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Record of a central Indo-Pacific corallimorph in the Lakshadweep atolls and its competition with the hard corals

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ABSTRACT

Coral reefs are disappearing worldwide because of mass bleaching, natural disasters, diseases and anthropogenic stressors. This leaves a large area of unutilised substratum, to which other benthic organisms, like corallimorpharians (CMs), anemones and macroalgae, can move in. In this article, we describe, for the first time, the competition for space between a CM and the hard corals in Kavaratti Atoll in the Indian Ocean. This is the first reported instance of an invasion of CM in the entire Lakshadweep Islands. The CM *Rhodactis bryoides* Haddon and Shackleton, 1893, is identified by morphological and molecular analysis. The species has not so far been reported from the western Indian Ocean area. We monitored the rate of invasion for six months to figure out the growth rate of CMs. This area did not have any prominent causative factors for CM outbreaks, such as external disturbances and nutrient enrichment. Yet our study showed that CMs are successful in the competition for space. More research needs to be done into the biology of this species, how it interacts with other benthic groups and how the environment facilitates its spread.

Keywords: Bioinvasion, Coral reefs, Corallimorpharia, Phase shift, *Rhodactis bryoides*

Introduction

Coral reefs are the most diversified ecosystems on Earth. The intensity and severity of anthropogenic climate change are unprecedented, exposing corals to circumstances unseen in millions of years (Hughes *et al.,* 2017). Added to this, space is the major limiting factor that slows down the growth of benthic organisms (Karlson and Hurd, 1993). As a result, the reef-building corals are diminishing, giving way to other creatures (Roff and Mumby 2012). It is anticipated that altering competitive dynamics in coral reefs would worsen ecosystem disruptions as ocean temperatures and acidification escalate (Kroeker *et al.,* 2013; Del Monaco *et al.,* 2017).

The outcome of competition for space in a reef is manifested in various ways. One consequence of competition is the shift in dominance of reef-building scleractinian corals to non-reef builders, generally known as a phase shift (Chadwick and Morrow, 2011). Done (1992) was the first to report this process in coral reefs by witnessing the rising dominance of macroalgae in a reef that was once coral-dominated. The phase shift is defined as "an extensive decrease in the coral cover coinciding with substantial increases in some alternative benthic organisms, due to a pulse or press disturbance, that have persisted >5 years" (Norstrom *et al.*, 2009). Whenever the notion of phase shift is applied to coral reefs, the implicit premise is that macroalgae are responsible for it. However, several other phase shifts are already happening in a reef ecosystem that has been less thoroughly explored and documented, particularly by other cnidarians such as corallimorphs (CMs) and anemones (Work *et al*., 2008). Phase shifts in which CMs surpass corals have already been observed in various reefs. Work *et al*. (2018) observed the proliferation of CMs associated with a shipwreck at Palmyra, where they hypothesised that the leaching of metals from the vessel hastened the phenomenon. The size of the CM colony at Palmyra expanded from 1 km^2 area in 2007 to 3 km^2 in 2011. Prolific multiplication by at least three mechanisms, namely sexual reproduction of planktonic larvae, clonal production *via* fission and budding, facilitates their rapid expansion (Work *et al*. 2018).

CMs have a worldwide distribution (Kuguru *et al*., 2004) and can be observed alone or in groups, covering large parts of coral reefs (Allen and Steene, 1994). It turns out that they are successful at competing with scleractinian corals in shallow water. CMs have polyps like corals but do not have calcified skeletons. These efficient competitors can move across the reefs, kill other organisms, and reproduce by cloning and budding. Reserving a significant portion of body mass during reproduction for dispersive larvae enables them to quickly take over valuable reef space, thus preventing other sessile animals from colonising reefs (Langmead and Chadwick-Furman, 1999a).

Our knowledge of the competition between CMs and other organisms in the tropical Indo-Pacific region is poor.

