Long-term blooming filamentous calcareous alga provides substrate for other coral-competitive macroalgae in the degraded lagoon of Dongsha Atoll (Pratas), Taiwan

Short title: Filamentous calcareous alga provides substrate for other coral-competitive macroalgae

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Abstract

Background: Red calcareous seaweeds of the genus *Galaxaura* have been associated with coral reef degradation. *Galaxaura* has low nutritional value for most herbivorous fishes and produces allelopathic chemicals in competition with corals. In this study, the abundance of the filamentous *Galaxaura divaricata* was surveyed on 13 spatially independent patch reefs across the lagoon of Dongsha Atoll, an isolated coral reef ecosystem in the northern South China Sea. Variations in *Galaxaura* cover on a degraded reef were monitored over a period of 17 months. Epiphytic macroalgae associated with *Galaxaura* were quantified, and species identifications aided through DNA barcoding.

Results: Patch reefs in the lagoon of Dongsha Atoll were degraded, exhibiting relatively low living coral cover (21 $\pm$ 3%), but high cover of macroalgae (30 $\pm$ 4%), and rubbles and dead coral (47 $\pm$ 4%). The distribution of *Galaxaura* was heterogeneous across the lagoon, with highest abundance in the southeast area. In that area *Galaxaura* has persistently bloomed on degraded reef for at least four years, covering up to 41% of the substrate. *Galaxaura* provides substrate for various macroalgae, 15 of which were identified to the species level, four to the genus level, one to the order Gelidiales, and one to the phylum cyanobacteria. Some of these epiphytes are allelopathic and known to frequently overgrow corals. For instance, the brown alga *Lobophora* sp28, third most common epiphytic macroalga on *Galaxaura*, frequently overgrows corals across the lagoon of Dongsha Atoll.

Conclusions: Our study demonstrated that an allelopathic and unpalatable seaweed, such as *Galaxaura* can bloom on degraded coral reefs for several years. The complex thallus-structure of *Galaxaura* provides suitable substrate for other macroalgae, some of which are noxious to corals.

By increasing the substrate availability for macroalgae, *Galaxaura* could facilitate the abundance of macroalgae, and decrease the recovery potential of degraded coral reefs.

Keywords: coral reef, epiphyte; *Galaxaura*; lagoon; macroalgae; phase-shift.

Introduction

Coral-macroalgae competition is a major ecological process on coral reefs [1,2]. However, climate change, overfishing, and anthropogenic pollution have driven corals worldwide to a decline and often facilitated macroalgae dominance on degraded reefs [3-9]. The replenishment of corals on degraded reefs is strongly influenced by the types of dominant macroalgae [10,11]. Macroalgae that produce noxious allelochemicals in competition with corals are considered most detrimental for the resilience of degraded coral reefs [10,12-14]. Allelopathic macroalgae may perpetuate their dominance on degraded reefs by inhibiting the process of successful recruitment of juvenile corals, the key process of coral reef recovery [15-17].

Species of the red, calcareous genus *Galaxaura* are common on coral reefs in the Pacific Ocean [18-22]. *Galaxaura* is one of the least nutritious macroalga to herbivores fish [23-26], and highly competitive with coral because of its allelopathic effects on coral and coral larvae [15,27]. Extracts of the lipid-soluble secondary metabolites of *Galaxaura filamentosa* were shown to cause bleaching and death of coral tissue upon direct contact [13-15,28], and deterred coral larvae from settlement [29]. It has been suggested that high abundance of *Galaxaura* on degraded reefs accounts for the inhibition of coral reef recovery [12,29]. More detailed investigations of the distribution and ecology of reef-associated seaweeds, such as *Galxaura*, and

their roles in outcompeting corals will provide valuable information for coral reef management and conservation [1,30].

Dongsha Atoll (also known as Pratas Islands) is the only large coral reef atoll (>500 km^2) in the northern South China Sea. The South China Sea is the largest tropical Pacific marginal sea in Southeast Asia [31], including numerous coral reef atolls and fringing reefs that are great natural resources, supplying large numbers of people with goods and services, such as fish and important ecological values [32-34]. The ring-shaped reef flat of Dongsha Atoll encircles a large lagoon with seagrass beds and hundreds of coral patch reefs [35]. The Lagoon patch reefs are structured into tops (1-5 m depth) and 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 [32,35-37]. The catastrophic mass bleaching event in 1998 and reoccurring bleaching events thereafter have caused severe mass mortalities of corals in the lagoon, followed by a marked increase of macroalgae [36,38].

The filamentous, calcareous macroalga *Galaxaura divaricata* is conspicuous on coral reefs in the lagoon of Dongsha Atoll [19] where it blooms in certain areas, overgrowing large parts of degraded reef substrate. Several macroalgae, e.g. *Sargassum* and *Lobophora*, are known to provide substrate and form habitats for epiphytic algae [39-41]. Increased substrate availability can lead to increased macroalgae biomass on coral reefs [1]. However, whether *Galaxaura* provides a suitable substrate for macroscopic epiphytes remains unexplored.

The aims of this study are to document the spatial patterns and persistence of *Galaxaura* blooms in the lagoon of Dongsha Atoll, show several aspects of *Galaxaura*-coral competition, and identify and quantify epiphytic macroalgae that grow on *Galaxaura*. Potential implications

of our observations, regarding the recovery potential of *Galaxaura* dominated reefs, and the role of *Galaxaura* as substrate for the facilitation of macroalgae abundance, are discussed.

Materials and methods

This study was conducted from April 2016 to September 2017 in Dongsha Atoll (Pratas Island) (Latitude 20°40'43"N, Longitude 116°42'54"E), an isolated coral reef atoll in the north of the South China Sea. The climate shows seasonal variability under the East Asian monsoon system, with a colder northeast monsoon season (as winter) and a warm southwest monsoon season (as summer) [31]. The ring-shaped atoll covers an area of approximately 500 km^2 and is situated 450 km southwest from the coast of Taiwan and 350 km southeast from Hong Kong (Fig 1). The outer reef flat is interrupted by two channels that are located north and south of a small islet (1.74km^2), allowing for water exchange between the lagoon and the open ocean [36,42]. The semi-closed lagoon is about 20 km wide with a maximum depth of 16 m deep near the center [36].

The abundance of the red, calcareous, filamentous seaweed *Galaxaura divaricata* was surveyed on 13 spatially independent lagoon patch reefs with SUBA (Fig 1B and S1 Table). Two 45-m transect lines were laid out across the reef top (1-5 m depth) and the reef slope (5-12 m depth) respectively. The percent cover of *Galaxaura*, living coral, macroalgae (MA; including low growing, filamentous turf algae [23, 24]), crustose coralline algae (CCA), and other substrate was estimated, using a 35 cm x 50 cm PVC quadrat [43]. Estimations were done at 1 m intervals and a total of 90 replicate quadrats were analyzed for each site. 'Other substrate' mainly constituted dead corals, rubbles, larger rocks covered with sediments and sparse turf algae, and

sand. The seawater temperature was measured every 30 min from March 2016 to September 2017, using Hobo temperature loggers that were fixed at the reef top and reef slope of each site.

