

RESEARCH ARTICLE

Filamentous calcareous alga provides substrate for coral-competitive macroalgae in the degraded lagoon of Dongsha Atoll, Taiwan

Carolin Nieder¹, Chen-Pan Liao^{2,3}, Chaolun Allen Chen^{4,5,6}, Shao-Lun Liu^{2*}

1 Leigh Marine Laboratory, Institute of Marine Science, University of Auckland, Leigh, New Zealand, **2** Department of Life Science & Center for Ecology and Environment, Tunghai University, Taichung, Taiwan, **3** Department of Biology, National Museum of Natural Science, Taichung, Taiwan, **4** Biodiversity Research Center, Academia Sinica, Taipei, Taiwan, **5** Institute of Oceanography, National Taiwan University, Taipei, Taiwan, **6** Department of Life Science, National Taiwan Normal University, Taipei, Taiwan

* shaolunliu@gmail.com



Abstract

Background

The chemically-rich seaweed *Galaxaura* is not only highly competitive with corals, but also provides substrate for other macroalgae. Its ecology and associated epiphytes remain largely unexplored. To fill this knowledge gap, we undertook an ecological assessment to explore the spatial variation, temporal dynamics, and diversity of epiphytic macroalgae of *Galaxaura divaricata* on patch reefs in the lagoon of Dongsha Atoll, a shallow coral reef ecosystem in the northern South China Sea that has been repeatedly impacted by mass coral bleaching events.

Methods

Twelve spatially independent patch reefs in the Dongsha lagoon were first surveyed to assess benthic composition in April 2016, and then revisited to determine *G. divaricata* cover in September 2017, with one additional *Galaxaura*-dominated reef (site 9). Four surveys over a period of 17 months were then carried out on a degraded patch reef site to assess the temporal variation in *G. divaricata* cover. Epiphytic macroalgae associated with *G. divaricata* were quantified and identified through the aid of DNA barcoding at this degraded site.

Results

Patch reefs in the Dongsha lagoon were degraded, exhibiting relatively low coral cover (5–43%), but high proportions of macroalgae (13–58%) and other substrate (rubble and dead corals; 23–69%). The distribution of *G. divaricata* was heterogeneous across the lagoon, with highest abundance (16–41%) in the southeast area. Temporal surveys showed consistently high covers (mean \pm SD = 16.9 \pm 1.21%) of *G. divaricata* for 17 months. Additional photographic evidence suggested that overgrowth of *G. divaricata* can persist for 3.5 years.

OPEN ACCESS

Citation: Nieder C, Liao C-P, Chen CA, Liu S-L (2019) Filamentous calcareous alga provides substrate for coral-competitive macroalgae in the degraded lagoon of Dongsha Atoll, Taiwan. PLoS ONE 14(5): e0200864. <https://doi.org/10.1371/journal.pone.0200864>

Editor: Sebastian C. A. Ferse, University of Bremen, GERMANY

Received: June 30, 2018

Accepted: May 5, 2019

Published: May 16, 2019

Copyright: © 2019 Nieder et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This study was financially support by Ministry of Science and Technology, Taiwan (104-2621-B-029-004; 105-2621-B-029-002; 106-2621-B-029-002; <https://www.most.gov.tw/>). The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Yet, *G. divaricata* provides substrate to other macroalgae (e.g., *Lobophora* sp.) that also limit the growth of corals.

Conclusions

Our study demonstrates that an allelopathic seaweed, such as *G. divaricata*, can overgrow degraded coral reefs for extended periods of time. By providing habitat for other harmful macroalgae, a prolonged *Galaxaura* overgrowth could further enhance the spread of macroalgae, and strengthen negative feedback loops, decreasing the recovery potential of degraded reefs.

Introduction

Coral-macroalgae competition is a natural ecological process on coral reefs [1]. However, anthropogenic disturbances, e.g., climate change, overfishing, and pollution, have intensified space competition between macroalgae and corals and in turn led to a phase shift from a coral-dominated to a macroalgae-dominated ecosystem [2]. The recovery of corals on degraded reefs is strongly influenced by the type of dominant macroalgae, i.e., allelopathic versus non-allelopathic [3,4]. Allelopathic macroalgae produce lipid-soluble secondary metabolites, e.g., loliolide derivatives or terpenes that are poisonous to corals (known as allelochemicals). Such allelochemicals are capable of bleaching and killing coral tissue [5], decreasing the photosynthetic efficiency of zooxanthellae [6], and altering the coral microbiome, ultimately decreasing coral health [7,8]. Allelopathic macroalgae are considered most detrimental for the resilience of coral reefs [9], as these types may perpetuate their dominance by deterring coral larval settlement, and inhibiting the growth and survival of juvenile recruits, key processes of coral reef recovery [10–12].

The red upright calcifying seaweed *Galaxaura* is known to be highly allelopathic against corals [13]. Life history of the genus *Galaxaura* can be grouped into two morphotypes, a smooth and a filamentous type. The latter is characterized by hairy branches that are covered with fine assimilatory filaments [14]. Extracts of the lipid-soluble secondary metabolites of *G. filamentosa* were shown to cause bleaching and death of coral tissue [13,15], and deterred coral larvae from settling [16]. It has thus been suggested that high abundance of *Galaxaura* on degraded reefs can inhibit the recovery of coral cover [4,9,16].

The filamentous morphotype of *G. divaricata*, is widely distributed in subtropical and tropical reef areas in the Pacific Ocean [17]. Filamentous *G. divaricata* is also common on coral reefs in the shallow lagoon of Dongsha Atoll [18]. Dongsha Atoll is the only large (> 500 km²) coral reef atoll in the northern South China Sea and represents a highly valuable hot-spot for marine biodiversity in this region [19]. A catastrophic mass bleaching in 1998 and reoccurring bleaching events thereafter have, however, caused severe mass mortalities of corals in the Dongsha lagoon, followed by a marked increase of macroalgae [20,21]. To date, little is known about state of recovery and dominant macroalgae in Dongsha lagoon patch reefs. The proliferation of *G. divaricata* on degraded reefs in the lagoon of Dongsha Atoll was first uncovered during a systematic macroalgae sampling expedition in February 2014 [18]. Similar to some well-documented macroalgae (e.g., crustose *Lobophora* or canopy-forming *Sargassum* and *Turbinaria*) that provide habitat for epiphytes [22–24] we observed that *G. divaricata* was also highly populated by epiphytic macroalgae. The dense epiphytic community associated with *G.*

divaricata might indicate a previously unappreciated role of *Galaxaura* as a habitat forming seaweed.

The goals of this study were to 1) assess the benthic composition of lagoon patch reefs, 2) document the spatial distribution of *G. divaricata* on patch reefs in the lagoon, 3) monitor changes of *G. divaricata* percent cover over time, and 4) quantify and identify the epiphytic macroalgae associated with *G. divaricata*. Understanding the dynamics *G. divaricata* and its role in providing new habitat for other macroalgae is important because the epiphytic community on *G. divaricata* could enhance macroalgae biodiversity on the reef, or provide trophic support for herbivores, while a facilitation of allelopathic algal types would decrease the resilience of coral reefs.

Materials and methods

Ethics statement

The ecological assessments and sample collections in this study were conducted with permissions of the Dongsha Atoll National Park.

Site description

This study was conducted from April in 2016 to September 2017 in the lagoon of Dongsha Atoll (also known as Pratas Island; 20°40'43" N, 116°42'54" E), which is an isolated coral reef atoll in the northern South China Sea. The atoll covers an area of approximately 500 km² and is situated 450 km southwest from the coast of Taiwan and 350 km southeast from Hong Kong (Fig 1A). The climate is seasonal and varies between a northeast monsoon winter (October–April) and southwest monsoon summer (May–September) [25]. Field work during the northeast winter monsoon is often restricted due to local weather conditions. The ring-shaped reef flat encircles a large lagoon with seagrass beds and hundreds of coral patch reefs [26]. Channels at the north and south of the small islet (1.74 km²) interrupt the reef flat and allow for water exchange between the lagoon and the open ocean. The semi-closed lagoon is about 20 km wide with a maximum depth of 16 m near the center [20]. The lagoon patch reefs are structured into reef tops (1–5 m depth) and reef slopes (5–12 m depth), and provide important habitat and sheltered nursery grounds for numerous marine organisms, such as green sea turtles and coral reef fish, including rays and sharks [26]. For background information the lagoon water temperature was measured at each survey site, every 30 min from March 2016 to September 2017 using HOBO Pendant Temperature/Light 8K Data Loggers (UA-002-08, Onset Computer Corporation, USA). Water temperatures were highest during the summer monsoon, averaging 30.1°C, and lowest during the winter monsoon, averaging 24.8°C. Maximum temperatures from July to August reached 34°C on reef tops and 32.7°C on reef slopes.

