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ORIGINAL PAPER

Highlighting competitive interactions between algae, corals, and herbivores in Bora Bora (French Polynesia)

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Abstract

Coral reefs, some of the most important marine ecosystems, are mainly structured by interactions between corals and benthic algae. The outcome of these interactions varies depending on the types of corals and algae involved. However, human activities, associated mainly with eutrophication and overfishing of herbivorous organisms, strongly impact the outcome of algae-coral interactions by promoting progressive replacement of corals by algae. The present study aimed to firstly establish the first inventory of algae-coral interactions at the species level on the Bora Bora reefs, and then experimentally determine the role of herbivorous species (sea urchins and *Trochus* shells) in the regulation of these complex algae-coral interactions. Firstly, visual surveys showed that the outcome of algae-coral interactions varied significantly according to the length of the algae-coral interaction border, and among algae-coral couples. For example, unhealthy coral colonies with large interaction borders were associated with a higher percentage of negative interactions. Then, using experimental enclosures for 70 days, we showed that the sea urchin *Tripneustes gratilla* controlled the proliferation of algae and thus allowed a better growth of *Acropora* corals. Overall, the present study suggests that conservation programs should rely on grazer densities as a Nature-Based Solution to attenuate global shifts from coral- to algal-dominance.

Keywords *Acropora pulchra* · Macroalgae · Sea urchins · *Tripneustes gratilla* · Bora Bora

Introduction

Coral reefs are hotspots of biodiversity and contribute to the wellbeing of millions of people through the ecosystem services they provide (Ramseyer et al. 2021). However, over the past decades, reef health has declined on a global scale (Hughes et al. 2017). 14% of the world's coral reefs disappeared between 2009 and 2018 (e.g., Costanza et al. 1997; Souter et al. 2021). Reduction of coral cover often leads to an increase of their main spatial competitors meaning algae (e.g., Mumby and Steneck 2008; Fong and Paul 2011) which in turn diminishes the space for coral larvae establishment leading to affected coral larvae recruitment and survival (e.g., Olsen et al. 2016). Many factors such as bleaching events (Jackson et al. 2014), ocean acidification (Godefroid et al. 2022), or diseases (Brandt et al. 2012) can cause the "phase shift" from coral- to macroalgal-dominated reefs. Moreover, other factors as eutrophication (Lapointe 1999)

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and overfishing of herbivores such as the long-spined sea urchin *Diadema antillarum* (Lessios 1988; Cook 2023) are responsible of the progressive replacement of corals by macroalgae (Nugues and Bak 2006). Today, algal growth often outcompetes corals while the spatial competition between algae and corals normally structures the overall dynamics of many reef ecosystems in the world (Miller 1998; Thinesh et al. 2019; Inagaki and Longo 2024).

The outcome of competitive interactions between algae and corals depends on the type of algae involved, such as macroalgae, turf algae, or crustose coralline algae (CCA). Some CCA have beneficial effects on corals, offering settlement space for coral larvae and supporting coral recruitment (Price 2010). Conversely, macroalgae like Halimeda spp. can block corals' access to light, reducing their photosynthetic capacity (Castro-Sanguino et al. 2016). Additionally, macroalgae and turf algae, which consist of diverse assemblages of filamentous species, can harm corals (Tebbett and Bellwood 2019) namely through the production of secondary metabolites that induce bleaching along the interaction borders (Rasher et al. 2011; Barott et al. 2009; Haas et al. 2010). These algae can also disrupt the microbial communities that normally protect corals from pathogens, further weakening coral health (Barott et al. 2012). The effects of algae interactions vary depending on coral type and size. Smaller and larger coral colonies tend to be better competitors (Barott et al. 2012), while encrusting corals are more successful in outcompeting turf algae, and branching corals often struggle to win these interactions (Swierts and Vermeij 2016).

Overall, the competitive interactions between algae and corals are always a topical debate. In addition, herbivores (fish, *Trochus* shells or sea urchin) can regulate this competition (e.g., Edmunds and Carpenter 2006, Mumby et al. 2006, Ling et al. 2018). A study conducted by Krimou et al. (2023) on Bora Bora Island highlighted experimentally, and at a relatively high density (i.e., 5 individuals.m^2), that *Tripneustes gratilla* and *Diadema setosum* sea urchins contributed to regulate the growth of different species of macroalgae, but the potential effects on coral growth were not tested. The local interactions between algae, corals and herbivores, although studied at smaller scales, have far-reaching implications for the structural complexity and resilience of coral reef ecosystems. These competitive interactions can serve as indicators of reef health. Persistent algal overgrowth can lead to macro-scale phase shifts, highlighting the need to study these interactions in detail.

Therefore, beyond a general objective devoted to the preservation of coral reefs, the present study aimed to (i) establish the first inventory of algae-coral interactions at the species level in Bora Bora reefs and evaluate the impact of few parameters on the outcome of algae-coral interactions, and (ii) experimentally determine the role of herbivorous species (sea urchins and *Trochus* shells) in the regulation of the complex algae-coral competitive interactions to maintain a balanced substrate between algae and corals.

