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Discussion

Levelling-up rhodolith-bed science to address global-scale conservation challenges



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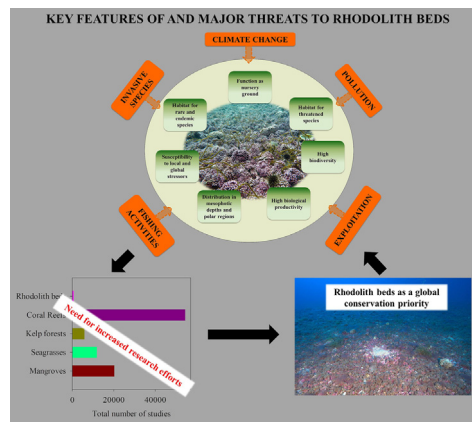
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HIGHLIGHTS

- Rhodolith beds (RBs) are globally extensive coastal habitats.
- We identify key features of RBs to qualify them as a global conservation priority.
- Research efforts on RBs lag far behind other coastal habitats.
- The lack of information hampers conservation of RBs, which is non-existent in most regions.
- This study calls for levelling-up research efforts to reach RB conservation needs.

GRAPHICAL ABSTRACT



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ABSTRACT

Global marine conservation remains fractured by an imbalance in research efforts and policy actions, limiting progression towards sustainability. Rhodolith beds represent a prime example, as they have ecological importance on a global scale, provide a wealth of ecosystem functions and services, including biodiversity provision and potential climate change mitigation, but remain disproportionately understudied, compared to other coastal ecosystems (tropical coral reefs, kelp forests, mangroves, seagrasses). Although rhodolith beds have gained some recognition, as important and sensitive habitats at national/regional levels during the last decade, there is still a notable lack of information and, consequently, specific conservation efforts. We argue that the lack of information about these habitats, and the significant ecosystem services they provide, is hindering the development of effective conservation measures and limiting wider marine conservation success. This is becoming a pressing issue, considering the multiple severe pressures and threats these habitats are exposed to (e.g., pollution, fishing activities, climate change), which may lead to an erosion of their ecological function and ecosystem services. By synthesizing the current knowledge, we provide arguments to highlight the importance and urgency of levelling-up research efforts focused on rhodolith beds, combating rhodolith bed degradation and avoiding the loss of associated biodiversity, thus ensuring the sustainability of future conservation programs.

1. Introduction

Filling essential knowledge gaps is a persistent scientific challenge for accurate species and habitat assessments and, subsequently, to improve regional and global conservation efforts (Broderick, 2015; IUCN, 2022). In this regard, deficits and biases of information hamper our understanding of the importance of specific habitats, their distribution, the associated species groups, and their ecological status, which in turn limits our ability in convincing society of the need for conservation actions and of securing the necessary funding. This matter is especially important in view of the continuously increasing threat of human activities to marine ecosystems, particularly those occurring in coastal and shelf waters. Coastal habitats, which include seagrass meadows, coral reefs, kelp forests and rhodolith beds, provide ecosystem functions and services of paramount importance at a global scale (Costanza et al., 1997; Macreadie et al., 2021). However, research efforts are unbalanced across these habitats, which are generally interconnected, resulting in major knowledge gaps that hinder conservation success.

Rhodolith beds (also known as maerl beds; Fig. 1) – reef-like habitats composed of free-living calcareous red algae and recognized global biodiversity hotspots and carbonate factories – are a prime example (Riosmena-Rodríguez et al., 2017). Based on the current state of the art regarding these habitats, we provide here multiple lines of evidence to support the importance and urgency for an increase in rhodolith-bed science towards equitable research efforts across coastal habitats. This will provide the empirical knowledge base required for a truly holistic conservation approach at local, regional and global scales.

Rhodolith beds are found from tropical to polar regions, covering an estimated area of 4.12 million km² worldwide (Fragkopoulou et al., 2021),

~20% larger than the estimated maximum global area of tropical coral reefs and 2.5–30 times larger than other well-studied coastal habitats, such as kelp forests, seagrass meadows and mangroves (Fig. 2A).

Attempts to raise awareness on the importance of rhodolith beds over the last two decades (e.g., Barbera et al., 2003; Hall-Spencer et al., 2008; Nelson, 2009; Nelson et al., 2012; Riosmena-Rodríguez et al., 2017) have led to an increase in research efforts (4-fold over the last 15 years; Rendina et al., 2022), though rhodolith-bed science lags still far behind other coastal habitats of comparable importance (Fig. 2B, C). As a result, many uncertainties regarding these habitats and their ecosystem functions and services persist.

Currently, one of the greatest challenges we face for rhodolith-bed conservation is the lack of accurate information on their distribution, extent and health status. Whereas their broad global distribution is widely acknowledged (Foster, 2001), recent global distributional models (Fragkopoulou et al., 2021; Rebelo et al., 2021) suggest that they may cover an even larger area than previously anticipated. As attention towards and recognition of these habitats has increased, so has the number of previously unknown rhodolith beds around the world. During the last five years, new discoveries have been reported for the Mediterranean (e.g., Bracchi et al., 2019, 2022; Rendina et al., 2020; Del Río et al., 2022), the Macaronesia and São Tomé and Príncipe region (Rebelo et al., 2018, 2022; Otero-Ferrer et al., 2020a, 2020b; Ribeiro and Neves, 2020; Neves et al., 2021; Cosme de Esteban et al., 2022), South Africa (Adams et al., 2020), the Western Indian Ocean (Ramah et al., 2021), Australia (Harvey et al., 2016), India (Sreeraj et al., 2018), Korea (Jeong et al., 2020, 2022), Brazil (Pereira-Filho et al., 2019; Negrão et al., 2021), and Alaska (Ward et al., 2021). Furthermore, the growing number of new, cryptic and endemic taxa being discovered in rhodolith beds indicates that much of