Spatial variation in benthic composition and *G. divaricata* cover of lagoon patch reefs

To assess the benthic composition of patch reefs in the lagoon of Dongsha Atoll, 12 spatially independent reefs were initially surveyed with SCUBA in April 2016 (Fig 1B and S1 Table). A 45-m transect was laid out across each reef area: reef top (2 m depth) and reef slope (10 m depth). The two transects were 10–20 m apart from each other. The percent cover of corals, total macroalgae (MA; all upright growing (including *G. divaricata*) and crustose non-coralline algae, and low growing, filamentous turf algae [27]), crustose coralline algae (CCA), and other substrate was estimated using a 35 cm x 50 cm PVC sapling frame [28]. Other substrate mainly consisted of dead coral, rubble, and rocks covered with sediments. Estimates were done *in-situ*

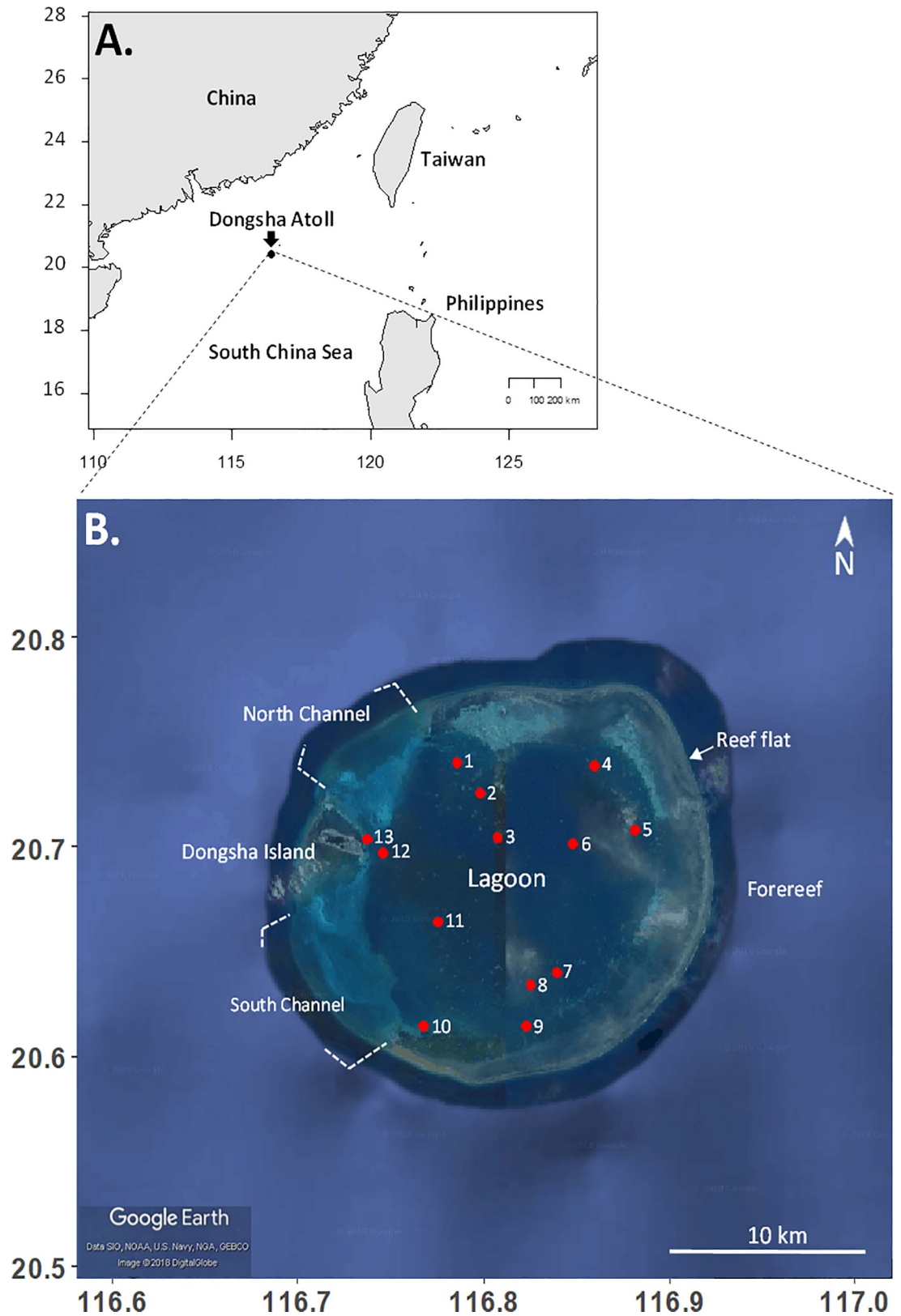


Fig 1. Study site. A) Geographical location of Dongsha Atoll in the northern South China Sea. B) Lagoon patch reef sites surveyed in this study.

<https://doi.org/10.1371/journal.pone.0200864.g001>

at 1 m intervals, for a total of 45 sampling frames analyzed per transect. The 12 sites were revisited in September 2017 to estimate the percent cover of *G. divaricata* and corals only, using the same survey method described above. An additional patch reef (site 9) was included, as this site was historically shown to be dominated by *G. divaricata* based on photo evidence, resulting in a total of 13 survey sites (Fig 1B and S1 Table). The diameter of haphazardly selected *G. divaricata* thalli were measured *in situ* at each site and classified as small (1–5 cm diameter), medium (>5–15 cm diam.), and large (>15–30 cm diam.).

Temporal variation in *G. divaricata* cover

To assess variations in *G. divaricata* cover over time, we selected the slope of a degraded patch reef (site 7) that was considerably overgrown by *G. divaricata* (14–18%) and had relatively low coral cover (13–19%). Percent cover of *G. divaricata* was estimated in April 2016 (the last month of the winter monsoon season), three times during the summer monsoon season (July and September 2016), and in September 2017, spanning a period of 17 months. Coral cover was also monitored during each survey to evaluate whether or not corals recovered over the course of this study. During each survey 45 photographs of the reef bottom were taken with an Olympus Stylus-TOUGH TG4 digital camera (25–100 lens, 35mm equivalent) mounted at 64 cm above the bottom onto a movable PVC-sampling frame (35 cm x 50 cm). A 45-m transect line was laid out along a marked trajectory to keep the survey area consistent among time points. For each survey the sampling frame was moved along the transect line and pictures were taken at every meter mark. Cover estimates were obtained from photographs using ImageJ software (version 1.52a) with a superimposed 10 x 10 reference grid, where 1 square represented 1% of the total grid area.

Epiphytic macroalgae associated with *G. divaricata*

In September 2017, thirty thalli of *G. divaricata* were collected from a degraded reef (site 7) with relatively high percent cover of *G. divaricata* (14–18%). *G. divaricata* thalli were haphazardly collected across the reef slope along a 45-m transect at 5 m depth. Epiphytic macroalgae were removed and identified to the closest identifiable taxonomic unit, using either the Dongsha seaweed guide book [18] or DNA barcoding. The presence and absence of each taxonomic unit was recorded, and the occurrence frequency (f) was calculated as follows: $f = c_i/n$, where c_i stands for the number of thalli that have the epiphyte taxonomic unit i , and $n = 30$, the total number of thalli analyzed. For DNA barcoding, macroalgae samples were preserved in silica gel after collection, and the total genomic DNA of samples was extracted with Quick-DNA Plant/Seed Miniprep Kit (Zymo Research Co., USA). Primers for the plastid gene specific amplifications were used as follows: *rbcL* F7/R753 for red algae [29], *rbcL* F68/R708 for brown algae [30], and *tufA* F210/R1062 for green algae [31]. The newly generated sequences were deposited in GenBank and searched using BLASTn against the GenBank database (S2 and S3 Tables). Sequence similarities of >98% were considered for species identification.

Statistical analysis

First, we explored spatial variation in benthic composition using nonmetric multidimensional scaling (NMDS) in the R package ‘vegan’ (version 2.5–4) [32]. Prior to this analysis, benthic cover was averaged within reef areas at each site and standardized using the Hellinger transformation. We then applied Spearman’s Mantel tests to determine whether spatial distance between surveyed areas correlated with Bray-Curtis dissimilarities for both reef tops and reef slopes.

Next, we examined the effects of two independent variables (i.e., area and site) and their interaction on benthic composition through space and time using linear models with the integration of Bayesian Markov Chain Monte Carlo (MCMC) methods in the R package ‘brms’ (version 2.7.0) [33]. The prior specification of the Bayesian MCMC analysis is provided in [S1 Text](#).