Materials and methods

Area of investigation

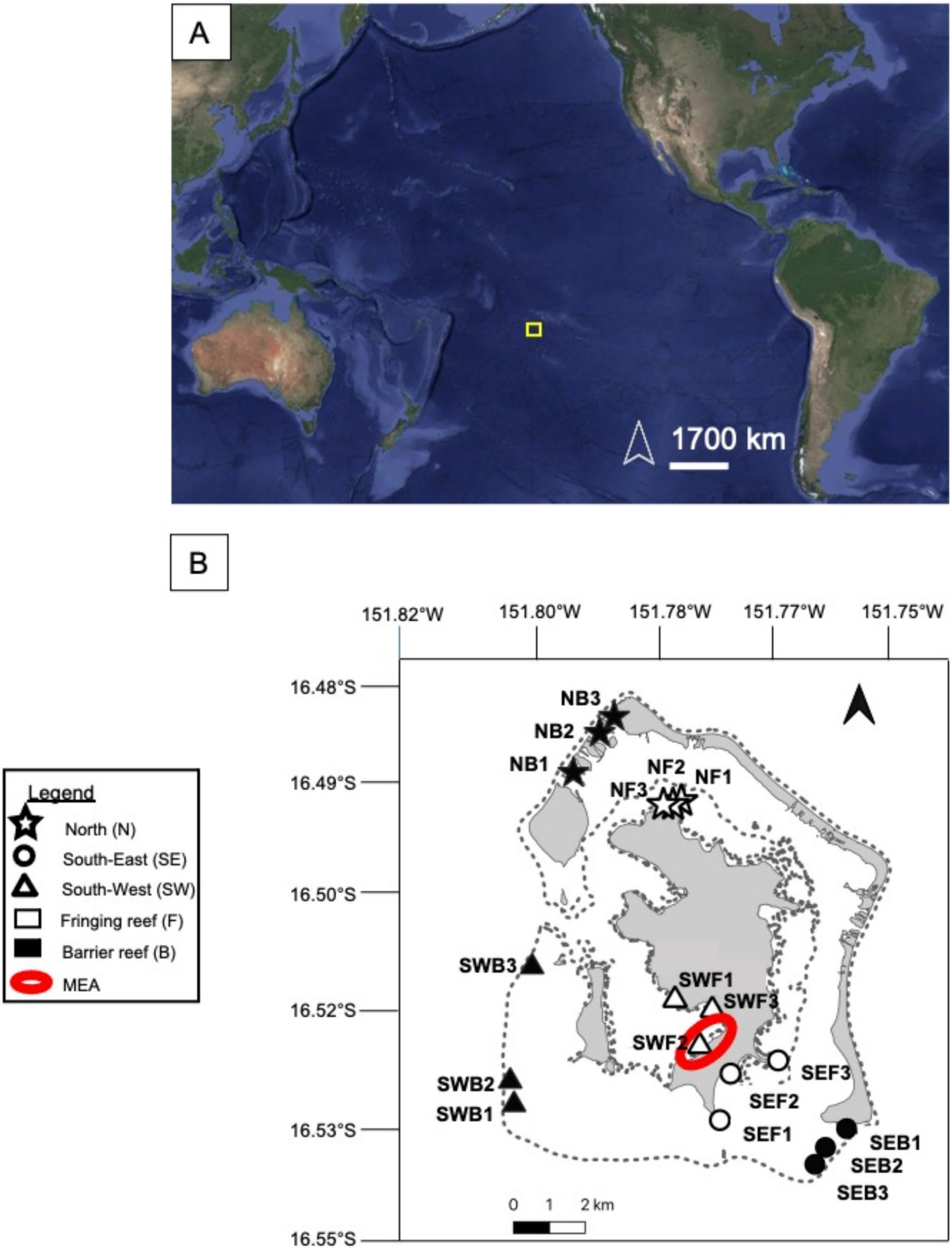
Bora Bora is a 20 km^2 tropical volcanic island located in the South Pacific Ocean (Fig. 1A) and more precisely in the Society archipelago of French Polynesia (16°29'S, 151°44'W). Coral reefs surrounding Bora Bora have a total area of 70 km^2 with four main geomorphological units (from the coast to ocean): the fringing reef, the channel, the barrier reef, and the outer slope (Lecchini et al. 2021).

In situ surveys

Surveys of algae-coral interactions were conducted in Bora Bora reef during the warm season from January to March 2023, by snorkeling. To include a possible spatial variability at the scale of the island, three radials on the North (N), South-West (SW) and South-East (SE) were chosen. On each radial, sampling was carried out on two different geomorphological units (or habitats): fringing reef (F) and barrier reef (B). For each habitat, three sites were selected, leading to a total of 18 studied sites (3 radials x 2 habitats x 3 sites) (Fig. 1B).

On each site, the living coral and algae, dead coral, sand, or rubble substrates were recorded along a 25-meter transect line, defining the percentage of cover for the different substrates along the transect. The substrate composition differs across habitats and radial regions (Table 1). In the fringing reef, the North sites are heavily dominated by dead coral, particularly at site NF2, where dead corals cover 94% of the area. In contrast, South-West and South-East fringing sites have a more balanced substrate distribution, with significant amounts of rubble and live coral, notably at SOF3, where live coral accounts for 35%. In the barrier reef, the North sites feature a mix of substrates, with live coral ranging from 43 to 57%. The South-West and South-East barrier sites show a similar pattern, although SOB2 is notable for having the highest live coral percentage at 60% (Table 1).

Fig. 1 (**A**) Location of Bora-Bora in the South Pacific Ocean. (**B**) Map of Bora-Bora showing the three radials (N, SE, SW) associated with two geomorphological units: fringing reef (F, in white) or barrier reef (B, in black). Grey shading represents land formed from coral, and grey dotted lines represent the limit of submerged coral reefs. Red circle shows the location of the experiment in the Marine Educative Area (MEA) ▶


A
1700 km
B
151.82°W
151.80°W
151.78°W
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16.52°S
16.53°S
16.55°S
NB3
NB2
NB1
NF2
NF1
NF3
SWB3
SWF1
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Legend
North (N)
South-East (SE)
South-West (SW)
Fringing reef (F)
Barrier reef (B)
MEA

Table 1 Percentage of substrate cover (dead coral, live coral, sand and rubble) recorded on the 18 sites for each radial and each habitat

Habitat	Radial	Site	Substrate (%)			
			Dead coral	Live coral and algae	Sand	Rubble
Fringing reef	North	NF1	67	12	4	17
		NF2	94	6	0	0
		NF3	9	28	55	8
	South-West	SOF1	6	51	1	42
		SOF2	10	39	0	50
		SOF3	19	35	21	25
	South-East	SEF1	14	18	38	30
		SEF2	20	31	16	34
		SEF3	45	34	7	14
Barrier reef	North	NB1	8	43	24	24
		NB2	17	55	5	23
		NB3	7	57	10	26
	South-West	SOB1	48	50	0	2
		SOB2	29	60	8	2
		SOB3	8	67	21	4
	South-East	SEB1	49	30	4	17
		SEB2	42	30	7	21
		SEB3	39	26	17	18

The category "live coral and algae" corresponds to a portion of the substrate where live coral and algae were found simultaneously during surveys

