



# Aggregations of free-living corals facilitate reef expansion at upper mesophotic depth off Poivre Island, Seychelles

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## Abstract

Free-living corals on unconsolidated substrates, such as sand and coral rubble, can play a key role in the outward expansion of coral reefs, yet their ecological significance at mesophotic depths remains poorly studied. Here, we present the first detailed documentation of aggregations of free-living corals at mesophotic depths (30–40 m) off Poivre Island, Seychelles, western Indian Ocean. Using manned submersibles and qualitative analysis of high-resolution video transects, we identified different benthic communities. Some of these communities were dominated by assemblages of free-living corals consisting of fungiids and a poritid, with a total of 13 species recorded. These free-living corals contributed substantially to live coral cover (estimated up to 75%) and provided new substrate for reef organisms, facilitating reef growth on unconsolidated sediments. Our findings offer the first direct evidence that free-living coral assemblages can enhance habitat complexity and live coral cover at upper mesophotic depths in the region. Although documented from a single site, our observations highlight the underappreciated ecological importance of free-living corals in deep reef environments and underscore the need for further quantitative research on their role in reef development and resilience.

**Keywords** Fungiidae · Mobility · Soft-bottom substrates · Substrate colonization · West Indian Ocean

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## Introduction

Research on Seychelles coral reefs (Western Indian Ocean) has historically concentrated on reef structure and coral communities, particularly during the late twentieth century (Braithwaite 1971; Stoddart 1984; de Kluijver 1994). Subsequent studies have focused on coral fauna composition, contributing significant insights into coral taxonomy and biogeography (Pillai et al. 1973; Rosen 1979; Wijsman-Best et al. 1980; Sheppard 1987; Selin et al. 1992; Hoeksema 1994; Hoeksema and Best 1994). Since the early 2000s, research has shifted towards understanding the degradation and recovery of reefs following major bleaching events, mostly in shallow waters (< 15 m) (Sheppard and Obura 2005; Spencer et al. 2000; Stobart et al. 2005; Chong-Seng et al. 2014; Harris et al. 2014; Cerutti et al. 2020; Gudka et al. 2020; Vessaz et al. 2022). As a result, deeper reef slopes and mesophotic coral ecosystems (30–150 m) remain largely unexplored in the Seychelles and across the broader Western Indian Ocean (Turner et al. 2017; Stefanoudis et al. 2023).

In these deeper zones, unconsolidated substrates such as sand, silt, and pebbles are common (Latypov 2007).

Many corals living on these substrates are free-living and form distinct species assemblages (Pichon 1974; Fisk 1983; Borghi et al. 2023; Mehrotra et al. 2023), with mushroom corals (Fungiidae) especially prominent in the Indo-Pacific (Pichon 1974; Claereboudt 1988; Latypov 2007; Prasetya et al. 2020). Juvenile mushroom corals are generally attached to solid substrates, often dead corals (Hoeksema and Yeemin 2011; Hoeksema and Benzoni 2013; Sayco et al. 2024). Species that normally remain attached can become dislodged and act as “coralliths,” behaving like free-living species (Capel et al. 2012; Kersting et al. 2017; Hoeksema et al. 2018b).

Free-living mushroom corals can move downslope, often aided by gravity, towards deeper and darker zones (Chadwick-Furman and Loya 1992; Ohara et al. 2021; Bayley and Mogg 2023). They can thrive in muddy or sandy habitats, shedding sediments if buried (Fisk et al. 1981; Johnson 1988; Bongaerts et al. 2012). Phototaxis may guide these movements (Yamashiro and Nishihira 1995; Lewis et al. 2025), and if overturned, they can right themselves, possibly aided by turbulent water (Jokiel and Cowdin 1976; Hoeksema and Bongaerts 2016). Once established on loose sediments, and in the absence of solid substrates for larval settlement, some free-living corals can reproduce asexually through budding (Hoeksema 2004; Hoeksema and Waheed 2011a) or by fragmentation (Yamashiro and Nishihira 1998; Hoeksema and Gittenberger 2010; Hoeksema and Waheed 2011b) resulting in dense aggregations and competition for space and overtopping (Littler et al. 1997; Hoeksema and Matthews 2011).