Prior to the analyses, the percent cover from each quadrat of transects was transformed using the logit transformation,

$$y = \text{Log}_e \left(\frac{p}{1-p} \right),$$

where p stands for cover ratio. If the observed data matched 0% or 100%, the percent covers were proportionally remapped to 0.05–99.95%. Four different linear models were compared:

$$M_1 : y_{ijk} = \mu_{ij} + \alpha(\text{area})_j + (\text{site})_i \sigma_i + (\text{area})(\text{site})_i \delta_i + \varepsilon_{ijk},$$

$$M_2 : y_{ijk} = \mu_{ij} + (\text{site})_i \sigma_i + (\text{area})(\text{site})_i \delta_i + \varepsilon_{ijk},$$

$$M_3 : y_{ijk} = \mu_{ij} + (\text{site})_i \sigma_i + \varepsilon_{ijk}, \text{ and}$$

$$M_4 : y_{ijk} = \mu_{ij} + \varepsilon_{ijk},$$

where y denotes the logit-transformed percent cover p of a specific benthic category on k^{th} quadrat in area j within site i , α denotes the fixed effect of area j , σ denotes the random intercept by site, and δ denotes the random slope against areas by site. The best model was selected based on Bayes factors. Overall, a multivariate mixed-effect linear model best fit the percent cover of corals, macroalgae, CCA, and other substrate, whereas a mixed-effect linear model best fit the percent cover of *G. divaricata*. Similarly, to examine temporal variation in the percent cover of *G. divaricata* and corals at site 7, we applied the multivariate fixed-effect linear model, except with time rather than area as the fixed factor and no random factor. In both our spatial and temporal analyses, pair-wise Bayesian MCMC tests were conducted to examine which pairs of surveyed areas were significantly different from each other. The tests were considered statistically significant if the effect size was greater than 0.2 (Cohen’s $d > 0.2$).

Results

Benthic composition

Our NMDS analysis revealed that macroalgae cover was highest (> 40%) on the reef top and reef slope of site 7 and on the reef tops of sites 1, 5, 10, and 12. Tops and slopes of sites 1 and 13 exhibited highest coral covers ([Fig 2A and 2B](#); [S1A Fig](#)). Notably, the reef top of site 1 was the only area showing both higher cover of corals and macroalgae ([Fig 2A](#); [S1A Fig](#)). Compared with corals and total macroalgae, we found that CCA cover was relatively low (< 3%) across sites. The average “other substrate” cover (mainly dead coral, rubble, and rocks) was generally high (> 40%) in over 50% of the surveyed areas. Our post-hoc tests showed that our 24 transects from reef top and slope across 12 sites could be grouped into 19 clusters ([Fig 2A](#)). Our Mantel test showed no correlation between spatial distances and benthic composition dissimilarities among sites in either reef top or slope (Mantel test; slope area, $r_s = 0.152$, $P = 0.132$; top area, $r_s = 0.032$, $P = 0.590$; [S2 Fig](#)).

Our linear model analyses showed that the area by site interaction effect had significant influence on the percent cover of corals, macroalgae, CCA, and other substrate ([S1A Fig](#);

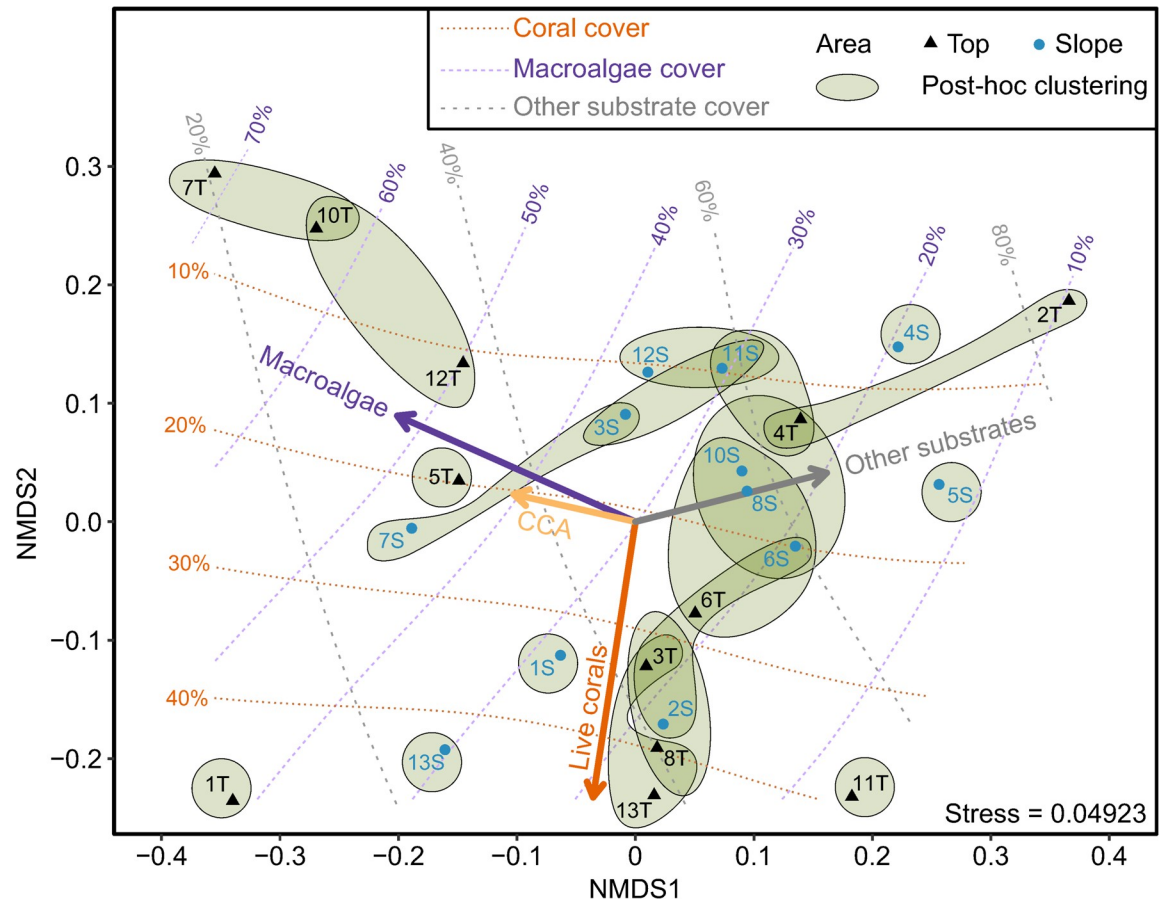


Fig 2. Spatial variation in benthic categories in the Dongsha lagoon. Two-dimensional nonmetric multidimensional scaling (NMDS) of average percent cover of corals, total macroalgae (upright/crustose non-coralline seaweeds and turf), crustose coralline algae (CCA) and other substrate among 24 groups (12 sites \times 2 area types). Thick arrows represent the vectors of weighted average scores of benthic categories. Green loops enclose groups with statistically similar composition by clustering analysis based on the Bayesian post-hoc analyses (posterior Cohen's $d > 0.2$); a loop enclosing only one group indicates that its composition is significantly different from all other groups. Dashed lines indicate the contours of percent cover projected onto two-dimensional NMDS space.

<https://doi.org/10.1371/journal.pone.0200864.g002>

BF > 150, BF of M_2 over M_3 in S4 Table). Our post-hoc analysis revealed a significant difference between top and slope in five sites for corals, seven sites for macroalgae and other substrate, and eight sites for CCA (S1A Fig). For instance, the interaction effect was evident in the percent cover of four different benthic categories (e.g., corals: top > slope in site 3 and slope > top in site 2; macroalgae and other substrate: top > slope in site 1 and slope > top in site 2; and CCA: with a much lower percent cover on the slope of site 4 compared to the slope of other sites) (S1A Fig). Overall, no clear spatial pattern was observed in benthic composition (S1B Fig).

Spatial variation in *G. divaricata* cover

The percent cover of *G. divaricata* among 13 sites was statistically significantly affected by the interaction between area (reef top and reef slope) and site (e.g., top > slope in site 5 and 6, and slope > top in site 7 and 8 in Fig 3A; BF > 150, BF of M_2 over M_3 in S5 Table). Our post-hoc tests showed that *G. divaricata* cover was not at all similar among the 26 transects (Fig 3). *G. divaricata* was most abundant on survey sites in the southeast lagoon, e.g., in site 9 (41%) and