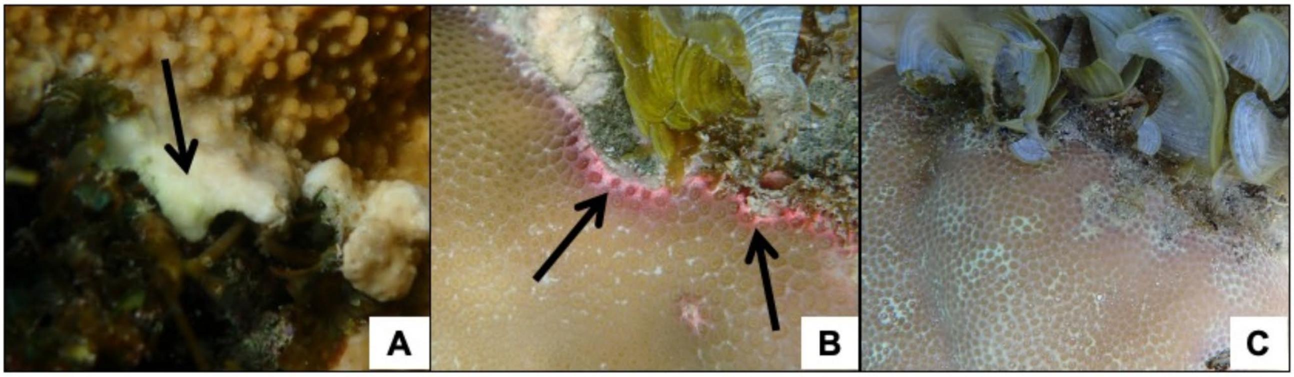

Fig. 2 Algae-coral interaction examples. Photos of negative interactions between (**A**) Montipora sp. (top), and *Turbinaria ornata* (bottom) and between (**B**) *Porites lutea* (bottom) and *Padina boryana* (top). (**C**) Photo of a neutral interaction between *Porites lutea* (bottom) and *Padina boryana* (top). Black arrows indicate areas of tissue damage (i.e., bleaching at the interaction border (**A**) and pink fluorescence indicating stress level (**B**)

Each living coral colony intercepting the 25-meter transect line was identified at the species level (or by the genus when coral species could not be visually identified), measured (maximum coral colony diameter) and its health percentage (ranging from 1 to 100%) was visually estimated. Algae in contact with the coral colony were identified at the species or family level for macroalgae and functional group for turf algae. The length of algae-coral interaction border was measured (method describer by Eich et al. 2019). We did not survey CCA since they can be taxonomically identified only through microscopic or genetic analysis. There are also strong species-specific differences in their effects on corals (Jorissen et al. 2020) and the difficulty in identifying specific CCA species in situ means that the type of interactions between CCA and corals can be easily missed or misinterpreted without proper laboratory verification (Twist et al. 2020; Piazza et al. 2021).

Each algae-coral interaction was classified according to Barott et al. (2012) as follows: (i) negative interaction: algae enter the coral zone and impacts it (bleaching, tissue damage, necrosis, fluorescence) (Fig. 2A and B); or (ii) neutral interaction: neither the coral nor the algae win the spatial competition (Fig. 2C). A single coral colony could be involved in multiple competitive interactions with different algae and different types of interactions, and all were considered. However, although we were looking for

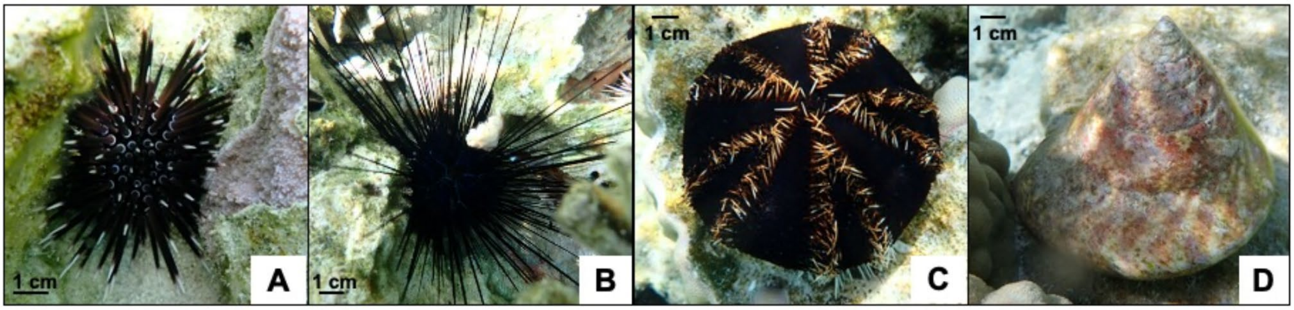

Fig. 3 Photos of the four target herbivorous species: (**A**) *Echinometra mathaei*, (**B**) *Diadema setosum*, (**C**) *Tripneustes gratilla* and (**D**) *Trochus niloticus* taken in the Marine Educative Area of Bora-Bora

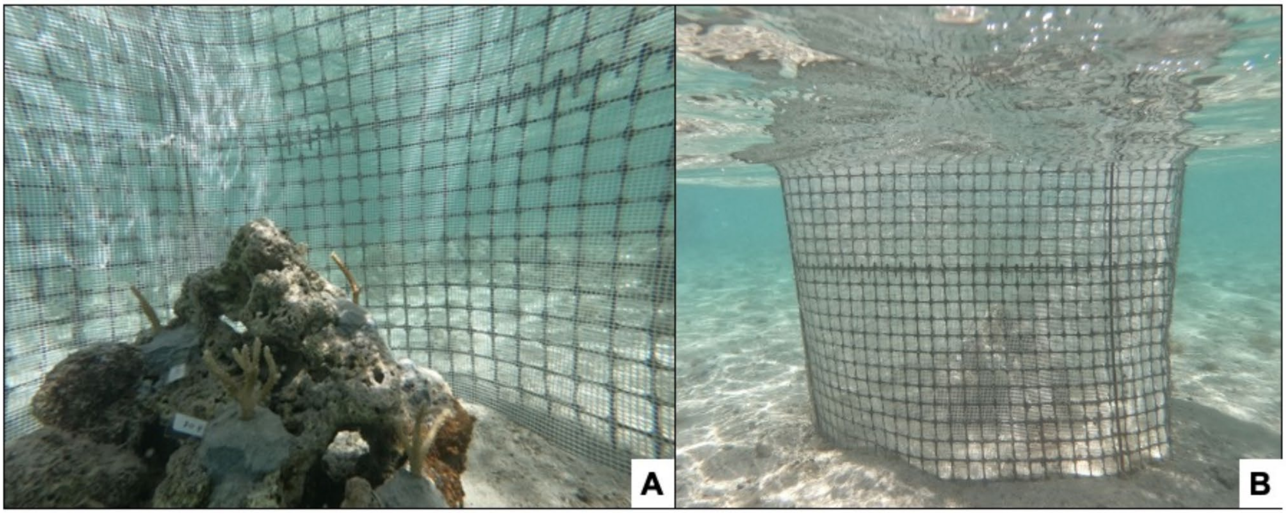

Fig. 4 Experimental set-up used to measure the effects of herbivory on algae colonization and coral health using a (**A**) dead coral patch with 6 coral fragments (**B**) enclosed by wire-mesh and metal stakes

