



Compounded effects of sea urchin grazing and physical disturbance on macroalgal canopies in the lagoon of Moorea, French Polynesia

Fabio Bulleri^{1,*}, Chloé Pozas-Schacre^{2,3}, Hugo Bischoff^{3,4}, Lorenzo Bramanti⁵,
Stephanie D'agata⁶, Julien Gasc^{2,3}, Maggy M. Nugues^{2,3}

¹Dipartimento di Biologia, Università di Pisa, CoNISMa, Via Derna 1, 56126 Pisa, Italy

²PSL Université Paris: EPHE-UPVD-CNRS, USR 3278 CRIOBE, Université de Perpignan, 66860 Perpignan, France

³Laboratoire d'Excellence Corail, 66860 Perpignan, France

⁴PSL Université Paris: EPHE-UPVD-CNRS, USR 3278 CRIOBE BP 1013, 98729 Papetoai, Moorea, French Polynesia

⁵Sorbonne Université, CNRS, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB,
66650 Banyuls-sur-Mer, France

⁶ENTROPIE (IRD, University of La Reunion, CNRS, University of New Caledonia, Ifremer), 97400 Saint-Denis,
La Reunion c/o IUEM, 29280 Plouzané, France

ABSTRACT: Release from herbivory is a factor underpinning coral replacement by macroalgae. Once macroalgae have achieved dominance, shifts back to the coral-dominated state can be hindered by stabilizing feedbacks. Thus, restoring herbivore assemblages alone can be insufficient to trigger coral recovery. However, herbivores could control macroalgal recovery in the aftermath of physical disturbances removing macroalgae. Diadematid urchins at Moorea (French Polynesia) have collapsed in the last decade. By means of a manipulative field experiment, we tested the interactive effects of physical disturbance and increased diadematid densities on macroalgae inside the lagoon. Massive *Porites* colonies, referred to as 'bommies', were assigned to 3 different macroalgal removal treatments (removal of stipes and fronds of the canopy-forming macroalgae *Turbinaria ornata* and *Sargassum pacificum*, total removal of erect macroalgae or untouched) and exposed to 3 different urchin densities (absent, low [~ 0.5 ind. m^{-2}], and intermediate [~ 1 ind. m^{-2}]). After 1 yr, sea urchins had no effect on the covers of *S. pacificum* and *T. ornata* when macroalgal canopies were left untouched. Urchins could control the recovery of *S. pacificum* on total macroalgal removal bommies, but not that of *T. ornata*. However, urchins, even when at intermediate densities, did not generate major changes in the structure of benthic assemblages on experimental bommies. Our study indicates that a moderate increase in diadematid densities is unlikely to reduce the extent of macroalgal stands in Moorea back reefs unless associated with the recovery of other herbivore guilds able to remove adult macroalgae (i.e. browsers).

KEY WORDS: Coral reefs · Macroalgae · *Turbinaria ornata* · *Sargassum pacificum* · Sea urchins · Disturbance · French Polynesia

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1. INTRODUCTION

Coral reefs worldwide are threatened by multiple anthropogenic stressors, often resulting in a shift in dominance from corals to macroalgae (Done 1992, McManus & Polsenberg 2004, Hughes et al. 2007,

Norstrom et al. 2009). Coral's ability to recover following mass mortalities due to extreme events, such as heatwaves, cyclones or predator outbreaks, appears to be reduced under weak grazing intensity and enhanced nutrient loading (Mumby & Steneck 2008, Graham et al. 2015; but see Szmant 2002). When con-

*Corresponding author: fabio.bulleri@unipi.it

sumer pressure is low, macroalgae can rapidly colonize space freed by disturbances (Diaz-Pulido & McCook 2002, Mumby et al. 2007, Adam et al. 2015, Schmitt et al. 2019). Thus, restoration of herbivore populations has been identified as a priority for sustaining coral reef resilience in the face of increasing intensity and frequency of extreme events (Mumby & Steneck 2008, Scheffer et al. 2008, Edwards et al. 2011, Ceccarelli et al. 2018, Schmitt et al. 2019).

Once dominance is achieved, macroalgae can trigger stabilizing feedbacks that prevent coral recovery and a shift back to a coral-dominated state. For instance, macroalgae can hinder coral recovery by facilitating the spread of coral diseases (Nugues et al. 2004, Bender et al. 2012), reducing the growth and survival of adult corals (Nugues & Bak 2006, Rasher & Hay 2010, Vega Thurber et al. 2012) and/or negatively affecting the recruitment and survival of juvenile corals (Kuffner & Paul 2004, Box & Mumby 2007, Beatty et al. 2018, Bulleri et al. 2018). In addition, adult stages of macroalgae can display herbivory resistance strategies via mechanical (i.e. tough, leathery tissues) and/or chemical defences (i.e. production of secondary metabolites) (Paul & Hay 1986, Hay & Fenical 1988, Stiger et al. 2004). Under some circumstances, herbivory can instead sustain the persistence of tropical brown seaweeds by enhancing both chemical and physical defences (Stiger et al. 2004, Bergman et al. 2016, Bittick et al. 2016).