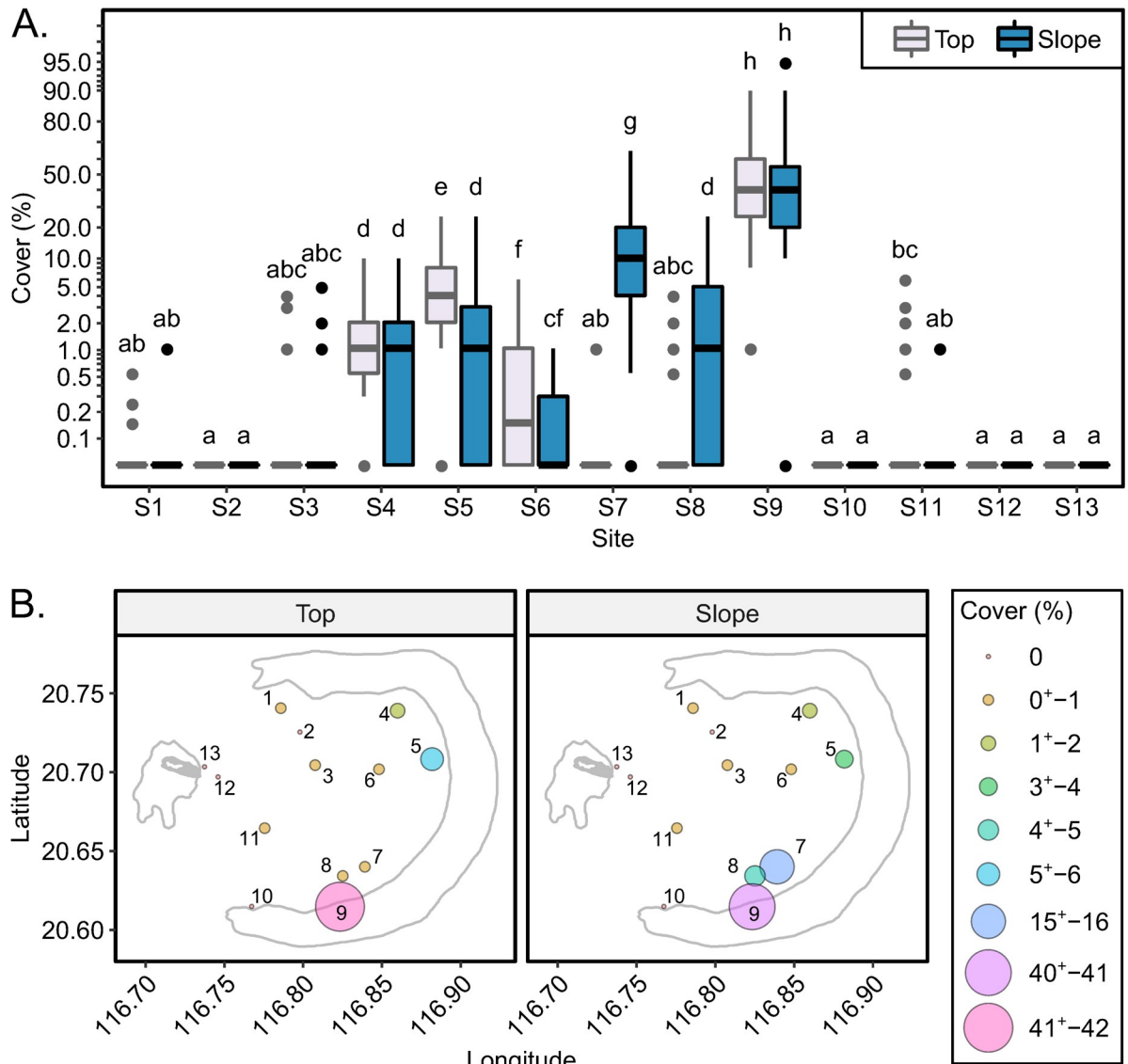


Fig 3. Spatial variation in *G. divaricata* in the Dongsha lagoon. (A) Boxplots showing variation in the percent cover of *G. divaricata* between reef top and slope among 13 sites. Labels denote the ranks of percent cover according to multiple comparisons among 26 transects. Labels that with different letters indicate a statistical difference (posterior Cohen’s $d > 0.2$) in the *G. divaricata* cover. (B) The average percent cover on the reef top and slope at each site are represented by circles with different colors and sizes.

<https://doi.org/10.1371/journal.pone.0200864.g003>

on the slope of site 7 (16%) (Fig 3A and 3B). Patch reefs in the northeast lagoon exhibited much lower cover of *G. divaricata* (range: 0.21–5.7%) (Fig 3A and 3B and S6 Table). Survey sites in the south, center, west, and north of the lagoon were characterized by the lowest cover of *G. divaricata* (range: 0–1.4%; Fig 3B and S6 Table).

During our survey, we observed that the thallus shape and size of *G. divaricata* varied across sites (S3 Fig). Small ball-shaped or slender thalli were dominant on patch reefs in the northeast lagoon, while medium ball-shaped and large, carpet-like thalli were exclusively present in the southeast lagoon. Our DNA barcoding analyses confirmed that all samples across sites were 100% identical in their *rbcL* sequences, indicative of conspecificity (S3 Table).

Temporal dynamics of *G. divaricata* cover

Our temporal survey at a *Galaxaura*-dominated reef (slope of site 7) revealed that the percent covers of *G. divaricata* and corals were similar among 4 time points (April 2016, July 2016, September 2016, and September 2017). The main effect (time points) contributed only 2% and 2.7% partial R^2 when fitting *G. divaricata* and coral covers, respectively, showing that both covers did not significantly change over a period of 17 months (BF < 0.001; Δ LOOIC = -9.36; Fig 4). Throughout the study, the mean *G. divaricata* cover remained relatively high ($16.45 \pm 1.17\%$), while mean coral cover was low ($15.91 \pm 0.6\%$). In addition, we provide photo-evidence from an additional patch reef (site 9, 3–5 m) overgrown by *G. divaricata*. Photographs of the site were taken in February 2014 and in September 2017, showing that the same *G. divaricata* overgrowth was present after 3.5 years (Fig 5A and 5B). *G. divaricata* frequently grew on live corals, where the holdfast penetrated the calcium-carbonate structure, creating a strong attachment to the corals (Fig 5C). In several cases we observed a fluorescent pink discoloration and bleaching of the coral tissue at the contact zone with *G. divaricata*, strongly indicative of allelopathic inhibition by *G. divaricata* (Fig 5D).

Epiphytic macroalgae associated with *G. divaricata*

We identified 21 taxonomic groups of macroalgae, including macroscopic filamentous cyanobacteria, in association with *G. divaricata* (Table 1 and S2 Table). Among these, 15 were identified to the species level, with seven species of red algae, three species of brown, and five species of green algae (Table 1 and S2 Table). The most common green macroalgae associated with *G. divaricata* were *Derbesia marina* (occurrence frequency: 37%) (Fig 6A), *Caulerpa chemnitzia* (27%) (Fig 6B), and *Boodlea composita* (20%). The most common brown macroalgae

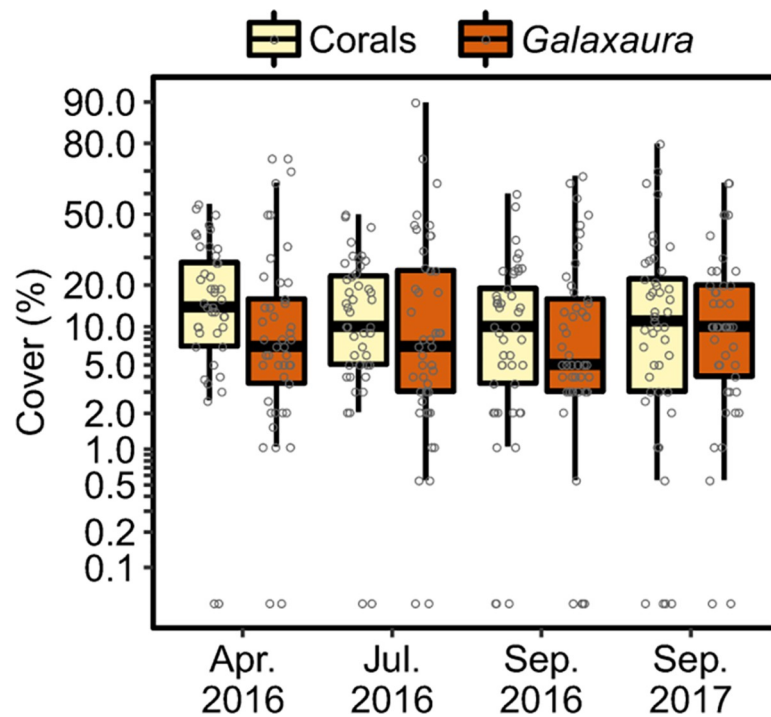


Fig 4. Temporal variation in *G. divaricata* on a degraded patch reef in the southeast Dongsha lagoon. Boxplots showing variation in the percent cover of two major benthic categories (corals and *G. divaricata*) among four time points over a period of 17 months (about 5 m depth at site 7).

<https://doi.org/10.1371/journal.pone.0200864.g004>



Fig 5. Observational photo-evidence of a prolonged *Galaxaura* overgrowth. A-B) A degraded patch reef in the southeast lagoon of Dongsha Atoll has been overgrown by *G. divaricata* for at least 3.5 years (3–5 m depth at site 9). Photos were taken in A) February 2014, with water temperature = 22.5°C; and B) in September 2017 with water temperature = 29°C. The holdfast of *G. divaricata* penetrates a branching *Porites* coral (*P. cylindrica*), creating small

holes (inset). D) Coral (*P. solida*) tissue discoloration and bleaching (arrows) following direct contact with *G. divaricata*, potentially caused by allelopathic chemicals.

<https://doi.org/10.1371/journal.pone.0200864.g005>

associated with *G. divaricata* were the brown algae *Lobophora* sp. (as *Lobophora* sp28 in [34]) (57%), *Padina* sp. (as *Padina* sp5 in [35]) (53%), and *Dictyota bartayresiana* (30%) (Fig 6C). The most common red macroalgae associated with *G. divaricata* were *Hypnea caespitosa* (100%) (Fig 6D), *Coelothrix irregularis* (87%), *Ceramium dawsonii* (43%). Lastly, epiphytic macroscopic cyanobacteria (> 1cm in height) had an occurrence frequency of 17%. Among these epiphytic macroalgae we observed that *Lobophora* (identified as *Lobophora* sp28; S2 Table) was also found to frequently overgrow corals in the Dongsha lagoon (Fig 7 and S4 Fig).