These free-living assemblages can be multi-species if sexual reproduction predominates, or be dominated by one or two species if asexual production prevails (Hoeksema and Benzoni 2013; Hoeksema and Gittenberger 2010; Hoeksema et al. 2018a, 2019b; Feingold et al. 2020). At high densities, free-living corals are vulnerable to predators such as *Drupella* snails and *Acanthaster* sea stars (Hoeksema et al. 2013; Scott et al. 2015). However, their relative mobility or “sessile dispersal” (Jackson 1986) provides an advantage, allowing them to avoid competition for space and other harmful interactions with reef organisms (Chadwick 1988; Chadwick-Furman and Loya 1992; Hoeksema and de Voogd 2012), enabling colonization of soft substrates that are rarely used by other corals (Goffredo and Chadwick-Furman 2000; Hoeksema et al. 2019a).

The skeletons of dead, sand-dwelling mushroom corals further contribute to benthic habitat complexity, providing settlement and shelter for various benthic invertebrates, which use them for (Hutchings 1981; Enochs 2012; Head et al. 2015), as well as sites for egg deposition

(Scott et al. 2017; Kaullysing et al. 2020). In addition, coral larvae readily settle on these skeletons (Norström et al. 2007; Yucharoen et al. 2015), promoting further expansion of reef surface area in deeper zones (Sheppard 1981).

Despite the ecological importance of free-living corals in mesophotic environments, the role of mushroom corals on deep unconsolidated substrates (> 25-m depth) remains poorly documented, particularly in relation to their life history, evolution, and competition for space with other benthic organisms (Hoeksema 2012; Hoeksema and Giyanto 2019).

Recent surveys of Seychelles reefs across a depth gradient (10–350 m) have revealed that mesophotic zones support distinct and functionally unique communities, with deep reefs hosting taxa of high functional and conservation importance, despite lower overall richness and abundance (Stefanoudis et al. 2023). Nevertheless, these habitats remain poorly studied, particularly in terms of the structure and dynamics of specific benthic assemblages. Against this backdrop, our study focuses on the aggregation of free-living corals uniquely encountered on the eastern slope of Poivre Island. Here, we provide new insights into the composition, environmental setting, and ecological significance of unconsolidated mesophotic reef habitats in the Western Indian Ocean, based on qualitative assessments from video transects.

