

# Coralline Algal Population Explosion in an Overgrazed Seagrass Meadow: Conditional Outcomes of Intraspecific and Interspecific Interactions

Isis Gabriela Martínez López,<sup>1,2\*</sup> Luuk Leemans,<sup>3</sup> Marieke M. van Katwijk,<sup>3</sup> S. Valery Ávila-Mosqueda,<sup>1</sup> and Brigitta I. van Tussenbroek<sup>1</sup>

<sup>1</sup>Unidad Académica de Sistemas Arrecifales-Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Prol. Av. Niños Héroes S/N Domicilio conocido, C.P. 77580 Puerto Morelos, Quintana Roo, México; <sup>2</sup>Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Delegación Coyoacán, Ciudad Universitaria, Ciudad de México, México; <sup>3</sup>Radboud Institute for Biological and Environmental Sciences, Radboud University, Nijmegen, The Netherlands

## ABSTRACT

Interactions such as mutualism and facilitation are common in ecosystems established by foundation species; however, their outcomes vary and show conditionality. In a Mexican Caribbean Bay, a seagrass-coralline algae (rhodoliths) mutualism protects the seagrass *Thalassia testudinum* from green turtle overgrazing. We postulate that the state of the seagrass meadow in this bay depends on the strengths of the interactions among seagrasses, green turtles, and coralline algae. Spatio-temporal changes through satellite imagery showed rhodolith bed developed rapidly from 2009 (undetected) to 2016 (bed of 6934 m<sup>2</sup>). Typically, such rapid expansion of the rhodoliths does not occur in sea-

grass meadows. An in situ growth experiment of coralline algae showed that a combination of reduction in light and wave movement (usual in dense seagrass meadows) significantly reduced their growth rates. In the rhodolith beds, the growth rates of the coralline algae *Neogoniolithon* sp. and *Amphiroa* sp. were high at 9.5 mm and 15.5 mm per growth tip y<sup>-1</sup>, respectively. In a second experiment, we found lower mortality in coralline algae within a rhodolith bed compared to algae placed outside the bed, likely explained by the reduced resuspension that we found in a third experiment, and this positive feedback may explain the high population increase in the rhodoliths, once established when the turtles grazed down the seagrass canopy. Therefore, the grazing-protection mutualism between seagrasses and coralline algae is thus conditional and came into existence under a co-occurrence of intensive grazing pressure and rapid population growth of coralline algae facilitated by positive feedback from increased growth and reduced sediment resuspension by the dense rhodolith bed.

Received 28 April 2023; accepted 1 April 2024

**Supplementary Information:** The online version contains supplementary material available at <https://doi.org/10.1007/s10021-024-00909-9-w>.

**Author Contributions:** BIT, IGML, and LL conceived the idea for the study; BIT, IGML, LL, and SVAM performed the research; BIT, IGML, LL, MMK, and SVAM analyzed the data; IGML led the writing of the manuscript; and BIT and MMK supervised the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

\*Corresponding author; e-mail: [igml\\_2015@comunidad.unam.mx](mailto:igml_2015@comunidad.unam.mx)

**Key words:** *Thalassia*; turtle herbivory; *Neogoniolithon*; rhodolith; sedimentation; light reduction; mutualism; positive feedback.

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## HIGHLIGHTS

- Coralline algae population increased explosively over few years.
- Reduction in light and wave movement decreased coralline algae growth rate.
- Coralline algae aggregations reduced sediment resuspension favoring their survival.
- When coexisting, turtle-seagrass-rhodolith interactions show conditional outcomes.

## INTRODUCTION

The outcomes of mutualistic interactions were traditionally considered fixed; however, the review by Bronstein (1994) was among the first to point out that the outcomes of potentially beneficial (and other types of) interactions are often not deterministic but context-dependent (that is, conditional outcomes). In plant communities, positive interactions such as mutualism and facilitation may act simultaneously with competitive interactions, and the overall effect of one plant species on another will depend on the relative strengths of the interactions in a given state of the environment (Callaway 1997). For example, Baraza and others (2007) found that spatial distribution of palatable and unpalatable plants influenced the foraging behavior of herbivores, which changed the probabilities of plant damage; the outcome was dependent on 1) plants palatability, 2) plants neighborhood, that is, presence/absence of unpalatable protective spiny plants and 3) difference in herbivore abundance (pressure). In addition, positive interactions will be influenced by the ability of plant species to modify their own environment, which is especially important for foundation species. Through such mechanisms of positive feedback, foundation species alter the environment facilitating not only their own existence but also that of other species (for example, Maxwell and others 2017). At the same time, the habitat-modifying ability of such plants will depend on their own biological and physical state in a given condition (Stachowicz 2001). This may lead to conditional positive feedback, as for example occurs in salt marshes, where the species *Spartina*

*anglica* modifies the environment through the enhancement of sediment accretion under specific abiotic conditions of hydrodynamics and topography, eventually allowing the formation of “sediment-accumulating dome-shaped tussocks” (van de Koppel and others 2012).

Recently, Leemans and others (2020) found a mutualistic interaction among seagrasses, loose-lying red calcareous algae (also known as coralline algae or rhodoliths), and green sea turtles in a Caribbean Bay. In this bay, the seagrass *Thalassia testudinum* was protected from overgrazing by the green turtles in dense rhodolith beds. The seagrass shoots, even those grazed short, reduced the removal of the coralline algae by waves or currents, thus creating the physical conditions for their accumulation, thereby allowing for the coexistence of both rhodolith beds and grazed seagrass meadows. In the beginning of rhodolith accumulation, the turtles were deterred completely, and they changed their feeding ground elsewhere in the bay; at a later stage when *T. testudinum* shoots grew well above the rhodolith bed, the turtles returned, but they left a higher canopy ( $> \sim 8$  cm, instead of 3 cm), which allowed for persistence of *T. testudinum* in the rhodolith bed, even under conditions of moderate turtle grazing. This mutualistic interaction is of relevance for seagrass and sea turtle management, as it may serve as a conservation measure to non-invasively persuade the green turtles to graze elsewhere, thereby protecting or restoring seagrass meadows overgrazed by green turtles (Leemans and others 2020).

Seagrasses are marine angiosperms that are the foundation species of vast meadows under the sea which host biodiverse communities and provide numerous ecosystem services (Nordlund and others 2016; Orth and others 2020). As it occurs with other foundation species, seagrasses alter their local environment through positive feedback mechanisms that promote their own survival and growth (Van der Heide and others 2011; Nyström and others 2012; Maxwell and others 2017). Seagrass canopy relieves hydrodynamic stress by attenuating currents and waves, which also improves light conditions by reducing suspended sediment and stabilizing the substrate (Van der Heide and others 2011; Adams and others 2016). In this way, seagrasses not only facilitate their growth and persistence, but also the occurrence or proliferation of countless other species intolerant to disturbed conditions (Stachowicz 2001; van der Heide and others 2011). Competitive interactions also shape the seagrass community (Williams 1987; Fourqurean and others 1995), including those between

seagrasses and calcareous algae such as competition for space, light, or nutrients (Williams 1990; Davis and Fourqurean 2001).

Unattached red calcareous (coralline) algae are foundation species of ecosystems made up by accumulations of living and dead thalli, called rhodolith or “maerl” beds; once having established a dense bed, the rhodoliths exercise a major influence on the structure and processes of the community. They produce enormous quantities of calcium carbonate and increase biodiversity by providing a habitat for a diverse community (Riosmena-Rodriguez and others 2017). To proliferate into beds, the coralline algae require a combination of sufficient light, nutrients, and water movement (Steller and Foster 1995; Wilson and others 2004). Particularly, water movement is a key factor in determining rhodolith coverage and biomass; too fast current velocity and individual thalli may be moved away from suitable zones, but too slow and coralline algae may be smothered by silt (Harvey and others 2017; Melbourne and others 2018). Rhodolith coverage ( $> 60\%$ , living and dead) has been associated with sites with lower current velocities ( $< 0.30 \text{ m s}^{-1}$ ; Dutertre and others 2015), while higher living rhodolith biomass ( $14.56 \pm 1.61 \text{ dry kg m}^{-2}$ ) has been reported under conditions of lower sedimentation rates ( $0.05 \text{ cm y}^{-1}$ ; Qui-Minet and others 2018).

