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Unexplored Refugia with High Cover of Scleractinian *Leptoseris* spp. and Hydrocorals *Stylaster flabelliformis* at Lower Mesophotic Depths (75–100 m) on Lava Flows at Reunion Island (Southwestern Indian Ocean)

Ludovic Hoarau [1,2,3,*], Héloïse Rouzé [3,4,5], Émilie Boissin [3,4,5], Nicole Gravier-Bonnet [5,6], Patrick Plantard [5], Camille Loisil [5], Lionel Bigot [1,3], Pascale Chabanet [1,3], Priscille Labarrère [2], Lucie Penin [1,3], Mehdi Adjeroud [1,3] and Thierry Mulochau [6,7]

1 UMR ENTROPIE, Université de La Réunion, IRD, CNRS, IFREMER, UNC, 97744 Saint Denis CEDEX 9, La Réunion, France; lionel.bigot@univ-reunion.fr (L.B.); pascale.chabanet@ird.fr (P.C.); lucie.penin@univ-reunion.fr (L.P.); mehdi.adjeroud@ird.fr (M.A.)
2 GPMDLR, 2 rue Evariste De Parny, 97420 Le Port, La Réunion, France; priscille.labarrere@reunion.port.fr
3 Laboratoire d'Excellence "CORAIL", 52 Avenue Paul Alduy, 66860 Perpignan, France; heloise.rouze@gmail.com (H.R.); eboissin@gmail.com (É.B.)
4 PSL Université Paris, CNRS-EPHE-UPVD, CRIOBE USR3278, 66860 Perpignan, France
5 Poisson Lune, 4 rue Benjamin Hoarau, 97430 Le Tampon, La Réunion, France; nickygravier@yahoo.fr (N.G.-B.); poissonlune974@gmail.com (P.P.); camille.loisil@gmail.com (C.L.)
6 Vie Océane, 6, avenue d'Aquitaine, 97427 Étang-Salé, La Réunion, France; biorecif@gmail.com
7 BIORECIF, 3 ter rue de l'Albatros, 97434 Saint-Paul, La Réunion, France
* Correspondence: ludovic-remy.hoarau@univ-reunion.fr or ludovic.remy.hoarau@gmail.com

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Despite increased attention over the last decade on Mesophotic Coral Ecosystems (MCEs) [1–4], the lower mesophotic zone (60–150 m depth) characterized by low light levels, though still sufficient for coral growth and from which distinct benthic communities occur [4], remains poorly studied. MCEs are particularly understudied at Reunion Island and more broadly in the southwestern Indian Ocean where currently a limited number of studies document the benthic communities at these depths. However, a recent study highlighted the overlooked diversity in the southwestern Indian Ocean with the report of a new record of the scleractinian coral *Leptoseris troglodyta* (65–90 m) in caves of Mayotte [5]. In addition, studies on some complex mesophotic habitats occurring on lava flows (e.g., structure, environmental conditions) are still missing for a complete understanding of MCEs' biodiversity [6]. In Reunion Island where a frequent volcanic activity is recorded at the southeastern part of the island, both species diversity and composition of coral assemblages on lava flows at shallow depths (0–30 m depth) are distinct from typical coral reef sites located on the western and southern coast of Reunion Island [7].

Combined with recent scientific programs and citizen science actions (e.g., Poisson Lune Association) aiming to explore and assess the biodiversity of MCEs in Reunion Island, the lower mesophotic zone was recently investigated across the island coasts (seven sites from the North-West to the South-East) using closed circuit rebreather (CCR) diving. Two dives with two CCR trimix tech divers equipped with cameras were conducted in September 2020 at Sainte-Rose (21°09′33″ S, 55°50′10″ E), on the southeastern leeward coast of the island. Two dive stations ~300 m apart from each other were investigated at depths 75–85 m and 90–100 m on a basaltic substrate, located nearby underwater lava flows from the eruptive event of 1977. Benthic assemblages were filmed (Supplementary Video S1), some specimens were collected for species identification, and fishes were filmed and photographed during ~15–20-min dives (total bottom time).