To assess variations over time we monitored the percent cover of *Galaxaura* and living coral across the slope of site 7 at 5 m depth in April, July, and September 2016 and in September 2017. 45 replicate photos were taken with an Olympus Stylus-TOUGH TG4 digital camera (25-100 lens, 35mm equivalent) mounted onto a PVC-quadrat at 0.64 cm above a sampling 35 cm x 50 cm quadrat [43], using the survey method described above. Percent cover estimations of *Galaxaura* were aided by superimposing a 10 x 10 reference grid onto each photograph, where 1 quadrat represented 1% of the total area.

To quantify epiphytic macroalgae associated with *Galaxaura*, we randomly collected 30 thalli of *Galaxaura* from site 7 at 5 m depth. The samples contained an equal proportion of small (6 ± 4 g), medium (23 ± 6 g), and large (49 ± 20 g) thalli. Epiphytic macroalgae were identified to the closest identifiable taxonomic unit, using either the guidebook [19] or DNA barcoding. The presence and absence of each taxonomic unit was recorded, and the occurrence frequency (f) was calculated as follows: $f = c\ (taxonomic\ unit_i)/n$, where $c\ (taxonomic\ unit_i)$ stands for the count number of thalli that have the epiphyte taxonomic unit i, and n stands for the total number of thalli analyzed.

Two-paired t-tests were used to detect significant differences of live coral, macroalgae, and CCA percent cover between reef tops and reef slopes. A two-way ANOVA and a post-hoc Tukey test were applied to test for significant differences of *Galaxaura* percent cover between reef top and reef slope and among sites. Percent cover of *Galaxaura* and living coral cover at site 7 from four surveys conducted over a 17-month period were analyzed using a two-way ANOVA, and p-values < 0.05 were considered significant.

127 Macroalgae samples were preserved in silica gel and species identified through DNA
128 barcoding [44]. DNA was extracted with Quick-DNA™ Plant/Seed Miniprep Kit (Zymo
129 Research Co., USA). Primers for the plastid gene specific amplifications were used as follows:
130 *rbc*L *F7/R753* for rhodophytes [45], *rbc*L *F68/R708* for Phaeophyceae [46], and *tufA*
131 *F210/R1062* for green algae [47]. The newly generated sequences were deposited in GenBank
132 and searched using BLASTn against the GenBank database (S2 and S3 Tables). Sequence
133 similarities of > 98% were considered for species identification.
134

135 **Results**

136 Seawater temperatures in the lagoon were highest during the southwest monsoon season
137 (June-Sept.), averaging 30.1°C, and lowest during the northeast monsoon season (Nov.-April),
138 averaging 24.8°C. In July and August, maximum temperatures reached 34°C on reef tops and
139 32.7°C on reef slopes. Across sites the average coral cover accounted for 21 ± 3% (± SE) of the
140 benthic substrate (range: 5-43%) (Table 1). Average coverage of the substrate was 30 ± 4%
141 (range: 13-58%) by macroalgae, and 2 ± 0.2% (range: 1-3%) by crustose coralline algae (CCA).
142 Dead corals, rubbles, larger rocks, and sand accounted for an average of 47 ± 4% (range: 23-69%)
143 of the substrate. Living corals dominated the reef substratum on two out of 13 patch reefs (sites 1
144 and 13), whereas dead corals, rubbles, larger rocks, and sand dominated the substrate on nine out
145 of 13 sites. Macroalgae cover exceeded live coral cover on seven out of 13 sites. No significant
146 difference in coral cover and macroalgae cover between reef tops and reef slopes was detected
147 (P-values = 0.394 and 0.552).

148 The percent cover of *Galaxaura divaricata* was significantly different between reef tops
149 and reef slopes (P-value < 0.01), as well as among the 13 survey sites (P-value < 0.001). The

post-hoc Tukey test showed that *Galaxaura* was more abundant on reef slopes than on reef tops (P-value <0.05). The percent cover of *Galaxaura* was classified as very low (0-1.5%), low (1.5-5%), moderate (5-20%), and high (>20%) (P-value < 0.05; post-hoc Tukey). *Galaxaura* was most abundant on patch reef sites in the southeast lagoon (Table 2). The percent cover of *Galaxaura* was highest at site 9 (41%) and on the slope of site 7 (16%). Patch reefs in the northeast lagoon exhibited moderate, low, and very low cover of *Galaxaura* (range: 0.21-5.7%). Survey sites in the south, center, west, and north section of the lagoon were characterized by very low cover of the alga (range: 0-1.4%). The thallus shape and size of *Galaxaura* varied across sites (S1 Fig). Medium (5-15 cm diameter), ball-shaped thalli and large (15-30 cm), carpet-like thalli were exclusively present in the southeast lagoon. Small (1-5 cm), ball-shaped thalli and small, slender thalli were dominant on patch reefs in the northeast lagoon. DNA barcodes revealed that all samples of *Galaxaura* from various sites across the lagoon were 100% identical in their *rbc*L sequences, indicative of conspecificity (S3 Table).

Our observations suggest that a *Galaxaura* bloom can persist for several years. Thick canopies of *Galaxaura* have overgrown dead *Acropora* rubbles for at least 4 years on a degraded patch reef in the southeast section of the lagoon, with 41 $\pm$ 25% *Galaxaura* cover and 5 $\pm$ 14% living coral cover (site 9, 3-5 m depth) (Fig 2A-B). *Galaxaura* was frequently observed in contact with coral, which in some cases showed beached and dead tissue underneath or in contact with *Galaxaura*. The holdfast of *Galaxaura* penetrates the calcium carbonate structure, creating a strong attachment to the coral (Fig 2C). In some cases, fluorescent pink and bleached coral tissue occurred in contact with *Galaxaura*, indicative of potential allelopathic effects of *G. divaricata* on corals (Fig 2D).

172 The percent cover *Galaxaura* did not vary significantly among surveys at site 7
173 conducted over a period of 17 months (Fig 3). The cover of *Galaxaura* and living corals did not
174 change significantly among surveys (P-value = 0.595). *Galaxaura* cover averaged 15.91 $\pm$ 0.6%
175 ($\pm$ SE), and coral cover remained low, averaging 16.45 $\pm$ 1.17%. Coral cover and *Galaxaura*
176 cover were not significantly different (P-value = 0.770), and no interaction between the two was
177 detected (P-value = 0.780).

