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Fish Herbivores Targeted by Fishing are Key to Benthic Algal Suppression in Barbados

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Author Contributions

AMC designed the experimental study in collaboration with FG and HV, collected and analyzed the data, and wrote the manuscript. NK contributed to data analysis, manuscript writing, and revisions. FG and HV reviewed the manuscript and supervised the project.

Abstract

Coral reefs have undergone phase shifts from coral to algal dominance due to anthropogenic pressures such as nutrient enrichment, overfishing, and climate change. Large herbivorous fishes play a critical role in preventing algal overgrowth, yet this top-down regulation is increasingly threatened by size-selective fishing. However, the role of herbivore body size and algal composition in mediating top-down control remains poorly understood, particularly in the Caribbean. We conducted a field experiment using exclusion cages of varying mesh sizes on a fringing coral reef on the west coast of Barbados to test the role of herbivore body size in regulating algal biomass and community composition. Algal biomass was significantly higher in all exclusion cages than in controls but did not differ between large and small mesh cages, suggesting that meso-herbivores (body depth >25mm, the size class targeted by Antillean fish pots) are primarily responsible for algal suppression on this reef, and that micro-herbivores (>13mm) cannot compensate for their loss. Percent cover surveys further revealed that controls maintained higher cover of crustose coralline algae (CCA), a facilitator

of coral larval settlement, while exclusion treatments showed increased turf algae and cyanobacteria. These patterns suggest that meso-herbivores selectively remove fast-growing, competitively dominant algae, thereby promoting CCA and constraining the proliferation of turf algae and cyanobacteria. Our results add to growing evidence for the disproportionate role of larger-bodied herbivores in regulating not only algal biomass but benthic community structure, providing the first experimental demonstration of this effect in Barbados and highlighting their importance in sustaining reef resilience under climate change.

1 Introduction

Coral reefs around the world have experienced phase-shifts from coral to algal dominance with profound consequences for their associated biodiversity (Hughes et al. 2018; Leong et al. 2018; Precht et al. 2020; Tebbett et al. 2018; Wicquart et al. 2025). These shifts have been driven by the combined effects of global and local stressors, with climate change-induced thermal bleaching emerging as the dominant source of coral mortality over the past two decades (Hughes et al. 2018; Eakin et al. 2026; Manzello et al. 2025). However, local anthropogenic influences can exacerbate or mediate reef responses to climate-driven disturbances. Terrestrial runoff increases nutrient input (Adam et al. 2021; Holbrook et al. 2022; Tomascik and Sander 1987) and overfishing decreases herbivory (Steneck et al 2018), both of which favor algal growth (D'Angelo and Wiedenmann 2014; Heath et al. 2014). Because local stressors are more directly manageable than global climate forcing, understanding how nutrient enrichment and herbivore depletion interact to regulate algal proliferation is critical for developing strategies that enhance reef resilience and help reefs recover from, or cope with, ongoing climate change. Studies investigating these interactions have quantified overall grazing pressure by fish herbivores and algal response (Ferrari et al. 2012; Swierts and Vermeij 2016; Clements et al. 2018; Leong et al. 2018; Mayakun et al. 2019), but we observe substantial variation in the effects of herbivore removal and nutrient enrichment on algal productivity (Burkepile & Hay

68 2006), stressing the need for a better understanding of factors driving variation in the strength of
69 trophic regulation.

70 The capacity of herbivory to regulate algal overgrowth on coral reefs is challenged by the decline of
71 herbivore populations (Edwards et al 2024; Feitosa et al. 2023), and by unprecedented levels of
72 nutrient enrichment that could stimulate algal growth beyond saturated levels of herbivory. Nutrient
73 enrichment in the absence of herbivores amplifies algal growth, suggesting that by losing herbivores,
74 a more dramatic effect in nutrient enrichment is produced (Gacia 1999; Smith et al. 2010; Evensen et
75 al. 2019). Having a community of fish herbivores that is not depleted by fishing should help mitigate
76 the effects of nutrient enrichment, as they feed off the excess algal growth, potentially making top-
77 down regulation (the control of algal growth by consumers) dominate over bottom-up forcing by
78 nutrient availability (Burkepile and Hay 2006). Nutrient concentrations on tropical reefs are often
79 spatially and temporally variable, and the relative importance of nutrient enrichment for driving algal
80 biomass remains debated. Several studies suggest that herbivory exerts stronger and more consistent
81 control over algal biomass than nutrient availability on coral reefs, including the Caribbean
82 (Burkepile & Hay 2006; Diaz-Pulido 2003; Ferrari et al. 2012; Holbrook et al. 2016). Notably, many
83 of these studies were conducted on Caribbean reefs where nutrient concentrations are already
84 chronically elevated (Cramer et al. 2026), meaning this apparent primacy of top-down control may
85 reflect regulation against a consistently high-nutrient backdrop.

86 The strength of top-down control on coral reefs is influenced by herbivore body size (Diaz-Pulido
87 2003; Gagnon et al. 2016). Body size influences both per capita rates of algal removal and the
88 functional role of the herbivore (Adam et al. 2015; Afeworki et al. 2013; Brandl et al. 2019). Algal
89 removal rates can increase non-linearly with body size (Lokrantz et al. 2008), resulting in a
90 disproportionate contribution of large fishes to algal removal (Shantz et al. 2020). Moreover, many
91 herbivorous fishes exhibit ontogenetic shifts in diet and feeding mode, and so small and large

92 individuals of the same species may differentially affect algae and coral (Holbrook et al. 2018;
93 Durante et al. 2019). Large herbivores like parrotfish and surgeonfish have been extirpated from
94 many reefs due to size-selective fishing that preferentially removes larger individuals (Bruno et al.
95 2019; Garcia et al. 2012). In the absence of large parrotfish species, the abundance of smaller
96 parrotfish species often increases in abundance (Clua & Legendre 2008; Shantz et al. 2020). Smaller
97 herbivorous fish, small herbivorous invertebrates, or juveniles of larger grazers ≤25 mm in body
98 depth (meso-grazers; Beermann et al. 2018), can in some cases significantly reduce algal growth on
99 coral reefs and slow the decline of reef-building corals (Kuempel & Altieri 2017; Holbrook et al.
100 2016). However, smaller herbivores cannot always fully compensate for the loss of large-bodied
101 species (Fong et al. 2020). Even if total fish biomass remains similar, the loss of large herbivores
102 may result in the loss of key functions (e.g., scraping or excavating algae to bare substrate)
103 (Bellwood et al. 2004). Changes in traits associated with grazing can have important implications on
104 resulting algal community structure, particularly in systems with low functional redundancy (Adam
105 et al. 2015; Brandl et al. 2019), such as the Caribbean (Bellwood et al. 2004).

