeleton remaining, though 1-week-old, single-polyp recruits under *C. binotatus* grazing had similar numbers of recruits that experienced mortality that were completely removed (i.e. no skeleton left).

Week old, single-polyp *G. retiformis* recruits had a much lower settlement density than the Acroporids, at 0.13 ± 0.04 recruits per cm^2 . These recruits were much smaller than their acroporid counterparts, at $0.30 \pm 0.09 \text{ mm}^2$, and experienced much higher mortality than acroporid recruits of the same age (Fig. 3c). Under *C. binotatus* grazing, median modelled probability of mortality was 88.9%, with $> 92\%$ certainty that this mortality was higher than all other treatments. *S. fasciatus* and the manual cleaning treatment also had relatively high modelled mortality rates, at 43.0% and 30.7%, respectively, though only *S. fasciatus* had evidence this represented an increase compared to the remaining three treatments ($P > 84\%$). Lowest modelled mortality was found in the *A. nigrofuscus* and *Z. scopas* treatments (6.3% and 5.1%, respectively), whilst the uncleaned treatment displayed a moderate mortality at 12.3%. Though these mortality rates were varied, they were still higher than those observed in *A. millepora* and *A. kenti*. All but one of the *G. retiformis* recruits that died in the experiment were completely removed.

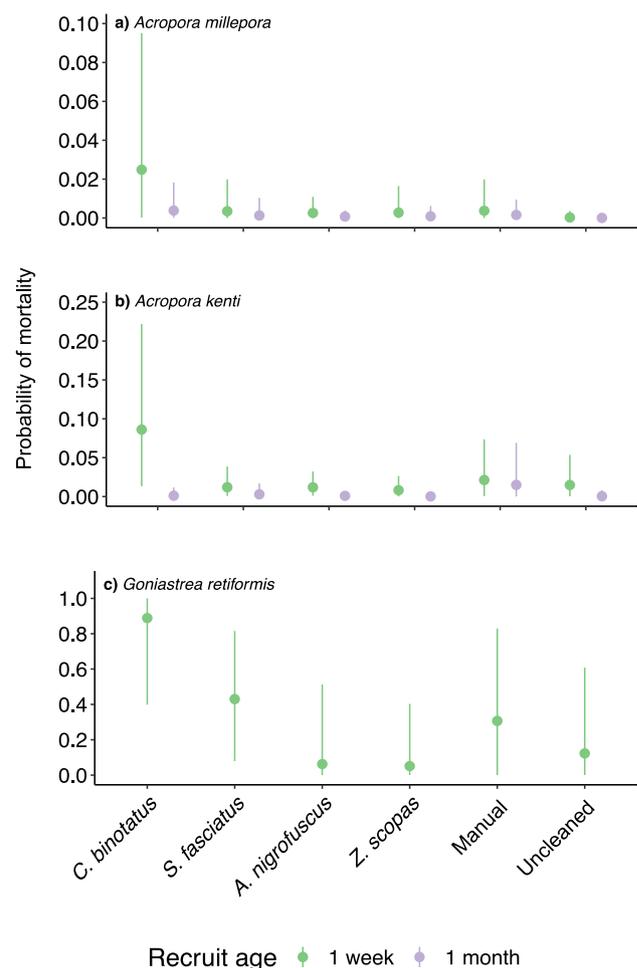


Fig. 3 Probability of mortality of coral recruits from different grazing treatments at 1-week (single-polyp recruits) and > 1 -month (multi-polyp recruits) post-settlement for **a** *Acropora millepora*, **b** *Acropora kenti* and **c** *Goniastrea retiformis*. Dots and bars represent modelled medians and 95% credibility intervals (calculated as highest posterior density interval)

Discussion

Overall, the two acroporid species displayed much lower mortality than the smaller *G. retiformis* recruits, though all corals experienced highest mortality under *Ctenochaetus binotatus* grazing. Month-old, multi-polyp *A. millepora* and *A. kenti* had lower mortality rates than their younger, single-polyp counterparts, and of those that experience mortality, younger recruits were more likely to be completely removed than month-old ones. Given the short duration of the experiment, it is unlikely that competition with algae was a major contributor to mortality, as typical algal competitive mechanisms such as overgrowth and abrasion take longer to have significant effects; thus, mortality can be attributed to natural attrition rates of recruits and disturbance from fish grazing or aquarist cleaning (Jorissen et al. 2020; McCook