The state and persistence of vegetative foundation species, such as seagrasses (for example, Valentine and Heck 1999), are often mediated by grazers. Green sea turtles (*Chelonia mydas*) are important megaherbivores in tropical and subtropical seagrass meadows (for example, Heithaus and others 2014; Christianen and others 2021). The green turtle is a species of large sea turtles, common throughout tropical and subtropical seas around the world. Green turtles may live up to 80 years, migrate long distances between hatching beaches and feeding grounds, and have high fidelity to their grazing ground (Esteban and others 2020). In the Caribbean, green turtles preferentially graze on *T. testudinum*, and if grazing intensity is low to moderate, they use a rotational (or cultivation) grazing strategy (Molina and van Tussenbroek 2014). But when the turtles become too abundant, they change their feeding strategy, resulting in overgrazing and even consuming entire plants including rhizomes, eventually leading to the collapse of the seagrass meadow (Christianen and others 2021). Under such a regime of overgrazing, Leemans and others (2020) demonstrated that in a dense rhodolith bed, the spiny structures of coralline algae induced avoidance behavior of the green

turtles, thereby protecting the seagrass meadows from collapse (that is disappearing entirely).

Here, we address how the state of the system (conditional outcome) described by Leemans and others (2020) depends on the strengths of the antagonistic, mutualistic and facilitative interactions among the seagrasses, green turtles and coralline algae in this tropical marine system. We question how the dense rhodolith bed came into existence, and how it could expand so fast, initiating the mutualism between the coralline algae and seagrasses that prevented the collapse of the seagrass meadow. We hypothesized that (1) the canopy of ungrazed seagrasses inhibits or reduces growth of the rhodoliths and geniculate coralline algae, and (2) a positive feedback explained the population explosion of the coralline algae, specifically, we hypothesized that the dense rhodolith bed may prevent sediment resuspension.

## MATERIAL AND METHODS

### Study Site

The study site was the north of Akumal Bay ( $20^{\circ}23'44.9'' \text{ N}$ ,  $87^{\circ}18'47.9'' \text{ W}$ ). It is a tropical small embayment protected by a fringing reef at 100–300 m from the coast. Akumal Bay is a popular tourist destination, particularly for snorkeling and turtle watching. Tourist demand and the consequent growth of coastal infrastructure have contributed to increase nutrient input by contaminated groundwater and, thus, the eutrophication of the system (Mutchler and others 2007; Baker and others 2010; Gil and others 2015; Hernández-Terrones and others 2015). In this bay, tidal regime is microtidal, semi-diurnal, with a mean tidal range of  $\sim 0.14 \text{ m}$ , and spring and neap tidal ranges of 0.3 and 0.08 m, respectively. Significant wave height in the reef-protected bay is  $\sim 0.2 \text{ m}$  ( $\pm \sim 0.03 \text{ m}$ ) and varies little between summer and winter (Osorio-Cano and others 2019). The seagrass meadow in the lagoon covers  $\sim 4\text{--}5 \text{ ha}$  in total and consists of *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme* with intermixed macroalgae typified by calcareous Chlorophytes and Rhodophytes, at 1.5 to 2.5 m depth (Lacey and others 2014; Molina-Hernández and van Tussenbroek 2014; Table 1). Seagrass meadows in Akumal Bay have been intensively grazed by a population of resident and visiting green turtles at least since 2007 (SEMARNAT 2015), shifting from a rotational grazing to a random grazing strategy (Molina-Hernández and van Tussenbroek 2014). Continuous grazing pressure by a (mainly) juvenile partially

**Table 1.** Mean Values ( $\pm$  SE,  $N = 4$ ) of Characteristics of Seagrasses in the Areas with and without Rhodoliths (Grazed by Turtles) at Akumal, from Core Samples (11.2 cm Diameter  $\sim$  30 cm Deep) Collected in October 2015, Processed following Molina-Hernández and van Tussenbroek (2014); Leemans and others (2020)

	<i>Thalassia testudinum</i>		<i>Syringodium filiforme</i>		<i>Halodule wrightii</i>	
	Inside rhodolith bed	Outside rhodolith bed	Inside rhodolith bed	Outside rhodolith bed	Inside rhodolith bed	Outside rhodolith bed
Length green leaf (cm)	11.0 $\pm$ 1.2	3.2 $\pm$ 0.3	13.3 $\pm$ 1.6	5.0 $\pm$ 0.4	8.2 $\pm$ 0.6	5.9 $\pm$ 0.4
Width green leaf (mm)	9.7 $\pm$ 0.6	5.5 $\pm$ 0.3	nd	nd	nd	nd
Shoot density (No. m <sup>-2</sup> )	659 $\pm$ 410	304 $\pm$ 110	355 $\pm$ 418	456 $\pm$ 88	330 $\pm$ 401	7790 $\pm$ 804
AG biomass (g m <sup>-2</sup> )	37.2 $\pm$ 13.3	1.9 $\pm$ 0.6	3.2 $\pm$ 1.9	0.9 $\pm$ 0.8	1.3 $\pm$ 0.9	6.1 $\pm$ 0.5
% AG/total biomass	12.5 $\pm$ 1.1	3.0 $\pm$ 0.3	12.0 $\pm$ 0.7	6.0 $\pm$ 0.8	7.3 $\pm$ 2.3	4.4 $\pm$ 0.4

*Dimensions were of the second newest leaf on a foliar shoot. nd not determined, AG above ground (green leaf sections).*

resident population of > 100 green turtles (Labrada-Martagón and others 2017) on the slow-growing climax seagrass *T. testudinum* caused a sharp decline of this species in 2012, causing it to become replaced then by the more grazing tolerant fast-growing species *H. wrightii* (Molina-Hernández and van Tussenbroek 2014). Under the continuity of these circumstances, a possible collapse of the seagrass system was expected, as has been reported for seagrass meadows under turtle overgrazing pressure (Christianen and others 2014); however, since 2014, *T. testudinum* recovered unexpectedly, increasing in biomass, shoot density and leaf size, simultaneously with a notorious increase in red coralline algae (*Neogoniolithon* sp. and *Amphiroa* sp.) forming a dense rhodolith bed.

### Expansion of the Rhodolith Bed

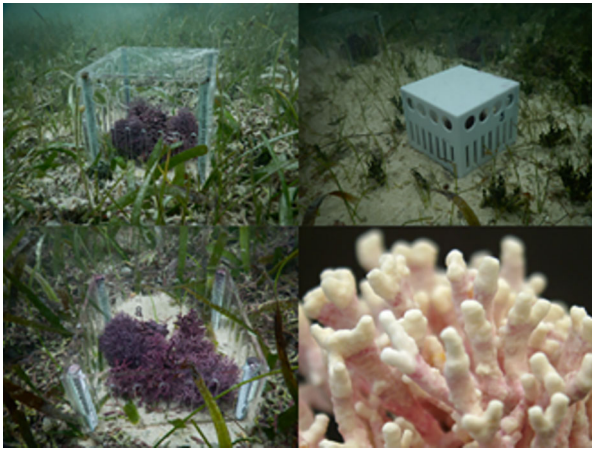
Spatio-temporal changes of the rhodolith bed were determined through analysis of a total of six satellite images from Planet Platform, Rapid Eye constellation. The satellite data from June 2009, February 2010, February 2012, February 2014, January 2015 and October 2016 consisted of 16-bit radiometric resolution with 5 bands: red (630–685 nm), green (520–590 nm), blue (440–510 nm), red edge (690–730 nm), and near infrared (760–850 nm), with a spatial resolution of 5  $\times$  5 m. SNAP software from the European Space Agency (ESA) was used for preprocessing, which consisted of masking the area of interest, sun glint correction, and water column correction using the depth invariant index (DII). A supervised classification

was performed in ENVI 5.3 software using red, green, blue and DII bands and the maximum likelihood algorithm (MLC). The cover of the benthic vegetation used to train the supervised classification was from three line transects set up in the area of interest in January 2016 (Banaszak and others 2016). By autonomous diving, 250 m long transects were placed at a direction of  $\sim$  140–180° to the coastline, with 100 and 200 m between transects, and each start and end point of the transects was georeferenced by GPS. Tape measures were placed over the bottom to mark the transects, and video and photographic recordings of the benthic vegetation were made.