106 Body size can also be a predictor of algal feeding preferences, with important consequences for algal
107 community structure. Herbivorous fishes are often highly selective in their diets and will
108 preferentially consume certain algal species based on their palatability, nutritional value, and
109 compatibility with their digestive system (Baker et al. 2017; Johnson et al. 2017; Nicholson &
110 Clements 2022). These preferences can shift with body size as bite size, jaw morphology, and
111 digestive capacity change ontogenetically (Adam et al. 2015; Brandl et al. 2019). Algae, in turn, vary
112 widely in their morphology, chemical defenses, and ecological effects on corals. For example, turf
113 algae and fleshy macroalgae differ in how they compete with corals via shading, abrasion or
114 allelopathy (McCook et al. 2001). Many algal species inhibit coral recruitment (Kuffner et al. 2006),
115 but some crustose coralline algae can promote settlement by coral larvae (Heyward & Negri 1999).

Because herbivore feeding preferences and feeding modes vary with body size, the size structure of the herbivore community, increasingly truncated by size-selective overfishing, can shape which algal groups dominate, mediating competition between benthic organisms, influencing rates of ecological processes, and shaping recovery trajectories following disturbances (Burkepile & Hay 2010; Humphries et al. 2014; Huntington et al. 2022; Ruttenberg et al. 2019).

This study was conducted inside a no-take Marine Protected Area on the West coast of Barbados, where fish herbivore populations are protected from size-selective fishing, allowing us to assess the role of herbivore body size in top-down control under conditions representative of an unfished fish herbivore community. This study used size-selective exclusion cages that specifically excluded fish herbivores targeted by Antillean fish pots, an important fishing gear used on Barbadian reefs (Mahon & Hunte, 2001; Robichaud et al. 1999; Schuhmann et al 2011, Vallès et al. 2025).

In this study, we tested the effect of herbivore size on algal biomass and composition on a fringing reef in a no-take area along the West coast of Barbados. We conducted a caging experiment using multiple mesh sizes to exclude either meso-herbivores (body depth > 25mm) or both meso- and micro-herbivores (body depth >13mm) from settlement tiles. Based on the literature, we predicted a gradient of algal biomass and community composition across treatments: from open controls, where intact herbivore communities maintain low algal biomass and high CCA cover, through large-mesh cages, where meso-herbivore exclusion was expected to increase algal biomass and reduce CCA in favor of turf algae, to small-mesh cages, where additional exclusion of micro-herbivores was expected to produce the strongest algal response if micro-herbivores contribute meaningfully to top-down control. A key question was whether small-mesh and large-mesh cages would differ, which would indicate that micro-herbivores can compensate for the loss of meso-herbivores. Our study documents the role of meso-herbivores in regulating the biomass and structure of algal communities in a Caribbean coral reef ecosystem.

2 Materials and Methods

2.1 Study Site

The study was conducted on the South Bellairs reef, a reef inside the only no-take area of Barbados (Mahon & Mascia 2003), just off the Bellairs Research Institute of McGill University, Holetown, Barbados. We chose this site because as a no-take area, adult fish herbivores are significantly more abundant (Chapman & Kramer 1999), and parrotfish size and biomass are greater than outside the no-take area (Vallès et al. 2015). Parrotfishes are particularly important functional herbivores on Caribbean reefs, as they remove algal biomass, crop turf algae, and in some cases excavate the substrate, thereby maintaining open space for coral recruitment and contributing to bioerosion and sediment production (Adam et al. 2015**)**. Historical (Allard 1994; Hunte & Wittenburg 1992; Tomascik & Sander 1985, 1987) and more recent (Simpson et al. 2023; Tosic et al. 2009) water quality surveys support that South Bellairs reef experiences a relatively high concentration of anthropogenic-derived dissolved nutrients (Cramer et al 2026; Hunte & Wittenburg 1992; Tomascik & Sander 1985, 1987; Simpson et al. 2023). Under this well-documented backdrop of relatively high nutrient levels, which is likely typical of many reef sites across the Caribbean (Cramer et al. 2026), we experimentally examined the extent to which fish herbivore assemblages unaffected by fishing exerted top-down control of benthic algae,

2.2 Size-specific herbivore exclusions

To test how fish herbivore size influences top-down control of algal growth, we deployed exclusion cages and control treatments containing experimental tiles on which algal abundance was monitored (Fig. 1). Cages were constructed from PVC pipe and hexagonal wire mesh and were designed to exclude herbivores based on body size using two mesh sizes. Small mesh cages (13 mm) excluded both micro- and meso-herbivores with body depths greater than 13 mm, while large mesh cages (25

mm) excluded only larger-bodied herbivores such as parrotfish, surgeonfish, and Bermuda chubs (Kuempel & Altieri, 2017). The 25 mm mesh size was deliberately selected to match that of traditional Antillean fish pots used by local fishers in Barbados (Schuhmann et al 2011), providing a realistic simulation of selective fishing (Fig. 1). Empirical sampling with this mesh size retained surgeonfishes as small as 9cm and parrotfishes as small as 15cm fork length (H.Vallès, unpublished data). We defined exclusion thresholds by body depth, as this determined whether a fish could pass through the mesh, but report fork-length equivalents as the more familiar metric of fishing selectivity.

