

HERBIVORY EFFECTS OF SEA URCHIN SPECIES ON A CORAL REEF (BORA-BORA, FRENCH POLYNESIA)

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KEYWORDS : Herbivorous ; Macroalgae ; Grazing ; *Tripneuste gratilla* ; *Diadema setosum* ; Bora-Bora

ABSTRACT

Macroalgae are becoming dominant on coral reefs worldwide, replacing corals as key habitat formers. Incrementing consumption rates by herbivores, such as sea urchins, has been identified as a viable strategy for promoting coral recovery. By means of a 28-day experiment, we assessed the grazing effects of the sea urchins, *Tripneustes gratilla* and *Diadema setosum*, on the macroalgal assemblages of shallow reefs at Bora-Bora (French Polynesia). In particular, each urchin species was either absent or maintained, using cages (n = 10), at a density of 5 individuals/m². *T. gratilla* exerted stronger negative effects than *D. setosum* on all the examined macroalgae (i.e., *Turbinaria ornata*, *Padina boryana*, *Halimeda spp*, *Dictyota spp*). In addition, the grazing effects by *T. gratilla* on macroalgae emerged shortly after the start of the experiment, more rapidly than those of *D. setosum*. Despite an apparent lower food preference for *T. ornata* in *D. setosum*, all macroalgae were consumed by both species and the composition of the macroalgal assemblages (i.e., the proportion of each species) did not change after 28 days. Overall, our study suggests that herbivorous sea urchins, when at relatively high densities, could contribute to sustaining coral-dominance on coral reefs by keeping macroalgae under control.

1. Introduction

Coral reefs are among the most productive and biodiverse ecosystems on the planet, providing a range of ecosystem services on which humanity depends (Spalding et al., 2001). Unfortunately, reef health is declining at a global scale, impinging on their ability to provide goods and services (Eddy et al., 2021). A variety of anthropogenic perturbations, acting at range of spatial scales, from global to local, can promote a shift in dominance from corals to macroalgae. In the aftermath of major events of disturbance, such as heatwaves and hurricanes, causing coral die-offs, freed space is typically colonized by filamentous ephemeral algae, that are rapidly replaced by longer-lived taxa, such as those belonging to the genera *Turbinaria*, *Sargassum*, *Lobophora*, *Dictyota* and *Padina* (e.g., Brown et al., 2018; Mumby et al., 2006). Chronic alteration of local environmental conditions, such as excessive nutrient loading, or the collapse of herbivores can then favour the persistence of macroalgae, reducing coral recovery. Once dominant, macroalgae can, in fact, directly or indirectly impact adult and juvenile corals, as well as the settlement of larvae, through shading, abrasion, transmission of diseases or microbes and through the release of allelochemicals (e.g., Hughes et al., 2007; Nugues et al., 2004; Vieira et al., 2016; Bulleri et al., 2018). Understanding the mechanisms that maintain the competitive balance in favour of hard corals is key to preventing phase shifts towards the algal- dominated state and to promote shifts back to the coral-dominated one.

Interactions between corals and macroalgae are often interpreted in terms of a competitive superiority of macroalgae under reduced herbivory or increased nutrient availability (McCook et al., 2001). In nondegraded reefs, the combination of bottom-up (e.g., limited nutrient supply) and top-down controls (e.g., high consumer pressure) can limit macroalgal proliferation (Valentine and Edgar, 2010). In addition to competitive inhibition by corals (McCook et al., 2001), herbivory is one of the critical factors that control macroalgal abundance in terms of biomass per unit area (Viviani et al., 2019). For instance, browsing fishes are often critical for maintaining coral-dominated reefs through their consumption of macroalgae (e.g., Fong and Paul, 2011; Hughes et al., 2007; Mumby et al., 2006). In particular, parrotfish, surgeonfish, rabbitfish and batfish are dominant herbivores in coral ecosystems (Bellwood et al., 2006; Tebbett, 2022) and thus play a pivotal role in the resilience of these highly threatened habitats (Bellwood et al., 2006; Bonaldo et al., 2014; Viviani et al., 2019). Sea urchins have been also shown to play an important role in controlling macroalgal biomass on coral reefs. For example, in the Caribbean, the recovery of *Diadema antillarum* has resulted in the reduction of macroalgae and in the recovery of coral cover (Edmunds and Carpenter, 2001). Likewise, some promising trials were performed with *Tripneustes gratilla* in Hawai'i, demonstrating that biocontrol through manual removal combined with hatchery raised urchins can be an effective management approach in controlling invasive macroalgae, with their cover reduced by 85% (Neilson et al., 2018).

Nonetheless, our understanding of their role in some tropical regions, such as the South Pacific remains limited. A recent study by Bulleri et al. (2022), performed in the lagoon of Moorea, has shown that diadematid urchins (i.e., *Diadema savignyi*, *Echinothrix diadema*, *E. calamaris*) had a limited ability to control macroalgal recovery when at relatively low densities (i.e., 1 individual/m²). The

present study aimed to experimentally assess the ability of another diadematid species, *Diadema setosum* (Leske 1778), to reduce the cover of erect macroalgae in the lagoon of Bora-Bora, when maintained at higher densities. The grazing effects of *D. setosum* was compared to those of *Tripneustes gratilla* (L. 1767), a species previously suggested to be an effective consumer of brown seaweeds in the Indian Ocean (Lison de Loma et al., 2002).

