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The *Millepora* Zone Is Back: Recent Findings from the Northernmost Region of the Maldives

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Abstract: Three species of the tropical hydrocoral genus *Millepora* were common and abundant in the Maldives before 1998, characterizing extensive shallow reef areas known as '*Millepora* zones'. The 1998 heat wave resulted in mass mortality of all the *Millepora* species, the characteristic *Millepora* zones disappeared, and only a few observations of isolated colonies were reported in the years ahead. A recent expedition (January 2024) to the northernmost region of the Maldives (Ihavandhippolhu Atoll) revealed new *Millepora* zones at 7–13 m depth, suggesting a potential repopulation of a vulnerable genus considered regionally extinct.

Keywords: hydrocorals; species distribution; new record; global warming; thermal anomaly; rarity; Indian Ocean

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Global ocean warming is exerting a significant impact on marine life, leading to marine ecosystems' alterations, such as rising temperatures, ocean acidification, and environmental degradation. These changes influence the species' behaviour, abundance, and distribution [1–3]. According to thermal niches and other biological traits [4], species may undergo phenological and distributional shifts or may change their abundance [1,5], and rare species may either face extinction or become more common [6]. Comparing historical and current records of marine benthic species distribution is crucial for detecting variations in biodiversity and understanding the causes of change [7,8].

Hydrozoans in the genus *Millepora* Linnaeus, 1758 (family Milleporidae, class Hydrozoa, phylum Cnidaria) are colonial, polypoid hydrocorals secreting a calcareous skeleton of an encrusting or upright form [9]. The numerous and highly toxic defensive polyps extending from the skeleton give their popular common names of stinging corals or fire corals [10]. All *Millepora* species are long-lived, zooxanthellate and hermatypic hydrocorals [11] and are considered a regular component of tropical coral reefs, from the surface up to a 40 m depth [12]. The genus *Millepora* is present in the Maldives with three species, *Millepora platyphylla* (Hemprich & Ehrenberg 1834), *M. tenera* (Boschma 1949) and *M. latifolia* (Boschma 1948) [9,13]. *Millepora platyphylla* is the most widely distributed in the Indo-Pacific, predominantly found on the surf-swept edges of reefs, shoals, and ledges with strong, turbulent water movement, and displaying a robust, bladed, or plate-like structure [12]. In contrast, the other two species—and especially *M. latifolia*—are characterized by delicate branches and thin, leafy forms, and exhibit a more confined distribution in the Indo-West Pacific, where they typically live in lagoons and sheltered waters [12]. Historical records from the early 20th century described *Millepora* species as abundant and frequent in the Maldives [14,15]. During the 1990s, *Millepora* spp. were often reported as characterizing extensive areas of the reef in very shallow waters (~3 m depth), called

'*Millepora* zones' [16,17]. While the literature lacks a precise definition of the *Millepora* zone, this can be identified as a reef portion dominated predominantly by hydrocorals in the genus *Millepora*, whose abundance in terms of surface covered or colonies density is high enough to characterize the reef. Prolonged thermal anomalies have already been shown to cause the expulsion of symbiotic dinoflagellates, compromising populations of hydrocorals during the past 30 years [18,19]. Around 32 °C, *Millepora* spp. exhibit a bleaching response to thermal stress that is similar to scleractinian corals [20]. In the Maldives, the severe heat wave of 1998 resulted in mass mortality of all the *Millepora* species [21], which almost disappeared in the whole archipelago [22]. Only single observations of a few sporadic colonies were reported in the years ahead in deeper waters (>7 m depth), always with less than 1% of the bottom coverage on the reef [13], thus providing evidence of the total disappearance of the characteristic *Millepora* zones. By 2013, *Millepora* spp. encounters were so infrequent that the genus was proposed as a case of local extirpation in the Maldives [23].

