

Invasion of coral reefs of Lakshadweep atolls by a central Indo-Pacific corallimorph

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Abstract

Worldwide, coral reefs are in decline due to mass bleaching, natural calamities, diseases, and anthropogenic stressors that expose large swathe of unutilized substratum which is later occupied by other benthic organisms like corallimorpharians, anemones, macroalgae etc. In the current work, we describe for the first time, the competitive interaction between a corallimorph and hard corals, observed in Kavaratti and Chetlat atolls in the tropical Indian Ocean, which is the first reported instance of an invasion of corallimorpharian in the entire Lakshadweep islands. The corallimorph, *Rhodactis bryoides* Haddon & Shackleton, 1893, is identified by morphological and molecular analysis. It is found that the species has no previous records from the western Indian Ocean region. Since the competitive interaction among reef organisms for space will have significant repercussions on the entire reef ecosystem in the future, we observed the pace of invasion for six months and calculated the relative abundance of the corallimorph using transects. None of the previous factors causing a corallimorpharia outbreak *viz.*, external disturbances and nutrient enrichment were observed in this region. However, these tropical atolls are prone to occasional bleaching during the summer seasons. Further investigation needs to be conducted on the biology of this species, the interaction with other benthic groups and the environmental descriptors promoting the invasion.

Introduction

Coral reefs are the most diverse ecosystems on earth, and thus a large number of interspecific and intraspecific interactions happen in these ecosystems (Karlson and Hurd 1993). Within this ecosystem, space availability is one of the major limiting factors that hinder the expansion of benthic organisms (Karlson and Hurd 1993). The structural framework of a coral reef ecosystem is composed of sessile organisms especially corals, crustose coralline algae, sponges, anemones, *etc.* Competitions among such organisms in coral reefs are multifaceted and are driven by both intrinsic and extrinsic factors. The results of such competitions are manifested in various ways. One such consequence of competition is the shift in dominance of reef-building corals to non-reef builders, which is generally known as phase-shift (Chadwick and Morrow 2011). A phase-shift can be defined as “extensive decreases in the coral cover coinciding with substantial increases in some alternative benthic organism, due to a pulse or press disturbance, that have persisted > 5 year” (Norström et al. 2009). Whenever we use the term ‘phase-shift’ concerning coral reefs, there is an underlying belief that it is the macroalgae that overgrow corals, but there are several other types of phase-shifts happening in a reef ecosystem especially by other cnidarians such as anemones and corallimorphs. These shifts are, however, underreported (Work et al. 2008). The exact reasons behind the phase shift from one type of cnidarians to another on a reef are still not well studied. A few studies suggest such possible reasons as bleaching, damage by typhoons, overfishing, excessive nutrient input, coastal development and tourism (Chen and Dai 2004; Kuguru et al. 2004).

Corallimorpharians are seen either as solitary individuals or in colonies that may cover large areas of coral reefs (Gerald and Roger 1994). They are found to be more competitive in shallow waters. CMs calcareous skeleton. Being capable of moving across the

reefs and destroying other organismal components and reproducing by means of cloning and budding, these efficient competitors occur in the reefs world-wide (Kuguru *et al.* 2004). Reserving a significant portion of body mass during reproduction for dispersive larvae production enables them to quickly take over valuable space of the reef, thus preventing other sessile animals from colonizing reefs (Langmead and Chadwick-Furman 1999). Phase shifts in which CMs are surpassing corals have already been observed in various reefs. Work *et al.* (2018) noted the flourishing of CMs associated with a shipwreck at Palmyra, where they infer that the phenomenon is aided by the leaching of metals from the vessel. In this instance, there was an expansion from one sq km. area in 2007 to 3 sq km in 2011. Prolific replication by at least three modes such as sexual reproduction of planktonic larvae, clonal production *via* fission, and budding aids them in such a quick spreading.

