

Limited interspecific variation in grazing susceptibility of the brown alga *Lobophora* to herbivory

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Abstract :

The genus *Lobophora* is a notable benthic algal component of tropical coral reefs, capable of dominating large reef areas following coral mortality and herbivory declines. The alga, however, has been the object of contradictory observations in terms of susceptibility to herbivory. Unaware of the species-richness of this genus, most studies referred to *Lobophora variegata*, a species assumed to present various morphotypes and chemotypes, occupying diverse ecological niches. Variation in susceptibility to herbivory has been consequently interpreted as intraspecific variation in terms of morphology and chemical composition as well as differences in herbivore guild compositions and diet across different locations (e.g., habitat, reef, region). Recent taxonomic studies of *Lobophora* disclosed a high species diversity, which could explain previous conflicting observations. The present study tested the grazing susceptibility of seven species of *Lobophora* (*L. dimorpha*, *L. hederacea*, *L. monticola*, *L. obscura*, *L. rosacea*, *L. sonderi* and *L. undulata*), which differ in growth form as well as in their chemical composition and fine-scale ecological niche on coral reefs in the southern lagoon in New Caledonia, to two important herbivores in New Caledonia, the rabbitfish *Siganus lineatus* and the sea urchin *Diadema setosum* using tank, cage, and *in situ* experiments. All seven *Lobophora* species were markedly consumed *in situ* and by the two herbivores. Differences in consumption among the *Lobophora* species were small but statistically significant. *Lobophora rosacea*, characterized by a distinct secondary metabolome, was significantly more consumed by the two herbivores. Conversely, *L. sonderi* was always among the least consumed species. These results point to the possible role of chemical defense, and suggest that *L. rosacea* may produce less or different chemical deterrents than the other *Lobophora* species, and that *L. sonderi* may produce deterrents active over a wider range of herbivores. However, the limited interspecific differences in consumption point to the greater importance of associational and spatial refuges as defense strategies against herbivores over chemical or morphological defenses in the genus *Lobophora*.

Highlights

► This is the first experimental study to specifically test interspecific grazing susceptibility in the brown alga *Lobophora*. ► Grazing susceptibility of seven *Lobophora* species was tested *in situ* and in controlled systems to two herbivores. ► All *Lobophora* species were markedly consumed by the herbivorous fish *Siganus lineatus* and the sea urchin *Diadema setosum*. ► Limited interspecific differences in consumption were observed between the seven *Lobophora* species in all experiments. ► Results indicate limited effects of morphology and chemical composition among species in their grazing susceptibility.

Keywords : Defense, Escape, Herbivory, *Lobophora*, Macroalgae

1. Introduction

The brown algal genus *Lobophora* J.Agardh (1894) (Dictyotales, Phaeophyceae) is a common seaweed of tropical coral reefs. Following natural and anthropogenic disturbances, it has recurrently bloomed in reefs that have shifted from coral- to macroalgal-dominated assemblages (e.g. De Ruyter van Steveninck & Breeman 1987b, Diaz-Pulido et al. 2009). These large-scale events illustrate how in normal conditions *Lobophora* cover is regulated by processes including herbivory and competition for space notably with corals. For instance, the mass mortality of *Diadema antillarum* in the Caribbean in the mid-80s (De Ruyter van Steveninck & Breeman 1987b, Steneck 1993) but also herbivore exclusion experiments (Kennelly 1991, Jompa & McCook 2002a, b, Diaz-Pulido & McCook 2003, Burkepile & Hay 2008, Morrow et al. 2011) resulted in a significant increase in *Lobophora* indicating the intense consumption necessary to restrict the algal cover.

