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New insights in benthic biodiversity of the saya de Malha Bank

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ABSTRACT

In the South West Indian Ocean, a unique, remote and atypical geomorphological structure, the Saya de Malha Bank, is considered as an underwater 'island' that plays a key role in understanding benthic biodiversity and connectivity processes in the Indian Ocean. In 2022, the Saya de Malha Bank has been explored during the Indian Ocean expedition led by Monaco Explorations. A team of the Muséum national d'Histoire Naturelle (Paris) and collaborators have explored the benthic diversity of the bank by deploying a combination of sampling methods, such as towed gears (dredge, trawl, and sledge) or by scuba-diving (on-sight, brushing and suction device samplings). A total of 81 stations have been sampled, comprising 35 shallow stations on the summit of the bank (19–58 m depth) and 46 stations gaining depth on the flanks of the bank (73–1141 m depth). From these sampling events, a large collection of marine invertebrates, fish and algae has been preserved for taxonomic (morphological and molecular) studies. The inventory of the benthic biodiversity of Saya de Malha is underway, but it is a long-term process. We propose here to focus on the most represented taxonomic groups (algae, molluscs, crustaceans, annelids and fish) by compiling the primary taxonomic data for the diversity metrics and highlighting some discoveries and potential species new to science. Although the inventory is far from complete, these first results emphasize the endemicity of the fauna and flora of the Saya de Malha Bank.

1. Introduction

Sampling, inventorying, naming and founding of new species to science are the stepping stones of Taxonomy but still challenging in the exploration of marine biodiversity (Appeltans et al., 2012). The Southwest Indian Ocean (SWIO) is a place where all these challenges converge to address knowledge of marine biodiversity. The SWIO can be recognized as original area because of its geomorphological and oceanographic features (Demopoulos et al., 2003). It is is located at the convergence of two main features: the Mozambique Channel and the Mascarene Plateau (Obura, 2012). While the Mozambique Channel is estimated to be more than 150-million-year-old, the Mascarene Plateau

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is a rather young structure (about 40-million-year-old, Leinweber et al., 2013). Seamounts in the SWIO are mostly distributed along ridges and in the Mozambique Channel, and their majority (68 %) is located in international waters (Marsac et al., 2020). One of the atypical features of the region is "underwater shoals", which are submerged shelf area, covering vast shallow areas with depths <200 m, rather than the limited surface area of seamount summits. These features, such as Walters Shoal (southern Madagascar Ridge) or the Saya de Malha Bank (Mascarene Ridge), are considered underwater 'islands' that play a key role in the connectivity processes at the scale of Indian Ocean (Obura et al., 2012).

The Saya de Malha Bank is the largest of the banks on the Mascarene plateau, with a surface area of about 40,000 km^2 (Obura et al., 2012; Ramah et al., 2021), lined up northwards by the Ritchie Bank and southwards by the Nazareth Bank. Considered as shallow seas, the Saya de Malha Bank is located between approximately 15 and 200 m deep, surrounded by a deep ocean. It is in the pathway of the South Equatorial Current (SEC), that dominates the oceanography of the Western Indian Ocean (WIO), and along with the Nazareth Bank, concentrates the flow of the SEC into a narrow passage between them at 12.5–13°S (Lutjeharms, 2006). The Bank thus has a major influence on the oceanography of the WIO and regions to the west. Regarding biogeography, the Saya de Malha Bank is located in the Mascarene Plateau Shelf province (Dunstan, 2024) and the ecoregion "Cargados Carajos/-Tromelin Island" characterised by low coral diversity and high endemism (Spalding et al., 2007; Obura, 2012).

Age, isolation, surface area: all these elements support the hypothesis that Saya de Malha could be an important centre of speciation and endemism of marine fauna and flora in the Indian Ocean. And yet, our knowledge of the fauna of the Mascarene plateau in general, and of Saya de Malha in particular, is limited for benthic fauna and flora. Most of the time in zoology, the relevant publications on a specific geographic region date back to the 19th century. In the case of Saya de Malha, most of the new species descriptions are recent, with less than 30 publications relevant of species descriptions as zoological references, including the descriptions of 22 species of molluscs, 16 species of fish, 10 species of crustaceans, 2 species of brachiopods, 2 species of corallines and 1 species of annelid (updated list, sup data 1). Beside descriptions of new species, and even at the era of big data on biodiversity, it is stunning to notice that biodiversity data of Saya de Malha Bank are scarce. As an example, a request for Saya de Malha on Ocean Biodiversity Information System database (OBIS, 2024), which brings together open-access data and information clearing-house on marine biodiversity for science, reveals a total 1885 records (*i.e.* species occurrences) of marine taxa for a depth range of 0–2000 m. These total records of marine fauna and flora are weak by comparison to others locations in WIO. For a total of 266 species referenced in this dataset, it is interesting to notice that main occurrences are for planktonic organisms (Copepods, Molluscs, Foraminifera). As an emblematic and economic taxon, "Fish" is also the most represented group with 35 % of total occurrences for 153 taxa (120 at species level). Knowledge of benthic invertebrates is clearly very incomplete (only 6 % of occurrences, 14 taxa, of which only 10 are at species level). Further information can be found in the literature. Vortsepneva (2008) has provided a list of marine taxa, both vertebrates and benthic invertebrates, in a summary report on Russian fishing expeditions (1961–1989) corresponding to a total of 228 species or morphospecies: 43 fish (including commercial species), 142 molluscs, 28 crustaceans, 3 echinoderms, 2 annelids and 10 species of seagrasses and algae. More recently, in 2018, from the EAF-Nansen Indian Ocean Research Expedition, Ramah et al. (2021) described the shallow benthic habitats of Saya de Malha (28–50 m) by video data analyses, as well as included information on diversity of seagrasses and algae (10 observed genera) and stony corals (13 observed genera). From the same expedition, ROV-image analyses have also enhanced the knowledge on Saya's deep-sea fauna (Bergstad et al., 2021) with the composition of the fauna observed on the slope of the bank (up to 1000 m depth) but still at higher-level taxonomical identification. However, these results provided new taxa occurrences of such as example for cnidarians (Actinaria, 7 genera; Octocorals Alcyonacea, 14 genera). Photographic catalogue illustrating the marine biodiversity of Saya de Malha Bank of Bhagooli et al. (2024) reported complementary information on shallow water sponges (14 species/morphospecies) as well as for echinoderms (14 species/morphospecies). However, biodiversity data of Saya de Malha Bank are still scarce and the state of our knowledge for a tropical bank as large as Switzerland, is far from complete.

The marine benthic biodiversity inventory performed by the scientific team of the Muséum national d'Histoire Naturelle (MNHN) implemented within the framework of the Saya de Malha project (Indian Ocean expedition, Monaco Explorations), aims to enrich our knowledge on marine biodiversity and to discover undescribed species. Over the last ca. 50 years the Tropical Deep-Sea Benthos programme (TDSB) conducted by MNHN scientists has explored the bathyal margins of islands and seamounts in the Indo-Pacific which is still a major frontier in marine biodiversity exploration. The core aim of TDSB program is to fill the gap of knowledge on deep-sea benthic fauna but also on overlooked marine biodiversity. In the SWIO, TDSB deep-sea cruises as well as the shore-based expeditions have been implemented since 2009 in the Mozambique channel (off Mozambique, Mayotte and Comoros), in North and South Madagascar, and more recently on Walters Shoal. Either shallow and deep-water samples have been acquired and studied from these areas (see Richer de Forges et al., 2013; Corbari et al., 2023; Corbari and Castelin, 2024). The exploration of Saya de Malha Bank is therefore an obvious place to add to our knowledge of the benthic biodiversity in the SWIO.

The objective of the inventory was to aim for exhaustiveness within the targeted taxonomic groups (algae, annelids, molluscs, crustaceans and fish) by integrating a wide range of sizes for all these taxa, with a particular focus on small-sized species (of the order of mm) for molluscs, crustaceans and annelids. These taxa, which are often small in size, have a high potential for diversity and are taxonomically challenging. They however are in reality the most important contributors to the diversity and richness of marine habitats (McClain et al., 2025). It is through an original and naturalistic approach based on the description of these taxa often considered neglected in conservation policies, as opposed to "flagship" species (*i.e.* corals, teleost fish). Beyond fundamental scientific questions (evolution, magnitude and richness of marine biodiversity, macro-ecology and discovery of unknown species), the taxonomic data (species occurrences) but also habitat data acquired during the expedition will help to meet conservation objectives.

2. Material and methods

2.1. Sampling methods

The MNHN sampling protocols deployed during TDSB[1] or "Our Planet reviewed"[2] programmes have been adapted for expeditions at high sea. Sampling has been carried out using two complementary approaches: diving methods for shallow habitats and deployment of towed gears for deep-sea environments, on selected areas to optimize all kinds of habitats: soft bottoms, rocky bottoms, phanerogam meadows, calcareous algae beds, bioconstructive and non-bioconstructive coral communities.

2.1.1. Diving methods (Fig. 1)

Large- and medium-sized specimens of selected species were visually documented by divers in representative habitats while trying to sample as many habitats as possible. A variety of techniques has been used to specifically sample micro-invertebrates.

Brushing method (Fig. 1A and B): This technique is dedicated to the

[1] https://www.mnhn.fr/en/tropical-deep-sea-benthos.
[2] https://www.mnhn.fr/en/our-planet-reviewed.