Discussion

Our study shows that most patch reefs in the lagoon of Dongsha Atoll are degraded. Many of the lagoon patch reefs (ca. 63% of the surveyed areas) exhibit relatively low coral cover (< 30%) and high proportions of macroalgae, dead corals, and rubble, all of which are signs of reef degradation [36]. This is consistent with previous surveys that reported degraded conditions of lagoon patch reefs at Dongsha Atoll [37,38]. The filamentous form of *Galaxaura divaricata* showed highest abundance in the southeast lagoon. *Galaxaura* overgrowth was also observed in other locations in the southeast lagoon in previous surveys (Keryea Soong,

Table 1. Occurrence frequency (%) of epiphytic macroalgae on *Galaxaura divaricata* from the slope of site 7.

Epiphyte taxon	Phylum	Occurrence frequency (%)
<i>Acanthophora spicifera</i> ^a	Red	3
<i>Ceramium dawsonii</i> (MH048927) ^b	Red	43
<i>Coelothrix irregularis</i> (MH048928)	Red	87
<i>Dichotomaria obtusata</i>	Red	3
Gelidiales	Red	27
<i>Gracilaria</i> spp.	Red	7
<i>Hypnea caespitosa</i> (MH048929, MH048930, MH048931)	Red	100
<i>Hypnea</i> sp. (MH048932)	Red	30
<i>Laurencia dendroidea</i>	Red	13
<i>Laurencia</i> spp.	Red	20
<i>Dictyota bartayresiana</i>	Brown	30
<i>Dictyota</i> spp.	Brown	13
<i>Lobophora</i> sp28 ^c (MH048934, MH048935, MH048936, MH048937)	Brown	57
<i>Padina</i> sp5 ^d (MH048933)	Brown	53
<i>Sargassum</i> spp.	Brown	3
<i>Boodlea composita</i>	Green	20
<i>Caulerpa chemnitzia</i> (MH048959)	Green	27
<i>Derbesia marina</i>	Green	37
<i>Phyllocladion anastomosans</i>	Green	10
<i>Valonia ventricosa</i>	Green	10
Cyanobacteria (filamentous > 1cm)	Cyanobacteria	17

^aIdentification of species and taxonomic groups according to [18].

^bGenBank number in parentheses based on species identifications through DNA barcoding.

^cDenomination according to [34].

^dDenomination according to [35].

<https://doi.org/10.1371/journal.pone.0200864.t001>

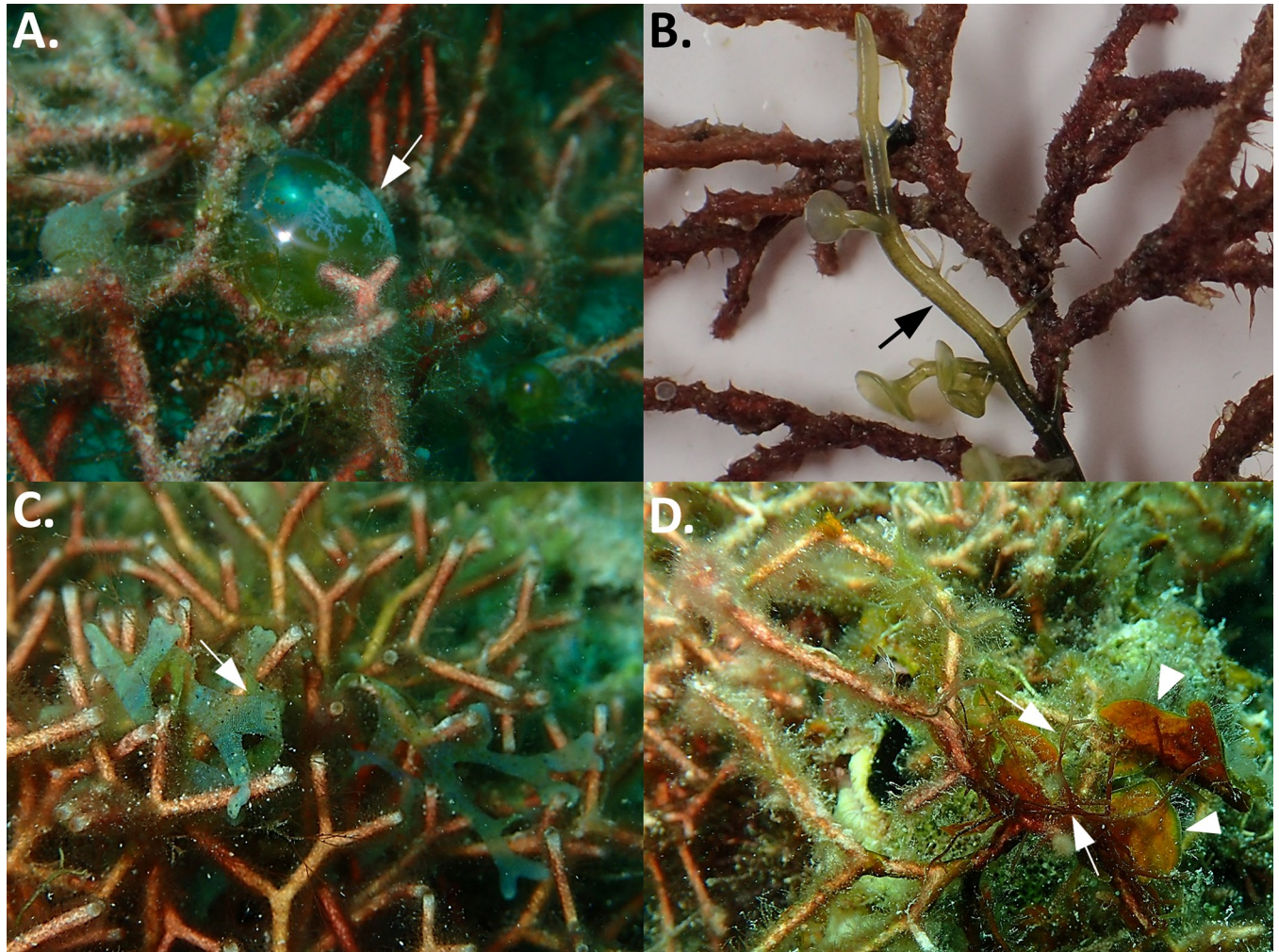


Fig 6. Examples showing epiphytic macroalgae that frequently grow on *G. divaricata*. A) *Valonia ventricosa*, B) *Caulerpa chemnitzia*, C) *Dictyota* sp., D) *Lobophora* sp. (arrowhead), and *Hypnea caespitosa* (arrow).

<https://doi.org/10.1371/journal.pone.0200864.g006>

personal communication; our own macroalgae inventory in 2012). The exact causes for this localized condition are not well understood. However, a potential explanation may be that the southeast lagoon is sheltered by a 2 km-wide reef flat, harboring very shallow (1–5 m) and calm waters that may provide suitable growth conditions for *G. divaricata*. The proliferation of macroalgae is likely the consequence of an initial coral decline [39,40]. The synergistic effects of thermal stress, overfishing, and typhoon damage may have caused the decline of the once pristine corals in the Dongsha lagoon, followed by a proliferation of *G. divaricata* and other macroalgae. Thermal stress on corals has increased over the past decades, with waters surrounding Dongsha Atoll warming at a faster rate than other areas of the South China Sea [37,41,42]. Recurrent bleaching events have caused high coral mortality and eradicated thermo-sensitive coral genera from the lagoon [43]. Overfishing and the extensive use of dynamite and cyanide, prior to the establishment of the Dongsha Atoll National Park in 2007 reduced fish, and destroyed large areas of coral framework [20,44]. Insufficient grazing by fish after disturbance can lead to the establishment and full outgrowth of macroalgae beyond their early stages [45]. *Galaxaura* is known to be largely unpalatable for various herbivorous fishes