positive interaction (the coral overgrows and outcompetes neighboring algae for spatial competition), no such positive interaction was observed during surveys. Only negative and neutral interactions could be analyzed in the light of coral colonies' health percentage, the length of the algae-coral interaction border, and among algae-coral couples.

Experiment on the effects of herbivory on algae colonization and coral health

In addition to in situ observation of algal-coral interaction, we experimentally determined the role of herbivorous species (sea urchins and *Trochus* shells) in the regulation of these complex algae-coral competitive interactions. Thus, the herbivory effects of.

Echinometra mathaei (test diameter = 3.85 ± 0.1 cm (mean ± SD) (Fig. 3A), *Diadema setosum* (4.9 ± 0.2 cm) (Fig. 3B), *Tripneustes gratilla* (8.37 ± 0.5 cm) (Fig. 3C), and *Trochus niloticus* (size = 9.25 ± 0.4 cm) (Fig. 3D) were tested by quantifying algae and coral growth. These selected species are of high commercial importance (i.e., *Trochus niloticus* - Lecchini et al. 2021) or key species for the ecosystem in terms of herbivory in Bora Bora (*Diadema setosum* and *Tripneustes gratilla* - Krimou et al. 2023). Indeed, in 2019, sea-urchins dominated the macro-invertebrate community, with *E. mathaei* and *T. gratilla* mainly present on barrier reefs (36% and 10% respectively of the total abundance of sea-urchins) whereas sea snails (Trochidae), valued for their shell and flesh, reduced in density by 4-fold since 2006 (Lecchini et al. 2021).

The experiment was carried out from February to April 2023. The 4 herbivorous species were collected by snorkeling on the fringing reefs of Bora Bora and relocated within a few hours into mono-specific enclosures made of wire-mesh (2 cm) and metal stakes (1.20 m) on the fringing reef of the Marine Educative Area (MEA, Fig. 1) of Bora Bora where they acclimated for 48 h (Fig. 4). MEA site mainly consists of dead coral substrate colonized mainly by four macroalgae (*Turbinaria ornata*, *Padina boryana*, *Halimeda spp.*, *Dictyota spp.*) (Krimou et al. 2023). The total percentage of algal cover as well as the percentage of the four main macroalgae found in the MEA were calculated for 20 coral patches based on photography analysis. This was performed using ImageJ by selecting the outline of each alga gathering with a freehand polygon. The total percentage of algal cover was respectively equal to (mean ± SD) 80.25 ± 2.31%, with 32.25 ± 2.55% of *Dictyota* spp., 18 ± 3.27% of *P. boryana*, 16 ± 3.11% of *T. ornata* and 12.75 ± 1.28% of *Halimeda* spp.

A total of 18 experimental enclosures of 1 m^3, spaced at least by one meter, were deployed over cleaned (with no algae) dead coral patches (from 50 to 70 cm long). Six coral fragments (between 5 and 7 cm long) from 6 *Acropora pulchra* colonies collected on the fringing reef of Bora Bora were placed on the surface of each patch with a mix of cement and SikaLatex® (Fig. 4). Three replicate enclosures were randomly assigned to one of the following conditions: presence of *D. setosum*; presence of *T. niloticus*; presence of *E. mathaei* and presence of *T. gratilla*. Two control conditions were added: Control_1 (no herbivore to test if there was no natural mortality of algae coming from various environmental factors) and Control_2 (no herbivore and rocks cleaned weekly to test that algae removal was responsible for coral growth). Each condition is represented by three replicates. The focus on coral growth, along with a cage size that allowed good water flow and access to the substrate, justified not adding a control for the effects of the enclosures on herbivores. This approach is supported by studies that have validated the caging method (Bulleri et al. 2022; Krimou et al. 2023). Previous studies showed that 5 individuals per m^2 of *D. setosum* are necessary to generate positive effects on coral cover through macroalgal control (Idjadi et al. 2010). To compare the herbivory efficacy of each specie and considering the size of our coral patches (from 50 to 70 cm long), two individuals per herbivorous species were kept in each enclosure. We did not include fish herbivory in our study due to significant technical challenges associated with caging experiments, particularly the survivorship of fish within the enclosures.

The total percentage of algal cover on each coral patch and the percentage of the four main algal species (i.e., *T. ornata*, *P. boryana*, *Halimeda spp.*, *Dictyota spp.*) were recorded at the beginning of the experiment (D_0) and every week thereafter over a period of 70 days, summing 10 weeks in total. Every week, five pictures of each coral patch were taken in the same place with a Black7 GoPro camera: 4 around the patch and one above it for all the 18 enclosures. The temporal dynamic of the surface occupied by each macroalgal was followed with picture analysis, using ImageJ by selecting the outline of each algal gathering with a freehand polygon.

Acropora corals are considered to have rapid growth, as the standard vertical growth for an arborescent coral colony can reach two to five cm in 70 days (Bosserelle et al. 2014). In this study, vertical growth of *Acropora* colonies was selected as the primary metric to assess coral health. Vertical branch elongation is widely recognized as a critical indicator of coral response to environmental stressors, including light competition and recovery from a disturbance (Kopecky et al. 2021). The choice of focusing on vertical growth also reflects the practical and non-invasive nature of this measurement, which is commonly used in field studies to assess coral health and monitor growth over time (Borgstein et al. 2020). While lateral growth is an important component of colony expansion, this study prioritized vertical measurements to align with previous research on coral recovery and competitive dynamics. Future studies could benefit from incorporating methods like 3D photogrammetry or surface area estimates to provide a more comprehensive view of coral growth (Lange and Perry 2020). Considering the duration of the experiment, *Acropora* corals were chosen for this study. Thus, every fragment of *A. pulchra* was measured (from the apex to the tip, cm) at the beginning and at the end of the experiment to evaluate their growth according to the presence or the absence of herbivorous species.