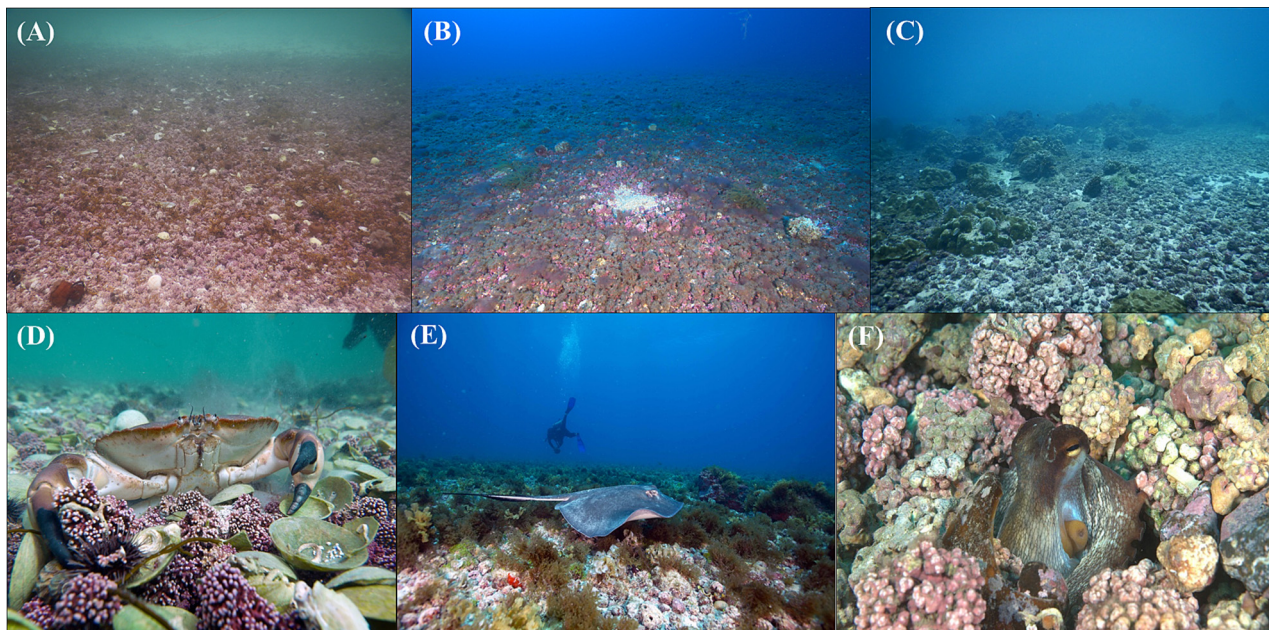


Fig. 1. Free-living coralline algae (rhodoliths, ~3–10 cm in diameter), covering extensive areas of the seafloor (A–C) and providing habitat for a high diversity of organisms (D–F). (A) Vega Island (Norway), (B) Madeira Island (Portugal), (C) Cocos Island (Costa Rica), (D) crab (*Cancer pagurus*) on an Arctic rhodolith bed in Norway, (E) sting ray (*Hypanus* sp.) on a tropical rhodolith bed in the Fernando de Noronha Archipelago (Brazil), and (F) octopus (*Octopus vulgaris*) on a warm-temperate rhodolith bed at Madeira Island (Portugal) (Photos by E. Rinde, P. Neves, C. Fernández-García, J. Hall-Spencer, Z. Matheus, and P. Neves, respectively).

their biodiversity is still unknown (e.g., Santos et al., 2016; Coutinho et al., 2021; Méndez Trejo et al., 2021; Senna et al., 2021; Sissini et al., 2022). Recent studies suggest that rhodolith beds may also act as seedbanks for recovering ecosystems, and as refugia for ecosystem resilience following acute (Fredericq et al., 2019) or chronic (Voerman et al., 2022a) environmental stress. Similarly, the significance of these habitats in sustaining fisheries is greatly underrated (Moura et al., 2021), and rhodolith beds may also be far more important in the global carbon budget than currently recognized (Amado-Filho et al., 2012a; Smith and Mackenzie, 2015; van der Heijden and Kamenos, 2015; Mao et al., 2020). The latter is a particularly pertinent

issue in the current era, as major efforts are underway to find nature-based solutions to offset anthropogenic carbon emissions and mitigate climate change (Hilmi et al., 2021).

Many features of rhodolith beds indicate their significant ecological and economic roles at the regional and global scale, but major knowledge gaps prevent efficient conservation and management efforts. In lacking the academic and societal charisma of other habitats (e.g., coral reefs), rhodolith-bed science has not developed at the same pace. We argue that it is essential to urgently overcome this, if we are to close the knowledge gaps and enable effective pan-habitat conservation measures to mitigate coastal ecosystem degradation.

