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ARTICLE

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Marine animal forest formed by gorgonians *Subergorgia* on near-shore mesophotic ecosystems in Reunion Island

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Abstract

Mesophotic coral ecosystems (MCEs), occurring between 30 and 150 m depth, are increasingly recognized for their ecological importance, yet they remain underexplored, particularly in the southwestern Indian Ocean. During benthic surveys conducted at depths ranging from 15 to 75 m off northwestern Reunion Island, we documented a dense and extensive marine animal forest (MAF) dominated by large arborescent octocorals *Subergorgia* cf. *suberosa*. This monospecific community formed a complex three-dimensional habitat spanning a substantial area at mesophotic depths over the northwestern abrupt slopes of Reunion Island. Colonies reached over 1.5 m in height, providing structural habitat for diverse fish and macroinvertebrate assemblages. A total of 53 fish species from 22 families were recorded in association with this MAF, alongside numerous epibionts and understory anthozoans. Despite its ecological value, this habitat faces significant anthropogenic pressures, particularly from fishing activities. Nearly 25% of photographed *S*. cf. *suberosa* colonies were entangled in fishing lines, with visible damage including tissue necrosis and polyp loss affecting up to 47% of colonies. These impacts, along with sedimentation from runoff, raise concerns for the long-term persistence of this mesophotic habitat-forming community, as long-lived, slow-growing organisms like gorgonians may be more impacted by these types of disturbances and take longer to recover than fast-growing organisms. Our findings represent the first quantitative assessment of *Subergorgia* dominance and associated biodiversity in this region and highlight its role as a potential refuge for shallow reef taxa. The ecological significance, spatial extent, and fragility of this MAF underscore the urgent need for spatially replicated surveys, targeted conservation strategies, and regulation of damaging activities such as fishing. We advocate for increased research efforts focused on mesophotic habitats, with particular attention to the population dynamics and ecological functions of large gorgonians, to better understand the role of MCEs in reef resilience under accelerating environmental changes.

KEYWORDS
benthic communities, biodiversity refuge, foundation species, gorgonians, marine animal forest, mesophotic coral ecosystems, octocorals, sessile organisms, southwestern Indian Ocean

Mesophotic coral ecosystems (MCEs) are characterized by the presence of sessile macrobenthic organisms found at depths between 30–40 m and 150 m in tropical and subtropical regions (Hinderstein et al., 2010; Pyle & Copus, 2019). Although in recent years knowledge of MCEs has increased, the diversity and ecological functions of these ecosystems remain poorly explored. Recent deep exploratory dives in the southwestern Indian Ocean region, using closed-circuit rebreathers, have extended previously known depth limits and the geographical range of reef-building corals (Boissin et al., 2021; Hoarau et al., 2021, 2024; Pichon et al., 2020) but have also led to the discovery of new unrecorded mesophotic benthic assemblages composed of Cnidarian species (Gravier-Bonnet et al., 2022; Hoarau et al., 2021, 2024). These baseline surveys of deep communities thereby identified MCEs as potential deep refuges for shallow reef organisms that suffer drastic environmental changes and anthropogenic impacts (Bongaerts et al., 2010; Glynn, 1996). This refuge potential likely warranting long-term persistence of marine populations (Bongaerts & Smith, 2019) has become a research and conservation priority (Keppel et al., 2012).