Statistical analysis

Only *Porites rus* and *Acropora hyacenthus* corals could be visually identified to species level. Due to the difficulties of visual identification, all *Porites* (other than *P. rus*) and *Montipora* corals were identified to the genus level. Other corals encountered were not part of analysis due to the lack of information. The effects of coral and algae species and of the type of interaction on the coral colonies' living percentage and length of algae-coral interaction border were investigated by running generalized linear models (GLMs) using the lme4 package (Bates et al. 2014). Coral living percentage or length of interaction were set as the dependent variables. The type of coral and the type of algae were set as categorical effects, as the type of interactions. Potential temporal correlation and the lack of independence in living percentage and length of interaction within each radial and geomorphological unit were accounted for by setting the site as a random effect. The model was fitted with a Poisson distribution for the percentage of living coral and with a Gaussian distribution for the length of interaction after a Log transformation of the data to approximate Normal distribution.

For the experiment on the effects of herbivory on algae colonization and coral health, a Cumulative Sum (CUSUM) method was used to analyze the temporal dynamic of the growth of macroalgae in the presence of each herbivorous species during the 70 days of the experiment. The CUSUM method is a sequential analysis technique designed to detect gradual or abrupt changes by accumulating deviations from a predefined mean, which is equal to zero in our study because for each treatment, the surface occupied by macroalgae at the beginning of the experiment is null. The CUSUM technique is particularly valuable for identifying changes that traditional statistical methods might miss, enhancing the sensitivity of our analysis (Regier et al. 2019).

All statistical analyses were conducted using R-Studio (R version 2022.02.3) at the significance level α = 0.05.

Results

Inventory of algae-coral interactions in the lagoon of Bora-Bora

No positive algae-coral interaction (i.e., coral wins) was observed during surveys. Only neutral and negative interactions (i.e., algae win) were identified (Fig. 5). Moreover, only *Porites rus* and *Acropora hyacenthus* corals could be visually identified to species level. Due to the difficulties of visual identification, all *Porites* (other than *P. rus*) and *Montipora* corals were identified to the genus level. Other corals encountered were not part of analysis due to the lack of information. Turf algae consistently had a negative impact on *Porites* coral, and more particularly on *Porites rus*. It also had a negative impact on *Montipora* (67% of turf-*Montipora* interactions) and on *Acropora hyacenthus* (53% of interactions). *Halimeda* spp. had a negative impact on all corals, except for *Montipora* (19% of *Halimeda-Montipora* interactions). *Dictyota* spp., which was the main algae that *P. rus* interacted with (71% of its interactions), was mostly negative for all corals. *Turbinaria ornata* had a mostly neutral impact on *Montipora* (70% of interactions) and negative impact on *Porites* (64%). *Padina boryana* was in 50% of cases negative for *Porites* corals (Fig. 5).

Coral colonies' health percentage showed no significant differences between coral species, algae species or type of outcome of interactions (Table 2). Length of algae-coral interaction border showed no significant differences between coral species or algae species. However, negative outcomes of interactions between corals and algae were significantly associated with longer algae-coral borders, when

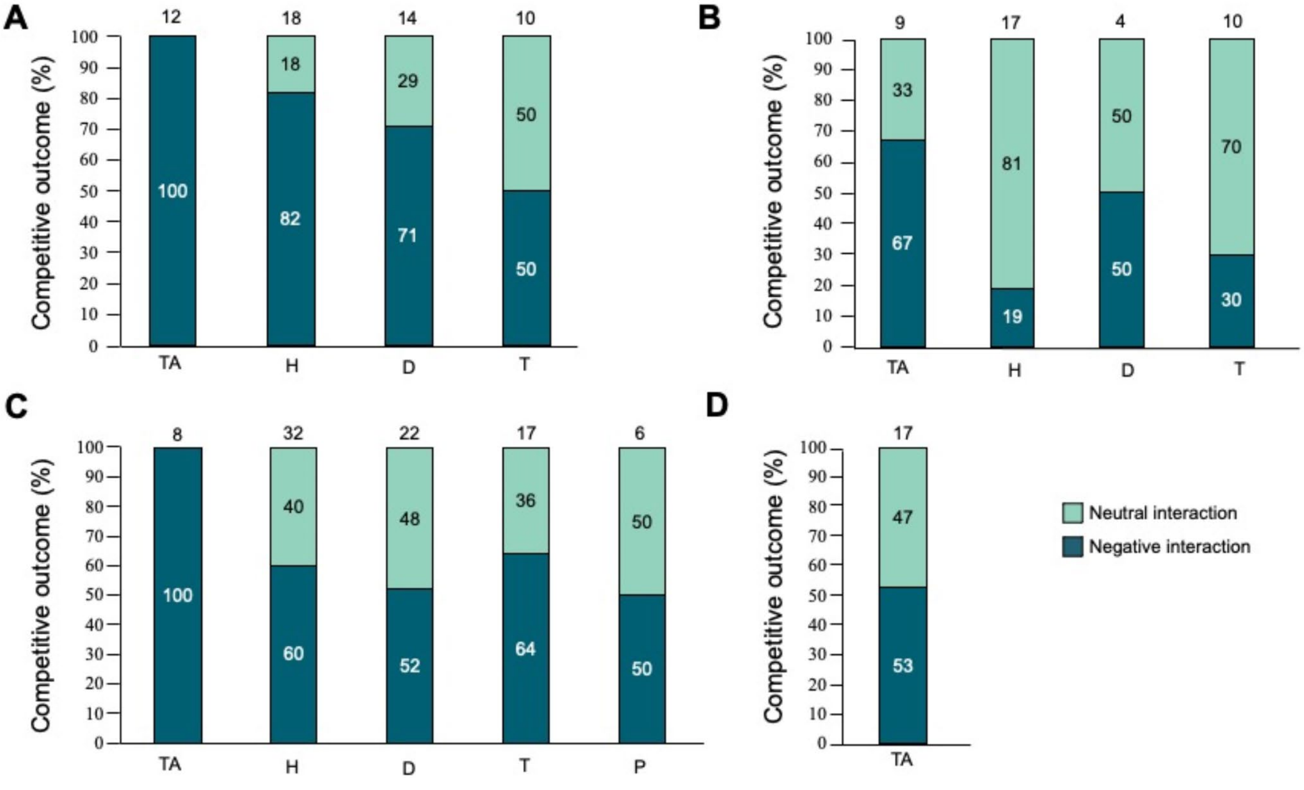

Fig. 5 Percentage of neutral and negative (algae wins against corals) interactions for (**A**) *Porites rus*, (**B**) Montipora, (**C**) Porites (other than *P. rus*) and (**D**) *Acropora hyacenthus* with turf algae (TA), *Halimeda spp.* (H), *Dictyota spp.* (D), *Turbinaria ornata* (T) and *Padina boryana* (P). Numbers on barplots indicate the percentage of neutral or negative (algae wins) interactions. Numbers above barplots indicate the number of interactions observed. Only colonies with at least one non-neutral algal interaction were considered