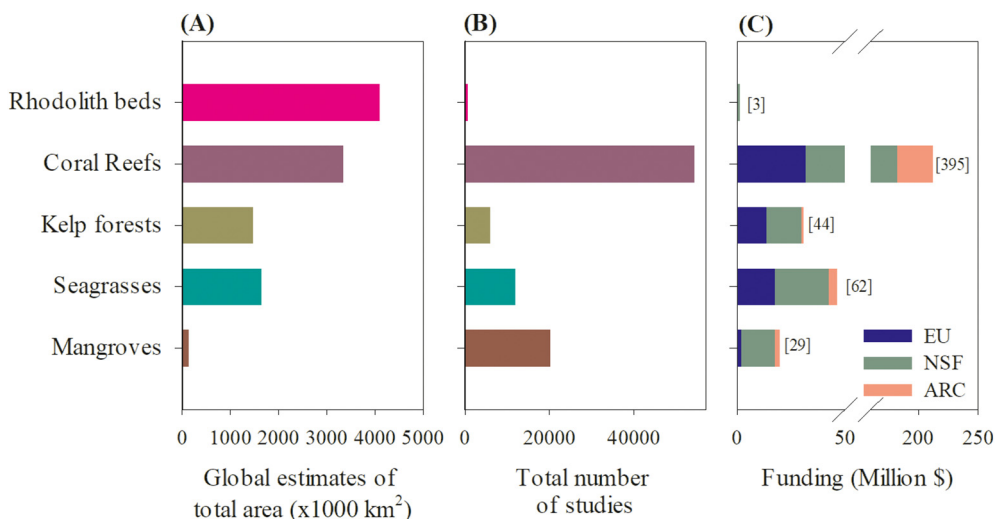


Fig. 2. Comparison of estimated total area, number of studies, and funding of key coastal habitats. (A) Global estimated total area, based on habitat distributional models (rhodolith beds - Fragkopoulou et al., 2021; tropical coral reefs - Kleypas, 1997; kelp forests - Jayathilake and Costello, 2020; seagrasses - Jayathilake and Costello, 2018; mangroves - Giri et al., 2011), (B) total number of studies (papers in the Web of Science database that included each habitat as a ‘topic’) published over the last three decades, and (C) total amount of funding and number of funded projects (in brackets) by three relevant international funding agencies, the European Union (EU, <https://cordis.europa.eu>), the National Science Foundation (NSF, <https://nsf.gov>), and the Australian Research Council (ARC, <https://dataportal.arc.gov.au>), between 2017 and 2022.

2. Rhodolith beds – Critical habitats for ocean conservation

Like tropical coral reefs, seagrass meadows and mangrove forests, rhodolith beds are considered as Small Natural Features (SNFs; Lundquist et al., 2017), defined as: ‘a site with ecological importance that is disproportionate to its size; sometimes because it provides resources that limit key populations or processes that influence a much larger area; sometimes because it supports unusual diversity, abundance, or productivity. The recognition and management of SNFs as distinct entities is primarily a means to facilitate pragmatic conservation of their associated biodiversity and ecosystem services.’ (Hunter Jr, 2017). However, unlike other marine SNFs, the available information regarding these habitats (e.g., their distribution, extension and ecological role) is still scarce (Nelson, 2009; Lundquist et al., 2017). Previously, Barbera et al. (2003) provided strong evidence that the biodiversity provision of rhodolith beds was under-estimated. Here, we extend that to the global context, arguing that we have sufficient evidence to classify rhodolith beds as ‘Ecologically or Biologically Significant Marine Areas’ (EBSAs), based on the seven criteria developed and adopted by the Convention on Biological Diversity (CBD, 2009) to identify priority areas for conservation (Fig. 3).

2.1. Uniqueness or rarity

This EBSA criterion applies to areas that contain (a) unique, rare or endemic species, populations or communities and/or (b) unique, rare or distinct habitats or ecosystems and/or (c) unique or unusual geomorphological or oceanographic features. In this context, rhodolith beds are recognized as a unique habitat that harbors many endemic species. For example, a recent global analysis revealed several rhodolith species that are endemic to a single biogeographical province (Rebello et al., 2021). Furthermore, many endemic or rare species are associated with these habitats. Examples from Brazilian rhodolith beds include the endemic kelp species *Laminaria abyssalis* (Amado-Filho et al., 2007), the rarely recorded polychaete

Nuchalosyllis cf. maiteae (Santos et al., 2016), and several endemic coral (Cavalcanti et al., 2013; Pereira-Filho et al., 2015, 2019; Amado-Filho et al., 2016; Negrão et al., 2021) and fish species (Moura et al., 2021). In the Mediterranean, the endemic deep-water kelp *Laminaria rodriguezii* (Barbera et al., 2003) and several species of endemic sponges (Longo et al., 2020) can be found on rhodolith beds, while in the NE-Atlantic the rare kelp *L. ochroleuca* and several rare rhodolith-associated seaweeds have been recorded (Peña et al., 2014; Braga-Henriques et al., 2022; Helias and Burel, 2023). At Cocos Island, Costa Rica, a new and endemic octocoral species, *Rhodolitica oculata*, has been found in association with rhodoliths (Breedy et al., 2021). In New Zealand and the Gulf of California, an endemic bryozoan species (*Celleporaria agglutinans*; MacDiarmid et al., 2012), rare sponge and echinoderm species (Nelson et al., 2012), and rare chiton species (Clark, 2000) have been recorded in rhodolith beds.

2.2. Special importance for life-history stages of species and naturalness

This EBSA criterion applies to areas that are needed for a population to survive and thrive. Rhodolith beds are important nursery grounds, as they increase habitat complexity and heterogeneity (Kamenos et al., 2003; Steller et al., 2003; Otero-Ferrer et al., 2019), resulting in higher food availability and safe refugia for recruitment and early developmental stages against predators (Kamenos et al., 2004a). Studies in northern Europe, the Gulf of California and Brazil showed that rhodolith beds function as nurseries for juvenile scallops, marine invertebrates and fishes (Kamenos et al., 2004b, 2004c; Steller and Cáceres-Martínez, 2009; Riosmena-Rodríguez and Medina-López, 2010; Costa et al., 2020; Navarro-Mayoral et al., 2020; Sánchez-Latorre et al., 2020). In the Gulf of California, 60% of all examined rhodolith-associated organisms were juveniles (Riosmena-Rodríguez and Medina-López, 2010). Rhodoliths also play a key role as seedbanks and temporary reservoirs of life history stages of ecologically important micro- and macroalgae (Fredericq et al., 2019).