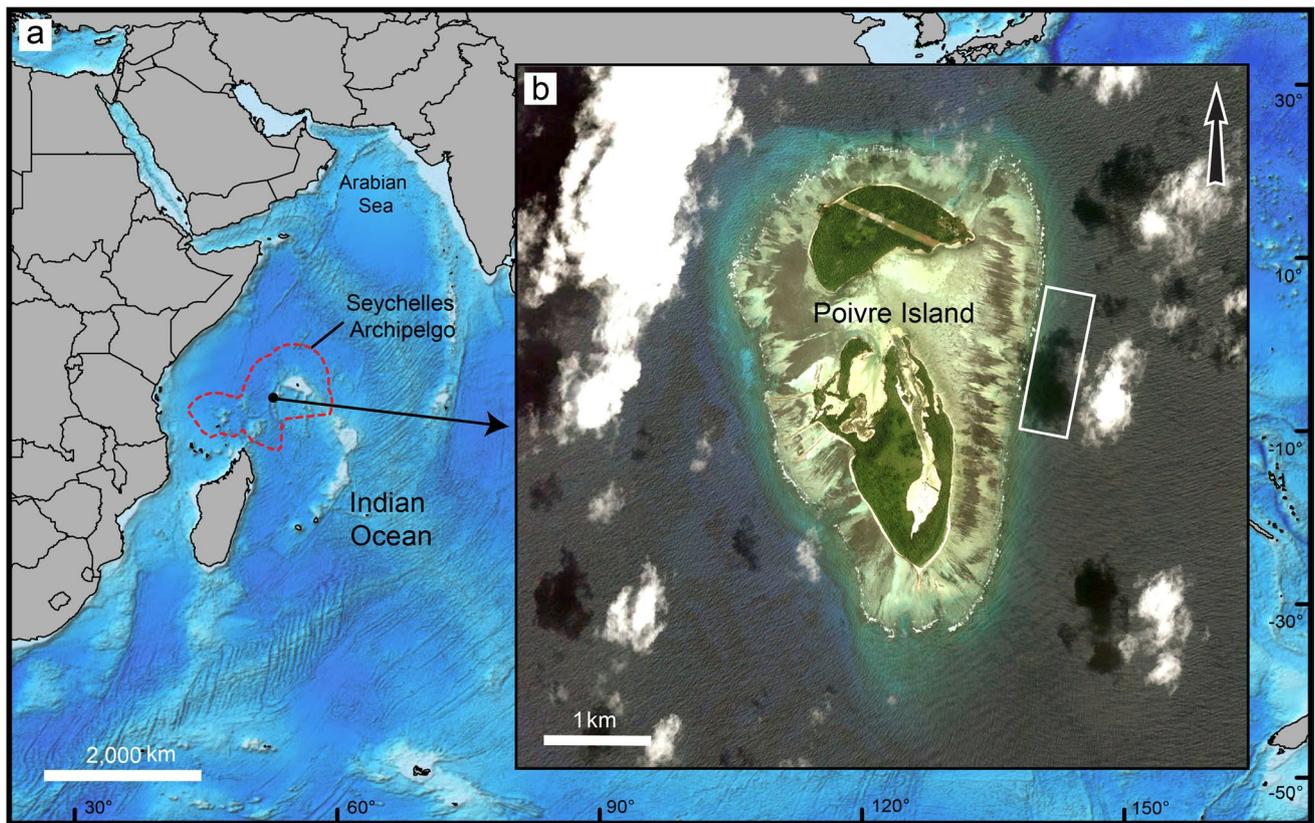
## Material and methods

### Field survey

As part of the First Descent: Seychelles expedition (5 March–18 April 2019; see Stefanoudis et al. 2023 for survey design and methods), benthic communities were surveyed at seven sites across six atolls in the Seychelles Outer Islands (Fig. 1a), using a combination of SCUBA, submersibles, and ROVs. At each site, video transects were conducted within a depth range of 10–350 m, resulting in a total of 108 transects (each 100–250 m in length) throughout the expedition. However, aggregations of free-living corals mainly consisting of fungiids were encountered exclusively on the eastern slope of Poivre Island at depths of 30–40 m (Fig. 1b). All transects from this site and depth band were analyzed in detail for the present study.

We describe these free-living coral aggregations, their environmental setting, and species composition based on qualitative assessments from video transects and observations made by submersible at approximately 1–2 m above the sea floor (see Electronic Supplementary Material, Videos S1 and S2).

Live coral cover was visually estimated from the video transect footage, based on the proportion of the visible



**Fig. 1** Location of the surveyed area; **a** Seychelles Archipelago in the western Indian Ocean; **b** Poivre Island, with the study area marked by a rectangle

substrate occupied by living corals. These estimates were qualitative and approximate, as no formal point-intercept or quantitative image analysis was conducted.

### Specimen identification

Species identification in this study was primarily qualitative and based on video transect imagery recorded by a submersible hovering 1–2 m above the seabed. Free-living coral species visible in the footage were identified to species level whenever possible. Identification was further supported by comparison with reference material from the coral collection at Naturalis Biodiversity Center in Leiden (catalog code RMNH.COEL), which includes dry coral skeletons collected during the RV Tyro cruise in the Seychelles as part of the Netherlands Indian Ocean Program (December 1992–January 1993; Hoeksema 1994; Hoeksema and Best 1994).

