Rhodolith beds (Corallinaceae, Rhodophyta): An important marine ecosystem of the Saya de Malha and Nazareth Banks

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Rhodoliths are unattached marine benthic crustose coralline red algae (Corallinaceae, Rhodophyta) nodules which are the foundation species of the rhodolith beds (Bruno and Bertness, 2001). These coralline red algae are formed by precipitating calcium carbonate ($CaCO_3$) within their cell walls (Foster, 2001). Rhodoliths depend strongly on water motion (currents) to enable their periodic rotation which allows them to be exposed to light on both sides (to photosynthesize) and to remain unburied by sediment (Hinojosa-Arango *et al*., 2009). These rhodolith beds (RBs) represent a key habitat worldwide and form an important ecosystem themselves (Schubert *et al*., 2019), and are associated with other tropical or polar benthic organisms such as sponges, corals, molluscs, seagrass, bryozoans and macroalgae, among others (Grall and Glemarec, 1997; Steller *et al*., 2003; Amado-Filho *et al*., 2012; Foster *et al*., 2013; Vilas-Boas *et al*., 2014; Ordines *et al*., 2015; Riosmena-Rodríguez *et al*., 2017). RBs also form part of the largest recognized macrophyte-dominated benthic communities, consisting of coralline algal reef, seagrass and kelp beds (Amado-Filho *et al*., 2012; Pena *et al*., 2014). They have been mainly reported around islands, capes, on submarine plateaus, seamounts, marine terraces, channels and banks (Basso *et al*., 2017).

While in-depth research on rhodoliths has mainly been concentrated in the Mediterranean, North Atlantic, and Pacific regions (Foster, 2001; Amado-Filho *et al*., 2012; Harvey *et al*., 2017), the only mention of these coralline algae from Saya de Malha (reported as red-pink *Lithothamnium*) was in Vortsepneva's review on previous expeditions carried out at this particular bank (Vortsepneva, 2008). Despite the fact that RB habitats are considered as a hotspot of biodiversity providing an array of ecosystem goods and services, such as fishery resources, soil conditioning, carbon trapping and climate regulation, among others (Jacquotte, 1962; Hall-Spencer *et al*., 2003; Cavalcanti *et al*., 2014; Basso *et al*., 2016; Krayesky-Self *et al*., 2017; Coletti *et al*., 2017; Schubert *et al*., 2020), not many studies have been conducted to properly understand their overall contribution to ocean ecology.

The Indian Ocean EAF-Nansen research expedition survey cruise in May 2018 helped to gather new information on RBs from the Saya de Malha and Nazareth Banks. With the help of a Remotely Operated Vehicle (ROV), RBs were mainly observed at eight locations within the Saya de Malha Bank namely SS4, SS34, SS36, SS37, SS38, SS39, SS40 and SS42 at depths ranging from 20-80 m and at three locations within the Nazareth Bank namely SS49, SS50 and SS52 at depths ranging from 53-126 m (Fig. 1). Rhodolith ball sizes ranged from approximately 0.5 to 4 cm. RBs have been reported to mostly occur at depths ranging between 30-75 m (Foster *et al*., 2013), but have also been recorded from as deep as 150 m (Aguilar *et al*., 2009) and forming beds of up to 10 m in thickness (Harvey *et al*., 2017). Although rhodoliths are most likely to occur in photic to mesophotic areas, they

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are acclimated to survive in restricted light ranges in deeper waters as well (Figueiredo *et al*., 2012). RBs are considered as a rich and important habitat harbouring high diversity and density of echinoderms and many other associated species (Steller *et al*., 2003; Gondim *et al*., 2014; Moura *et al*., 2021).