2. Material and methods

2.1. AREA OF INVESTIGATION AND SAMPLE COLLECTION

Bora-Bora (16°30' S, 151°45' W), often called the 'Pearl of the Pacific', is a high volcanic island in French Polynesia (Gabrie et al., 1994). Coral reefs surrounding Bora-Bora have an area of approximately 70 km², with four main geomorphological units (from the coast to ocean): fringing reef, channel, barrier reef, and outer slope (Lecchini et al., 2021). The present study was performed from April to July 2022 on a fringing reef at the Marine Education Area (MEA) of Bora-Bora High School (Fig. 1). The site is dominated by dead coral reefs mainly colonized by four macroalgal species (i.e., *Turbinaria ornata*, *Padina boryana*, *Halimeda spp*, *Dictyota spp*).

Tripneustes gratilla (Fig. 2a) is one of the four sea urchin species of the genus *Tripneustes* (Kroh and Mooi, 2023). This species is globally distributed on coral reefs (Kroh and Mooi, 2023), it feeds mainly at night and is primarily an opportunistic omnivore displaying a range of diets in wild and aquaculture environments. While the diet of juveniles of *T. gratilla* is mainly composed by sessile diatoms, adult individuals feed on macroalgae (reviewed in Lawrence and Agatsuma, 2020). In particular, adult *T. gratilla* forage close to the substratum, ingesting leaves of *Thalassia hemprichii*, *Halimeda sp.*, *Syringodium isoetifolium* and coral rubble. *Diadema setosum* (Fig. 2b) is a species of Diadematidae, a common urchin family in tropical seas. In some regions, such as the Caribbean, Taiwan and Easter Island they have been shown to play a key role in controlling macroalgal development and, hence, in sustaining high coral cover (e.g., De Ruyter et al., 1986; Myhre and Acevedo-Gutierrez, 2007). Species belonging to this family have also been reported as important agents of coral bioerosion (Carreiro-Silva and McClanahan, 2001; Glynn, 1997).

The densities of both sea urchin were low at the study site, i.e., < 0.001 individual/m² (Lecchini et al., 2021).

2.2. EXPERIMENTAL DESIGN AND SAMPLING PROTOCOL

Adult sea urchins (*T. gratilla*: n = 94, size = 7 ± 1 cm - mean ± SD; *D. setosum*: n = 60, test diameter = 6 ± 1 cm) were collected by snorkelling on the fringing reefs of Bora-Bora, temporarily stored in coolers containing seawater at ambient temperature and relocated within a few hours in mono-specific enclosures made of wire mesh (5 cm) and metal stakes (40 to 70 cm) on the fringing reef of the Marine

Educative Area of Bora-Bora, where they acclimated for 24 h. They were then kept for another 24 h in similar types of enclosures, but built on sand and, hence, without macroalgae. Thirty experimental enclosures were deployed over dead coral patches of 1 m² to 4 m² that, at the start of the experiment, had an overall macroalgal cover above 80%. The cages were spaced at least three meters apart. Ten replicate enclosures were randomly assigned to each of the following urchin treatments: 1) presence of *T. gratilla*; presence of *D. setosum*; 3) no sea urchins (i.e., Control). Each urchin species was kept at a density of 5 individuals/m². Previous studies performed in Jamaica showed that a high density (e.g., *D. setosum*: 5 ind/m²) was necessary to generate positive effects on coral cover through macroalgal control (Idjadi et al., 2010; Sammarco, 1980).

The total percentage of algal cover inside enclosures (Fig. 3) and the percentage of each algal species (*T. ornata*, *P. boryana*, *Halimeda* spp., *Dictyota* spp.) were recorded before the start of the experiment (Day 0) and, thereafter, every four days over a period of 28 days, for a total of 9 sampling events. The same observer (S. Krimou) positioned herself in front of each enclosure and visually quantified the percentage of

macroalgae, by choosing 10 random visual intercept points on each of the four sides and on the top of the coral patches present at different points (method adapted from Dethier et al., 1993). Moreover, the observer had trained before the beginning of the experiment by comparing her visual estimates with data obtained from photo-quadrats and Image J processing.

All urchins survived the experiment and were released close to collection areas after 28 days.

Figure 1. Map of Bora Bora (A) and location of the study site in the Marine Educative Area (B).



Figure 2. Photos of *T. gratilla* (A) and *D. setosum* (B) in the Marine Educative Area of Bora-Bora (Photo by S. Krimou).