### Experiment 1: Do Abundant Seagrasses Inhibit the Growth of Coralline Algae?

Samples of *Neogoniolithon* sp. and *Amphiroa* sp. were collected from the rhodolith bed and placed in large flat plastic trays filled with fresh seawater with a concentration of 20 mg/L Alizarin Red-S and containing an air pump. Alizarin Red-S is incorporated in the calcareous skeleton of the algae when they photosynthesize during the day. After one day almost all the pigment had been absorbed by the algae and the procedure was repeated. On the third day, the stained algae were placed in small areas (15  $\times$  15 cm) in the rhodolith bed, where the coralline algae were previously removed, and where seagrasses were absent or in low abundance (up to 3 foliar shoots of *S. filiforme* or *H. wrightii*). To mimic seagrass effects, stained algae were placed in groups of 8 (4 medium-sized individuals of each





**Figure 1.** Coralline algae growth experiment. **A** Reduction of wave movement WR, **B** reduction of wave movement and sunlight WR + LR, and **C** control, **D** *Neogoniolithon* sp. stained with Alizarin Red-S, after 10 weeks of growth; white tips are newly formed sections.

species), and each group was covered by 1 of 3 types of open-bottom acrylic boxes ( $15 \times 15 \times 15$  cm) anchored to the sediment (Figure 1). Boxes had slits and holes in the sides, designed to annihilate water movement by waves and currents, but still allowing for gas exchange with surrounding water. The first type of box was transparent, reducing total average water flow by 85% (WR; Supporting material), the second was opaque (white acrylic), partly blocking sunlight in addition to reducing water movement (WR + LR). Light reduction boxes attenuated photosynthetically active radiation (PAR, 400–700 nm) by 60% (measured with an Odyssey Photosynthetic Active Radiation Logger), which was within the light reduction range by *Thalassia testudinum* canopies in the region reported by Enríquez and Pantoja-Reyes (2005). Finally, the control treatment (C) consisted of open and transparent boxes ( $15 \times 15 \times 6$  cm height). Each treatment had 15 replicates; thus, in total 45 boxes were placed haphazardly in the field. Experiment maintenance consisted of cleaning the tops of boxes of the first and second treatment approximately every 4 days with a soft sponge to remove fouling epibiota.

The algae were positioned in the field in August 2015 and collected 69 days later in November 2015, after which they were placed in a 7.5% sodium hypochlorite (Clorox) solution for 120 min, that bleached the algae and revealed the Alizarin Red-S-stained calcareous skeleton (Figure 1d). After bleaching, the thalli were washed 3 times with water to remove all hypochlorite and dried.

All algae from the same box were fragmented by hand and mixed, and 120 branches per species were selected haphazardly to measure the length of the new growth section (length growth tip in mm) of the ramification (obvious as a white section above the stained part) with a dial caliper (precision 0.02 mm). The new growth from 11 dyed *Neogoniolithon* sp. individuals of the control treatment was separated from the old tissue with sharp pliers, and both old and new tissue were weighed to determine relative growth rate (RGR); for *Amphiroa* sp. samples, RGR was not calculated because separating new from old growth was not possible.

### Experiment 2: Do Coralline Algae Benefit from Dense Aggregations?

To test whether coralline algae in dense aggregations have lower mortality as compared to areas with few coralline algae, so to establish whether positive feedback may occur, we collected coralline algae (*Neogoniolithon* sp. and *Amphiroa* sp.) from the rhodolith bed using six  $15 \times 15$  cm quadrats. The samples were divided in two equal parts and placed in numbered bags. One half of these samples was placed in  $15 \times 15$  cm boxes (as those in control treatment of experiment 1) and positioned within the rhodolith bed, while the second half was placed in  $15 \times 15$  cm boxes in a nearby area without coralline algae (sparsely covered by grazed *Thalassia testudinum* and *Halodule wrightii*). The specimens in equal halves of the samples were assumed to have the same proportional dead to live tissue. The algae were retrieved after 15 days and placed in numbered Ziploc bags for transport. In the laboratory, samples were separated in three morphospecies: (1) compact hemispherical clumps *Neogoniolithon* sp. without branches, (2) branching *Neogoniolithon* sp., and (3) branching geniculate *Amphiroa* sp. The proportion of white tissue (dead) respect to all tissue (live pink + dead white tissue) was determined visually on the hemispherical clumps *Neogoniolithon* sp., branching *Neogoniolithon* sp. and branching geniculate *Amphiroa* sp. were broken, and branch sections were separated in white (dead) or pink (alive). All samples were dried for 48 h in a drying oven at 60 °C. Dry weights and the proportion of live tissue per each morphospecies were determined.

### Experiment 3: Mechanism of Positive Feedbacks in Rhodolith Beds: Reduced Sediment Resuspension

To test whether dense and bed forming aggregations of coralline algae reduce resuspension as compared to small patches ( $1 \text{ m}^{-2}$ ) of coralline algae in sparsely grazed *Thalassia testudinum* and *Halodule wrightii*, we established twenty  $1 \times 1 \text{ m}$  plots in two different conditions in September 2015. The first condition consisted in ten plots haphazardly established within the sparse and grazed seagrass section and outside the rhodolith bed. Within the  $1 \times 1$  plots, coralline algae of both species ( $\sim 95\%$  *Neogoniolithon* sp. and  $\sim 5\%$  *Amphiroa* sp.) were placed manually until reaching a  $\sim 5 \text{ cm}$  thick layer of algae, which was the average thickness of the rhodolith bed. For the second condition, which served as control, the remaining ten plots were placed within the well-developed rhodolith bed (3–6.8 cm thick layer), and where *T. testudinum* was also grazed (see Lee-mans and others 2020 for further details). Within each plot, two 5 ml Eppendorf tubes (sediment traps; Johnson and others 2019) were placed on small stakes considering the upper level of the tubes to be  $\sim 7 \text{ cm}$  above the sea floor. After 14 days, Eppendorf tubes were retrieved in order to determine sediment dry weight within them. Laboratory processing consisted of placing Eppendorf tubes in a drying oven to determine their dry weight with sediment, to later remove the sediment and repeat the procedure to determine the weight of the Eppendorf tubes.

### Statistical Analysis

Data were analyzed with R (v. 3.6, R Development Core Team 2017) and Statistica (8.0 StatSoft Power Solutions, Inc.). Mean  $\pm$  standard deviation (SD) was used to show the variability of parameters in this study. For experiment 1, when  $N$  is given for nested data, it refers to the number of boxes per treatment not to the total number of tip length measurements ( $n$ ). When SD is given for nested data, it is of subject means. To compare treatments with nested and random factors a generalized linear mixed model (hereafter GLMM) was used, followed by a pairwise comparisons. A GLM two-way ANOVA was used for experiment 2 to test differences in the proportion of live tissue per coralline algal morphotype (*Neogoniolithon* sp. in its hemispherical clumps or branched type, and *Amphiroa* sp.), and per condition (inside a rhodolith bed or outside). For data of experiment 3, a two-sample  $t$ -

test was performed to determined differences in sediment dry weight in sediment traps (Eppendorf tubes) inside a rhodolith bed or outside the coral-line algae aggregation. The data for each plot (gr of dry sediment per tube) were pooled to obtain one datum per plot. Assumptions of normality were tested through Shapiro–Wilk normality test, and Levene test was performed to test equal variance. Probable outliers were identified with Dixon’s  $Q$ -test (CL = 95%) and removed due to suspected procedural errors. Two C, one WR and four WR + LR replicates were excluded for *Neogoniolithon* sp. GLMM analysis; three C, one WR and four WR + LR boxes were excluded for *Amphiroa* sp. GLMM analysis. Length growth (mm) data were log transformed (experiment 1), and a BoxCox transformation was performed to sediment dry weight (gr) because of differences in variance between groups (experiment 3).

## RESULTS

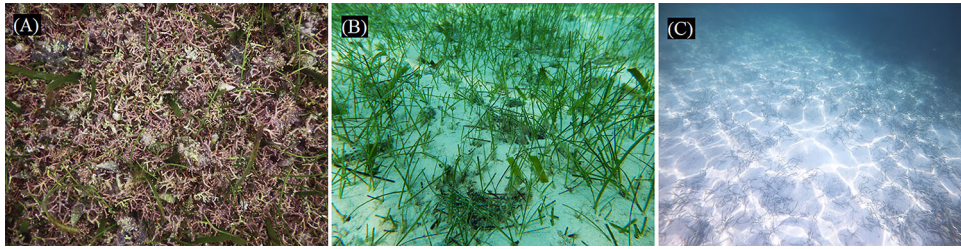
### Expansion of the Rhodolith Bed

Satellite imagery and in situ verification of the benthic cover discerned three classes classified as: 1. rhodolith bed, consisting of a dense (usually 100%) cover of coralline algae (*Neogoniolithon* sp. and *Amphiroa* sp.) with or without sparse seagrasses; 2. seagrass meadow, usually consisting of sparse mixed vegetation dominated by *Halodule wrightii* and in low densities *Thalassia testudinum* and *Syringodium filiforme*; and 3. sand areas with  $< 30\%$  vegetation cover (Figure 2).