The study showed that RBs found on both banks provided a benthic substrate to sustain other organisms such as echinoderms, asteroids, sea cucumbers, sponges, corals, seagrass, fish, and seaweed (Fig. 2B-D, F-H and Fig. 3C-H). Studies in the Gulf of California demonstrated that sea urchins help rhodoliths by turning them, in a process called bioturbation, during feeding and movement, which contributes to bed integrity (James, 2000). RBs provide a safe and important ground for juvenile echinoderms (Riosmena-Rodriguez and Medina-Lopez, 2010). The RBs at location SS42 (Fig. 2B) on the Saya de Malha Bank and location SS50 (Fig. 3D) at the Nazareth Bank may be considered as a niche for echinoderm assemblages, while the other locations show the importance of RBs for the sustainability of many other organisms at the banks.

In addition to their structural complexity and their importance to continental shelf biodiversity, RBs are considered as important carbonate factories (Amado-Filho *et al*., 2012). This is similar to coral reefs which have been reported to be a major coastal $CaCO_3$ manufacturers (Spalding and Grenfell, 1997; Vecsei, 2000, 2004a, b) through evidence built on their global distribution (Spalding and Grenfell, 1997; Vecsei, 2000, 2004a, b) estimations of their mineralization rates (Kinsey and Hopley, 1991; Milliman, 1993; Milliman and Droxler, 1996; Kleypas, 1997). Similarly, RBs contribute considerably to continental shelf ecosystem $CaCO_3$ cycles owing to their high community $CaCO_3$ production and dissolution rates (Foster, 2001; Martin *et al*., 2007; Martin and Gattuso, 2009). Ample evidence indicates that the capture and

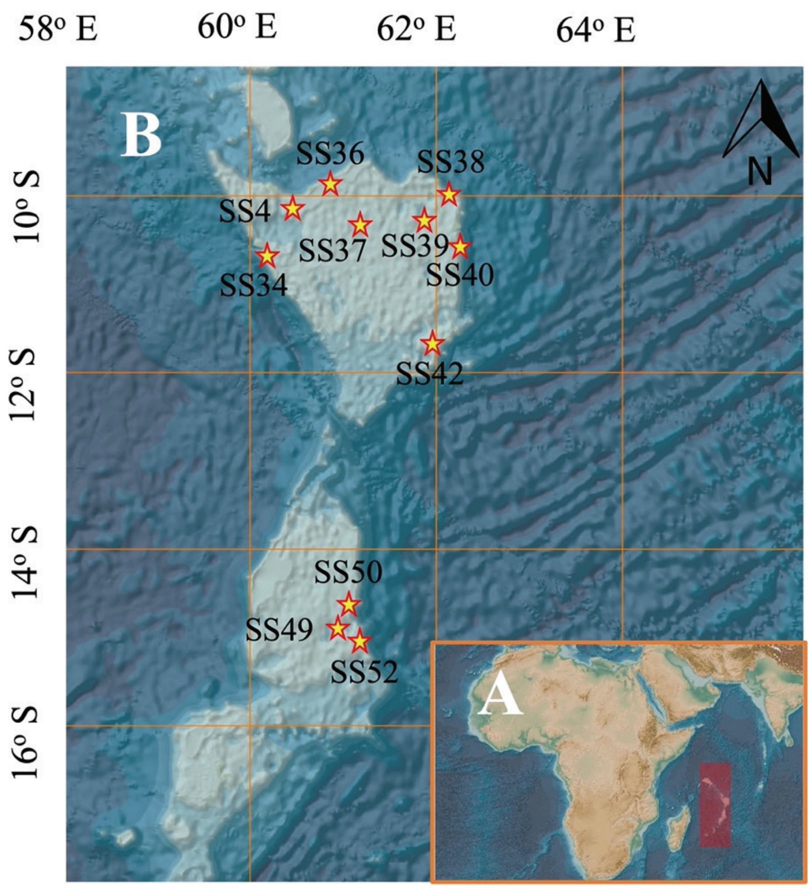

Figure 1. Map showing the locations of the rhodolith beds. A: Western Indian Ocean map showing the location of Saya de Malha and Nazareth Banks in the red-shaded box. B: Map showing the 11 locations (indicated by yellow and red border stars) where rhodolith beds were observed using the ROV. Map prepared using the GEBCO Bathymetry Grid layer data 2020.