178 In our epiphyte survey we identified 21 taxonomic groups of macroalgae in association
179 with *Galaxaura*. Among those groups, we identified 15 to the species level, four to the genus
180 level, one to the order Gelidiales and one to the phylum cyanobacteria (Table 3 and S2 Table).
181 Among the 15 identified species, red algae were most abundant (10), followed by brown algae
182 (5), and green algae (5). The most common species associated with *Galaxaura* were the red
183 algae *Hypnea caespitosa* [48] (100% relative abundance) (Fig 4D), *Coelothrix irregularis* (87%),
184 *Ceramium dawsoniia* (43%) and the brown algae *Lobophora* sp28 [49] (57%) (Fig 4D), *Padina*
185 sp5 [50] (53%), and *Dictyota bartayresiana* (30%). The most common green algae associated
186 with *Galaxaura* were *Derbesia marina* (37%), *Caulerpa chemnitzia* (27%) (Fig 4B), and
187 *Boodlea composita* (20%). Epiphytic macroscopic cyanobacteria (filamentous > 1cm) had a
188 relative abundance of 17%. *Lobophora* sp28, third most common macroalga on *Galaxaura*, was
189 identified to frequently overgrow corals across the lagoon of Dongsha Atoll (Fig 5 and S2 Fig).
190

191 Discussion

192 The results of the benthic surveys indicate that coral reefs in the lagoon of Dongsha Atoll
193 are highly degraded, with high abundance of dead corals, rubbles, larger rocks, and sand (47%).
194 Our observation is consistent with previous surveys that noted signs of coral degradation in the

lagoon, with an extremely large proportion of coral rubbles and dead corals [36,51,52]. The majority of patch reef sites exhibited a coral cover of lower than 25%, which is considered degraded [53]. Coral reefs in the South China Sea have been facing increasing chronic and acute thermals stress over the past decades [33,38,51,54]. The summer mean sea surface temperature shows an average upward trend of 0.2°C / decade, with waters surrounding Dongsha Atoll warming at a faster rate than other areas of the South China Sea [33]. Prior to the 2007 establishment of Dongsha Atoll Marine National Park, Dongsha Atoll was heavily overfished, and large coral reef areas were destroyed through dynamite and cyanide fishing [36,52,54,55]. According to a previous survey coral cover and the number of new small corals were especially low on patch reefs in the south section of the lagoon [56]. Recurrent coral bleaching events [36,38,57], coral damage by annual typhoons, and destructive fishing practices may have acted synergistically, leading to the failure of recovery for some of the lagoon patch reefs. Coral cover and coral recruitment rate was especially low on patch reefs in the southeast lagoon [56].

Species of the red calcareous alga genera *Galaxaura* occur in two morphological forms, a smooth and a filamentous form, which is characterized by fine, assimilatory filaments [21]. Our observations suggested that, under certain conditions, the filamentous *Galaxaura divaricata* can become dominant on degraded reefs and form long-standing canopies that grow frequently in contact with corals. *Galaxaura* was heterogeneously distributed across the lagoon, and bloomed on degraded patch reefs in the southeast section, where it attained largest thallus sizes. Maybe something like this:

Our observations further show the persistence of *Galaxaura* on degraded reefs both over a 17-month period and for at least four years. However, our data do not resolve potential seasonal variations of *Galaxaura* during the cooler northeast monsoon season. In the tropical

218 waters of Florida, U.S., *Galaxaura* shows seasonal persistence with no significant change in
219 abundance among seasons [58].

220 The causes for *Galaxaura* blooms in the southeast area of the Dongsha lagoon are not
221 understood. The dominance of macroalgae, such as *Galaxaura*, on degraded reefs is probably the
222 consequence rather than the cause of initial coral decline [1,30,59,60]. There are several potential
223 factors that could facilitate a *Galaxaura* outgrowth after a disturbance, including shallow, calm,
224 and sheltered habitats, and nutrient-rich waters with high turbidity. Other members of the
225 *Galaxauraceae* family, such as *Tricleocarpa*, are known to prefer sheltered habitats [61], and
226 bloom under high water turbidity and low irradiance [62]. The southeast section of the lagoon,
227 where *Galaxaura* is most abundant, is sheltered by the relatively wide reef flat (2 km), and
228 characterized by shallow waters (1-5 meter) and low current [63]. *Galaxaura* was absent from
229 environments with strong water currents, i.e. west lagoon, channels, and forereef, where strong,
230 erosive currents [35,63] may create unfavorable conditions for *Galaxaura* to establish.

231 Due to limited water exchange with the open ocean, coral communities and associated
232 fauna of the shallow, semi-closed lagoons are highly vulnerable to heat stress, eutrophication,
233 and hypoxia [64-66], especially under the backdrop of climate change [67]. Recurrent mass
234 mortality events in the Dongsha lagoon in 2014 and 2015 killed thousands of fish, cephalopods,
235 gastropods, and crustaceans, and eradicated more than 25 km^2 of seagrass, potentially caused by
236 hypoxia [35,68]. During our 2017 survey we recorded extremely low densities of
237 macroinvertebrates, including echinoids, sea cucumbers, lobsters, and giant clams (Table S4).
238 *Galaxaura filamentosa* was among the very few macroalgae that proliferated in the Hikeru the
239 lagoon of French Polynesia, following a hypoxia-induced mass mortality event [18]. Elevated

240 nutrients from seagrass die offs in the southeast lagoon and a potentially higher resistance to
241 hypoxia may be additional factors promoting blooms of *Galaxaura.*

242 A long-term bloom of *Galaxaura* is likely to have profound implications on the recovery
243 potential of degraded reefs. The observations of this study further suggest that *Galaxaura*
244 *divaricata* is potentially allelopathic in competition with corals. Allelopathic competition with
245 corals has previously been demonstrated for *Galaxaura filamentosa* [12,14,15,27-29]. Extract of
246 *G. filamentosa* were shown to inhibit the settlement of *Acropora tenuis* larvae [29]. The
247 susceptibility of coral to algal overgrowth depends on the type of coral [1,59] and the coral
248 colony form. Branching corals appear most vulnerable to algal overgrowth [69]. In the lagoon of
249 Dongsha Atoll *G. divaricata* frequently grew in contact with massive and branching *Porites*, e.g.,
250 *P. lobata*, *P. cylindrica,* and *P. solida.* Previous studies in the tropical Pacific reported similar
251 observations, where *Porites*, in particular *Porites cylindrica*, was frequently found in contact
252 with the allelopathic *Galaxaura filamentosa*, suggesting that *Porites* may be relatively tolerant to
253 *Galaxaura* allelopathic chemicals [15]. *Acropora* corals are fast growing and considered
254 competitive against macroalgae overgrowth [59]. However, the majority of the thermal-
255 susceptible Acroporid species were eradicated following reoccurring bleaching events since 1998
256 [36,57]. The coral community in the lagoon of Dongsha Atoll has since been dominated by more
257 thermal tolerant genera, such as *Porites*, *Echinopora*, *Pavona*, and *Turbinaria* [51]. These coral
258 genera are rather slow-growing, and thought to be less competitive to macroalgae overgrowth
259 [17,59]. Unlike crustose coralline algae (CCA), *Galaxaura* does not stabilize the coral reef
260 matrix, and a long-term bloom of *Galaxaura* is likely to exacerbate the flattening of the complex
261 three-dimensional coral reef structure, which may have consequences for reef biodiversity,
262 ecosystem functioning and associated services [64,70].

263 Insufficient grazing after disturbance can lead to the establishment and full outgrowth of
264 macroalgae beyond their initial stages [30]**.** *Galaxaura* is known to be largely unpalatable for
265 various herbivorous fishes due to its calcareous thallus and low nutritional content
266 [23,25,26,71,72]. Once established, large macroalgae are less efficiently consumed by
267 herbivorous fishes [30,73]. Local herbivorous fish population on *Galaxaura*-dominated reefs in
268 the Dongsha lagoon may not be effective to prevent or reverse the space monopolization by
269 *Galaxaura* [30,74]. It is suggested that *Galaxaura* can alter the chemical microclimate on
270 degraded reefs with potential implications on fish behavior. Butterfly fishes and other
271 corallivores avoid corals in close association with *Galaxaura filamentosa*, making it potentially
272 difficult for these trophic guilds to find food [75,76]. Water soluble chemicals of *Galaxaura*
273 *rugosa* negatively impact the predator risk assessment of damselfish by nullifying their
274 perception of predator warn odors [11]. In summary, the long-standing canopies of *Galaxaura*
275 are likely to hamper coral larvae recruitment through allelopathic recruitment inhibition [29],
276 ultimately preventing coral reef recovery [1,15].