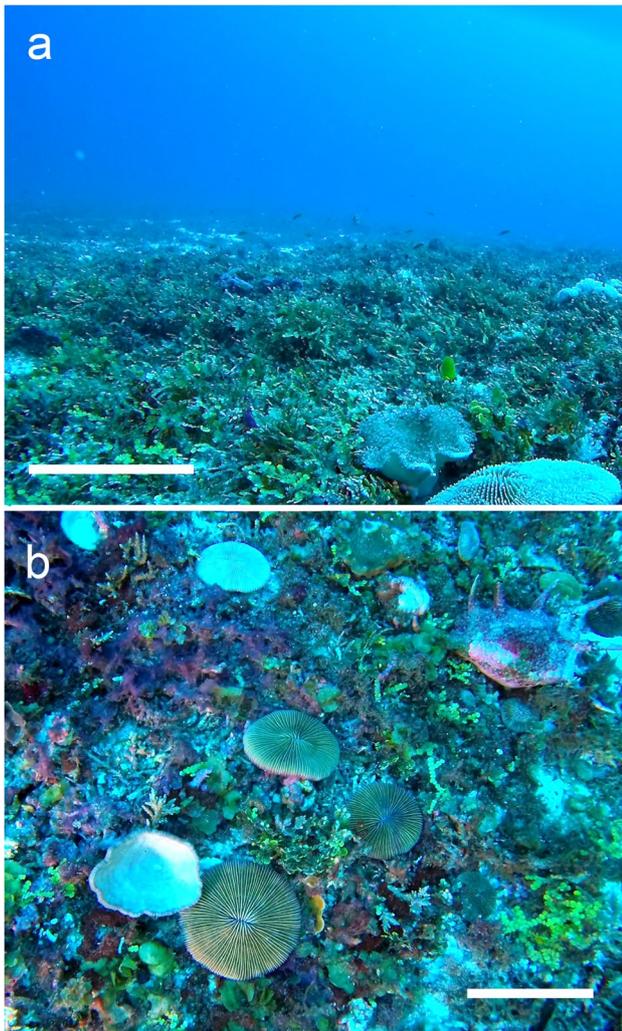
Species identifications based on video imagery are inherently limited by the resolution and viewing angles of the footage, as well as by the absence of physical specimens for detailed morphological or molecular confirmation. Only a subset of species could be confidently identified; where possible, identifications were cross-referenced with historical collections as reference material. Consequently, some

taxa are listed as provisional and should be interpreted with caution. Due to the qualitative nature of the video analysis, presence/absence and abundance data were not systematically quantified.