In the last 3 decades, coral reefs along the island of Moorea (French Polynesia) have been repeatedly impacted by major physical (i.e. cyclones) and biotic disturbance events (i.e. outbreaks of the predatory crown-of-thorns sea star) that have caused a dramatic decline of live coral cover (Adjeroud et al. 2009, Kayal et al. 2012, Lamy et al. 2016). Although some coral recovery has been documented on the outer reefs (Edmunds 2022), lagoonal environments are still locally dominated by macroalgal stands formed by the brown seaweeds *Turbinaria ornata* and *Sargassum pacificum* (often indicated with the heterotypic synonym *S. mangarevense*) (Adjeroud et al. 2018, Bulleri et al. 2018, Davis 2018, Schmitt et al. 2019). Recent work by Schmitt et al. (2019) has shown that low herbivore pressure underpins the current dominance of canopy-forming macroalgae in lagoons, suggesting that, due to hysteresis, a disproportionate increase in herbivory would be necessary to shift the system to a non-macroalgal state.

In general, germlings or juvenile thalli are more susceptible to herbivory since they are less well defended mechanically and/or chemically (Duggins 1981, Stiger et al. 2004, Davis 2018). Thus, assessing

the role of grazers in controlling macroalgal recovery in the aftermath of major physical disturbances, either natural (e.g. cyclones, storms) or anthropogenic (e.g. eradication campaigns), that remove extant macroalgal stands composed of mature thalli (Han et al. 2016, Schmitt et al. 2021), has been paramount for devising management strategies aimed at sustaining coral reef resilience (Adam et al. 2011, Bulleri et al. 2018, Schmitt et al. 2021). Sea urchins, despite being given less attention than fishes, have been shown to play a key role in sustaining coral cover on Caribbean and Indo-Pacific reefs through macroalgal control (Myhre & Acevedo-Gutierrez 2007, Idjadi et al. 2010, Neilson et al. 2018, Cano et al. 2021, Manuel et al. 2021). Evidence from both tropical and temperate areas suggests that, despite their potential to destroy marine forests when at high density, sea urchins have a limited ability to feed upon adult stages of macroalgae (Duggins 1981, Agnetta et al. 2015, Briggs et al. 2018). By contrast, due to their scraping feeding habit, they are very effective in preventing seaweed recovery, even when at relatively low densities (Bulleri & Benedetti-Cecchi 2006), through the removal of juvenile stages which are generally less resistant to herbivory. In this light, the effects of enhancing sea urchin populations could vary according to local disturbance regimes to which macroalgal stands are exposed.

The Diadematidae are a family of sea urchins including genera, such as *Diadema*, which are common in tropical oceans (Lessios et al. 2001). Most of the evidence of the key role of diadematids in sustaining high coral cover and recruitment has been produced by studies on *D. antillarum* in the Caribbean (Bellwood et al. 2004, Cano et al. 2021, Stockton & Edmunds 2021). In French Polynesia, populations of diadematids, and in particular that of *D. savignyi*, can occur at 2 stable states: high density (~ 11 ind. m^{-2}) and low density (~ 1 ind. m^{-2}) (Han 2016). Species belonging this family, such as *D. savignyi*, *Echinothrix diadema* and *E. calamaris*, were present at relatively high densities in lagoon patch reefs up to about one decade ago (Peyrot-Clausade et al. 2000, Han 2016), but they are now found at densities lower than those characterizing the low state described by Han (2016) (Carpenter R of Moorea Coral Reef LTER 2020). The decline of diadematids may have contributed to backreef dominance by brown seaweeds. Although adult thalli of *T. ornata* are chemically and mechanically defended against herbivores (Stiger et al. 2004), juveniles (< 2 cm) are susceptible to grazing (Davis 2018). Likewise, *S. pacificum* is actively consumed by some fish species (Sura et al. 2021). However, little is

known about the role of diadematid sea urchins in controlling macroalgae in reef patches inside lagoons of French Polynesia.

We used a manipulative field experiment to test the interactive effects of macroalgal removal and sea urchin densities on the dynamics of macroalgae. We hypothesised that sea urchins would be unable to reduce the cover of extant macroalgal canopies, but they could prevent their recovery following an acute disturbance. More specifically, we tested 2 intensities of macroalgal removal and predicted that urchin ability to control the recovery of macroalgal canopies would be greater in areas from which macroalgae were totally removed than those in which only the erect part of the thallus was removed. In the second case, re-growth of the erect parts from the holdfast and growth of understory juvenile individuals could, in fact, speed up recovery. Since the strength of herbivore control on primary producers is density-dependent (Dang et al. 2020), we also predicted that urchin ability to control macroalgal recovery in canopy removal or total removal treatments would increase with urchin density.

2. MATERIALS AND METHODS

2.1. Study site and data collection

This study was carried out in the lagoon of Taareu (17° 29' 15.21" S, 149° 51' 21.25" W), on the north coast of Moorea, French Polynesia, from November 2019 to November 2020. During the period of study, there were no extreme climatic events, such as marine heatwaves, cyclones or heavy rains (authors' pers. obs.). Back reef seabeds, at a depth of 2–3 m, are a mosaic of sand, coral rubble and rock, characterized by the presence of massive *Porites* colonies (often referred to as coral bommies), with a diameter up to 4 m and a height up to 2 m (Lenihan et al. 2011, Bulleri et al. 2018, Schmitt et al. 2019). The top half of these coral bommies is often colonized by lush canopies formed by *Turbinaria ornata* and *Sargassum pacificum* (Bulleri et al. 2018, Schmitt et al. 2019, 2021). In the inner barrier, the density and fertility of both species fluctuates (albeit moderately) among seasons, with thallus density and fertility peaking in the cool and warm season, respectively (Stiger & Payri 1999, 2005).