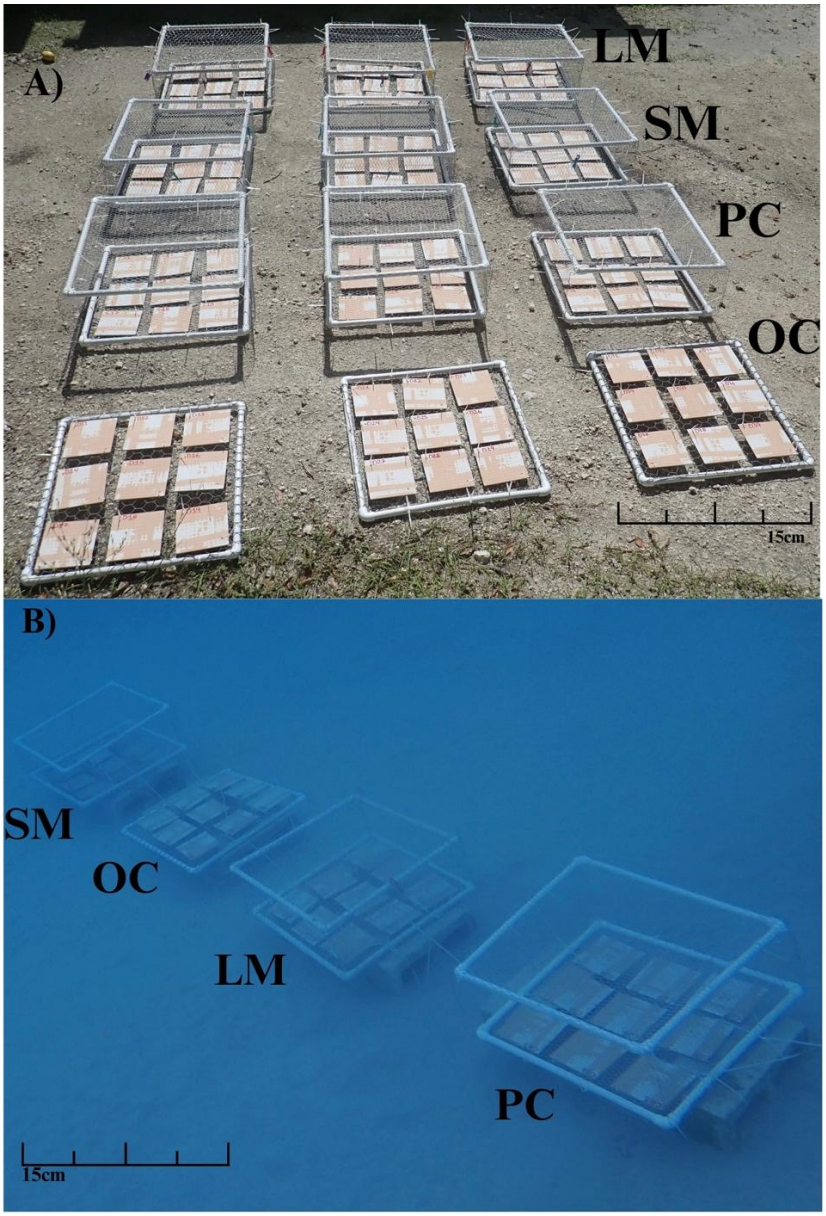


Fig. 1 (a) Above water photograph of 3 blocks of replicates not yet randomized. (b) Photograph of randomized experimental block located at the end of sand and groove formations underwater. Caged large mesh (LM), Caged small mesh (SM), Partial Cage (PC), Control (OC).

To account for potential non-grazing effects of the cages, such as changes in light, sedimentation, or water flow, we included partial cages as procedural controls. These cages were enclosed only on the top and bottom and open on the sides. We used the small mesh (13 mm) for partial cages to match the more restrictive treatment, allowing us to isolate the effect of herbivore exclusion while holding mesh size constant. This choice avoids confounding effects due to mesh size differences, and previous studies have shown that mesh size does not influence the outcome of partial controls (Tebbett et al. 2018). Open cages, consisting of a single bottom mesh panel to secure the tiles, served as fully open controls. In each cage and control treatment, nine terracotta tiles were secured at the base and used to monitor algal growth over time (Fig. 1 & 2).