277 *Galaxaura divaricata* provides a suitable substrate to host a variety of macroalgae. Some
278 of the identified macroalgae on *Galaxaura* are widely important in coral overgrowth in response
279 to disturbances, and are known for their allelopathic inhibition coral larvae recruitment, e.g.
280 *Lobophora* [77,78], *Dictyota bartayresiana* [79,80], and cyanobacteria [81,82]. Here, we firstly
281 report that the yet undescribed species, *Lobophora* sp28 [49], third most abundant macroepiphyte
282 on *Galaxaura*, was frequently observed to overgrow and kill corals, preferentially branching
283 *Porites* spp. (primarily *P. cylindrica*) through epizoism (**Figs 5 and S2**). Similarly, *Lobophora*
284 *hederacea* overgrows and kills corals in New Caledonia through epizoism [83].

285 *Galaxaura* is known to be of low preference to various herbivorous fishes due to its
286 calcification [84,85] and low nutritional value [25,84,86,87]. *Galaxaura* was proposed to provide
287 associational refuge to more palatable macroalgae [86]. For instance, rabbitfishes prefer
288 *Caulerpa* and *Dictyota* [88,89], but avoid *Galaxaura* [23]. These epiphytic macroalgae thus
289 could indirectly gain the benefit by growing between the branches of *Galaxaura*, as they are less
290 likely to be spotted by herbivorous fish. Commensalistic interactions are important for the
291 establishment of less common, nutrient-rich seaweeds that grow in association with common,
292 nutrient-poor seaweeds [80]. Even if the common seaweeds lowered the growth rate of the less
293 common ones (competition), evidence suggest that the benefits provided by macroalgae
294 associations outweigh the drawbacks through competition [80,90]. Moreover, the microscopic
295 filaments of *Galaxaura* may facilitate the attachment of macroalgae spores, while the calcium
296 carbonate branches may provide structural support for other macroalgae. Considering that an
297 increase in substrate availability can enhance the biomass of macroalgae on the reef [1], we
298 hypothesize that, by providing a suitable and sheltered substrate for epiphytic macroalgae,
299 *Galaxaura* may facilitate the diversity and abundance of macroalgae on degraded reefs. This
300 study is merely observational and does not provide experimental evidence for the facilitation of
301 macroalgae diversity and abundance by *Galaxaura.* However, the abovementioned hypotheses
302 would be of great interest awaiting future validation.
303

304 ## Conclusions

305 Our observations illustrated that the allelopathic and unpalatable seaweed *Galaxaura*
306 *divaricata* can become dominant on degraded reefs in shallow, sheltered environments. On
307 degraded coral reefs, the dominant macroalgae have a profound impact on coral recruitment and

coral recovery. Allelopathic and unpalatable macroalgae such as *Galaxaura* were proposed to perpetuate their dominance on degraded reefs by chemically inhibiting the process of coral recruitment. Thus, a long-term dominance by the allelopathic, nutrient-poor *Galaxaura* could provide a negative feedback, perpetuating reef degradation. In addition, we suggest that *Galaxaura* provides a suitable substrate for a variety of macroalgae, potentially facilitating macroalgae growth and abundance on degraded reefs. Several common macroepiphytes on *Galaxaura* have been proven to be allelopathic in competition with corals and inhibit coral larvae settlement. Thus, degraded coral reefs dominated by *Galaxaura* may fail to recover, and face a substantial decline in biodiversity of corals, fishes, and other associated fauna, which may have far-reaching effects on coral reef ecosystem functioning and services. Macroalgal assemblages, such as the *Galaxaura*-macroepiphyte system, warrant further investigation to better understand the interactions between macrophyte inhabitants and habitat forming seaweeds and their ecological implications. There are 439 listed coral reef atolls on earth; among them are 335 with open or semi-enclosed lagoons [91]. Atoll lagoons are highly productive and serve as valuable and nursery habitat for marine life; however, they are most vulnerable to the effects of climate change [18,66,67]. Results from our study can be informative for the management and conservation of lagoons and shallow, inshore coral reef ecosystems, especially for coral reefs in the South China Sea and the Pacific Ocean, where *Galaxaura* is a common seaweed.

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Tables

Table 1. Cover[a] (%) of live coral, macroalgae (MA), crustose coralline algae (CCA), and other substrate on 13 patch reefs in the lagoon of Dongsha Atoll, South China Sea.

	Location	Coral	MA	CCA	Other[b]
1	North	40 ± 24	35 ± 23	1.93 ± 2.18	23 ± 23
2	North	22 ± 25	13 ± 12	2.57 ± 5.58	63 ± 32
3	North	24 ± 22	29 ± 23	1.47 ± 2.39	46 ± 24
4	Northeast	10 ± 15	20 ± 16	1.37 ± 2.42	69 ± 22
5	Northeast	17 ± 19	29 ± 25	1.62 ± 1.91	53 ± 32
6	Northeast	24 ± 20	19 ± 15	2.15 ± 3.01	55 ± 25
7	Southeast	14 ±17	58 ± 24	2.79 ± 2.59	25 ± 22
8	Southeast	29 ± 29	20 ± 14	2.07 ± 2.15	50 ± 33
9	Southeast	5 ± 14	41 ± 25	0.84 ± 0.89	53 ± 25
10	Center	10 ± 13	43 ± 27	3.33 ± 3.07	43 ± 25
11	Center	24 ± 27	18 ± 19	1.07 ± 1.27	56 ± 25
12	West	11 ± 19	42 ± 24	2.46 ± 2.94	45 ± 26
13	West	43 ± 25	22 ± 18	3.00 ± 3.63	32 ± 29
	mean ± SE	**21 ± 3**	**30 ± 4**	**2.05 ± 0.21**	**47 ± 4**

[a]Data are mean (%) ± SD of 90 replicate quadrats.
[b] "Other substrate" constituted mainly dead coral, larger rocks covered with sediments and sparse turf algae, rubbles and sand.

579 **Table 2. Cover (%) of *Galaxaura divaricata* on 13 patch reefs in the lagoon of Dongsha Atoll,**

580 **South China Sea.**

Site	Location	Patch reef area		Cover rank
		Top (1-5 m)	Slope (5-10 m)	
1	North	0.02	0.02	very low
2	North	0	0	very low
3	North	0.27	0.31	very low
4	Northeast	1.52	1.4	very low - low
5	Northeast	5.69	3.37	low - moderate
6	Northeast	0.79	0.21	very low
7	Southeast	0.02	15.86	moderate
8	Southeast	0.17	4.31	very low - low
9	Southeast	41.87	40.87	high
10	South	0	0	very low
11	Center	0.46	0.02	very low
12	West	0	0	very low
13	West	0	0	very low

581 [a]Data are mean (%) of 45 replicate quadrats for reef top and reef slope respectively.