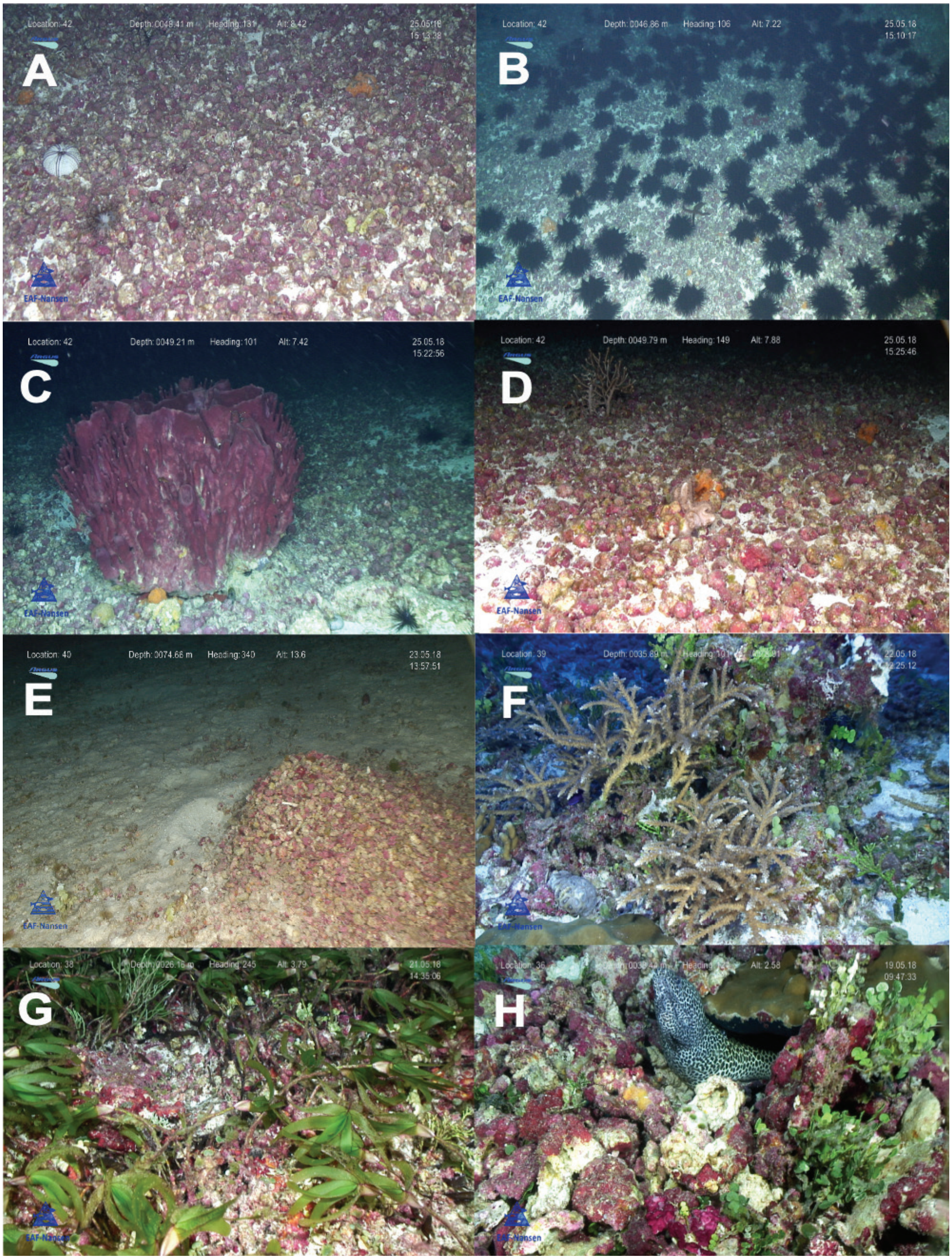

Figure 2. Rhodolith beds (RBs) at Saya de Malha Bank. A. Location 42 at a depth of 48.41 m - Sponge and echinoderms on RB; B. Location 42 at a depth of 46.86 m – Group of echinoderms on RB.; C. Location 42 at a depth of 49.21 m – Demospongia growing on RB; D. Location 42 at depth of 49.79 m – Octocoralia, soft corals and sponge growing on RB; E. Location 40 at a depth of 74.66 m – Rhodoliths clustered forming a mount; F. Location 39 at a depth of 35.89 m - *Acropora* sp. and *Porites* sp. growing on rhodoliths; G. Location 38 at a depth of 26.16 m – Seagrass *Thalassodendron ciliatum* growing on RB; H. Location 36 at a depth of 38.44 m - Moray eel (*Gymnothorax* sp.) using rhodoliths as habitat. Photos were taken using the Argus Remotely Operated Vehicle (ROV) during the expedition.