The Maldives Archipelago forms the central part of the Chagos-Maldives-Laccadive ridge in the central Indian Ocean, extending from 7°07′ N to 0°42′ S and from 72°33′ to 73°45′ E. Comprising approximately 1120 islands, the Maldives form a single atoll chain in both the northern and southern regions, with a double atoll chain in its central part. In January 2024, the "Up North expedition" was carried out in Ihavandhippolhu Atoll, the northernmost area of the Maldives (Figure 1). This remote atoll is located in a scantly anthropized region where tourism frequentation is lower than in all the other central and southern atolls [24]. The expedition aimed to explore and survey those reefs in the region that were described, for the first time, in 2011 [23]. Underwater visual surveys were carried out on ten reefs, from the reef flat up to a 30 m depth (Table 1), to collect data on the abundance (expressed as % cover) and the composition of the reef communities. Visual surveys also aimed at verifying the presence of the three *Millepora* species that had never been reported in the northern Maldives after 1998 [23]. In the presence of *Millepora* spp., the % cover was visually estimated using the plain view technique [25]. Divers hovered 1–2 m above the seafloor observing an area of about 20 m^2 in three replicates (spaced tens of meters apart) at each of the ten reef sites investigated.

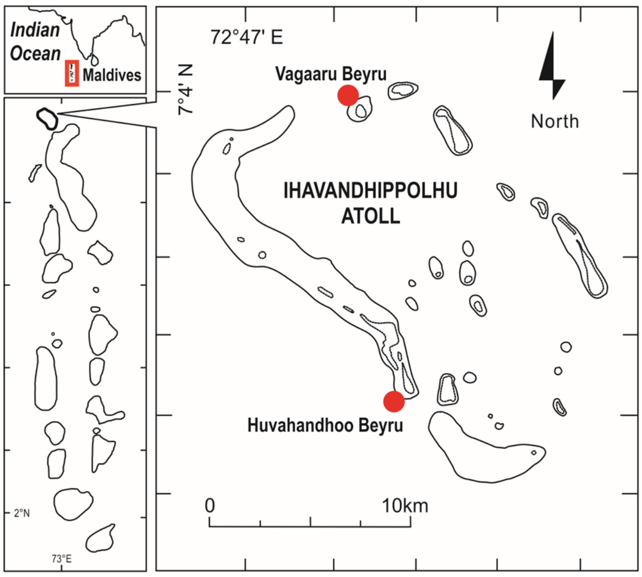

Figure 1. Map of the Maldives Archipelago with a zoom on Hiavandhippolhu Atoll. The red circles are the two sites where colonies of *Millepora* spp. have been found in January 2024.

Table 1. Geographic location of the ten reefs investigated during the "Up North Expedition" in the Ihavandhippolhu Atoll. The two reefs where the *Millepora* zones were found are in bold.

Site Name	Coordinates
Manafaru	06°59.674′ N; 72°56.657′ E
Uligamu Ethere	07°05.309′ N; 72°54.934′ E
Muladhoo Ethere	07°01.650′ N; 72°59.005′ E
Medafushi	07°00.605′ N; 72°55.844′ E
Huvahndhoo Ethere	06°57.518′ N; 72°54.507′ E
Huvahandhoo Beyru	**06°57.080′ N; 72°53.976′ E**
Galandhoo Beyru	06°56.596′ N; 72°59.174′ E
Vagaaru Beyru	**07°05.980′ N; 72°52.410′ E**
Uligamu Beyru	07°04.816′ N; 72°56.136′ E
Gambas	07°01.616′ N; 72°59.722′ E