Grazing experiments resulted in contrasting observations in terms of consumption, with studies showing low (Pillans et al. 2004) to high (Lewis 1985) preference for *Lobophora* relative to other macroalgae, but also large differences in *Lobophora* consumption by members of the same family (Pillans et al. 2004, Bennett et al. 2010), or even from the same species (De Ruyter van Steveninck & Breeman 1987a, b, Morrison 1988, Solandt & Campbell 2001, Tuya et al. 2001). Contrasting observations in terms of *Lobophora* consumption have been ascribed to chemical and morphological differences among different morphotypes/ecotypes of the species *L. variegata*. Some authors attributed the low preference for *Lobophora* by herbivores (e.g., sea urchin, fishes and sea snails; Bolser & Hay 1996, Pillans et al. 2004, Ng et al. 2013) to the presence of feeding deterrents such as polyphenolic secondary metabolites (e.g., phlorotannins; Targett et al. 1995, Bolser & Hay 1996, Arnold &

Targett 1998, 2000). In this sense, Bolser and Hay (1996) attributed the greater consumption of *Lobophora* by *Diadema antillarum* in temperate (North Carolina) versus tropical (Bahamas) regions to the higher concentrations of phlorotannins. In addition, *Lobophora* resistance to herbivory was associated to its morphology, i.e., structural defense (Littler 1980, Steneck & Watling 1982). Coen and Tanner (1989) showed differential susceptibilities to herbivory by fish and crabs among different morphotypes. Conversely, Vergés et al. (2011) did not find differences in consumption between reef flat-decumbent and lagoon-ruffled morphotypes.

Previous work on *Lobophora* susceptibility to herbivory has used individuals from the same species (i.e., *L. variegata*) with intraspecific variations (i.e., contrasting morphotypes, chemotypes and growing at different depths or locations (Coen & Tanner 1989, Vergés et al. 2011)). However, in the light of recent molecular studies, which revealed high species diversity in *Lobophora*, with over 100 species worldwide (Vieira et al. 2016, Vieira et al. 2017, Vieira et al. 2018, Camacho et al. 2019, Vieira et al. 2019), these previous studies were most likely studying different species of *Lobophora*, and thus were comparing grazing susceptibility among different species and not among different morphotypes or chemotypes of a single species.

With our best knowledge of *Lobophora* species diversity, the present study aims to test interspecific variation in susceptibility to herbivory. A review on the species diversity in New Caledonia indicated that the genus contains at least 31 species in this archipelago located East of Australia, and that *Lobophora* species have developed very specific ecological niches together with morphologies. Seven species commonly found in the Southwestern lagoon of New Caledonia and presenting characteristic morphologies and ecologies (Vieira et al. 2014) were selected for this study (*L. dimorpha* C.W.Vieira, Payri & De Clerck, *L. hederacea* C.W.Vieira,

Payri & De Clerck, *L. monticola* C.W.Vieira, Payri & De Clerck, *L. obscura* (Dickie) C.W.Vieira, De Clerck & Payri, *L. rosacea* C.W.Vieira, Payri & De Clerck, *L. sonderi* C.W.Vieira, De Clerck & Payri and *L. undulata* C.W.Vieira, Payri & De Clerck; Figs 1, S1). Morphologies range from tightly crustose (e.g., *L. obscura*) to stipitate (e.g., *L. sonderi*) forms with intermediate growth forms including procumbent (e.g., *L. dimorpha*), decumbent (e.g., *L. hederacea*, *L. undulata*, *L. monticola*) and ruffled (e.g., *L. rosacea*). The rigidity of their thallus is linked to their thickness also varying among species (Table 1). These species grow on different substrates and reef types, characterized by specific depth, hydrodynamism, herbivory intensity and benthos composition (Vieira et al. 2014). For instance, *L. obscura* commonly grows on coral rubbles and rocks at shallow depths where herbivory is rather low because of high wave exposure. In contrast *L. rosacea* and *L. hederacea* grow in coral dominated habitat down to 5 meters where herbivory is more intense, niched amongst branching corals. *Lobophora hederacea* is commonly found in the inner barrier reef, while *L. rosacea* is more common on fringing and islet reefs within the lagoon. In contrast, *L. sonderi* grows in low herbivory and less exposed habitats (e.g., leeward side of islets) such as in macroalgal beds typically dominated by *Sargassum* and *Turbinaria* or on sand bottoms below 5 meters depth. Some species also present different ecotypes such as *L. rosacea* either found nested amongst coral branches or epiphytic on *L. sonderi* (Fig. S1f). Metabolomics fingerprints of six New Caledonian species of *Lobophora* (*L. dimorpha*, *L. hederacea*, *L. obscura*, *L. rosacea*, *L. sonderi* and *L. undulata*,) provide evidence for clear chemical compositional differences among species (Vieira et al. 2016b). These metabolomics analyses showed that these six