582

583 **Table 3. Relative abundance (%) of epiphytic macroalgae on *Galaxaura divaricata* from a**

584 **degraded patch reef.**

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

585 Macroscopic epiphytes were identified from 30 thalli of *G. divaricata* from site 7 at 5 m depth.
586 [a]Identification of species and taxonomic groups according to [19].
587 [b]GenBank number in parentheses based on species identifications through DNA barcoding.
588 [c]Denomination according to [49].
589 [d]Denomination according to [50].
590

Figure legends

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.

Fig 2. *Galaxaura divaricata* overgrowth of corals. A-B) *Galaxaura* has overgrown a degraded patch reef in the southeast lagoon of Dongsha Atoll for at least 4 years (site 9, 3-5 m depth). C) The holdfast of *G. divaricata* penetrates into a branching Porites coral (*Porites cylindrica*), creating small holes (inlet). D) Coral (*Porites solida*) tissue bleaching (arrows) following direct contact with *Galaxaura*, allelopathic chemicals produced by the alga.

Fig 3. Long-lasting bloom of *Galaxaura divaricata* on site 7 in the southeast lagoon of Dongsha Atoll. The percent cover of *G. divaricata* did not change significantly among surveys conducted over a period of 17 months (P-value > 0.05; Two-way ANOVA). Data are mean + SE of 45 replicate quadrats.

Fig 4. Examples showing epiphytic macroalgae that frequently grow on *Galaxaura divaricata*. A) *Valonia ventricosa*, B) *Caulerpa chemnitzia*, C) *Dictyota* sp., D) *Lobophora* sp28 [49] (arrow head), and *Hypnea caespitosa* (arrow).

Fig 5. 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 wide spread in the shallow lagoon of Dongsha Atoll.

Supplementary information

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

Site	Latitude	Longitude
1	20°44'26.28"	116°47'8.879"
2	20°43'31.62"	116°47'52.679"
3	20°42'16.14"	116°48'27.419"
4	20°44'20.52"	116°51'35.699"
5	20°42'29.88"	116°52'54.599"
6	20°42'6.72"	116°50'53.279"
7	20°38'24"	116°50'20.999"
8	20°38'3.12"	116°49'30.479"
9	20°36'52.86"	116°49'24.179"
10	20°36'53.4"	116°46'2.399"
11	20°39'52.2"	116°46'32.159"
12	20°41'49.2"	116°44'45.659"
13	20°42'12.36"	116°44'14.639"

617 **S2 Table. Information and Genbank numbers of macroalgae samples used for DNA**

618 **barcoding in this study.**

Species	Phylum	Voucher#	Date	Site	Area	Substrate	Marker	GenBank#
Ceramium dawsonii	Red	KO208	Oct-16	7	slope	*G. divaricata*	*rbc*L	MH048927
Coelothrix irregularis	Red	K0206	Oct-16	7	slope	*G. divaricata*	*rbc*L	MH048928
Hypnea caespitosa	Red	K0204	Oct-16	7	slope	*G. divaricata*	*rbc*L	MH048929
Hypnea caespitosa	Red	K0203	Oct-16	7	slope	*G. divaricata*	*rbc*L	MH048930
Hypnea caespitosa	Red	SD17120	Aug-17	7	slope	*G. divaricata*	*rbc*L	MH048931
Hypnea sp.	Red	K0205	Oct-16	7	slope	*G. divaricata*	*rbc*L	MH048932
Lobophora sp28[a]	Brown	SD17023	Aug-17	7	slope	*G. divaricata*	*rbc*L	MH048934
Lobophora sp28	Brown	SD17021	Aug-17	7	slope	*G. divaricata*	*rbc*L	MH048935
Lobophora sp28	Brown	SD17019	Aug-17	7	slope	*G. divaricata*	*rbc*L	MH048936
Lobophora sp28	Brown	SD17017	Aug-17	7	slope	*G. divaricata*	*rbc*L	MH048937
Lobophora sp28	Brown	K0173	Apr-16	7	slope	Coral	*rbc*L	MH048940
Lobophora sp28	Brown	SD17058	Aug-17	9	slope	Coral	*rbc*L	MH048941
Padina sp5[b]	Brown	SD17114	Aug-17	7	slope	*G. divaricata*	*rbc*L	MH048933
Caulerpa chemnitzia	Green	SD17117	Aug-17	7	slope	*G. divaricata*	*tufA*	MH048959

619 [a]Denomination according to [49].
620 [b]Denomination according to [50].
621

622 **S3 Table. Information and Genbank numbers of *Galaxaura divaricata* samples from**

623 **various locations in the lagoon of Dongsha Atoll that were used for DNA barcoding in this**

624 **study.**

Species	Voucher#	Date	Site	Area	Substrate	Thallus size	Marker	GenBank#
G. divaricata	K0210	Apr-16	7	slope	rock	medium	*rbc*L	MH048946
G. divaricata	R90B12	Feb-14	9	top	rock	large	*rbc*L	MH048942
G. divaricata	SD17048	Aug-17	9	slope	rubble	large	*rbc*L	MH048957
G. divaricata	SD17098	Aug-17	6	top	rock	small	*rbc*L	MH048943
G. divaricata	SD17099	Aug-17	1	top	rock	small	*rbc*L	MH048956
G. divaricata	SD17100	Aug-17	5	top	rock	small	*rbc*L	MH048955
G. divaricata	SD17101	Aug-17	5	top	rock	small	*rbc*L	MH048958
G. divaricata	SD17102	Aug-17	5	slope	rock	medium	*rbc*L	MH048954
G. divaricata	SD17103	Aug-17	1	slope	rock	small	*rbc*L	MH048953
G. divaricata	SD17104	Aug-17	6	slope	rock	medium	*rbc*L	MH048952
G. divaricata	SD17105	Aug-17	5	slope	rock	medium	*rbc*L	MH048951
G. divaricata	SD17106	Aug-17	6	slope	rock	small	*rbc*L	MH048950
G. divaricata	SD17107	Aug-17	6	slope	rock	small	*rbc*L	MH048944
G. divaricata	SD17110	Aug-17	6	top	coral	medium	*rbc*L	MH048949
G. divaricata	SD17112	Aug-17	4	slope	rock	medium	*rbc*L	MH048948
G. divaricata	SD17113	Aug-17	4	slope	rock	small	*rbc*L	MH048947