Millepora spp. were found at Huvahandhoo Beyru, at a 7–10 m depth, and at Vaagaru Beyru, at a 10–13 m depth (Table 1). In both sites, the hydrocoral dominated a specific portion of the reef between 7 to 13 m depth, where it showed high densities and locally covered nearly 100% of the substrate, thus creating the characteristic *Millepora* zones. When averaging the % cover of the *Millepora* spp. across the ten reefs surveyed in Ihavandhippolhu Atoll, a mean cover value of 3.3 ± 2.3% was registered (Figure 2). A taxonomic identification of the specimens found was unlikely, given the difficult taxonomic resolution of the *Millepora* genus [26,27] and the uncertain identification based on images collected underwater. Considering the morphologic plasticity of the genus showcasing highly variable phenotypic forms across a broad spectrum of depths and environmental conditions [28], we tentatively identified *Millepora* cf. *platyphylla* on Huvahandhoo Beyru reef, based on its plate-like structure, and *Millepora* cf. *tenera* on Vaagaru Beyru reef, based on a more branched habitus (Figure 3).

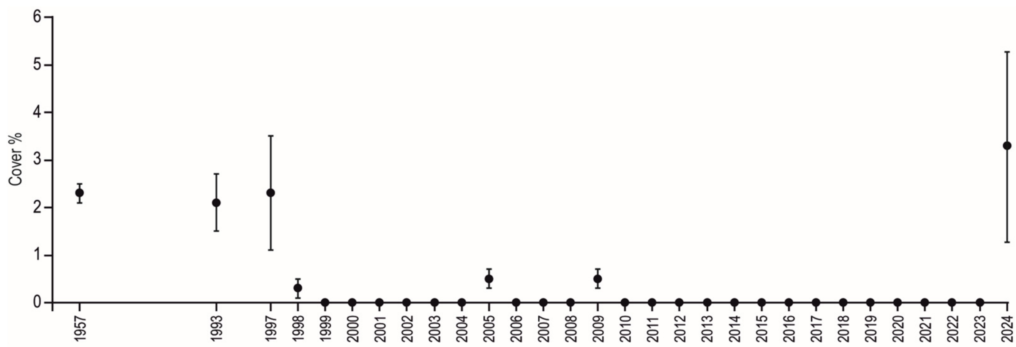

Figure 2. Historical reconstruction of *Millepora* spp. sightings in the Maldives. Where only one colony was documented, a % cover of 0.5% was assigned. Note that the scale on the x-axis is not uniform. Data sources: 1957 [29]; 1993 [30]; 1997–2014 [22]; 2015–2023 [24,31,32]; 2024 (this study).

The high susceptibility of *Millepora* spp. to water warming and thermal anomalies is widely reported (e.g., [11] and references therein). Re-discovering dense reef zones with *Millepora* spp. in the northernmost region of the Maldives is particularly noteworthy, as it marks a unique finding after the 1998 heatwave. Before our findings, the most recent record of *Millepora* in the northern region of the Maldives dates to 2009, when a single colony of *M. platyphyllia*, at approximately 7 m depth, was observed [13]. The regeneration of a characteristic *Millepora* zone likely involved a period of adaptation, between 1998 and 2024. Also, it likely *required* a shift in the depth range preferred by the species, from the very shallow waters of the reef flat (around 3 m depth)—typical of the historical occurrences of the *Millepora* zones in the Maldives—to deeper waters at around 7–13 m depth. These findings recall the still-debated Deep Reef Refugia Hypothesis [33–35]. The concept of providing an 'escape from disturbances' was initially introduced by Glynn (1996) [36], suggesting that coral communities at a 'moderate depth' may find protection from rapid ocean warming. Moving to major depths could be crucial for the local persistence of heat-sensitive marine organisms in the face of climate change conditions [24,37–39]. The *Millepora* zones persist within the euphotic zone; however, there is a slight yet significant depth variation due to evident environmental distinctions between the reef flat areas (approximately 3 m depth) and the reef edge and slope (approximately 7–13 m depth) in shallow Maldivian reefs [11,22].