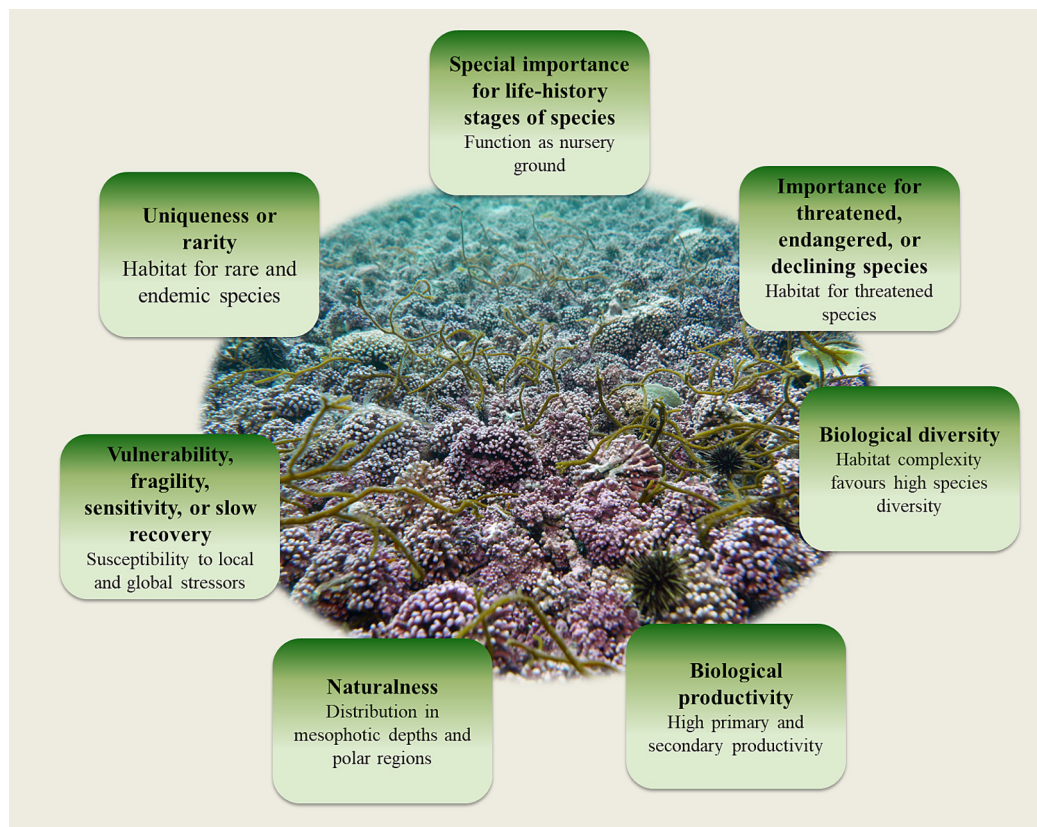


Fig. 3. Key ecosystem features of rhodolith beds and their relevance according to the ‘Ecologically or Biologically Significant Marine Areas’ criteria (in bold), used to identify key areas for biodiversity conservation (CBD, 2009) (Photo provided by J. Hall-Spencer).

The EBSA criterion defines an area with a comparatively higher degree of naturalness, as a result of the lack, or low level of, human-induced disturbance or degradation. The low light tolerance of rhodoliths allows them to thrive in the mesophotic zone (e.g., Villas-Boas et al., 2014; Bélanger and Gagnon, 2021; Voerman et al., 2022b). In these deeper waters, rhodolith beds acquire inherent protection against the chronic and acute stressors of the shallow-water coastal zone (e.g., marine heatwaves, land pollution, clam dredging). Moreover, rhodolith beds are found in polar regions (Teichert et al., 2012; Peña et al., 2021a), and around isolated oceanic archipelagos (Fragkopoulou et al., 2021), far away from the most intensive human pressures. Even in shallow waters, rhodolith beds can retain a high degree of naturalness, where conservation protection has been rigorously implemented (Barbera et al., 2003).

2.3. Importance for threatened, endangered, or declining species and/or habitats

This EBSA criterion applies to an area containing habitat for the survival and recovery of endangered, threatened, declining species, or areas with significant assemblages of such species. Rhodolith beds harbour a large biodiversity, including species categorized as threatened or endangered at the national and international level. For example, a number of fish species, categorized as vulnerable and endangered (ICMBio, 2022; IUCN, 2022), are found in Brazilian rhodolith beds (e.g., *Hypanus marianae*, *Scarus trispinosus*, *Epinephelus morio*; Moura et al., 2021) and in shallow coastal beds of Principe Island (e.g., *Balistes truncatus*, *Ginglymostoma cirratum*; Otero-Ferrer et al., 2020b). Furthermore, the Brazilian red list of threatened species (ICMBio, 2022) includes several species reported in association with rhodolith beds, such as the echinoderms *Linckia guildingii* and *Lytechinus variegatus* (Gondim et al., 2014; Guabiroba et al., 2022).