In 2009, no rhodolith bed was detected by satellite imagery. In 2011, the abundance of the coralline algae increased and a small ( $\sim 900 \text{ m}^2$ ) rhodolith patch was visible in the center of the bay surrounded by a heavily grazed seagrass meadow, as was identified during field surveys (see also Molina-Hernandez and van Tussenbroek 2014). The rhodolith bed increased rapidly in size to  $2367 \text{ m}^2$  in 2014 (Figure 3), and to  $6025 \text{ m}^2$  in 2015. The population growth rate leveled off from 2015 until 2016 when it covered an area of  $6934 \text{ m}^2$  (Figure 3).

### Experiment 1: Do Abundant Seagrasses Inhibit the Growth of Coralline Algae?

The applied treatments (combination of reduction in light and wave movement) had a significant effect on growth for both *Neogoniolithon* sp. (GLMM:  $F_{(2,35)} = 8.9$ ,  $p < 0.001$ ), and *Amphiroa* sp. ( $F_{(2,34)} = 29.2$ ,  $p < 0.001$ ). Light reduction affected



**Figure 2.** Benthic cover classes: **A** Rhodolith bed; here with foliar shoots of the seagrass *Thalassia testudinum*; **B** seagrass meadow; here with dominance of *Halodule wrightii* and low densities of *T. testudinum* and *Syringodium filiforme*; and **C** sand areas with < 30% of vegetation cover.

growth tissue more than wave reduction (Figure 4). While wave reduction (WR treatment) only slowed down *Amphiroa* sp. growth (13%), additional light reduction (WR + LR treatment) slowed down the growth of both *Amphiroa* sp. (41%) and *Neogoniolithon* sp. (27%). Mean increase in tip length during the study period was approx.  $1.80 \pm 0.13$  (mean  $\pm$  SD) mm for *Neogoniolithon* sp. and  $2.92 \pm 0.14$  mm for *Amphiroa* sp., corresponding with  $9.52$  and  $15.45$  mm tip  $y^{-1}$  for *Neogoniolithon* sp. and *Amphiroa* sp., respectively. In the control treatment (C), the dominant *Neogoniolithon* sp. increased  $10.3\% \pm 5.5$  from its live initial biomass (pink photosynthesizing sections of the thalli) in 10 weeks.

### Experiment 2: Do Coralline Algae Benefit from Dense Aggregations?

Coralline algae inside the rhodolith bed had significantly lower tissue mortality than the algae placed outside the rhodolith bed (GLM two-way ANOVA  $F_{(1,30)} = 23.8$   $p < 0.001$ ). Differences between morphospecies and the interaction of treatment and morphospecies were not significant (Table 2); however, *Amphiroa* sp. had higher proportion of live tissue than *Neogoniolithon* sp. in both conditions (Figure 5).

### Experiment 3: Mechanism of Positive Feedbacks in Rhodolith Beds: Reduced Resuspension?

After 14 days of the experiment, significant differences ( $t_{16} = -7.0$   $p < 0.001$ ) were found between the sediment accumulated in the Eppendorf tubes of the two conditions. The tubes placed in the plots within the sparse and grazed seagrass meadow (and where the coralline algae were deposited manually) had significantly more sediment (mean  $\pm$  SD =  $0.2091 \pm 0.1017$  dry g), in comparison with the sediment accumulated in the tubes placed in the plots where the rhodolith bed

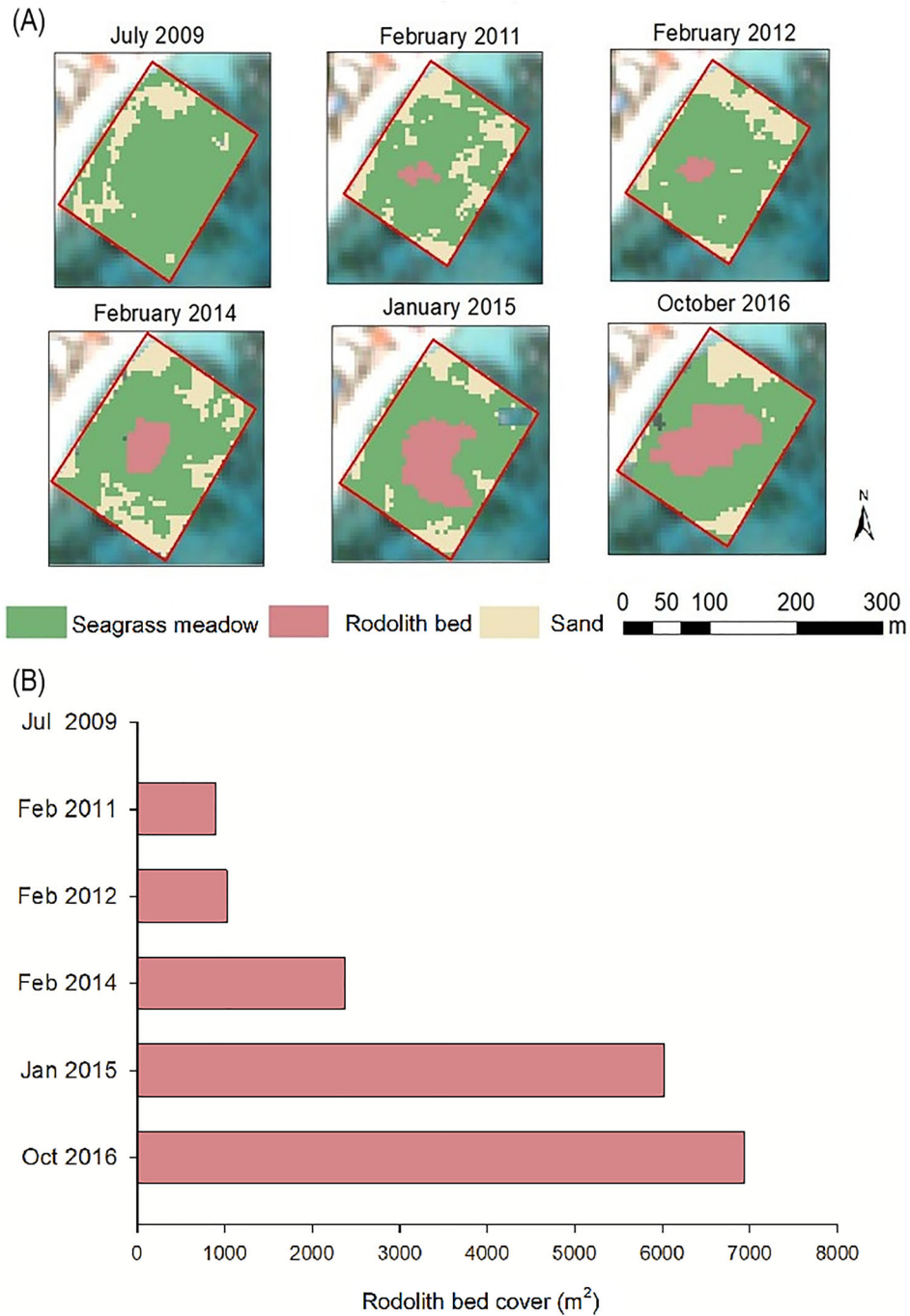
was naturally present (mean  $\pm$  SD =  $0.05 \pm 0.02$  dry g).

