



Going further on herbivore fishing: the removal of smaller fishes from algal-dominated reefs

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ABSTRACT: Overfishing of large herbivorous fishes is connected to the rise of algal-dominated states on coral reefs. The recovery of their populations is challenging, and future herbivore assemblages may be composed of smaller fish. With fisheries now targeting these smaller-sized herbivore populations, coral reef benthic communities may face unknown outcomes. We performed caging experiments in algal-dominated reefs of Northeastern Brazil, that have been depleted of large herbivorous fishes, to appraise the effects of removing small herbivores on benthic community composition and succession. Full cages simulated herbivore removal, and partial cages and open plots functioned as controls. In total, 36 experimental plots were monitored for 1 yr, accounting for the influence of seasonal changes in local conditions of temperature and turbidity. Overall macroalgal cover did not change between experimental treatments, but filamentous algae increased 5-fold inside full cages by the end of the experiment, surpassing articulated coralline forms as the dominant group. Higher temperatures during the dry season promoted filamentous algae when the top-down control of the herbivores was removed, while a reverse pattern was observed when fishes were allowed to feed inside plots. Small herbivores accelerated benthic succession, facilitating the dominance of articulated coralline algae as the climax community. Our findings oppose previous studies performed at sites with high abundances of large-bodied fishes, where herbivory decreased overall macroalgal cover, promoted filamentous and crustose coralline algae and delayed community succession. The further depletion of smaller-bodied herbivores can trigger shifts in benthic community dynamics that interact with water temperature, which may have implications for reef resilience in an ocean-warming scenario.

KEY WORDS: Herbivory · Fishing effects · Phase shift · Coral reefs · Parrotfish · Surgeonfish · Damselfish · Functional ecology · Brazilian reefs · Community ecology

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1. INTRODUCTION

The role of herbivorous fish has been a recurring subject in coral reef studies for the past 2 decades (Bonaldo et al. 2014, Hoey & Bonaldo 2018, Lange et al. 2020). They have been regarded as one of the essential components for reef functioning, and their feeding activities are thought to regulate core ecological processes (Adam et al. 2015a, Harborne & Mumby 2018, Topor et al. 2019). Attributable to these fishes are the mediation of benthic competition by

macroalgae removal, promoting reef builders such as coral and crustose coralline algae (CCA), production and transport of reef sediments and predation on coral and sponges (Mumby & Steneck 2008, Graham et al. 2013, Cordeiro et al. 2020). However, variable degrees in the delivery of these functions have been increasingly identified, and both experimental and observational works point toward the functional complementarity of piscine herbivores (Burkepile & Hay 2008, 2010, 2011, Adam et al. 2015b, 2018, Capitani et al. 2021). Many factors are linked to the

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variation among herbivorous fishes in their relative contribution to reef functions (Bonaldo et al. 2014, Feitosa et al. 2021); among them, fish body size is a determinant of the nature and intensity of the impact of herbivore feeding on the reef (Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Cardozo-Ferreira et al. 2018, Robinson et al. 2020).

Seminal and more recent studies attempting to classify herbivores into functionally meaningful groups are somewhat tied to fish body size. For instance, the largest parrotfishes have jaws powerful enough to penetrate the reef matrix while feeding and are regarded as 'excavators' (Bonaldo et al. 2014, Siqueira et al. 2019b), being linked to functions such as bioerosion, corallivory and removal of algae (Siqueira et al. 2019a). Much smaller fish, such as surgeonfishes of the genus *Ctenochaetus*, are classified as 'brushers' and only participate in the transport of sediments (Goatley & Bellwood 2010, Siqueira et al. 2019b). Additionally, larger individuals of the same species make a disproportionately higher contribution in their roles as algae removers or bioeroders, at least in parrotfish (Bruggemann et al. 1996, Lokrantz et al. 2008, Ong & Holland 2010, Yarlett et al. 2018; similar metrics for other herbivores such as surgeonfish are still not available given methodological difficulties, as discussed in Tebbett et al. 2022). Estimations are that a 50% decrease in the mean body size of a parrotfish population as a result of fishing can result in a 90% loss of some functions performed by these fish (Lokrantz et al. 2008). Therefore, the roles of herbivorous fish communities are strongly determined by species composition and fish body size. At the same time, fish size also determines fishing interest, as larger species and individuals are selectively captured. Consequently, highly fished herbivore communities are prone to be disproportionately composed of smaller-sized fish, such as juveniles of larger species (e.g. parrotfishes and surgeonfishes) and adults of smaller species (e.g. damselfish) (Edwards et al. 2014, Robinson et al. 2019a, 2020), resulting in a potential shift in the functional performance of herbivore assemblages.

In the literature, smaller herbivores have been sporadically noted to have a greater influence on macroalgal removal than expected from their size. There are instances where smaller-bodied herbivorous fishes have been responsible for higher grazing rates than larger fish (Robinson et al. 2020), delivering enough grazing potential to prevent macroalgal dominance after massive coral bleaching events (Kuempel & Altieri 2017) or being major contributors to the formation and structuring of habitats (Madin et

al. 2019). Identifying the dimension of algal control by these smaller fish in impacted reefs can contribute to the comprehension of subsequent ecological trajectories in environments increasingly exposed to anthropogenic stress (Kuempel & Altieri 2017), and the current understanding of these processes is still incipient. Assessing the importance of these smaller species on macroalgal consumption and their influence on the composition of benthic communities is essential, mainly because fishing can impact smaller species once large herbivore stocks are depleted (Bejarano et al. 2019, Robinson et al. 2019b).

Most reefs in Brazil are distributed only a few kilometers or less from the coastline (see Leão et al. 2003) and are intensively affected by the historical subsistence of coastal communities on fishing. Parrotfishes have been increasingly targeted in these inshore reefs in recent decades (Bender et al. 2014, Previero 2014), with growing interest in the exportation of their catches (Marques & Ferreira 2010, MPA 2012). As a result, large-sized parrotfish stocks are depleted in several sites and captures and fish size are drastically diminishing over time (Bender et al. 2014, Roos et al. 2020). Other smaller-bodied herbivore species that have been of little interest to fisheries in the past, such as surgeonfish (Ferreira & Maida 2006), are increasing in importance to fisheries (Cunha et al. 2012). Additionally, Brazilian reef fish communities are much less rich in herbivore species than other systems (Ferreira et al. 2004, Siqueira et al. 2019a). The loss of these few large-sized herbivorous species has likely contributed to changes in benthic communities in Brazilian reef systems.

The rise of alternative stable states to coral dominance has been attributed to several processes that contribute to reductions in coral cover and the increase of macroalgae. Besides the release of top-down control of macroalgae due to overfishing, bottom-up nutrient enrichment of macroalgae as a result of eutrophication and side-in perturbations directly affecting coral, such as diseases, predator outbreaks, thermal and sedimentation stress, and natural disasters are also a cause of coral demise (Precht et al. 2020). When multiple impacts are in place, measuring the causes of coral cover reductions and predicting the trajectories of dominant taxa on tropical reefs is a complex task, and it is still a matter of debate how extensive and persistent the macroalgal dominance is (see Jackson et al. 2014 and Precht et al. 2020 for opposing views of the Caribbean region). Nevertheless, the loss of coral cover is a worldwide trend that has risen in recent decades; estimates are that corals currently cover about 50–75% less of the

substrate than they did in the past (Gardner et al. 2003, Bruno & Selig 2007, Bruno et al. 2009, Schutte et al. 2010, De'ath et al. 2012, Jackson et al. 2014, Hughes et al. 2018), and they have been replaced by macroalgae more often than by any other sessile organism (Norström et al. 2009, Jackson et al. 2014). Hence, understanding the dynamics of the new ecological relationships established in macroalgal-dominated states is paramount, especially those related to the top-down control exerted by herbivores.

Despite the lack of long-term quantitative records, there are indications that a reduction in live coral cover also occurred in Brazilian reefs, leading to phase shifts to stable states of macroalgal or zoanthid dominance (Cruz et al. 2015, 2016, 2018, Soares et al. 2021, 2022). Coral cover diminished from approximately 25% in the 1960s to less than 5% in the 2000s on the northeastern coast (Ferreira & Maida 2006, Laborel-Deguen et al. 2019), and these reefs are currently highly dominated by macroalgae, which covers more than 60% of all Brazilian reefs (Aued et al. 2018, Ferreira et al. 2021). This system is often overlooked in global perspectives of the macroalgae dominance spread (such as Bruno et al. 2009); however, it could serve both as an early warning of possible future scenarios for other systems and as a model for studies aspiring to provide new perspectives on ecological outcomes in impacted reefs.

Herein, we experimentally assessed the consequences of going further and fishing down smaller herbivores for reefs dominated by macroalgae. This subject was addressed with 3 main questions: (1) what is the effect of smaller-bodied fish on benthic algal communities, and (2) how is the delivery of their herbivory influenced by local conditions? (3) When a new bare substrate is available, are small herbivores capable of influencing community assembly?