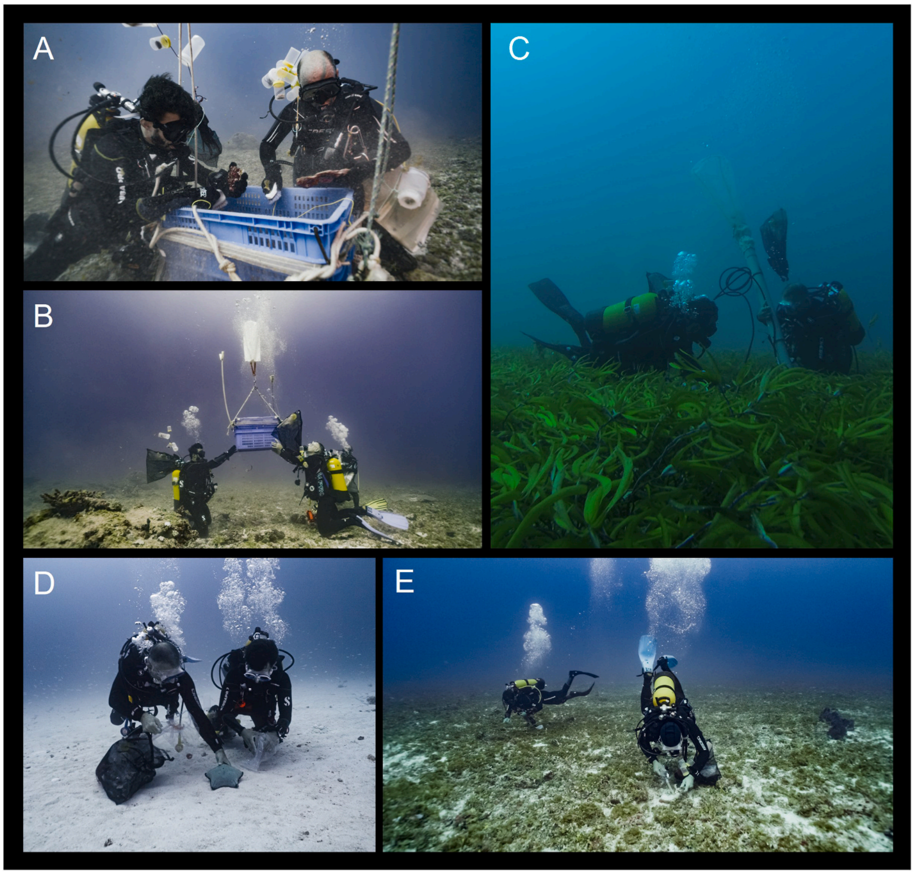

Fig. 1. Diving sampling and methods. A, B: brushing method. C: suction sampling. D, E: On-sight collections. Photo authors: S. Bender (A, B, D, E), B. Gouillieux (C).

sampling of the epibiont fauna, which adheres strongly to the substrate. It consists of cleaning a surface, usually large blocks or pebbles, with a hard-plastic brush over a brush basket. Loose rocks and coral rubble are placed in the basket and vigorously brushed by hand. The cleaned rock is returned to its location, and the residue accumulates in the net. The brushing basket consists of a 500-micron-mesh net protected inside and outside by sturdy laundry baskets. Underwater, the small blocks are brushed over two open-worked stacking baskets. The assembly is weighted by 8 kilos of lead fixed at each corner at the bottom of the basket. A brushing sample typically covers 1–2 square meters of seafloor and generates 1–5 L of bottom material.

Suction sampling (Fig. 1C): The suction sampler is operated on soft seafloor substrate, to collect the upper 1–2 cm of material and the thin layer of ooze and microalgae found in rock crevices. A suction sample typically covers 1–2 square meters of seafloor and generates 2–15 L of bottom material. The air from a diving tank is delivered through a medium pressure hose at 7 bar to the base of a 2 m long PVC tube with a diameter of about 10 cm. As the air rises into the pipe, which should be as vertical as possible, it relaxes the piston. Particles and objects in the vicinity of the opening are sucked in and retained in a 1 mm mesh net. This tool does not, however, allow the sessile fauna to be removed.

On-sight collections (Fig. 1D and E): Most organisms blend into their environment to often achieve perfect mimicry with their hosts. On-sight collection requires know-how, experience and intuition: the choice of blocks to be turned, attention to differences in sediment granulometry, camouflaged species or individuals (homochromy or mimicry), etc. Only experienced divers and collectors are able to spot commensals, parasites and animals living in symbiosis.

2.1.2. *Sampling with towed gears (Fig. 2)*

The panel of towed gears was deployed according to depth, morphology of the seafloor and the nature of the bottom. The Warén dredge was deployed on rocky and steep bottoms while the beam trawl and the sledge were deployed on soft bottoms. The complementation of towed gears was optimized on each selected site through a large depth range.

Sledge (Fig. 2A): It is the appropriate apparatus to collect efficiently the small-sized swimming macrofauna living in the benthic boundary layer, the so called suprabenthos. It is equipped with two superimposed 500 μm mesh-size nets to sample simultaneously two water layers from 25 to 60 cm and from 77 to 112 cm above the seafloor (Brenke, 2005). The cod ends are equipped with net-buckets containing a 300 μm mesh window. The gear is towed on the seafloor at 1–2 knots. To avoid contamination by planktonic organisms during the deployment into the water column, a lever mechanism is attached to the front doors, which are closed while the gear has no contact to the bottom. Additionally, the use of a pinger attached in its chassis allows checking in time the deployment of the sledge to assure the accuracy of its position during the haul.

Dredge (Fig. 2B): It is a small dredge with an opening of 80 cm but heavy enough (100 kg) to allow sampling of hard substrates (small stones, gravel). The Warén dredge consists of a strong metallic frame behind which is placed a net to retain sediment and fauna. The frame is connected to a wire and hauled by a boat at slow speeds (1–2 knots), sometimes slower depending on seafloor roughness. The bag of the dredge is composed of several layers; an inner bag made of smaller mesh size (3–5 mm) is protected by 1–2 outer layers with a larger mesh size (20–50 mm) and a stronger weave. In the Warén dredge used during the TDSB programme and related expeditions, the external layer is made of a strong metallic ring net.

Beam trawl (Fig. 2C and D): Suitable for scientific research, it is a small trawl, towed over a distance between 1 and 2 nautical miles, on

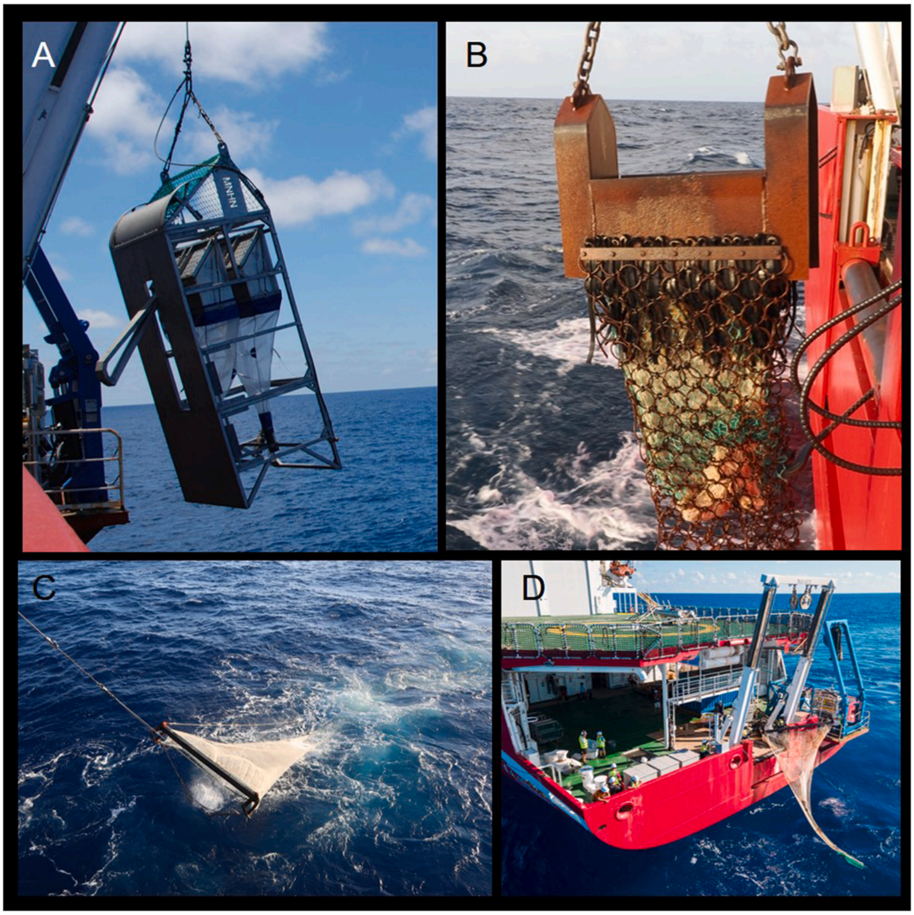

Fig. 2. Deep-sea sampling by towed gears. A: sledge. B: Warén dredge. C, D: beam trawl. Photo authors: I. Frutos (A), L. Corbari (B, C), N. Mathys (D).

soft substrates. The beam trawl is composed of a 4 m wide wooden beam that is affixed onto heavy iron runners located at both ends of the bar. These runners serve as skis so that the trawl can glide along the sea floor. The height of the iron side-skis (0.5 m, length 0.45 m, giving an effective height of 0.35 m) defines the vertical opening of the net, the beam determines the horizontal opening of the net. The heavy weight of the runners at the base of the opening of the net settles the trawl and keeps it well on the ground. A fine-mesh net (15 and 12 mm) is attached to this system; the ground rope of the net is strengthened with chain to allow it to dig into the sediment and stir up organisms or substrate on and in the sediment. A tickler chain (4.5 m long, 10 kg) is placed before the net. A conical net proper is located behind the ground rope. This conical shape allows for good filtration of the water and guides the organisms caught in the net towards the cod-end of the trawl. The cod-end is double-layered, with an inner finer mesh bag. The trawl is connected to the warp of the ship by two 4 m long wires, forming a triangle with the beam (crowfoot).

2.2. *Sampling area (Fig. 3)*

A total of 81 sampling stations has been performed on the Saya de Malha Bank in the four areas selected for their potential co-occurrences of diving sites with deeper areas suitable for sampling with towed gears (Northern, Eastern, Western and Southern areas). A log-book containing the procedure (diving, towed gears), the station coordinates (latitude, longitude and depth), a brief description of the sampling site and the type of sample has been maintained on board. The station codes are preceded by a two-letter prefix that refers to the type of gear/method used: CP, beam trawl; DW, Warén dredge; EB, benthic sledge; YR, on-sight collection; YB, brushing sample; and YS, suction sample. This station code is reported on label associated to each specimen or batch of specimens sorted on board (see Figs. 4G and 6A, C). The expedition name in the MNHN databases is called SAYA and all the metadata, photos and information related to the sampling stations are available online at https://expeditions.mnhn.fr/campaign/saya.

2.3. *On-board processing of biological samples and data (Fig. 4)*

For each collection operation (diving or towed), the content of the samples is photographed to document the nature of the substrate.

Sorting of bulk samples from scuba-diving (brushing, suction samples): The bulk samples are sieved and split into different sized fractions on board. Bottom samples and residues are sieved fresh in seawater and fractioned through a set of sieves from 10 mm to 0.5 mm mesh-size. Then, both the light (containing algae and polychaetes) and heavy fractions (containing sediment and shells) from each sieve are separated. The coarse fractions are sorted with the naked eye, fractions smaller than 5 mm are sorted with dissecting microscopes. The freshly sorted catch is screened for remarkable species/specimens that will be channelled to the photography and/or barcoding team. The remaining specimens, as well as the empty shells, are preserved in ethanol for post-expedition sorting.