2.4. Biological diversity

This EBSA criterion applies to areas that contain comparatively higher diversity of ecosystems, habitats, communities, or species, or have higher genetic diversity. Rhodolith beds, like coral reefs, are biodiversity hotspots because they create living habitats with high structural heterogeneity (Kamenos et al., 2003; Otero-Ferrer et al., 2019), which is reflected in a higher associated biodiversity than common adjacent substrata (Steller et al., 2003; Teichert, 2014; Neves and Costa, 2022). For instance, Nelson et al. (2014) found 103 macroalgal species associated with northern New Zealand rhodolith beds, equivalent to ca. 30% of the local macroalgal flora. Similarly, Peña et al. (2014) recorded 350 macroalgal species on rhodolith beds in the NE Atlantic, which corresponds to 30% of the total seaweed diversity found in this region. For the worldwide largest rhodolith bed in Abrolhos, Brazil, 150 macroalgal species and 127 fish species have been reported (Brasileiro et al., 2016; Simon et al., 2016; Moura et al., 2021). Likewise, a high variety of rhodolith-bed associated infauna and epifauna (e.g., sponges, nematodes, polychaetes, crustaceans, molluscs, and echinoderms) has been found wherever in the world studies have taken place (Hall-Spencer, 1998; Steller et al., 2003; Sciberras et al., 2009; Neill et al., 2015; Bassi et al., 2020; Navarro-Mayoral et al., 2020; Sánchez-Latorre et al., 2020; Veras et al., 2020; Stelzer et al., 2021; Voerman et al., 2022a). Furthermore, Méndez Trejo et al. (2021) found species- and location-specific differences in the cryptofauna associated with two different rhodolith-forming species. Last, but not least, in contrast to other coastal habitats, such as seagrass meadows and kelp forests, rhodolith beds are usually formed by several different species of coralline algae, belonging to different families and even orders. For example, in Brazil, rhodolith communities can be composed of ten or more species (Costa et al., 2014; Holz et al., 2020).

2.5. Biological productivity

This EBSA criterion defines areas containing species, populations, or communities with comparatively higher natural biological productivity. Indeed, compared to sand or muddy seabeds, the habitat formed by rhodolith beds has higher primary and secondary productivity. Primary producers,

including rhodoliths themselves but also associated macro- and microalgae, contribute substantially to habitat primary productivity and biogenic carbonate production (Martin et al., 2007; Amado-Filho et al., 2012a; Schubert et al., 2019; Teed et al., 2020; Qui-Minet et al., 2022). Moreover, provision of complex habitat structures increases the faunal biomass in rhodolith beds and, consequently, their associated secondary productivity (Bordehore et al., 2003; Steller et al., 2003; Gabara et al., 2018; Moura et al., 2021; Neto et al., 2021; Stelzer et al., 2021).

2.6. Vulnerability, fragility, sensitivity, or slow recovery

This EBSA criterion defines areas that contain a relatively high proportion of sensitive habitats, biotopes or species that are functionally fragile (i.e., highly susceptible to degradation or depletion by human activity or by natural events), or with slow recovery.

Rhodolith beds are highly vulnerable to global (e.g., ocean warming and acidification) and local stressors (e.g., nutrient or organic pollution, mining exploitation and fishing activities). In particular, ocean acidification is likely to result in a decline of rhodolith-associated carbonate production and the loss of dead rhodoliths, due to increased carbonate dissolution (Basso, 2012; Martin and Hall-Spencer, 2017; Burdett et al., 2018). Moreover, rhodoliths are fragile and easily damaged by commercial fishing activities, using bottom trawling, hydraulic gear and scallop dredges. This leads to significant impacts due to algal breakage and removal (as by-catch), resulting in decreased habitat complexity, rhodolith burial, and subsequent death (Hall-Spencer and Moore, 2000; Kamenos et al., 2003; Bernard et al., 2019). Rhodolith beds are also vulnerable to exploitation activities (mining, gas- and oil-exploitation) due to elevated risk of sedimentation and habitat destruction (Villas-Boas et al., 2014; Figueiredo et al., 2015; Osterloff et al., 2016) and exhibit a high sensitivity to fish and mussel aquaculture (Hall-Spencer et al., 2006; Sanz-Lázaro et al., 2011; Aguado-Giménez and Ruiz-Fernández, 2012; Legrand et al., 2021).

Altogether, when considering the generally slow growth rates of rhodoliths (0.2–1.5 mm per year; Blake and Maggs, 2003; Bosence and Wilson, 2003), the recovery time from those impacts can span centuries to millennia (Hall-Spencer and Moore, 2000). Rhodolith beds have thus been classified as a non-renewable resource (Barbera et al., 2003).

3. Ecosystem services

As outlined above, rhodolith beds are essential habitats for associated biodiversity, which includes a high diversity of commercially important species and their early developmental stages (e.g., fish and scallop species; Hall-Spencer et al., 2006; Steller et al., 2003; Kamenos et al., 2004a, 2004b, Costa et al., 2020, Moura et al., 2021). Rhodolith beds tend to support larger abundances and richness of epifaunal organisms relative to adjacent bottoms (Riosmena-Rodríguez et al., 2017; Otero-Ferrer et al., 2019). Rhodolith beds are, furthermore, important for ecological and genetic connectivity with other habitats (e.g., seagrass beds, mangroves, coral reefs), by ensuring the survival of juvenile fish, providing corridors for reef fish migration towards spawning grounds and increasing the abundance of reef species (Costa et al., 2020; Moura et al., 2021; Carneiro et al., 2022). Hence, they are vital habitats for sustainable fisheries. Their economic importance, in terms of *Provisioning Services*, is also associated with the direct exploitation of rhodoliths and their associated species for several industrial sectors, such as agriculture (fertilizers, soil pH control and limestone production), cosmeceuticals (toothpaste, bath salts), food (food supplement), and biomedicine (bone implants, antimicrobial agents, antioxidants) (Blunden et al., 1975; Dias, 2000; Amado-Filho and Pereira-Filho, 2012). For example, the extract of the rhodolith-forming species *Lithothamnion calcareum* has been shown to be effective in suppressing proliferation of human colon cancer cell lines in vitro (Aslam et al., 2009) and, hence, could be used as a dietary supplement for chemoprevention against colon polyp formation (Aslam et al., 2010). Additionally, several studies, using geniculate coralline algae, have shown their extensive biological activity, including antibiofilm (Salem et al., 2020), anticancer (Harada and Kamei,

1997; Gheda et al., 2018), antimalarial (Stout et al., 2010), antioxidant (Matloub et al., 2015), antiviral (Matloub et al., 2015) and larvicidal activities (Jagadeesan et al., 2015).