2. MATERIALS AND METHODS

2.1. Study area

The present study was performed on the Tamandaré reef complex, ILTER (International Long Term Ecological Research) Site 18. The Tamandaré reef complex is situated off the northeastern coast of Brazil, where most hermatypic coral reefs in the southwestern Atlantic are located. The area has a coastal tropical climate with average air temperatures near 30°C during the dry season (November–May) and 24°C during the rainy season (June–

October) (Maida & Ferreira 1997). Given a distinctive coral fauna, these reefs grow as isolated columns that can reach 5–6 m and then laterally expand just below the surface, creating large reef flats (Dominguez et al. 1990, Ferreira et al. 1995, Maida & Ferreira 1997). Algae dominate among organisms covering the reef flat, of which articulated coralline algae are the most abundant group, primarily composed of *Halimeda opuntia* and *Jania* spp. (~40–70%; Feitosa et al. 2012, Feitosa & Ferreira 2015). Sessile animals are only found in minor proportions; zoanthids and corals occur sparsely and comprise ~2% of benthic cover (Feitosa & Ferreira 2015).

The study area is within a no-take zone of the Tamandaré Fortress Municipal Park, where fishing and tourism activities have been prohibited since 1999 in an area of approximately 3 km², including 5 extensive reefs and several reef patches. The area is also part of the Multiple Use Costa dos Corais Marine Protected Area (APACC) and is considered a zone of protection of marine life (ZPRE) under its management plan. The region contains typical coastal reefs of the Southwestern Atlantic Region, where reefs occur very close to the coastline (less than a few km apart) and are found in shallow waters (less than 7 m deep). In Brazilian reefs, fishing pressure on herbivores is most substantial on these inshore reefs (Roos et al. 2020). For instance, parrotfish densities inside the APACC's no-take area reach ~12 ind. per 100 m² at most, whereas in highly fished areas, parrotfishes are found in densities as low as 2 ind. per 100 m² (Fig. A1 in the Appendix). Conversely, parrotfish densities of 30–40 ind. per 100 m² are common in sites with lower fishing incidence elsewhere in Brazil (raw data used in Araújo et al. 2020), highlighting that reefs in the study area could not reach parrotfish densities comparable to those sites even after 20 yr of fishing prohibition under intensive enforcement in the no-take area. Five parrotfish species are present in the study area (*Sparisoma amplum*, *S. axillare*, *S. frondosum*, *Scarus trispinosus* and *S. zelindae*), with *S. axillare* being the most abundant species in herbivore assemblages, mainly juveniles (Feitosa & Ferreira 2015). Surgeonfishes are highly dominant in these assemblages; *Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus* occur at an average of ~18 ind. per 100 m² on Costa dos Corais reefs (Fig. A1). Herbivorous fishes with total lengths (TLs) greater than 20 cm are scarce across all APACC fished sites, whereas the density of fishes smaller than this threshold is still comparable among both fished and unfished sites (Fig. A1). Here, we aimed to evaluate the effect of the further removal of these smaller

fishes through the experimental procedures described below.

2.2. Experimental design and data collection

Two reef patches about 100 m apart were selected inside the no-take area for experimental procedures (Fig. 1). As the present study aimed to evaluate the effects of fishing smaller herbivores, we considered 3 main points: (1) experiments should be placed inside an area with lower densities of large-bodied parrotfish (i.e. individuals with TL greater than 20 cm) that has high densities of both smaller parrotfish and surgeonfish (less than 20 cm TL) in comparison to surrounding fished reefs (Lippi et al. 2022; Fig. A1); (2) these sites should be placed inside a no-take area to allow for the above conditions and reduce possible human interference; and (3) experiments should exclude herbivores within a size that would be of fishing interest but allow fishes too small to be targeted for fisheries to feed inside the plots. Therefore, cages were designed with 3 cm mesh nets, the same nets used by local fishermen to make fishing traps that capture parrotfishes above 15 cm TL (described in Ribeiro 2004). Fully caged treatments then allowed damselfishes and small juvenile parrotfish and surgeonfish to feed inside the plots, as they are not targeted by fisheries. This mesh size has also been found to balance potential artefacts caused by mesograzers (e.g. crustaceans and gastropods) that could

use cages as refuges from predators (Lewis 1986) and has been proven in previous works to exert minimal interference to algal development (McClanahan et al. 2002, 2003, Sotka & Hay 2009, Bennett et al. 2010, Shantz et al. 2019), water flow and sedimentation rates (Miller & Hay 1998, Miller et al. 1999, Smith et al. 2001, McClanahan et al. 2003).

The experimental design consisted of 3 treatments: (1) full cages, which simulated the depletion of small herbivores; (2) partial cages, which were covered with nets only on the sides, which evaluated artefacts of allochthonous material on the grazing behavior of fish not targeted in this study; and (3) open plots, which were utilized as controls. Even though fully and partially caged plots did not allow the entrance of sea urchins, they were rarely observed at our field sites during the maintenance of cages and monitoring of open plots; thus, their influence on the benthic community in the experiments was considered negligible. Full and partial cages had 40 × 40 × 25 cm stainless steel frames fixed to the substrate by 15 cm stainless steel stakes. Cage walls were made of a plastic net with 3 cm mesh, mounted over frames and held in place with cable ties. The net extended over the surrounding substrata (~10 cm) to prevent fish penetration underneath the cages. Open plots were marked on the reef by placing nails at 4 opposite corners of a 40 × 40 cm square. All plots were cleared of fouling organisms every 2 wk to prevent shading. Net cleaning was performed by removing the cable ties and nets, which were brushed *in situ* away from

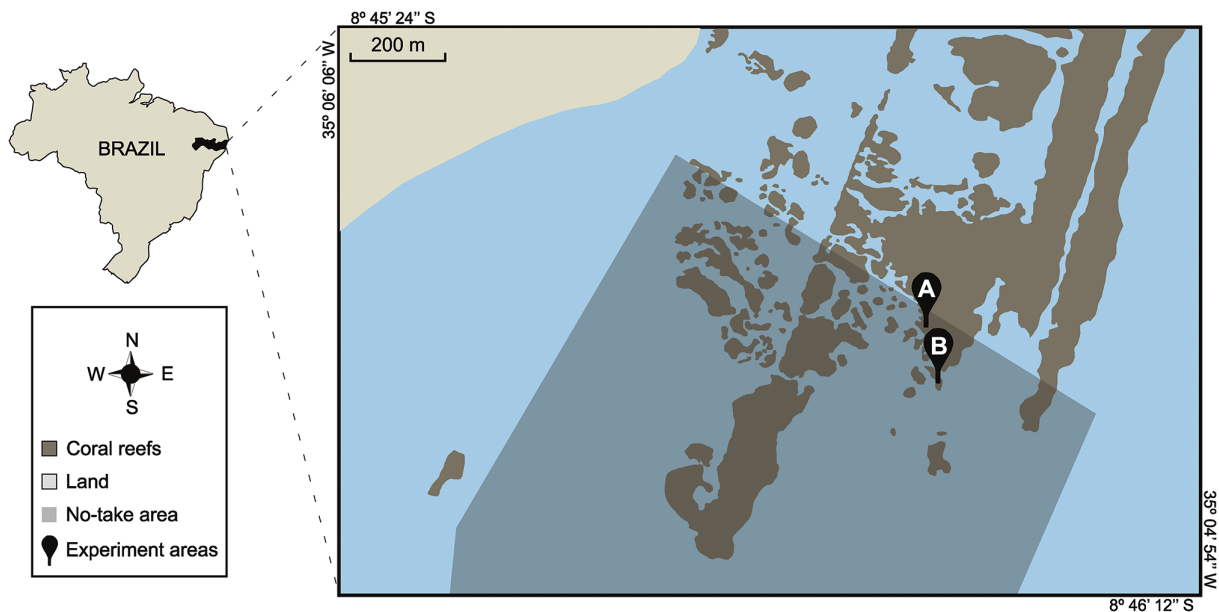


Fig. 1. Study area within the limits of the Costa dos Corais Marine Protected Area. A and B are sites selected for experiment installation

Table 1. Algal genera, classified into functional-form groups (modified from Littler & Littler 1984). NI: not identified

Filamentous	Articulated coralline	Foliose	Coarsely branched
Acrochaetaceae NI	<i>Amphiroa</i>	<i>Dictyopteris</i>	<i>Acanthophora</i>
<i>Aglaothamnion</i>	<i>Halimeda</i>	<i>Dictyota</i>	<i>Botriocladia</i>
<i>Antithamnion</i>	<i>Jania</i>		<i>Caulerpa</i>
<i>Antithamnionella</i>			<i>Gelidiella</i>
<i>Bryopsis</i>			<i>Gracillaria</i>
<i>Calithamnion</i>			<i>Hypnea</i>
<i>Ceramium</i>			<i>Laurencia</i>
<i>Champia</i>			<i>Palisada</i>
<i>Cladophora</i>			
<i>Dipterosiphonia</i>			
Ectocarpaceae NI			
<i>Gelidium</i>			
<i>Griffithsia</i>			
<i>Gymnothamnion</i>			
<i>Herposiphonia</i>			
<i>Heterosiphonia</i>			
<i>Neosiphonia</i>			
<i>Polysiphonia</i>			
<i>Pterocladia</i>			
<i>Spyridia</i>			
<i>Wrangelia</i>			

plots to prevent fouling organisms from falling inside the area of the experiment. No fish were allowed to feed inside the plots during net cleaning. With this design, 36 experimental plots were placed in the 2 selected sites (18 plots per site; Fig. 1) and monitored for 12 mo (April 2013 to April 2014). The reef patches were about 100 m in diameter, and plots were equally distributed across their tops. Plots were randomized in relation to treatment and were placed at least 5 m apart from each other. Half of the plots (equally distributed across treatment and sites) were completely scraped after 6 mo, and samples were used to estimate the biomass of algae (in September 2013). The remaining plots were continuously monitored for the full year. After the complete removal of all organisms, scraped plots with bare substrata were monitored to evaluate potential herbivory effects on benthic community succession until the end of the experiment.