A few reports say they take up much space in reefs and may eliminate reef-building corals from the shallow reef substratum (Langmead and Chadwick-Furman, 1999b). For example, a study by Den Hartog (1994) from the reefs of Seychelles revealed polyps of *Rhodactis howesii* overgrown in considerable patches of the reef and killed stony corals. There are other examples from the Maldives (Moosleitner, 1989) and Malaysia (Ridzwan, 1993) that demonstrate the potential of CMs to damage and outcompete scleractinian corals. Also, a recent study by Prakash *et al*. (2022) at the neighbouring Agatti Island of Lakshadweep showed an outbreak of corallimorph-sea anemones.

Lakshadweep Archipelago, which comprises 36 islands and several submerged reefs and seamounts, forms the northern-most portion of the Chagos-Maldives-Lakshadweep Ridge, the longest atoll system on Earth. They are diverse and rich and have significant endemicity of marine fauna, especially those associated with the reef ecosystems (Anakha *et al*., 2021). Due to the apparent spatial continuity of these ridge-associated reef ecosystems, the repercussions of an event like an invasion of the kind dealt with in this study could be effected across vast areas of this atoll chain and points out the requirement of early identification and monitoring of such incidents.

Meterials and methods

Study site

The surveys were conducted during April 2019 and October 2019 in Kavaratti Atoll, located off the south-west of India in the Lakshadweep Sea. Kavaratti has a coral lagoon of around 5 km^2 and hosts the largest human population among the islands (Prakash *et al*., 2015). The lagoon is roughly oval-shaped, with a low-lying island located on its east. The shallow reef in the lagoon is dominated to a large extent by *Porites cylindrica*.

Survey and sample collection

We surveyed 17 stations, of which 11 were located inside the lagoon and six in the forereef (Fig. 3). The survey was done as part of a coral resilience assessment study. During the study, we observed unusual growth of CM at lagoon station 8 (L8), which is located in shallow waters near the shore. The benthic survey was conducted by the line intercept transect method (English *et al*., 1997). Three transects of 10 m length placed 5 m apart were used to assess coral and other benthic coverage at 17 stations. Further, we conducted a detailed survey using permanent linear transects in this station to determine the outcome of the competition between the corals and CM over a period of six months.

The depth and benthic characters of the site were recorded. CM samples were collected using a chisel. The samples were then transferred to 95% ethanol. *In situ* photographs were taken to furnish the competitive success of CMs over scleractinian corals.

Identification

CM samples collected were examined for their morphological characters following Carlgren (1949). Molecular analysis was also carried out to confirm the species identity. 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 Acuna *et al*. (2007). The primer sequences are Acuna 18S (5'CACCGCCCGTCGCTACTACCGATTGAATGG3') and Acuna 28S (5'CCGCTTCACTCGCCGTTACTAGG GGAATCC3'). PCR was performed using Q5 high-fidelity DNA polymerase (NEB). The PCR conditions used were: initial denaturation at 95°C for 3 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 55°C for 30 s and extension at 72°C for 45 s and an additional extension for 5 min at 72°C after the end of the 35 cycles. The amplified PCR fragments were purified and cloned into pJET1.2 cloning vector and transformed into *Escherichia coli* (Top10). Plasmids were purified from transformed clones and were Sanger sequenced (AgriGenome Labs Pvt. Ltd., Kochi). DNA sequences were assembled using the SeqMan program (DNASTAR) combined with manual proofreading to ensure the sequences were correct before submitting to GenBank. A 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 and Scleractina were used. In the 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 using the Maximum Likelihood method and the Tamura-Nei model (Tamura and Nei, 1993). Initial tree(s) for the heuristic search were obtained by applying Neighbor-Joining and BioNJ algorithms to a matrix of pair-wise distances estimated using the Tamura-Nei model and then selecting the topology with a superior log likelihood value.

Community analysis

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

Relative abundance (RA) = (Pi/Ptotal) x 100

where, Pi = Pooled live coverage of the i^{th} species from all transects at a given site, and P_{total} = Pooled total coverage of living substratum 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), Common (RA=1-10), Abundant (RA=10-20) and Dominant (RA>20).

Results

The CM species of our study were identified as *Rhodactis bryoides*.

Systematics

Kingdom: Animalia

Phylum: Cnidaria

Class: Anthozoa

Order: Corallimorpharia

Family: Discosomidae

Genus: *Rhodactis* Milne Edwards and Haime, 1851

Species: *Rhodactis bryoides* Haddon and Shackleton, 1893

Materials examined

A large colony of CM was selected at Kavaratti Atoll (10.5539⁰N, 72.6263⁰E), for further studies. Samples were collected by hand using a chisel, carefully detaching individual CM polyps.