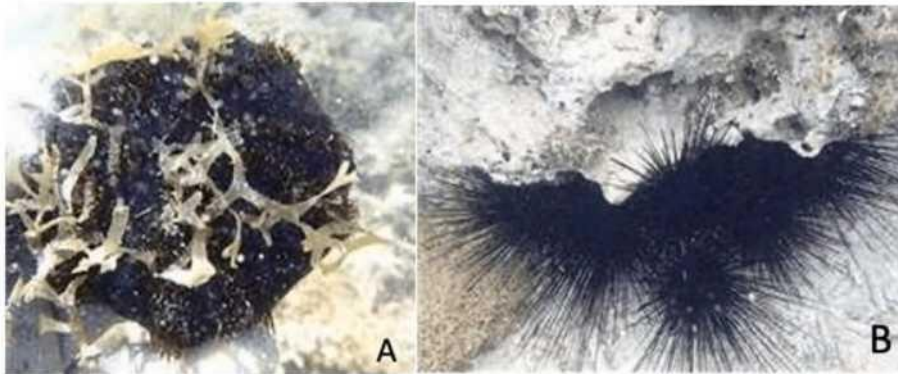
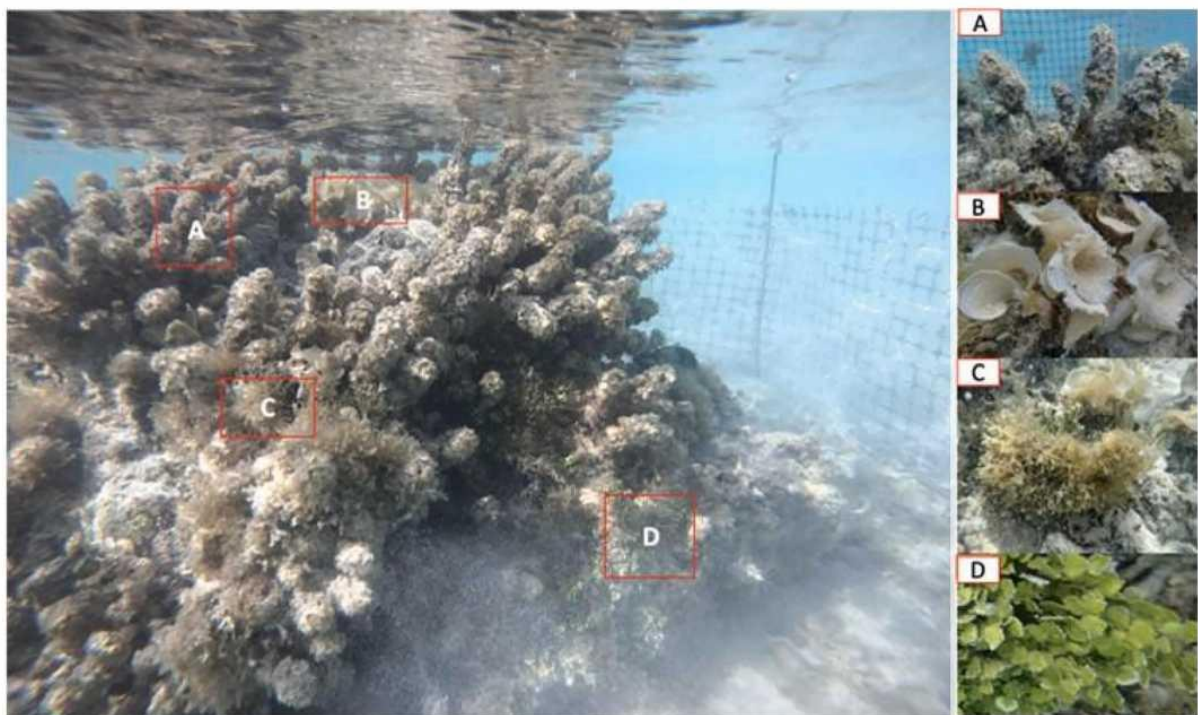


Figure 3. Location of macroalgae on a coral patch and pictures of the most abundant macroalgae species in the study area (MEA): *Turbinaria ornata* (A), *Padina boryana* (B), *Dictyota* spp. (C), *Halimeda* spp. (D). (Picture by S. Krimou).



2.3. STATISTICAL ANALYSIS

Shapiro-Wilk tests were used to check for the normal distribution of the total percentage cover of macroalgae in *T. gratilla*, *D. setosum* and control enclosures (*T. gratilla*, $W = 0.95$, $p\text{-value} = 0.006$; *D. setosum*, $W = 0.95$, $p\text{-value} = 0.003$; Control, $W = 0.95$, $p\text{-value} = 0.004$). Parametric test assumptions were not met, so non-parametric tests were used. A Kruskal-Wallis test showed no differences in the total percentage of macroalgae among the three treatments at Day 0 (Kruskal-Wallis, $\chi^2 = 1.74$, $df =$

2, p -value = 0.42). Thus, for each condition, the total percentage of macroalgae was compared between the first and last day (D0 vs. D28) using Wilcoxon -rank tests. The grazing rate was then calculated as the slope of the linear regression between macroalgal cover and time (i.e., from D0 to D28). A Kruskal-Wallis test, followed by a Dunn post hoc test, was then performed to compare the slopes of the linear regression across the three treatments. Finally, the percentage cover of each macroalgal species (*T. ornata*, *P. boryana*, *Halimeda* spp, *Dictyota* spp) at D0 versus D28 were compared for each of the three treatments (*T. gratilla*, *D. setosum* and Control) with Pearson's χ^2 tests. All the statistics were performed with R version 4.1.1 (2021).

3. Results

3.1. TEMPORAL DYNAMICS OF MACROALGAL GRAZING BY SEA URCHINS

In *T. gratilla* enclosures, macroalgal cover (Fig. 4) significantly decreased from $88.2 \pm 3.3\%$ (mean \pm SD) at D0 to $26.1 \pm 3.5\%$ at D28 (Wilcoxon signed-rank test; $V = 55$, $p = 0.006$). There was also a significant decrease of macroalgal cover in *D. setosum* enclosures ($V = 55$, $p = 0.006$), which was, however, smaller (i.e., from $93.1 \pm 2.5\%$ at D0 to $68.9 \pm 6.1\%$ at D28). In control enclosures, the change in macroalgal cover, although significant ($V = 34.5$, $p = 0.025$) was moderate (i.e., from $91.3 \pm 20\%$ at D0 to $83.9 \pm 3.2\%$ at D28).