Sorting of samples from towed gears (trawls, dredges): Bulk samples and residues are sieved fresh in seawater and separated into fractions through a set of sieves from 20 mm to 0.5 mm mesh-size, and the light fraction (containing notably small crustaceans) and heavy fractions (containing sediment, shells and other macro-organisms) from each sieve are separated. The coarse fractions are sorted with the naked eyes, fractions smaller than 5 mm are sorted under stereomicroscopes. The freshly sorted catch is screened for remarkable species/specimens that will be channeled to the photography and/or barcoding team. All the specimens are sorted by main taxonomic groups.

Preservation of sledge samples: Bulk samples from both nets are processed separately. They are washing and the sample is sieved in seawater on a sieve of 300 μm mesh-size for removing potential mud. Due to the tropical climatic conditions, deep-sea samples were transferred to a cold environment for sieving and being subsequently stored. Whole samples are preserved in 95 % ethanol. For a more efficient preservation, ethanol was replaced after 24 h. The sorting is performed back to the laboratory.

Photography: To supplement *in situ* photography (of large species and habitats), we documented directly on-board some species of invertebrates. Special attention was devoted to crustaceans, photography of fresh living specimens is particularly important for the documentation of colour patterns, crucial for taxonomic studies.

Barcoding and preservation for morphological analysis: Special attention was given to preserve the specimens in an optimal way for both morphological and molecular study. Most organisms were preserved in ethanol 80 % or 95 % except seaweed that were pressed as herbarium voucher with a subsample preserved in silica gel dedicated to genetic analysis. Special attention was paid for molluscs. For optimal preservation, the organism must not be retracted deep inside the shell, especially if it possesses an operculum; species-level taxonomy requires examination of the intact shell. A long-time experience on this group revealed that gastropods should be removed from their shells for an optimal preservation of the tissues. Different procedures have been developed on-board such as relaxation of the animal in Magnesium Chloride or micro-wave procedure for removing the tissues (Galindo et al., 2014). We used a combination of dissection methods to ensure proper preservation of tissues and preservation of shell characters. Tissues and shells are preserved together in ethanol 95 %.

For traceability of the samples and specimens, during the different processing steps on board, we use a labelling system that includes: (a) cruise name and station code; (b) specimen identifier; (c) photo identifier if relevant.

3. Results

3.1. Sampling effort and habitats (Figs. 3 and 5)

The MNHN exploration of the Saya de Malha Bank is characterised by four main explored areas (Fig. 3) and by the sampling effort deployed in each zone. On the 81 sampling stations, a total of 35 stations has been sampled by diving methods, whereas deeper areas sampled by towed gears represent 46 stations. The Northern area is located between the Southern part of Ritchie Bank and the northernmost part of the Saya Bank. In this area, a total of 17 sampling stations has been performed corresponding to 9 diving operations (19–58 m depth) and 8 deep-sea samplings with towed gears (192–1441 m depth). Because of the hardness of the bottom, dredging has been mainly performed (5 stations with DW codes). The trawling station CP5412 (1396–1441 m depth) is located in the channel between the Ritchie and Saya de Malha banks. The exploration of the western area corresponds to 12 sampling stations with 6 diving operations (37–50 m depth) and 6 samplings with towed gears (110–220 m depth). The eastern zone was more devoted to shallow water samplings, as it contains more accessible areas suitable for diving (18 diving operations, 24–47 m depth) but also for towed gears such as the sledge which has been deployed around 73 m depth (3 stations with code EB). The largest explored area was the southern zone. This area was deeper and by consequence the sampling by diving has been limited (2 operations at 47 m depth). Instead, a total of 26 towed gears has been deployed from 150 to 1087 m depth, comprising 3 operations located in the channel between the Saya and the Nazareth banks as well as in the northernmost part of the Nazareth Bank.

The shallow waters habitats of the Saya de Malha Bank (Fig. 5) are characterised by the extensive and dense meadow composed by the

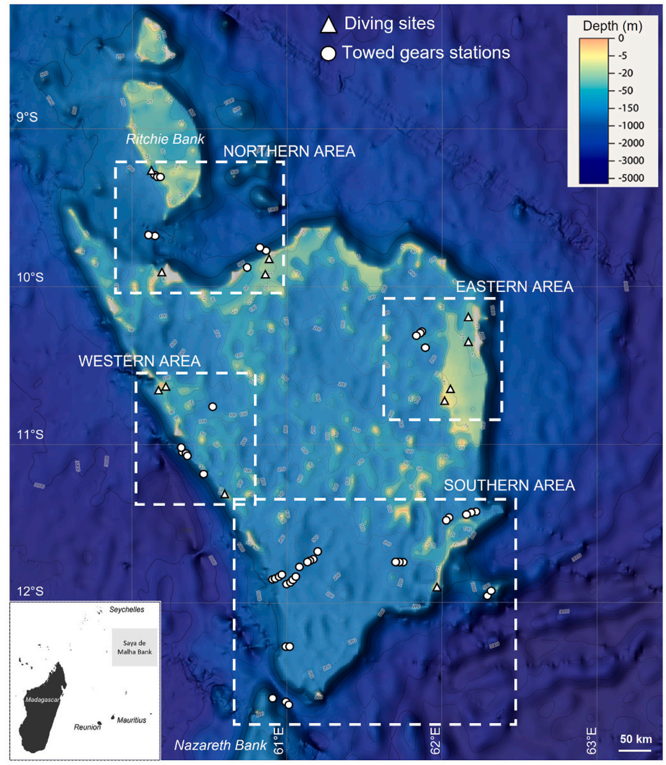

Fig. 3. MNHN exploration on Saya de Malha Bank represented by the four explored areas and the corresponding sampling methods (diving and towed gears deployments). All station data available at https://expeditions.mnhn.fr/campaign/saya. Map from GEBCO.

marine phanerogam *Thalassodendron ciliatum* (Fig. 5A–B). This flowering plant has roots that allow it to attach to the substrate. Both asexual multiplication by « boutures » and sexual reproduction occurs thanks to inconspicuous flower that have not been observed during the expedition. Asexual multiplication is supposedly more frequent that sexual reproduction leading to the presence of clonal individuals. *Thalassodendron ciliatum* formed a seascape that can be qualified as a dense underwater forest which has been observed in the Northern explored area during the expedition. From place to place this forest is punctuated by some reef patches where some corals can be observed on a white sand that likely resulted from coral abrasion. In the shallow habitats of the northern part (Fig. 5C–D), the divers have also observed detrital reef flat with macroalgae and turf and reef flats with algae and sponges. The eastern habitats (Fig. 5E) were more characterised by reef slope with spurs and furrows or buttresses and valleys with macroalgae, digitate, massive and encrusting corals. Sandy plains of reef slopes with sparse endogeal fauna have been mainly observed in the western area (Fig. 5F). The exploration of the upper slope and margin of the Saya de Malha Bank using towed gear has yielded a wide variety of deep-water samples that have been imaged directly on board, providing additional information on the nature of the substrate and megafaunal assemblages (Fig. 6). In the northern explored area, the deepest sampling (Fig. 6B) is characterised by the presence of globigerina mud and pumice stones whereas most of the samples collected around 200–300 m depth indicated the presence of small rocky substrates and gravels. The samplings by towed gears in the eastern area were shallow (73 m depth), with a fine sandy substrate. Most sites in the western and southern zones were sampled by dredging due to the presence of hard bottoms. Excluding sampling with the suprabenthic sledge, usually deployed on the same site as the beam trawl, 60 % of samplings on the explored area was carried out by dredging.

Fig. 4. MNHN on board workflow and samples processing. A, B: bulk samples respectively from Waren dredge and succion sampler; C, F: Primary sorting of samples; D, E, G: splitting and labelling specimes; H, I: sorting under stereomicroscope of fine fraction from bulk samples collected by diving (brushing and succion samples). Photo authors: MNHN team.

3.2. Biodiversity, preliminary results by taxa

3.2.1. Seagrasses and algae (Fig. 7)

The only other account for Seaweeds of Saya de Malha Bank that we are aware of all comes from Gardiner's expedition that were further studied by Gepp, A. & Gepp, E.S. (1908) for green algae and Weber-van Bosse, A. (1913) for red algae. A total of 6 taxa were observed during our dives (Fig. 7, Table 1). In between individuals of *Thalassodendron ciliatum*, we uncovered rhodoliths formed mostly by coralline algae and Peyssonneliales which are often referred to under the vocable Crustose Coralline Red Algae (CCRA). These calcified algae contribute to the cementation of the Saya de Malha reef. In addition, free forms called rhodoliths accumulate on the seabed, constituting an important local carbon sink. The observation of the seabed while diving had led us to believe that the coralline algae on the Saya de Malha Bank were highly diversified. We set out to test this hypothesis using the tools of molecular systematics and the first results of DNA sequencing of reference markers for molecular systematics analyses have been obtained for red coralline algae. Among the 33 specimens sequenced, species delimitation tools revealed the presence of 17 species (5 Sporolithales, 4 Corallinales, 8 Hapalidiales). An analysis of the sequences on a global scale shows that none of these species have been collected yet outside the Saya de Malha Bank. They are often closely related to species from other seamounts or islands in the Indian Ocean, such as the Seychelles, Mauritius, Saint Brandon or Chagos, but never identical. It would therefore appear that Saya de Malha Bank is sufficiently isolated from other emergent or submerged lands in the Indian Ocean to harbor endemic red algae. Red algae are known for their poor dispersal abilities, but it is likely that this pattern of diversity is also that of other moderately dispersing groups.

3.2.2. Molluscs (Fig. 8)

A total of 47 species of molluscs was collected on Saya de Malha Bank by Gardiner's Sealark expedition in 1905, and 130 species by the Soviet R/V Odyssey in 1984. A rough estimate is that 300 to 400 species were sampled during the Saya de Malha expedition in 2022. There is practically no overlap between the fauna from diving depths (20–50 m) and the fauna from deeper water (70 m and deeper) sampled by dredges and trawls. Roughly half of the species were sampled during the dives, and the other half by dredging and trawling. Two species-rich families straddle both depths zones, albeit with different species: the Marginellidae and the Columbellidae, represented by respectively ca 20 and 10–15 species (Fig. 8). Most are small to minute, with adult sizes in the range of 2–15 mm, and it is remarkable that the Sealark expedition of 1905 had collected respectively none and one species, demonstrating the efficiency of the collecting and sorting methods used during the MNHN marine benthic biodiversity inventory. Likewise, the Muricidae and Fasciolariidae, with respectively ca 15 and 10 species, also occur at all depths and are represented by quite a few specimens. By contrast, the families Triphoridae and Cerithiopsidae, represented respectively by ca. 15 and ca. 10 species, are almost entirely confined to the shallow areas. The turrid families, generally extremely diverse in both shallow and deep water, are altogether represented by 20–30 species. Special attention has been given during the dives to nudibranchs and other seaslugs, represented by ca. 40 species, plus another 10 in the dredges and the trawls.