Table 2 Summary of the generalized linear model analysis performed on (A) the coral colonies' health percentages and (B) the length of algae-coral interaction border. *Acropora*, *Dictyota* spp and negative interactions were set as the reference groups for coral species, macroalgae and type of interaction, respectively

(A)		Estimate	SE	z values	*P*
	Intercept	0,59	3,03	0,195	0,84
Coral	Montipora	−0.50	3,21	−0.15	0,87
	Porites	0,6	3,07	0,19	0,84
	Porites rus	0,76	3,09	0,24	0,81
Macroalgae	*Halimeda spp*	−1.24	0,94	−1.32	0,19
	Padina boryana	−0.53	1,06	−0.49	0,62
	Turbinaria ornata	−0.91	1,03	−0.87	0,38
	Turf algae	1,19	3,12	0,38	0,70
Interaction	Neutral	0,044	0,4	0,11	0,91
(B)		Estimate	SE	t values	P
	Intercept	0,31	0,36	0,87	0,38
Coral	Montipora	0,064	0,36	0,17	0,86
	Porites	0,16	0,34	0,47	0,64
	Porites rus	0,097	0,34	0,28	0,78
Macroalgae	*Halimeda spp*	0,064	0,13	0,48	0,63
	Padina boryana	−0.022	0,14	−0.16	0,87
	Turbinaria ornata	−0.072	0,14	−0.52	0,60
	Turf algae	0,12	0,34	0,35	0,72
Interaction	**Neutral**	**−0.11**	**0,053**	**−2.10**	**0,035**

Significant differences are highlighted in bold

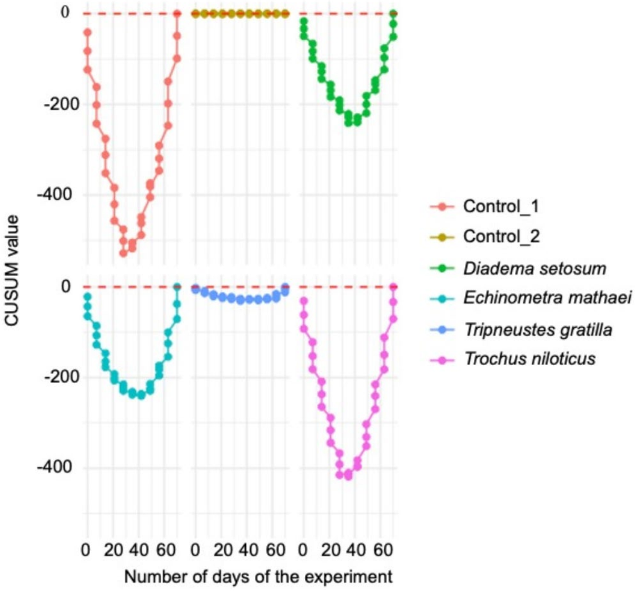

Fig. 6 Cumulative Sum (CUSUM) Analysis of the total percentage of algal cover according to (A) Control_1 (no herbivore to test if algal proliferation was responsible for preventing coral growth), (B) Control_2 (no herbivore and rocks cleaned weekly to test that algal proliferation control was assigned to herbivory activity) and the presence in enclosures of C) *Diadema setosum*, D) *Echinometra mathaei* E) *Tripneustes gratilla*, F) *Trochus niloticus* from D_0 to D_{70}. The dotted red line represents the predefined mean value equal to zero

compared to borders associated with neutral interactions (Table 2).

Effects of the grazing activity on macroalgae colonization and coral health

The CUSUM values for the Control_1 enclosures (no herbivore to test if algal proliferation was responsible for preventing coral growth) show a negative trend over time, with a decline from D_0 to D_{40}, followed by an upward shift toward zero between D_{40} and the experiment's conclusion at D_{70} (Fig. 6A). This pattern reflects natural macroalgal colonization in the absence of herbivores. By D_{70}, the substrate becomes saturated with algae and therefore the growth gradually declines. Conversely, the CUSUM values for Control_2 enclosures (no herbivore and rocks cleaned weekly to test that algal proliferation control was assigned to herbivory activity) remain stable around the predefined mean value (zero), as macroalgal growth was actively prevented (Fig. 6B). These CUSUM plots for Control_1 and Control_2 validate the reliability of the observations under the four experimental conditions involving herbivores.

The CUSUM plots for *Diadema setosum* (Fig. 6C), *Echinometra mathaei* (Fig. 6D), and *Trochus niloticus* (Fig. 6F) exhibit downward and upward trends similar to Control_1, indicating that these herbivores can partially regulate algal growth early in the experiment but are insufficient to prevent substrate saturation by D_{70}. In contrast, the CUSUM values for *Tripneustes gratilla* remain close to zero throughout the 70-day experiment, indicating strong and consistent regulation of macroalgal overgrowth by *T. gratilla*, maintaining an equilibrium (Fig. 6E).

These increases were only due to *Padina boryana* and *Dictyota spp.* macroalgae growth (Fig. 7). As an example, in *T. gratilla* and *E. mathaei* enclosures, *Padina boryana* represented respectively 77.33% and 61.81% of the total cover of macroalgae. For Control_2 condition, no macroalgae growth was observed (Fig. 7).