Our understanding of the competitive interaction of CMs *vs* other sessile organisms in the tropical Indo-Pacific region is scanty. Only a few reports from this region state that they are an important occupier of space in coral reefs and may eliminate reef-building corals from the shallow reef substratum (Langmead and Chadwick-Furman 1999). For example, a study by den Hartog (1980) from the reefs of Seychelles revealed polyps of *R. howesii* overgrown considerable patches of the reef and apparently killed stony corals. Further, there are reports from Maldives (Moosleitner 1989) that clearly state the ability of CMs to damage and overgrow scleractinian corals.

Materials And Methods

Study sites

The study was conducted during November-April 2019 at Kavaratti atoll of Lakshadweep islands, located off the southwest of India in the Lakshadweep Sea. Kavaratti is an atoll with a coral lagoon of around five sq km and hosts the largest human population among the islands (Prakash *et al.* 2015). The lagoon is roughly oval-shaped with the low-lying sandy island located on its south-west. Observations are made in situ by snorkelling at depths of less than 1 meter close to the beach. The shallow reef in this area is dominated to a large extent by healthy *Porites cylindrica*.

Survey and sample collection

We surveyed 17 stations as part of a coral resilience assessment study when we observed unusual growth of CM on a particular patch of the reef near the shore, shallow waters. The coverage of CM was documented by the line intercept transect method (English *et al.* 1997). Three transects of 10-meter length placed 5 meters apart are used to assess coral and CM coverage. Further, we conducted a detailed survey using permanent transects in this station for six months to determine the progression of CM occupancy.

The depth and benthic characters of the site were recorded. Corallimorpharian samples were collected using a chisel. The samples were then transferred to 95% ethanol. In situ photographs were taken to document corallimorpharians over scleractinian corals.

Identification

Corallimorpharian species were identified from the collected samples, and its morphological characters were examined following Haddon & Shackleton (1949). Molecular analysis was also carried out to confirm the species. For molecular identification, Corallimorphs were collected from Kavaratti atoll and were preserved in 95% ethanol. Total DNA was extracted from approximately 30 mg of ethanol preserved tissue using DNeasy Blood and Tissue kit (QIAGEN), following the manufacturer's protocol. The nuclear ribosomal cluster fragments were amplified using the primer pairs designed by Acuña et al. (2007). The primer sequences are Acuna 18S (5'CACCGCCCGTCGCTACTACCGATTGAATGG3') and Acuna 28S (5'CCGCTTCACTCGCCGTTACTAGGGGAATCC3'). PCR was performed using Q5 high fidelity DNA polymerase (NEB). The PCR conditions were; an initial denaturation for 3 minutes at 95°C, followed by 35 cycles, with denaturation for 30 seconds at 95°C, annealing at 55°C for 30 seconds and extension for 45 seconds at 72°C, and an additional extension for 5 minutes at 72°C after the end of the 35 cycle. The amplified PCR fragments were purified and cloned into pJET1.2 cloning vectors and transformed into *Escherichia coli* (Top10). Plasmids were purified from transformed clones and were Sanger sequenced (AgriGenome Labs Private Limited, Cochin). DNA sequences were assembled using the SeqMan program (DNASTAR) combined with manual proofreading before submitting to GenBank. Sequence similarity search was performed using the NCBI BLAST. The nuclear ribosomal cluster fragment sequences belonging to the anthozoa subclass Hexacorallia were used for estimating evolutionary relationships. All the sequences were aligned and trimmed using Bioedit version 7.2.5. The trimmed sequences were used for Evolutionary analyses using MEGA X (Kumar et al. 2018). The nuclear ribosomal cluster fragment sequences belonging to the Anthozoa subclass Hexacorallia belonging to the orders Corallimorpharia, Antipatharia, Actinaria, Zoantharia, Scleractina were used, in case of Zoantharia as full nuclear ribosomal cluster fragment sequence was not available, the full-length sequence was constructed by contig aligning multiple sequences belonging to the same organism. *Paraglomus* sp. Belonging to the Kingdom Fungi was used as an outgroup. The evolutionary history was inferred by using the Maximum Likelihood method and the Tamura-Nei model (Tamura & Nei 1993). Initial tree for the heuristic search were obtained applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Tamura-Nei model, and then selecting the topology with superior log likelihood value.