The grazing rate (quantified as the change of macroalgal cover through time; Fig. 4) differed significantly among treatments (Kruskal- Wallis; $\chi^2 = 22.2$, $df = 2$, $p < 0.0001$). There was a significant difference in the rate of macroalgal grazing between *T. gratilla* and the control (Dunn's post-hoc test: $Z = 4.64$, $p < 0.0001$) and between *T. gratilla* and *D. setosum* ($Z = 2.91$, $p = 0.0054$). By contrast, the grazing rate did not differ between *D. setosum* and the control ($Z = 1.90$, $p = 0.057$).

3.2. MACROALGAL CONSUMPTION

Changes in the percentage cover of each of the macroalgae species between the beginning and end of the experiment (D0 vs. D28) showed that *T. ornata* was consumed more by *T. gratilla* ($4 \pm 2\%$ consumed after 1 day to $82 \pm 19\%$ consumed after 28 days) than by *D. setosum* ($2 \pm 1\%$ at D1 to $19 \pm 14\%$ at D28) (Fig. 5). In control enclosures, *T. ornata* cover decreased by $7 \pm 1\%$ after 28 days. The three other macroalgal species (*P. boryana*, *Halimeda* spp, and *Dictyota* spp) were also more consumed by

T. gratilla than *D. setosum*, while their covers changed little in the absence of sea urchins (Fig. 5).

None of the three treatments showed a significant difference in macroalgal composition between D0 and D28 (Pearson's tests, *T. gratilla*: $\chi^2 = 5.76$, $df = 3$, $p = 0.12$; *D. setosum*: $\chi^2 = 0.97$, $df = 3$, $p = 0.81$; Control: $\chi^2 = 0.17$, $df = 3$, $p = 0.98$) (Fig. 6).

Figure 4. Total percentage (mean \pm SD) of macroalgal cover for all replicate enclosures with *Triploneustes gratilla*, *Diadema setosum* and the no sea urchins control from D0 to D28. Linear regression equations = *T. gratilla* : $y = -2,17x + 84,28$; *D. setosum* : $y = -0,71x + 89,46$; Control: $y = -0,25x + 91,39$.

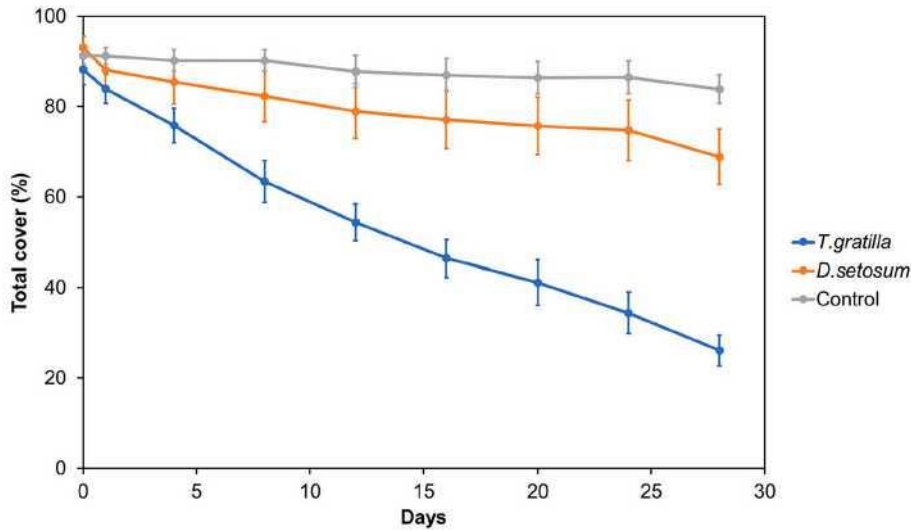


Figure 5. Consumption percentage of each macroalgae species (mean \pm SD) over time in the three conditions (*T. gratilla*, *D. setosum*, control enclosures).