### Results

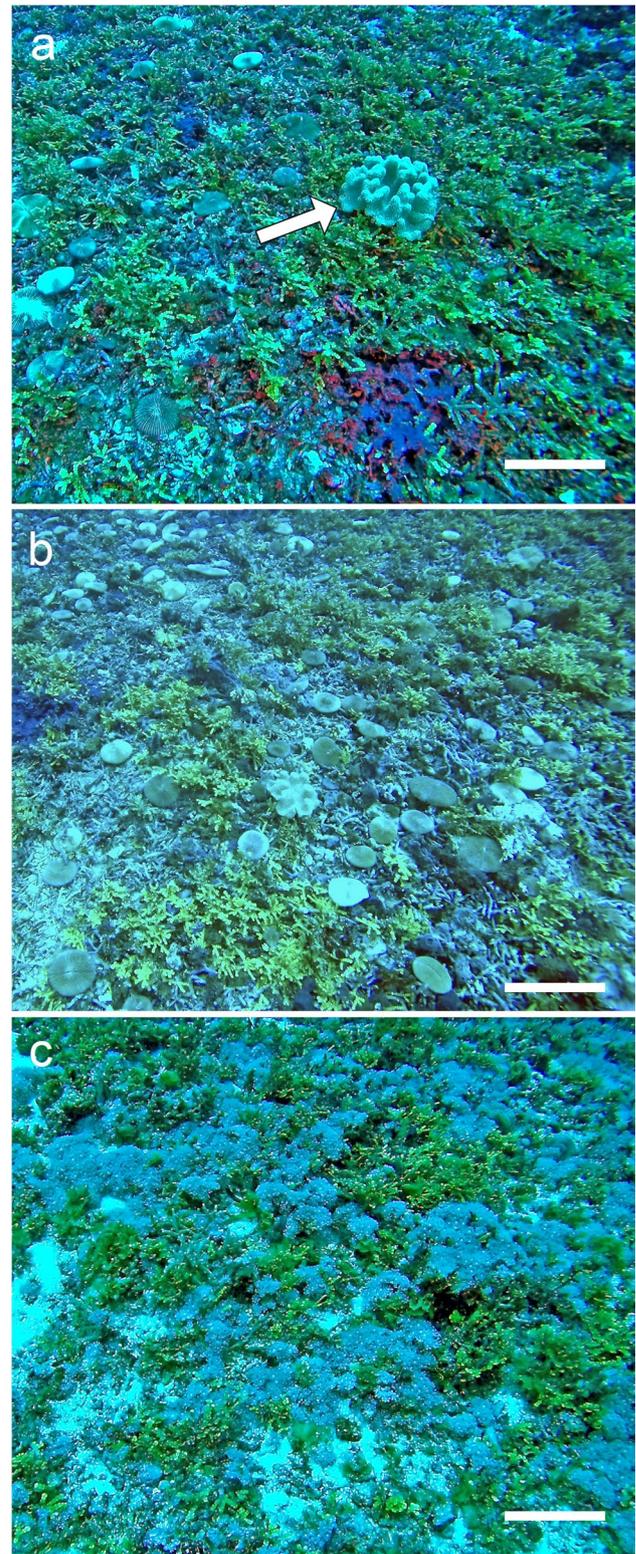
The lower reef slope (> 30-m depth) gradually declined and exhibited little variation in coral height, resulting in a reef surface with low structural complexity (i.e., low rugosity) (Fig. 2). Substrate cover ranged from 60 to 80% across the area. The coral community was patchy, interspersed with sand pockets and rubble fields, and primarily composed of low, branching *Acropora* colonies. In the shallower slope areas, ahermatypic soft corals such as *Scleronephthya*, *Sarcophyton*, and several xeniids, like *Ovabunda* and *Xenia*, dominated the benthic cover (Fig. 3). The site also featured a field of the green alga *Halimeda* sp. and a few aggregations of xeniid soft corals (Fig. 3C, D).

Free-living corals, predominantly fungiids, were found on all available substrates, including sand and rubble. These corals occurred at visually high densities, with live cover estimated to reach up to 75% at the site, based on qualitative