During the warm season, in early November 2019, 36 medium-sized bommies with a surface of 5–6 m² and colonized by a dense canopy formed by *T. ornata* (mean ± SE cover: 49.5 ± 2.7 %, n = 144) and *S. paci-*

ficum (35.69 ± 2.6 %, n = 144) were randomly selected across a 200 × 200 m area. Bommies were marked for relocation with marine epoxy putty and fishing floaters. Each bommie was assigned to 1 of the 9 treatments generated by crossing 3 levels of algal removal treatment and 3 levels of density of diadematid sea urchins, including the species *Diadema savignyi*, *Echinothrix diadema* and *E. calamaris*. Algal removal treatment levels included (1) macroalgal assemblages left untouched (=control); (2) removal of stipes and fronds of canopy-forming macroalgae (*T. ornata* and *S. pacificum*), leaving the holdfasts and the understory macroalgal community untouched (=canopy removal); and (3) total removal of erect macroalgae, including the canopy-forming holdfasts and the understory species (=total macroalgal removal). Urchins were either (1) absent or kept at either (2) low urchin density (3 ind. bommie⁻¹; i.e. about 0.5 ind. m⁻²) or (3) intermediate urchin density (6 ind. bommie⁻¹; i.e. about 1 ind. m⁻²). Data from several sites in Moorea, collected within the framework of The Moorea Coral Reef Long-term Ecological Research (MCR LTER) (Carpenter R of Moorea Coral Reef LTER 2020), indicate diadematid densities close to zero between 2016 and 2019 (*D. savignyi*: 0.035 ± 0.0002 ind. m⁻²; *E. diadema*: 0.058 ± 0.002 ind. m⁻²; *E. calamaris*: 0.004 ± 0.0001 ind. m⁻²; cumulative density of diadematids: 0.098 ± 0.002 ind. m⁻²; n = 480). These values are well below the low-density state for *D. savignyi* (1.34 ± 0.52 ind. m⁻²) according to Han (2016). Generating high diadematid densities such as those recorded in the past (i.e. exceeding 10 ind. m⁻²; Han 2016) was not possible due to the current scarcity of these sea urchins. Nonetheless, by generating low and intermediate urchin densities roughly corresponding to a 5- and a 10-fold increase from current densities, we simulated a realistic scenario, close to the low diadematid density state. The 3 sea urchin species were treated as a guild since, due to low relative abundances, experimental densities could not be generated by the addition of individuals of a single species. Urchins with a test diameter of 5–6 cm were collected at night from nearby reefs along the north and east coasts of the island and randomly translocated onto experimental bommies.

Although several studies have manipulated sea urchin densities by using fences (Dang et al. 2020, Dajka et al. 2021), artificial constraint of their movements can influence their behaviour and foraging (Vadas et al. 1986). Likewise, cages might create artefacts by excluding fish herbivores that can use back-reef habitats for shelter and foraging under natural settings, as well as urchin predators (e.g. *Bal-*

istapus undulates). Diadematids have been reported to have a small home range, with night foraging bouts limited to the area surrounding the refuges (Carpenter 1984, Young & Bellwood 2011). In addition, coral bommies were generally separated by coral rubble or sandy areas which, representing low-quality habitat, were expected to reduce sea urchin movement. Sea urchin abundances were, however, adjusted at fortnightly intervals throughout the duration of the study, through either the removal or addition of specimens. Adjustments every 2–3 wk were sufficient to maintain sea urchin density treatments, apart from the period between 20 March and 4 May 2020 in which visits to the field were prevented by COVID-19 restrictions (Fig. 1).

Before the start of the experiment, the covers of *T. ornata*, *S. pacificum*, *Lobophora* sp., crustose coralline algae (CCA), algal turfs, coral and bare space supported by each of the 36 bommies were quantified visually in 4 randomly selected 50 × 50 cm quadrats supporting a 25 sub-quadrat grid. For each sub-quadrat, the cover of each taxon was given a score of 0 (absent), 1 (¼ of the space occupied), 2 (½ of the space occupied), 3 (¾ of the space occupied) or 4 (complete occupation of the space) and the percentage cover was calculated by summing over the whole set of sub-quadrats (Dethier et al. 1993). A 2-way permutational multivariate analysis of variance (PERMANOVA), including the factors algal removal treatment and urchin density, showed that before the

start of the experiment there were no differences in benthic assemblages among bommies assigned to different treatments (Table S1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m697/p045_supp.pdf). Likewise, a 2-way ANOVA showed no differences in the covers of *T. ornata* and *S. pacificum* across bommies before the start of the experiment (Table S2).

Benthic assemblages on experimental bommies were then visually sampled through photo-quadrats in May, August and November 2020, corresponding to 6, 9 and 12 mo after the start of the experiment. For each sampling time, 5–7 pictures were randomly taken on the top half of each bommie, using a Canon PowerShot S100 camera equipped with a distancer and a 20 × 20 cm PVC frame. Species abundances were calculated on a PC screen, using the same visual technique previously described for estimating benthic species cover before the start of the experiment (Dethier et al. 1993). Except for *S. pacificum* and *T. ornata*, macroalgal species were included for analysis into broad morpho-functional groups, namely CCA, sub-canopy macroalgae and algal turfs. The sub-canopy macroalgae included *Dictyota* spp., *Padina boryana*, *Halimeda* spp., *Lobophora* spp., *Amanesia rhodantha*, *Spatoglossum asperum* and some non-identified articulated corallines, coarsely branched and thin-tubular sheet-like species (Steneck & Dethier 1994). Algal turfs included filamentous forms and *Acanthophora spicifera*, a species that forms

mats (Fong et al. 2003) that trap sediments (F. Bulleri pers. obs.) and has previously been categorized as turf-forming (Sangil & Guzman 2016). The cover of cyanobacteria (max. cover: 6.8%; mean cover: 0.19 ± 0.1 ; $n = 108$) and that of sessile invertebrates, such as coral (alive or dead), tridacnids, sponges and vermetids (max cover: 7.9%; mean cover: 0.69 ± 0.14 %; $n = 108$), were generally low and therefore not further analyzed. Also, the percentage cover of primary surfaces, either dead coral or rock (i.e. unoccupied by any macroscopic organism or colonized by a very thin biofilm), was quantified and hereafter referred to as bare space. The proportion of sampling units occupied by holes and cracks or too dark (i.e. shaded) to allow species identification was quantified and the per-