## DISCUSSION

### Population Explosion of Coralline Algae

The grazing-protection mutualism between seagrasses and coralline algae in the study area came into existence under a co-occurrence of increasing grazing pressure and rapid areal expansion of the rhodolith bed. The rapid increase in the coralline algae was likely forced by a combined effect of the improved light climate after grazing of the canopy by the green turtles, and a positive feedback leading to a decrease in sediment resuspension and lower mortality of the coralline algae once they reached a critical density. In 2009, when turtle grazing on the seagrass was still moderate, the coralline algae were sparse, and individual thalli occurred mostly scattered at the edges of the seagrass meadow, forming no detectable rhodolith bed. From 2010 to 2011 until 2015, the coralline algae formed a dense aggregation of  $6025$  m<sup>2</sup> with a 3.0–6.8 cm thick layer (with average calcified biomass of  $5.6$  dry kg m<sup>-2</sup>, 95% accounted for by *Neogoniolithon* sp.; Leemans and others 2020). In this rhodolith bed, the dominant species, *Neogoniolithon* sp., increased  $10.3\% (\pm 5.5\%)$  with respect of its live initial biomass (pink photosynthesizing sections of the thalli) in 10 weeks, which corresponds with a relative growth rate (RGR) of  $0.14$  (% d<sup>-1</sup>), implying that the algae doubled their size in 495d ( $\sim 1$  y and 4 months), as the old calcareous skeletons remained mostly intact. This RGR explains the rate of size increase in the rhodolith bed ( $0.14\%$  d<sup>-1</sup> from 2011 until 2015, when the size increased from  $900$  to  $6025$  m<sup>2</sup> in 4 y). This increase in rhodolith bed size corresponds with an annual production of  $3512$  g CaCO<sub>3</sub> m<sup>-2</sup>, as 94.3% of the biomass is calcium carbonate (Vázquez-Elizondo and Enriquez 2017), which is more than four times the annual production of  $815$  g CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> for





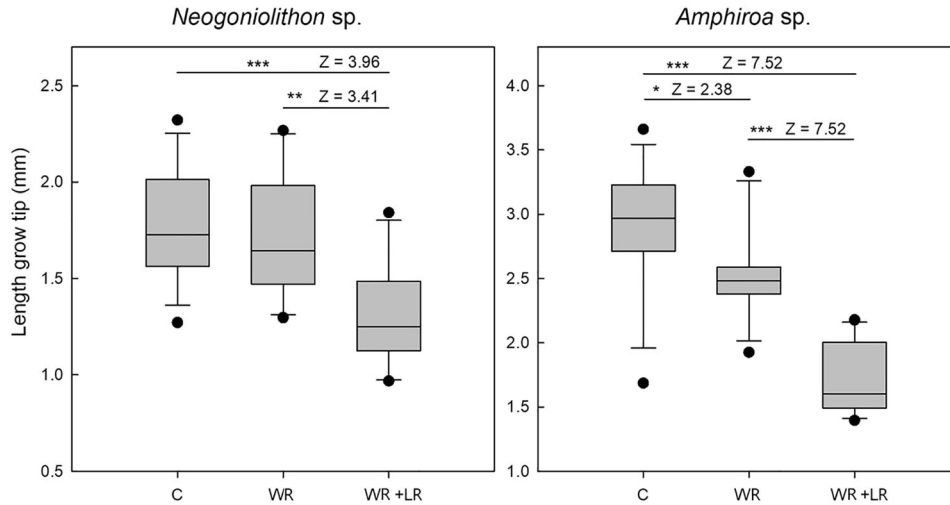
**Figure 3.** Development of rhodolith bed, detected by satellite imagery over 7-year period in the North section of Akumal Bay. **A** Image series of benthic classes (see Results). **B** Cover of the satellite detected rhodolith bed from 2009 to 2016.

another important calcifying algae in tropical reef systems, *Halimeda incrassata*, in a Caribbean seagrass meadow found by Van Tussenbroek and Van Dijk (2007). The expansion of the rhodolith bed leveled off in 2016 (Per. Obs.), as in certain places near the edges of the rhodolith bed the absence of grazing appeared to result in *T. testudinum* achieving densities sufficiently high to shade the coralline

algae, inhibiting further expansion. Alternatively, intermittent green turtle grazing on *T. testudinum* and consequential shading of the coralline algae may result in a stable coralline algal turnover, stabilizing the size of the rhodolith bed.

The mean growth rates of the coralline algae in this study at 9.5 (*Neogoniolithon* sp.) and 15.5 (*Amphiroa* sp.) mm tip  $y^{-1}$  are in the high range,





**Figure 4.** Box plot of mean length growth after 69 d, in the tips of *Neogoniolithon* sp. and *Amphiroa* sp. after treatment (Experiment 1: C control, WR wave reduction, WR + LR wave and light reduction). Mean  $\pm$  standard deviation (SD). Lines over bars indicate which groups significantly differ. Asterisks indicate significance level of the difference between treatments (\* < .001).

**Table 2.** Results of GLM Two-Way ANOVA on the Proportion of Live Tissue of Coralline Morphospecies (Compact Hemispherical Clumps *Neogoniolithon* sp. Without Branches, Branching *Neogoniolithon* sp., and Branching Geniculate *Amphiroa* sp.) Inside or Outside the Rhodolith Bed (Treatment).

Effect	df	SS	MS	F	p
Treatment	1	0.29167	0.29167	23.789	<b>0.000033</b>
Coralline morphospecies	2	0.07298	0.03649	2.976	0.066199
Treatment*coralline morphospecies	2	0.00902	0.00451	0.368	0.695242
Error	30	0.36782	0.01226		

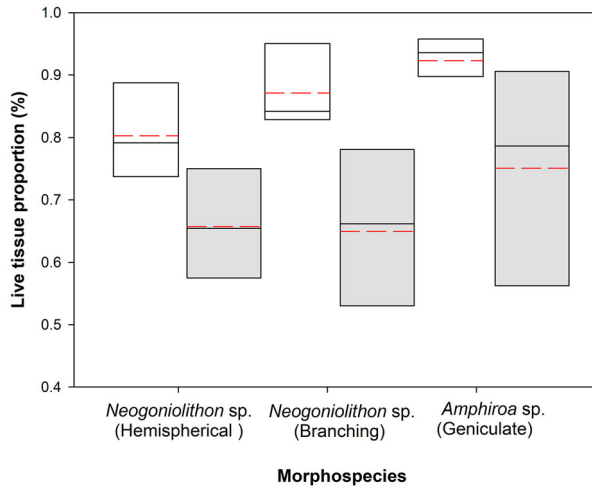
Significantly different at  $\alpha = 0.05$  (in bold type).

compared with rhodoliths elsewhere. Steller and others (2007) reported a growth rate (mean  $\pm$  SD) of  $5.02 \pm 1.16$  mm tip  $y^{-1}$  for *Lithophyllum margaritae* (summer season) in the south of the Gulf of California, while Caragnano and others (2016) reported growth rates ranging from  $8.74$  mm  $y^{-1}$  for *Lithophyllum kotschyannum*,  $13.92$  mm  $y^{-1}$  for *Porolithon onkodes*, and  $9.25$  mm  $y^{-1}$  for *Neogoniolithon* sp in the Red Sea. The high growth rates values in this study may be attributed to the shallow depth (2–3 m), as often rhodoliths are found at greater depths > 5 m where light may be limiting growth (Foster 2001).

High nutrient input in Akumal bay may also help to explain the fast growth of the coralline algae, although increasing eutrophication is not a suspected cause of the timing of the observed coralline algae population increase, as nutrient levels in Akumal have been high for at least 15 years (Mutchler and others 2007; Baker and others 2010;

Hernández-Terrones and others 2015). In addition, in typically oligotrophic systems, eutrophication initially results in an increase in foliar biomass of the seagrasses, and thereby potentially shading the coralline algae (Cortés and others 2019).