625

626

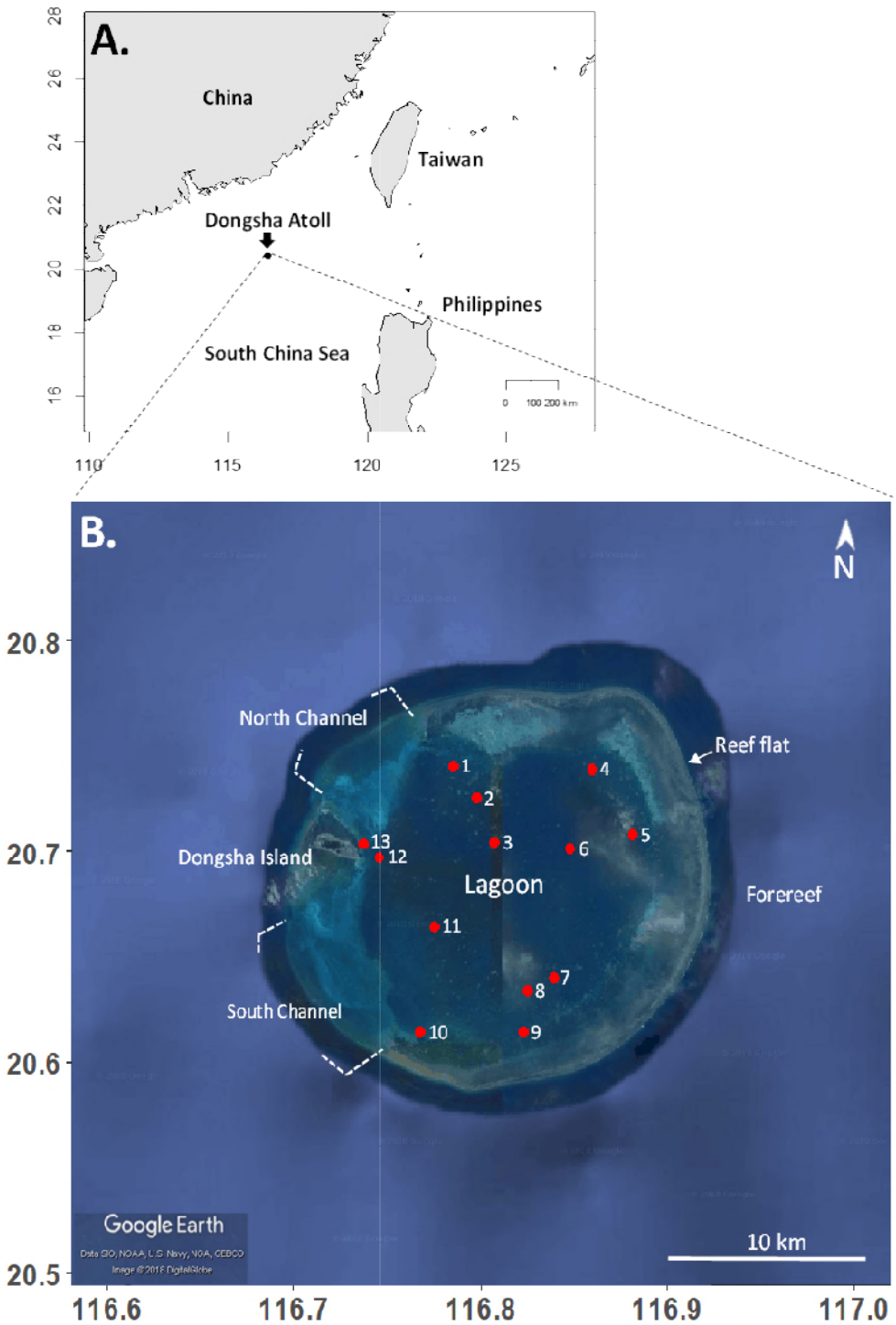
S4 Table. Paucity of macrobenthic invertebrates in the lagoon of Dongsha Atoll.

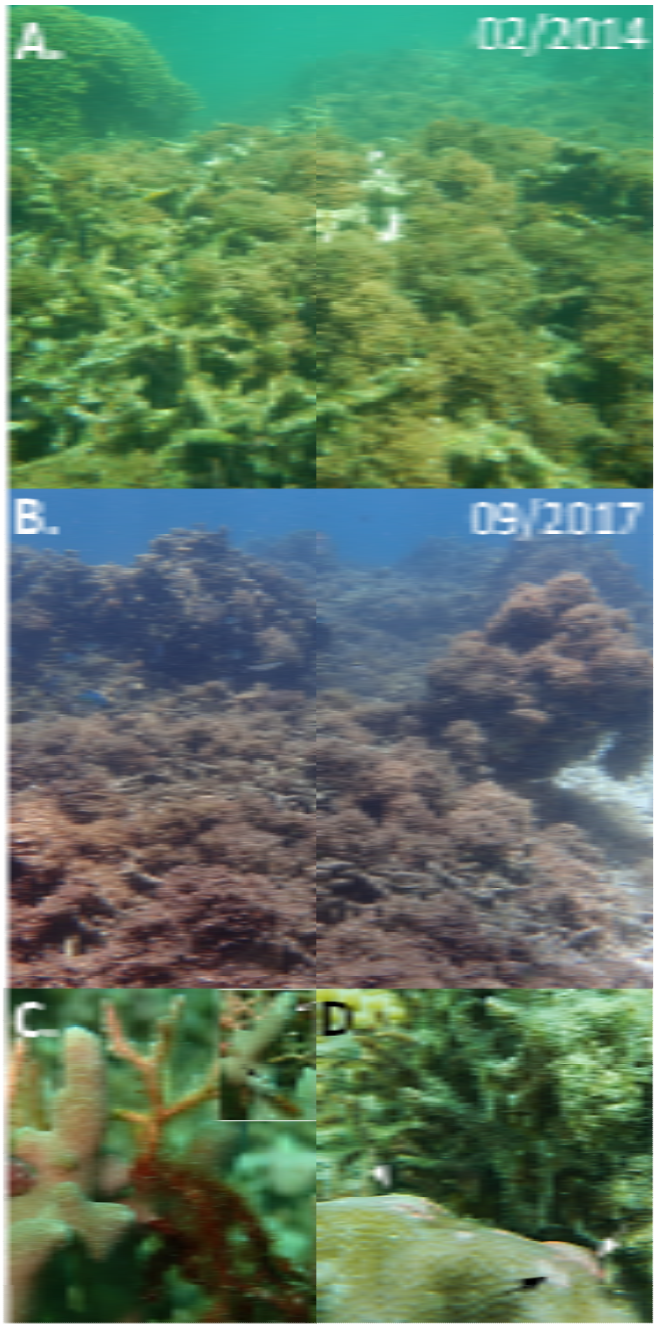
Macrobenthic fauna	Count	Density (individual/ 100 m^2)
Diadema savignyi	3	0.03
Diadema setosum	1	0.01
Echinometra mathaei	126	1.26
Echinothrix calamaris	3	0.03
Tripneustes gratilla	4	0.04
Culcita novaeguineae	54	0.54
Echinaster luzonicus	2	0.02
Fromia spp.	8	0.08
Linckia multifora	15	0.15
Holothuria	0	0
Cypraea tigris	3	0.03
Giant clam	34	0.34
Lambis spp.	3	0.03
Lobster	0	0