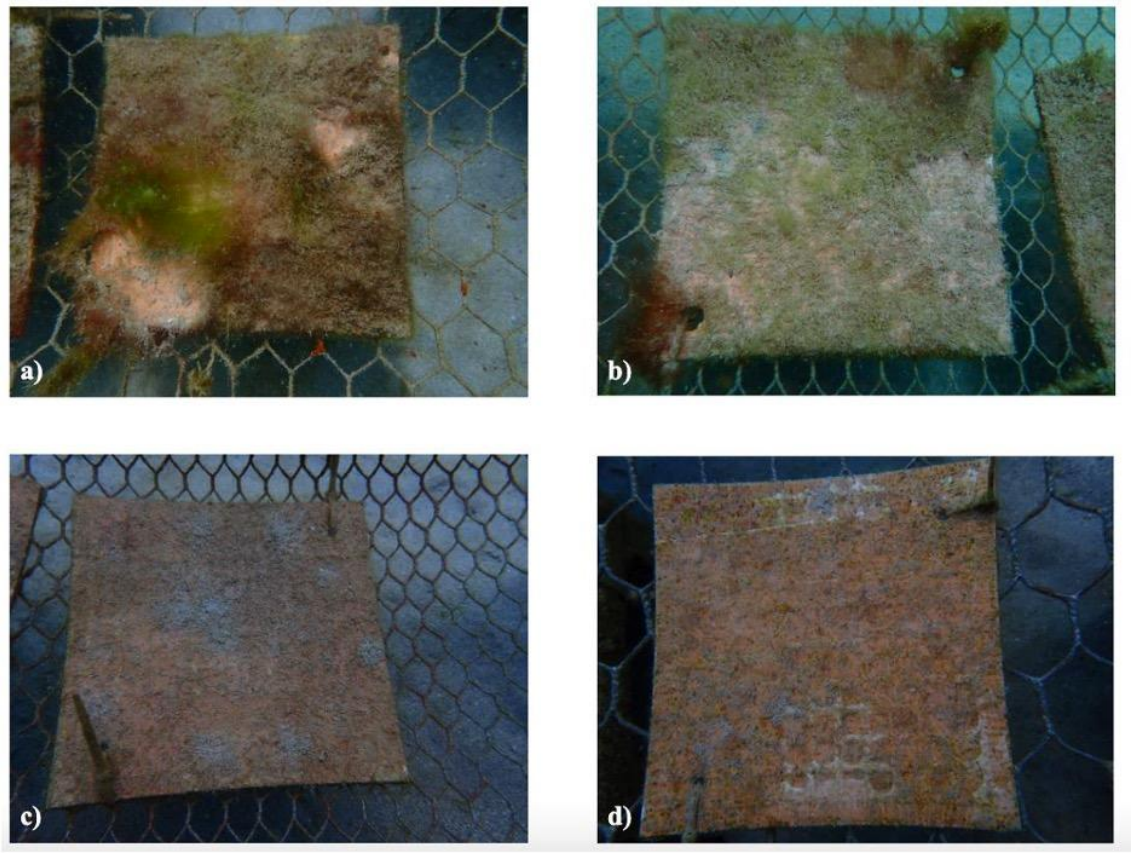


Fig. 2 Tile Comparison after 8 weeks. a) Large Mesh Closed Cage, b) Small Mesh Closed Cage, c) Partial Cage (Procedural Control), d) Open Cage control.

We conducted our experiment from July-September 2021. We placed cages in open areas on spur and groove formations, about 100 meters from shore, in relative proximity to the coral substrate (5-10 meters), but not too close in order to prevent damage to any coral substrate during installation, and to prevent damselfishes from taking over the tiles and creating gardens inside the cages (Randazzo Eisemann et al. 2019). A total of 24 cages were built and divided into six blocks. Each block contained each level of our exclusion treatment levels: Caged large mesh size (LM), caged small mesh size (SM), partial cage as our procedural control (PC) and uncaged open plot control (OC) (Fig. 1). The treatment position was randomized in each block. We installed the cages over the course of two days at depths between 6 and 10 meters. Two breezeblocks were used to secure each cage to the seafloor. Block sites were distanced so that one block site was not visible from the other (>15 m apart).

2.3 Algal Abundance

We tested for time-dependent effects of our experimental treatments by collecting tiles starting four weeks after cage installation. Three tiles were removed from each cage biweekly for the remainder of the sampling period that lasted eight weeks. For each sampling week (three total), tiles were randomly chosen across all 24 cages. Tiles were then placed into individually labelled treatment bags and brought back to the lab for analysis. In the lab, algae were scraped off tiles and dried in a drying oven at 60°C for 48 hours. Dry weights were measured using a precision balance. After the 8-week sampling period, we incinerated samples in a Muffle Furnace at 575°C for 4 hours to obtain Ash Free Dry Weight (AFDW). We weighed samples immediately after incineration to minimize reabsorption of moisture.

We further assessed the effect of our experimental treatments on algal composition and cover using non-destructive photographic sampling. Photos were taken weekly from Week 2 to Week 8 for a total duration of eight weeks. Each tile was photographed once per week. Due to the bi-weekly removal of tiles for Ash Free Dry Weight (AFDW) analysis, some tiles were only photographed until Weeks 4, 6, or 8.

Photographs were taken using an Olympus TG-4 camera at an approximately fixed distance and angle perpendicular to the tile surface (Fig. 2). To measure percent cover, images were analyzed in CoralNet using predefined substrate categories: Sand/ Bare Substrate, Turf Algae, Fleshy Algae, Foliose Algae, Brown Fleshy Algae, Crustose Coralline Algae (CCA), Cyanobacteria and Lobophora. All images were manually checked for accurate classification, and one observer annotated the images, with a second observer reviewing the classifications for quality control. Quality control was conducted on all annotated images, and discrepancies were corrected prior to analysis. Inter-observer agreements exceeded 90% across substrate categories.

2.4 Statistical Analyses

2.4.1 The effect of herbivore size on algal growth

To test for the effect of herbivore size on algal growth, we fitted a generalized linear mixed-effects model with a Gamma error distribution and a log link in R (R Core Team, 2026) using the glmmTMB package (Brooks et al. 2026). Ash free dry weight (AFDW) was used as the response variable because values were positive and continuous, and model comparison and diagnostics indicated that a Gamma model provided a better fit than a Gaussian alternative. Fixed effects included sampling Week (weeks 4, 6 and 8), Cage treatment (large mesh closed cage, small mesh closed cage, partially caged/ procedural control, open cage/positive control), and their interaction. Week was treated as a categorical factor. Random intercepts were included for CageID and Block.

The model specification was as follows:

$$\mathbf{AFDW} \sim \mathbf{Week} * \mathbf{Cage} + (\mathbf{1}|\mathbf{CageID}) + (\mathbf{1}|\mathbf{Block})$$

Post hoc pairwise comparisons of estimated marginal means were conducted using the emmeans package (Lenth 2026) with Tukey adjustment to test for differences among cage treatments within each week and among weeks within each cage treatment. Compact letter displays were used to summarize significant treatment differences within weeks.

2.4.2 The effect of herbivore exclusion and size on algal percent cover and composition

To test for the effect of herbivore exclusion on algal percent cover and composition, we fitted a linear mixed-effects model in R using the nlme package (Pinheiro et al. 2026). Percent cover was treated as a continuous response variable. Fixed effects included sampling Week (weeks 2 to 8), Cage treatment (large-mesh exclusion, small-mesh exclusion, partial cage, and open control), and their interaction. Random intercepts for Block and CageID nested within Block accounted for the hierarchical structure of the experiment.

The model specification was as follows:

$$\mathbf{Percent\ Cover} \sim \mathbf{Week} * \mathbf{Cage} + (\mathbf{1}|\mathbf{Block}) + (\mathbf{1}|\mathbf{Block}:\mathbf{CageID})$$

We modelled algal percent cover separately for each algal category. For the focal analyses presented in the main text, separate models were fitted for CCA, cyanobacteria, and turf algae. For descriptive summaries of benthic composition, total algal cover was calculated as the sum of all algal groups. Model suitability was assessed by inspecting raw distributions, quantile-quantile plots, and residuals versus fitted values. Post hoc pairwise comparisons of estimated marginal means were calculated

using the emmeans package (Lenth et al. 2026), and multcomp (Hothorn et al. 2026) was used to generate compact-letter displays for pairwise Tukey-adjusted treatment differences within each week.