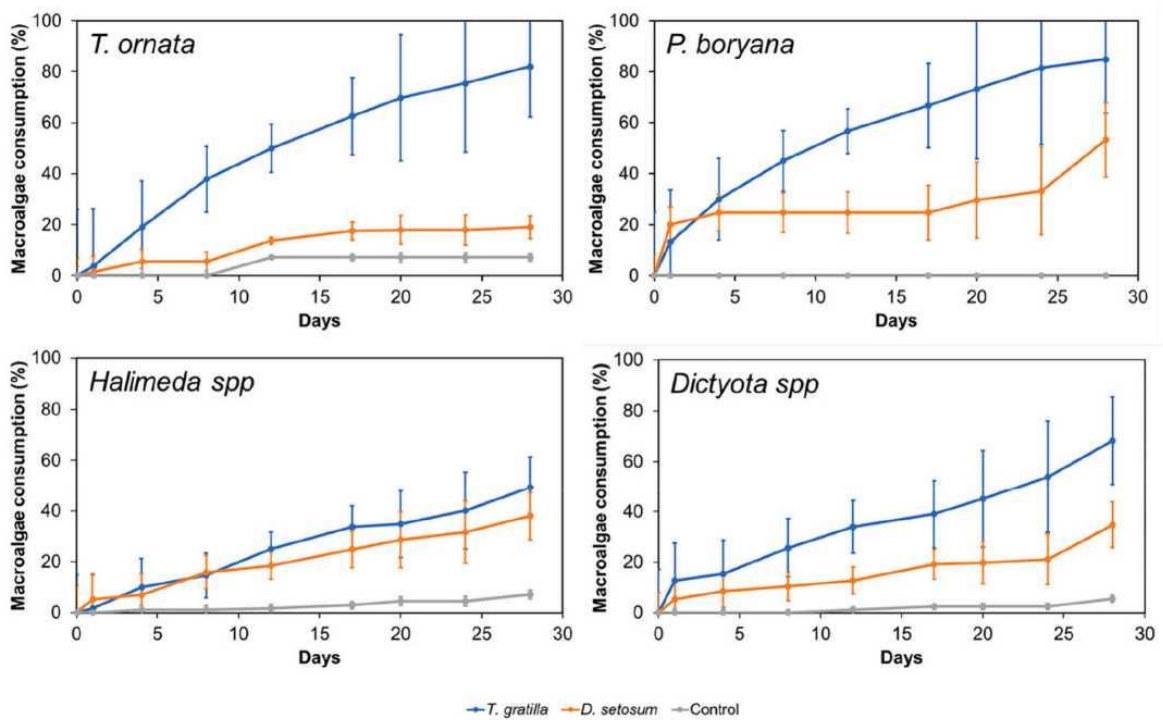
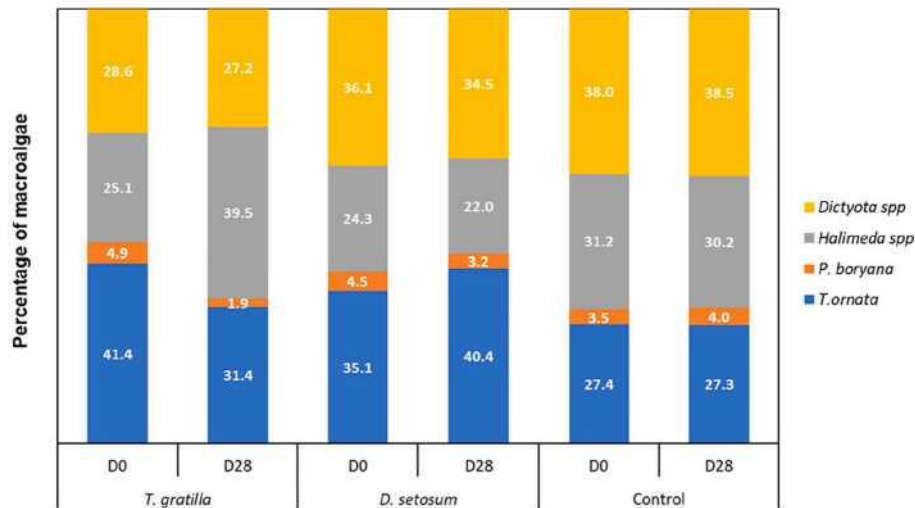


Figure 6. Average percentage stacked bar plot of each macroalgae species present in the three experimental enclosures at day 0 and after 28 days of grazing.



4. Discussion

Herbivory has long been recognized as a major determinant of plant community organization in both terrestrial (Harper, 1969) and marine environments (Crisp, 1964). Echinoids are among the most important groups of benthic grazers in temperate and tropical marine ecosystems (Lawrence and Sammarco, 2020). Our results showed that the efficiency and rate of grazing of *T. gratilla* were significantly greater than those of *D. setosum* (Figs. 4, 5), despite the specimen of both species that were used were adults. Indeed, in our enclosures, *T. gratilla* caused a decrease in total macroalgal cover from 88% to 26% in just 28 days. Our results are in contrast with those of Carpenter (1997), who found that the effects of grazing of *T. gratilla* were weaker in comparison to those of different *Diadema* spp. On the other hand, other in situ experiments have brought evidence that *T. gratilla* could markedly reduce macroalgal biomass within cages (e.g., Chon, 2014; Conklin and Smith, 2005; Westbrook et al., 2015). At La Reunion Island, Lison de Loma et al. (2002) found that *T. gratilla* actively selects food items, exhibiting a marked preference for *T. ornata*. We found no significant preference of *T. gratilla* for a specific macroalgal species since the proportions of macroalgal species did not change between the start and the end of the study (see Fig. 6). *T. gratilla* may benefit from a mixed diet that would provide a more balanced nutrition and, potentially, a dilution of toxic secondary metabolites produced by some of the macroalgal species, such as Dycytiales (Bernays et al., 1994; Hay, 1996).

In *D. setosum* enclosures, the magnitude of the decrease in total macroalgal cover, although significant, was smaller. Weaker effects of *D. setosum* in comparison with *T. gratilla* could be a result of an active avoidance of *T. ornata*, as previously documented (Coppard and Campbell, 2007; Dajka et al., 2021). *T. ornata* is, in fact, mechanically and chemically defended against herbivores

(Sakanishi et al., 2020; Stiger et al., 2004). Although the composition of the macroalgal assemblage at the end of the study, in terms of the proportion of each species, was not significantly different from the beginning, *D. setosum* appeared to consume *P. boryana*, *Halimeda* spp, and *Dictyota* spp more than *T. ornata*. This could be explained by *T. ornata* providing refuge against grazing for palatable macroalgae, as suggested by previous studies (Bittick et al., 2010; Bulleri et al., 2022; Davis, 2018).