A mesophotic coral community consisting of significant coral cover and abundance of zooxanthellate scleractinian corals and azooxanthellate hydrocorals was discovered (Figure 1). The dominant benthic assemblage includes encrusting, foliaceous, and thin plate corals of the genus *Leptoseris* (Agariciidae) extending horizontally and of calcareous branching hydroids, commonly named lace corals (Stylasteriidae), belonging to *Stylaster flabelliformis* (Lamarck, 1816) erected vertically. Encrusting sponges, crustose coralline, macro and turf algae filled the rest of the available substrate space (Figure 1b–f). *Leptoseris* and *Stylaster* colonies were both abundant and densely aggregated with a visually estimated cover reaching up to ~70–90% and ~10–20%, respectively. *Leptoseris* spp. formed horizontal large dark brown plates and tiers (>40 cm in diameter) while the white-pink fan-shaped *Stylaster* grows vertically in one plane above substrate crests (up to 60 cm tall), between *Leptoseris* plates and mostly perpendicularly to the main current direction (Figure 1c,d). Most corals were alive although some parts of some colonies of *Stylaster* were dead with their skeleton colonized with algae, sponges, and other hydroids (Figure 2a). The extent of this mesophotic benthic formation composed with *Leptoseris* spp. and *Stylaster flabelliformis* is estimated to be over 15,000 m^2.

Our surveys with collected specimens revealed an extension of vertical range distribution of several coral species at Reunion Island with new maximum depth records (comparison with review in [8]). New depth records for *Leptoseris hawaiiensis* Vaughan, 1907 and *Leptoseris scabra* Vaughan, 1907 are reported for Reunion Island at 75–100 m depths, corals that were previously reported locally at 60 m and 70 m depths, respectively. According to Boschma [9], who studied previous literature and provided a precise description of *S. flabelliformis* while revising the collections of the Muséum National d'Histoire Naturel MNHN, *S. flabelliformis* is recorded from the Mascarene Islands of Mauritius and Reunion Island. Apart from the specimens collected in Mauritius and initially described by Lamarck (1816), the only others identified with certainty are those collected in Reunion Island at 292 m depth. The specimens were described with more details by Milne Edwards and Haime [10]. No more specimens were reported then in the scientific literature though *Stylaster* were documented during ROV surveys conducted between 100 and 400 m depths on the volcanic slopes of Reunion Island in 2009 [11]. Therefore, the colonies of *S. flabelliformis* collected at 95 m depth during the CCR dives are the first new specimens studied since the nineteenth century.

Zooxanthellate scleractinian corals are rarely found at dense aggregations at the lowest mesophotic depths. However, on rare occasions, the coral cover may be high at these depths. For instance, dense fields of up to 100% cover of *Agaricia* colonies were observed at 70–85 m depth at Curaçao [12] or a high cover of *Leptoseris* communities at Hawaiian Islands at 70–90 m depth [13,14], and a mixture of corals, *Leptoseris*, *Pachyseris*, and *Montipora*, on Myrmidon Reef (Great Barrier Reef) at 60 m depth [15]. Deep-water corals on young geological and prehistoric lava flows in Hawaii may also present large numbers and sizes of Coralliidae colonies [6]. This is the first documented record of such original benthic community composition with a high cover and size of both *Leptoseris* and *Stylaster* colonies on mesophotic lava flows. For *S. flabelliformis*, the spatial aggregation may be explained by its reproductive cycle and settlement pattern as it is a gonochoristic brooding species whose planula larvae are able to settle as soon as they leave the mother colony. The settlement of stylasterid larvae occurs on the available space, sheltered between and below the horizontal plates of *Leptoseris* or in small cavities of the bottom, as attested by the presence of small colonies (shown in Figure 1e,f). The presence of short-lived and non-dispersive larvae in their life cycle explains the high regional endemicity and limited distribution of stylasterid species worldwide as well as at the regional scale [16,17]. High densities of stylasterids providing structure-forming components as described herein were found in deep waters in the Straits of Florida and North Alaska, USA [18].