3 Results

3.1 Algal Biomass

Our controlled field experiment revealed that excluding herbivores substantially increased algal biomass (Fig. 3, Table 1). Both large- and small- mesh exclusion cages consistently supported the highest algal biomass across the three sampling periods, whereas open cage controls maintained the lowest algal biomass (Fig. 3). There was no significant difference in AFDW between large and small mesh cages (Fig. 3, Table 1). By week 8, algal biomass in the large-mesh treatment was approximately 22 times higher than in open controls.

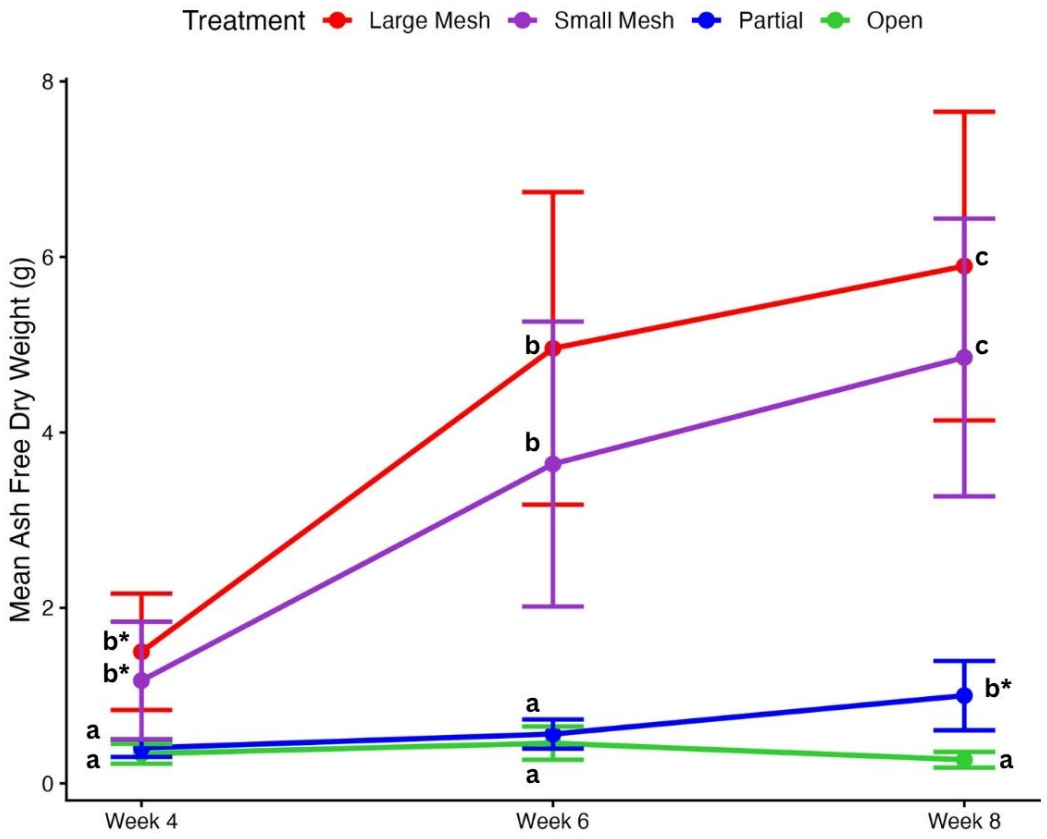


Fig. 3 Mean Ash Free Dry Weight (AFDW) across cage treatments over three sampling periods (weeks 4, 6 and 8). Points and error bars show mean ± 95% confidence intervals. Different lowercase letters indicate significant differences among cage treatments within the same week. Weeks with an asterisk were statistically different from other weeks within each cage treatment.

The effect of grazers on algal biomass was significant at our first sampling date, 4 weeks after the start of our experiment, and was observed in both large and small mesh exclusion cages compared to open controls, with these trends persisting through weeks 6 and 8 (Table 1). Partial cages initially mirrored open cage controls, showing no significant differences in AFDW during weeks 4 and 6. However, by week 8, algal biomass increased significantly in partial cages while continuing to decrease in open controls.

Table 1. Results of the Generalized Mixed Effects Model to predict the effect of grazer size and herbivorous grazing on algal growth inside a benthic coral reef community based on AFDW. *p<0.05; **p<0.01; ***p<0.001.

Fixed effects	Estimate	Std. Error	t value	Pr(>|z|)	
(Intercept)	-1.11911	0.21307	-5.252	1.50E-07	***
Large Mesh Cage	1.6941	0.25805	6.565	5.21E-11	***
Partial Cage	0.17127	0.25581	0.67	0.50317	
Small Mesh Cage	1.1816	0.25703	4.597	4.28E-06	***
Week 6	0.22345	0.23024	0.97	0.3318	
Week 8	-0.18371	0.23306	-0.788	0.43055	
Large Mesh Cage x Week 6	0.72456	0.32946	2.199	0.02786	*
Partial Cage x Week 6	0.07998	0.32343	0.247	0.80469	
Small Mesh Cage x Week 6	0.91405	0.3275	2.791	0.00525	**
Large Mesh Cage x Week 8	1.38916	0.32873	4.226	2.38E-05	***
Partial Cage x Week 8	1.07277	0.33011	3.25	0.00116	**
Small Mesh Cage x Week 8	1.72122	0.32919	5.229	1.71E-07	***

3.2 Algal Percent Cover

Our controlled field experiment revealed that herbivore exclusion (large- and small-mesh exclusion cages) substantially increased percent cover of turf and cyanobacteria over time (Fig. 4), whereas crustose coralline algae (CCA) had negligible cover in both large- and small-mesh exclusion cages throughout the experiment (Fig. 4). In contrast, open and partial cages supported significantly higher CCA cover beginning at Week 4, and these differences persisted through Weeks 6 and 8 (Fig. 4 and 5). Open and Partial cages showed significant week-to-week increases in CCA cover.