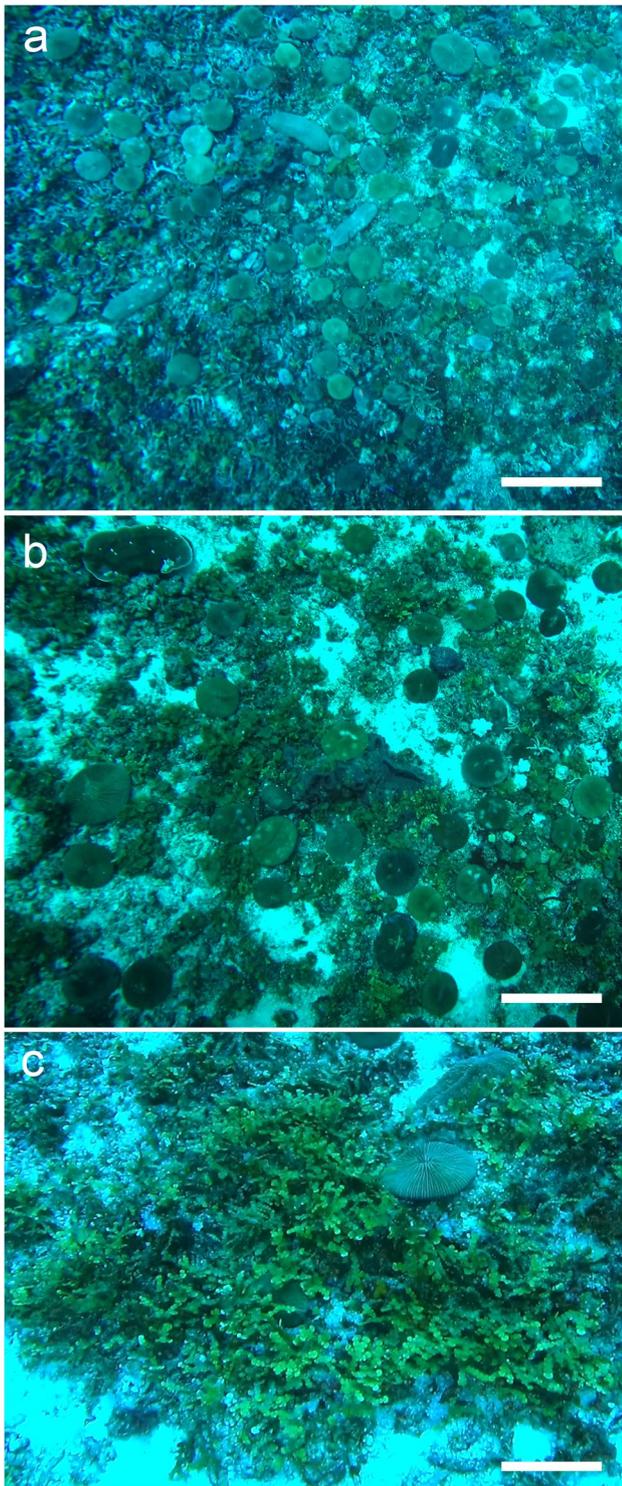


**Fig. 2** Upper mesophotic reefscape (30–40-m depth) off Poivre Island, Seychelles; **a** overview of the reef base below the reef slope, with part of a mushroom coral (*Danafungia scruposa*) in the foreground; **b** close-up of the coral community with mushroom corals (several *Lithophyllon repanda*, a bleached *Pleuractis granulosa*, and an overturned *Halomitra pileus*), some green algae (*Halimeda* sp.), a large gastropod (*Lambis* sp.), and branching corals (*Acropora* sp.). Scales:  $\approx$  20 cm

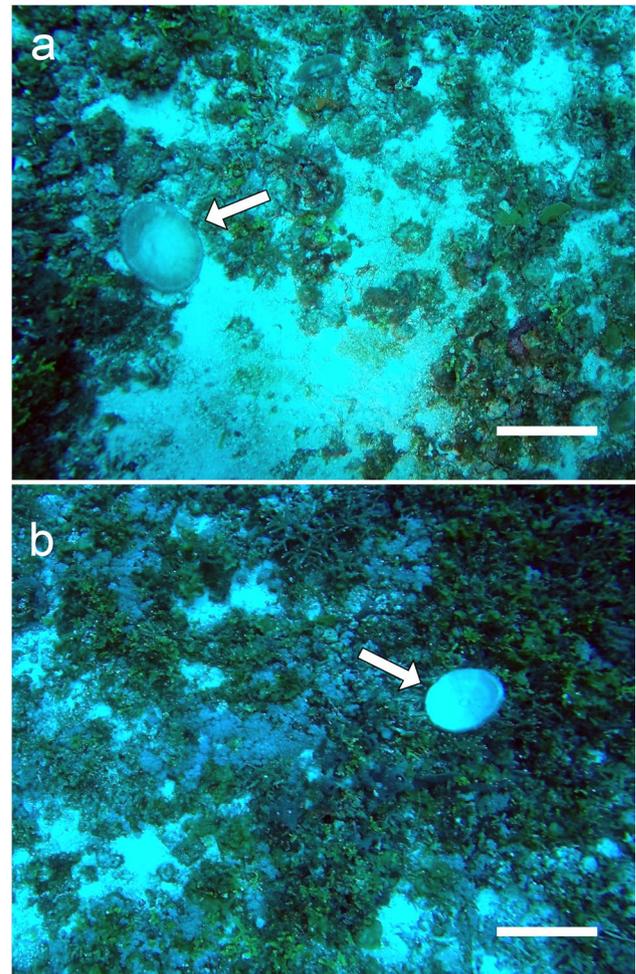
video assessment. No overtopping among individuals was observed (Fig. 4). The free-living coral assemblages included species from two scleractinian families: Fungiidae and Poritidae. The Fungiidae family was represented by 12 species: *Danafungia horrida* (Dana, 1846), *D. scruposa* (Klunzinger, 1879), *Fungia fungites* (Linnaeus, 1758), *Halomitra pileus* (Linnaeus, 1758), *Herpolitha limax* (Esper, 1792), *Lithophyllon concinna* (Verrill, 1864), *L. repanda* (Dana, 1846), *Lobactis scutaria* (Lamarck, 1801), *Pleuractis granulosa* (Klunzinger, 1879), *P. seychellensis* (Hoeksema, 1993), *Sandalolitha dentata* (Quelch, 1884), and *S. robusta* (Quelch, 1886). The Poritidae was only represented by