Arborescent octocorals (often referred to as gorgonians), that belong to the order Malacalcyonacea (McFadden et al., 2022), are important components of macrobenthic communities on many shallow (Fabricius & Alderslade, 2001) and mesophotic (sub)-tropical coral reefs worldwide (Benayahu et al., 2019). In some regions, gorgonians can dominate the seascape, as is well documented for instance in the shallow-mesophotic reefs in the tropical Caribbean basin and the Red Sea (Benayahu et al., 2019; Rossi et al., 2017; Williams et al., 2015). Moreover, the decline in shallow scleractinian corals and the concomitant increasing abundances of octocorals in other tropical regions (Lenz et al., 2015; Ruzicka et al., 2013; Stobart et al., 2005) will likely allow for this community to transition over time and favor the rise of octocoral forests (Lasker et al., 2020). As for scleractinians, gorgonians are structurally and functionally crucial within reef benthic communities (Nelson & Bramanti, 2020; Slattery & Lesser, 2021). The formation of such complex biogenic structures has deep evolutionary roots, as animals like corals, sponges, and bivalves have been building three-dimensional "forests" in the sea almost continuously since the Early Cambrian ~520 million years ago (Mya) (Kiessling, 2009). These habitats enhance structural complexity and offer shelter to a wide array of marine species, thereby supporting high levels of associated biodiversity (Figure 1). Functional significance and structural complexity were recently identified as the two key criteria defining marine animal forests (MAFs) (Orejas et al., 2022). Identifying and characterizing gorgonian forests is thus essential to understanding the structure and dynamics of MCEs and to guiding conservation efforts for these ecologically important communities.

Here we provide an initial report of an impressive octocoral MAF from benthic community surveys led in 2021–2022 of northwestern Reunion Island in the southwestern Indian Ocean. We used digital still photographic