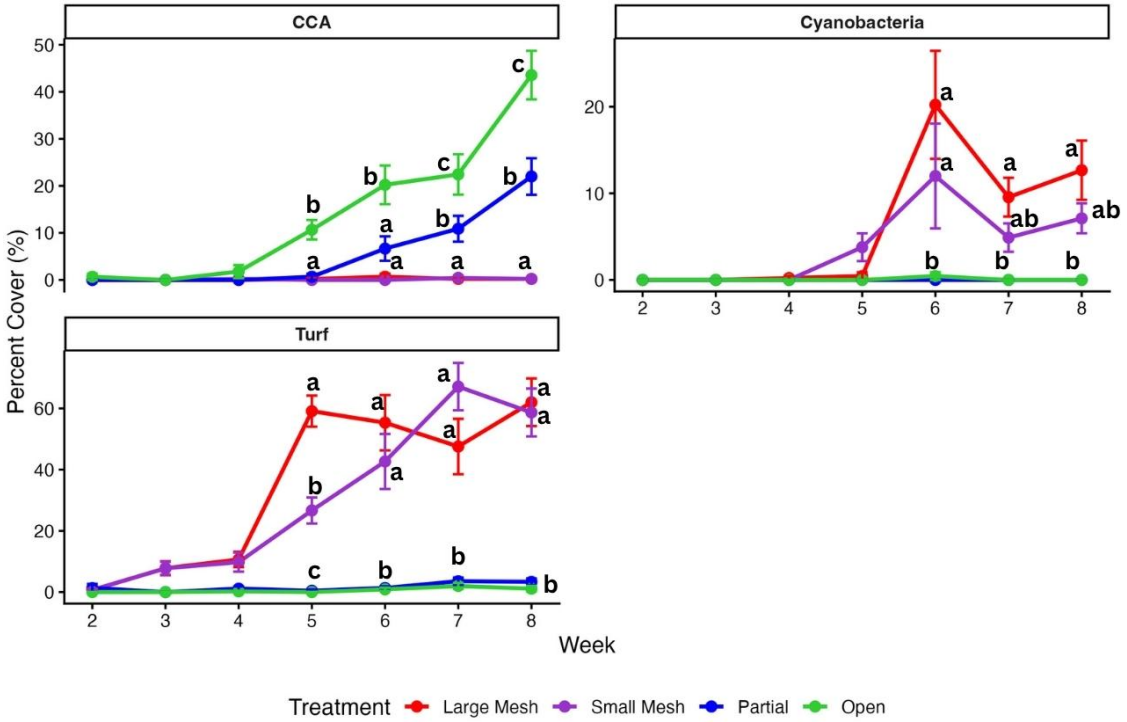


Fig. 4 Temporal trajectories of percent cover for CCA, Turf, and Cyanobacteria across four herbivore-exclusion treatments. Points represent mean percent cover ± standard error (n = 18 per treatment per week), and lines connect treatment means through time. Different lowercase letters indicate significant treatment differences within a given week at $p<0.05$; letters are shown only for weeks in which the overall treatment effect was significant. Overlapping lines were only represented with one letter.

Turf algae rapidly increased in response to herbivore exclusion. By Week 5 both large- and small-mesh cages had significantly greater turf cover than partial and open controls and maintained higher turf cover through the end of Week 8 (Fig. 5). Mean turf cover reached 59.1% in large mesh cages and 26.7% in small mesh cages, compared with 0.4% in partial cages and 0% in open controls. Across all exclusion treatments there was a significant increase in turf cover from Week 4 to 5. Weeks 6 and 7 in the mesh cages denote additional significant weekly gains, whereas partial and open cages showed little week-to-week change over the 8-week sampling period and showed consistently lower cover (Fig. 4).

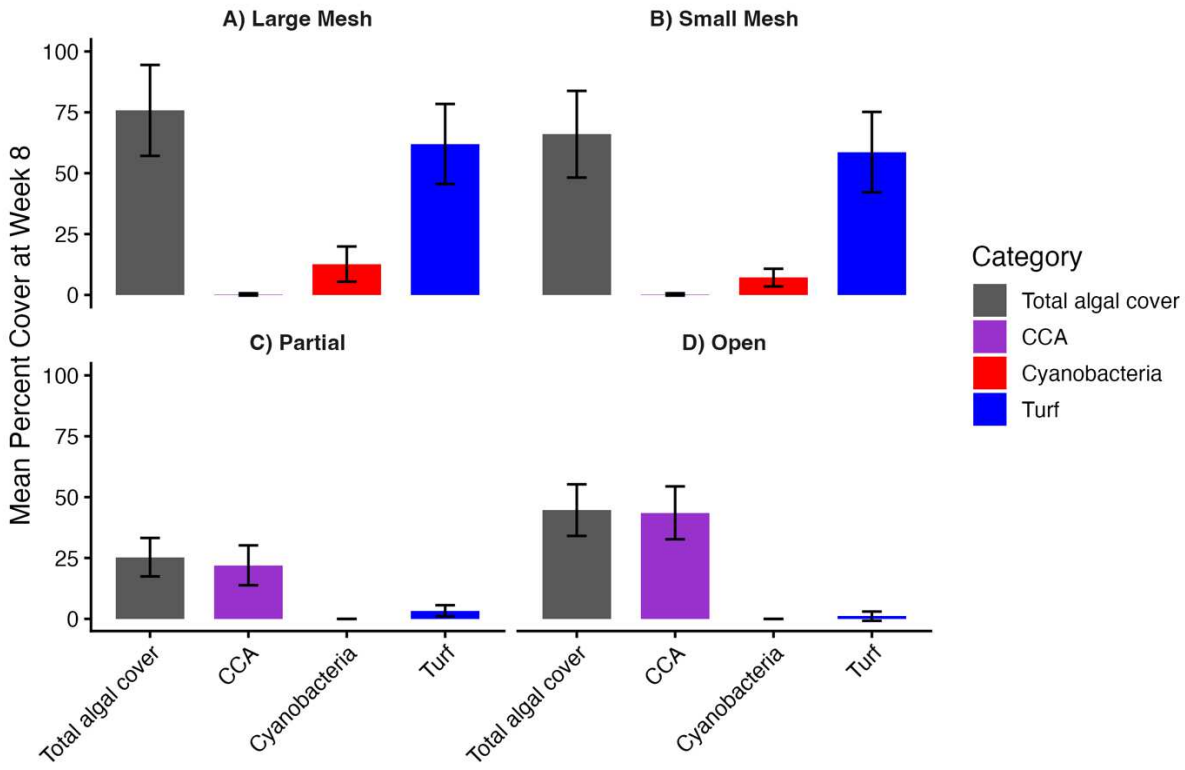


Fig. 5 Mean percent cover of selected algal categories at week 8 across cage treatments. Panels correspond to A, Large Mesh; B, Small Mesh; C, Partial; and D, Open. Bars represent mean percent cover ± 95% confidence intervals for total algal cover, calculated as the sum of all algal groups except sand (or just CCA, Cyanobacteria, Turf).