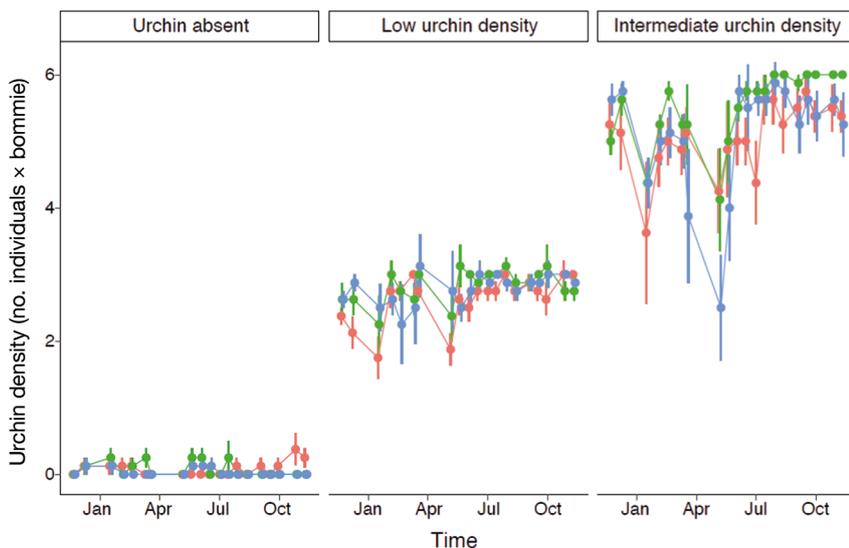


Fig. 1. Temporal dynamics of urchin densities on experimental bommies assigned to different algal removal treatments (red: control; green: macroalgal canopy removal; blue: total macroalgal removal) and urchin density (absent, low and intermediate). Urchin densities could not be maintained in the period 20 March–4 May due to COVID-19 restrictions. Data are means \pm SE; $n = 4$

centage cover of each taxon was then adjusted according to the total surface sampled.

2.2. Statistical analyses

2.2.1. Multivariate analyses

Variations in the structure of benthic assemblages across treatments were assessed with permutational analysis of variance on Bray-Curtis dissimilarities calculated on untransformed data, including algal removal treatment and urchin density as fixed and crossed factors. Since our data were not independent through time due to the repeated sampling of the same bommies, we ran a separate analysis for each time of sampling. Multivariate patterns were visualized using non-metric multidimensional scaling. Multivariate analyses were run using the software Primer and Permanova+ v.1.0.1 (PRIMER-e).

2.2.2. Univariate analyses

To test for the effects of algal removal treatment and urchin density on the percentage covers of benthic groups, we employed a generalized linear mixed model with a beta error distribution and a logit link function, using the R package 'GlmTMB' v.1.0.2.90 (Brooks et al. 2017). To reduce model complexity, coral bommies were considered experimental units ($n = 4$) and data were averaged for each bommie at each sampling time. Algal removal treatment, urchin density and time were included as fixed effects, with time also included in the random part of the model to take into account repeated sampling of the same replicates (i.e. the bommies). Since the beta distribution does not allow for values of 0 or 1, percentage covers were linearly transformed according to Douma & Weedon (2019) as follows:

$$\text{cover}' = \frac{\text{cover} \times (n - 1) + \frac{1}{C}}{n}$$

where n is the total number of observations and C is the number of categories (8 taxa in our case). For each response variable, we used Akaike's information criterion to compare the fit of a model assuming the same dispersion for all treatments to those of models allowing dispersion to vary either across combinations of levels of algal treatment and urchin density or across combinations of all 3 factors (i.e. algal treatment, urchin density and time) (Douma & Weedon 2019). We then performed Type III Wald chi-

squared tests for fixed effects included in the best-fit model (Table S3), using the 'Anova' function in the R package 'car' v.3.0-10 (Fox & Weisberg 2019). Pairwise comparisons between levels of significant factors were performed using the function 'emmeans' using the Tukey multiplicity adjustment method in the R package 'emmeans' v.1.6.0 (Lenth 2020).

Model assumptions were checked with QQ plots and plots of standardized residuals versus the expected values, using the R package 'DHARMA' v.0.4.1, which employs a simulation-based approach (Hartig 2020). The same R package was used to run a Kolmogorov-Smirnoff test to formally assess heteroscedasticity and goodness-of-fit tests on the simulated residuals to check for over-dispersion and outliers. These diagnostics showed no violation of model assumptions (Figs. S2–S7). All univariate analyses were run in RStudio v.1.3.1093 (RStudio Team 2020)

3. RESULTS

Multivariate analyses (PERMANOVAs and post hoc pairwise tests) showed that benthic assemblages varied significantly among bommies exposed to different algal removal treatments at all times of sampling, while they were not affected by our manipulation of urchin density (Table 1, Fig. 2).