Diagnosis

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 so closely that it is difficult to distinguish the individual polyps. We observed all these characters in the corallimorpharian in our study area, which confirms their position under the genera *Rhodactis.* The species exhibits more significant intraspecific morphological variation that hinders species-level identification.

Molecular identity and evolutionary relationships of taxa

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 a 5' end of the 28S gene, the two internally transcribed spacers (ITS-1 and ITS-2) and the complete 5.8S gene. The assembled and manually proofread sequences were deposited in GenBank with Accession no. MW375770. Sequence similarity search using NCBI BLAST gave a similarity of 99.32% with *Rhodactis bryoides* (GenBank Accession: Ab441417). The evolutionary history was inferred 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 and our sequence *Rhodactis bryoides*_CMFRI (MW375770) occupied the Corallimorpharia Clade and it clustered together with *Rhodactis bryoides* Ab441417.

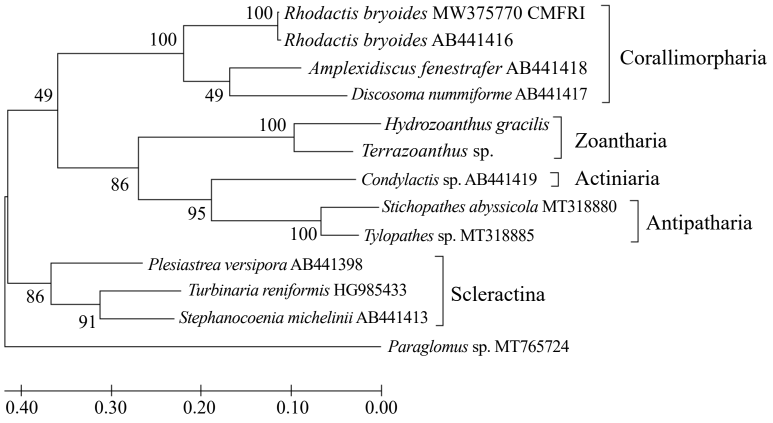


Fig. 1. Phylogenetic tree inferred using the Maximum Likelihood method depicting the relationship of *Rhodactis bryoides* MW375770 CMFRI with that of other Hexacorallia. The percentage of trees in which the associated taxa clustered together is shown next to the branches

Percentage coverage and relative abundance

The LIT survey revealed the total coverage of the CM as 50.98% of all living substratum (Table 1). The live coral coverage was 45.67%. *R. bryoides* were categorised as 'dominant' as per their relative abundance in the station. *R. bryoides* coverage rose from 42.5 to 53% towards the end of the six months, which is an 11% rise in coverage. The stony coral *Porites cylindrica* covers almost all the living coral on this reef patch, making up almost all of it. From our observations, we found that CMs were very good at competing with *P. cylindrica* and that is why CMs have grown so quickly in this area.

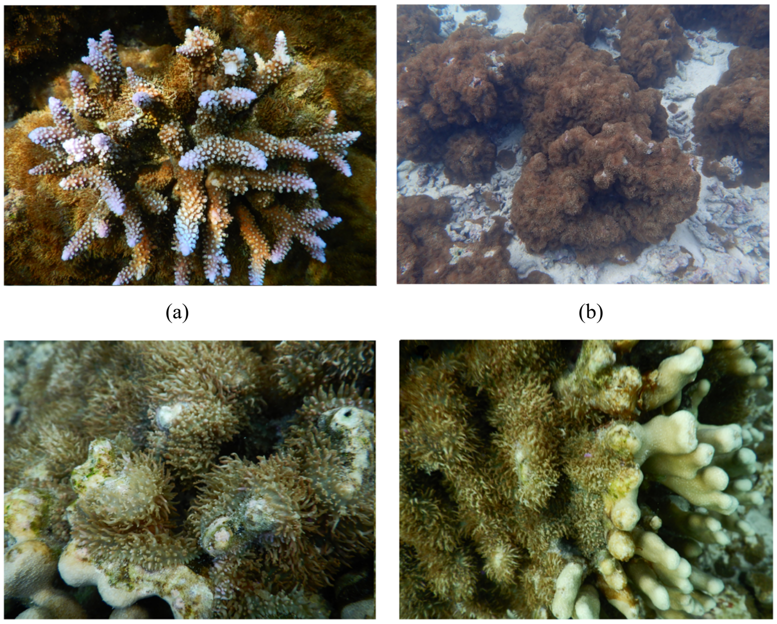
The survey also found that *R. bryoides* has been quickly taking over the benthic space and competing with the more common species *P. cylindrica* and other branching acroporids for space. There were both live and healthy corals that *R. bryoides* grew on. First, it killed the coral tissues and then it took over the corals (Fig. 2). A band of dead coral tissue was visible at the leading edge of the progression of *R. bryoides* growth (Fig. 2c, d).