Our results are in accordance with a recent study (Bulleri et al., 2022), conducted at Moorea (another island in French Polynesia), revealing no effect of diadematids (*Diadema savignyi*, *Echinothrix diadema* and *E. calamaris*) on the covers of canopies formed by *T. ornata* and *Sargassum pacificum* these urchins are present at low densities (i.e., 1 ind/m²). Stronger effects of diadematids on macroalgae have emerged at higher densities (e.g., Dajka et al., 2021; Dang et al., 2020) than those examined in our study (5 ind/m²). Thus, the effects of diadematids on erect macroalgae appear density-dependent and there could be thresholds below which their grazing effects are negligible. The slight reduction in macroalgal cover at a *D. setosum* density of 5 ind/m² does not align with the findings of previous studies (Idjadi et al., 2010; Sam-marco, 1980), indicating that 3-4 individuals/m² would be necessary to generate effects on macroalgal control. Our results rather support the postulation that the ability of diadematids to reduce macroalgal cover would be dependent upon the maintenance of higher densities of individuals and the composition of macroalgal assemblages (Bulleri et al., 2022; Carpenter and Edmunds, 2006; Dang et al., 2020). In the present study area, it may therefore be appropriate to consider sea urchins cage culture in order to use urchins to assure an efficient grazing impact.

5. Conclusions

In summary, our study suggests that the strength of the effects of grazing by sea urchins are markedly species-specific. Increasing the abundance of *T. gratilla* appears functional for the reduction of the canopy stands formed by *T. ornata*, a species that, by virtue of its low palatability, is consumed by a reduced group of browsing fishes, namely *Naso lituratus* and *Calotomus carolinus* (Schmitt et al., 2021). Reducing the dominance of *T. ornata* may facilitate the grazing activity of other grazers, including diadematids, on less defended macroalgae. Stronger negative effects of diadematids on macroalgae can be expected at high densities, but these could come at a cost to corals, due to their bioerosive activity. Additional studies with a higher density of sea urchins could be pursued to see the effect of group and species behavior in the grazing of macroalgae.

CRedit authorship contribution statement

Stephanie Krimou: Investigation, Formal analysis, Writing - original draft, Writing - review & editing. Emma Gairin: Investigation, Formal analysis, Writing - original draft, Writing - review & editing. Laura Gautrand: Investigation. Jerome Sowinski: Investigation, Resources, Supervision. Mila Trotier: Investigation. Lana Minier: Investigation. Hugo Bischoff: Investigation. Vincent Sturny: Investigation,

Resources, Funding acquisition. Tehani Maueau: Investigation. Vili- ame Waqalevu: Investigation. Fabio Bulleri: Writing - review & editing. Xavier Raick: Formal analysis, Writing - original draft, Writing - review & editing. Frédéric Bertucci: Formal analysis, Visualization, Writing - review & editing. David Lecchini: Conceptualization, Funding acquisition, Methodology, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Stephanie Krimou reports financial support was provided by Bloody Mary. David Lecchini reports financial support was provided by Fondation de France (2019-08602). David Lecchini reports financial support was provided by French Biodiversity Office. Lana Minier reports financial support was provided by Polynésienne des Eaux. David Lecchini reports financial support was provided by French National Research Agency. Lana Minier reports financial support was provided by French National Research Agency.

Acknowledgements

We would like to thank the staff of Espace Bleu, Polynésienne des Eaux, la Vai Ma Noa Bora-Bora and the Commune de Bora-Bora for their help. This work has received several grants: Bloody Mary's, Fondation de France (2019-08602), Office Français de la Biodiversité (AFB/2019/ 385 - OFB.20.0888), Polynésienne des Eaux, ANR-19-CE34-0006-Man- ini and ANR-19-CE14-0010-SENSO, ANRT grant (CIFRE 2021/1268).

References

- Bellwood, D.R., Hughes, T.P., Hoey, A.S., 2006. Sleeping functional group drives coralreef recovery. *Curr. Biol.* 16, 1434-2439. <https://doi.org/10.1016/j.cub.2006.10.030>.
- Bernays, E., Bright, K., Gonzalez, N., Angel, J., 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75, 1997-2006. <https://doi.org/10.2307/1941604>.
- Bittick, S., Bilotti, N., Peterson, H., Stewart, H., 2010. *Turbinaria ornata* as an herbivory refuge for associate algae. *Mar. Biol.* 157, 317-323. <https://doi.org/10.1007/s00227-009-1319-6>.
- Bonaldo, R., Hoey, A., Bellwood, D., 2014. The ecosystem roles of parrotfishes on tropical reefs. *Oceanogr. Mar. Biol.* 52, 81-132. <https://doi.org/10.1201/b17143-3>.
- Brown, K.T., Bender-Champ, D., Kubicek, A., van der Zande, R., Achlatis, M., Hoegh- Guldberg, O., Dove, S.G., 2018. The dynamics of coral-algal interactions in space and time on the southern great barrier reef. *Front. Mar. Sci.* 5, 181. <https://doi.org/10.3389/fmars.2018.00181>.

Bulleri, F., Thiault, L., Mills, S.C., Nugues, M.M., Eckert, E.M., Corno, G., Claudet, J., 2018. Erect macroalgae influence epilithic bacterial assemblages and reduce coral recruitment. *Mar. Ecol. Prog. Ser.* 597, 65-77. <https://doi.org/10.3354/meps12583>.

Bulleri, F., Pozas-Schacre, C., Bischoff, H., Bramanti, L., D'agata, S., Gasc, J., Nugues, M., 2022. Compounded effects of sea urchin grazing and physical disturbance on macroalgal canopies in the lagoon of Moorea, French Polynesia. *Mar. Ecol. Prog. Ser.* 697, 45-56. <https://doi.org/10.3354/meps14137>.