Community analysis

The relative abundance (RA) of all corals and corallimorpharians in the study area calculated (Rilov and Benayahu 1998):

$$\text{Relative abundance (RA)} = (P_i / P_{\text{total}}) \times 100$$

where, P_i = pooled living coverage of the i th species from all transects at a given site and P_{total} = pooled total living coverage of all coral and corallimorpharian in all transects at a given site.

Resulting values were converted into abundance categories (%) viz., rare ($0 < RA < 0.1$), uncommon ($RA = 0.1 - 1$) and dominant ($RA > 20$).

Results

Systematics

Kingdom: Animalia

Phylum: Cnidaria

Class: Anthozoa

Order: Corallimorpharia

Family: Discosomidae

Genus: *Rhodactis* Milne Edwards & Haime, 1851

Species: *Rhodactis bryoides* Haddon & Shackleton, 1893

Materials examined

A large patch covering approximately 0.32 hectares of CM was observed at Kavaratti atoll (10.5539° N, 72.6263° E), and a small patch recorded at Chetlat atoll (11.6953° N, 72.7092° E).

Morphological and Molecular characterisation and Evolutionary relationships

The corallimorpharian genera *Rhodactis* comes under the family Discosomatidae. They have peculiar morphological characters that differentiate them from the remaining three families of the Order Corallimorpharia. Marginal tentacles of *Rhodactis* species are digitiform while distal tentacles are branched and papilliform. Tentacle-free zones are absent in the oral disk. They usually grow on hard surfaces crowded together so closely that it is difficult to distinguish the individual polyps. *R. bryoides* has a hypocateriform body, and the parapet markedly crenulated. The prominent tentacles are compound and are arranged in multiple radial lines. The diameter of a number of discs were measured and were found within a range of 26-35mm. Most of these characters were in congruence with the original description of *R. bryoides* (Haddon & Shackleton 1893).

The nuclear ribosomal cluster fragments were successfully amplified using the primer pairs Acuna 18S and Acuna 28S, giving a PCR product of 879 bp. The amplified region contains 3' end of the 18S and 5' end of the 28S gene, the two internally transcribed spacers (ITS-1 & ITS-2), and the complete 5.8S gene. The assembled and manually proofread sequences were deposited in GenBank with accession number: MW375770. Sequence similarity search using NCBI BLAST gave a similarity of 99.32% with *Rhodactis bryoides* (GenBank Accession: Ab441417). The evolutionary history was inferred by using the Maximum Likelihood method and Tamura-Nei model using MEGA X (Kumar et al. 2018) (Fig. 1). All the organisms formed separate clades corresponding to their orders, our sequence *Rhodactis bryoides*_CMFRI (MW375770) clustered with *Rhodactis bryoides* (Ab441417) in the Corallimorpharia Clade, and it clustered together with *Rhodactis bryoides*

(Ab441417). Based on both morphological and molecular characteristics the identity of the organism was established as *Rhodactis bryoides*.

Percentage Coverage and Relative abundance

The LIT survey revealed the total coverage of the CM as 50.98% out of all living substratum. The live coral coverage was 45.67%. The *R. bryoides* was categorised as 'dominant' as per their relative abundance in the station. The permanent quadrats revealed an increase of the *R. bryoides* coverage from 42.5% to 53% at the end of the sixth month means an 24.7% increase. Out of all living coral, almost 80% of this particular reef patch is covered by *P. cylindrica*. From our observation, we found that CMs are highly competitive with *P. cylindrica*, which justify the rapid growth of CMs in this particular area.