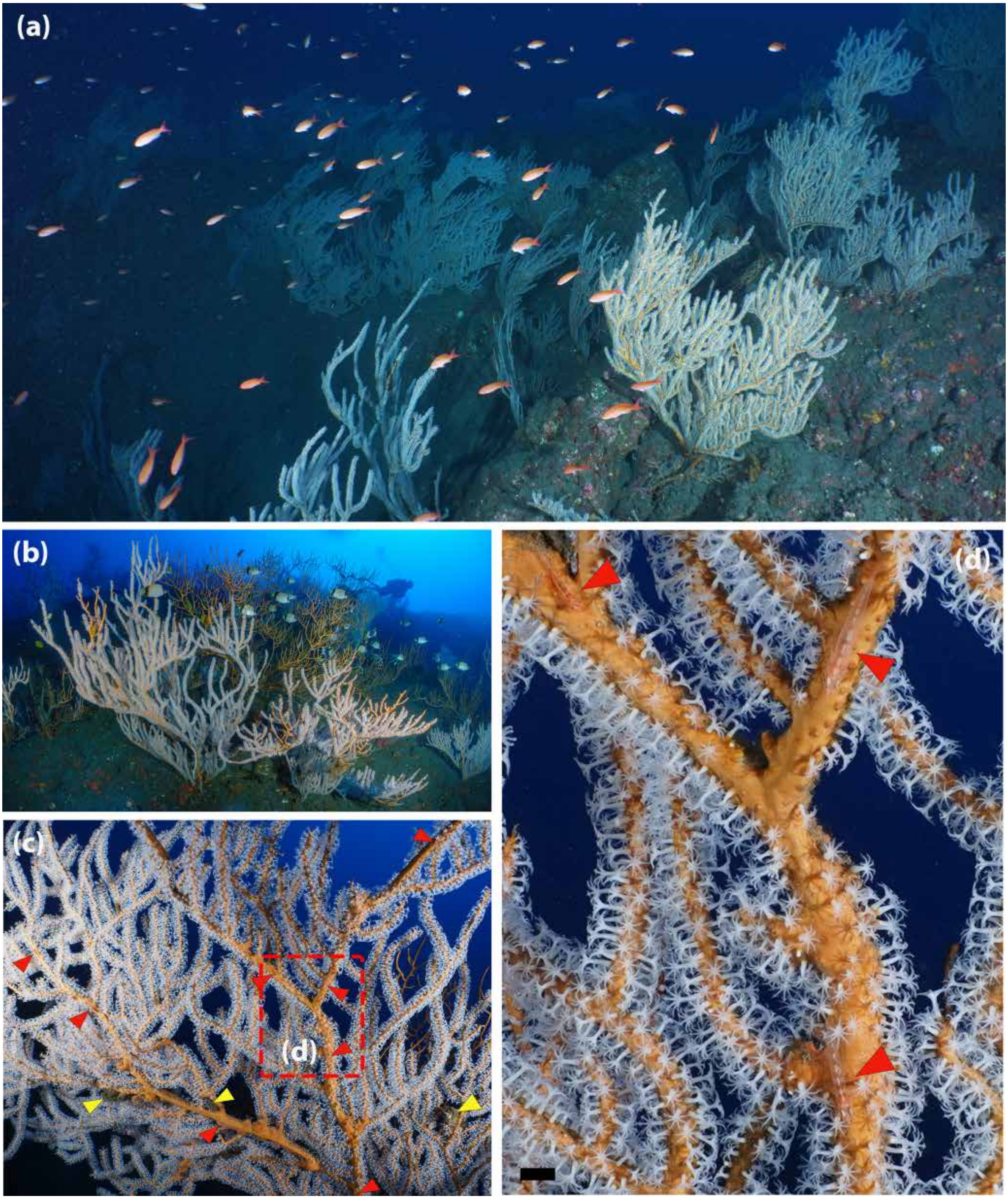

FIGURE 1 Marine animal forest (MAF) formed by dense aggregations of large gorgonians *Subergorgia* cf. *suberosa* in the mesophotic zone in Reunion Island. (a) Above view at 50 m depth with a school of planktivorous fishes *Pseudanthias cooperi*. (b) Large individuals (>1.5 m height) of *S.* cf. *suberosa* with a school of reef fishes *Chaetodon dolosus*, *Chaetodon kleinii* and *Heniochus diphreutes*. (c, d) Enlarged views of *S.* cf. *suberosa* branches with epibionts bryozoans and mollusks *Pteria* sp. (yellow arrows) sheltering a variety of animals including the large whip goby *Bryaninops* aff. *amplus* (red arrows). Scale bar in (d) corresponds to 0.5 cm. Photo credits: Hendrik Sauvignet (a, c, d) and Christophe Ediar (b).

imaging to assess the presence, density, cover, and composition of coral communities in areas with complex topography at 15–75 m depth. The monospecific community of arborescent octocorals revealed by the surveys was identified as *Subergorgia suberosa* (Pallas, 1766) (Figure 1). *Subergorgia* colonies grow in one plane and develop lateral to dichotomous branches on which a narrow furrow can be distinguished (Fabricius & Alderslade, 2001; Figure 1). Some of the colonies were visually estimated to reach over 1.5 m in height and 1 m in width, and nearly half (38/77) of the haphazardly measured *S.* cf. *suberosa* had a height greater than 0.5 m. This remarkable seascape, characterized by large-sized octocorals, is an important three-dimensional habitat that might provide a refuge from predators, shelter, and feeding substrate for fishes and diverse taxonomic groups of macroinvertebrates (Figure 1b–d). This MAF was estimated to cover a zone of at least 200,000 m^2 (area estimated based on mapping; Appendix S1: Figure S1) which should be considered for greater conservation attention. The genus *Subergorgia* was once considered rare among the octocorals of Reunion Island (Benayahu & van Ofwegen, 2012). However, our findings suggest it may be more locally widespread, particularly in the mesophotic zone. The density of *S.* cf. *suberosa* peaked at 45 m depth with a mean density (±SE) of 6.1 ± 1.0 colonies m^{-2} (Appendix S1: Table S2). The shallowest part of our study site (10–20 m) is dominated by sediment-resistant encrusting and massive scleractinian corals, along with *Millepora* hydrozoan plates covering large boulders (see photo at 15 m depth in Figure 2). Yet, a few colonies of *S.* cf. *suberosa* were also observed, hinting at a broader distribution than previously assumed.