*Neogoniolithon* sp. and *Amphiroa* sp. in the Mexican Caribbean were reported with relatively high minimum photosynthetic requirements, but these species are equipped with optical attributes, such as a thick light-scattering  $CaCO_3$  skeleton (*Neogoniolithon* sp.) or delicate highly ramified thalli (*Amphiroa* sp.), which aid in effective absorption of light. In our study, *Neogoniolithon* sp. was affected by reduction in light and wave (WR + LR), which caused 27% growth reduction when compared with only wave reduction (WR) and control treatment (C); *Amphiroa* sp. was affected by wave reduction (13% decrease in growth compared to control) and combined wave and light reduction decreased growth by 41%. The levels of light



**Figure 5.** Box plots of live tissue proportion (%) in the three coralline algae morphotypes inside (white boxes) and outside (gray boxes) the rhodolith bed after 15 d (Experiment 2). Red dashed lines denote mean values, and black solid lines represent median values.

reduction in this study were in the same order of magnitude as the light reduction by seagrass canopies; thus, shading by seagrass canopy likely reduces the growth rates of the coralline algae. Reductions in growth rate may prevent the formation of dense coralline algal aggregations; however, seagrasses are also beneficial to coralline algae (see also Harvey and others 2017) as their canopies relieve hydrodynamic stress by attenuating currents and waves (van der Heide and others 2011), and their rhizomes improve sediment stabilization even when the meadows are under intensive grazing (high turtle density) or a rotational grazing regime (Christianen and others 2013; Johnson and others 2019), which favors coralline algae that are highly susceptible to sedimentation (Riosmena-Rodríguez and others 2017). Also, seagrasses, either grazed or not, prevent coralline algae from being flushed away (Leemans and others 2020). We expected an effect of wave movement reduction on the algae, as Riosmena-Rodríguez and others (2017) reported that occasional rotation of the thalli is necessary to prevent sedimentation and to allow light to reach all surfaces of the thalli, although excessively strong water motion may break thalli preventing rhodoliths from forming (Case Marrak 1997). In the rhodolith bed, *Neogoniolithon* sp. was not affected by reduction of wave movement (WR) alone, and *Amphiroa* sp. only slightly; possibly because sedimentation rates were already lower in the rhodolith bed.

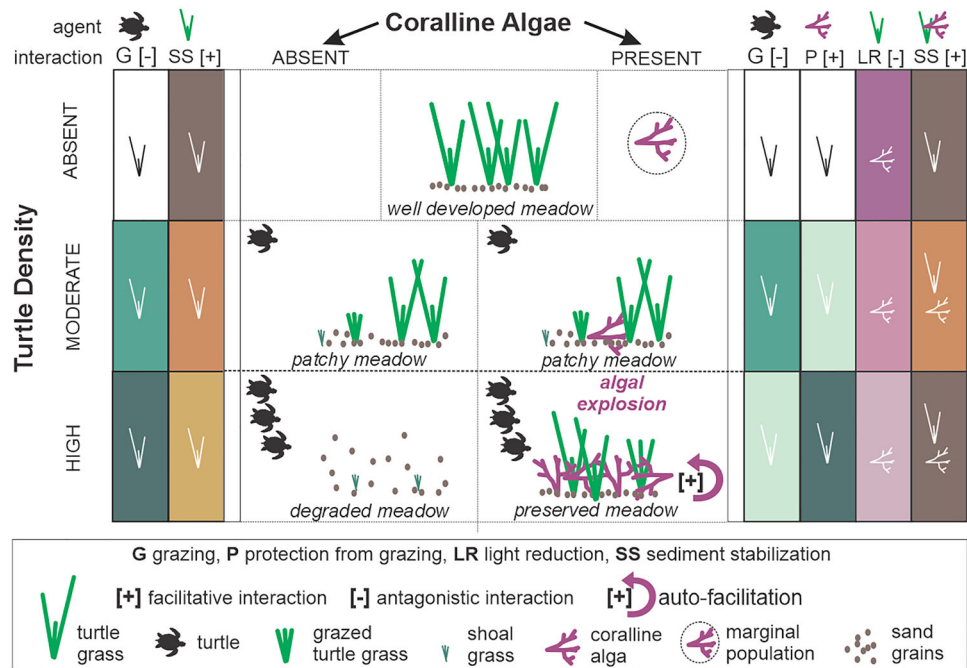
Positive (“amplifying”) and negative (usually “stabilizing”) feedbacks are an integral part of

natural systems and may involve biological, physical and chemical processes (Nyström and others 2012; Kéfi and others 2016). Positive feedback mechanisms often emerge in cases in which organisms significantly modify their environment, thereby facilitating their own optimal development. Such mechanisms typically cause a complex, nonlinear response of ecosystems to changes in their environment (van der Heide and others 2011). Through positive feedbacks, many foundation species like reef-forming corals, giant kelps, seagrasses and bed-forming coralline algae can make an originally stressful or almost inhospitable habitat more suitable not only for them, but also for other species (Kéfi and others 2016). We demonstrated that even 1 m<sup>2</sup> plots with a ≥ 5 cm thick layer of coralline algae had higher sediment resuspension rates than those inside the rhodolith bed, it is likely that larger sized beds are needed to sustain this positive feedback through reduction of sediment load on the coralline algae. During field inspections, we observed that the coralline algae at the edges of the 1 × 1 m<sup>2</sup> plots in the sparse seagrass bed were gradually buried by the surrounding fine sediments, which is known to induce mortality of coralline algae (Melbourne and others 2018). We found that coralline algae within the rhodolith bed had significantly lower mortality than those placed manually in the sparse seagrass meadow, supporting our hypothesis that through self-facilitation, coralline algae improved seabed stabilization, thereby reducing resuspension and creating a self-sustaining positive feedback with consequential population explosion.

## Conditional Outcomes

Bronstein (1994) predicted that mutualistic interactions are likely more dynamic if the relationships 1) are facultative, 2) involve a third species, and 3) are density-dependent. All three conditions were present in our studied system. The mutualistic interaction between turtle grass *Thalassia testudinum* and coralline algae, in which the coralline algae protect the seagrass from grazing and the seagrass allows for aggregation of the algae through prevention of excessive sediment resuspension or being removed by waves, is facultative; both the turtle grass and coralline algae occur without the other in a wide range of biotic and abiotic conditions.

The third species involved is the green turtle *Chelonia mydas*; and the mutualism between the turtle grass and coralline algae occurs only when a dense seagrass canopy is cropped continuously by



**Figure 6.** Conditional outcomes of the state of the seagrass meadow, with or without coralline algae, with different green turtle densities. Darker colors of the lateral columns indicate stronger interactions: the symbols in the cells of the column indicate the component affected by the interactive process. When turtle densities are low or moderate, the state of the seagrass meadow is the same with or without coralline algae. When turtle density is high and coralline algae are absent, the seagrasses are overgrazed, and the system degrades or collapses. When the coralline algae are present, continuous cropping will decrease shading by the seagrass canopy, allowing for faster algal growth, resulting in a coralline algal population explosion due to positive feedback through reduction of sediment resuspension, which results in a mutualistic steady state in which coralline algae protect the seagrasses from overgrazing by turtles, although moderate grazing by turtles may continue.

the turtles as a result of an increase in turtle density. When the density of the turtles in Akumal Bay increased to such a level that they recurred to prolonged grazing, then the canopy was reduced for sufficient time allowing for a significant increase in the coralline algae density. At this level, turtle monitoring efforts in Akumal Bay reported between ~ 70 and ~ 90 different turtles during a sensing period of various months (in unpublished reports by park managers, NGOs, and so on), and Labrada-Martagón and others (2017) captured (and recaptured) 166 turtles over a period of 10 y in the bay. And once the coralline algae had formed a dense rhodolith bed, the protection from turtle grazing became effective (Leemans and others 2020).

When coexisting, turtle grass, coralline algae, and sea turtles are connected through multiple interactive mechanisms (Figure 6). From our results, we postulate that incidentally present coralline algae start to expand when grazing of the seagrass canopy leads to a better light climate (this study). This leads to vigorous expansion of the rhodolith bed, likely

due to a combination of self-facilitation (positive feedback resulting from reduced resuspension, this study) and facilitation by seagrass to not be flushed away by water movement (Leemans and others 2020). But the grazing protection may eventually lead to seagrass recovery and thus shading by the canopy; in other words, this interaction may become progressively more antagonistic for the coralline algae. Such interactive feedbacks may present boom and bust situations (van der Heide and others 2007; Kéfi and others 2016); but the seagrasses do not entirely inhibit the growth of the coralline algae, and the turtles continued to crop the upper parts of the foliar shoots that emerged from the rhodolith bed (Leemans and others 2020), which may aid in maintaining the coralline-seagrass-turtle coexistence.

### CONCLUDING PARAGRAPH

Akumal Bay is quite unique (Mexican Caribbean), as in that the seagrass meadow, only ~ 4.5 ha large hectares, sustains a relatively large persistent

(mainly juvenile) turtle population, and has been registered eutrophication at least since 2008 (Baker and others 2010). Most seagrass meadows in the Mexican Caribbean are more extensive (for example, Guimaraes and others 2021), where the turtles adopt a rotational grazing regime (Molina Hernandez and van Tussenbroek 2014; Martínez Lopez and others 2019). Seagrasses and coralline algae coexist in many places without the formation of a rhodolith bed; likely a unique combination of factors is necessary for such a formation to come into existence. Usually, environments that allow for fast coralline algae growth in seagrass meadows, such as low sedimentation, sufficient light and moderate nutrient availability, also favor dense seagrass canopies. Only the presence of a third agent such as sea turtles, exerting excessive grazing pressure, may allow for coralline algal proliferation in such a system. In the last decades, green turtle densities have been increasing and their increasing impacts on seagrass meadows worldwide is becoming more notorious (Christianen and others 2021); therefore, we expect that systems with coralline algal explosions, such as that seen to occur in Akumal, may become more common in the near future.