In the summit area, the bivalves are mostly cemented: *Tridacna* (2

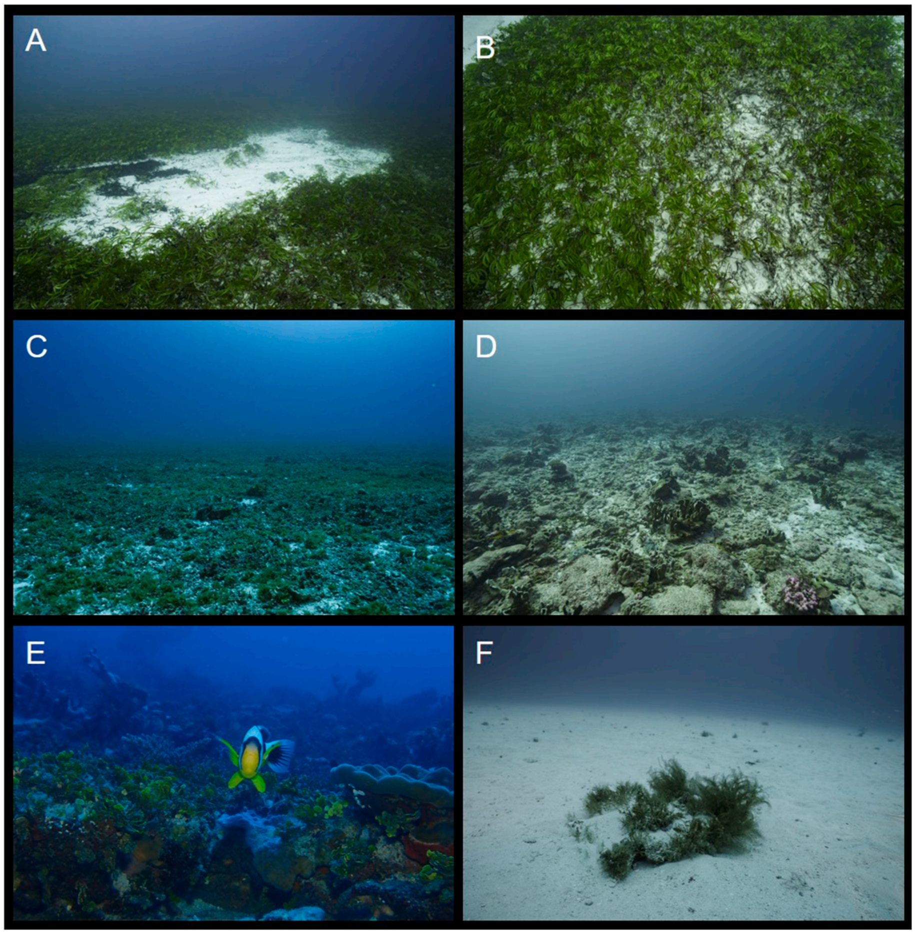

Fig. 5. Shallow water habitats. Northern area. A, B: station YR07 (25 m depth); C: station YR01 (42 m depth); D: station YR09 (20 m depth); Eastern area. E: station YR12 (27 m depth); Western area. F: station YR03 (43 m depth). Photo author: S. Bender.

species, see below), *Malleus*, 2 species of large oysters; or are byssally attached: *Pteria* (2 or 3 species, bysally attached to hydroids or gorgonians), *Pinctada* (pearl oyster, a single specimen). However, single loose valves of cockles (Cardiidae) and Glycymeridae indicate that further infaunal bivalves are present in the area. In deeper water, bivalve assemblages with *Bentharca*, *Microcardium*, Verticordiidae, Poromyidae, and *Cuspidaria* are encountered on soft bottoms.

Just as importantly, some families are noticeably absent. Among the families of « seashells », the herbivorous family Strombidae, characterized by long-distance dispersing larvae, is unexpectedly remarkably scarce, with only 2 juveniles *Strombus* (s.l.) and 3 adult *Lambis* (2 species) found ; the predatory miters (family Mitridae) are altogether missing ; only three species of Terebridae were documented, and the necrophagous Nassariidae are also almost completely absent, both in shallow and in deep-water : no *Nassaria*, a couple of species of *Nassarius*, one species of *Phos*. The larger species of the family Cerithiidae are almost completely absent, but one *Bittium*-like species is very common in the summit area. The vetigastropods (Trochidae, Fissurellidae) are remarkably poorly diverse in the summit area. The absence of Pyramidellidae is noticeable but may in part be explained by the absence of mud/silt bottoms in shallow water.

Among the remarkable catches, the lepetelloids are small limpets specialized in feeding on/degrading organic substrates. Species of *Lepetella* feed on empty tubes of the polychaete *Hyalinoecia*, and what may represent a new species was found at CP5412 (1396–1441 m depth). Species of *Bathysciadium* live exclusively on cephalopod beaks decaying on the bottom in deep water. No species was previously known from the tropical Indian Ocean, but one species probably new to science was sampled at DW5445 in 430 m. Species of *Addisonia* live exclusively in spent elasmobranch (rays and sharks) egg-cases. What may be a new species of this genus, or even a new genus, was found in a spent chimaera egg-case at CP5403 in 875 m.

In the group of emblematic species, the giant clam *Tridacna rosewateri* was discovered by divers during the Soviet expedition of 1988, and it was again found by us in the shallowest parts of the Saya de Malha Bank. Its distinctiveness has been genetically confirmed. Elsewhere, it is a species known only from Nazareth Bank (Cargados Carajos) and Tromelin. It can thus be considered to be iconic of the coral reef depths on Saya de Malha. A second species of giant clam, *T. squamosa*, is also present on Saya. *Conus primus* was described based on specimens allegedly collected in 80–98 m, it is known from a handful (7 or 8) specimens collected during Soviet times, and never seen subsequently. The SAYA expedition collected one freshly dead empty shell while diving at 42 m.

3.2.3. *Crustaceans* (Figs. 9–10)

Only a few crustacean species are known from the Saya de Malha bank. Including species recently described from the bank (see data sup. 1), literature data and occurrences from international databases, fewer than 50 species of benthic crustaceans have been reported from Saya de Malha Bank.

A total of 650 lots of crustaceans were collected during the SAYA expedition in 2022, originating from sampling by scuba diving and towed gears. A rough estimate was that about 200 species were sampled during the expedition. On board, we estimated in terms of relative abundance that 56 % of the total sampled specimens of crustaceans were

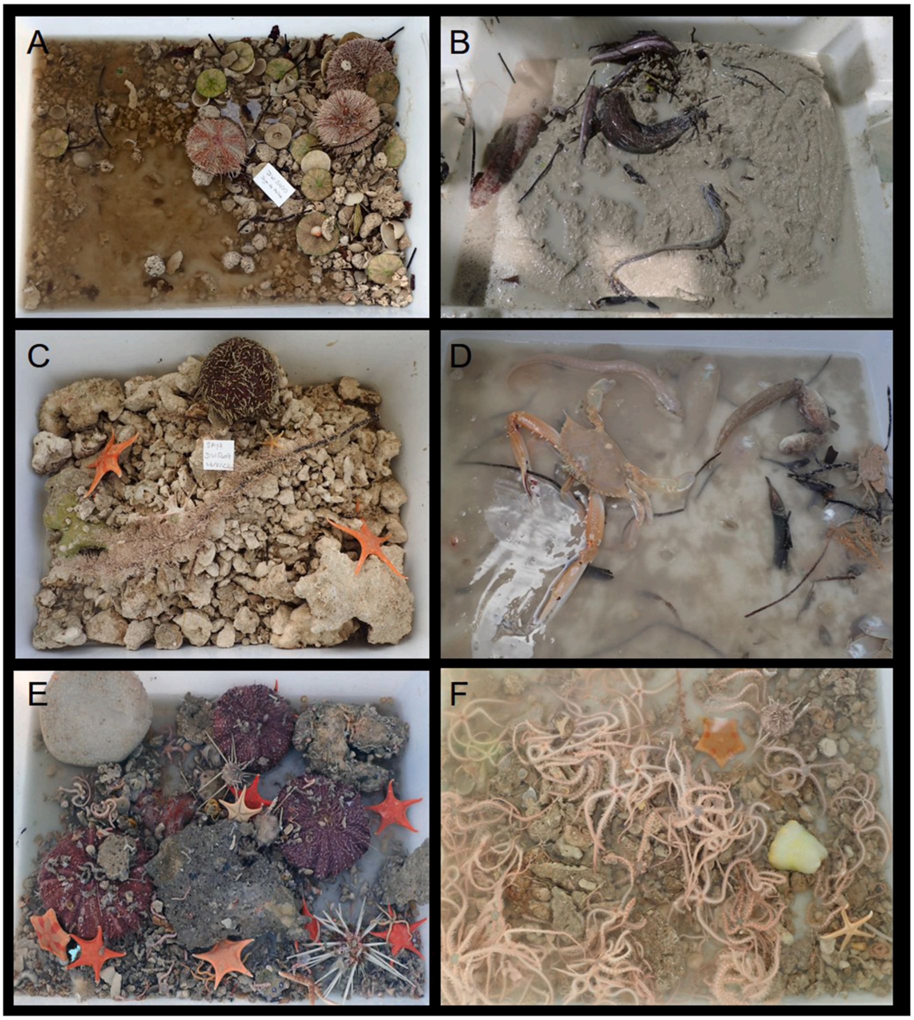

Fig. 6. Deep-sea samples collected by towed gears. Northern area. A: station DW5400 (277–295 m depth), B: station CP5412 (1396–1441 m depth); Western area. C: station DW5407 (193–198 m depth); Eastern area. D: station CP5414 (76–77 m depth); Southern area. E: station DW5441 (300–305 m depth), F: station DW5440 (272–273 m depth). Photo author: L. Corbari.