**Fig. 3** Mesophotic multi-species assemblages off Poivre Island, Seychelles; **a** *Sarcophyton* sp. (arrow) surrounded by branching corals (*Acropora* sp.); **b** mix of free-living mushroom corals and *Acropora* sp. on dead coral and the green alga *Halimeda* sp.; **c** an aggregation of the xeniid soft coral *Ovabunda* sp. (arrows), in a shallower part of the mesophotic reef slope. Scales:  $\approx$  20 cm



**Fig. 4** Multi-species assemblages of free-living mushroom corals on unconsolidated substrates at upper mesophotic depths (30–40 m), off Poivre Island, Seychelles; **a** upper zone consisting mainly of dead coral rubble, scale  $\approx$  50 cm; **b** lower zone primarily composed of sand, scale  $\approx$  50 cm, **c** green alga (*Halimeda* sp.) present among mushroom corals, scale:  $\approx$  20 cm



**Fig. 5** Examples of overturned and tilted free-living mushroom corals at upper mesophotic depths off Poivre Island, Seychelles; **a** *Halomitra pileus*, upside down; **b** *Fungia fungites*, upside down. Scales:  $\approx$  20 cm

*Goniopora stokesi* (Milne Edwards & Haime, 1851). Among all free-living species *L. repanda* was the most abundant, followed by *H. limax*, *D. scruposa*, *P. seychellensis*, and *L. scutaria*.

Asexual reproduction was observed in *Sandalolitha dentata*, the only mushroom coral species displaying this mode of reproduction. Three large and thin specimens were observed, all regenerated from a small fragment and lacking a central (primary) mouth, indicating that they originated from fragmentation (Hoeksema and Dai 1991). Additionally, two colonies of *Goniopora stokesi* were found on sand showing asexual reproduction by budding.

Less than 1% of the assemblage comprised mushroom corals observed in an upside-down or tilted position (Figs. 2b and 5), mostly large individuals of *D. scruposa*, *F. fungites*, *H. pileus*, *L. repanda*, *P. granulosa*, and *S. robusta*.

## Discussion

High densities of free-living coral assemblages on the lower reef slopes at upper mesophotic depths (> 30 m) off Poivre Island were composed of multiple species, colonizing unconsolidated substrates by sessile dispersal and contributing to the outward expansion of live coral cover and laying the foundation for new reef growth. While previous research has suggested that free-living corals could contribute to reef formation on lower reef slopes and reef bases in the western Indian Ocean (Sheppard 1981), this process has not been documented or illustrated in the Seychelles. Furthermore, only a few studies have examined the role of mushroom corals in Indo-Pacific mesophotic coral communities at the species level (Lane and Hoeksema 2016; Muir et al. 2018; Hoeksema et al. 2019; De Palmas et al. 2021).

A total of 13 free-living coral species were recorded in this survey, including 12 fungiids and one poritid, *Goniopora stokesi*. In comparison, 18 free-living mushroom coral species were found in the Seychelles during the 1992–1993 survey (Hoeksema 1994; Hoeksema and Best 1994). Free-living *Goniopora stokesi* has been previously reported in the Seychelles (Rosen and Taylor 1969; Hoeksema and Best 1994). This species is capable of reaching high densities due to asexual reproduction and covering large areas of unconsolidated substrate (Sheppard 1981; Hoeksema and Waheed 2011a; Reimer et al. 2020).