#### ACKNOWLEDGEMENTS

We thank Maria Guadalupe Barba Santos for supporting this study in the field and laboratory. We are grateful to Edgar Escalante Mancera and Miguel Ángel Gómez Reali who helped with the calculation of water movement reduction of the acrylic boxes used in Experiment 1. Isis Gabriela Martínez López received PhD fellowship support from The Mexican Consejo Nacional de Ciencia y Tecnología (CONACyT), the part of the work was financed by SEMARNAT (PROCER/CCER/DRPYCM/02/2016). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

#### FUNDING

The funding was provided by Secretaría de Medio Ambiente y Recursos Naturales, PROCER/CCER/DRPYCM/02/2016.

#### DATA AVAILABILITY

<https://doi.org/10.17026/dans-25z-w37w>

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#### REFERENCES

- Adams Mp, Hovey RK, Bruce LC, Ghisalberti M, Lowe RJ, Gruber RK, Ruíz-Montoya L, Maxwell PS, Callaghan DP, Kendrick GA, O'Brien KR. 2016. Feedback between sediment and light for seagrass: Where is it important? *Limnology and Oceanography*. 61:1937–1955. <https://doi.org/10.1002/lno.10319>
- Baker DM, Jordán-Dahlgren E, Maldonado MA, Harvell CD. 2010. Sea fan corals provide a stable isotope baseline for assessing sewage pollution in the Mexican Caribbean. *Limnology and Oceanography*. 55:2139–2149. <https://doi.org/10.4319/lo.2010.55.5.2139>.
- Banaszak AT, BI van Tussenbroek, AC Claudia Padilla Sosa. 2016. Determinación del estado de conservación y caracterización de los ecosistemas en los dos principales polígonos de observación y nado con tortuga en el refugio para la protección de especies-bahía Akumal. Informe final de Programa de Conservación de especies en Riesgo (PROCER), ejercicio fiscal 2016. Financiado por SEMARNAT (PROCER/CCER/DRPYCM/02/2016).
- Baraza E, Zamora R, Hódar JA, Gómez JM. 2007. Plant–herbivore interaction: beyond a binary vision. <https://doi.org/10.1201/9781420007626-16>
- Bronstein JL. 1994. Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution*. 9(6):214–217. [https://doi.org/10.1016/0169-5347\(94\)90246-1](https://doi.org/10.1016/0169-5347(94)90246-1).
- Callaway RM. 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia*. 112:143–149. <https://doi.org/10.1007/s004420050293>.
- Caragnano, A., D. Basso y G. Rodondi. 2016. Growth rates and ecology of coralline rhodoliths from the Ras Ghamila back reef lagoon, Red Sea. *Marine Ecology*. 37:(4):713–726. <https://doi.org/10.1111/maec.12371>
- Case Marrak E. 1997. The relationship between water motion and rhodolith movement in the Southwestern Gulf of California, Mexico. Moss Landing Marine Laboratories.
- Christianen MJA, van Belzen J, Herman PMJ, van Katwijk MM, Lamers LPM, van Leent PJM, Bouma TJ. 2013. Low-canopy seagrass beds still provide important coastal protection services. *PLoS ONE*. 8(5):e62413. <https://doi.org/10.1371/journal.pone.0062413>.
- Christianen MJA, Herman PMJ, Bouma TJ, Lamers LPM, van Katwijk MM, van der Heide T, Mumby PJ, Silliman BR, Engelhard S, van de Kerk M, Kiswara W, van de Koppel J.



2014. Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. *Proceedings of the Royal Society B* 281:20132890. <https://doi.org/10.1098/rspb.2013.2890>.
- Christianen MJA, van Katwijk MM, van Tussenbroek BI, Pagès JF, Ballorain K, Kelkar N, Arthur R, Alcoverro T. 2021. A dynamic view of seagrass meadows in the wake of successful green turtle conservation. *Nature Ecology & Evolution*. 5:553–555. <https://doi.org/10.1038/s41559-021-01433-z>.
- Cortés J, Oxenford HA, van Tussenbroek BI, Jordán-Dahlgren E, Cróquer A, Bastidas C, Ogden JC. 2019. The CARICOMP network of Caribbean Marine laboratories (1985–2007): history, key findings, and lessons learned. *Frontiers in Marine Science*. 5:519. <https://doi.org/10.3389/fmars.2018.00519>.
- Davis BC, Fourqurean JW. 2001. Competition between the tropical alga *Halimeda incrassata* and the seagrass, *Thalassia testudinum*. *Aquatic Botany*. 71:2017–2232. [https://doi.org/10.1016/S0304-3770\(01\)00179-6](https://doi.org/10.1016/S0304-3770(01)00179-6).
- Dutertre M, Grall J, Ehrhold A, Hamon D. 2015. Environmental factors affecting maerl bed structure in Brittany (France). *European Journal of Phycology*. 50(4):371–383. <https://doi.org/10.1080/09670262.2015.1063698>.
- Enríquez S, Pantoja-Reyes NI. 2005. Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass *Thalassia testudinum*. *Oecologia* 145:235–243. <http://doi.org/10.1007/s00442-005-0111-7>.
- Esteban N, Mortimer JA, Stokes HJ, Laloë JO, Unsworth RKF, Hays GC. 2020. A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels. *Marine Biology*. 167–183. <https://doi.org/10.1007/s00227-020-03786-8>.
- Foster MS. 2001. Rhodoliths: between rocks and soft places. *Journal of Phycology*. 37:659–667. <https://doi.org/10.1046/j.1529-8817.2001.00195.x>.
- Fourqurean JW, Powell GVN, Kenworthy WJ, Zieman JC. 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrass *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos*. 72(2):349–358. <http://doi.org/10.2307/3546120>.
- Gil MA, Renfro B, Figueroa-Zavala B, Penié I, Dunton KH. 2015. Rapid tourism growth and declining coral reefs in Akumal, Mexico. *Marine Biology*. 162:2225–2233. <https://doi.org/10.1007/s00227-015-2748-z>.
- Guimaraes M, Zúñiga-Ríos A, Cruz-Ramírez CJ, Chávez V, Odéris I, van Tussenbroek BI, Silva R. 2021. The conservation state of coastal ecosystems on the Mexican Caribbean coast: environmental guidelines for their management. *Sustainability* 13(5):2738. <https://doi.org/10.3390/su13052738>.
- Harvey AS, Harvey RM, Merton E. 2017. The distribution, significance and vulnerability of Australian rhodolith beds: a review. *Marine and Freshwater Research*. 68:411–428. <http://doi.org/10.1071/MF15434>.
- Heithaus MR, Alcoverro T, Arthur R, Buckholder DA, Coates KA, Christianen MJA, Kelkar N, Manuel SA, Wirsing AJ, Kenworthy WJ, Fourqurean JW. 2014. Seagrasses in the age of sea turtle conservation and shark overfishing. *Frontiers in Marine Science*. 1. <https://doi.org/10.3389/fmars.2014.00028>
- Hernández-Terrones LM, Null KA, Ortega-Camacho D, Paytan A. 2015. Water quality assessment in the Mexican Caribbean: Impacts on the coastal ecosystem. *Continental Shelf Research*. 102:62–72. <https://doi.org/10.1016/j.csr.2015.04.015>.
- Johnson RA, Gulick AG, Boltan AB, Bjorndal KA. 2019. Rates of sediment resuspension and erosion following green turtle grazing in a shallow Caribbean *Thalassia testudinum* meadow. *Ecosystems* 22:1787–1802. <https://doi.org/10.1007/s10021-019-00372-y>.
- Kéfi S, Holmgren M, Scheffer M. 2016. When can positive interactions cause alternative stable states in ecosystems? *Functional Ecology*. 30:88–97. <https://doi.org/10.1111/1365-2435.12601>
- Labrada-Martagón V, Tenería FAM, Herrera-Pavón R, Negrete-Philippe A. 2017. Somatic growth rates of immature green turtles *Chelonia mydas* inhabiting the foraging ground Akumal Bay in the Mexican Caribbean Sea. *Journal of Experimental Marine Biology and Ecology* 487:68–78. <https://doi.org/10.1016/j.jembe.2016.11.015>.
- Lacey EA, Collado-Vides L, Fourqurean JW. 2014. Morphological and physiological responses of seagrasses (Alismatales) to grazers (Testudines: Cheloniidae) and the role of these responses as grazing patch abandonment cues. *Revista De Biología Tropical* 62:1535. <https://doi.org/10.15517/rbt.v62i4.12844>.
- Leemans L, Martínez I, van der Heide T, van Katwijk MM, van Tussenbroek BI. 2020. A mutualism between unattached coralline algae and seagrasses prevents overgrazing by sea turtles. *Ecosystems*. <https://doi.org/10.1007/s10021-020-00492-w>.
- Martínez-Lopez IG, van Den Akker M, Walk L, van Katwijk MM, van der Heide T, van Tussenbroek BI. 2019. Nutrient availability induces community shifts in seagrass meadows grazed by turtles. *PeerJ*. 7:e7570. <https://doi.org/10.7717/peerj.7570>.
- Maxwell PS, Eklöf JS, van Katwijk MM, O'Brien KR, de la Torre-Castro M, Boström C, Bouma TJ, Krause-Jensen D, Unsworth RKF, van Tussenbroek BI, van der Heide T. 2017. The fundamental role of ecological feedback mechanism for the adaptive management of seagrass ecosystem- a review. *Biological Reviews of the Cambridge Philosophical Society*. 92(3):1521–1538. <https://doi.org/10.1111/brv.12294>.
- Melbourne LA, Denny MW, Harniman RL, Rayfield EJ, Schmidt DN. 2018. The importance of wave exposure on the structural integrity of rhodoliths. *Journal of Experimental Marine Biology and Ecology*. 503:109–119. <https://doi.org/10.1016/j.jembe.2017.11.007>.
- Molina-Hernández ALM, van Tussenbroek BI. 2014. Patch dynamics and species shifts in seagrass communities under moderate and high grazing pressure by green sea turtles. *Marine Ecology Progress Series*. 517:143–157. <https://doi.org/10.3354/meps11068>.
- Mutchler T, Dunton KH, Townsend-Small A, Fredriksen S, Rasser MK. 2007. Isotopic and elemental indicators of nutrient sources and status of coastal habitats in the Caribbean Sea, Yucatan Peninsula, Mexico. *Estuarine, Coastal and Shelf Science*. 74:449–457. <https://doi.org/10.1016/j.ecss.2007.04.005>.
- Nordlund LM, Koch EW, Barbier EB, Creed JC. 2016. Seagrass ecosystem services and their variability across genera and geographic regions. *PLoS ONE*. 11(10):e0163091. <https://doi.org/10.1371/journal.pone.0163091>.
- Nyström M, Norström AV, Blenckner T, de la Torre-Castro M, Eklöf JS, Folke C, Österblom H, Steneck RS, Thyresson M, Troell M. 2012. Confronting feedbacks of degraded marine ecosystems. *Ecosystems*. 15:695–710. <https://doi.org/10.1007/s10021-012-9530-6>.
- Orth RJ, Lefcheck JS, McGlathery KS, Aokl L, Luckenbach MW, Moore KA, Oreska, MPJ, Snyder R., Wilcox DJ, Lusk B. 2020. *Science Advances*. 6(41):1–10. <https://doi.org/10.1126/sciadv.abc6434>