The cover of *Turbinaria ornata* differed significantly among bommies exposed to different levels of algal removal treatment (Table 2, Fig. 3a). In particular, it was highest on canopy removal bommies, intermediate on controls and lowest on total removal bommies, consistently through time (Table S4). The analysis also showed significant effects of urchins which varied through time. However, post hoc tests did not identify significant differences among urchin densities (Table S4).

There was a significant effect of the interaction between algal removal treatment and urchin density on the cover of *Sargassum pacificum* (Table 2, Fig. 3b). Increasing urchin density had no effect on control or canopy removal bommies, whereas at intermediate densities, urchins reduced the cover of this macroalga on total removal bommies (Table S4). Control bommies supported a higher cover of *S. pacificum* than total or canopy removals when urchins were either absent or at low density. In contrast, at intermediate urchin density, the cover of *S. pacificum* was significantly lower on total removal than control or canopy removal bommies.

Increasing sea urchin density and initial macroalgal removal treatments had limited effects on sub-

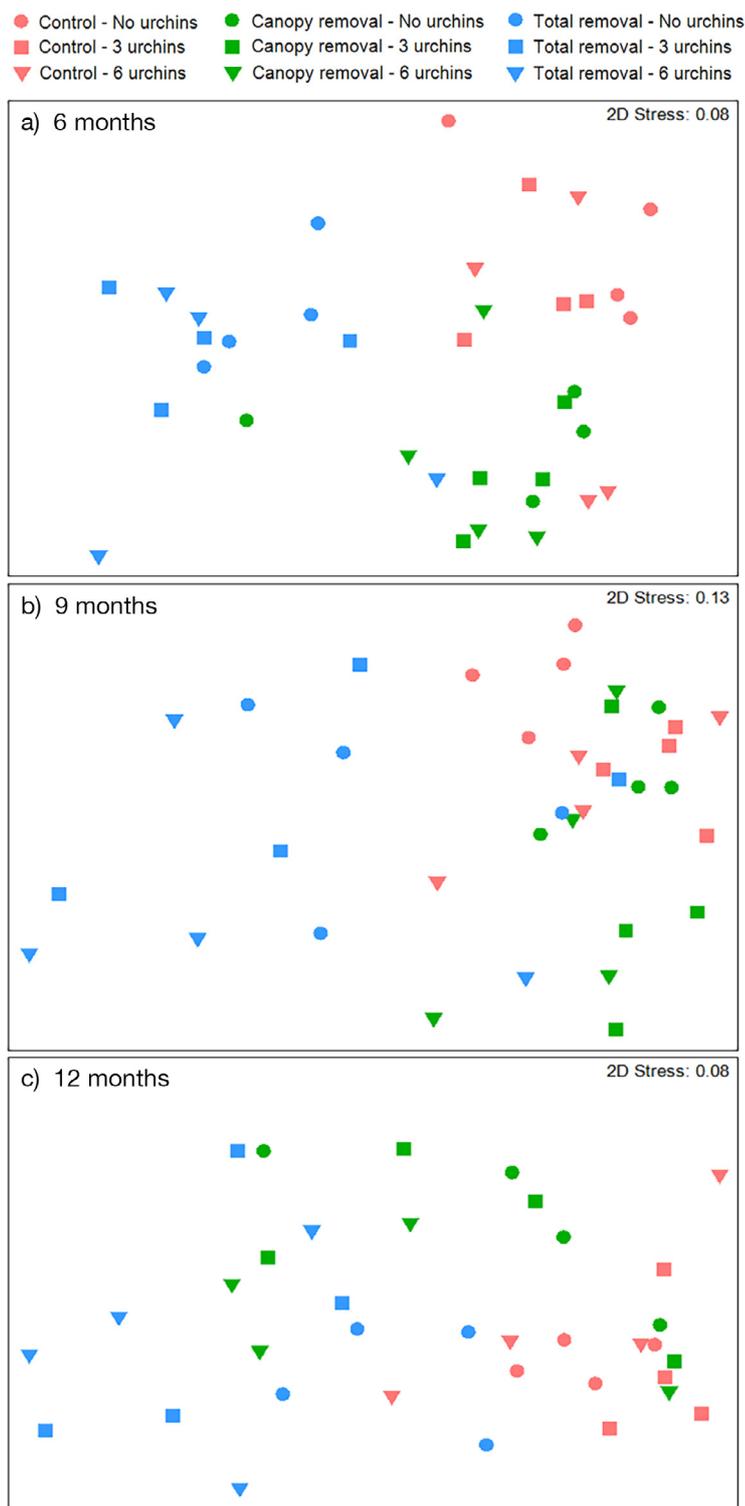


Fig. 2. Two-dimensional non-metric multidimensional scaling plot on untransformed data comparing benthic assemblages on experimental bommies assigned to different combinations of algal removal treatment (control, canopy removal and total removal) and urchin density (circles: absent; squares: low; triangles: intermediate), separately for (a) 6 mo, (b) 9 mo and (c) 12 mo after the start of the experiment

canopy macroalgae, whose cover changed through time (Table 2, Fig. 3c). Algal removal treatments had no effects on turfs (Table 2, Fig. 3d). In contrast, there were significant effects of sea urchins, which varied through time. The cover of algal turfs was lower on bommies without urchins than in those supporting low urchin densities after 6 mo from the start of the experiment, but not thereafter (Table S4). Differently, the cover of CCA was not affected by sea urchins, but it was greater on total removal bommies than on control or canopy removal ones consistently through time (Tables 2 & S4, Fig. 3e).