et al. 2001). The reduction in mortality in the month-old, multi-polyp recruits is consistent with previous research which has shown once recruits reach the 6–8 polyp stage they are much less likely to die from over-grazing pressure (Christiansen et al. 2009; Doropoulos et al. 2012), possibly due to the 1-week-old recruits not having completely developed skeletal structures (Babcock et al. 2003; Yuan et al. 2018). *G. retiformis* also had much higher rates of mortality, and of the recruits that experienced mortality the majority were completely removed. The acroporid recruits were far larger than *G. retiformis*, at $\sim 1.4 \text{ mm}^2$ in surface area compared to $\sim 0.3 \text{ mm}^2$, which follows the principle that smaller recruits are more vulnerable to over-grazing.

The different feeding strategies of the fishes incorporated in this study (i.e. “brushers”, “croppers” and “concealed croppers” (Tebbett et al. 2022)) are the likely explanation for why coral recruit mortality rates varied between fish species, though there was also a large variation between the impacts of the two brusher species. Fishes classified as brushers target detritus and sediment typically at the base of the algae matrix, though they can incidentally remove more loosely attached algae (Tebbett et al. 2017a, 2022), whilst croppers typically nip at algae above the substratum with little detritus or sediment found in their gut (Purcell and Bellwood 1993; Tebbett et al. 2017b, 2022). The brusher fishes in this experiment (*C. binotatus* and *S. fasciatus*) had wider jaws than the cropper (*A. nigrofuscus*) or concealed cropper (*Z. scopas*). They also had much larger bite-scars than *A. nigrofuscus*, and other brusher species like *Ctenochaetus striatus* have been reported as having much larger jaw openings (180°) than *A. nigrofuscus* (113°) (Purcell and Bellwood 1993). The smooth concrete tiles used to settle the corals also meant that recruits had no access to microhabitats which can provide refugia from fish grazing (Brandl et al. 2013; Trapon et al. 2013). Thus, *A. nigrofuscus* and *Z. scopas*'s feeding methods coupled with their smaller jaw and bite sizes likely indicate that these fish rarely came into direct contact with the coral recruits in this experiment even when grazing near them, resulting in the lower mortality rates than either *C. binotatus* and *S. fasciatus*.

However, as noted above, feeding strategy alone is not solely responsible for coral mortality patterns, as both *C. binotatus* and *S. fasciatus* are classified as “brushers” yet had markedly different impacts on recruit survival. Different feeding rates and “brushing” methods between the species likely created the observed differences in recruit mortality. A higher feeding rate means greater likelihood of the fish coming into contact with the corals, and though there was variation among the individual fish, *C. binotatus* took significantly more bites on the coral tiles than *S. fasciatus* in the recorded period. *C. binotatus* also had a greater reduction in fouling coverage than *S. fasciatus*, further suggesting that grazing was either lower or at least less effective in the

latter. Interestingly, whilst the individuals in this experiment had similar jaw widths, *C. binotatus* had a lower mean bite-scar area, at around half the size of *S. fasciatus*. Potentially, this greater bite size of *S. fasciatus* may explain their lower grazing rate, as per bite they can harvest a greater mass of algae, which coupled with their smaller body size means they consume a higher relative percentage of their body mass than *C. binotatus* with each bite. Whilst both brushers, these fishes also function in slightly different manners. As per Christiansen et al. (2010) and observations of feeding from our videos, *S. fasciatus* apply both premaxillary and dentary jaws to the substrate, then pull the jaws towards each other whilst pulling backwards with their bodies, using their angled teeth to comb through algal filaments for food. In contrast, *Ctenochaetus* brushers have long, comb-like teeth which they use in a ‘brush-pan and dust’ method, where the dentary jaw is used to scrape the substrate and collect detritus against a collection plate in the premaxillary jaw (Fishelson and Delarea 2013; Tebbett et al. 2018). It may be that *S. fasciatus*'s feeding method has a lower impact on the coral recruits, despite covering a larger average area. This different “brushing” method, coupled with a lower feeding rate, likely contributes to the lower mortality rates observed under *S. fasciatus* grazing.