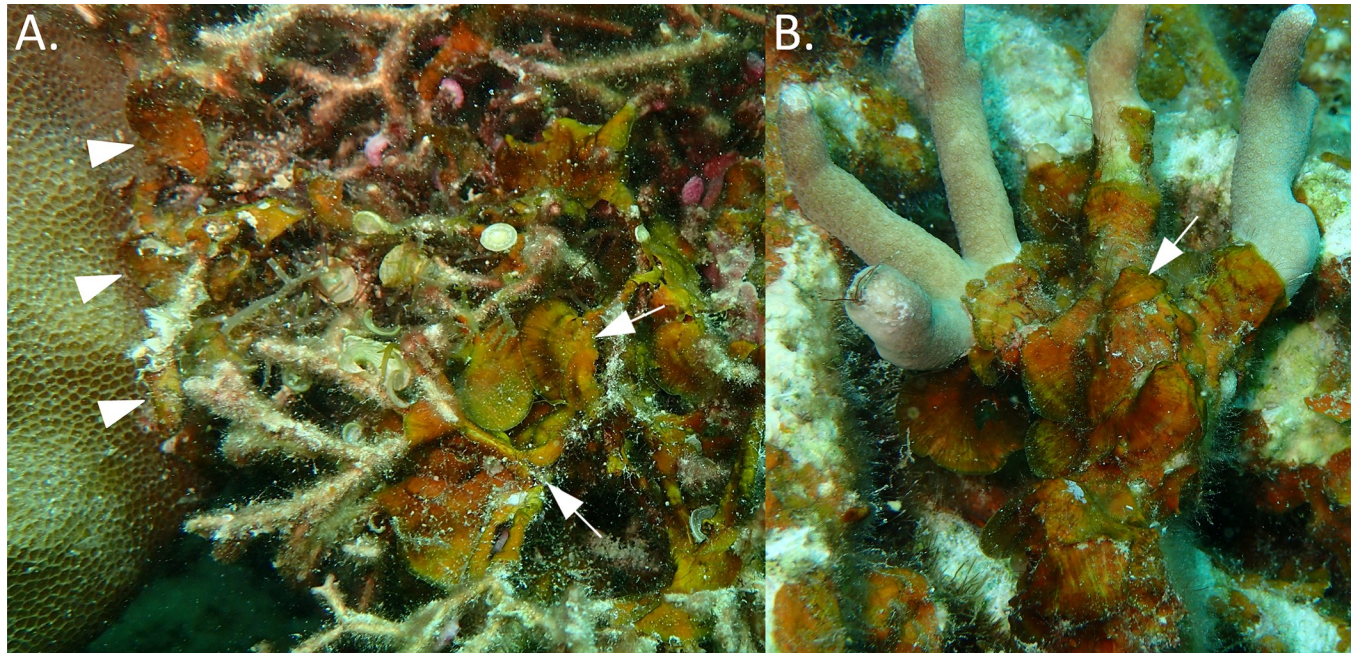


Fig 7. Coral overgrowth by *Lobophora* sp28. A) Example showing *Lobophora* sp28 growing on *Galaxaura divaricata* (arrows), and in contact with coral (*Porites solida*) (arrowheads). B) Coral overgrowth (*Porites cylindrica* in this case) by *Lobophora* sp28 is widespread in the shallow lagoon of Dongsha Atoll.

<https://doi.org/10.1371/journal.pone.0200864.g007>

due to its calcareous thallus and low nutritional content [46–48]. Local herbivorous fish population in the Dongsha lagoon may not be effective to control the outgrowth of *Galaxaura* in certain areas.

Semi-closed lagoons are highly vulnerable to eutrophication and hypoxia, especially under the backdrop of climate change [49,50]. Reoccurring events of hypoxia during hot summers in 2014 and 2015 have caused substantial mass-die offs of the coral associated fauna and flora in the Dongsha lagoon [51]. Particularly, densities of macroinvertebrates, including echinoids, sea cucumbers, lobsters, and giant clams are extremely low (S7 Table). *Galaxaura* appears to be well adapted to hypoxic conditions. For instance, *G. filamentosa* was one of the few algae to proliferate after a mass-die off caused by hypoxia in an atoll lagoon in French Polynesia [52].

Although the filamentous *G. divaricata* is a common allelopathic seaweed in subtropical and tropical waters, it has never been reported as a nuisance in overgrowing coral reefs. Our observations are the first to report a prolonged *G. divaricata* overgrowth in degraded coral reefs. For instance, the *G. divaricata* cover was equally high on a degraded reef after 17-months. We further provide photo-evidence from another patch reef showing that the same *G. divaricata* overgrowth was present to a similar extend after 3.5 years. The photos clearly show that *G. divaricata* dominated the reef substrate of the site in both, the cooler northeast monsoon (winter) season (Fig 5A, water temperature: 22.5°C), and the warmer southwest monsoon (summer) season (Fig 5B, water temperature: 29°C). Due to challenging weather conditions, we were only able to conduct our quantitative temporal survey in April, the last month of the winter season, and therefore we cannot rule out potential variations in *G. divaricata* cover over the full length of that season. Expanding temporal surveys in the future will be worth of doing to confirm the long-term persistence of *G. divaricata* overgrowth.

It is important to note that only two out of 13 survey sites showed substantial overgrowth by *G. divaricata*. Thus, the dominance of *G. divaricata* is not a generalized condition across

the entire lagoon of Dongsha Atoll. Rather, it represents a much localized condition found at certain sites in the southeast lagoon.

High abundance of filamentous *G. divaricata* may have profound implications for the recovery potential of those patch reefs experiencing a prolonged *Galaxaura* overgrowth in the lagoon of Dongsha Atoll. Owing to its allelopathic effects on corals long-standing canopies of *G. divaricata* are likely to hamper coral recruitment ultimately preventing coral recovery [16,53]. As a caveat of this study, it is important to note that we did not attempt to isolate and identify allelopathic chemicals in *G. divaricata*. But, previous studies have identified lipid-soluble terpenoid compounds from filamentous *Galaxaura* cell extracts as allelochemicals that were capable of bleaching and killing coral tissue [13]. It is also known that *Galaxaura* can change the chemical microclimate on degraded reefs with adverse effects on fish feeding behavior [4]. For instance, butterflyfish and other corallivores avoid corals in close association with *Galaxaura*, making it potentially difficult for these trophic guilds to find food [54,55]. Unlike other calcifying algae such as coralline algae, *Galaxaura* does not stabilize the reef matrix. Thus, a prolonged *Galaxaura* overgrowth may contribute to the erosion and flattening of the reef structure, which negatively impacts biodiversity, and trophic support for coral associated organisms [56].

The filamentous *G. divaricata* is used as habitat by a variety of macroalgae. The availability of new habitat for epiphytic macroalgae provided by a prolonged *Galaxaura* overgrowth could have several implications for the ecology and recover potential of the reef. For instance, nutrient rich epiphytes could provide trophic support for herbivorous fishes and invertebrates, such as crustaceans and mollusks [24,57,58]. On the other hand, the association with the unpalatable *Galaxaura* may provide a refuge from herbivory for certain palatable algae [40,59,60], and facilitate their establishment on the reef, increasing macroalgae biodiversity [61]. The facilitation of harmful, allelopathic algal types could decrease the resilience and promote alternative stable states on coral reefs [62]. Some of the identified *G. divaricata* epiphytes, such as cyanobacteria [11], *Dictyota* [63], and *Lobophora* [10,64] are widely shown to overgrow corals after disturbance, and are known for their allelopathic inhibition of coral larvae recruitment. Here, we firstly report that an undescribed species *Lobophora* sp. (as *Lobophora* sp28 in [34]), the third most abundant macroalga on *G. divaricata*, overgrows and kills corals in the Dongsha lagoon through epizoism (Fig 7 and S2 Fig). Moreover, the microscopic filaments of *G. divaricata* may facilitate the attachment of macroalgae spores, while the calcified branches may provide structural support for fine, filamentous macroalgae. Considering that an increased substrate availability can promote macroalgae biomass on coral reefs, we hypothesize that, by providing a habitat for epiphytic macroalgae, *G. divaricata* may facilitate the diversity and abundance of macroalgae on degraded reefs. This study is merely observational and does not provide experimental evidence for the facilitation of macroalgae diversity and abundance by *G. divaricata*. However, the abovementioned hypotheses would be of great interest awaiting future validation.

Conclusions

Our observations illustrated that the allelopathic and unpalatable filamentous seaweed, *Galaxaura divaricata*, can become dominant on degraded reefs in shallow, sheltered, and calm environments. We show that *G. divaricata* provides suitable substrate for a variety of macroalgae, further facilitating macroalgae growth and abundance on degraded reefs. Thus, a prolonged proliferation of *Galaxaura* could potentially enhance negative feedback loops, thereby perpetuating reef degradation. Several common epiphytic macroalgae on *Galaxaura* are allelopathic and known to frequently overgrow corals. Macroalgal assemblages, such as the *Galaxaura*-

epiphyte system, warrant further investigation to better understand their ecological implications on the resilience of coral reefs, especially of shallow atoll lagoons. There are 439 listed coral reef atolls on earth; among them are 335 with semi-enclosed lagoons [65]. Atoll lagoons are highly productive and serve as valuable nursery habitat for marine life; however, they are most vulnerable to the effects of climate change [50,66]. Results from our study can be informative for the management and conservation of lagoons and shallow, inshore coral reef ecosystems, especially in the South China Sea and the Pacific Ocean, where filamentous *Galaxaura* is very common.

Supporting information

S1 Fig. Percent cover (A) and spatial patterns (B) of corals, macroalgae, crustose coralline algae (CCA), and other substrate on reef top and slope across 13 sites. Color and size of the circles are proportional to the percent cover.