Cyanobacteria cover increased in herbivore exclusion cages beginning in Week 5 but remained near zero for partial and open control treatments throughout the experiment (Fig. 4). During weeks 6-8 cyanobacteria cover was highest in the large mesh cages (12.7% at week 8), followed by the small mesh cages (7.1% at week 8), and effectively absent in the open and partial controls (0% at week 8) (Fig. 5).

4 Discussion

We found that in a no-take reef in Barbados, meso-herbivores (>25 mm body depth), typically targeted by fish pots, were responsible for suppressing algal growth. Excluding meso-herbivores increased algal growth by 22-fold relative to controls, but additionally excluding micro-herbivores (25-13mm) did not further increase algal growth. Excluding herbivores also changed algal composition: crustose coralline algae dominated in the presence of herbivores, whereas turf algae and cyanobacteria dominated in their absence. Our study suggests that the presence of fish herbivores falling within the size range targeted by fishing could provide important context to reconcile observed variation in the strength of top-down control of algal overgrowth and community structure in coral reef ecosystems of Barbados. Our findings reveal the potential for a disproportionate importance of meso-herbivores relative to micro-herbivores for top-down regulation. They also show how algal regulation results in shifts in algal community composition, with potential implications for the turf-sediment complex and interspecific interactions that can mediate coral reef resilience. Our study provides important insights for marine conservation in Barbados and for fisheries management of meso-herbivores targeted by Antillean fish pots.

4.1 Herbivore Body Size and Top-Down Control

The role of consumer body size in mediating top-down control is well-documented across marine systems (Diaz & McQuaid, 2011). In rocky shore systems, for example, larger grazers have been

shown to drive the strength of trophic control in ways that smaller consumers cannot replicate (Tejada-Martínez et al. 2016). On coral reefs, studies have found that large-bodied parrotfish and surgeonfish account for the majority of grazing, with feeding rates scaling with body size (Bellwood & Choat, 1990; Burkepile & Hay, 2008; Adam et al. 2018; Fong et al. 2016). In the Caribbean, reefs with populations of these larger-bodied herbivores currently subjected to low or no fishing pressure maintain lower macroalgal cover and higher coral recruitment compared to fished reefs where size-selective overfishing has reduced mean herbivore body size (Mumby et al. 2007; Steneck et al. 2018; Shantz et al. 2020).

Our results show that grazing by meso-herbivores, such as parrotfish and surgeonfish, suppresses algal growth, even in a nutrient-rich environment. These families are among those typically retained in Antillean fish pot catches in Barbados (Vallès et al. 2025), linking the size class responsible for top-down control to the one targeted by local fishing. This was evidenced by consistently greater algal biomass in both large- and small-mesh cages compared to partial and open controls, and by the absence of any further increase when micro-herbivores were additionally excluded, highlighting the insufficiency of micro-herbivores in regulating algal growth on their own. Multiple factors can explain the lack of top-down control from micro-herbivores. Invertebrate or small-bodied fish micro-herbivores that retained access to large-mesh cages were either not sufficiently abundant at our study site, had limited mobility to reach cages, or were not sufficiently efficient as grazers to provide any additional control over algal growth compared to small-mesh cages (Beermann et al. 2018). The mechanisms underlying this net effect will require further assessments of relative abundances and differences in foraging behavior between micro- and meso-herbivores.

It is worth noting that our small-mesh (13 mm) and large-mesh (25 mm) treatments were chosen to reflect the body depth thresholds relevant to Antillean fish pots widely used in Barbadian coastal fisheries, with meso-herbivores corresponding closely to the size class retained and removed by this

gear (Robichaud et al. 1999; Mahon & Hunte, 2001). Our exclusion thresholds therefore approximate an ecologically and economically meaningful size cutoff: the fish that fishing pressure selectively targets. The fact that meso-herbivores, rather than micro-herbivores, account for the overwhelming majority of top-down control suggests that current fishing practices, even outside no-take zones, are likely removing the size class of herbivores most responsible for algal regulation.

4.2 Shifts in Algal Community Composition and Implications for Coral Reef Resilience

The role of consumers in mediating species interactions and composition of their resources is key for understanding the strength of trophic regulation and its broader community implications (Smith et al. 2010; Ruttenberg et al. 2019). Our experimental results revealed shifts in algal community composition in addition to overall abundance, underscoring the cascading effects of herbivore exclusion on coral reef ecosystems (Jessen & Wild, 2013). CCA, a key reef-builder, declined significantly in the absence of herbivory but remained stable in our control cages, supporting the idea that grazing pressure selectively favors less competitive algal groups (Littler et al. 2006; Burkepile & Hay, 2009; but see Teichert et al. 2020). Specifically, CCA cover decreased substantially within exclusion cages, whereas turf algae expanded rapidly over the eight-week experiment, reinforcing a shift towards turf dominance. This antagonistic response aligns with the Relative Dominance Model (Littler & Littler, 1984; Littler et al. 2006), which predicts shifts from CCA to more competitive turf algae or macrophytes under herbivore exclusion and increasing nutrient inputs (Smith et al. 2010; Ruttenberg et al. 2019)

Shifts in algal community composition are likely to have broader community-level consequences beyond increases in algal abundance. Turf algae accumulate fine sediments within their filamentous structure, forming a turf-sediment complex (Bellwood et al. 2004; Goatley & Bellwood, 2012) that can suppress coral survival, growth, and recruitment through sedimentation, reduced light

availability, and allelopathic interactions (Kuffner et al. 2006; McCook et al. 2001; Speare et al. 2019). CCA, in contrast, is widely recognized as a facilitator of coral larval settlement (Heyward & Negri, 1999). The replacement of CCA by turf algae and cyanobacteria under meso-herbivore exclusion therefore suggests that loss of this size class may reduce reef resilience not only by increasing total algal biomass, but also by shifting benthic communities towards states less favorable for coral recovery. Reef systems that have crossed into turf dominance may face a compounded recovery challenge, as the sediment legacy embedded in turf mats must also be cleared before coral larvae can successfully settle and survive (Speare et al. 2019).