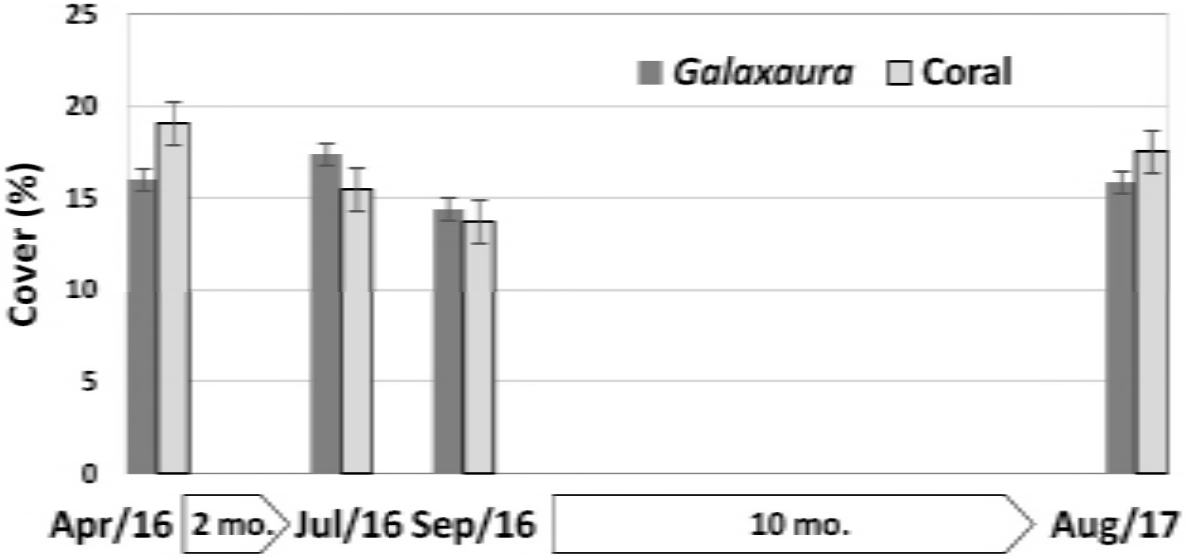
Data derived from a belt transect survey of 13 patch reefs and seven seagrass beds (10,000 m^2 total area surveyed) across the lagoon of Dongsha Atoll in September 2017.

S1 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.

S2 Fig. Coral overgrowth by *Lobophora* sp28. A) Coral overgrowth (*Porites cylindrica* in this case) by *Lobophora* sp28 is a wide spread in the lagoon of Dongsha Atoll. B) The same coral showing dead tissue (arrow) after removal of the algae.

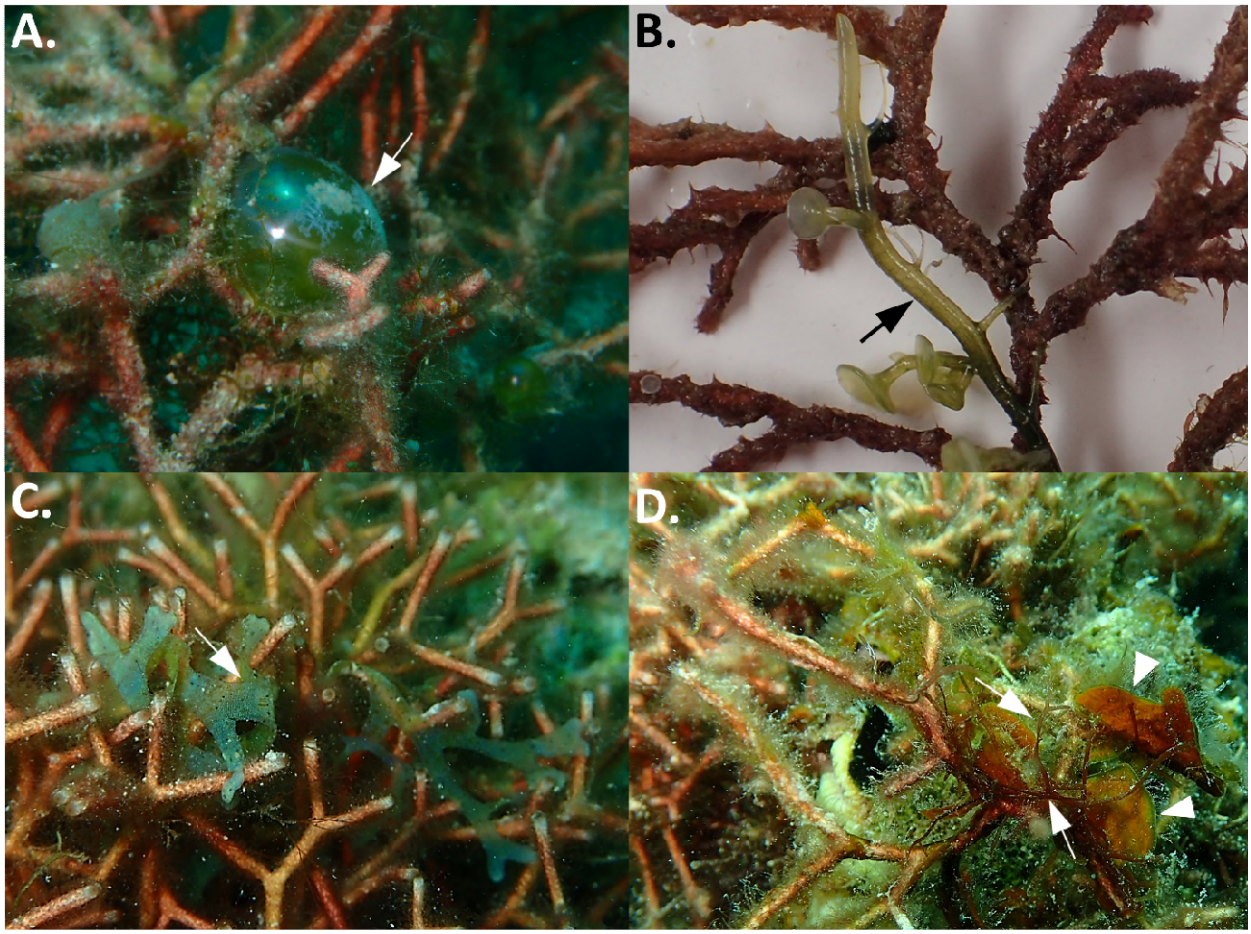

A.
China
Taiwan
Dongsha Atoll
Philippines
South China Sea
0 100 200 km
28
26
24
22
20
18
16
110
115
120
125
B.
N
North Channel
Reef flat
Dongsha Island
Lagoon
Forereef
South Channel
1
2
3
4
5
6
7
8
9
10
11
12
13
Google Earth
10 km
20.8
20.7
20.6
20.5
116.6
116.7
116.8
116.9
117.0