(TIF)

S2 Fig. Correlation between geographical distance and benthic composition dissimilarity among 12 sampling sites. Regression lines and 95% confidence bands were estimated by the locally weighted scatterplot smoothing (LOESS) method.

(TIF)

S3 Fig. Various sizes and thallus shapes of *Galaxaura divaricata* from different locations in the lagoon of Dongsha Atoll. A-B) Small, ball-shaped thalli, and C-D) small, slender thalli were dominant on patch reefs in the north and northeast lagoon. E) Medium, ball-shaped thalli, and F) large carpet-like thalli were exclusively present in the southeast section of the lagoon.

(TIF)

S4 Fig. Coral overgrowth by *Lobophora* sp28. A) Coral overgrowth (*Porites cylindrica* in this case) by *Lobophora* sp28 is widely spread in the lagoon of Dongsha Atoll. B) The same coral showing dead tissue (arrow) after the removal of the algae.

(TIF)

S1 Table. GPS coordinates of patch reef survey sites in the lagoon of Dongsha Atoll, South China Sea (Taiwan).

(DOCX)

S2 Table. Information and Genbank numbers of macroalgae samples used for DNA barcoding in this study.

(DOCX)

S3 Table. Information and Genbank numbers of *Galaxaura divaricata* samples from various locations in the lagoon of Dongsha Atoll that were used for DNA barcoding in this study.

(DOCX)

S4 Table. Model fit statistics of percent cover of benthic categories (corals, total macroalgae, CCA, and other substrate) for reef top and reef slope among 12 sites.

(DOCX)

S5 Table. Model fit statistics of *Galaxaura divaricata* percent cover for reef top and reef slope among 13 sites.

(DOCX)

S6 Table. Relative percent cover (% mean \pm SD, n = 45) of *Galaxaura divaricata* on 13 patch reef sites in the lagoon of Dongsha Atoll, South China Sea.

(DOCX)

S7 Table. Paucity of macrobenthic invertebrates in the lagoon of Dongsha Atoll.

(DOCX)

S1 Text. Detailed information of statistical analyses and results.

(DOCX)

Acknowledgments

The authors would like to thank our colleagues of the joint project: “Patterns of Resilience in Dongsha Atoll Coral Reefs” for their collaboration and great support throughout this study. We thank Prof. Keryea Soong and staff of the Dongsha Atoll Research Station, the Dongsha Atoll National Park, the Coastal Guard Administration, and the Ministry of Marine Affairs for logistic support. We would like to thank Dr. Ming-Jay Ho, Miss Yen-Jia Chen, Prof. George P. Lohmann and Mr. Cherng-Shyang Chang for their assistance with benthic surveys, as well as Miss Chieh-Hsuan Lee and Miss Pin-Chen Chen for assistance with fieldwork and DNA bar-coding. We thank Miss Diana LaScala-Gruenewald for her edits of the manuscript. This study was financially supported by the Ministry of Science and Technology, Taiwan to SLL.

Author Contributions

Conceptualization: Carolin Nieder, Chaolun Allen Chen, Shao-Lun Liu.

Data curation: Carolin Nieder, Shao-Lun Liu.

Formal analysis: Carolin Nieder, Chen-Pan Liao, Shao-Lun Liu.

Funding acquisition: Shao-Lun Liu.

Investigation: Carolin Nieder, Shao-Lun Liu.

Methodology: Carolin Nieder, Chen-Pan Liao, Shao-Lun Liu.

Supervision: Chaolun Allen Chen, Shao-Lun Liu.

Validation: Carolin Nieder, Chaolun Allen Chen, Shao-Lun Liu.

Visualization: Carolin Nieder, Chaolun Allen Chen.

Writing – original draft: Carolin Nieder.

Writing – review & editing: Chen-Pan Liao, Chaolun Allen Chen, Shao-Lun Liu.

References

1. McCook L, Jompa J, Diaz-Pulido G. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*. 2001; 19: 400–417.
2. Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, et al. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Bio*. 2007; 17: 360–365.
3. Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanogr Mar Biol Annu Rev*. 2008; 46: 25–63.
4. McCormick MI, Barry RP, Allan BJ. Algae associated with coral degradation affects risk assessment in coral reef fishes. *Sci Rep*. 2017; 7: 16937. <https://doi.org/10.1038/s41598-017-17197-1> PMID: 29208978

5. Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME. Macroalgal terpenes function as allelopathic agents against reef corals. *Proc Natl Acad Sci.* 2011; 108: 17726–17731. <https://doi.org/10.1073/pnas.1108628108> PMID: 22006333
6. Andras TD, Alexander TS, Gahlana A, Parry RM, Fernandez FM, Kubanek J, et al. Seaweed allelopathy against coral: surface distribution of a seaweed secondary metabolite by imaging mass spectrometry. *J Chem Ecol.* 2012; 38: 1203–1214. <https://doi.org/10.1007/s10886-012-0204-9> PMID: 23108534
7. Nugues MM, Smith GW, Hoodonk RJ, Seabra MI, Bak RP. Algal contact as a trigger for coral disease. *Ecol Lett.* 2004; 7: 919–923.
8. Thurber RV, Burkepile DE, Correa AM, Thurber AR, Shantz AA, Welsh R, et al. Macroalgae decrease growth and alter microbial community structure of the reef-building coral, *Porites astreoides*. *PLoS One.* 2012; 7: e44246. <https://doi.org/10.1371/journal.pone.0044246> PMID: 22957055
9. Morrow KM, Bromhall K, Motti CA, Munn CB, Bourne DG. Allelochemicals produced by brown macroalgae of the *Lobophora* genus are active against coral larvae and associated bacteria, supporting pathogenic shifts to vibrio dominance. *Appl Environ Microbiol.* 2016; 83: 10.1128.
10. Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS. Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar Ecol Prog Ser.* 2006; 323: 107–117.
11. Webster FJ, Babcock RC, Van Keulen M, Loneragan NR. Macroalgae inhibits larval settlement and increases recruit mortality at Ningaloo Reef, Western Australia. *PloS One.* 2015; 10: e0124162. <https://doi.org/10.1371/journal.pone.0124162> PMID: 25898011
12. Liu S, Liao LM, Wang W. Conspicuity of two morphologically distinct calcified red algae from the northwest Pacific Ocean: *Galaxaura pacifica* and *G. filamentosa* (Galaxauraceae, Rhodophyta). *Bot Stud.* 2013; 54: 1. <https://doi.org/10.1186/1999-3110-54-1> PMID: 28510896
13. Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME. Macroalgal terpenes function as allelopathic agents against reef corals. *Proc Natl Acad Sci.* 2011; 108: 17726–17731. <https://doi.org/10.1073/pnas.1108628108> PMID: 22006333
14. Rasher DB, Hay ME. Chemically rich seaweeds poison corals when not controlled by herbivores. *Proc Natl Acad Sci.* 2010; 107: 9683–9688. <https://doi.org/10.1073/pnas.0912095107> PMID: 20457927
15. Dixson DL, Abrego D, Hay ME. Reef ecology. Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. *Science.* 2014; 345: 892–897. <https://doi.org/10.1126/science.1255057> PMID: 25146281
16. Rasher DB, Hay ME. Seaweed allelopathy degrades the resilience and function of coral reefs. *Commun Integr Biol.* 2010; 3: 564–566. <https://doi.org/10.4161/cib.3.6.12978> PMID: 21331240
17. Wendy Guiry in Guiry M.D. & Guiry G.M. Algaebase. World-wide electronic publication, National University of Ireland, Galway. Searched on 13 December 2018. Algaebase. 2018. Available: <http://www.algaebase.org>.
18. Wang WL, Liu SL, Li TH. Seaweeds of Dongsha Atoll in the South China Sea. Kaohsiung, Taiwan: Marine National Park Headquarters; 2015.
19. Huang D, Licuanan WY, Hoeksema BW, Chen CA, Ang PO, Huang H, et al. Extraordinary diversity of reef corals in the South China Sea. *Mar Biodivers.* 2015; 45: 157–168.
20. Dai C. Dongsha Atoll in the South China Sea: Past, present and future. Islands of the World VIII International Conference “Changing Islands—Changing Worlds” 1–7 November 2004, Kinmen Island (Quemoy), Taiwan.
21. DeCarlo TM, Cohen AL, Wong GT, Davis KA, Lohmann P, Soong K. Mass coral mortality under local amplification of 2° C ocean warming. *Sci Rep.* 2017; 7: 44586. <https://doi.org/10.1038/srep44586> PMID: 28333165
22. Fricke A, Titlyanova T, Nugues M, Bischof K. Depth-related variation in epiphytic communities growing on the brown alga *Lobophora variegata* in a Caribbean coral reef. *Coral Reefs.* 2011; 30: 967–973.
23. Prince JS, O’Neal SW. The ecology of Sargassum pteropleuron Grunow (Phaeophyceae, Fucales) in the waters off South Florida: I. Growth, reproduction and population structure. *Phycologia.* 1979; 18: 109–114.
24. Bittick SJ, Clausing RJ, Fong CR, Scoma SR, Fong P. A Rapidly Expanding Macroalga Acts as a Foundational Species Providing Trophic Support and Habitat in the South Pacific. *Ecosystems.* 2018: 1–9.
25. Wang B, Zhang Y, Lu M. Definition of South China Sea monsoon onset and commencement of the East Asia summer monsoon. *J Clim.* 2004; 17: 699–710.
26. Chou Y. Dongsha Atoll Research Station-A steady research platform in South China Sea. *Kuroshio Science.* 2016; 10–1: 23–27.
27. Connell S, Foster M, Airoidi L. What are algal turfs? Towards a better description of turfs. *Mar Ecol Prog Ser.* 2014; 495: 299–307.