Rhodolith beds also provide *Cultural Services*, as stranded rhodoliths can make up a large proportion of beach deposits (Harvey et al., 2018; Rebelo et al., 2022). Well-known examples are the so-called “Popcorn Beaches” in the Canary Islands, where some beaches can be composed of up to 5000 stranded rhodoliths per square meter (Rebelo et al., 2022).

Certain key features of rhodolith beds, such as their large primary and secondary productivity (*Supporting Services*), suggest that they have the potential to contribute significantly to the global carbon cycle (a *Regulation Service*), a topic that is currently gaining attention, as a nature-based solution (Blue Carbon ecosystems) to mitigate anthropogenic CO₂ emissions. Rhodolith beds may play a globally significant role in the carbon cycle that is poorly accounted for in Blue Carbon policy (see also Laffoley, 2020), despite some significant features that are directly related to Blue Carbon dynamics:

- (1) Considerable amounts of particulate organic carbon accumulate between and underneath rhodolith nodules through settlement (Neto et al., 2021; Stelzer et al., 2021), leading to storage of organic carbon over millennia (Mao et al., 2020);
- (2) Direction and magnitude of rhodolith-bed carbon fluxes (carbon ‘sink-source’ duality), which are associated to community productivity (Martin et al., 2007; Qui-Minet et al., 2022);
- (3) High carbonate production rates and build-up of large carbonate stocks (Amado-Filho et al., 2012a; van der Heijden and Kamenos, 2015; Teed et al., 2020). Individual-community longevity (centuries to millennia) means that this inorganic carbon is locked away as both living and dead biogenic carbonate deposits (e.g., estimated 200 Gt CaCO₃ on the Brazilian coastal shelves; Kempf, 1970);
- (4) Slow dissolution of non-living carbonate deposits due to microbial respiration, a process that increases alkalinity and captures CO₂, and which will accelerate in the future due to ocean acidification (Kamenos et al., 2013; Burdett et al., 2018).

4. Under threat – Impacts and vulnerability of rhodolith beds

Rhodolith beds face a series of anthropogenic pressures and threats that fall into four categories (Halpern et al., 2015): land-based stressors (nutrient pollution, organic/inorganic pollution), ocean-based stressors (ocean-

based pollution, by offshore mariculture, mining, gas and oil exploitation, and invasive species), fishing (destructive fishing activities), and climate change (Fig. 4).

Land-based pollution includes: untreated sewage, agricultural run-off, oils and heavy metals from industry, and sediment washed from coastal developments and logging. In this regard, evidence has shown that (i) rhodolith beds are susceptible to coastal eutrophication, as increased nutrient levels negatively affect rhodolith performance (Schubert et al., 2019; Bélanger and Gagnon, 2020; Koerich et al., 2021), and (ii) they are threatened by large-scale catastrophic events, such as the 2015’s Doce River mining dam collapse in Southeast Brazil (Francini-Filho et al., 2019; Magris et al., 2019; Holz et al., 2020), which dramatically increased metal-contaminated coastal pollution and suspended sediment loads (Hatje et al., 2017).

Ocean-based stressors include the spread of invasive species, offshore mariculture, and ocean-based pollution. The available evidence shows records of the spread and impact of non-native macroalgae and gastropods in NE Atlantic beds (Grall and Hall-Spencer, 2003; Peña et al., 2014). For example, the invasive gastropod *Crepidula fornicata*, introduced in Brittany, France, has been shown to overgrow living rhodoliths, leading to smothering and ultimately death (Grall and Hall-Spencer, 2003). Similar negative impacts have been recorded, caused by the invasive filamentous red algae *Womersleyella setacea* and *Acrothamnion preisii* in the Mediterranean (Ferrer et al., 1994; Sciberras and Schembri, 2007). Furthermore, negative impacts of fish and mussel farming on rhodolith beds have been widely reported (e.g., Barbera et al., 2003; Hall-Spencer et al., 2006; Peña and Bárbara, 2008; Sanz-Lázaro et al., 2011; Aguado-Giménez and Ruiz-Fernández, 2012; Legrand et al., 2021). Beds below these mariculture installations are exposed to increased organic enrichment (e.g., fish faeces, uneaten food) and fine sediment load, leading to increased biofouling and reduced performance of the rhodoliths and their burial, respectively, which ultimately leads to death.

Extractive industries, particularly offshore oil and gas exploitation and the direct mining of rhodoliths, cause significant impacts to rhodolith beds, through the discharges of drill cuttings, sediment dislodgement and direct habitat destruction (Nilssen et al., 2015; Reynier et al., 2015). The harvest of rhodoliths has serious consequences for the long-term health of the beds, as rhodoliths have very slow growth rates. The extraction leads not only to the loss of habitat complexity and associated biodiversity, but causes also physical disturbances that promote massive sediment