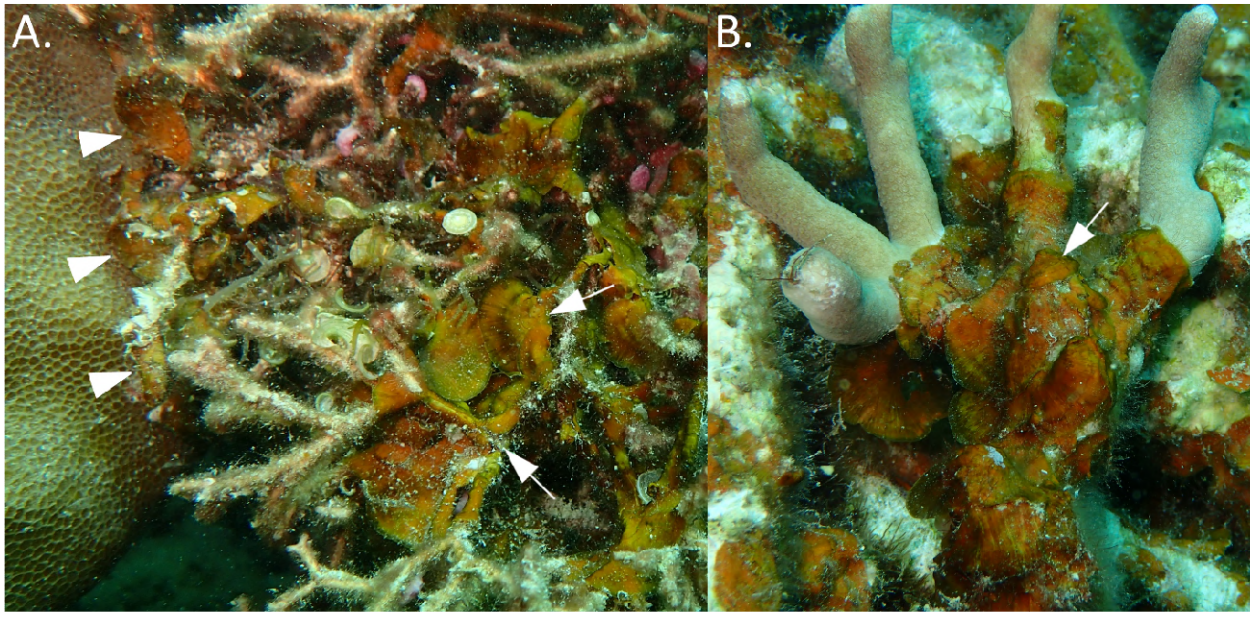

A.
02/2014
B.
09/2017
C.
D.

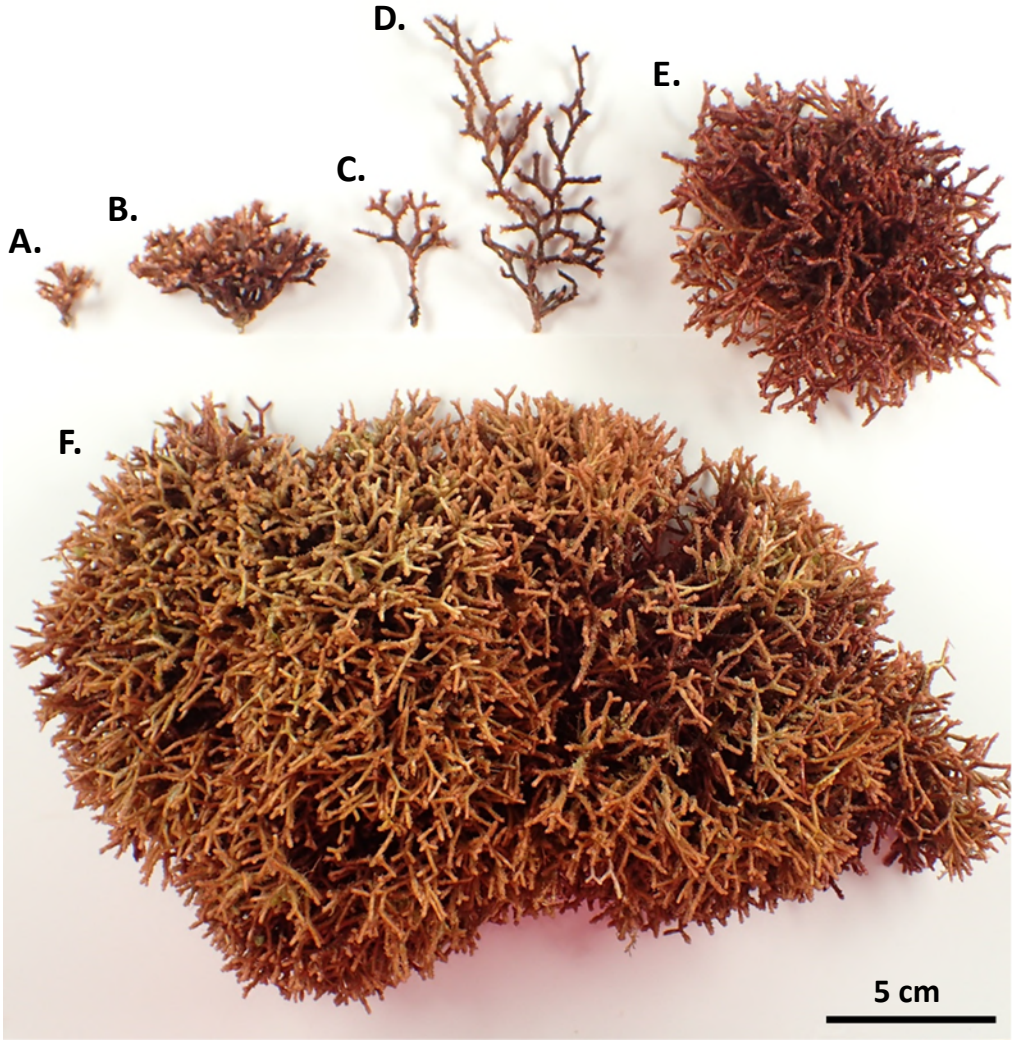

25
20
15
10
5
0
Cover (%)
Galaxaura
Coral
Apr/16
2 mo.
Jul/16
Sep/16
10 mo.
Aug/17

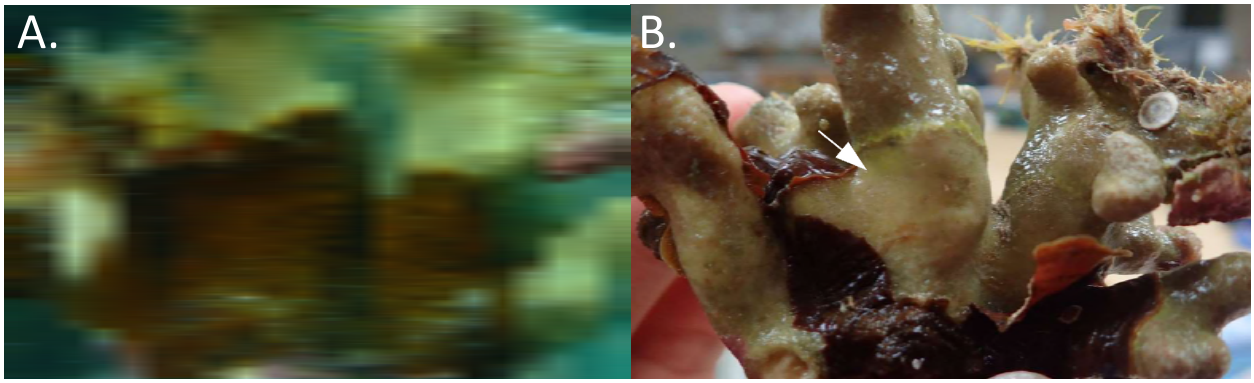
643

644


A.
B.
C.
D.


A.
B.


A.
B.
C.
D.
E.
F.
5 cm



651