Further, the survey revealed that *R. bryoides* is rapidly covering the available benthic space and competing with the abundant species *Porites cylindrica* and some other branching acroporids. *R. bryoides* invade live and healthy corals by killing the coral tissues first and then overgrowing it (Fig. 2). A band of dead coral tissue was visible at the leading edge of the progression of *R. bryoides* growth (Fig. 2c, d).

Other than Kavaratti, we conducted further surveys in Kalpeni, Amini, Agatti and Chetlat atolls and encountered the same CM at Chetlat. The growth of corallimorph at Chetlat is comparatively less; nevertheless, their competition with corals was noticed. We have recorded their overgrowth on *Lobophyllia cf. corymbosa* and *Porites cylindrica* colonies.

Discussion

For the first time, we report the occurrence of a CM species and its competitive success over corals at Lakshadweep atolls. No previous studies had observed the presence and competitive invasion of CMs in any of these atolls even though some of these atolls were previously subjected to thorough surveys. Although the occurrence of other *Rhodactis* sp. was reported from various reefs in the western Indian Ocean, there are no previous records of *R. bryoides* from this region. *R. bryoides* has previously been recorded from the central Indi-Pacific Ocean. First described from the Torres Strait (Haddon & Shackleton 1893), this species remains less known till date, having a few records from the western Pacific Ocean regions such as Australia, Mariana Islands, Coral Sea and the South China Sea off Vietnam (Paulay et al. 2003; GBIF 2019). It is morphologically distinct from the four other morphologically similar congeners (Chen & Miller 1996). In the nearby atolls of Maldives, the presence of an ambiguous *Rhodactis* sp. (then doubtfully identified as *Discosoma cf. rhodostoma*) was previously reported and speculated to be causing a phase shift (Zahir et al. 2009).

Various species of corallimorpharia live solitary in deeper waters or as colonies in the shallow waters. *Rhodactis bryoides* is a colonial corallimorph, and they inhabit shallow waters. Corallimorpharians have a worldwide distribution, with many of the colonial corallimorpharia occurring in the tropics primarily aided (artog 1980). Longitudinal fission occurring in the larger

polyps is the most common form of asexual reproduction (Chen et al. 1995b; Chadwick-Furman & Spiegel 2000; Chadwick-Furman et al. 2000). Corallimorpharians also show inverse budding which is achieved when a nodule of the pedal disk rises up and pinch off from the maternal polyp (Chen et al. 1995b). Different modes of asexual reproduction help corallimorpharians to increase their population size. Doubling time of *Rhodactis rhodostoma* is significantly higher than Scleractinians (Chadwick-Furman & Spiegel 2000). Corallimorpharians are known to exhibit a higher biomass turnover than Scleractinians in less than five weeks (Chadwick 1987). Consequently, they are expected to be more efficient and successful competitors for space on tropical reefs.

We strongly believe that the present occurrence of *R. bryoides* is a case of invasion in this region. For a non-indigenous species to become invasive, there must be a source, it should survive and thrive in the new place. Whether a species has successfully or unsuccessfully invaded elsewhere can substantiate if it is invasive or not (Mc Neelay 2000; Norström et al. 2009). Evidence from our study indicates that they are actively reproducing within a short time span, successfully establishing a population by effectively outcompeting the dominant coral species. This is apparent from the permanent quadrat data, where an increase of ~25 % of coverage was noticed in a short duration of six months.

However, from the currently available data, it is not possible to elaborate on the triggering factors behind the invasion and the seemingly successful initial level of proliferation of this corallimorph at Kavaratti. We recorded *R. bryoides* towards the shore of Kavaratti, where the depth of the lagoon is minimal (<1m). The coral colonies at that location were found to be healthy except at the area of the corallimorph invasion. There are studies describing the capacity of CMs to thrive in hostile conditions which give them an advantage over Scleractinians (Muhando et al. 2002). They prefer nutrient-rich areas with low visibility, which helps them outcompete hard corals as the latter requires clear and low-nutrient water (Kuguru et al. 2004). Usually, most Scleractinians have limited success in shallow waters as they are exposed to air and sunlight and wave damage. However, this part of the reef was found to be devoid of any such stressors. The reef at which *R. bryoides* was located is beyond the level of a neap tide exposure. Further, hardly any anthropogenic disturbances were noticed at the site. Being tropical in location, the reefs of Lakshadweep are prone to bleaching, associated with ENSO and multiple bleaching events had been recorded from 1998 till date (Arthur 2008; Arora et al. 2019). Nevertheless, *R. bryoides* was observed to be overgrowing live corals rather than growing on the dead ones. Hence, the findings point to a successful invasion of *R. bryoides* in a healthy reef patch without any apparent facilitation by extrinsic factors, but rather by the inherent biological ability of that species to outcompete the corals.