It should be noted that species-level identifications in this study were primarily based on qualitative video imagery; actual diversity, particularly of smaller or cryptic taxa, may be underestimated, and some identifications remain provisional. Species absent from the present survey are generally small and may have been overlooked or unrecognized in the footage. *Cycloseris* species, for example, are too small to be identified with a submersible hovering at a height of over 2 m above the sea floor. Some of these species have been reported from the Seychelles in earlier studies (Wijsman-Best et al. 1980; Hoeksema 1994; Latypov 2007). These species are typically observed from a close distance, often during SCUBA dives at shallow depths (Hoeksema et al. 2019; Feingold et al. 2020), although mesophotic records from ROV surveys have also been reported (Hoeksema et al. 2019). *Polyphyllia talpina* was also absent in the current study, although a single specimen was dredged from 40-m depth during the 1992–1993 survey in the Seychelles (Hoeksema 1994).

Some mushroom coral records from the Seychelles reported in earlier studies, but absent in the present survey, were based on misidentifications. For instance, Latypov (2007) reported 13 fungiids from the Seychelles, including *Herpolitha weberi* (van der Horst, 1921), which is a synonym of *H. limax* (Hoeksema 1989). A record of *Zoopilus*

*echinatus* (Dana, 1846) from the Seychelles (Friedlander et al. 2015) was based on the misidentification of a large specimen of *H. pileus* that apparently originated from a regenerated fragment, as also observed in Madagascar and Fiji (see Pichon 1974; Littler et al. 1997).

Two free-living species were represented by a few specimens that originated from asexual reproduction: *Sandallitha dentata* by fragmentation and *Goniopora stokesi* by budding (as mentioned above). Other species that frequently reproduce through fragmentation were not observed.

Several large mushroom corals were found overturned, possibly due to the activity of foraging animals, such as fishes, suggesting that these corals can move or be displaced by external forces (Jokiel and Cowdin 1976; Gittenberger and Hoeksema 2013), despite the reef slopes not being steep at upper mesophotic depths. This overturning indicates that the free-living corals at the surveyed depths are mobile and capable of sessile dispersal (Jackson 1986), supporting their ability to colonize sand and rubble substrates.

The results of the present survey support the hypothesis that settlement and movement of free-living corals at greater depths contribute to the gradual expansion of coral reef surfaces, a process not previously documented at mesophotic depths in the Seychelles. Globally, aggregations of free-living corals are uncommon at these depths, and reef expansion through sessile dispersal is likely to be slow. Nevertheless, our findings reveal that free-living corals play a unique and underappreciated role in shaping reef communities by colonizing unconsolidated substrates beyond the limits of most attached species. These findings align with recent trait-based assessments of Seychelles reefs (Stefanoudis et al. 2023), which highlight the functional distinctiveness and conservation value of deep reef communities, even where taxonomic richness is comparatively low.

Overall, this study provides the first detailed documentation of species-rich free-living coral aggregations on unconsolidated substrates at mesophotic depths in the Seychelles. The ecological role of these assemblages, particularly in facilitating reef expansion and enhancing benthic complexity, deserves further investigation, especially given the increasing threats to reef habitats in the region. These observations reinforce the view that mesophotic reefs, although often overlooked, are functionally important components of coral reef ecosystems in the Western Indian Ocean. Future research, especially quantitative surveys across a broader range of sites and depths, will be crucial to fully understand the prevalence, ecological significance, and conservation needs of these free-living coral assemblages.

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## Declarations

**Conflict of interest** The authors declare no competing interests.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

**Sampling and field studies** All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the “Acknowledgements,” if applicable.

**Data availability** All data generated or analyzed during this study are available as supplementary material or can be requested from the first author.

**Author contribution** K. S.-N. and B. W. H. conceived and designed the research and analysis; K. S.-N. and B. W. H. analyzed the data; L. C. W. provided materials and funds; K. S.-N. and B. W. H. wrote the first draft of the manuscript; K. S.-N., L. C. W., P. V. S., S. T., and B. W. H. edited the manuscript and approved its submission.

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