represented by decapods. At that time, it was difficult to provide a precise estimation because small fractions (suction or brushing samples) and bulk samples (such as from the suprabenthic sledge) were not fully sorted. Now and at this stage of the inventory (far from complete), 561 taxonomic lots (*i.e.* corresponding to a number of same individuals from the same station with the assignation of taxonomic rank), representing a total of 5125 specimens, have been integrated in the MNHN crustacean collection database.[3] Decapod crustaceans account for 57 % of all crustacean lots recorded, corresponding to date to 974 specimens and 80 taxa (taxonomic rank from family to species level). Among the remarkable crustaceans, 17 specimens of the crabs of the family Leucosiidae have been collected during the expedition (7 sampling events by towed gears, depth range 193–305 m). They have been assigned to *Praebebalia extensiva* Rathbun (1911) (Fig. 9A, identification B. Galil). In 1905, six specimens of *Praebebalia extensiva* were collected off Saya de Malha, and Providence, Seychelles (type locality), by the 'Sealark' expedition, and described by Rathbun (1911). Since the 2022 expedition on Saya de Malha Bank, no other specimens were known. The specimens recently collected increase our knowledge of the species (depth range and distribution) and the species is now re-described (Galil, 2025). In the same family, the rare species *Merocryptus boletisculpta*, re-described from Walters shoal (Fig. 9B; Galil, 2019) has also been collected during the SAYA expedition, extending greatly the distribution range of the species. The inventory of decapods is not yet complete but new species or potential new species are already in the hands of taxonomists. For example, the crab of the family Ethusidae (Fig. 9C) has been designated as new for science by the specialist of the group (P. Castro, pers-comm) and the squat lobsters Galatheoids (families Galatheidae, Munididae and Munidopsidae) are a group supporting high rates of diversity and new species descriptions are expected (Macpherson & Rodríguez-Flores, pers-comm.). In the framework of the integrative taxonomy, the production of genetic data on this group has revealed a species richness of more than 25 species (instead of 15 species discriminated at morphological level). These include strong hypotheses for species new for science, especially in the genus *Coralliogalathea* which is a small-sized and cryptic genus of Galatheidae (Fig. 9D).

In terms of crustaceans Peracarida, 2349 specimens have been processed and preliminarily identified during the working time on board. Within the six orders of Peracarida represented in the samples (Lophogastrida, Mysida, Amphipoda, Cumacea, Isopoda, and Tanaidacea, see Fig. 10), amphipods (64.3 %) and isopods (19.4 %) are the most frequent findings, in contrast with tanaidaceans (1.5 %) and lophogastrids (0.1 %). In fact, amphipods occurred in 27 of the 31 stations processed meanwhile lophogastrids are only in two of them (CP5431 and EB5427).

[3] https://science.mnhn.fr/institution/mnhn/collection/iu/item/search/form.

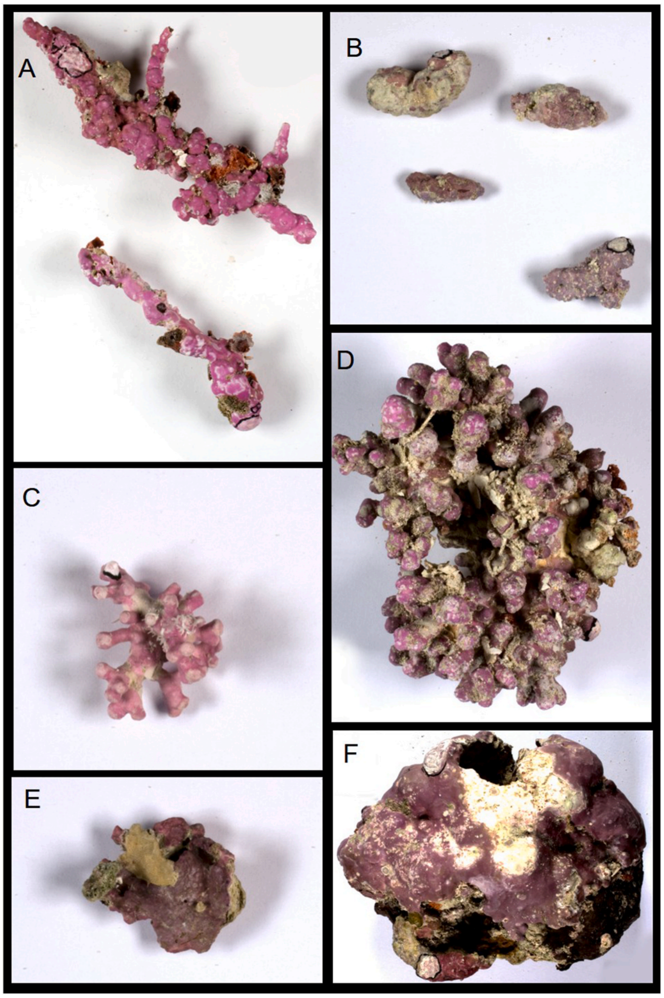

Fig. 7. Rhodophyta, Corallinophycidae. A: *Lithothamnion* sp. (MNHN-PC-PC0638852); B: Mastophoraceae (MNHN-PC-PC0638740); C: Hapalidiales (MNHN-PC-PC0638741); D: *Harveylithon* sp. (MNHN-PC-PC0638757); E: Sporolithales (MNHN-PC-PC0638723); F: *Sporolithon* sp. (MNHN-PC-PC0638823). Photo author: G. Marani.

According to the sampling methods, diving methods provide low amount of peracarids (6 YS: 45 individuals; 3 YB: 53 individuals; 6 YR: 13 individuals), when compare with the towed sampling gears (15 DW: 450 individuals; 10 CP: 499 individuals), especially with the sledge (1 EB: 1288 individuals). Consequently, the number of peracarids from the samples located at the top of the bank are significantly lower than from the stations at upper bathyal depths (200–1000 m), where the sampling effort is only possible by means of towed gears (239 *vs* 2060 individuals). Despite the preliminary level of faunal identification, a high diversity is already observed especially in the best represented groups. Thus, Amphipoda is represented by at least 35 families, of which 21 belong to suborder Amphilochidea, 12 to Senticaudata and 1 to Hyperiidea, the latter represented by 3 specimens. It is noteworthy the efficient sampling of *Polycheria* sp. (fam. Dexaminidae) and *Leucothoe* sp. (fam. Leucothoidae) in diving samples and of *Rhachotropis* sp. and *Cleonardo* sp. (fam. Eusiridae) by means of towed gears. Isopoda is mostly represented by the suborder Asellota characterizing the deep-sea samples, meanwhile Cymothoida (Family Anthuridae and Gnathiidae), Sphaeromatidea and Valvifera are in the shallow areas of the bank ().

3.2.4. *Annelids (Fig. 11)*

Only two species of polychaetes were reported from the soviet expeditions in the area (Vortsepneva, 2008). In total, 331 lots of annelids were collected during the Saya de Malha part of the leg. These lots can contain from 1 to about 30 specimens (this latter mostly for small annelids). About a third of these lots remain unsorted and will be part of a dedicated workshop, the remaining ones have been sorted at least to the family level (20 families represented). Some specimens of the family Polynoidae (Fig. 11B, C, 124 lots total) were identified to the genus level but many specimens in the family remain to be identified more precisely (74 lots). A special attention was also given to associations of polychaetes with other invertebrates: holothurians, starfish, other annelids, stylasterid corals and black corals. The collections already allowed the description of a new species of Iphionidae, *Iphione corbariae* (Fig. 13). Collected at 150–170 m, it was so far only found on the Saya de Malha Bank (Salazar-Vallejo et al., 2024). Originally described from the Seychelles, *Hermenia neoverruculosa* (Polynoidae) is here reported for the first time in another location. Commonly found in the Western Pacific, *Lepidonotus cristatus* (Polynoidae) has also been collected at various intertropical locations in the Atlantic Ocean, Indian Ocean and at Saya de Malha during our expedition.

Table 1
List of red and green algal species collected by Mr. Stanley Gardiner 1905 and identified by Annett Weber-van Bosse (1913). Valid names referred to Algaebase and Worms. *Asterisk indicates taxa observed by the MNHN team during the Saya de Malha expedition in 2022.

Taxa in Weber-Van Bosse	Current synonym
RED ALGAE	
Galaxaura fastigiata	*Tricleocarpa cylindrica* (J.Ellis & Solander) Huisman and Borowitzka, 1990
Galaxaura obtusa	*Dichotomaria obtusata* (J.Ellis & Solander) Lamarck, 1816
Eucheuma cottonii	*Kappaphycopsis cottonii (*Weber Bosse) Dumilag and Zuccarello, 2022 Type Information: Lectotype locality: Saya de Malha in the Indian Ocean north of Mauritius; (Doty, 1988: 177) Lectotype: Stanley Gardiner; In 26 fathoms of water; Leiden Herbarium; 938.316–220 (Doty, 1988: 177) Notes: An isotype is deposited in the British Museum.
Fauchea microspora	*Gloiocladia microspora* (Rodríguez y Femenías) (Berecibar et al., 2009)
Gloiderma expansum	*Sciadophycus expansus* (Weber Bosse) A.J.K.Millar, 2001
Chylocladia perpusilla	*Chylocladia perpusilla* Weber-van Bosse, 1913, Type locality: Saya de Malha Bank; (Silva & al., 1996: 349)
Dictyurus purpurascens *	*Dictyurus purpurascens* Bory de Saint-Vincent, 1834
Cryptonemia seminervis	*Cryptonemia seminervis* (C.Agardh) J.Agardh, 1846
Cryptonemia sp.	–
Peyssonnelia coccinea	*Sonderopelta capensis* (Montagne) A.D.Krayesky, 2009
Peyssonnelia harveyana	*Peyssonnelia harveyana* P.L.Crouan & H.M.Crouan ex J. Agardh, 1851
Cruoriopsis crucialis	*Peyssonnelia armorica* (P.Crouan & H.Crouan) (Weber-van Bosse, 1913)
GREEN ALGAE	
Struvea gardineri *	*Phyllodictyon gardineri* (A.Gepp & E.S.Gepp) (Kraft and Wynne, 1996)
Microdictyon pseudohapteron *	*Microdictyon pseudohapteron* A.Gepp & E.S.Gepp and Gepp, 1908
Struvea orientalis *	*Phyllodictyon orientale* (A.Gepp & E.S.Gepp) (Kraft and Wynne, 1996)
Bryopsis indica	*Bryopsis indica* A.Gepp & E.S.Gepp and Gepp, 1908
Cladocephalus excentricus *	*Cladocephalus excentricus* A.Gepp & E.Gepp and Gepp, 1908
Avrainvillea gardineri *	*Avrainvillea gardineri* A.Gepp & E.S.Gepp and Gepp, 1908

3.2.5. *Fish (Fig. 12)*

The fish specimens collected during the SAYA expedition, along with associated genetic samples, are currently housed at the National Taiwan University Museums (NTUM). In total, 196 fish specimens were collected (three of which were photographed only) from 39 stations at depths ranging from 76 to 1441 m. Tissue samples from 172 specimens were preserved for genetic studies. Based on the classification system proposed by Near and Thacker (2024), the collection encompasses 19 orders, 45 families, 74 genera, and at least 98 species (Sup. data 2).