Substrate cover was the metric used to evaluate herbivory effects through experiments, monitored every 2 wk with photoquadrats, and analyzed using CPCe v.4.1 (Kohler & Gill 2006). A total of 100 points per cage were randomly selected in this software, where benthic organisms underneath each point were identified. Samples for biomass estimation (collected in September 2013) were frozen and taken to the laboratory, where macroalgal species were iden-

tified to the lowest taxonomic level possible. Algal samples were dried at 60°C for 24 h and weighed (0.01 g precision), and dry weights were used to measure biomass. For substrate cover and biomass measures, algal species were assigned to ecological groups according to their morphological and functional forms: filamentous, articulated coralline, foliose, coarsely branched or crustose coralline (modified from Littler & Littler 1984). The functional-form thick leathery algae were not observed in our plots. Genera included in each functional-form category are listed in Table 1, except for CCA (Order Corallinales), which were not identified to genus level.

2.3. Environmental variables

Environmental parameters that could also influence macroalgal growth and/or herbivory were acquired through remote sensing. Images derived from Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA's Aqua satellite were utilized for estimating sea surface temperature (SST), chlorophyll *a* (chl *a*) concentration, photosynthetically active radiation (PAR), particulate organic carbon (POC) and particulate inorganic carbon (PIC). This radiometer is present in both Terra and Aqua satellites and provides complete global coverage in 1–2 d intervals. Mapped images with a 4.63 km resolution (Level 3) containing monthly averages for the selected parameters were processed through the software SeaDas v.7.0.2. By using monthly averages, missing or red-flag data could be avoided. These parameters were tested for collinearity before model fitting using Pearson's correlation coefficient. In this analysis, chl *a*, PAR, POC and PIC were significantly correlated; therefore, only POC was included in further analyses because this variable is linked both with primary production and turbidity (Slaets et al. 2014, Kharbush et al. 2020).

2.4. Data analyses

Our first 2 questions—the effects of herbivory by small fishes on benthic communities and their interaction with other environmental drivers—were tested using linear mixed-effects modeling (LME), fitting one model to each functional group. This ap-

proach permitted the inclusion of both categorical and continuous variables in a repeated measures design, most appropriate for monitoring the algal community using non-independent samples over time. For model fitting, and following analysis using data derived from percentage cover estimation, response variables were logit-transformed before analysis, which increases analytical power more than other methods such as arcsine transformation (Warton & Hui 2011). Predictors included the categorical factor 'treatment', consisting of the 3 experimental procedures applied, whose levels were coded 'cage' for full cages, 'partial' for partial cages and 'open' for open plots. The environmental parameters (SST and POC) were included as continuous variables in the model. Time of closure was also considered a continuous variable (referred to as 'time' in models), expressed as days from experiment installation. The spatial variation of sites and temporal dependence of each plot (from the repeated measures design) were included as random effects in the models, following a nested structure (plots nested in sites). Interactions between the factor 'treatment' and the continuous predictive variables were also accounted for in full models. LME models were fitted in 'lme' function of the package 'nlme' (Pinheiro et al. 2020) in R software (R Core Team 2020). These full models were tested for performance against generalized linear models fitted with the 'glmer' function of the package 'lme4' (Bates et al. 2015), which were fitted using raw cover data as response variables and indicating the distribution family as binomial and logit as the link function. After inspection of the residuals of models using both approaches, the ones fitted here were found to perform the best. The selection of predicting variables in LMEs was based on Akaike's information criterion, using the function 'dregde' from the 'MuMin' package (Bartoń 2020) in R.

To test if herbivore influence on algal cover extended to their biomass, each functional form was tested for differences in mean dry weight between treatments through 1-way ANOVAs, utilizing the scraped macroalgae samples collected after the first 6 mo of caging, as mentioned above. Biomass data for each algal type was investigated for normality through Q-Q plots, Shapiro-Wilk tests and fitted normal distributions, while Bartlett's tests indicated homoscedasticity.

A permutational multivariate analysis of variance (PERMANOVA) was applied to compare changes in the cover of functional forms of benthic organisms after the last 6 mo of experimentation, testing if small herbivores could drive changes in benthic commu-

nity succession (the third question underlined in this study). The factor 'treatment' had the same levels described above, and sites were considered strata of permutations. Changes in the community over time were observed with a non-metric multidimensional scaling (nMDS) analysis. The PERMANOVA analysis was performed through the 'adonis' function, while the nMDS was fitted with the 'metaMDS' function, both using Bray-Curtis similarity and performed using the 'vegan' package (Oksanen 2019) in R.

3. RESULTS

Benthic cover of algal functional groups was mostly influenced by treatment. Filamentous and coarsely branched algal cover decreased in partial and open plots, whereas the cover of articulated coralline and foliose algae increased (Fig. 2). The significant interaction between time and treatment indicates that these shifts in algal cover occurred gradually throughout the experiments, intensifying over time. SST only consistently affected the cover of filamentous algae, and these effects differed between herbivory treatments. POC only had an effective influence on articulated coralline algae; POC promoted the cover of these algae inside all plots, as the interactions with treatments were not significant. Reef-building organisms, i.e. CCA and coral, presented minor changes with all factors analyzed (Fig. 2). As results obtained from partial and open plots were similar in their responses, we considered that no artefacts related to the placement of foreign material on reefs were found and that the effects of caged treatments were successfully attributed to the removal of the fishes targeted in the design of experimental procedures. Results from LME fitting are shown in Tables S1–S6 in the Supplement at www.int-res.com/articles/suppl/m713p117_supp.pdf.

As expected, algae significantly dominated all experimental plots regardless of the manipulation of herbivore pressure. The main functional groups were filamentous, articulated coralline and foliose algae, which invariably occupied over 70% of available substrate cover from the beginning of experimental trials. Nevertheless, the dominant group changed considerably between treatments. At the beginning of the experiment, filamentous algae represented only around 10% of the plots. After 1 yr of experimentation, the influence of small herbivores maintained filamentous cover around the same values, but herbivore exclusion resulted in caged plots having around 50% of filamentous algae cover

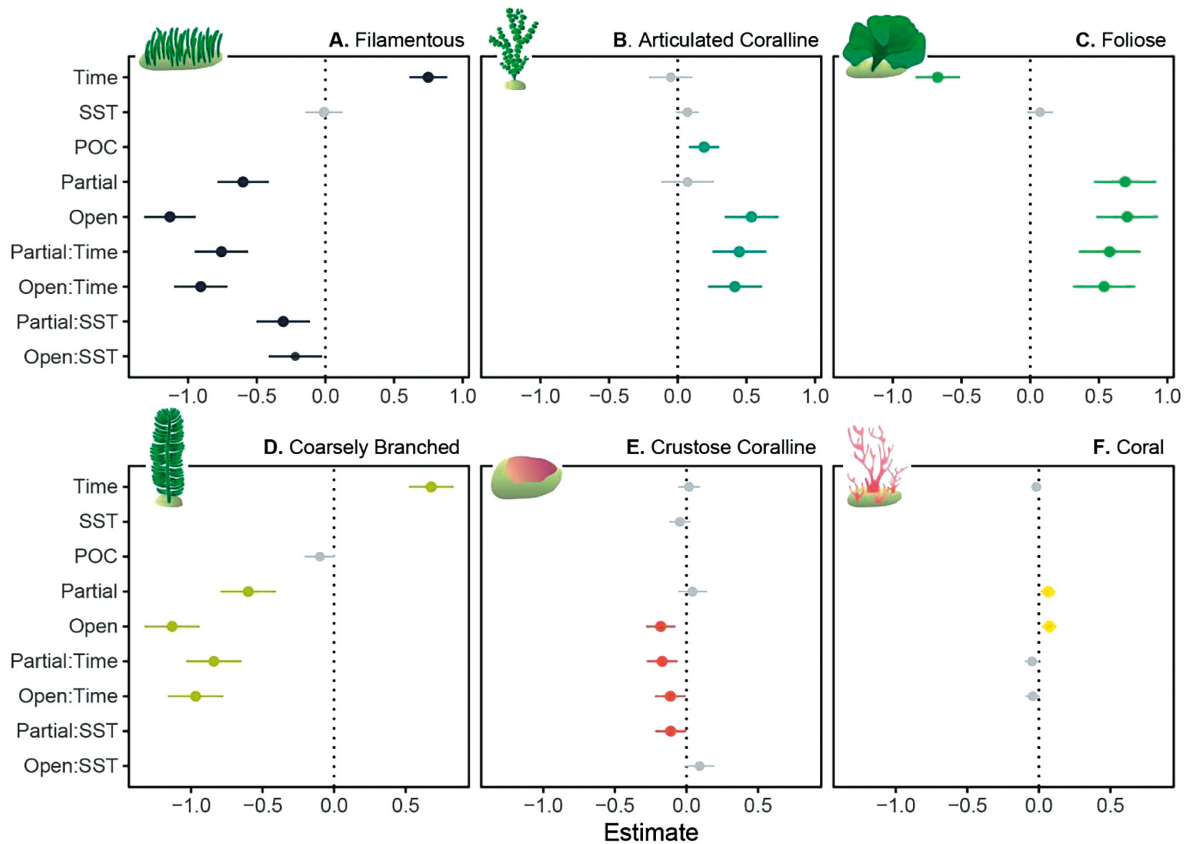


Fig. 2. Effects of time (days from experiment installation), sea surface temperature (SST), particulate organic carbon (POC) and experimental treatment on the cover of (A) filamentous algae, (B) articulated coralline algae, (C) foliose algae, (D) coarsely branched algae, (E) crustose coralline algae and (F) coral. Linear mixed-effects modeling coefficients are standardized for the selected factors. Intercept values are based on the treatment 'cage'; thus, estimates for 'partial' and 'open' are based on comparison to this level. Only variables selected to compose models are displayed; non-significant variables appear in grey. Error bars: confidence intervals