Fifty-eight percent of photographed *S.* cf. *suberosa* were colonized with at least one epibiont. Mollusks *Pteria* sp. were also frequently observed as epibionts on gorgonians (Figure 1c). The echinoderms *Cenometra* cf. *emendatrix* (Crinoidea) and *Astroboa* sp. (Ophiuroidea) were observed on branches of *S.* cf. *suberosa*. *Ophiothela* aff. *mirabilis* (Ophiuroidea) was also found in large densities (>100 individuals) on *S.* cf. *suberosa* colonies. On the understory assemblage, other recorded octocoral genera and species were all azooxanthellate and comprised whip, bushy colonies and fans from the Ellisellidae, Acanthogorgiidae, Melithaeidae, and Paramuriceidae families (Appendix S1: Table S1). Other macrobenthic anthozoan species were observed within the understory canopy of *S.* cf. *suberosa*, such as the azooxanthellate scleractinian *Tubastraea aurea*, but also zooxanthellate scleractinians such as *Leptoseris* spp. and *Horastrea indica*, a western Indian Ocean endemic coral (Obura, 2012). *Madracis hellana*, a rare mesophotic Pocilloporidae (Appendix S1: Figure S2), *Coscinaraea monile*, *Porites lutea*, *Favites pentagona*, *Pachyseris speciosa*, and Fungiidae species were also observed in the understory of the MAF. Three Antipatharia, *Stichopathes* sp., *Cirripathes* sp., and *Cupressopathes* sp., were also recorded within the MAF but at low densities (Appendix S1: Table S1).

Regarding vertebrates, a total of 53 fish species from 22 families were recorded in association with this gorgonian forest (Appendix S1: Table S1). The fish that were identified included planktivorous fish represented by schools of small species (e.g., *Pseudanthias cooperi*, *Heniochus diphreutes*) (Figure 1a,b), corallivorous fish (i.e., *Chaetodon kleinii*) (Figure 1b), and herbivorous fish such as unicornfish and surgeonfish (e.g., *Naso hexacanthus*, *Acanthurus mata*). Some carnivorous and commercial species targeted by local fisheries were also photographed, such as *Lutjanus argentimaculatus*, *Carangoides fulvoguttatus*, and *Variola louti*. Other coral reef species such as *Aulostomus chinensis*, *Bryaninops amplus*, *Oxycirrhites typus*, *Arothron hispidus*, and *Taeniurops meyeni* were also observed sheltering above or in-between *Subergorgia* branches (Figure 1c,d). Corals are widely recognized as hosts for diverse and often cryptic epibiotic communities. For example, McCloskey (1970) reported 309 species and over 56,000 individuals associated with just eight colonies of a non-reef-building temperate coral in North Carolina, highlighting the exceptional biodiversity potential of coral-associated habitats. In this context, our own assessment likely represents a conservative estimate, as many cryptic, nocturnal, or small-bodied organisms may have gone undetected during the surveys.

Horizontal photographs of *S.* cf. *suberosa* colonies ($n = 77$) show that 24.7% were entangled in fishing lines. In some colonies, polyps of *S.* cf. *suberosa* were retracted over parts or throughout the entire colony as a direct response to the physical impacts of the fishing lines on the colonies (Figure 3). The impact of fishing lines was evident at various depths, with numerous colonies mechanically dislodged and branches broken (Figure 3a,d,e). As recently observed on coral reefs worldwide, this threat of macroplastics, and specifically with fishing activities as the main source, peaks at mesophotic depths (Pinheiro et al., 2023). Conversely, partial or total loss of polyps concerned almost half (46.8%) of photographed *S.* cf. *suberosa*, which is likely responsible for the partial or total necrosis of tissues that occurred on 35.1% of colonies and seems to increase with depth (Appendix S1: Table S2). Strings of fine particles, detrital materials, or algal turf overgrowth were also evident at the surface of these affected colonies (Appendix S1: Figure S3). Seasonal trade-wind regimes and large-scale synoptic patterns strongly influence rainfall variability across