Our results show that in a no-take coral reef chronically exposed to strong nutrient enrichment, meso-herbivores can suppress the growth of turf-sediment complexes that decrease coral survival, growth, and recruitment. Yet Bellairs, despite hosting some of the healthiest populations of parrotfish and surgeonfish in Barbados, has continued to lose coral cover, and recent surveys indicate that its protected status has not been sufficient to prevent this decline (Vallès et al. 2025). This discrepancy between the strong top-down control we document, and the ongoing degradation of the reef itself is likely attributable to a mismatch of scales. Our study resolves a process that acts locally and over a short period, whereas coral reef health is shaped by drivers operating across spatial and temporal scales, including nutrient enrichment, disease, storms, and extreme thermal events (Bieg et al. 2024; Tomascik & Sander, 1985; Tosic et al. 2009; Wicquart et al. 2025). Our study stresses the need to understand the interaction between local stressors such as top-down trophic regulation and larger-scale climate events to mitigate the impact of climate change on coral resilience and restoration.

4.3 Context-dependence, Fishing Pressure, and Implications for Marine Conservation in Barbados

Barbados provides an important case study for examining the interaction between local fishing pressure and reef trophic dynamics. The relative importance of top-down and bottom-up control on Barbadian reefs has been debated for several decades (Bieg et al. 2024; Cramer et al. 2026), with early work attributing elevated algal cover to nutrient enrichment rather than reduced grazing (Bell & Tomascik, 1994; Tomascik & Sander, 1985, 1987) and later work linking benthic change to the loss of grazing following the 1983 *Diadema antillarum* die-off (Hunte & Wittenburg, 1992; Allard, 1994). Resurveying west coast reefs including Bellairs, Allard (1994) found algal change to be more strongly associated with reduced urchin densities than with eutrophication levels and concluded that herbivorous fish had been unable to compensate for the loss of *Diadema* grazing, plausibly because trap fishing had already depressed their abundance.

Barbadian reefs remain subject to artisanal and commercial fishing pressure, and size-selective fishing has been shown across the Caribbean to shift herbivore populations towards smaller-bodied individuals (Hawkins & Roberts, 2004). Antillean fish pots, a gear long used in Barbadian shallow reef habitats, retain fish above a size threshold set by mesh aperture (Mahon & Hunte, 2001), that was approximated by our exclusion treatments. The size class we show to be primarily responsible for algal regulation therefore corresponds to the size class that trap gear selectively removes. Our experiment was conducted within a no-take zone where this fishing pressure is absent, and the strong top-down control we observed may therefore not be representative of fished reefs in Barbados. Barbados is currently restructuring the governance and regulation of its fisheries sector under a new national fisheries policy (Cox et al. 2026), and empirical studies such as this one could help inform the development of gear regulations aimed at protecting the herbivore size classes most important for algal control.

Our results can be read as an indicator of the strength of top-down regulation that is eroded when meso-herbivores are removed by fishing outside MPAs. Studies from comparable Caribbean systems

have documented reduced herbivore body size and grazing rates on fished reefs relative to protected ones, with associated increases in algal cover and decreases in juvenile coral density (Burke et al. 2011; Steneck et al. 2018; Wilson et al. 2021). Our results illustrate a key underlying mechanism: the reduction in body size via the experimental exclusion of meso-herbivores, the size class targeted by Antillean fish pots, drives the collapse of top-down control, micro-herbivores having no impact on algal biomass or composition.

Integrating fish herbivore body size into MPA selection and management strategies can help achieve MPA objectives of promoting coral resilience, as supported by studies showing increased juvenile coral density in well-managed fisheries (Steneck et al. 2018). However, given the variation in body-size dependence of herbivory reported in the literature, conservation strategies should rely of regional assessment of body-size impact of herbivory. Management efforts must also be adapted to size-dependent herbivory given evidence that compliance and enforcement, rather than MPA size or age alone, are key drivers of large herbivore biomass across Caribbean MPAs (Skinner et al. 2026).

Our results provide site-specific experimental support for including the protection of meso-herbivorous fish among management priorities. Taken together, our findings highlight the role of herbivores targeted by fishing in regulating both the biomass and composition of benthic algae on coral reefs and illustrate the importance of considering both herbivore traits (body size) and algal community structure (species composition) to explain observed variation in the strength of top-down control, with important implications for the development of conservation strategies. However, because our experiment was conducted over a small spatial extent and a short time frame, these effects are best interpreted as one component of a broader set of processes. Bottom-up drivers such as nutrient loading and water quality operate over larger areas and longer periods and may exert comparable or greater influence on algal biomass and composition (Adam et al. 2021; Cramer et al. 2026), including the fringing reefs of Barbados itself (Tosic et al. 2009). With Barbados committed

to increasing protection from less than 1% to approximately 30% of its waters (The Nature Conservancy, 2022a, 2022b), understanding the interactions among local stressors such as herbivory, water quality, and larger-scale climate events across a range of scales remains an urgent priority for mitigating the impact of climate change on coral resilience and restoration.

5 Statements and Declarations

5.1 Funding

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5.2 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

5.3 Ethics Approval

Not applicable. This study did not involve the capture, handling, or sampling of vertebrate animals; exclusion cages only altered the access of free-ranging herbivores to settlement tiles.

5.4 Data Availability Statement

The data and R code used in this study are available in Zenodo at https://doi.org/10.5281/zenodo.21416592.

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