(Fig. 3A). Open and partial plots increased in articulated coralline algae over time, which surpassed 60% of cover, whereas caged plots remained with less than 40% (Fig. 3B). Similarly, the cover of foliose algae oscillated around 25% under the influence of herbivory, but without this pressure, it decreased after 6 mo until stabilizing at 10% inside full cages (Fig. 3C). Coral, CCA and coarsely branched algae were found to cover exceptionally low percentages of the substrate (<5% each), and despite changes in cover over time, no particular trends could be detected.

SST only affected filamentous algal cover but interacted with herbivory to determine the composition of benthic cover in plots. SST values presented a cyclic pattern, peaking between February and May, with a minimum around September (Fig. 3D). Increased temperatures promoted filamentous algae without herbivore pressure; a reverse pattern was observed when fish fed inside open and partial plots (Fig. 3E).

Despite changes in substrate cover, algal biomass analyses revealed distinctive effects of herbivory. Filamentous and foliose algae had significantly greater biomass inside caged plots, roughly duplicating the values observed in other plots (Table 2). Articulated coralline and coarsely branched functional forms did not differ between treatments (based on ANOVA tests), as values for these algae were highly variable. Still, the biomass of these functional groups was also greater inside fully caged treatments.

Bare substrate colonization also differed between treatments: partial and open plots followed a similar community succession pattern over 6 mo, different from full cages (Fig. 4A). As identified in PERMANOVA analysis, resulting communities that colonized the bare substrate were significantly distinct by the end of the experiment (Table S7). Filamentous algae were responsible for most of the initial colonization of the plots. Inside all treatments, more than 50% of the substrate was covered by this functional

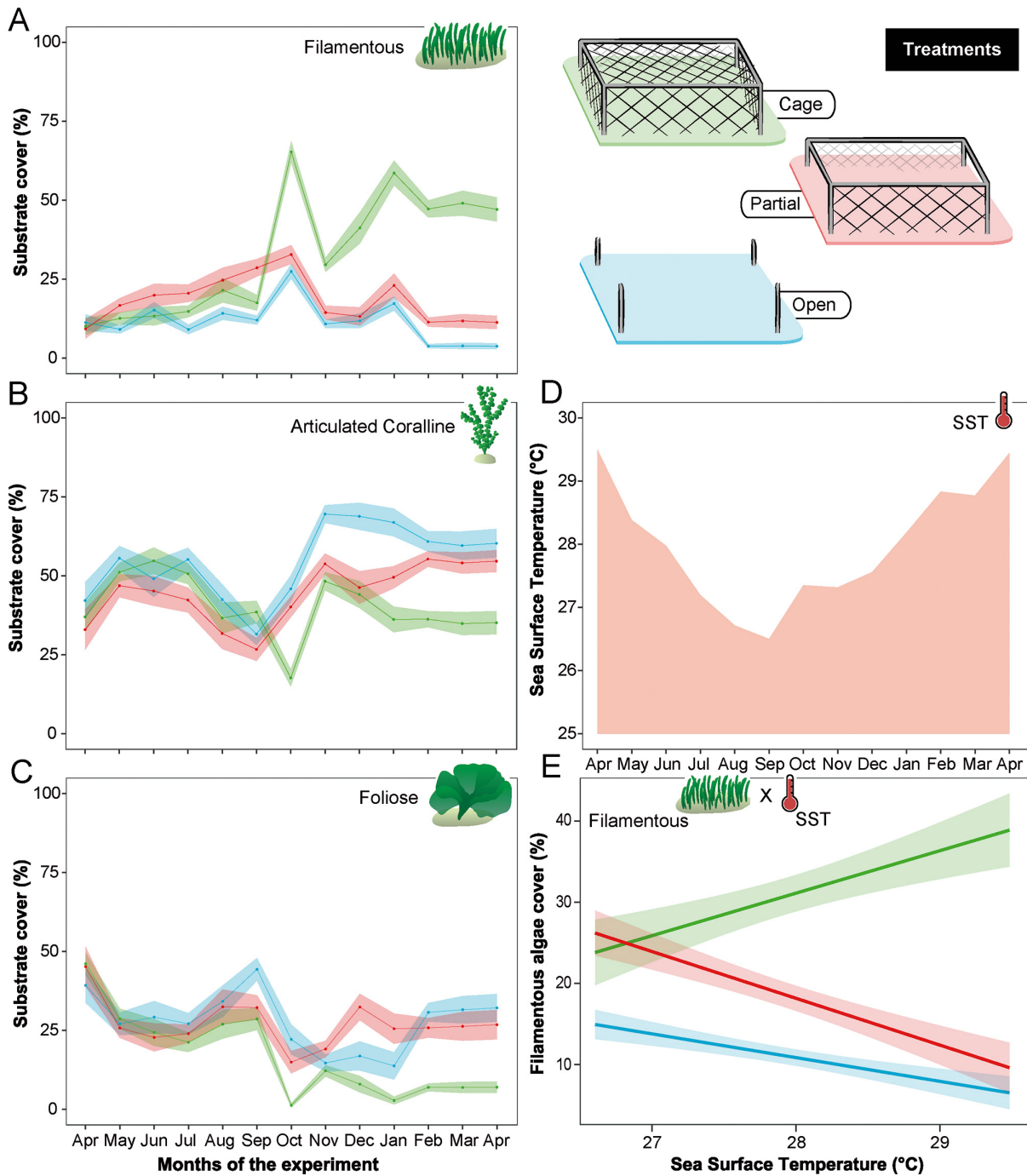


Fig. 3. Substrate cover of the most abundant functional forms of algae, and sea surface temperature (SST) variation during experiments. Mean cover (\pm SE) of (A) filamentous, (B) articulated coralline and (C) foliose algae by month of experimentation. Changes in monthly averages of SST and the relationship between filamentous algae and SST are shown in (D) and (E), respectively; shading in (E) shows confidence intervals. Line colors represent experimental treatments

group by the first month (Fig. 4B–D). Foliose algae also readily colonized the available substrata. After 2 mo, articulated coralline algae started to cover greater portions of the benthos, which increased inside all plots until stabilizing by the fourth month.

However, articulated coralline algae covered about 30% of the substrate in caged plots, while in partial and open plots, these algae reached more than a 2-fold increase in cover. Other functional groups covered very small portions of the substrate throughout

Table 2. ANOVA analyses of the biomass of algal functional forms between treatments. The last columns give the mean values (\pm SE) of algal biomass inside each treatment. Homogenous groups identified in pairwise comparisons are shown as super-script letters above biomass values; ns: not significant

	df	SS	MS	F	p	Cage	Open	Partial
Filamentous	2	11.1	5.55	6.63	<0.05	4.7 \pm 0.3 ^A	1.2 \pm 0.3 ^B	2.6 \pm 0.5 ^B
Articulated coralline	2	2189.76	1094.88	1.11	ns	47.8 \pm 16.5	9.0 \pm 4.3	26.2 \pm 10.4
Foliose	2	42.04	21.08	67.26	<0.05	8.8 \pm 1.2 ^A	1.3 \pm 0.1 ^B	5.6 \pm 0.3 ^B
Coarsely branched	2	18.6	9.28	0.84	ns	3.5 \pm 2.2	0.9 \pm 0.1	0.8 \pm 0.1

the experiment (<5%). It is noteworthy that no corals were recruited inside any plot, despite the fact there was still bare substrate available after the first 3 mo of experimentation.