A significant growth of *A. pulchra* coral fragments between the start and end of the experiment was observed for control 2 condition (i.e., no herbivore and weekly cleaned rocks) (Wilcoxon signed-rank test between the start and end sizes; V = 50, p-value = 0.002), as well as in *D. setosum* enclosures (Wilcoxon signed-rank test; V = 37.5, p-value = 0.001) and *T. gratilla* enclosures (Wilcoxon signed-rank test; V = 52.5, p-value = 0.002) (mean growth in 70 days: 2.1 cm ± 0.5; 2.8 cm ± 0.6; 3 cm ± 0.9 respectively). No significant growth of the coral fragments was observed for *T. niloticus* enclosures (Wilcoxon signed-rank test; V = 55, *P* = 0.058), for *E. mathaei* enclosures (Wilcoxon signed-rank test; V = 60.5, p-value = 0.058), and for control

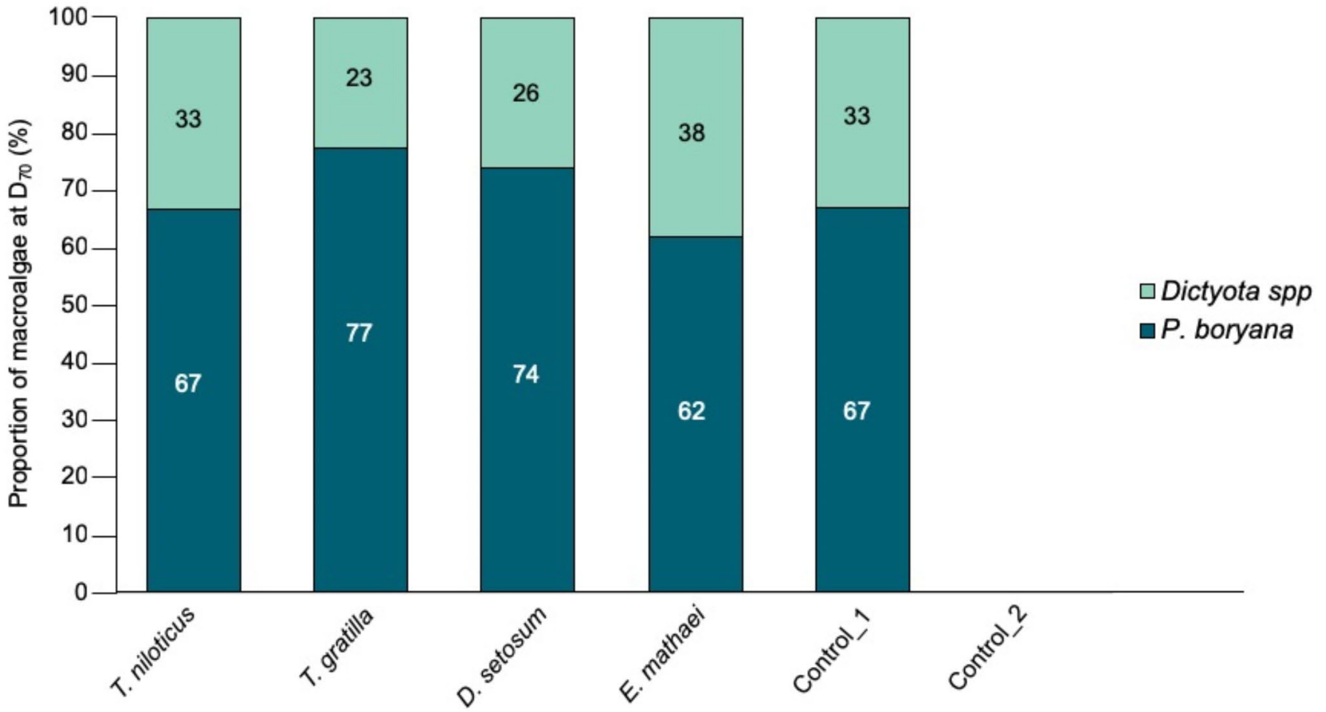

Fig. 7 Average percentage of *Padina boryana* and *Dictyota* spp. cover in the different enclosures at D_{70} of the experiment. In Control_2 condition (no herbivore and rocks cleaned weekly to test that algae removal was responsible for coral growth), no macroalgae growth was observed hence why there is no value for this condition

1 condition (i.e., no herbivore) (Wilcoxon signed-rank test; V = 49, p-value = 0.1) (mean growth in 70 days: 1.4 cm ± 0.3; 1.3 cm ± 0.3; 1.6 cm ± 0.9 respectively).

Discussion

Bora Bora, like many coral reef systems, faces several challenges that impact its coral assemblages and recovery, as well as the herbivorous populations that are crucial for maintaining reef health. Multiple monitoring programs showed that the corals in Bora Bora are in good health (Lecchini et al. 2021). However, some hypoxic and high-temperature events in 1984, 2001 and 2020 resulted in high mortality of fish and macro-invertebrates as well as a strong coral bleaching (all species except Porites) on the southern part of Bora Bora (Salvat et al. 2002; Lecchini et al. 2020). Although coral reefs of Bora Bora are currently in good health, their fragile balance requires a deeper understanding of their functioning, particularly in terms of the algae-coral equilibrium. If this balance is disrupted, it could lead to a phase shift, resulting in significant changes in biodiversity.

Although eighteen transects and numerous coral and algae species were investigated, no positive algae-coral interaction (i.e., coral wins) was reported in Bora Bora reef. Among all marine benthic algae, mostly crustose coralline algae (CCA) have been reported in the literature to have a positive interaction with corals (Barott et al. 2012). Indeed, CCA, which were not included in the survey reported here, are known to contribute to reef construction (Littler and Littler 1984), as well as to provide substrate for coral larvae settlement (Price 2010). However, it is important to recognize that other forms of algae, while less frequently reported, may also engage in neutral or positive interactions with corals under specific environmental conditions. McCook et al. (2001) described scenarios where turf algae and small macroalgae patches coexist with corals, especially in nutrient-poor environments, without significant negative impacts. They also highlighted indirect facilitative mechanisms, where algae create habitat for herbivores that help maintain coral health by controlling harmful algal overgrowth. Some species of macroalgae may also provide settlement substrates for coral larvae in specific conditions, while others might offer ecological benefits such as habitat structure or reduction of sedimentation, indirectly promoting coral resilience (Inagaki and Longo 2024). In our study, only neutral and negative interactions (i.e., algae win) were identified in Bora Bora. The outcome of algae-coral interactions had no effect on coral colony health, while the length of algae-coral interactions border was significantly longer in negative outcomes. Our observations also suggest differences among algae-coral couples (Fig. 5). For example, turf algae, *Halimeda* spp. and *Dictyota* spp. had a negative impact on all studied coral genera (*Porites*, *Montipora* and *Acropora*). In contrast, *Turbinaria ornata* had variable impacts on corals, and had a mostly neutral impact on *Montipora* corals. Lastly, *Padina boryana* was in 50% of cases negative for *Porites* corals. (Fig. 5).