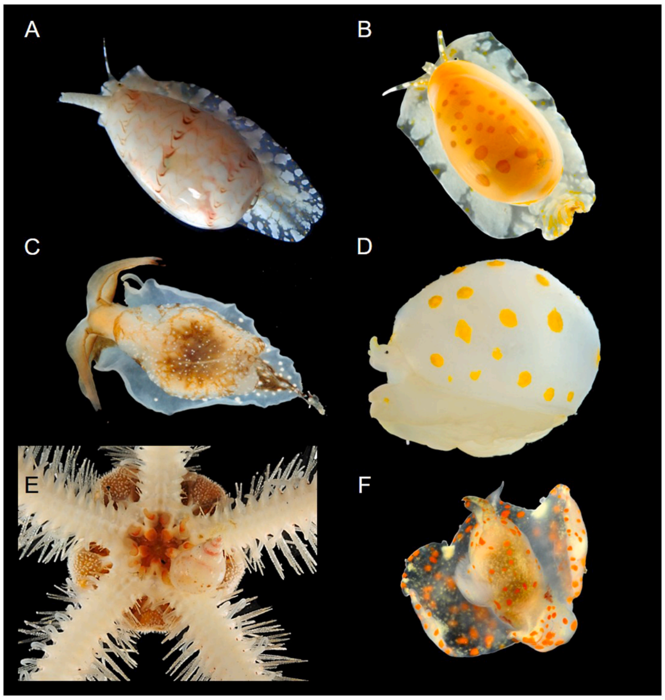

Fig. 8. Mollusca. Pictures on specimens were taken on board immediately after sampling. A: A new species of Persicula [family Cystiscidae], 6 mm (station YR05, 24 m); B: A new species of Closia [family Marginellidae], 10.6 mm (station CP5421, 215 m); C: Bathyhedyle boucheti, a giant acochlidiacean previously known only from off Mozambique (station CP5431, 254–261 m); D: A new deep-sea species of Velutinidae (station DW5411, 192–216 m); E: a gastropod of the family Eulimidae parasitic on the ventral side of an ophiuroid (station DW5440, 272–273 m); F: shell-less but not a nudibranch: a swimming seaslug of the family Gastropteridae (station CP5426, 216–222 m). Photo author: G. Moutardier.

Among these, five specimens were identified only to the familial level, while 45 were identified to the generic level. Identification of 34 specimens was further validated using genetic analysis, specifically the mitochondrial cytochrome *c* oxidase subunit I (*COI*) DNA barcoding marker.

The order Carangiformes is the most species-rich, with 20 species, all belonging to the suborder Pleuronectoidei (flatfishes). This is followed by Scorpaeniformes, represented by 12 species, and Gadiformes, with nine species. At the family level, the most species-rich group is Bothidae (lefteye flounders) (Fig. 12A), comprising eight species. This is followed by Cynoglossidae (tonguefishes), Macrouridae (grenadiers), and Triglidae (gurnards or sea robins) (Fig. 12D), each represented by seven species. Among the identified species, several were originally described based on specimens collected from the Saya de Malha Bank, and most are likely endemic to the region. Notable examples include *Parabothus malhensis* (Regan, 1908), *Poecilopsetta normani* Foroshchuk and Fedorov (1992), *Ocosia possi* Mandrytsa and Usachev (1990), *Pterygotrigla jacad* Richards and Yato (2014), *Antigonia quiproqua* Parin and Borodulina (2006), and *Neobythites malhaensis* Nielsen (1995), as illustrated in Fig. 12. Many of these species were previously known from only a few specimens, with some represented solely by the type series. Visual documentation of these taxa was also limited, often restricted to type illustrations. The SAYA expedition provided an invaluable opportunity to obtain fresh specimens and genetic materials, as well as high-quality photographs of these poorly known species, significantly advancing our understanding and documentation of their genetic and morphological diversity, as well as their taxonomy.

Particularly noteworthy is the occurrence of several species previously not known to inhabit the western Indian Ocean. For instance, ten specimens of the duckbill *Chrionema chlorotaenia* McKay (1971) (Fig. 12G) were collected during the expedition. Originally described from northwestern Australia, this species has been documented across the central Indo-West Pacific, including Japan, Taiwan, and the Arabian Sea (Fricke and Eschmeyer, 2025). A genetic distance comparison based on *COI* revealed negligible differences (*p*-distance <0.002) between the specimens from Saya de Malha and Taiwan, marking the first record of this species in the western Indian Ocean. Similarly, *Lophiodes endoi* Ho

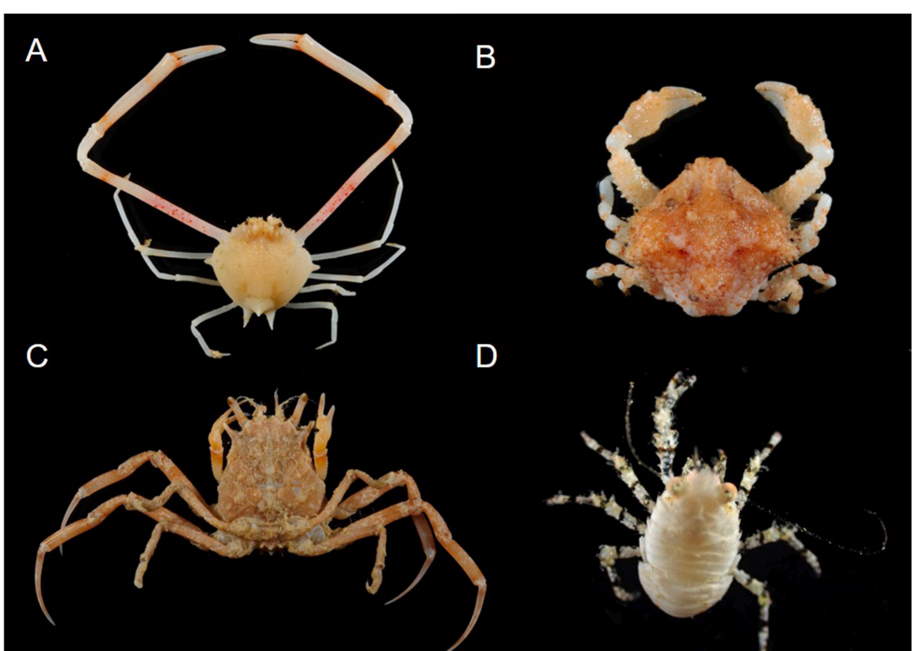

Fig. 9. Crustaceans Decapoda. Pictures on specimens were taken on board immediately after sampling. A: *Praebebalia extensiva* Rathbun (1911) (Family Leucosiidae), MNHN-IU-2022-265; B: *Merocryptus boletisculpta* Zarenkov, 1994 (Family Leucosiidae), MNHN-IU-2022-218; C: *Ethusa* sp. (Family Ethusidae), MNHN-IU-2022-290; D: *Coralliogalathea* sp. (Family Galatheidae), MNHN-IU-2022-206. Photo author: L. Corbari.

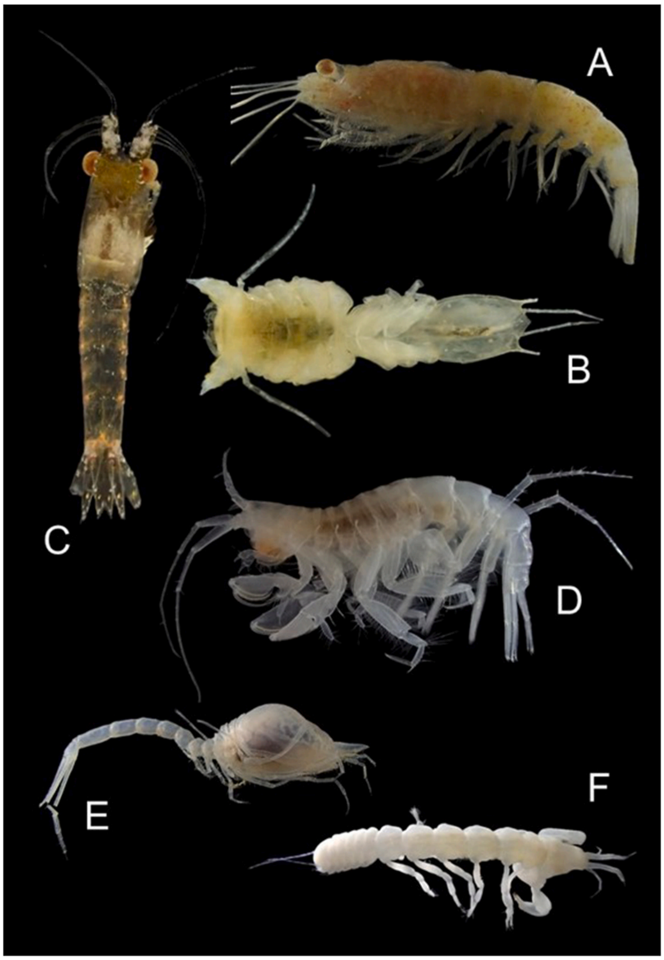

Fig. 10. Crustaceans Peracarida. Pictures on specimens were taken on board immediately after sampling. A: Lophogastrida (Family Lophogastridae) MNHN-IU-2022-254; B: Isopoda (Family Munnopsidae) MNHN-IU-2022-196; C: Mysida (Family Mysidae) MNHN-IU-2022-244; D: Amphipoda (Family Oedicerotidae) MNHN-IU-2022-259; E: Cumacea (Family Diastylidae) MNHN-IU-2022-316; F: Tanaidacea (Family Neotanaidae) MNHN-IU-2022-194. Photo authors: L. Corbari (A), I. Frutos (B–F).

and Shao (2008) (Endo's anglerfish; Lophiidae) was previously known only from the central Indo-West Pacific, with its range extending from Australia to Japan. During this expedition, a single specimen of this species was captured (Fig. 12J), and its genetic distance from conspecific individuals in Taiwan and Japan was minimal (0.014). This finding indicates a significantly broader distribution of the species across the Indo-West Pacific, extending into the western Indian Ocean.