4. DISCUSSION

Our results demonstrated a significant effect of herbivory; small-sized herbivores, such as surgeon-

fish and small parrotfish, were responsible for controlling the biomass and cover of filamentous algae, especially when SSTs were warmer during the dry season. Such control promoted an increased cover of articulated coralline and foliose algae; nonetheless, a small part of their biomass was consumed. Other functional groups had extremely low percentage cover, particularly the reef-building CCA and corals. The herbivory by smaller fishes accelerated the successional stages of benthic communities, facilitating

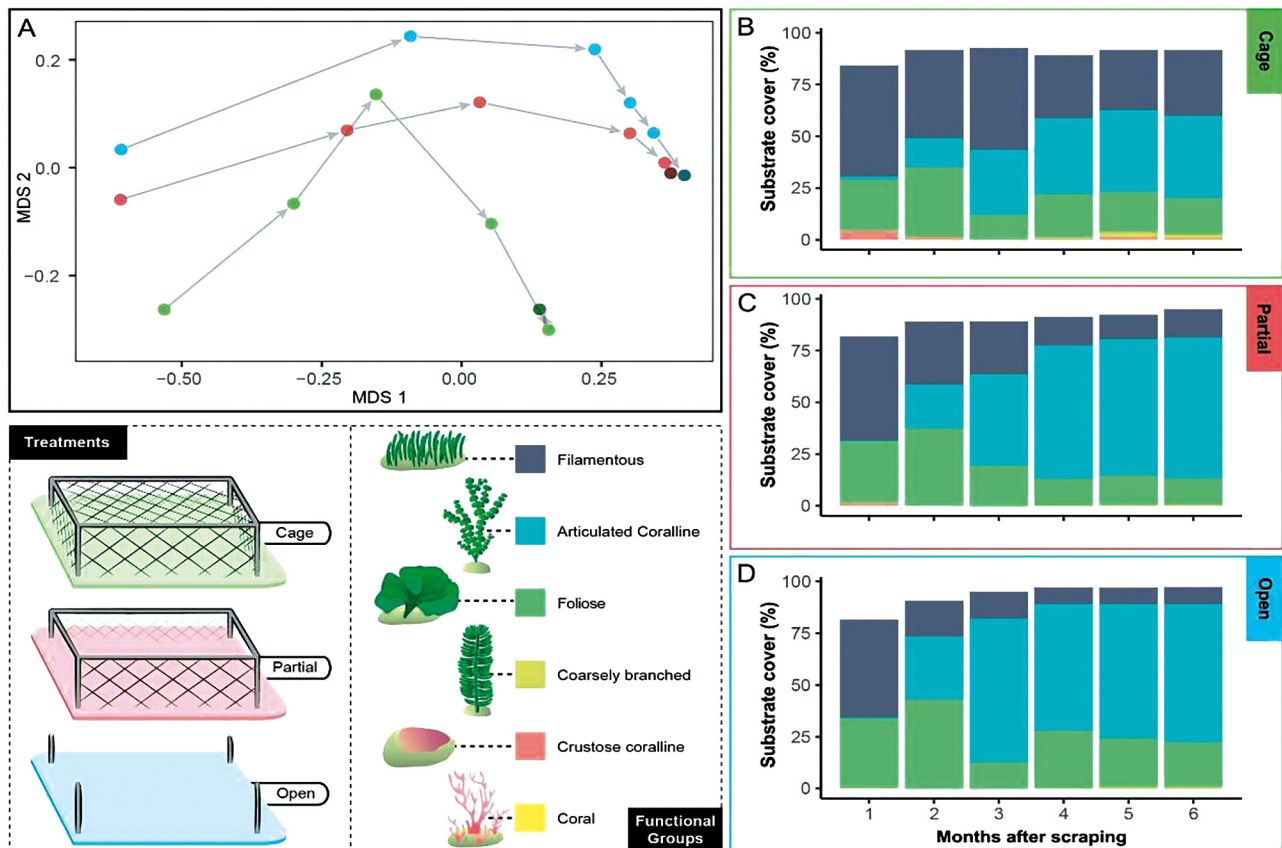


Fig. 4. Functional-form succession of the bare substrate subjected to experimental treatments. (A) non-metric multidimensional scaling (MDS) shows temporal changes in community composition from the beginning (left) to the end of the experiment (darker dots on the right); colors represent each treatment. The mean percentage of substrate cover by each form is shown for (B) cages, (C) partial and (D) open plots; colors indicate functional groups of benthic organisms

the dominance of articulated coralline algae as a climax community. Regardless of herbivory influence, no indications of coral or CCA recruitment were observed throughout the study, a possible effect of overall low coral cover in the selected sites. Our findings are remarkably the opposite of studies performed at sites where large parrotfish abundance is high: in those sites, herbivory promoted filamentous and CCA, decreasing overall macroalgae cover and delaying community succession (Paddack et al. 2006, Burkepile & Hay 2008, 2010, Smith et al. 2010, Ferrari et al. 2012, Duran et al. 2016, Shantz et al. 2019). The experimental removal of large herbivores appraised in previous studies led to similar responses, even when field sites ranged from environments with high coral cover (e.g. Smith et al. 2010, Ferrari et al. 2012) to areas primarily dominated by macroalgae (e.g. Paddack et al. 2006, Duran et al. 2016, 2018). This indicates that large herbivores are responsible for the well-known effects of herbivory, especially the control of higher-canopy macroalgae such as articulated corallines. As such, a positive feedback to the expansion and persistence of macroalgal dominance may be created by fishing: the removal of large herbivores not only releases the top-down suppression of articulated coralline algae but may further promote its dominance, facilitated in communities where herbivorous fishes are limited to small-bodied representatives, as seen here. Additionally, the articulate coralline algae *Halimeda* can induce negative impacts on coral populations by triggering virulent diseases (Nugues et al. 2004, Smith et al. 2006) and reducing coral recruitment on suitable substrates (Nugues & Szmant 2006). This alga is largely dominant in Brazilian reefs (Aued et al. 2018) and has increased on many reefs over the last several decades (Bruno et al. 2014), and these processes may be associated with its spread.

While calcification is an effective approach applied by articulated coralline algae to halt fish feeding, filamentous algae are recognized to have minimal herbivore-deterrent strategies (Littler et al. 1983, Littler & Littler 1984, Hay 1991). Therefore, the consumption of filamentous algae promoted by small herbivores in the present study can be performed by a vast array of species (Mendes et al. 2018, Ferreira 2019, Leitão et al. 2023). In our study area, damselfishes and juvenile parrotfishes compete to feed almost exclusively on filamentous algae (Feitosa et al. 2012, Feitosa & Ferreira 2015); in the case of parrotfishes, this can be promoted by their preference to forage on cyanobacteria mats, which are often found in association with filamentous algae (Clements et al. 2017,

Cissell et al. 2019, Nicholson & Clements 2020). In general, smaller fish avoid large, established articulated coralline and other erect macroalgae patches as feeding grounds (Hoey & Bellwood 2011, Robinson et al. 2019b). Small herbivores seem to segregate in functional roles from larger individuals, even intraspecifically, and larger fish have a disproportionately higher contribution to the removal of algae (Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Bonaldo et al. 2014). When large fishes are removed, the remaining herbivore assemblage cannot sustain previous consumption rates on a diverse set of macroalgae groups. In addition, it is feasible that the reduced competition encourages smaller fish to focus their feeding on the more palatable filamentous algae.

Small herbivores had a clear role in structuring algal communities. Still, differences in benthic composition among reefs are context-dependent, varying also with other factors such as temperature, turbidity, and anthropogenic interference (Mumby 2006, Williams et al. 2013, Duran et al. 2016, Hughes et al. 2018, Robinson et al. 2018, Bruno et al. 2019). One intriguing aspect observed here is that temperature affected filamentous algae only in an interaction with small-herbivore pressure. Filamentous algae cover was reduced with increasing temperature in plots under herbivore influence, but the exact opposite occurred when herbivores were excluded (Fig. 4E). Rising temperatures can promote algal and cyanobacteria growth (Ferrari et al. 2012, Duran et al. 2016, Biscaia Zamoner et al. 2021) but they can also enhance the feeding rates of herbivores (Ferreira et al. 1998, Floeter et al. 2005, Longo et al. 2019). This interaction points towards a role for small herbivores in buffering the effects of temperature rise on algal cover. This central function may be of particular importance, considering that warming waters are quickly becoming a major cause of coral reef demise (Heron et al. 2017, Hughes et al. 2018, 2019). Recent reports on the status of reefs worldwide have indicated that algal cover has increased as much as 20% in recent decades, a trend associated with increased sea temperatures (Souter et al. 2021). Indeed, herbivorous fish have less intense effects in colder waters (Lefèvre & Bellwood 2010, Duran et al. 2016, Cordeiro et al. 2020); however, global warming can lead to the introduction of tropical functions to temperate reefs (Zarco-Perello et al. 2020). Unforeseeable outcomes for benthic communities can arise in the aftermath of this unprecedented assembly of herbivores.

Small herbivores also influenced the succession of benthic communities and facilitated the growth of articulated coralline algae inside open and partial

plots by consuming the pioneer filamentous algae. Community succession experiments developed in Florida and Caribbean reefs also identified articulated coralline algae as dominant features of climax communities (Ferrari et al. 2012, Duran et al. 2016, Shantz et al. 2019). However, the dominance of articulated coralline algae is related to weak herbivory pressure (Duran et al. 2016), reinforcing our view that small-bodied herbivores cannot control these late-successional algae. As much as reductions in biomass of algal forms other than filamentous were observed here (Table 2), small fish herbivory is certainly not enough to control the overall algae growth. Large herbivores prevent macroalgal communities from developing to later successional stages, as seen in previous works (Hixon & Brostoff 1996, Thacker et al. 2001). Ferrari et al. (2012) and Duran et al. (2016) found that nutrient enrichment also accelerated the dominance of articulated coralline algae, which developed in 4 mo under this condition. Herein, a state of articulated coralline algae dominance was attained in the same period. We do not rule out the influence of nutrient input in our study area, as there is intense runoff from nearby rivers that receive emissions of non-treated sewage and excessive fertilizers (Maida & Ferreira 1997, Leão et al. 2016).