From the initial observations itself, it was evident that the dominant *P. cylindrica* is losing the fight for space. Since competition for space is a never-ending process in coral reefs (Muko et al. 2001), the CMs use several life-history traits that allow them to overgrow the shallow reef substrate. They are competitively superior to some coral species and have well-suited anatomy which gives them an edge in the battle for space. Their elongated marginal tentacles help them to kill Scleractinian corals. (Langmead and Chadwick-Furman 1999). Additionally, clonal replication ability of CMs allows them to rapidly

Loading [MathJax]/jax/output/CommonHTML/jax.js man and Spiegel 2000). CMs successfully use their

mesenterial filaments and acrospheres as weapons against their adjacent organisms in the competition for space (Chadwick 1987; Langmead & Chadwick-Furman 1999a). Naturally, mesenterial filaments were used in digestion, but when they come in contact with a Scleratinian coral, CMs gather the mesenterial filaments in mouth or body walls and extrude onto the opponent's body (Chadwick 1987). The mesenterial filaments come in contact with the enemy causing tissue necrosis; prolonged contact may lead to death (Chadwick 1987; Kuguru et al. 2004).

An established invasive corallimorpharia will be very difficult to be expunged, especially from a highly connected ecosystem such as coral reefs. Nevertheless, the extent of damage to the coral reefs it can cause may justify efforts to control further spread and manage established populations. If this situation continues, given this rapid pace of expansion, we can expect that the CMs might be able to destroy the entire reef by overthrowing the coral within a few years. This can further lead to a phase shift in the reef, as noted in other coral reefs (Kuguru et al. 2004; Work et al. 2018; Zahir et al. 2009). Understanding the biology of this species, the interaction with other benthic groups, and the environmental descriptors promoting the invasion is vital in prioritising the management actions. The Lakshadweep atolls' strategic position and their connectivity to many nearby atolls and fringing reefs (Athira 2018) call for the immediate adoption of coordinated and integrated invasive species management strategies.

Declarations

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Compliance with ethical standards

Conflict of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Human and animal rights

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The study does not involve human participants and/or animals

Ethical approval

Non-applicable

Consent to participate

Non-applicable

Consent for publication

All authors are consenting to publish the manuscript.

Availability of data and material

Not applicable

Code availability

Not applicable

Authors' contributions

Field work and data preparation were performed by Alvin A. Study was conceived by Sreenath K. R. Analysis of data was performed by Joshi K. K. Molecular analysis was performed by Pradeep M. A. & Nisha E. A. The manuscript was written by Aju K. R. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Table

Table 1. Relative abundance of different species coverage at the selected reef patch

Species	Relative abundance (RA)	Abundance category
<i>Rhodactis bryoides</i>	50.98	Dominant
<i>Porites cylindrica</i>	35.42	Dominant
<i>Porites lutea</i>	6.031	Common
<i>Pocillopora damicornis</i>	0.1944	Uncommon
<i>Porites sp.</i>	0.7837	Uncommon
<i>Acropora muricata</i>	1.07	Abundant
<i>Pavona venosa</i>	2.15	Abundant