Despite their different feeding methods and impact on recruits, only *C. binotatus* and *A. nigrofuscus* reduced fouling coverage on the coral tiles over the 24-h exposure, with coverage increasing in the uncleaned treatment due to the fast growth of filamentous algae. Whilst the other treatments (*Z. scopas*, *S. fasciatus* and manual aquarist cleaning) did not reduce fouling coverage, they did prevent it from increasing as observed in the uncleaned tanks. Growth of fouling on surfaces during coral grow-out will be dependent on what fouling community is initially present, which will vary depending on the conditioning practices of different facilities. However, even on relatively clean settlement surfaces, fouling by filamentous algae develops in the weeks post-settlement (Guest et al. 2013). Here, we froze tiles to reduce competition between algae and recruits, resulting in an early successional environment for the settled corals. Tebbett et al. (2017b) reported that *C. striatus* is more adept at clearing early successional (< 6 weeks old), loosely attached algal turfs compared to *A. nigrofuscus*, who were better at cropping older, well-attached turfs (Marshall and Mumby 2012; Tebbett et al. 2017b), consistent with observations of this study.

Whilst the uncleaned tanks had low mortality for all recruit species, uncontrolled fouling in the first 6-month post-settlement can lead to increased mortality and reduced growth of coral recruits, particularly if fouling species such as *Dictyota* sp. propagate, which are resistant to smaller, less disruptive grazers (Craggs et al. 2019; Neil et al. 2024; Webster et al. 2015). Manual cleaning had mixed effects on

the recruits, with acroporids displaying lower mortality than the *G. retiformis* recruits, though intensive manual labour is prohibitively expensive for large-scale operations (Baria-Rodriguez et al., 2019). Therefore, practitioners must strike the balance of introducing grazers early enough that they effectively control fouling species whilst minimising impact on the recruits. From the data presented in this study, the ideal introduction point of fish grazers is after the recruits have reached the multi-polyp stage at around 1-month post-settlement for fast growing coral species. However, past work has shown that small invertebrate herbivores (gastropod, juvenile sea urchins) are sufficient to control early successional algae such as filamentous algae whilst minimising impact to corals in the early stages (< 2 months) of grow-out (Craggs et al. 2019; Neil et al. 2024, 2021). Therefore, the introduction of fish could be safely delayed until even later to further reduce impact on the corals.

From this study, *A. nigrofuscus* represented the best trade-off between removing a significant amount of fouling from the tiles whilst minimising mortality of the faster-growing acroporid recruits. *G. retiformis* also experienced lower mortality in the *A. nigrofuscus* treatment, though it was generally more vulnerable to grazing than the acroporids; thus, it would likely be best for practitioners to wait until the recruits reach the multi-polyp stage before introducing this fish. From past studies on *G. retiformis*, this would take > 1 month, with the exact timing depending on the grow-out practices and recruit growth rates of different facilities (Neil et al. 2024). Developing a microherbivore and fish grazer pipeline would be ideal, where small invertebrate herbivores are introduced to the recruits < 1-month post-settlement to control early stage algae; then, larger fish grazers brought in as the recruits become larger and the fouling community matures. Indeed, *A. nigrofuscus* was found to mostly remove turf algae, which complements the filamentous algae control that can be provided by invertebrate herbivores such as small gastropods (Neil et al. 2024). Though the exact combination and type of grazers and timing of introduction will vary between facilities, as a general rule, if culturing coral recruits with invertebrate herbivores and fish in succession practitioners should wait to introduce fish until after 2-month post-settlement, or even later if culturing slower growing species that have not reached the multi-polyp stage.

Overall, our results show that fish grazers can reduce the coverage of fouling algae in coral culture, and mortality of coral recruits is minimised when exposed to cropper or concealed cropper grazers as opposed to brushers. Co-culturing coral recruits with a less disruptive species like the cropper *A. nigrofuscus* provides an effective way to reduce algae growth whilst minimising disturbance to corals. Delaying the introduction of fishes until at least after 1-month post-settlement can significantly reduce coral mortality in response to grazing. The outcome of this work provides a

valuable guideline for introducing fish into recruit grow-out for coral aquaculture practitioners.

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Data and code availability Code and data are available via https://github.com/blue-bio/fish_recruit_public. Data are also available via the AIMS Data Centre <https://doi.org/10.25845/Z1RD-9R72>.

Declarations

Competing interest The authors declare that no competing interests exist.

Ethical approval All research was conducted in accordance with the Great Barrier Reef Marine Park Authority permits (G23/49085.1, G21/45348.1 and G21/38062.1) and James Cook University Animal Ethics permit (A2920).

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