Regardless of the fact the succession experiment was initiated during September–October, during the spawning period of some local coral species (Pinheiro 2006), not a single recruit settled inside the plots. A low larval supply is a feasible reason for the widespread scenario of low coral cover across the Brazilian coast (Aued et al. 2018). Additionally, macroalgal dominance is already a recognized factor in suppressing coral settlement, growth and survivorship through space competition, allelochemical production, disease transmission and overgrowth (Karez et al. 2004, Smith et al. 2006, Worm & Lotze 2006, Hughes et al. 2007, Dixson et al. 2014, Zaneveld et al. 2016). Thus, management actions for Brazilian reefs that aim to increase coral cover to previous levels must also consider assisted coral reproduction, active removal of algae and the recovery of large herbivore populations as strategies to succeed.

The effects of herbivory are context-dependent, varying according to environmental conditions and herbivore community characteristics (Robinson et al. 2018, Russ et al. 2018, Cardozo-Ferreira et al. 2018, Bruno et al. 2019, Wilson et al. 2021). Herein, we observed that increasing herbivore fishing and depleting smaller-bodied fishes can affect benthic communities, altering the patterns of community succession and, in an interaction with higher tempera-

tures, may have implications for reef resilience in an ocean warming scenario. Strategies to protect herbivore populations inside and outside Marine Protected Areas are urgent (Mumby 2006, Bozec et al. 2016, Topor et al. 2019), especially in areas with low functional redundancy. If those measures are taken early, and effective conservation of both small and large herbivores is guaranteed, reef resilience in the face of rising temperatures is more conceivable (Topor et al. 2019, Taylor et al. 2020). Nevertheless, these solutions alone cannot prevent phase shifts, and policies to reduce global warming and nutrient input on coral reefs are mandatory, so that the services provided by reef ecosystems are maintained.

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LITERATURE CITED

- ✦ Adam TC, Burkepile DE, Ruttenberg BI, Paddock MJ (2015a) Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar Ecol Prog Ser* 520:1–20
- ✦ Adam TC, Kelley M, Ruttenberg BI, Burkepile DE (2015b) Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia* 179:1173–1185
- ✦ Adam TC, Duran A, Fuchs CE, Roycroft MV, Rojas MC, Ruttenberg BI, Burkepile DE (2018) Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. *Mar Ecol Prog Ser* 597:207–220
- ✦ Araújo ME, Mattos FMG, Melo FPL, Chaves LCT and others (2020) Diversity patterns of reef fish along the Brazilian tropical coast. *Mar Environ Res* 160:105038
- ✦ Aued AW, Smith F, Quimbayo JP, Cândido DV and others (2018) Large-scale patterns of benthic marine communities in the Brazilian province. *PLOS ONE* 13: e0198452

- Bartoń K (2020) MuMIn: multi-model inference. R package version 1.43.17. <https://cran.r-project.org/package=MuMIn>
- ✦ Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67: 1–48
- ✦ Bejarano S, Pardede S, Campbell SJ, Hoey AS, Ferse SCA (2019) Herbivorous fish rise as a destructive fishing practice falls in an Indonesian marine national park. *Ecol Appl* 29:e01981
- ✦ Bender MG, Machado GR, Silva PJA, Floeter SR, Monteiro-Netto C, Luiz OJ, Ferreira CEL (2014) Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the Southwestern Atlantic. *PLOS ONE* 9:e110332
- ✦ Bennett S, Vergés A, Bellwood DR (2010) Branching coral as a macroalgal refuge in a marginal coral reef system. *Coral Reefs* 29:471–480
- ✦ Biscaia Zamoner J, Aued AW, Macedo-Soares LCP, Pico-lotto VAP, Eiras Garcia CA, Segal B (2021) Integrating oceanographic data and benthic community structure temporal series to assess the dynamics of a marginal reef. *Front Mar Sci* 8:762453
- ✦ Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. *Mar Ecol Prog Ser* 360: 237–244
- ✦ Bonaldo RM, Hoey AS, Bellwood DR (2014) The ecosystem roles of parrotfishes on tropical reefs. *Oceanogr Mar Biol Annu Rev* 52:81–132
- ✦ Bozec YM, O'Farrell S, Bruggemann JH, Luckhurst BE, Mumby PJ (2016) Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proc Natl Acad Sci USA* 113:4536–4541
- ✦ Bruggemann JH, van Kessel AM, van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. *Mar Ecol Prog Ser* 134:59–71
- ✦ Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLOS ONE* 2:e711
- ✦ Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90: 1478–1484
- ✦ Bruno JF, Precht WF, Vroom PS, Aronson RB (2014) Coral reef baselines: How much macroalgae is natural? *Mar Pollut Bull* 80:24–29
- ✦ Bruno JF, Côté IM, Toth LT (2019) Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? *Annu Rev Mar Sci* 11:307–334
- ✦ Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proc Natl Acad Sci USA* 105:16201–16206
- ✦ Burkepile DE, Hay ME (2010) Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLOS ONE* 5:e8963
- ✦ Burkepile DE, Hay ME (2011) Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* 30:351–362
- ✦ Capitani L, Roos N, Longo GO, Angelini R, Schenone L (2021) Resource-to-consumer ratio determines the functional response of an herbivorous fish in a field experiment. *Oikos* 130:2100–2110
- ✦ Cardozo-Ferreira GC, Macieira RM, Francini-Filho RB, Joyeux JC (2018) Inferring labrid functional roles through morphological and ecological traits. *Mar Ecol Prog Ser* 588:135–145
- ✦ Cissell EC, Manning JC, McCoy SJ (2019) Consumption of benthic cyanobacterial mats on a Caribbean coral reef. *Sci Rep* 9:12693
- Clements KD, German DP, Piché J, Tribollet A, Choat JH (2017) Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. *Biol J Linn Soc* 120: 729–751
- ✦ Cordeiro CAMM, Harborne AR, Ferreira CEL (2020) The biophysical controls of macroalgal growth on subtropical reefs. *Front Mar Sci* 7:488
- ✦ Cruz ICS, Loiola M, Albuquerque T, Reis R and others (2015) Effect of phase shift from corals to Zoantharia on reef fish assemblages. *PLOS ONE* 10:e0116944
- ✦ Cruz ICS, Meira VH, de Kikuchi RKP, Creed JC (2016) The role of competition in the phase shift to dominance of the zoanthid *Palythoa* cf. *variabilis* on coral reefs. *Mar Environ Res* 115:28–35
- ✦ Cruz ICS, Waters LG, Kikuchi RKP, Leão ZMAN, Turra A (2018) Marginal coral reefs show high susceptibility to phase shift. *Mar Pollut Bull* 135:551–561
- Cunha FEA, Carvalho RAA, Araújo ME (2012) Exportation of reef fish for human consumption: long-term analysis using data from Rio Grande do Norte, Brazil. *Bol Inst Pesca* 38:369–378
- ✦ De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci USA* 109: 17995–17999
- ✦ Dixon DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. *Science* 345:892–897
- ✦ Dominguez JML, Bittencourt ACSP, Leão ZMAN, Azevedo AEG (1990) Geologia do quaternário costeiro do Estado de Pernambuco. *Rev Bras Geocienc* 20:208–215
- ✦ Duran A, Collado-Vides L, Palma L, Burkepile DE (2018) Interactive effects of herbivory and substrate orientation on algal community dynamics on a coral reef. *Mar Biol* 165:156
- ✦ Duran A, Collado-Vides L, Burkepile DE (2016) Seasonal regulation of herbivory and nutrient effects on macroalgal recruitment and succession in a Florida coral reef. *PeerJ* 4:e2643
- ✦ Edwards CB, Friedlander AM, Green AG, Hardt MJ and others (2014) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proc R Soc B* 281:20131835
- ✦ Feitosa JLL, Ferreira BP (2015) Distribution and feeding patterns of juvenile parrotfish on algal-dominated coral reefs. *Mar Ecol* 36:462–474
- ✦ Feitosa JLL, Concentino AM, Teixeira SF, Ferreira BP (2012) Food resource use by two territorial damselfish (Pomacentridae: Stegastes) on south-western Atlantic algal-dominated reefs. *J Sea Res* 70:42–49
- ✦ Feitosa JLL, Chaves LCT, Queiroz-Véras LVMV, Miranda RJ, Ormond CGA, Ferreira BP (2021) Effects of social organization on the feeding of the striped parrotfish, *Scarus iseri*. *Coral Reefs* 40:951–957
- ✦ Ferrari R, Gonzalez-Rivero M, Ortiz JC, Mumby PJ (2012)

- Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae. *Coral Reefs* 31:683–692
- Ferreira GCC (2019) Ecologia nutricional de peixes nominalmente herbívoros no Atlântico Sudoeste. PhD thesis, Federal University of Espírito Santo, Vitória
- Ferreira BP, Maida M (2006) Monitoring Brazilian coral reefs—status and perspectives. Biodiversity Series No. 18. Ministerio do Meio Ambiente—MMA, Brasília
- Ferreira BP, Maida M, Souza AET (1995) Levantamento inicial das comunidades de peixes recifais da região de Tamandaré-Pernambuco. *Bol Téc Cient CEPENE* 3: 213–230
- Ferreira CEL, Peret AC, Coutinho R (1998) Seasonal grazing rates and food processing by tropical herbivorous fishes. *J Fish Biol* 53:222–235
- ✦ Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC, Journal S, Jul N (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *J Biogeogr* 31:1093–1106
- Ferreira BP, Coxey MS, Gaspar ALB, Silveira CBL and others (2021) Status and trends of coral reefs of the Brazil region. In: Souter D, Planes S, Wicquart J, Logan M, Obura D, Staub F (eds) Status of coral reefs of the world: 2020. Australian Institute of Marine Science, Townsville, p 3–12
- ✦ Floeter SR, Behrens MD, Ferreira CEL, Paddock MJ, Horn MH (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar Biol* 147:1435–1447
- ✦ Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- ✦ Goatley CHR, Bellwood DR (2010) Biologically mediated sediment fluxes on coral reefs: sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*. *Mar Ecol Prog Ser* 415:237–245
- ✦ Graham NAJ, Bellwood DR, Cinner JE, Hughes TP, Norström A, Nyström M (2013) Managing resilience to reverse phase shifts in coral reefs. *Front Ecol Environ* 11: 541–548
- Harborne AR, Mumby PJ (2018) FAQs about Caribbean parrotfish management and their role in reef resilience. In: Hoey A, Bonaldo R (eds) Biology of parrotfishes. Taylor & Francis Group, Boca Raton, FL, p 383–406
- ✦ Hay ME (1991) Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, p 96–119
- Heron SF, Eakin CM, Douvère F, Anderson K and others (2017) Impacts of climate change on world heritage coral reefs: a first global scientific assessment. UNESCO, Paris
- ✦ Hixon MA, Brostoff WN (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecol Monogr* 66:67–90
- ✦ Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: A critical feedback on coral reefs? *Ecol Lett* 14:267–273
- ✦ Hoey AS, Bonaldo RM (2018) Biology of parrotfishes. CRC Press, Boca Raton, FL
- ✦ Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D and others (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17:360–365
- ✦ Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2018) Global warming transforms coral reef assemblages. *Nature* 556:492–496
- ✦ Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2019) Global warming impairs stock–recruitment dynamics of corals. *Nature* 568:387–390
- Jackson J, Donovan M, Cramer K, Lam V (eds) (2014) Status and trends of Caribbean coral reefs: 1970–2012. Global Coral Reef Monitoring Network, Washington DC
- ✦ Karez R, Engelbert S, Kraufvelin P, Pedersen MF, Sommer U (2004) Biomass response and change in composition of ephemeral macroalgal assemblages along an experimental gradient of nutrient enrichment. *Aquat Bot* 78: 103–117
- ✦ Kharbush JJ, Close HG, Van Mooy BAS, Arnosti C and others (2020) Particulate organic carbon deconstructed: molecular and chemical composition of particulate organic carbon in the ocean. *Front Mar Sci* 7:518
- ✦ Kohler KE, Gill SM (2006) Coral point count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci* 32:1259–1269
- ✦ Kuempel CD, Altieri AH (2017) The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Sci Rep* 7:39670
- Laborel-Deguen F, Castro CB, Nunes FD, Pires DO (2019) Recifes brasileiros: o legado de Laborel. Museu Nacional, Rio de Janeiro
- ✦ Lange ID, Perry CT, Morgan KM, Roche R, Benkwitt CE, Graham NA (2020) Site-level variation in parrotfish grazing and bioerosion as a function of species-specific feeding metrics. *Diversity (Basel)* 12:379
- Leão ZMAN, Kikuchi RKP, Testa V (2003) Corals and coral reefs of Brazil. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, p 9–52
- ✦ Leão ZMAN, Kikuchi RKP, Ferreira BP, Neves EG and others (2016) Brazilian coral reefs in a period of global change: a synthesis. *Braz J Oceanogr* 64:97–116
- ✦ Lefèvre CD, Bellwood DR (2010) Seasonality and dynamics in coral reef macroalgae: variation in condition and susceptibility to herbivory. *Mar Biol* 157:955–965
- ✦ Leitão M, Hackradt CW, Lima e Silva Í, Ciancio JE, Félix-Hackradt FC (2023) Effect of human impact on coral reef herbivorous fish niche. *Mar Biol* 170:59
- ✦ Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monogr* 56: 183–200
- ✦ Lippi DL, Coxey MS, Rooker JR, Rezende SM and others (2022) Use of acoustic telemetry to evaluate fish movement, habitat use, and protection effectiveness of a coral reef no-take zone (NTZ) in Brazil. *Mar Ecol Prog Ser* 688: 113–131
- ✦ Littler MM, Littler DS (1984) Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. *J Exp Mar Biol Ecol* 74:13–34
- ✦ Littler MM, Taylor PR, Littler DS (1983) Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2: 111–118
- ✦ Lokrantz J, Nyström M, Thyresson M, Johansson C (2008) The non-linear relationship between body size and function in parrotfishes. *Coral Reefs* 27:967–974
- ✦ Longo GO, Hay ME, Ferreira CEL, Floeter SR (2019) Trophic interactions across 61 degrees of latitude in the Western Atlantic. *Glob Ecol Biogeogr* 28:107–117
- ✦ Madin EMP, Precoda K, Harborne AR, Atwood TB, Roelfsema CM, Luiz OJ (2019) Multi-trophic species interactions shape seascape-scale coral reef vegetation patterns. *Front Ecol Evol* 7:102

- Maida M, Ferreira BP (1997) Coral reefs of Brazil: overview and field guide. Proc 8th Int Coral Reef Symp, Panama City 1:263–274
- Marques S, Ferreira BP (2010) Composição e características da pesca de armadilhas no litoral norte de Pernambuco—Brasil. Bol Téc Cient CEPENE 18:49–60
- ✦ McClanahan TR, Cokos BA, Sala E (2002) Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. Mar Pollut Bull 44:441–451
- ✦ McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones SH IV (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Mar Ecol Prog Ser 261:135–147
- ✦ Mendes TC, Ferreira CEL, Clements KD (2018) Discordance between diet analysis and dietary macronutrient content in four nominally herbivorous fishes from the Southwestern Atlantic. Mar Biol 165:180
- ✦ Miller MW, Hay ME (1998) Effects of fish predation and seaweed competition on the survival and growth of corals. Oecologia 113:231–238
- ✦ Miller MW, Hay ME, Miller SL, Malone D, Sotka EE, Szmant AM (1999) Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. Limnol Oceanogr 44:1847–1861
- MPA (Ministério da Pesca e Aquicultura do Brasil) (2012) Boletim estatístico da Pesca e Aquicultura. MPA, Brasília
- ✦ Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecol Appl 16:747–769
- ✦ Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol Evol 23:555–563
- ✦ Nicholson G, Clements K (2020) Resolving resource partitioning in parrotfishes (Scarini) using microhistology of feeding substrata. Coral Reefs 39:1313–1327
- ✦ Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Mar Ecol Prog Ser 376:295–306
- ✦ Nugues MM, Szmant AM (2006) Coral settlement onto *Halimeda opuntia*: A fatal attraction to an ephemeral substrate? Coral Reefs 25:585–591
- ✦ Nugues MM, Smith GW, Van Hooidek RJ, Seabra MI, Bak RPM (2004) Algal contact as a trigger for coral disease. Ecol Lett 7:919–923
- Oksanen J (2019) vegan: ecological diversity. R package version 2.5-6:11. <https://CRAN.R-project.org/package=vegan>
- ✦ Ong L, Holland KN (2010) Bioerosion of coral reefs by two Hawaiian parrotfishes: species, size, differences and fishery implications. Mar Biol 157:1313–1323
- ✦ Paddock MJ, Cowen RK, Sponaugle S (2006) Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. Coral Reefs 25:461–472
- Pinheiro BR (2006) Recrutamento de corais no recife da Ilha da Barra–Tamandaré/PE. MSc thesis, Universidade Federal de Pernambuco, Recife
- Pinheiro J, Bates D, DebRoy S, Sarkar D (2020) nlme: linear and nonlinear mixed effects models. R package version 3.1-147. <https://CRAN.R-project.org/package=nlme>
- ✦ Precht WF, Aronson RB, Gardner TA, Gill JA and others (2020) The timing and causality of ecological shifts on Caribbean reefs. Adv Mar Biol 87:331–360
- Previero M (2014) A pesca do budião-azul (*Scarus trispinosus* Valenciennes, 1840) no maior complexo coralíneo do Atlântico Sul. MSc thesis, Universidade Estadual de Maringá
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ribeiro FP (2004) Composição da biocenose e abundância relativa de peixes capturados com covos nos estados do Rio Grande do Norte e Pernambuco (Brasil). Bol Téc Cient CEPENE 12:113–128
- ✦ Robinson JPW, Williams ID, Yeager LA, McPherson JM, Clark J, Oliver TA, Baum JK (2018) Environmental conditions and herbivore biomass determine coral reef benthic community composition: implications for quantitative baselines. Coral Reefs 37:1157–1168
- ✦ Robinson JPW, Wilson SK, Jennings S, Graham NAJ (2019a) Thermal stress induces persistently altered coral reef fish assemblages. Glob Change Biol 25:2739–2750
- ✦ Robinson JPW, Wilson SK, Robinson J, Gerry C and others (2019b) Productive instability of coral reef fisheries after climate-driven regime shifts. Nat Ecol Evol 3:183–190
- ✦ Robinson JPW, McDevitt-Irwin JM, Dajka JC, Hadj-Hammou J and others (2020) Habitat and fishing control grazing potential on coral reefs. Funct Ecol 34:240–251
- ✦ Roos NC, Taylor BM, Carvalho AR, Longo GO (2020) Demography of the largest and most endangered Brazilian parrotfish, *Scarus trispinosus*, reveals overfishing. Endang Species Res 41:319–327
- ✦ Russ GR, Payne CS, Bergseth BJ, Rizzari JR, Abesamis RA, Alcala AC (2018) Decadal-scale response of detritivorous surgeonfishes (Family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. J Fish Biol 93:887–900
- ✦ Schutte VGW, Selig ER, Bruno JF (2010) Regional spatiotemporal trends in Caribbean coral reef benthic communities. Mar Ecol Prog Ser 402:115–122
- Shantz AA, Ladd MC, Burkepile DE (2019) Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. Ecol Monogr 90:e01403
- ✦ Siqueira AC, Bellwood DR, Cowman PF (2019a) Historical biogeography of herbivorous coral reef fishes: the formation of an Atlantic fauna. J Biogeogr 46:1611–1624
- ✦ Siqueira AC, Bellwood DR, Cowman PF (2019b) The evolution of traits and functions in herbivorous coral reef fishes through space and time. Proc R Soc B 286: 20182672
- ✦ Slaets JIF, Schmitter P, Hilger T, Lamers M, Piepho HP, Vien TD, Cadisch G (2014) A turbidity-based method to continuously monitor sediment, carbon and nitrogen flows in mountainous watersheds. J Hydrol (Amst) 513:45–57
- ✦ Smith JE, Smith CM, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342
- ✦ Smith JE, Shaw M, Edwards RA, Obura D and others (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. Ecol Lett 9:835–845
- ✦ Smith JE, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507
- ✦ Soares MO, Rossi S, Gurgel AR, Lucas CC and others (2021) Impacts of a changing environment on marginal coral reefs in the Tropical Southwestern Atlantic. Ocean Coast Manage 210:105692
- ✦ Soares MO, Kitahara MV, Santos MEA, Bejarano S, Rabelo EF, Cruz ICS (2022) The flourishing and vulnerabilities