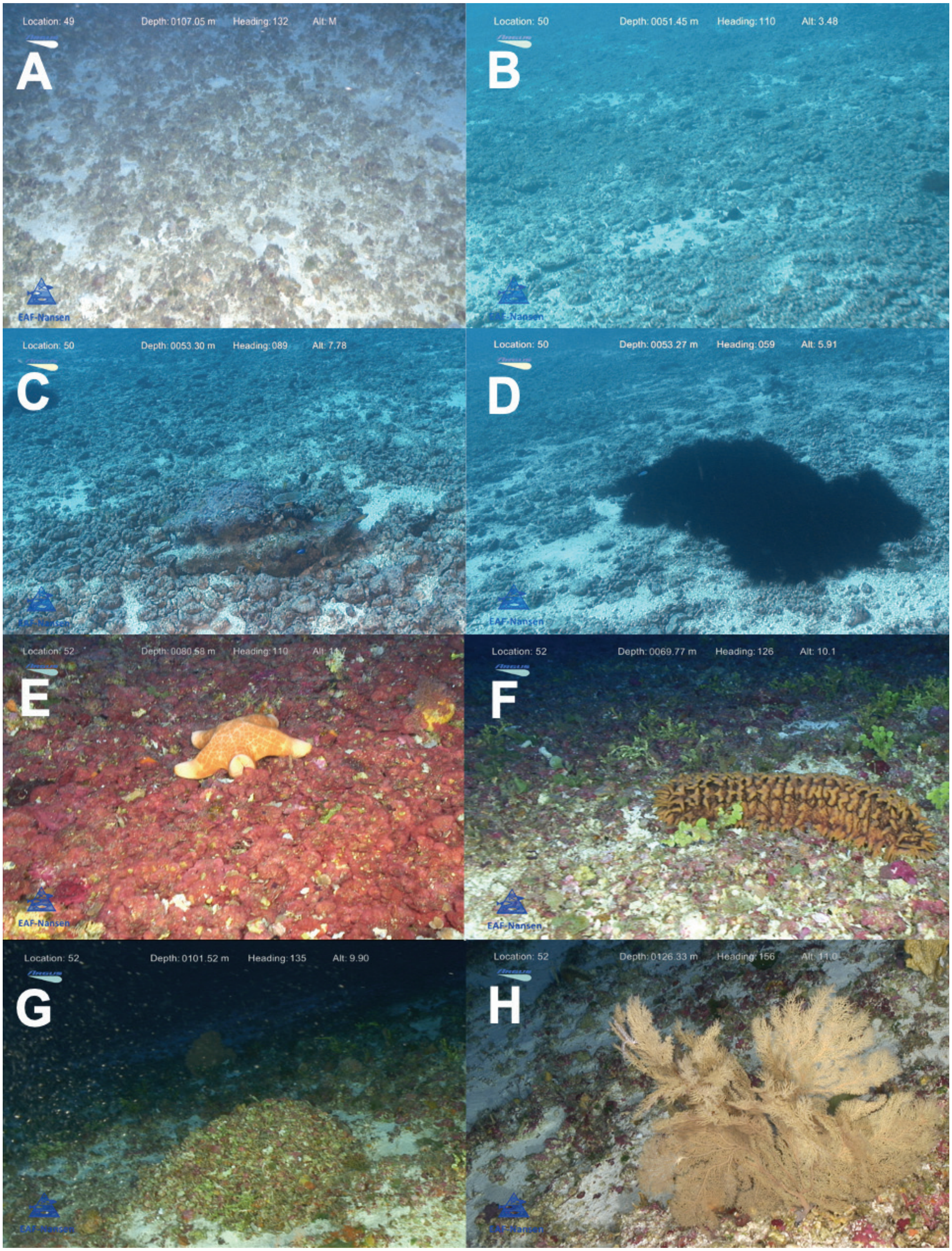

Figure 3. Rhodolith beds (RBs) at Nazareth Bank. A. Location 49 at a depth of 107.05 m – RB overview; B. Location 50 at a depth of 51.45 m – RB overview; C. Location 50 at a depth of 53.30 m – Coral (Tabular *Acropora* sp.) growing on RB; D. Location 50 at a depth of 53.27 m – Group of echinoderms on RB; E. Location 52 at a depth of 80.58 m – cushion seastar on RB; F. Location 52 at a depth of 69.77 m – Sea cucumber (*Thelenota ananas*) on RB; G. Location 52 at a depth of 101.52 m – Rhodoliths clustered forming a mount with coralline algae (*Halimeda* sp.) colonising the mount; H. Location 52 at a depth of 126.33 m – Gorgonian sea fan growing on RB. Photos were taken using the Argus Remotely Operated Vehicle (ROV) during the expedition.

storage of atmospheric carbon dioxide by RBs over time are comparable, both in efficiency and area, to those of coral reefs (Amado-Filho *et al*., 2012). Studies have shown that the RB on the Abrolhos Shelf (approximate area of 200,000 km^2) was able to produce a total of 0.025 Gt yr^{-1} (1.060.7 kg m^{-2} yr^{-1}) of $CaCO_3$ (Amado-Filho *et al*., 2012), almost equivalent to the yearly total $CaCO_3$ produced by Caribbean coral reefs (0.04-0.08 Gt yr^{-1} or 1.3-2.7 kg m^{-2} yr^{-1}) (Vecsei, 2004a, b) and the estimated mean calcification rate of 1.5 kg m^{-2} yr^{-1} produced by global coral reefs (Andersson *et al*., 2005). RBs are however at risk from disturbances such as climate change, global warming, and associated ocean acidification, as well as from other disturbances with anthropogenic sources such as sedimentation, and fishery trawling (Foster *et al*., 2013; Harvey *et al*., 2017; Schubert *et al*., 2019). Rhodoliths grow only a few millimeters per year (Foster *et al*., 2013) and these disturbances affect their recruitment, development, health, and survival rate which may lead increased competition from space competitors such as fleshy algae (Martin and Hall-Spencer, 2017; Carvalho *et al*., 2020) in shallower areas.

This first documentation of RBs from the Saya de Malha and Nazareth Banks provides the basis for future research and conservation work on RBs in this part of the world. RBs at the two banks may be considered as marine biodiversity hotspots that function as seedbanks, habitat, nursery grounds, refugia and areas of high carbonate production. The vast number of organisms that RBs host, including sponges and other macroalgae, may also provide new opportunities for bioprospecting in the future. However, there is a need for directed research to fully understand the physical integrity, ecological balance and community structure of RBs over time in order to better conserve and protect these important, yet poorly studied and understood ecosystems on the Saya de Malha and Nazareth Banks.

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