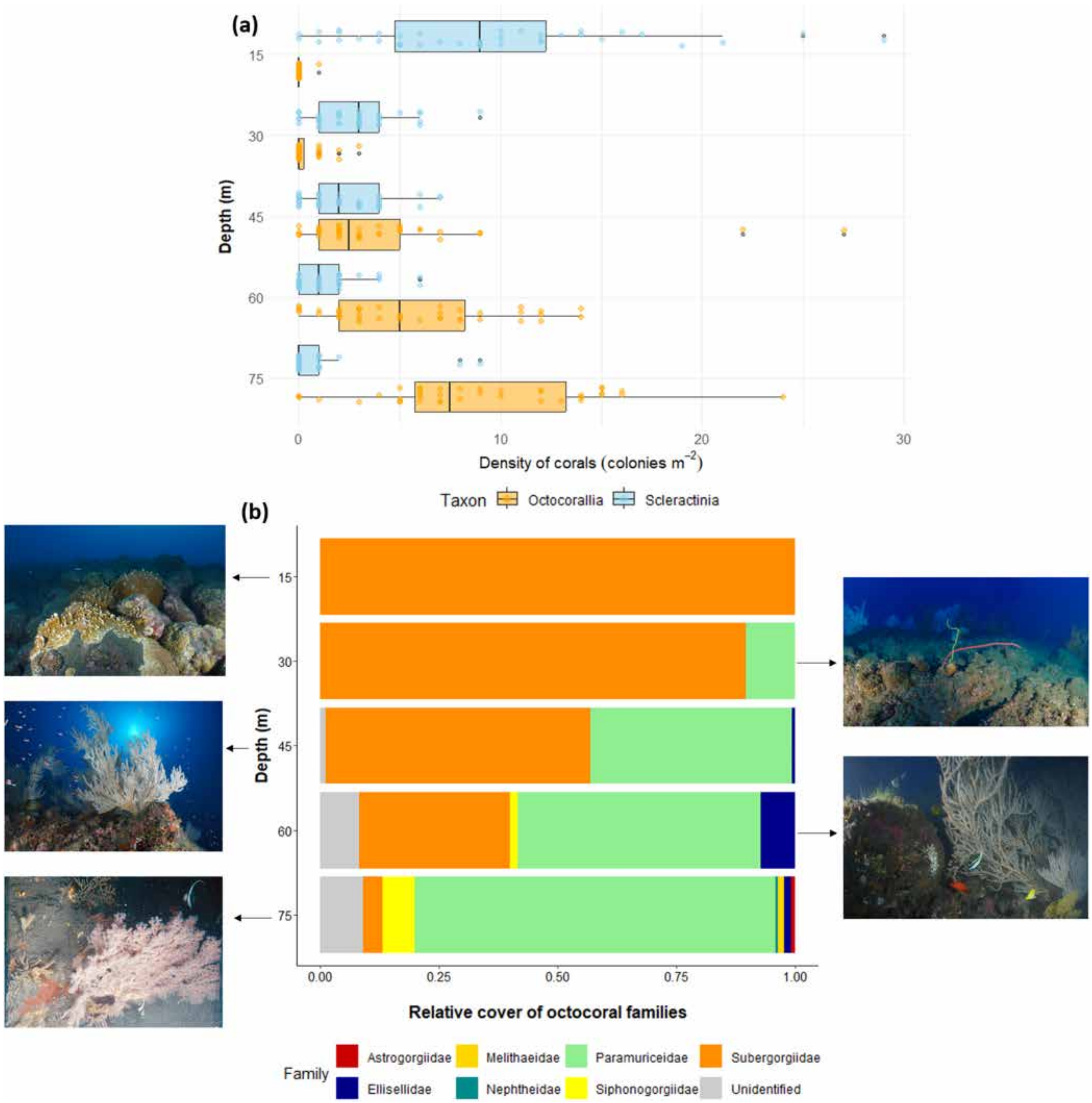

FIGURE 2 (a) Distribution of density of Scleractinia and Octocorallia and (b) relative cover (in percentage) of octocoral families at a western port in Reunion Island with corresponding representative seascape photographs at shallow depths at 15 m, in the upper limit of mesophotic zone at 30 and 45 m depths, and in the lower mesophotic zone at 60 and 75 m depths. The densities and cover were estimated from 40 horizontally oriented photoquadrats per depth (total area per depth = 10 m^2). Photo credits: Hendrik Sauvignet and Ludovic Hoarau.

Reunion Island. During the wet season, when rainfall is most intense and variable, sedimentation in the northwestern part of the island could be significant, particularly near perennial rivers, where increased runoff may affect turbidity, light availability, temperature, and nutrient distribution (Réchou et al., 2019). The octocoral canopy may also alter sedimentation resulting in greater levels of turbulence within the canopy, which may affect the recruitment success of other benthic organisms, leading to changes in reef structure dynamics (Cerpovicz & Lasker, 2021). Given their slow growth rate and reproductive mode, gorgonians are highly susceptible to physical disturbances from anthropogenic debris (notably fishing lines), and changes in physicochemical properties of the water column, both of which can impair their recovery.