- of zoantharians on Southwestern Atlantic reefs. *Mar Environ Res* 173:105535
- ✦ Sotka EE, Hay ME (2009) Effects of herbivores, nutrient enrichment, and their interactions on macroalgal proliferation and coral growth. *Coral Reefs* 28:555–568
- ✦ Souter D, Planes S, Wicquart J, Logan M, Obura D, Staub F (2021) Status of coral reefs of the world: 2020. Australian Institute of Marine Science, Townsville
- ✦ Taylor BM, Benkwitt CE, Choat H, Clements KD, Graham NAJ, Meekan MG (2020) Synchronous biological feedbacks in parrotfishes associated with pantropical coral bleaching. *Glob Change Biol* 26:1285–1294
- ✦ Tebbett SB, Siqueira AC, Bellwood DR (2022) The functional roles of surgeonfishes on coral reefs: past, present and future. *Rev Fish Biol Fish* 32:387–439
- ✦ Thacker RW, Ginsburg DW, Paul VJ (2001) Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. *Coral Reefs* 19: 318–329
- ✦ Topor ZM, Rasher DB, Duffy JE, Brandl SJ (2019) Marine protected areas enhance coral reef functioning by promoting fish biodiversity. *Conserv Lett* 12:e12638
- ✦ Warton DI, Hui FKC (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3–10
- ✦ Williams GJ, Smith JE, Conklin EJ, Gove JM, Sala E, Sandin SA (2013) Benthic communities at two remote Pacific coral reefs: effects of reef habitat, depth, and wave energy gradients on spatial patterns. *PeerJ* 1:e81
- ✦ Wilson MW, Gaines SD, Stier AC, Halpern BS (2021) Variation in herbivore grazing behavior across Caribbean reef sites. *Mar Biol* 168:53
- ✦ Worm B, Lotze HK (2006) Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnol Oceanogr* 51: 569–579
- ✦ Yarlett RT, Perry CT, Wilson RW, Philpot KE (2018) Constraining species-size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates. *Mar Ecol Prog Ser* 590:155–169
- ✦ Zaneveld JR, Burkepille DE, Shantz AA, Pritchard CE and others (2016) Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat Commun* 7:11833
- ✦ Zarco-Perello S, Carroll G, Vanderklift M, Holmes T, Langlois TJ, Wernberg T (2020) Range-extending tropical herbivores increase diversity, intensity and extent of herbivory functions in temperate marine ecosystems. *Funct Ecol* 34:2411–2421

Appendix

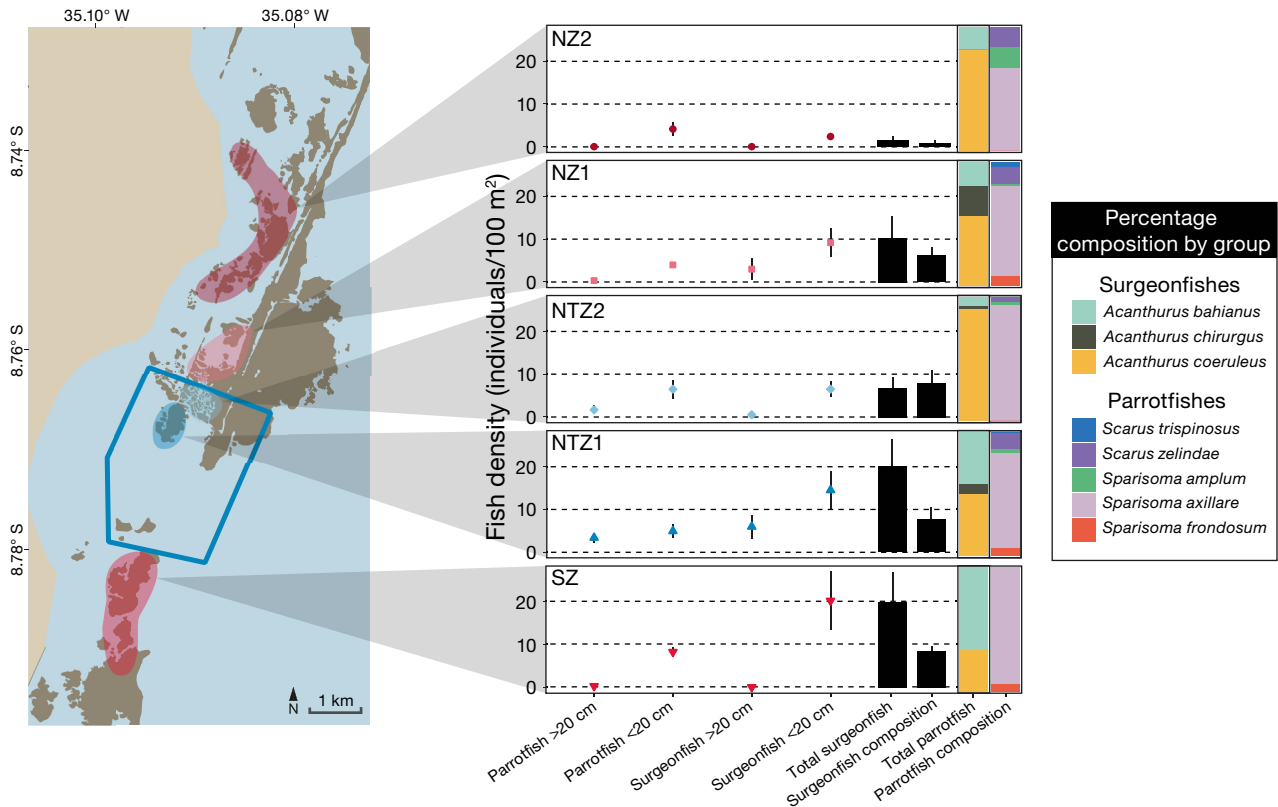


Fig. A1. Herbivore densities across several zones in the study area. Left panel: shades of red indicate zones outside the no-take area; shades of blue represent zones inside the no-take area. Symbol shapes and bars in the right panel: mean (\pm SE) values, with colors corresponding to the areas shown on the left. Densities are presented per herbivore group, categorized by total length (20 cm threshold). Panels and shapes represent zones following Lippi et al. (2022): North Zone 2 (NZ2), North Zone 1 (NZ1), No-take Zone 2 (NTZ2—the area chosen for installing the experimental plots), No-take Zone 1 (NTZ1) and South Zone (SZ). Data for these plots were derived from 2 yr of monitoring (2013–2014) the sites using visual censuses with belt transects (20 \times 5 m, n = 63)

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