The analysis showed significant effects of the interaction among algal removal treatment, urchin density and time on the amount of bare space. On control and canopy removal bommies, there were no effects of increasing urchin densities at any time (Table S4). In contrast, 9 and 12 mo after the start of the experiment, there was more bare space on total removal bommies maintained at either low or intermediate urchin densities than on those without urchins (Tables 2 & S4, Fig. 3f).

4. DISCUSSION

The effects of increasing sea urchin density varied between canopy-forming species and according to the intensity of the algal removal treatment applied at the onset of the experiment. When macroalgal canopies were left untouched, the addition of sea urchins had no effect on the covers of both *Sargassum pacificum* and *Turbinaria ornata*. Instead, urchins were effective in reducing the recovery of *S. pacificum* on bommies initially exposed to the total macroalgal removal, whereas they had weak effects on the recovery of *T. ornata*. However, the effects of increasing sea urchins on the entire benthic community were negligible compared with those of the macroalgal removal. Such results cast doubts on the effectiveness of a moderate increase in diadematid urchin density, as produced by our experiment, in facilitating a shift towards coral dominance.

Table 1. PERMANOVA assessing the effects of algal removal treatment and urchin density on the structure of benthic assemblages on experimental bommies, separately for each time of sampling. Post hoc pairwise tests are reported for significant factors; *** $p < 0.001$

Source of variation	df	6 mo		9 mo		12 mo	
		MS	Pseudo- F	MS	Pseudo- F	MS	Pseudo- F
Algal removal (Ar)	2	10328.00	18.747***	6101.90	9.053***	6686.50	10.809***
Urchin density (Ud)	2	756.24	1.373	1189.50	1.765	717.46	1.160
Ar \times Ud	4	429.05	0.779	657.90	0.976	687.03	1.111
Residual	27	550.92		674.03		618.58	
Pairwise tests							
Comparisons		t	p	t	p	t	p
Canopy removal—total removal		4.411	0.001	3.154	0.001	2.580	0.004
Canopy removal—control		3.107	0.001	1.639	0.048	2.306	0.011
Total removal—control		5.104	0.001	3.543	0.001	4.886	0.001

Stability in macroalgal dominance can be sustained by a low susceptibility of adult stages to herbivory (Briggs et al. 2018). Avoidance of mature thalli of large furoids, such as *Sargassum* spp. and *T. ornata*, by *Diadema savignyi* and *Echinotrix* species has been previously documented (Coppard & Campbell 2007, Dajka et al. 2021). Both seaweeds, and in particular *T. ornata*, are well defended against herbivores both mechanically and chemically (Stiger et al. 2004, Sakanishi et al. 2020). Juveniles of *T. ornata* are exposed to lower consumption rates when protected by adult thalli (Davis 2018). Since palatable

macroalgae can be exposed to weaker herbivory when hidden amongst unpalatable species (Hay 1986), *S. pacificum* could benefit from the association with *T. ornata* when growing in mixed canopies. Thus, although palatable to some herbivores (McClanahan et al. 1994, Mantyka & Bellwood 2007, Rasher et al. 2013, Sura et al. 2021), dense stands of *T. ornata* and *S. pacificum* would be able to persist under increased urchin density by virtue of their intrinsic resistance to herbivory, but also due to intra-specific and inter-specific associational refuges. Loss of browsing herbivores able to consume mature

Table 2. Type III ANOVA results for fixed effect parameters included in the generalized linear mixed model testing effects of time, algal removal treatment and urchin density on percentage covers of benthic groups. CCA: crustose coralline algae

Source of variation	df	<i>Turbinaria ornata</i>		<i>Sargassum pacificum</i>		Sub-canopy	
		χ^2	p	χ^2	p	χ^2	p
Intercept	1	465.01	<0.0001	3.18	0.075	74.77	<0.0001
Time (Ti)	2	21.55	<0.0001	1.29	0.525	7.41	0.025
Algal removal (Ar)	2	21.04	<0.0001	11.98	0.003	0.39	0.822
Urchin density (Ud)	2	2.42	0.300	4.73	0.094	0.19	0.910
Ti \times Ar	4	3.61	0.462	7.68	0.104	4.52	0.340
Ti \times Ud	4	11.81	0.019	4.57	0.334	2.47	0.650
Ar \times Ud	4	6.38	0.173	12.60	0.013	2.12	0.713
Ti \times Ar \times Ud	8	3.43	0.905	8.24	0.410	5.12	0.745
Source of variation	df	Algal turf		CCA		Bare space	
		χ^2	p	χ^2	p	χ^2	p
Intercept	1	60.26	<0.0001	44.27	<0.0001	61.41	<0.0001
Ti	2	23.89	<0.0001	5.73	0.057	0.29	0.866
Ar	2	0.72	0.699	10.12	0.001	3.20	0.202
Ud	2	0.38	0.828	3.60	0.166	1.22	0.544
Ti \times Ar	4	9.39	0.052	5.20	0.267	20.75	0.000
Ti \times Ud	4	14.91	0.005	2.70	0.610	4.77	0.312
Ar \times Ud	4	3.53	0.473	3.58	0.465	12.85	0.012
Ti \times Ar \times Ud	8	13.71	0.090	9.99	0.265	16.30	0.038