- Osorio-Cano JD, Alcérreca-Huerta JC, Mariño-Tapia I, Osorio AF, Acevedo-Ramírez C, Enriquez C, Costa M, Pereira P, Mendoza E, Escudero M, Astorga-Moar A, López-González J, Appendini CM, Silva R, Oumeraci H. 2019. Effects of roughness loss on reef hydrodynamics and coastal protection: approaches in Latin America. *Estuaries and Coasts* 42:1742–1760. <https://doi.org/10.1007/s12237-019-00584-4>.
- Qui-Minet ZN, Delaunay C, Grall J, Six C, Cariou T, Bohner O, Legrand E, Davoult D, Martin S. 2018. The role of local environmental changes on maerl and its associated non-calcareous epiphytic flora in the Bay of Brest. *Estuarine Coastal and Shelf Science*. 208:140–152. <https://doi.org/10.1016/j.ecss.2018.04.032>.
- Riosmena-Rodríguez R, Nelson W, Aguirre J. 2017. Rhodolith/Maerl beds: a global perspective. USA: Springer. [https://doi.org/10.1007/978-3-319-29315-8\\_11](https://doi.org/10.1007/978-3-319-29315-8_11).
- SEMARNAT. 2015. Estudio técnico justificativo para declarar Área de refugio para proteger tortuga verde, tortuga Carey y tortuga caguama; cuatro especies de corales, tres especies de mangle; tres especies de pastos marinos, todos ubicados en el área marina conocida como Bahía de Akumal, Quintana Roo, México.
- Stachowicz JJ. 2001. Mutualism, facilitation, and the structure of ecological communities. *BioScience*. 51:235. [https://doi.org/10.1641/0006-3568\(2001\)051\[0235:mfatso\]2.0.co;2](https://doi.org/10.1641/0006-3568(2001)051[0235:mfatso]2.0.co;2).
- Steller D, Hernández-Ayón J, Riosmena-Rodríguez R y Cabello-Pasini A. 2007. Effect of temperature on photosynthesis, growth and calcification rates of the free-living coralline alga *Lithophyllum margaritae*. *Ciencias Marinas*. 33(4): 441–456. <https://doi.org/10.7773/cm.v33i4.1255>
- Steller DL, Foster MS. 1995. Environmental factors influencing distribution and morphology of rhodoliths in Bahía Concepción, B.C.S, México. *Journal of Experimental Marine Biology and Ecology*. 194:201–212. [https://doi.org/10.1016/0022-0981\(95\)00086-0](https://doi.org/10.1016/0022-0981(95)00086-0)
- Valentine JF, Heck KL Jr. 1999. Seagrass herbivory: evidence for the continued grazing of marine grasses. *Marine Ecology Progress Series*. 176: 291–302. <https://www.jstor.org/stable/24831891>
- van der Heide T, van Nes EH, Geerling GW, Smolders AJP, Bouma TJ, van Katwijk MM. 2007. Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. *Ecosystems*. 10:1311–1322. <https://doi.org/10.1007/s10021-007-9099-7>
- van der Heide T, van Nes EH, van Katwijk MM, Olff H, Smolders AJP. 2011. Positive feedbacks in seagrass ecosystems - Evidence from large-scale empirical data. *PLoS ONE*. 6:1–7. <https://doi.org/10.1371/journal.pone.0016504>.
- van der Koppel J, Bouma TJ, Herman PM. 2012. The influence of local- and landscape-scale processes on spatial self organization in estuarine ecosystems. *The Journal of Experimental Biology*. 2015:962–967. <https://doi.org/10.1242/jeb.060467>.
- Van Tussenbroek BI, Van Dijk JK. 2007. Spatial and temporal variability in biomass and production of psammophytic *Halimeda incrassata* (Bryopsidales, Chlorophyta) in a Caribbean reef lagoon. *Journal of Phycology*. 43(1):69–77. <https://doi.org/10.1111/j.1529-8817.2006.00307.x>.
- Vásquez-Elizondo RM, Enríquez S. 2017. Light absorption in coralline algae (Rhodophyta): a morphological and functional approach to understanding species distribution in a coral reef lagoon. *Frontiers in Marine Science*. 4:1–17. <https://doi.org/10.3389/fmars.2017.00297>.
- Williams SL. 1990. Experimental studies of Caribbean seagrass bed development. *Ecological Monographs*. 60(4):449–469. <https://doi.org/10.2307/1943015>.
- Williams SL. 1987. Competition between the seagrass *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. *Marine Ecology Progress Series*. 35: 91–98. <http://www.jstor.org/stable/24825013>
- Wilson S, Blake C, Berges JA, Maggs CA. 2004. Environmental tolerances of free-living coralline algae (maerl): implications for European marine conservation. *Biological Conservation*. 120:283–293. <https://doi.org/10.1016/j.biocon.2004.03.001>