Figures

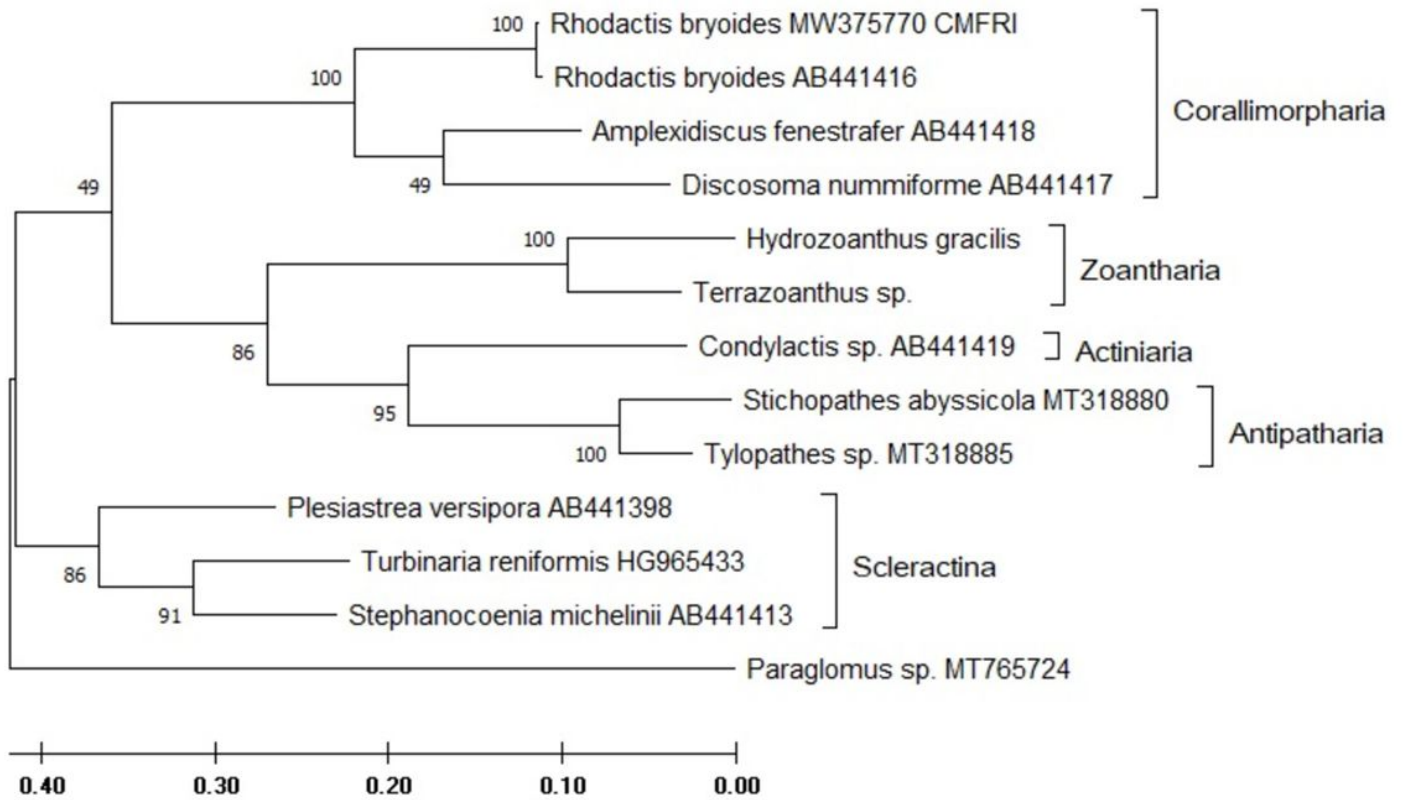


Figure 1

Phylogenetic tree inferred using the Maximum Likelihood method depicting the relationship of *Rhodactis bryoides* MW375770 CMFRI with that of other Hexacorallia. The percentage of trees in which the associated taxa clustered together is shown next to the branches