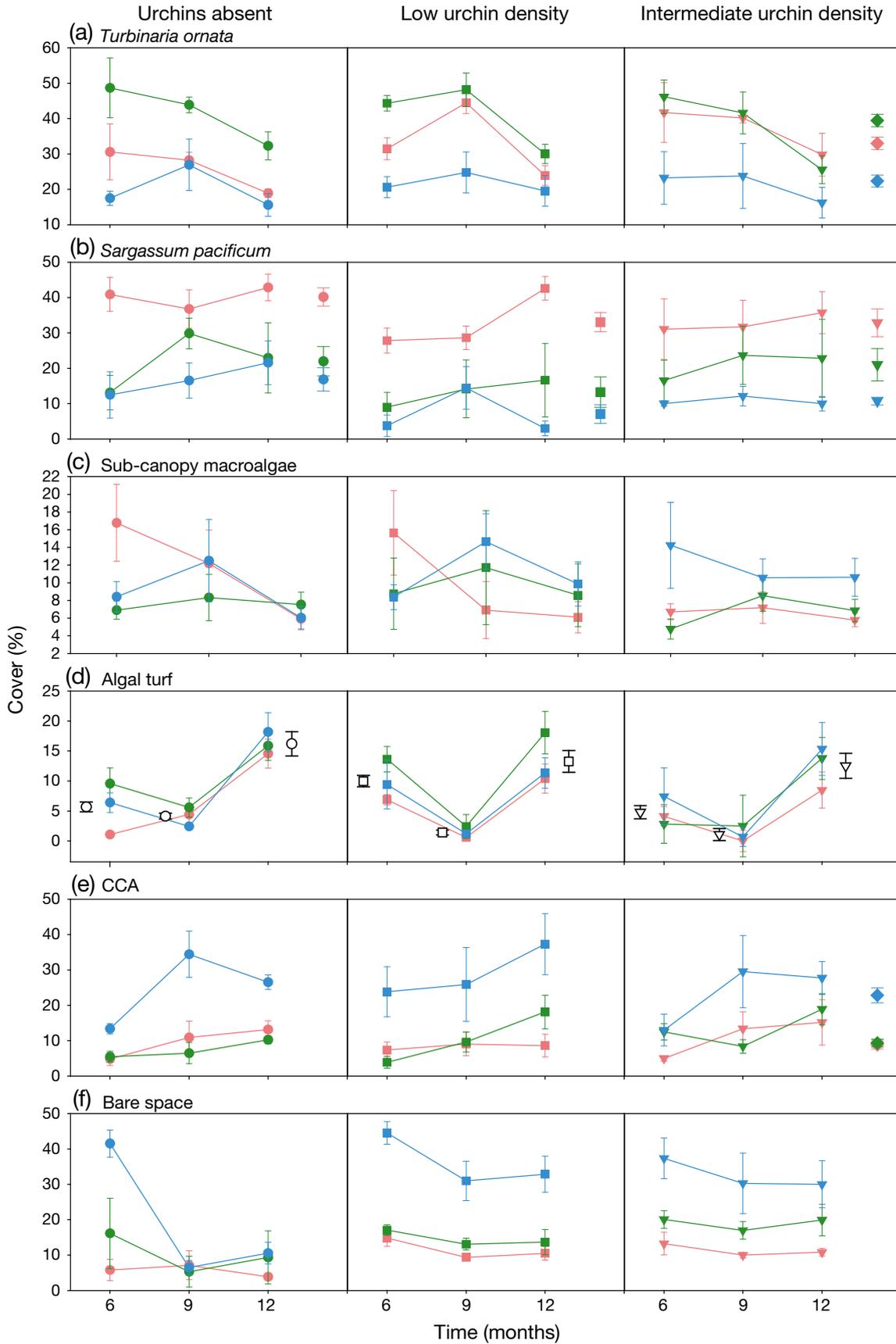


Fig. 3. Percentage cover of (a) *Turbinaria ornata*, (b) *Sargassum pacificum*, (c) sub-canopy algae, (d) turfs, (e) crustose coralline algae (CCA) and (f) bare space on experimental bommies assigned to different combinations of algal removal treatment (red: control; green: macroalgal canopy removal; blue: total macroalgal removal) and urchin density (circles: absent; squares: intermediate) as a function of time (6, 9 and 12 mo after the start of the experiment). Data are means \pm SE; n = 4. To facilitate interpretation of the results, we also report means \pm SE for each algal removal treatment across urchin densities, and times for (a) *T. ornata* and (e) CCA as diamonds at the right of the intermediate urchin density panel (n = 36); for each combination of levels of algal removal treatment and urchin densities across time for (b) *S. pacificum*, as symbols at the right hand of each urchin density panel (n = 12); and for each level of urchin density across algal removal treatments and separately for each time for (d) algal turfs as hollow symbols (n = 12).

macroalgae has been shown to be a key driver of macroalgal dominance on reefs worldwide, including Moorea (Burkepile & Hay 2010, Han et al. 2016, Burkepile et al. 2020, Schmitt et al. 2021). Our study confirms that a moderate increase in diadematid urchins in the lagoons of Moorea cannot compensate for the decline of browsing fishes, such as *Naso lituratus* and *Calotomus carolinus* (Schmitt et al. 2021) or that of the urchin *Tripneustes gratilla*, a species that actively forages on *T. ornata* (de Loma et al. 2002).