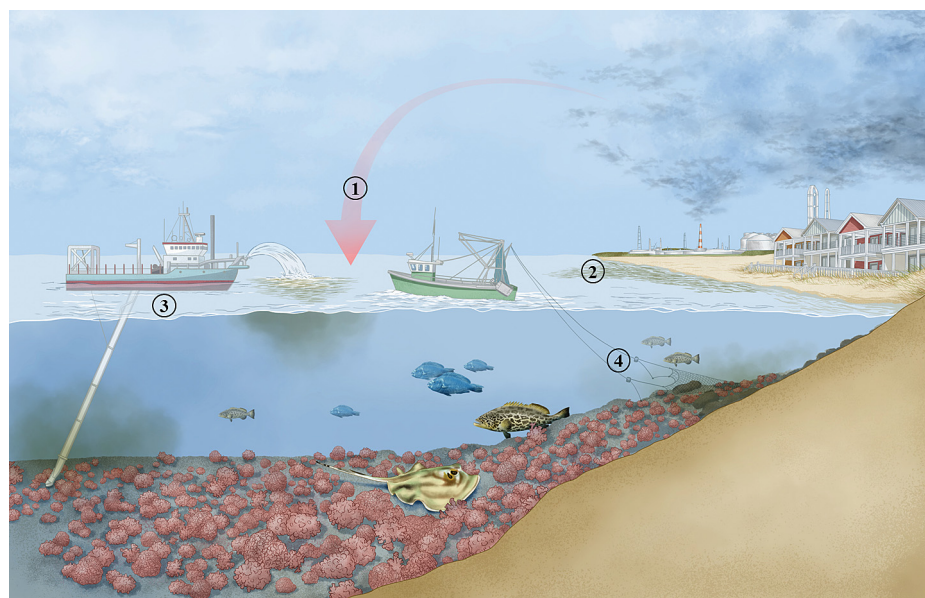


Fig. 4. Schematic illustration of the threats to rhodolith-bed habitats. (1) Global-change related stressors (e.g., ocean warming and acidification), (2) coastal pollution, (3) exploitation activities (e.g., mining, oil- and gas exploitation), and (4) destructive fishing activities (e.g., bottom trawling) (Illustration by ©Lúcia Antunes, www.luciaantunes.com).

dislodgement, resulting in burial and subsequent death of rhodoliths in adjacent areas (Villas-Boas et al., 2014; Figueiredo et al., 2015; Osterloff et al., 2016). Undoubtedly, the exploitation of this non-renewable resource represents an everlasting threat, which is exacerbated by the lack of protection of these habitats through efficient conservation measures (Berchez et al., 2022; Paiva et al., 2023). Another threat to rhodolith beds is the pollution associated with accidental oil spills. Examples are the BP Deepwater Horizon oil spill in the NW Gulf of Mexico in April 2010 that drastically affected rhodolith beds associated with deep bank habitats (Fredericq et al., 2014), and the so far most extensive oil spill recorded in tropical oceans that occurred on the Brazilian continental shelf (2019/2020) (Escobar, 2019), threatening marine ecosystems, including coral reefs and rhodolith beds (Magris and Giarrizzo, 2020; Sissini et al., 2020; Soares et al., 2022).

Well-acknowledged are the significant impacts that certain fishing activities can have on rhodolith beds. Mobile bottom-contacting gears, such as beam-trawls and clam-dredges induce profound and long-lasting effects due to habitat destruction and the suspension of large sediment clouds into the water column that smothers rhodoliths (e.g., De Grave and Whitaker, 1999; Hall-Spencer and Moore, 2000; Barbera et al., 2003; Hauton et al., 2003; Kamenos et al., 2003; Cabanellas-Reboredo et al., 2018; Coquereau et al., 2017; Bernard et al., 2019; Farriols et al., 2021). Also, artisanal fisheries, such as small-scale hookah diving fisheries in the Gulf of California, can have severe effects on rhodolith beds (Urrea et al., 2018), as do disturbances caused by boat moorings and anchoring (Tompkins and Steller, 2016; Gabara et al., 2018; Broad et al., 2020; Dolinar et al., 2020). These disturbances can cause crushing, fragmentation and mobilization of rhodoliths at a localized scale, which has been shown to reduce habitat complexity and associated biodiversity (Tompkins and Steller, 2016; Gabara et al., 2018), and can affect rhodolith physiological performance (Dolinar et al., 2020).

On top of all these pressures, rhodolith beds are also threatened by ongoing and predicted climate change, including ocean warming and acidification (Martin and Hall-Spencer, 2017). Many coralline algal taxa are indeed especially vulnerable to these changes (Peña et al., 2021b). Model projections for 2100 suggest up to an 84% decline in suitable area for rhodolith beds in Scotland (Simon-Nutbrown et al., 2020) and a decline of 26–44% of their estimated global area (Fragkopoulou et al., 2021). In this context, experimental evidence shows that rhodoliths, regardless of region or latitude, are highly susceptible to ocean acidification (OA), which reduces their calcification and growth rates (e.g., Jokiel et al., 2008; Büdenbender et al., 2011; Nelson et al., 2012; Noisette et al., 2013; Legrand et al., 2017; Sordo et al., 2018; Qui-Minet et al., 2019) and weakens their structural integrity (Burdett et al., 2012; Ragazzola et al., 2012; Kamenos et al., 2013). It has been shown that this relates to the composition of their skeletons, in form of the most soluble carbonate in seawater (high Mg-calcite), and that the susceptibility to dissolution increases with Mg-substitution in the calcite (Andersson et al., 2008). Brazilian rhodolith species appear to have a higher Mg content, potentially making them even more susceptible to near-future ocean acidification (Carvalho et al., 2022). Moreover, in situ CO₂ enrichment on a rhodolith bed showed that OA will potentially cause a shift from rhodolith-bed net carbonate production to net dissolution (Burdett et al., 2018). In fact, dead rhodolith thalli that can represent a significant proportion of the rhodolith-bed substrate (e.g., 50–85%, Harvey and Bird, 2008; Bracchi and Basso, 2012; Chimienti et al., 2020) have been shown to be particularly vulnerable to OA (>10× increase in CaCO₃ dissolution; Kamenos et al., 2013). This, together with a decreased calcification and growth rate of the living rhodoliths will result in a decrease in habitat complexity and, consequently, in a significant disruption in the provision of associated ecosystem services.