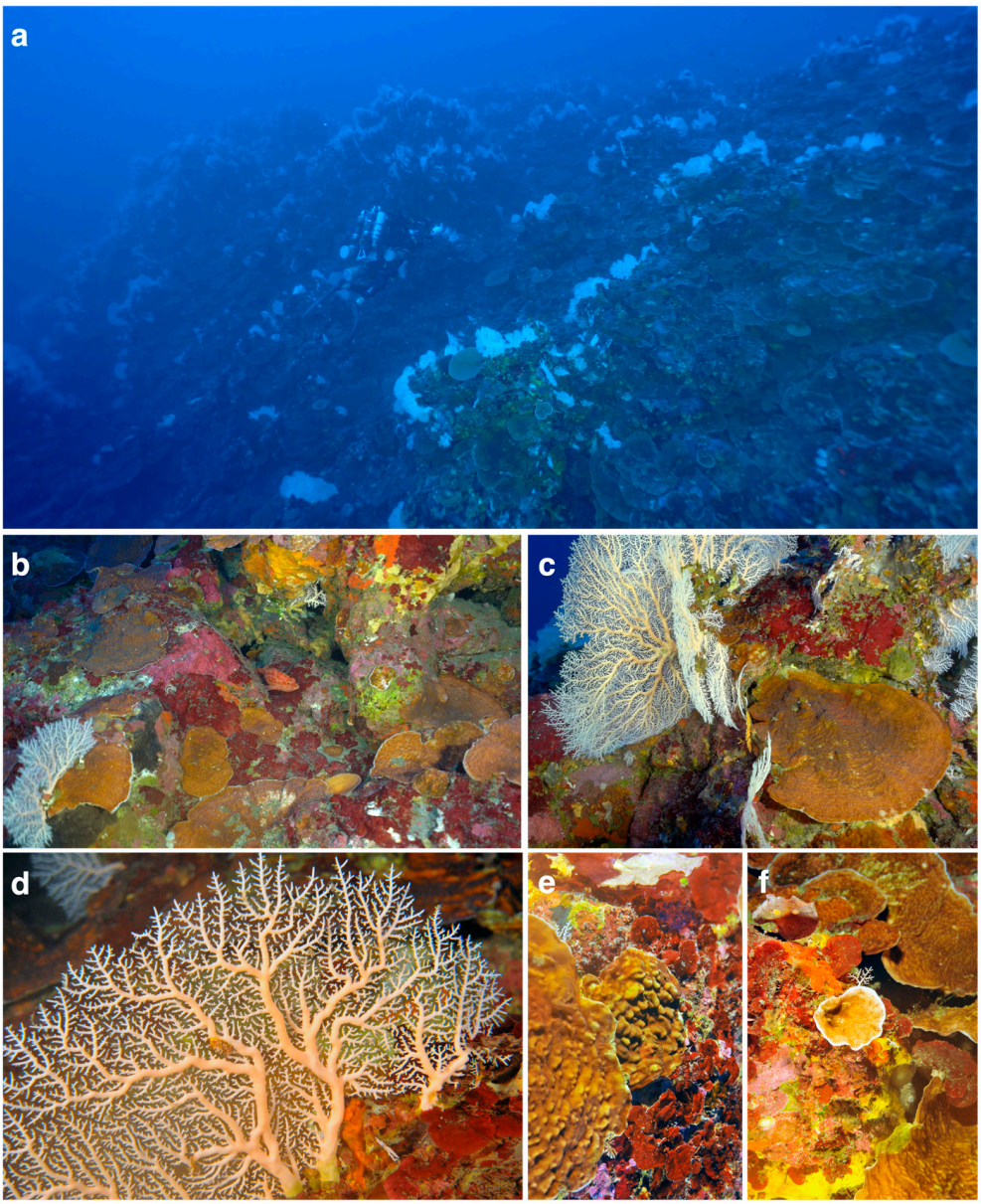

Figure 1. Benthic community on lava flow at 83–95 m depth on the leeward eastern coast of Reunion Island (Sainte-Rose) composed of dense aggregations of tall lace corals *Stylaster flabelliformis* and large zooxanthellate scleractinian corals *Leptoseris* spp. (**a**) Overall Mesophotic Coral Ecosystem (MCE) overview on the lava flow steep slope extending down to 100 m depth (*Stylaster* colonies in white). Close-up views of large plates of (**b**) *Leptoseris* spp. and (**c**) *S. flabelliformis* above a large plate and encrusting colonies of *Leptoseris* sp. along with sponges, crustose coralline, and turf and macro-algae. (**d**) Colony close-up view of *S. flabelliformis*. (**e**,**f**) The diversity of *Leptoseris* spp. composed with thin plates, encrusting, vases, and tiered colonies.