species displayed characteristic secondary metabolomics profiles, with one species, *L. rosacea*, particularly standing out (Fig. S2).

The present study aims to test the grazing susceptibility of seven *Lobophora* species from New Caledonia to two important herbivores in New Caledonia, the rabbitfish *Siganus lineatus* and the sea urchin *Diadema setosum* using tank, cage, aquarium and *in situ* experiments. The study has for dual objectives to test the consumption of *Lobophora* by different herbivores and to compare the relative preference for species that are morphologically and chemically different.

3. Material and methods

Three grazing experiments were performed in the southwest lagoon of New Caledonia in April 2014, in the fish farm Aqualagon (Baie N'go, New Caledonia), in the natural environment, and aquariums of the Institut de Recherche pour le Développement (IRD) in Noumea. In all experiments, *Lobophora* thalli from different species were alternatively and equidistantly disposed along lines in a semi-random manner, i.e., while we made sure that individuals from the same species were never next to each other, the placement of species was random to avoid any bias. All experiments lasted 24 h.

3.1. Lobophora sampling

Seven *Lobophora* species (*L. dimorpha*, *L. hederacea*, *L. monticola*, *L. obscura*, *L. rosacea*, *L. sonderi* and *L. undulata*,) were collected on SCUBA in different localities (Table S1) within the southwestern lagoon of New Caledonia on the 16th of April 2014. *Lobophora* samples were collected, kept in a cooler, for less than 2 h, until treatment in the lab.

3.2. Fish farm experiments

The grazing experiments in the fish farm were conducted in fish tanks (3 m³; Fig. S3a) and in circular open-water fish cages (8 m in diameter x 6 m in depth) with a single species of rabbitfish (Fig. S3b), *Siganus lineatus* (Valenciennes, 1835), a common fish in New Caledonia and identified as a prominent herbivore in the Great Barrier Reef (Mantyka & Bellwood 2007). *Lobophora* species were inserted in three-stranded polypropylene lines. For the tank experiments, the lines were 1 m long and the samples were fixed 10 cm from each other. For the cage experiments, the lines were 5 m long and specimens were fixed every 15 cm. The lines were disposed vertically in the tubs and net pens. Grazing susceptibility of *Lobophora* was tested on juveniles and commercial size of *S. lineatus*, in the tanks (2 adult tanks, 1 juvenile tank) and the cage (2 juvenile cages, 1 adult cage). The density of fishes in the adult tanks was of 3-5 fish.m⁻³ and in the juvenile tank of around 25 fish.m⁻³.

3.3. In situ experiments

In situ experiments took place in different reefs in front of Noumea. Triplicates of 20 m lines were deployed at five different sites (Table S2). *Lobophora* thalli were inserted every 25 cm between strands of three-stranded polypropylene lines (Fig. S3c). We used ten replicates per species, resulting in 80 algal thalli per line. Lines were fixed horizontally by metal rods, at 1 m above the lagoon floor.

3.4. Aquarium experiments

Grazing experiments in the aquarium were conducted with the sea urchin *Diadema setosum* (Lesk, 1778), a common grazer in the Pacific tropical region. The seven *Lobophora* species were alternatively stapled along a nylon fishing line, and fixed on the aquarium bottom using diving weights (Figs S3d, S4). Nine lines (which represent nine replicates per species) were distributed in three aquariums, which represent a

total of 21 *Lobophora* specimens (i.e., 7 species × 3 replicates) per aquarium (Fig. S4). In each aquarium four individuals of sea urchins were put together (Fig. S4).