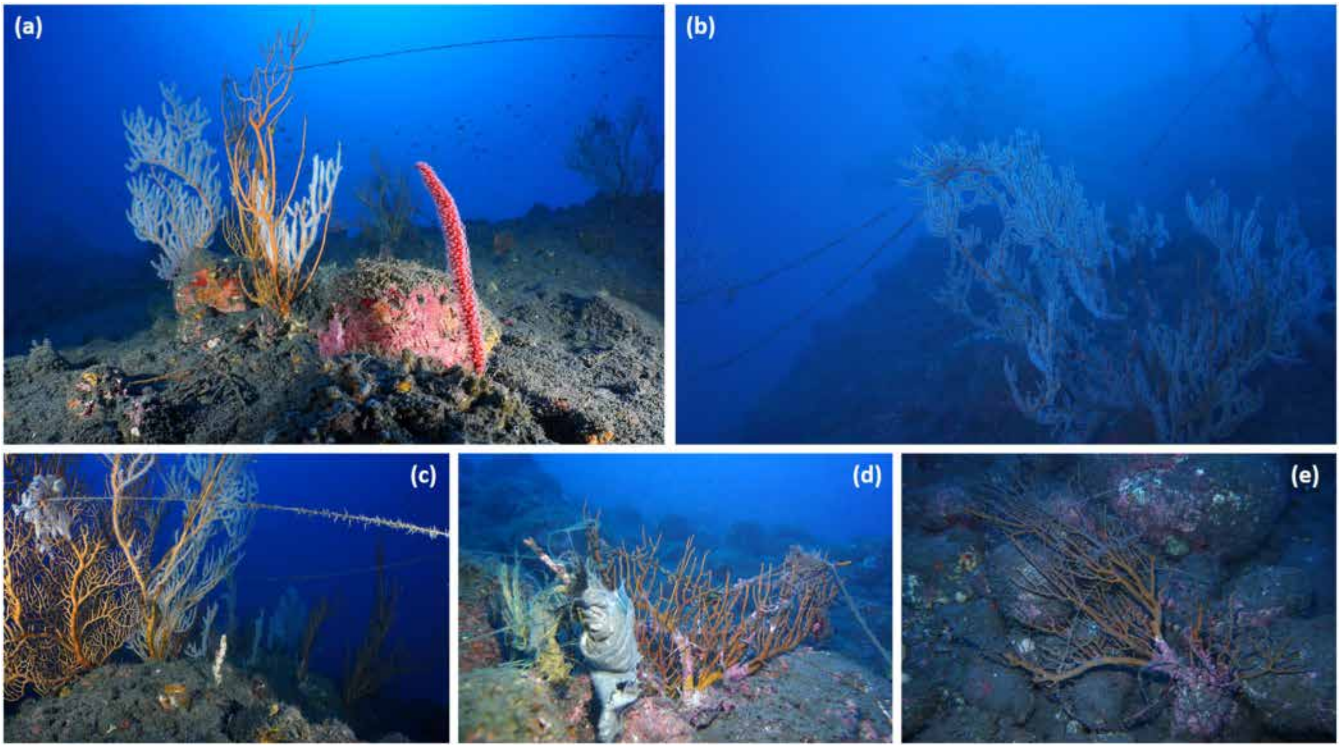

FIGURE 3 Examples of damages to entanglements on *Subergorgia* cf. *suberosa*. Some large colonies (>50 cm height) are entangled by long fishing lines at (a) 30 m, (b) 45 m, and (c) 60 m depth. (d) Colonies are entangled in lost lines and tissues and colonized by turf and coralline algae and (e) mechanically dislodged. Photo credits: Hendrik Sauvignet (a, c) and Ludovic Hoarau (b, d, e).

Our findings suggest 45–60 m as the optimal depth for *Subergorgia* (Figure 2; Appendix S1: Table S2). *Subergorgia* colonies also occur in crevices and in caves on other shallow sites around Reunion Island (10–20 m depths; L. Hoarau, personal observation), suggesting that this species is sciaphilic in shallow waters. Increasing abundance along mesophotic depths is a common pattern in the Indo-Pacific octocorals of the genera *Acabaria*, *Subergorgia*, and *Junceella* (Paulay et al., 2003). *Subergorgia* is common among Indo-Pacific octocorals and is noted as a common gorgonian in MCEs of the Chagos Archipelago, northwestern Indian Ocean (Andradi-Brown et al., 2019). These octocorals can form dense communities in various habitats from shallow crevices to caves and are generally distributed at depths of 20–30 m but can be found as deep as 115 m (Loya et al., 2019; Rowley et al., 2019).

We report a remarkable and vast MAF that is predominantly composed of dense and large *Subergorgia* in the mesophotic zone harboring a high diversity of other taxa, which consequently forms a distinct MCE in the southwestern Indian Ocean. We hypothesize that this distinct MAF with high tridimensional complexity might provide potential refuges for shallow reef biodiversity. Given that Reunion Island supports high heterogeneity of benthic assemblages of MCEs among island sites (Gravier-Bonnet et al., 2022; Hoarau et al., 2021, 2024) and our study lacks spatial replicability, the acquisition of further knowledge about spatial variance