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

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

Different kinds of CMs live solitary in deeper waters or in groups in shallow waters. *R. bryoides* is a CM that lives in groups and they live in shallow water. CMs can be found all over the world, but many of the colonial CMs are found in the tropics as they reproduce asexually (Den Hartog, 1980). It is most common for larger polyps to split longitudinally. This is the most common type of asexual reproduction (Chen *et al*., 1995; Chadwick-Furman and Spiegel 2000; Chadwick-Furman *et al*., 2000). CMs 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*., 1995). Different modes of asexual reproduction help CMs to increase their population size. The doubling time of *Rhodactis rhodostoma* is significantly higher than Scleractinians (Chadwick-Furman and Spiegel, 2000). CMs are known to have more biomass turnover in less than five weeks (Chadwick, 1987) and because of this, they are expected to be better competitors for space on tropical reefs.

R. bryoides has only a few previous global records from the eastern Indian Ocean and the western Pacific Ocean. First described from the Torres Strait (Haddon and Shackleton, 1893), it remains less known to date, having very few records from the western Pacific Ocean regions such as the Mariana Islands, the Coral Sea and the South China Sea off Vietnam (Paulay *et al*., 2003; GBIF, 2019). It is morphologically distinct from the four other similar congeners (Chen and Miller, 1996).


(a) (b)

(c) (d)

Fig. 2. *R. bryoides* growth on (a) *Acropora* sp.; (b - d) *Porites cylindrica*

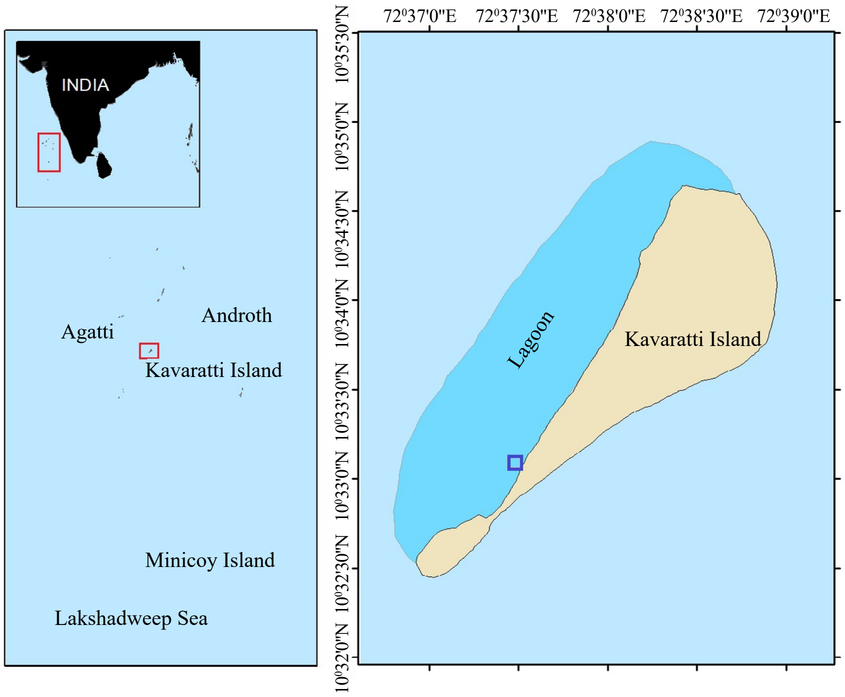


Fig. 3. Study site in Kavaratti Island (Corallimorph growth observed area highlighted in the blue square)