3.4. Algal consumption rates

To measure the algal biomass consumed, we measured the algal dry-blotted weight before and after the grazing experiments to the nearest 0.001 g. Given the significant differences of thallus size and thicknesses, we also calculated the percentage of alga consumed. ANOVA's were performed on both the total consumed biomass and the percentage consumed. Results for each experiment (*in situ*, fish farm and aquarium) were pooled and averaged.

3.6. Statistical analyses

Normality of results was tested with the Shapiro-Wilk test. If the responses violated parametric assumptions, grazing results were evaluated using the Kruskal-Wallis H tests followed by Tukey honest significant difference (HSD) post hoc comparisons test for significant Kruskal-Wallis findings. If data respected the parametric assumptions, a one-way ANOVA was performed followed by the Tukey post hoc HSD test for significant ANOVA findings. Statistical analyses were performed using the computing environment R (R Development Core Team 2013).

4. Results

4.1. Fish farm grazing experiment

All *Lobophora* species were consumed by *S. lineatus*, with an average consumption of algal material ranging from 48 ± 23 (\pm s.d.; *L. dimorpha*) to 158 ± 54 mg (*L. monticola*); and percentage of alga consumed ranging between 38 ± 26 (*L. undulata*) and 53 ± 30 % (*L. rosacea*) (Fig. 2a). Considering the percentage of the alga

consumed, no significant differences were observed among six *Lobophora* species (*L. obscura*, *L. monticola*, *L. sonderi*, *L. hederacea*, *L. dimorpha*, *L. undulata*) with an average of alga consumed of 39 ± 26 % (ranging from 37 to 41 %) (Fig. 2a). With an average of 53 ± 30 %, *L. rosacea* consumption was significantly higher than the other *Lobophora* species (one-way ANOVAs, $p=9.92.e-14$ (percentage consumed)).

4.2. *In situ* grazing experiment

All *Lobophora* species were consumed during the *in situ* experiments, with an average consumption of algal material for each species ranging between 34 ± 20 (*L. dimorpha*) and 116 ± 42 mg (*L. monticola*); and in percentage of alga consumed ranging between 47 ± 23 (*L. sonderi*) to 69 ± 20 % (*L. monticola*) (Fig. 2b). Significant differences in consumption were observed for *in situ* grazing experiments among the seven species of *Lobophora* (Fig. 2b) (one-way ANOVAs, $p<2e-16$ (biomass consumed) and $p=5.27e-14$ (percentage consumed)). *Lobophora monticola*, *L. hederacea* and *L. obscura* were significantly more consumed than the other species, when considering the percentage of biomass consumed.

4.3. Aquarium grazing experiment

All *Lobophora* species were consumed by the sea urchin *D. setosum*, with an average consumption of algal material for each species ranging between 31 ± 3 (*L. dimorpha*) and 120 ± 12 mg (*L. rosacea*); and in percentage of alga consumed ranging between 66 ± 7 (*L. monticola*) and 83 ± 8 % (*L. rosacea*) (Fig. 2c). Significant differences in consumption (Fig. 2c) were observed among the seven species of *Lobophora* (one-way ANOVAs, $p=0.00704$ (biomass consumed) and $p<2e-16$ (percentage consumed)). No significant differences were observed among *L. obscura*, *L. monticola* and *L. sonderi*, nor between *L. hederacea* and *L. dimorpha*. *Lobophora*

undulata followed by *L. rosacea* were significantly more consumed than the rest of the *Lobophora* species.