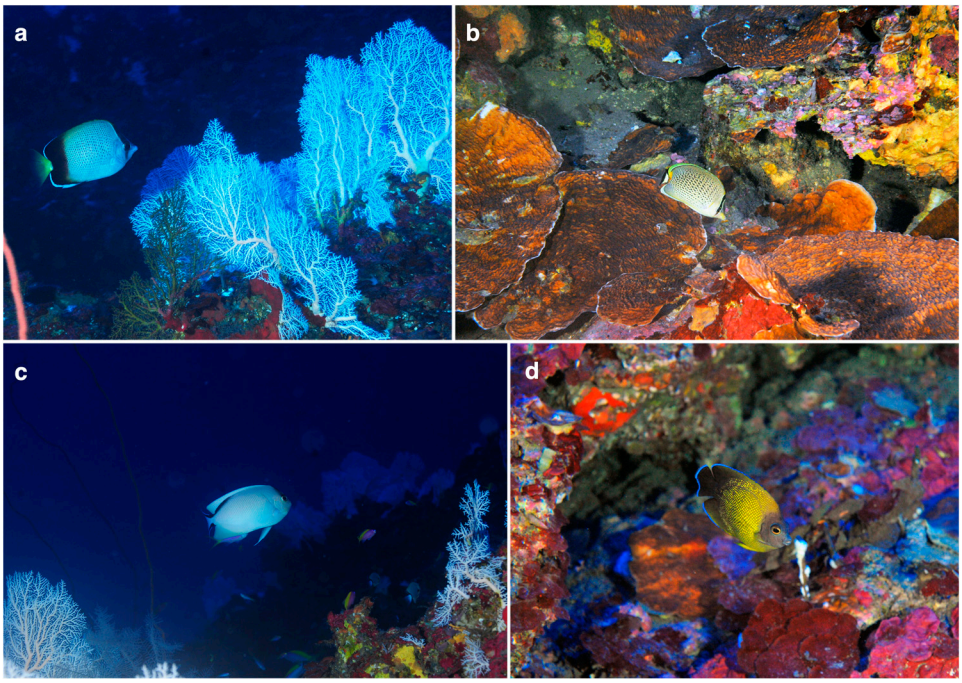

Figure 2. Some of the fishes associated to *Leptoseris* spp. and *S. flabelliformis*. (**a**) *Chaetodon dolosus*, (**b**) *C. guttatissimus*, (**c**) *Genicanthus caudovittatus* ♀with *Pseudanthias evansi* in the background, and (**d**) a rare endemic species angelfish species *Apolemichthys guezei*.

Such mesophotic coral assemblages on lava flow of Sainte-Rose constitutes a tridimensional complex structuring habitat providing shelter for benthic invertebrates and fish fauna. The numerous fish species observed in this mesophotic coral assemblage belong to (i) depth-generalist species (0 to >60 m depth) common in the western Indian Ocean (e.g., *Chaetodon dolosus* Ahl, 1923 (Figure 2a)), (ii) Indo-Pacific species previously known with a more limited vertical distribution (e.g., *Chaetodon guttatissimus* Bennett, 1832 described until 0–25 m depth; *Genicanthus caudovittatus* (Günther, 1860) at 15–70 m depth in the western Indian Ocean; *Pseudanthias evansi*, (Smith, 1954) at 4–40 m depth in the Indian Ocean (Figure 2b,c)), and (iii) rare and endemic species from Reunion Island at depths of 60–80 m [19] to 90 m [20] (e.g., *Apolemichthys guezei* (Randall and Maugé, 1978) photographed at 95 m depth (Figure 2d)). These findings support a high potential of deep refugia for fish and invertebrates provided by the coral assemblage and highlight the distinctness of MCEs [1–4] that constitute relevant habitats for an underestimated number of species.

Our observations are preliminary results from scientific programs aimed at studying biodiversity, structure, and functioning of Reunion Island MCEs. More surveys should be conducted in the lower mesophotic zone as increasing sampling efforts would rapidly improve our knowledge on the ecology of species (i.e., their vertical distribution and habitats) and thus better determine their status for conservation. Given the limited number of CCR dives and time spent at lower mesophotic depths, original information regarding diversity and community structure of Reunion Island mesophotic corals and fishes were collected here through videos and photos, improving our understanding on these distinct ecosystems [3,4]. At the moment, no protection measures specifically target the lower depths of MCEs around Reunion Island. Adequate conservation tools should be implemented to protect these unique and fragile habitats as a mean to protect their structural complexity and associated underexplored biodiversity.

Supplementary Materials: The following is available online at https://www.mdpi.com/1424-2818/13/4/141/s1, Video S1: Video footage of coral communities on a steep slope lava flow at 85 m depth, Sainte-Rose, Reunion Island.

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