In contrast, the dragonet *Draconetta xenica* Jordan and Fowler (1903) (Draconettidae), a small-sized species widely distributed across the Indo-West Pacific, was also captured during the expedition. This species is the sole recognized member of the genus *Draconetta*. However, when its *COI* sequence was compared with sequences from individuals in the western Pacific, a striking level of genetic divergence was observed, with an estimated divergence of 13.8 %. This is approximately five times higher than the 3 % threshold commonly used to delineate species in marine fishes based on the *COI* locus (Ward, 2009). This finding highlights a previously overlooked hidden diversity within this species, and potentially within other species recorded from the Saya de Malha Bank.

Moreover, several species are known from the Saya de Malha Bank or its adjacent waters, but their distinct characteristics warrant further investigation into their identities. For example, the brown lanternshark *Etmopterus compagnoi* Fricke and Koch (1990) (Etmopteridae), originally described based on the specimens collected from southern South Africa, would not be so surprising to capture it in this region. However, the body of our specimen is uniformly black (Fig. 12I), in contrast to the bicolored body of the holotype (based on illustrations). Additionally, our specimen exhibits a stouter body. The identity of this specimen is currently under investigation.

Another example is the searobin *Satyrichthys laticeps* (Peristediidae), of which we captured three specimens. This species can be easily identified based on the unequal size of the midline parietal bones (Kawai, 2013), and the species is known to be widespread across the Indo-West Pacific (Kawai and Richards, 2022). However, our specimens are orange-red in overall coloration (Fig. 12H), differing from the typical pinkish-red coloration observed in specimens from the northwestern Pacific. Genetic distance comparisons between one of our specimens and other congeners (downloaded from BOLD) revealed that our specimen was closely related to those from off South Africa (p-distance <0.001), but more distantly related to the Australian specimens (p-distance $\sim$ 0.010) and Philippine specimens (p-distance $\sim$ 0.023). This suggests that *S. laticeps* may represent a species complex, and specimens from different regions should be carefully compared for accurate species identification and for phylogeographic investigation.

3.3. Databasing and accessibility of the data

All data from the MNHN marine benthic biodiversity inventory (Expedition SAYA) are available for the scientific community, either through MNHN collection databases or international databases (*i.e.* species occurrences via GBIF,[4] Genetic data via Genbank or Bold system). To ensure the traceability of these data, MNHN has set up different data management systems involving interconnected databases. The data flow is managed within the different databasing systems, from the field (survey or cruises) to the publication and dissemination of the data. Two main data portal are available: (i) expedition database devoted to cruise, survey information, geographic data and onboard pictures of the samples, as well as documents related to the cruise proposal, permits and communication (http://expeditions.mnhn.fr/); (ii) collection database for taxonomic data and species occurrences, where are recorded the specimens (and their associated collection data and photo) collected by the MNHN during the last decades (https://science.mnhn.fr/all/search).

A total of 1612 lots of specimens (*i.e.* number of specimens from the same station with the assignation of taxonomic rank) corresponding to a total of 6962 specimens has been integrated in the MNHN collection.[5] We estimate that it represents about 60 % of the specimens sampled on Saya de Malha. 83 % of this material is identified at Family, Genus and/or species level, representing at the moment 280 species/morphospecies for molluscs and crustaceans. Up to now, three species new for science have been described from specimens collected by MNHN during the SAYA expedition, for the groups of molluscs, crustaceans and annelids (Fig. 13, sup data 1). The sorting is ongoing and the small-sized samples are still processed (*i.e.* annelids, suprabenthic sledge samples). Primary morphological identifications have been carried out on board, but the priority for the scientists was to preserve the samples/specimens as much as possible before the DNA degradation. The production of genetic data is ongoing and specimen delimitations must then be confirmed by using DNA sequences combined with observation of anatomical characters in the framework of the integrative taxonomy.

4. Discussion and conclusions

The marine benthic biodiversity inventory performed by the MNHN team, was based on an original sampling strategy, combining sampling methods, such as towed gears (dredge, trawl, and sledge) and by scuba-diving (on-sight, brushing and suction device samplings). The total of 81

[4] https://www.gbif.org.

[5] https://science.mnhn.fr/all/list?country=JMA%20Maurice/Seychelles.

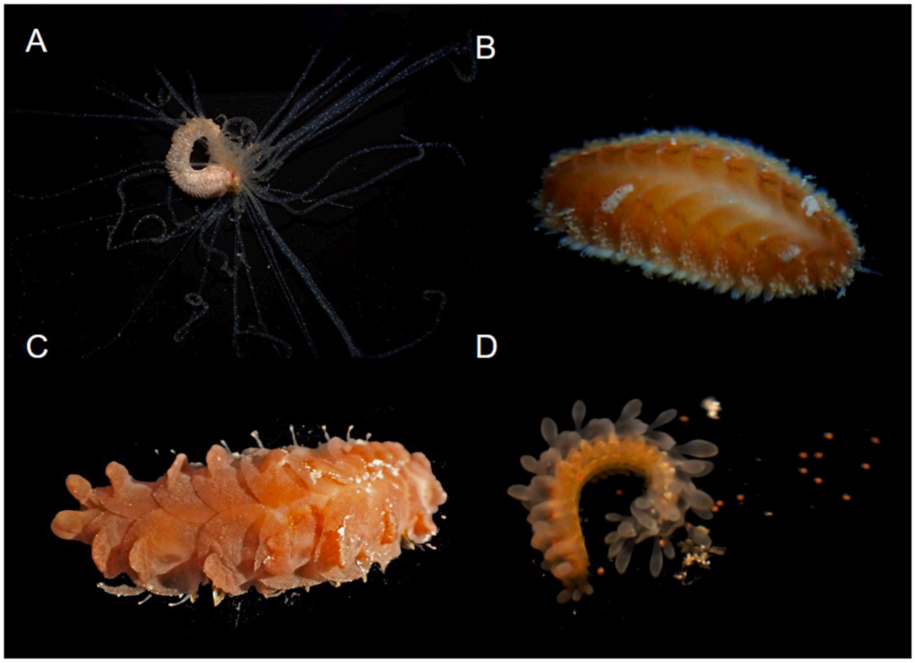

Fig. 11. Annelids Polychaeta. Pictures on specimens were taken on board immediately after sampling. A: *Eupolymnia* sp. (Family Terebellidae); B: *Iphione* sp. (Family Iphionidae); C: *Lepidonotus cristatus* (Family Polynoidae); D: *Asterophilia* sp., associated with a starfish (Family Polynoidae). Photos author: S. Hourdez.

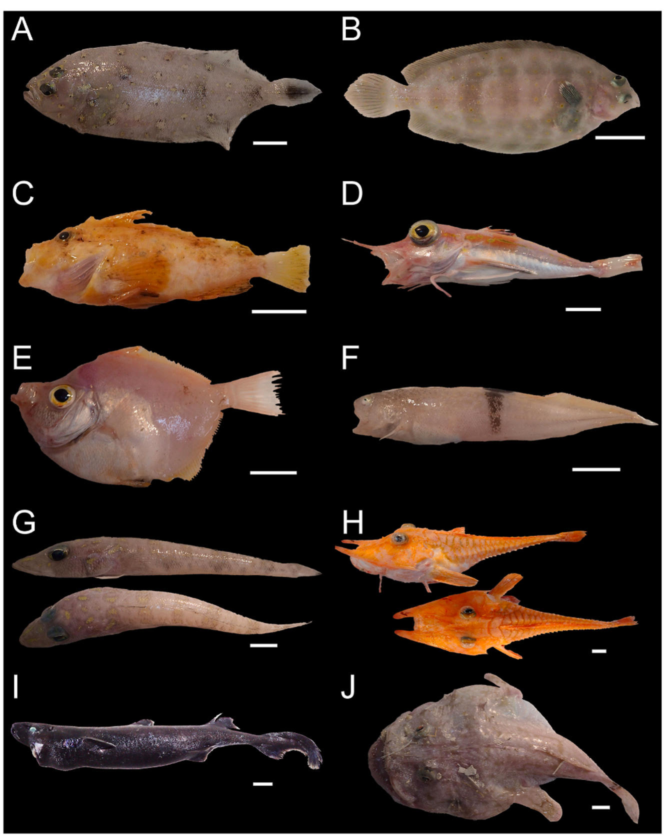

Fig. 12. Photography of selected fish specimens captured during the SAYA expedition. A, *Parabothus malhensis*, WIO794. B, *Poecilopsetta normani*, WIO828. C, *Ocosia possi*, WIO813. D, *Pterygotrigla jacad*, WIO843. E, *Antigonia quiproqua*, WIO894. F, *Neobythites malhaensis*, WIO852. G, *Chrionema chlorotaenia*, WIO869 (upper, lateral view; lower, dorsal view). H, *Satyrichthys* cf. *laticeps*, WIO770 (upper, lateral view; lower, dorsal view). I, *Etmopterus compagnoi*, WIO900. J, *Lophiodes endoi*, WIO885. Scale bars = 2 cm. Photo authors: MNHN team.

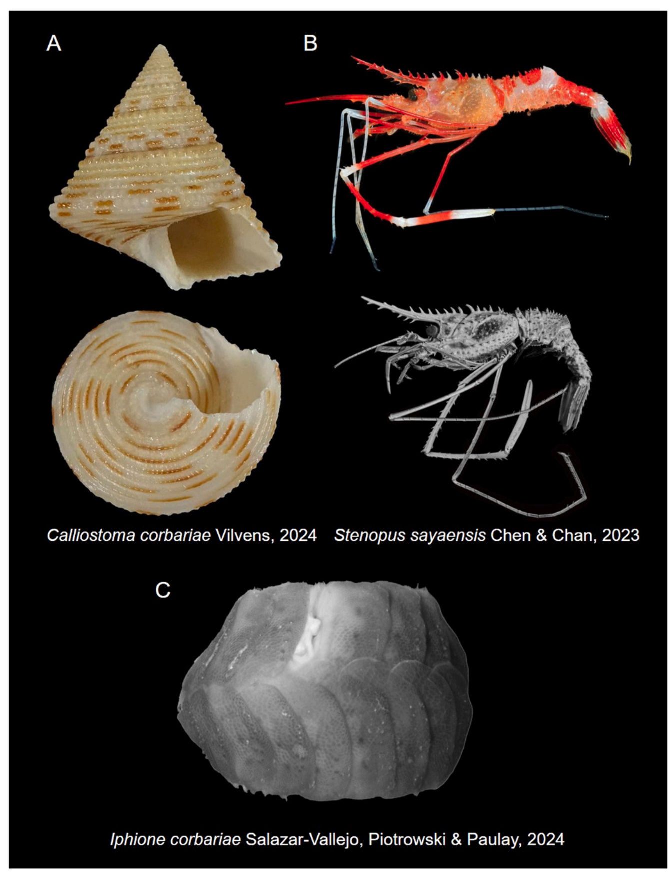

Fig. 13. New species described from MNHN samplings. A: Mollusca, Gastropoda, Calliostomatidae, *Calliostoma corbariae* Vilvens (2024); B: Crustacea, Decapoda, Stenopodidae, *Stenopus sayaensis* Chen and Chan (2023); C: Annelida, Phyllodocida, Iphionidae, *Iphione corbariae* Salazar-Vallejo et al., 2024, photos modified from original publications.

sampling stations included 35 shallow stations on the summit of the bank (19–58 m depth) and 46 stations gaining depth on the flanks of the bank (73–1141 m depth). From these sampling events, a large collection of marine invertebrates and algae has been preserved for taxonomic (morphological and molecular) studies.