5. Discussion

5.1. Interspecific differences in grazing susceptibility

The present study assessed the susceptibility to herbivory of seven different species of *Lobophora* presenting contrasting morphologies, chemical compositions and ecologies. We experimentally forced the contact between algae and herbivores, which naturally would not necessarily be the case. All *Lobophora* species were markedly consumed with small but significant interspecific differences, *in situ* and by two important herbivores in New Caledonia, the rabbitfish *S. lineatus* and the sea urchin *D. setosum*. Differences in the significantly most consumed species in the three experiments (*L. rosacea* by *S. lineatus*; *L. monticola*, *L. hederacea* and *L. obscura in situ*; *L. undulata* and *L. rosacea* by *D. setosum*) may indicate slight differences in food preferences among herbivores. *Lobophora rosacea* was nonetheless significantly more consumed by the two herbivores, and *L. sonderi* was among the least consumed in all experiments.

5.2. Chemical defenses?

The chemical composition analyses from Vieira et al. (2016) revealed two main trends: (1) each species is characterized by a distinct chemical composition, and (2) major differences are found in the chemical composition of *L. rosacea* compared to the other *Lobophora* species. While the differences are small, both the fish farm and aquarium experiments revealed statistically significant differences in consumption

rates among species. Moreover, in both cases, *L. rosacea* was the first or second most eaten species within the *Lobophora* genus. These results may point to a correlation between chemical composition and herbivore consumption, suggesting that *L. rosacea* produces less or different chemical deterrents than the other species, and that these are less effective against the two tested herbivores. Conversely, the fact that *Lobophora sonderi* was in all experiments among the least consumed species could indicate that this species is chemically better defended against a wider range of herbivores than the other *Lobophora* species.

5.3. Refuge over defense?

The limited interspecific differences in grazing susceptibility suggests that morphological or chemical differences among *Lobophora* species do not remarkably affect *S. lineatus* and *D. setosum* food choice. This leads us to dispute that while chemicals and morphological defenses have been suggested previously as major strategies against herbivores, they may eventually play a limited role as a strategy against herbivory in *Lobophora* species. Alternatively, and largely overlooked until now, refuge would appear to be an important strategy against herbivores. We argue that species from the genus *Lobophora* adopt two major refuge strategies, namely (1) spatial and (2) associational refuge as chief stratagems against herbivory. A review of the diversity of the genus in New Caledonia, showed that *Lobophora* species had distinct habitat and substratum preferences (e.g., bedrocks, coral rubbles, live and dead corals; Vieira et al. 2014).

5.4. Spatial and associational refuges

Spatial refuge has been evidenced by De Ruyter van Steveninck and Breeman (1987a) who showed that *Lobophora* abundance was negatively correlated with *Diademum*

antiallarum density. In Curaçao, the erect golden-brown *Lobophora* species has refuge from herbivores in deep waters. In New Caledonia, *L. obscura* is mainly found in shallow wave-washed habitats consisting of bedrock, rocks, coral rubbles. The latter has thick blades and adheres strongly to the substratum, which is characteristic of intertidal populations and considered to be adaptations to increased water motion and desiccation (Norton et al. 1981). In this habitat, herbivore presence is limited due to high hydrodynamism. Consequently, *L. obscura* finds spatial refuge from herbivores in this habitat.

Lobophora hederacea, *L. monticola*, *L. undulata* and *L. rosacea* are commonly found associated to branching corals and notably the genera *Acropora*, *Montipora*, *Porites*, *Stylophora*, *Pocillopora* and *Seriatopora* (Diaz-Pulido et al. 2009, Bennett et al. 2010, Vieira et al. 2014, Vieira et al. 2015). *Lobophora rosacea* adopts a ruffled form and grows mainly amongst *Acropora* coral branches. The other *Lobophora* species are usually decumbent, attached by their basal part to coral branches, or form crusts predominantly at the basal part of the coral branches, where access by large herbivores is difficult. In the Great Barrier Reef, populations of *Lobophora* growing amongst branching *Acropora* were less consumed than populations located in planar habitats, suggesting that branching corals act as a refuge for *Lobophora* from herbivores (Bennett et al. 2010). Jompa and McCook (2002a) also concluded that the coral *Porites cylindrica* structure provides a refuge for *Lobophora* from herbivory. The refuge role played by branching corals is furthermore supported by the rare presence of *Lobophora* with other coral forms in the same habitat (author's personal observations).