Our results align with the literature (e.g., Littler and Littler 1984; Barott et al. 2012). Macroalgae and turf algae, although they both contribute significantly to primary production, are known to be the most abundant competitors that corals face (Haas et al. 2010). *Halimeda-Porites* interactions resulted in frequent discoloration and tissue loss on coral colonies in Bora Bora. Indeed, long-term algal physical contact stops light required for polyp photosynthesis and alters coral health (Thinesh et al. 2019). Similarly, Titlyanov et al. (2007) showed a reduced growth of *Porites* corals in contact with *Dictyota* spp. algae through allelochemical mechanism and abrasion. Kaullysing et al. (2016) showed that *Padina boryana* overgrowth on corals could be responsible for a decreased resistance to stress for coral colonies, resulting in higher vulnerability to *Drupella cornus* corallivores predation in Mauritius. However, studies have reported methods for corals to cope with algae competitive interactions, for instance through an "escape in height" strategy for branching corals (Meesters et al. 1996) or mucus secretion (Lang and Chornesky 1990). Nevertheless, the increasing abundance of algal turfs and macroalgae on coral reefs (Sandin et al. 2008) threatens the balance between growth and investment in defenses of coral colonies. Overall, our study only describes a snapshot of algae-coral interactions based on visual surveys. Monitoring the long-term fate of individual colonies would shed more light on interaction outcomes. Future studies should also include detailed surveys of CCA, possibly involving laboratory identification techniques to investigate their interactions with coral species in Bora Bora.

In addition, our study showed a significant effect of grazing of *T. gratilla* by limiting the colonization of algae to 7.5% of the total cover of coral patches after 70 days, as compared to a colonization of over 90% in the absence of herbivores over the same period (Figure S1) and the CUSUM plot showed that *T. gratilla* could control algae overgrowth and make it stable through time (Fig. 6E). Significant branching coral growth was observed in *T. gratilla* enclosures, which is comparable to the growth reported by Bosserelle et al. (2014) (2 to 5 cm in 70 days). *Diadema setosum* also limited algae colonization and promoted coral growth, but to a lesser extent than *T. gratilla*. Other studies have also highlighted that adult *D. setosum* play a key role in controlling macroalgal development and therefore in sustaining high coral cover in the Caribbean, Taiwan, and Easter Island (De Ruyter et al. 1986). Coyer et al. (1993) showed that high densities of sea urchins can remove algae, thereby reducing coral mortality due to algal overgrowth and allowing corals to increase in abundance in Anacapa Island, California. Overall, our results are in accordance with these several previous herbivory studies. However, not all herbivorous species may favor coral growth through their regulation of algal development. At the density of 2 individuals per m^2, the grazing rate of *E. mathaei* and *T. niloticus* did not prevent algae from colonizing coral patches (respectively up to 55% and 65% at D70) and no significant growth of coral fragments was observed. However, Villanueva et al. (2013) showed that *T. niloticus*, at the density of four individuals per m^2, limited the turf algal cover and therefore could enhance survivorship of coral spat in caged culture. Thus, at sufficiently high densities and against the correct target (turf algae), this mollusk could be used to control turf algae proliferation, in addition to another grazer species consuming macroalgae. Although our study focuses on the effect of sea urchins and mollusks grazing activity on coral health, it is essential to mention that herbivorous fish often complement other grazers, such as sea urchins, by targeting different types of algae and offering a more continuous regulation of algal growth promoting coral health (Francis et al. 2019). For example, in Palmyra Atoll, coral growth was higher when algae were removed in the presence of fish-mediated herbivory, namely species of Scaridae and Acanthuridae such as *Acanthurus coeruleus*, *Sparisoma aurofrenatum* and *Scarus croicensis*, reinforcing the role of fish herbivory in reef health across the Pacific (López-Jiménez et al. 2020). These global dynamics of algae-coral-herbivorous fish interactions highlight the critical role of herbivorous fish in sustaining coral resilience and preventing phase shifts towards algal dominance.

To conclude, the extent of the borders between corals and algae seem to influence the outcome of algae-coral interactions outcome. Moreover, algae-coral-herbivore interactions are acting at the species level. For example, *T. gratilla* grazers were efficient in terms of limiting macroalgae colonization which aligns with the study of Lewis and Smith (2019). Our study highlighted that *T. gratilla* herbivory was especially efficient on *P. boryana*, and thus allowing *A. pulchra* coral fragments growth. However, human activities exacerbate negative effects of certain macroalgae on coral reefs, leading to changes in coral reef community composition, from coral to algal dominance (e.g., Mumby 2006; Hughes et al. 2007; Mumby and Steneck 2008). Thus, in the context of global changes, such observations in Bora Bora show the importance of considering the species level for algae-coral-herbivore interaction studies, and thus highlight the importance of preserving herbivore biodiversity, as macroalgal dominance can reduce coral growth rates and increase coral mortality, which can change the composition of communities and lower biodiversity (Clements and Hay 2019). Many herbivorous species could be used as new Nature-based Solutions for limiting algae proliferation on isolated Pacific Islands (Duvat and Magnan 2019). Our research on algae-coral competition offers crucial insights into how localized algal dominance could drive broader ecological changes on reefs. The persistence of competitive algal overgrowth on corals observed in our study suggests that, under certain conditions, these interactions could lead to a reduction in coral cover across reef systems. Such a shift could have cascading effects on reef biodiversity and ecosystem services, suggesting that preserving herbivorous populations may restore coral resilience and improve ecosystem function (Donovan Mary et al. 2023; Cook et al. 2024). This may lead managers and scientists to pursue coral reef monitoring in terms of the balance between algae and corals, and to establish appropriate conservation measures for key herbivorous species on this iconic island.

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Data availability Data can be provided on reasonable request.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethics approval All applicable guidelines for the care and use of animals were followed.

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