Carpenter, R.C., 1997. Invertebrate predators and grazers. In: Birkeland, C. (Ed.), *Life and Death of Coral Reefs*. Springer US, Boston, MA, pp. 198-229. https://doi.org/10.1007/978-1-4615-5995-5_9.

Carpenter, R.C., Edmunds, P.J., 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. *Ecol. Lett.* 9, 271-280. <https://doi.org/10.1111/j.1461-0248.2005.00866.x>.

Carreiro-Silva, M., McClanahan, T.R., 2001. Echinoid bioerosion and herbivory on Kenyan coral reefs: the role of protection from fishing. *J. Exp. Mar. Biol. Ecol.* 262, 133-153. [https://doi.org/10.1016/S0022-0981\(01\)00288-X](https://doi.org/10.1016/S0022-0981(01)00288-X).

Chon, G., 2014. Optimizing biocontrol: Assessing benthic community changes with different sizes and densities of *Tripneustes gratilla* on patch reef dominated by invasive *Kappaphycus* spp. In: Kane'ohe Bay, Hawai'i. Hawai'i Pacific University.

Conklin, E.J., Smith, J.E., 2005. Abundance and spread of the invasive red algae, *Kappaphycus* spp., in Kane'ohe bay, Hawai'i and an experimental assessment of management options. *Biol. Invasions* 7, 1029-1039. <https://doi.org/10.1007/s10530-004-3125-x>.

Coppard, S.E., Campbell, A.C., 2007. Grazing preferences of diademateid echinoids in Fiji. *Aquat. Bot.* 86, 204-212. <https://doi.org/10.1016/j.aquabot.2006.10.005>.

Crisp, D. (Ed.), 1964. *Grazing in Terrestrial and Marine Environments: A Symposium of the British Ecological Society*. Blackwell, Oxford.

Dajka, J.-C., Beasley, V., Gendron, G., Graham, N., 2021. Investigating sea urchin densities critical to macroalgal control on degraded coral reefs. *Environ. Conserv.* 48 (2), 136-141. <https://doi.org/10.1017/S037689292000051X>.

Dang, V.D.H., Cheung, P.-Y., Fong, C.-L., Mulla, A.J., Shiu, J.-H., Lin, C.-H., Nozawa, Y., 2020. Sea urchins play an increasingly important role for coral resilience across reefs in Taiwan. *Front. Mar. Sci.* 7, 581945 <https://doi.org/10.3389/fmars.2020.581945>.

Davis, S.L., 2018. Associational refuge facilitates phase shifts to macroalgae in a coral reef ecosystem. *Ecosphere* 9, e02272. <https://doi.org/10.1002/ecs2.2272>.

Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M., 1993. Visual versus random-point percent cover estimations: 'objective' is not always better. *Mar. Ecol. Prog. Ser.* 96, 93-100. <https://doi.org/10.3354/meps096093>.

Eddy, T.D., Lam, V.W.Y., Reygondeau, G., Cisneros-Montemayor, A.M., Greer, K., Palomares, M.L.D., Bruno, J.F., Ota, Y., Cheung, W.W.L., 2021. Global decline in capacity of coral reefs to provide ecosystem services. *One Earth* 4, 1278-1285. <https://doi.org/10.1016/j.oneear.2021.08.016>.

Edmunds, P.J., Carpenter, R.C., 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proc. Natl. Acad. Sci.* 98, 5067-5071. <https://doi.org/10.1073/pnas.071524598>.

Fong, P., Paul, V., 2011. Coral reef algae. In: Dubinsky, Z., Stambler, N. (Eds.), *Coral Reefs: An Ecosystem in Transition*, pp. 241-272. https://doi.org/10.1007/978-94-007-0114-4_17.

Gabrie, C., Planes, S., Baldwin, J., Bonvallot, J., Chauvet, C., Vernaudon, Y., Payri, C., Galzin, R., 1994. Study of the coral reefs of Bora-Bora (society archipelago, French Polynesia) for the development of a conservation and management plan. *Ocean Coast. Manag.* 25, 189-216. [https://doi.org/10.1016/0964-5691\(94\)90056-6](https://doi.org/10.1016/0964-5691(94)90056-6).

Glynn, P.W., 1997. Bioerosion and coral-reef growth: A dynamic balance. In: Birkeland, C. (Ed.), *Life and Death of Coral Reefs*. Chapman & Hall, New York, pp. 69-98.

Harper, J., 1969. The role of predation in vegetational diversity. In: *Diversity and Stability in Ecological Systems*. 22nd Symp. U.S. Brookhaven Nat. Lab, Upton, NY, pp. 48-62.

Hay, M., 1996. Marine chemical ecology: what's known and what's next? *J. Exp. Mar. Biol. Ecol.* 200, 103-134. [https://doi.org/10.1016/S0022-0981\(96\)02659-7](https://doi.org/10.1016/S0022-0981(96)02659-7).

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschanivskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17, 360-365. <https://doi.org/10.1016/j.cub.2006.12.049>.

Idjadi, J.A., Haring, R.N., Precht, W.F., 2010. Recovery of the sea urchin *Diadema antillarum* promotes scleractinian coral growth and survivorship on shallow Jamaican reefs. *Mar. Ecol. Prog. Ser.* 403, 91-100. <https://doi.org/10.3354/meps08463>.

Kroh, A., Mooi, R., 2023. World Echinoidea Database. *Tripneustes gratilla* (Linnaeus, 1758). Accessed through: World Register of Marine Species at: <https://www.marine-species.org/aphia.php?p=taxdetails&id=212453> (accessed 21.02.2023).