It was suggested that palatable prey may typically be protected from consumers by living in association with less preferred prey (e.g., Poore & Hill 2005). *Lobophora*

sonderi usually grows in sand-covered habitats, characterized by low grazing intensity, amidst other algae such as *Turbinaria* and *Sargassum*, both tough spiky and upright brown algae, which are less edible because of morphological and chemical defenses (Bittick et al. 2010). *Turbinaria ornata* has been previously reported to represent a herbivory refuge for associated algae (Hay 1986, Bittick et al. 2010). This refuge is not only associational but also spatial, as algal beds outside coral reefs experience low grazing intensity. *Lobophora rosacea*, which presents two distinct ecotypes, either finds refuge with branching *Acropora* or in algal beds as an epiphyte to *L. sonderi*.

6. Conclusion

The present contribution represents the first experimental study to specifically test interspecific grazing susceptibility in the brown alga *Lobophora*. This study primarily showed that all *Lobophora* species were markedly consumed by *S. lineatus* and *D. setosum*, and that interspecific differences were limited. Although trivial, the trends of two species, *L. rosacea* and *L. sonderi*, may point to the role of chemical defense. Significantly more consumed by the two herbivores and characterized by a distinct secondary metabolome, *L. rosacea* may produce less or different chemical deterrents than the other *Lobophora* species. On the contrary, significantly less consumed in all experiments, *L. sonderi* may produce chemicals deterrents active against a wide range of herbivores. While it was previously suggested that *Lobophora* resists herbivory by relying essentially on chemical deterrents and structural defense, present results suggest that differences in morphology and secondary metabolome may play a rather limited role in defense against herbivores. Instead, *Lobophora* may primarily find refuge from herbivory by growing in specific habitats or associated to

certain organisms. Future studies need to identify exactly which herbivores feed on *Lobophora* spp. in the natural environment, and determine if these herbivores vary among species of *Lobophora*.

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Figures captions

Figure 1. External morphology of the six *Lobophora* species (*L. obscura* (a), *L. undulata* (b), *L. hederacea* (c), *L. rosacea* (d), *L. dimorpha* (e), *L. sonderi* (f), *L. monticola* (g)) used in the grazing experiments.

Figure 2. Grazing experiments results with seven *Lobophora* species in three grazing experiments: natural environment (a), fish farm (b), and sea-urchin aquarium experiments (c). Barplots represent the average percentage of alga consumed. Letters indicate distinct groupings based on post-hoc statistical comparison among *Lobophora* species. Error bars represent standard deviation of the mean.

Figure S1. Habit photographs of the six *Lobophora* species (*L. obscura* (a), *L. undulata* (b), *L. hederacea* (c), *L. rosacea* (d), *L. sonderi* (e), *L. rosacea* (left arrow) epiphytic on *L. sonderi* (right arrow) (f), *L. monticola* (g)) used in the grazing experiments.

Figure S2. Principal Component Analysis (PCA) of metabolomic profiles of six *Lobophora* species used in the grazing experiments. *Lobophora monticola* is missing from this analysis. **L. rosacea* niched amongst corals. ***L. rosacea* epiphytic on *L. sonderi*.

Figure S3. Pictures of fish farm experiment (a), rabbitfish (b), natural environment experiment (c) and aquarium experiment (d).

Figure S4. Diagram of experimental setup for the sea-urchin aquarium grazing experiment. Three nylon fishing lines were disposed to the bottom of the aquarium fixed on each extremity by diving weights. *Lobophora* thalli from different species were randomly stapled at equidistance along the lines.