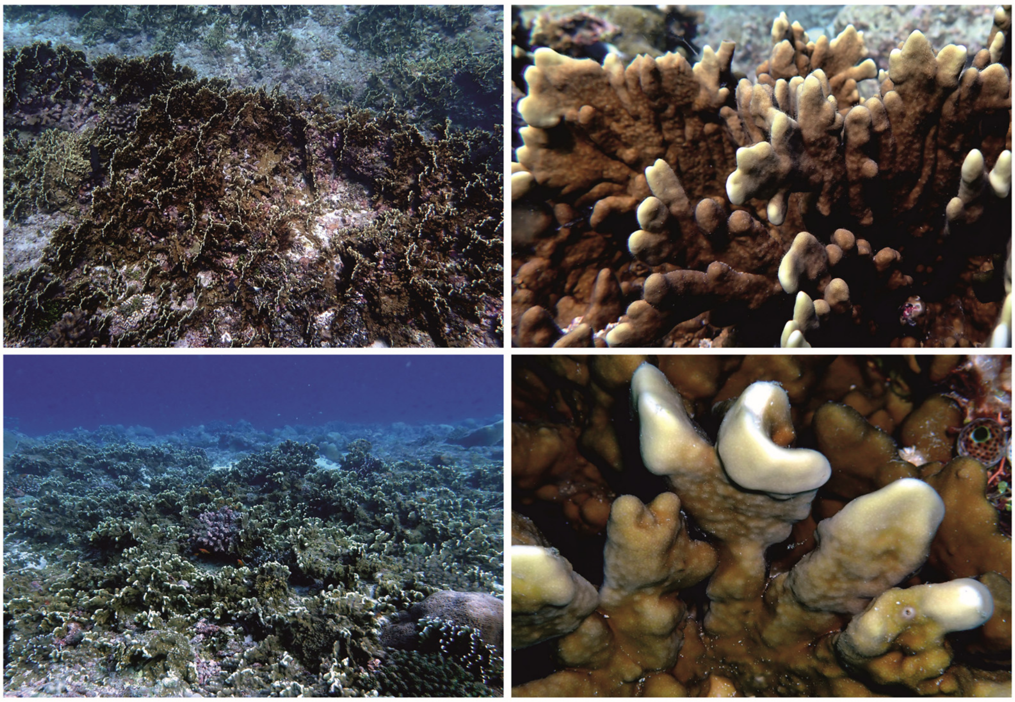

Figure 3. Plate-like structure of *Millepora* cf. *platyphylla* colonies found on Huvahandhoo Beyru reef (**upper** panels), and the more branched habitus typical of *Millepora* cf. *tenera* found on Vaagaru Beyru reef (**lower** panels).

The two *Millepora* zones were observed in exposed ocean reefs, which contrasts with the previous sightings of *Millepora* spp. colonies and *Millepora* zones that had always been mainly found in sheltered (lagoon) reefs (e.g., [16]). During the last severe bleaching event of 2016, exposed ocean reefs experienced fewer impacts than lagoon reefs, resulting in lower coral mortality [24,31]. The intense monsoonal ocean currents, driving movements of upwelling currents and bringing cooler water, were recognized as one of the main reasons for the higher resistance of corals in ocean reefs [40]. The return of the *Millepora* zones in Hiavandhippolhu Atoll sparks hope for a potential repopulation of a vulnerable genus that was considered regionally extinct. Moreover, the branching structures formed in the wide *Millepora* zones enhance substrate complexity, thereby promoting the development of diverse and abundant fish and macro-invertebrate communities. The return of this formation in a remote region of the Maldives suggests that the combined effect of local human disturbances and climate change in the more developed central and southern atolls might prevent, or at least slow down, the recovery of the most vulnerable species to thermal stress [6,41]. Periodic surveys carried out in the central and the southern atolls of the Maldives during the last 26 years did not report any single colony of the *Millepora* spp. [22,24,31]. Regular monitoring and genetic analysis will be essential for identifying *Millepora* species in the northernmost Maldivian region, understanding local populations, and assessing their potential recovery across the entire archipelago.

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