Lawrence, J.M., Agatsuma, Y., 2020. *Tripneustes*. In: Lawrence, J.M. (Ed.), *Sea Urchins, Biology and Ecology*. Academic Press, pp. 681-703.

Lawrence, J.M., Sammarco, P.W., 2020. Effects of feeding on the environment: Echinoidea. In: Jangoux, M., Lawrence, J.M. (Eds.), *Echinoderm Nutrition*. CRC Press, London, pp. 499-519.

Lecchini, D., Bertucci, F., Schneider, D., Berthe, C., Gache, C., Fogg, L., Waqalevu, V., Maueau, T., Sturny, V., Bambridge, T., Sang, G.T., 2021. Assessment of ecological status of the lagoon of Bora-Bora Island (French Polynesia). *Reg. Stud. Mar. Sci.* 43, 101687 <https://doi.org/10.1016/j.rsma.2021.101687>.

- Lison de Loma, T., Conand, C., Harmelin, M., Ballesteros, E., 2002. Food selectivity of *Tripneustes gratilla* (L.) (Echinodermata: Echinoidea) in oligotrophic and nutrient- enriched coral reefs at La Reunion (Indian Ocean). *Bull. Mar. Sci.* 70, 927-938.
- McCook, L., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400-417. <https://doi.org/10.1007/s003380000129>.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R. W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311, 98-101. <https://doi.org/10.1126/science.1121129>.
- Myhre, S., Acevedo-Gutierrez, A., 2007. Recovery of sea urchin *Diadema antillarum* populations is correlated to increased coral and reduced macroalgal cover. *Mar. Ecol. Prog. Ser.* 329, 205-210. <https://doi.org/10.3354/meps329205>.
- Neilson, B.J., Wall, C.B., Mancini, F.T., Gewecke, C.A., 2018. Herbivore biocontrol and manual removal successfully reduce invasive macroalgae on coral reefs. *PeerJ* 6, e5332. <https://doi.org/10.7717/peerj.5332>.
- Nugues, M.M., Smith, G.W., van Hooidek, R.J., Seabra, M.I., Bak, R.P.M., 2004. Algal contact as a trigger for coral disease. *Ecol. Lett.* 7, 919-923. <https://doi.org/10.1111/j.1461-0248.2004.00651.x>.
- Ruyter, De, van Steveninck, E.D., Bak, R.P.M., 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Mar. Ecol. Prog. Ser.* 34, 87-94. <https://www.jstor.org/stable/24824955>.
- Sakanishi, Y., Tanaka, K., Kasai, H., Tanaka, J., 2020. Characterization of thallus mechanical and physiological traits of tropical furoids: a preliminary study. *Psychol. Res.* 68, 208-215. <https://doi.org/10.1111/pre.12425>.
- Sammarco, P., 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *J. Exp. Mar. Biol. Ecol.* 45, 245-272. [https://doi.org/10.1016/0022-0981\(80\)90061-1](https://doi.org/10.1016/0022-0981(80)90061-1).
- Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Adam, T.C., 2021. Evaluating the precariousness of coral recovery when coral and macroalgae are alternative basins of attraction. *Limnol. Oceanogr.* 67, S285-S297. <https://doi.org/10.1002/lno.11929>.
- Spalding, M., Ravilious, C., Green, E.P., 2001. *World Atlas of Coral Reefs*. University of California Press, Berkeley.
- Stiger, V., Deslandes, E., Payri, C., 2004. Phenolic contents of two brown algae, *Turbinaria ornata* and *Sargassum mangarevense* on Tahiti (French Polynesia): interspecific, ontogenic and spatio-temporal variations. *Bot. Mar.* 47, 402-409. <https://doi.org/10.1515/BOT.2004.058>.
- Tebbett, S.B., 2022. *The functioning of future coral reefs: fishes, sediments and productivity* (phd). James Cook University. <https://doi.org/10.25903/1mnx-mn17>.

Valentine, J., Edgar, G., 2010. Impacts of a population outbreak of the urchin *Tripneustes gratilla* amongst Lord Howe Island coral communities. *Coral Reefs* 29, 399-410. <https://doi.org/10.1007/s00338-010-0610-9>.

Vieira, C., Engelen, A.H., Guentas, L., Aires, T., Houlbreque, F., Gaubert, J., Serrao, E.A., De Clerck, O., Payri, C.E., 2016. Species specificity of bacteria associated to the Brown seaweeds *Lobophora* (Dictyotales, Phaeophyceae) and their potential for induction of rapid coral bleaching in *Acropora muricata*. *Front. Microbiol.* 7, 316. <https://doi.org/10.3389/fmicb.2016.00316>.

Viviani, J., Moritz, C., Parravicini, V., Lecchini, D., Siu, G., Galzin, R., Viriot, L., 2019. Synchrony patterns reveal different degrees of trophic guild vulnerability after disturbances in a coral reef fish community. *Divers. Distrib.* 25, 1210-1221. <https://doi.org/10.1111/ddi.12931>.

Westbrook, C.E., Ringang, R.R., Cantero, S.M.A., Toonen, R.J., 2015. Survivorship and feeding preferences among size classes of outplanted sea urchins, *Tripneustes gratilla*, and possible use as biocontrol for invasive alien algae. *PeerJ* 3, e1235. <https://doi.org/10.7717/peerj.1235>.