Discussion

There are several studies which observe the competitive success of CMs over hard corals at various locations (Table. 2). For the first time, we report the occurrence of a CM and its competitive success over corals in Lakshadweep. Some of these atolls were subjected to thorough surveys in the past, but no observations exist regarding the presence or invasion of CMs in any of them (Suresh, 1991; George, 2008). The occurrence of other *Rhodactis* sp. was reported from various reefs in the western Indian Ocean; however, there were no previous records of *R. bryoides*. In the nearby atolls of Maldives, the presence of an ambiguous *Rhodactis* sp. (then doubtfully identified as *Discosoma* cf. *rhodostoma*) was previously reported and was speculated to be causing a phase shift (Zahir *et al*., 2009).

From the currently available data, it is impossible to elaborate on the exact triggering factors behind the invasion and the seemingly successful initial level of proliferation of the CM at Kavaratti. We observed *R. bryoides* towards the shore of the island, where the lagoon is shallow (approximately <1m), but not exposed during low tides. The coral colonies at this location were healthy except in the area of the CM invasion. Studies described the capacity of CMs to thrive in hostile conditions, which gives 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 become frequently exposed to air and wave damage.

Table 2. Major works on competitive interaction of Corallimorphs and Scleractinian corals

Location	Corallimorph species	Authors
Maldives	*Rhodactis.* sp	Moosleitner (1989)
Malaysia	*Rhodactis howesii, Discosoma dawydoffi*	Ridzwan (1993)
Seychelles	*Rhodactis howesii*	Den Hartog (1994)
Eliat, Red sea	*Rhodactis rhodostoma*	Langmead and Furman (1999a)
Tanzania	*Rhodactis rhodostoma*, *Rhodactis mussoides*, *Ricordea yuma*, *Actinodiscus unguja* and *Actinodiscus nummiforme*	Muhando *et al.* (2002)
Palmyra Atoll	*Rhodactis howesii*	Work *et al.* (2008); Carter (2014)
Maldives	*Discosoma* cf. *rhodostoma*	Zahir *et al.* (2009)
Kavaratti, Lakshadweep	*Rhodactis bryoides*	Current study

However, the reef where *R. bryoides* was recorded during the present study, is not exposed even during neap tides and the reef breaks protect it from waves. Further, hardly any anthropogenic disturbances were noticed at the site, yet CMs successfully replaced the corals. Hence, the findings point to a successful invasion of *R. bryoides* in a healthy reef patch without any apparent assistance of exogenous forces, but rather due to the species' innate biological ability to outcompete the corals.

The competition for space is a never-ending process in coral reefs (Muko *et al*., 2001). The initial observations showed that the dominant *P. cylindrica* is losing the fight for space. The CMs are able to successfully use several life-history traits that help them to overgrow the shallow reef substrate. They are competitively superior to some coral species and have well-suited anatomy, giving them an edge in the fight for space. Their elongated marginal tentacles help them to kill Scleractinian corals (Langmead and Chadwick-Furman, 1999b). Additionally, the clonal replication ability of CMs allows them to rapidly colonise the spaces on the reefs (Chadwick-Furman and Spiegel, 2000). CMs successfully use their mesenterial filaments and acrospheres as weapons against adjacent organisms in the competition for space (Chadwick, 1987; Langmead and Chadwick-Furman, 1999a). Naturally, mesenterial filaments are used for ingestion, but when they come in contact with a Scleractinian coral, CMs gather the mesenterial filaments in the mouth or body walls and expel them onto the opponent's body (Chadwick, 1987). The mesenterial filaments cause tissue necrosis, while prolonged contact may lead to death (Chadwick, 1987; Kuguru *et al*., 2004). Given the quick rate of expansion reported in this study, we may anticipate that, if this situation persists, the CMs may be able to destroy the entire reef patch within a few years by overthrowing the coral. This can further lead to a phase shift in the shallow reefs of Kavaratti Lagoon, as has been observed in numerous other coral reefs.

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