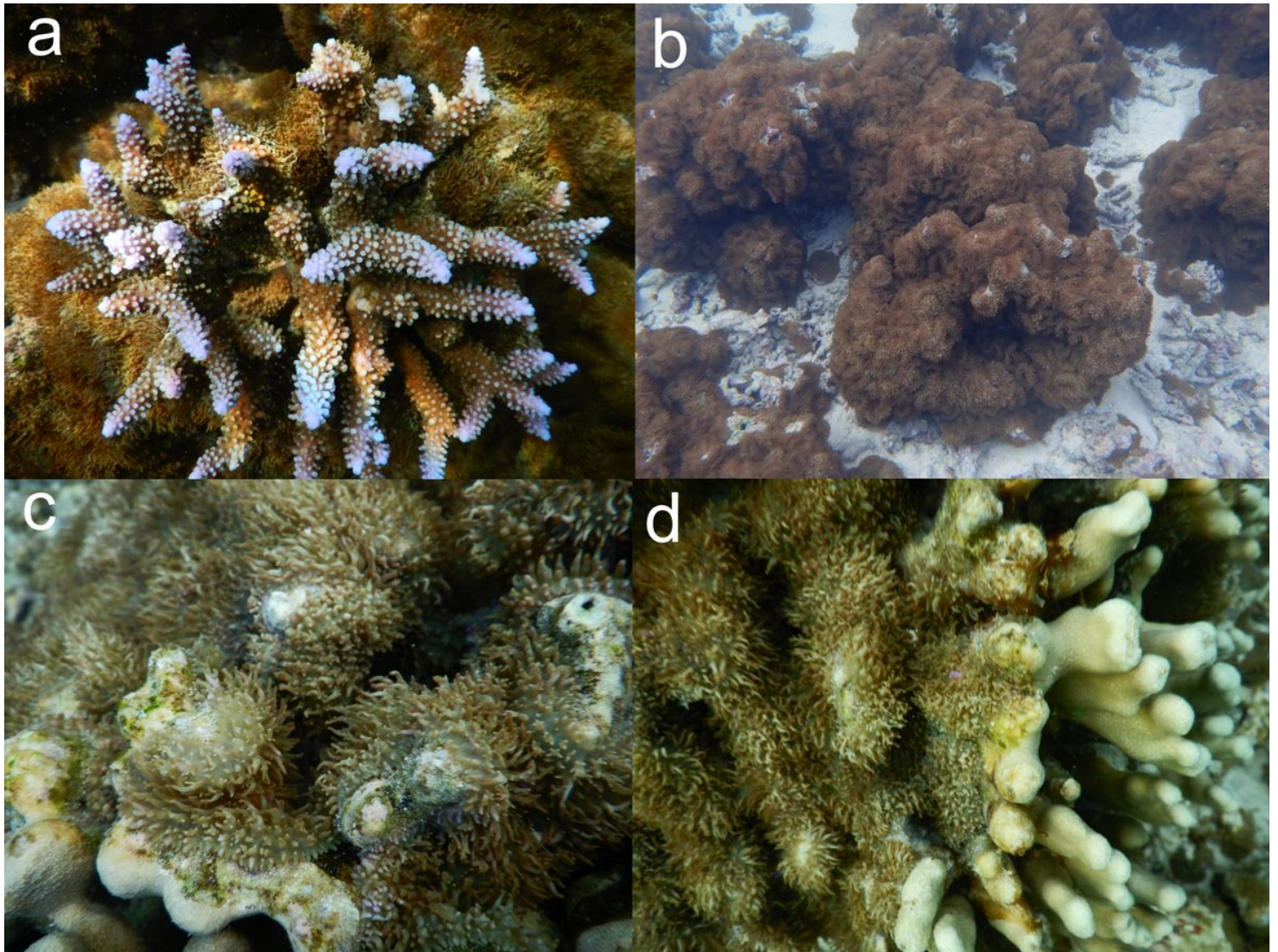


Figure 2

R. bryoides growth on (a) *Acropora* sp.; (b - d) *Porites cylindrica*