Tables

Table 1. Description of the *Lobophora* species tested in the grazing experiments

	Morphology	Thickness (μm)	Habitat	Substrate
<i>L. dimorpha</i>	Procumbent, Stipitate	101.2 \pm 12.8	Coral dominated	Coral basal part, bedrock
<i>L. hederacea</i>	Shelf-like (decumbent), Crustose	188.6 \pm 26.1	Coral dominated	Coral basal part, live coral branches
<i>L. monticola</i>	Shelf-like (decumbent)	152.9 \pm 24.4	Coral dominated	Dead coral basal part, live coral branches
<i>L. obscura</i>	Crustose	291.6 \pm 39.8	Shallow exposed reefs coral rubbles	Dead coral, coral rubble, bedrock, rock
<i>L. rosacea</i>	Fasciculate (ruffled), Decumbent	146.5 \pm 16	Coral dominated, macroalgal beds	Coral basal part
<i>L. sonderi</i>	Stipitate	211.2 \pm 8.2	Macroalgal beds, sand bottoms	Bedrock, loose rock, sand
<i>L. undulata</i>	Shelf-like (decumbent)	214 \pm 52.3	Coral dominated	Coral basal part

Table S1. Sites where the *Lobophora* species were collected in the southwestern lagoon of New Caledonia

Species	Locality	Latitude	Longitude
<i>Lobophora dimorpha</i>	Senez	-22.220141	166.33441
<i>Lobophora hederacea</i>	Grand recif Abore	-20.7161	165.141
<i>Lobophora monticola</i>	Baie Sainte Marie	-22.297713	166.481639
<i>Lobophora obscura</i>	Ricaudy	-22.315317	166.457717
<i>Lobophora rosacea</i>	Ricaudy	-22.315317	166.457717
<i>Lobophora sonderi</i>	Crouy	-22.3517	166.3514
<i>Lobophora undulata</i>	Ilot Laregnere	-22.288783	166.427983

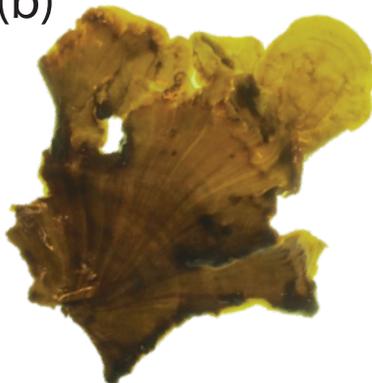
Table S2. *In situ* sites location

Reef name	Reef type	Habitat	Depth (m)	Latitude	Longitude	Duration
Crouy	Patch reef	Algae bed	2	22°21.114	166°21.084	48h
Larégnère	Islet reef	Sandy bottom	2	22°19.524	166°18.953	48h
Canard 1	Islet reef	Coral reef	2	22°18.840	166°26.266	48h
Canard 2	Islet reef	Coral reef	4	22°18.855	166°26.289	48h
Canard 3	Islet reef	Coral reef	7	22°18.858	166°26.317	72h
Senez	Patch reef	Coral reef	2	22°17.760	166°19.975	72h
Abore	Back reef	Coral reef	1	22°27.001	166°22.271	24h

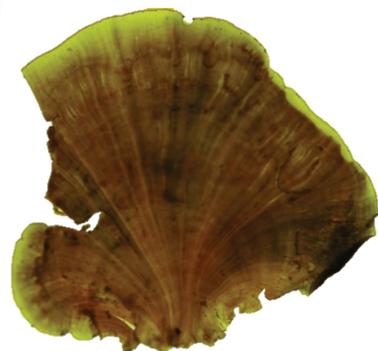
(a)



(b)



(c)



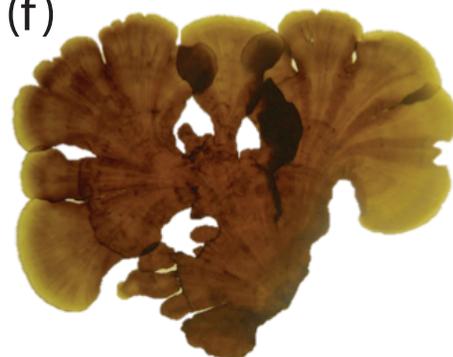
(d)



(e)



(f)



(g)