28. Preskitt LB, Vroom PS, Smith CM. A rapid ecological assessment (REA) quantitative survey method for benthic algae using photo-quadrats with scuba. *Pac Sci*. 2004; 58: 201–209.
29. Freshwater DW, Rueness J. Phylogenetic relationships of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on *rbcL* nucleotide sequence analysis. *Phycologia*. 1994; 33: 187–194.
30. Draisma SG, Prud'Homme van Reine, Willem F, Stam WT, Olsen JL. A reassessment of phylogenetic relationships within the Phaeophyceae based on RUBISCO large subunit and ribosomal DNA sequences. *J Phycol*. 2001; 37: 586–603.
31. Famà P, Wysor B, Kooistra WH, Zuccarello GC. Molecular phylogeny of the genus *Caulerpa* (Cauleriales, Chlorophyta) inferred from chloroplast *tufA* gene1. *J Phycol*. 2002; 38: 1040–1050.
32. Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara R, et al. Package 'Vegan'. Community ecology package, version. 2013;2.
33. Lin L, Zhang J, Hodges JS, Chu H. Performing Arm-Based Network Meta-Analysis in R with the pnet-meta Package. *J Stat Softw*. 2017; 80: 10.
34. Vieira C, Camacho O, Sun Z, Fredericq S, Leliaert F, Payri C, et al. Historical biogeography of the highly diverse brown seaweed *Lobophora* (Dictyotales, Phaeophyceae). *Mol Phylogenet Evol*. 2017; 110: 81–92. <https://doi.org/10.1016/j.ympev.2017.03.007> PMID: 28279809
35. Silberfeld T, Bittner L, Fernández-García C, Cruaud C, Rousseau F, de Reviers B, et al. Species diversity, phylogeny and large scale biogeographic patterns of the genus *Padina* (Phaeophyceae, Dictyotales). *J Phycol*. 2013; 49: 130–142. <https://doi.org/10.1111/jpy.12027> PMID: 27008395
36. Gomez ED, Yap HT. Monitoring reef condition. In: Kenchington RA, Hudson ET. editors. *Coral Reef Management Handbook*, UNESCO Regional Office for Science and Technology for Southeast Asia (ROSTSEA); 1988. pp. 171–178.
37. Tkachenko KS, Soong K. Dongsha Atoll: A potential thermal refuge for reef-building corals in the South China Sea. *Mar Environ Res*. 2017; 127: 112–125. <https://doi.org/10.1016/j.marenvres.2017.04.003> PMID: 28395870
38. Morton B. Dongsha Atoll, South China Sea: Ground Zero! *Mar Pollut Bull*. 2002; 44: 835–837. PMID: 12405206
39. Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, et al. Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. *PLoS One*. 2009; 4: e5239. <https://doi.org/10.1371/journal.pone.0005239> PMID: 19384423
40. Roff G, Doropoulos C, Zupan M, Rogers A, Steneck RS, Golbuu Y, et al. Phase shift facilitation following cyclone disturbance on coral reefs. *Oecologia*. 2015; 178: 1193–1203. <https://doi.org/10.1007/s00442-015-3282-x> PMID: 25761445
41. DeCarlo TM, Karnauskas KB, Davis KA, Wong GT. Climate modulates internal wave activity in the Northern South China Sea. *Geophys Res Lett*. 2015; 42: 831–838.
42. Zuo X, Su F, Wu W, Chen Z, Shi W. Spatial and temporal variability of thermal stress to China's coral reefs in South China Sea. *Chinese Geogr Sci*. 2015; 25: 159–173.
43. Li J, Lee T, Tew KS, Fang L. Changes in the coral community at Dongsha Atoll, South China Sea from 1975 to 1998. *Acta Zoologica Taiwanica*. 2000; 11: 1–15.
44. Morton B, Blackmore G. South China Sea. *Mar Pollut Bull*. 2001; 42: 1236–1263. PMID: 11827109
45. Bozec Y, Doropoulos C, Roff G, Mumby PJ. Transient grazing and the dynamics of an unanticipated coral–algal phase shift. *Ecosystems*. 2018: 1–16.
46. Mantyka CS, Bellwood DR. Macroalgal grazing selectivity among herbivorous coral reef fishes. *Mar Ecol Prog Ser*. 2007; 352: 177–185.
47. Rasher DB, Hoey AS, Hay ME. Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology*. 2013; 94: 1347–1358. PMID: 23923498
48. Duffy JE, Hay ME. Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology*. 1994; 75: 1304–1319.
49. Charpy L, Dufour P, Garcia N. Particulate organic matter in sixteen Tuamotu atoll lagoons (French Polynesia). *Mar Ecol Prog Ser*. 1997: 55–65.
50. Andréfouët S, Dutheil C, Menkes CE, Bador M, Lengaigne M. Mass mortality events in atoll lagoons: environmental control and increased future vulnerability. *Global Change Biol*. 2015; 21: 195–205.
51. Gajdzik L, DeCarlo TM. The perfect calm: Reoccurring mass die-offs on a remote coral atoll. *Matters*. 2017; 3: e201707000003.
52. Adjeroud M, Andréfouët S, Payri C. Mass mortality of macrobenthic communities in the lagoon of Hikueru atoll (French Polynesia). *Coral Reefs*. 2001; 19: 287–291.

53. Bonaldo RM, Hay ME. Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PLoS One*. 2014;9.
54. Brooker RM, Brandl SJ, Dixon DL. Cryptic effects of habitat declines: coral-associated fishes avoid coral-seaweed interactions due to visual and chemical cues. *Sci Rep*. 2016; 6: 18842. <https://doi.org/10.1038/srep18842> PMID: 26725835
55. Brooker RM, Sih TL, Dixon DL. Contact with seaweed alters prey selectivity in a coral-feeding reef fish. *Mar Ecol Prog Ser*. 2017; 580: 239–244.
56. Alvarez-Filip L, Dulvy NK, Gill JA, Cote IM, Watkinson AR. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc Biol Sci*. 2009; 276: 3019–3025. <https://doi.org/10.1098/rspb.2009.0339> PMID: 19515663
57. Thomsen MS, Hildebrand T, South PM, Foster T, Siciliano A, Oldach E, et al. A sixth-level habitat cascade increases biodiversity in an intertidal estuary. *Ecol Evol*. 2016; 6: 8291–8303. <https://doi.org/10.1002/ece3.2499> PMID: 27878096
58. Marzinelli EM, Burrows MT, Jackson AC, Mayer-Pinto M. Positive and negative effects of habitat-forming algae on survival, growth and intra-specific competition of limpets. *PLoS One*. 2012; 7: e51601. <https://doi.org/10.1371/journal.pone.0051601> PMID: 23251589
59. Löffler Z, Bellwood D, Hoey A. Associations among coral reef macroalgae influence feeding by herbivorous fishes. *Coral Reefs*. 2015; 34: 51–55.
60. Bittick SJ, Bilotti ND, Peterson HA, Stewart HL. *Turbinaria ornata* as an herbivory refuge for associate algae. *Mar Biol*. 2010; 157: 317–323.
61. Hay ME. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *Am Nat*. 1986; 128: 617–641.
62. Briggs CJ, Adam TC, Holbrook SJ, Schmitt RJ. Macroalgae size refuge from herbivory promotes alternative stable states on coral reefs. *PLoS One*. 2018; 13: e0202273. <https://doi.org/10.1371/journal.pone.0202273> PMID: 30226879
63. Paul VJ, Kuffner IB, Walters LJ, Ritson-Williams R, Beach KS, Becerro MA. Chemically mediated interactions between macroalgae *Dictyota* spp. and multiple life-history stages of the coral *Porites astreoides*. *Mar Ecol Prog Ser*. 2011; 426: 161–170.
64. Vieira C, Thomas OP, Culioli G, Genta-Jouve G, Houlbrequé F, Gaubert J, et al. Allelopathic interactions between the brown algal genus *Lobophora* (Dictyotales, Phaeophyceae) and scleractinian corals. *Sci Rep*. 2016; 6: 18637. <https://doi.org/10.1038/srep18637> PMID: 26728003
65. Goldberg W. Atolls of the world: revisiting the original checklist. Atoll Res Bull No. 610. Washington, D. C.: Smithsonian Institution Scholarly Press; 2016.
66. Altieri AH, Gedan KB. Climate change and dead zones. *Global Change Biol*. 2015; 21: 1395–1406.