After an intensive sampling of the nature that was undertaken on Saya de Malha, the questions that naturally arise are: how complete is our inventory of the benthic invertebrates and algae? What have we missed?

In the framework of Mollusc's taxonomy, Sirenko (1993) recorded many species of « seashells » in the shallowest part of the Bank (« 12 m ») that have not been found. This may reflect the fact that none of the dives were shallower than 20 m, and we would then have missed a segment of the reef fauna. For instance, the Sealark expedition of 1905 had recorded the small abalones *Haliotis pustulata* and *H. ovina*, and the Soviet expeditions had recorded *Haliotis* cf. *varia*, whereas we did not get abalones at all. Conversely, we noted the almost absence of strombs, and this is confirmed by earlier expeditions: a single species of stromb and no *Lambis* had been found by the Sealark expedition of 1905.

Of special interest are various species of « seashells » that were described in the 1990s based on material collected by Russian or Ukrainian vessels, either as a result of the Soviet research expeditions, or as a by-catch of commercial trawlers. We did find *Conus primus*. We possibly found (pending confirmation of the identification) *Closia limpida*, *Fusinus malhaensis*, and *Murex surinamensis*. But we did not find *Amalda danilai*, *A. trippneri*, *Conus gordyi*, *Haustellum bondarevi*, *H. danilai*, *Lyria bondarevi*, *L. doutei*, *L. surinamensis, Morum vicdani*, *Perotrochus metivieri*, *Phalium vector*, and *Semicassis bondarevi*. In addition, Khromov and co-authors (Khromov et al., 1991; Filippova and Khromov, 1991) described 4 species of cuttlefish (*Sepia bathyalis*, *S. mascarensis*, *S. saya* and *S. tala*); we probably did not use the right gear to sample *Sepia*, but got *Sepia* (a single specimen) on one occasion, and this may represent one of Khromov's species. In other words, and although our sampling was far more detailed than what had been achieved in the 1980s–1990s, we did not find the majority of the species of seashells known before the 2022 expedition. This may be explained by the fact that we didn't reach the right depth (80–200 m) in the right sector of the shoal, which suggests a great diversity of habitats on a shoal of this size. It may also be because the Russian/Ukrainian collections were the result of hundreds of commercial otter-trawl hauls that covered a much larger surface area of the bottom of the area, unmatched by our beam trawl. Finally, one cannot avoid noting the occurrence of some remarkable taxa that were found only once and never again, for example we found an abundance of a species of *Turritella* on a bottom of fine calcareous mud in 80 m, which was not found anywhere else. To summarize, all this points out to a probably much more diverse fauna of perhaps 1000 species of molluscs, of which we found between a quarter and a third. The explorations carried by our expedition, combining bulk sampling, sieving on a fine mesh, and sorting with stereomicroscopes, has undoubtedly documented hundreds of species for the first time on Saya de Malha. But clearly more dives in the shallowest part of the Bank, and more hauls by dredging/trawling would be needed for a full inventory.

In the case of peracarid crustaceans the lack of knowledge is critical on the Saya de Malha Bank. Despite the expeditions performed at the bank, only a few records of peracarid crustaceans, mostly pelagic species, have been reported. Thirty-five species of hyperiid amphipods recorded from the Searlak expedition (Walker, 1909), eigth species of lophogastrids and five of mysids both reported after 17th cruise of Russian vessel *Vitjaz* (Vereshchaka, 1995), and one unidentified isopod recorded by video imaging during EAF-*Nansen* expedition (Bergstad et al., 2021) set up the peracarid fauna known in the bank. As pointed out by Rogers (2018), such as scarcity of data on seamount studies is reflected in species inventories where focus on small-sized fauna is commonly neglected, although they can constitute hotspots of biodiversity (Frutos and Sorbe, in rev.). The accomplishment of species identification after Saya expedition will enlarge the Peracarida species inventories of the SW Indian Ocean.

In general, the complementarity of sampling methods not only provide a major collection of specimens, and consequently higher diversity rates, but also an additional information on species behaviour and biology, a great challenge in deep-sea peracarid species (Frutos et al., 2022). Thus, the amount of Peracarida specimens collected with Warén dredge or beam trawl is low when compared with sledge catches, due to their bigger mesh-size nets, but specimens exceptionally retained will be larger sizes (Corbari et al., 2024). Additionally, the two superimposed nets of the sledge allow estimating the swimming capability of the species and its vertical distribution from the seafloor (San Vicente et al., 2014; Frutos and Sorbe, 2022). The use of the information resulted of this combination of different equipment types to sample along with molecular and morphological characters, will enhance the integrative approach for the description of new species of Saya expedition. Furthermore, overlapping methods (scuba-diving and towed gears) in the shallow stations located on the summit of the bank could display associations between peracarids and sedentary epibenthic fauna (i.e, corals, sponges), a symbiotic relationship well-known for amphipods and isopods to get food or shelter (Vader and Krapp-Schickel, 1996; Frutos et al., 2017; Taboada et al., 2019; Navarro-Mayoral et al., 2024; Tandberg and Vader, 2024).

How much of the invertebrate fauna of Saya de Malha can be considered endemic to Saya de Malha Bank?

In a biogeographic perspective, endemism can be defined in two ways: (i) spatial endemism for species occurring in a given geographical area whatever its size (some species are regional endemics versus local endemics); (ii) ecological endemism for species specific to a particular type of habitat (*i.e.* vent species, biological associations, parasites, etc.). This ecological endemism or narrow endemism, related to the specialization of a species, can be assessed by comparing the different types of habitats where the species is harvested. Questioning the endemism of the benthic marine fauna and flora of Saya de Malha Bank is, at this stage, would be premature as declaring a species endemic assumes that (i) the taxonomy of the fauna at species level has been elaborated and (ii) other locations in this sector of the Indian Ocean have been sufficiently studied (Costello et al., 2017). This is of course still far from being the case as long as the collections of the Agulhas II expedition have not been worked up. However, the biogeography of the area should be studied further, and even if the taxonomic data provided by the 2022 Saya expedition are not yet complete, it will provide new insights into the structure and composition of marine biodiversity in the South West Indian Ocean.

In the case of molluscs, we have over 500 specimens/samples of molluscs specifically prepared for DNA sequencing, and the results of this sequencing will also shed light on the possible isolation of Saya de Malha populations of already known species. Because of the accretionary growth of their shell, the gastropods are uniquely suited to discuss issues of larval dispersal and potential endemism. Several families (Tonnoidea, Architectonicidae) are well-known for their long-distance teleplanic larvae and vast geographical ranges: their occurrence on Saya de Malha would represent an extreme of "non-endemism". Endemism would be expected to occur in species with paucispiral protoconch indicative of non-planktotrophic larval development, an extreme of which is represented by the three narrow-range volutes (which we did not find) with crawl-away juveniles; non-planktotrophy is the rule also in the family Marginellidae, which is well represented on Saya de Malha. In between these two extremes, a number of families may exhibit one or the other of the two developmental modes, and a number of species of, e.g., Columbellidae, Fasciolariidae, Turridae, were noticed with paucispiral protoconchs, and represent putative new species endemic to Saya de Malha.

The 2022 expedition to the Saya de Malha Bank resulted in the collection of a remarkable number of fish species, many of which were poorly known, some previously undocumented in the region, and several potentially undescribed. With the specimens and accompanying genetic samples obtained, further studies hold the potential to uncover the hidden diversity of this understudied area. In the case of crustaceans, all Peracarida, as brooders, are carrying embryos in a ventral pouch formed by oostegites until juveniles are released. Such as characteristics along with their high capabilities of swimming, make them good candidate as model for studies on connectivity, and eventually assessing endemism. Due to the lack of knowledge of such an interesting group after all precedent expeditions carried out in Saya de Malha Bank, our study will provide the baseline of knowledge on species distribution in the area to further biogeographical comparisons. For molluscs, we can speculate that perhaps up to 20 % of the molluscs living on Saya de Malha are endemic species new to science. It is too soon to estimate this percentage for the others taxa of the collection of marine invertebrates and algae, but three species new to science have already been described, the mollusc Calliostomatidae, *Calliostoma corbariae* Vilvens (2024); the crustacean Stenopodidae, *Stenopus sayaensis* Chen and Chan (2023) and the annelid Iphionidae, *Iphione corbariae* Salazar-Vallejo et al., 2024, (Fig. 13; updated list in sup. data 1). It is noteworthy that a new mollusc species from Saya de Malha Bank has been recently described (*Chicomurex kozlovi* Bondarev, 2023) from the expeditions conducted by research organizations of the Ministry of Fisheries of the USSR (Expedition of R/V Gordy, Gydronavt Base, Sevastopol in 1989). This suggests that in the near future, either from the 2022 expedition or even from the Russian ones, many species from the Saya de Malha Bank, new to science will be described. The challenge will be to properly describe them in the context of the "taxonomic impediment".

CRediT authorship contribution statement

L. Corbari: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **P. Bouchet:** Writing – review & editing, Writing – original draft, Validation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **L. Le Gall:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **S. Hourdez:** Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **I. Frutos:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **B. Gouillieux:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **E. Vassard:** Writing – review & editing, Writing – original draft, Visualization, Methodology. **G. Moutardier:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation, Conceptualization. **W.-J. Chen:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **S.-L. Ng:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **R. Bhagooli:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **S. Ramah:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation. **D. Kaullysing:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **V. Munbodhe:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation. **C. Labonte:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation. **R. Boone:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **S. Bender:** Visualization, Methodology.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Corbari Laure reports article publishing charges and travel were provided by Monaco explorations. Has patent pending to. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr2.2025.105500.

Data availability

All date are open access in MNHN databases.

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