Incrementing sea urchin density had no effect on the recovery of *T. ornata*. Although *T. ornata* germling dispersal from parental plants is limited (<90 cm from parental thalli) (Stiger & Payri 1999), the recolonization of total macroalgal removal bommies 6 mo after the start of the experiment could indicate a supply from nearby canopy stands or from floating rafts. The timing of a physical disturbance event can determine patterns of recovery according to the phenological characteristics of species (Kennelly & Larkum 1983, Bulleri et al. 2002). Starting our experiment in the warm season might have generally facilitated the recovery of *T. ornata* and *S. pacificum* by making free space available just before their peak in fertility (Stiger & Payri 1999, 2005). Alternatively, the recovery of this seaweed might have been promoted by banks of microscopic forms, which have been documented in several macroalgae (Hoffmann & Santelices 1991), including *T. ornata* (Stiger & Payri 2005). Improvement of environmental conditions (e.g. light levels) following the removal of adult stands may have stimulated growth resumption in microscopic juvenile stages that could not be eliminated by our total macroalgal removal and/or escaped from grazing in crevices and holes. There was, however, no significant increase in the cover of *T. ornata* in the following period, with covers on total macroalgal removal bommies generally not exceeding 20%, irrespective of urchin densities. Slightly smaller cover values at the end of the experiment (November 2020), particularly evident on canopy removal and control bommies, could be explained by the natural decline in the abundance of this seaweed during warmer months (Stiger & Payri 1999, 2005).

By contrast, urchins were effective in controlling the cover of *S. pacificum* on total macroalgal removal bommies, increasing bare space availability. Most herbivore feeding preference trials have been performed using adult macroalgal thalli (Coppard & Campbell 2007, Lewis & Smith 2019). However, the efficacy of structural and chemical defences in both *S. pacificum* and *T. ornata* increases ontogenetically and is lower in recruits and juveniles than in mature

thalli (Stiger et al. 2004, Davis 2018). Thus, seaweeds that are actively avoided at adult stages might be included in herbivore diets at earlier life stages, before herbivore-resistance mechanisms are fully developed. This could be the case for *S. pacificum* which, by the end of the experiment, was virtually absent from total macroalgal removal bommies maintained at either low or intermediate urchin densities. Our results suggest that even a moderate increase in grazing pressure from sea urchins could be sufficient to control the recovery of this species in lagoonal environments.

Urchin densities in our experiment were lower compared to those examined in other studies (Han 2016, Dang et al. 2020, Dajka et al. 2021). Sea urchin effects on macroalgae generally scale with their density (Benedetti-Cecchi et al. 1998, Carpenter & Edmunds 2006, Dang et al. 2020), and evidence from coral reefs in the Caribbean, Taiwan and Easter Island suggests that diadematid sea urchins can contribute to stabilizing the coral-dominated state by maintaining macroalgae in check (Carpenter & Edmunds 2006, Idjadi et al. 2010, Easton et al. 2018, Dang et al. 2020, Nozawa et al. 2020). For instance, in the Caribbean, the recruitment and growth of juvenile coral colonies was significantly increased when urchin densities were between about 3 and 4 ind. m⁻² (Sammarco 1980, Idjadi et al. 2010), while it was depressed at higher urchin densities due to biological disturbance (Sammarco 1980, Dang et al. 2020). In our study, using higher densities was impractical and likely would have generated unrealistic conditions given the current rarity of diadematid urchins in the lagoons of Moorea.

Interestingly, there were no effects of sea urchins on sub-canopy algae in canopy or total macroalgal removal bommies, even when the removal of canopies exposed these brown (*Dictyota* spp., *Padina boryana*, *Lobophora* spp., *Spatoglossum asperum*) and red seaweeds (e.g. *Corallina* spp., *Jania* sp., *Amansia rhodantha*) to intense predation also by herbivorous fishes (Bittick et al. 2010). As grazers, sea urchins were expected to feed on algal turfs (Manuel et al. 2021). Although limited to the first time of sampling (i.e. 6 mo after the start of the experiment), they had a positive effect on these algal forms — both on control and canopy removal bommies — likely releasing them from competitors. Nonetheless, the cover of algal turfs was generally limited, rarely exceeding values greater than 20%.

The control of *S. pacificum* recovery by sea urchins resulted in an increase in bare space on total macroalgal removal bommies, which, irrespective of sea urchin densities, also supported a greater cover of

CCA. However, such increase in the availability of macroalgal-free surfaces may not be sufficient to facilitate coral recruitment, since covers of *T. ornata* as low as 10 % can be enough to reduce larval settlement and enhance the mortality of juvenile coral colonies (Schmitt et al. 2021). *T. ornata* has been shown to alter the structure of epilithic microbial biofilms on nearby open surfaces through indirect mechanisms, likely through the exudation of labile dissolved organic carbon, allelochemicals, free-living microbes and exosomes (Barott & Rohwer 2012, Jorissen et al. 2016, Morrow et al. 2017), hindering recruitment success of coral larvae (Bulleri et al. 2018).

In summary, our study suggests that a recovery of diadematid populations to density levels that could be realistic in the short-term, given the current rarity of these urchins, is unlikely to be efficient in promoting coral recovery through the provisioning of free space, unless associated with the restoration of other guilds of herbivores able to remove adult macroalgae (i.e. browsers) and, likely, reductions in nutrient loading (Graham et al. 2015, MacNeil et al. 2019, Adam et al. 2021). Higher diadematid densities might be, however, more effective in controlling macroalgal canopies. Finally, the increment in the cover of *T. ornata* on bommies initially exposed to the removal of canopies indicates that eradication campaigns consisting in the removal of stipes and fronds of adult thalli do not represent a viable option for controlling this species.

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