of MCEs at the scale of the island (but see in Hoarau et al., 2024) should be prioritized in order to successfully implement conservation actions. Our results constitute the first assessment of the abundance of a foundation species and associated fauna in this MAF and establish the baseline for understanding possible future changes associated with human activities. Conservation strategies should reduce the risk of mechanical damage, in particular by regulating fishing activities and anchorages where gorgonian forests are present. Moreover, when evident alterations are documented, restoration actions should be implemented to recover the integrity of such gorgonian forests.

We highlight the critical need to expand marine research efforts to include deeper mesophotic environments and emphasize once again the importance of mesophotic reef communities for biodiversity and the establishment of MCEs as a priority in conservation (Soares et al., 2020). Further research is also needed to clarify the structure and ecological functions of these distinct MCEs, with a focus on the dynamics and the demography of *S.* cf. *suberosa* populations. These studies are urgently needed to enhance our understanding of *Subergorgia*'s life history and to better consider this unique MAF of the underexplored mesophotic zone and to address the impacts of fishing lines, which compromise its health and resilience, especially under acceleration of environmental changes. Continuous monitoring of remarkable marine habitats across depths is required to assess the response of foundation benthic communities to future extreme events and to confirm their role as a refuge mechanism for other depth generalist species living in shallow habitats.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Hoarau et al., 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.15583490.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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