The increase in seawater temperature, gradually (ocean warming), or during heatwave events, appears to induce highly variable responses in rhodoliths (reviewed in Martin and Hall-Spencer, 2017). For example, evidence shows that events of anomalously high temperatures (i.e., marine heatwaves) induce significant negative effects on primary and carbonate production in subtropical and temperate rhodoliths (Schubert et al., 2019, 2021), while temperate species express a seasonal variation in their

responses to increased seawater temperature (Legrand et al., 2017; Qui-Minet et al., 2019). In contrast, subarctic (*Lithothamnion glaciale*) rhodoliths are seemingly resilient to changes in sea temperature over a relatively broad thermal range, with sustained growth even at temperatures above those normally observed during most of the year in Newfoundland coastal waters and northwards (Bélanger and Gagnon, 2021). This wide range of responses conveys our need for a better understanding of the vulnerability and resilience of rhodolith beds to ocean warming.

5. Current conservation status of rhodolith beds

Rhodolith beds are currently exposed to a wide range of threats, requiring effective conservation. The urgency of this is ever-increasing, given the continued threat of climate change on low-latitude distributional contraction and potential poleward expansion (if migration rate is fast enough), which may increase their presence in regions of high bottom trawling activity (Fragkopoulou et al., 2021). These localized and intense disturbances, alongside with other chronic threats (see above) jeopardize the long-term survival of rhodolith beds, their associated flora and fauna and the services provided.

Unfortunately, while the conservation value of these important and fragile habitats has been recognized in some regions, global-scale actions to conserve rhodolith beds are very few, compared to other coastal habitats. Relatively recent efforts have been made to protect these habitats in Europe, which are now recognized as a conservation priority at national and international scales (Hall-Spencer et al., 2008; JNCC, 2016a, 2016b; Basso et al., 2016; European Commission, 2018; Scottish Government, 2018). They are protected under the EU Habitats Directive and the OSPAR Commission in the North-East Atlantic (added 2004 to the OSPAR list as ‘*Threatened and/or Declining habitats*’; Hall-Spencer et al., 2008; European Commission, 2018) and listed as ‘*vulnerable*’ or ‘*endangered*’ in the European red list of habitats, issued by the IUCN (Annex A; Gubbay et al., 2016). Furthermore, at a regional scale, they are included in the Convention for the Protection of the Mediterranean Sea Against Pollution (Barcelona Convention), in an Action plan for the ‘*Protection of the Coralligenous and other Calcareous Bio-concretions in the Mediterranean*’, within the framework of the United Nations Environment Programme Mediterranean Action Plan (UNEP-MAP; UNEP/MAP, 2017) and are considered ‘*Priority Marine Features*’ in Scotland (Scottish Government, 2018). Similarly, in a few other regions of the world, rhodolith beds have been recognized as habitats for conservation. In Brazil, they are included in some multiple-use marine protected areas (e.g., Costa das Algas; Costa Gastão et al., 2020), as protected features (‘*bioclastic and lithoclastic sedimentary formations*’, <https://www.icmbio.gov.br/apacostadasalgas>), in Mexico, a few protected areas in the Gulf of California (Loreto, Espirito Santo Island, San Pedro Martir Island, and Revillagigedo Islands) have included rhodolith beds as habitats for conservation (Riosmena-Rodríguez et al., 2010), and in New Zealand they have been recognized as sensitive marine habitats by the Ministry for the Environment for a decade (MacDiarmid et al., 2013) and are incorporated in regional coastal plans.

Despite these efforts, few rhodolith beds are specifically protected. Instead, many are indirectly protected from certain impacts, because of restrictions informed by other local features. Examples in Europe include: (i) rhodolith beds are indirectly protected by the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats), since they provide habitat for certain species listed as ‘*strictly protected*’ or ‘*protected*’ in the appendices of the convention (for example, the rare Mediterranean kelps *Laminaria rodriguezii* and *L. ochroleuca*), (ii) in NW Spain, 28% of the known rhodolith beds are located within protected areas (Peña and Bárbara, 2009), (iii) they occur within marine protected areas of the Madeira archipelago (Natural Marine Park of Cabo Girão, Marine Protected Area of Porto Santo; Desertas and Selvagens Islands Natural Reserves, Ribeiro and Neves, 2020; Neves et al., 2021), (iv) the prohibition of bottom trawling in waters <50 m, operative across EU Mediterranean member states since 1994 (EC Regulation 1626/1994), provides an indirect protection, though more recently destructive fishing activities have been

specifically prohibited over Mediterranean rhodolith beds (EC Regulation 1967/2006). However, the latter represents an ineffective measure due to the lack of relevant data regarding rhodolith-bed spatial distribution (Basso et al., 2016). In addition, (v) two maerl-bed forming species, *Lithothamnion corallioides* and *Phymatolithon calcareum* are listed in the Annex V of European Community Habitats Directive 1992 as species, whose exploitation requires management, and the maerl community is an important feature of Natura 2000 sites.

Similarly, in other regions of the world, rhodolith beds are recognized as key biogenic habitats in need of conservation, but not afforded any specific protection. As in Europe, they are protected only when they incidentally occur in existing marine reserves, as for example in Australia (Harvey et al., 2016), New Zealand (e.g., Kapiti Island, Tonga Islands Marine Reserves, Kermadec-Rangitahua Ocean Sanctuary; Anderson et al., 2019), and Brazil (Fernando de Noronha; Amado-Filho et al., 2012b). While in Brazil, which harbors the largest known rhodolith beds worldwide (Amado-Filho et al., 2017), a high proportion of rhodolith beds are indirectly protected due to their presence in no take marine protected areas in some Brazilian ecoregions, in others, their presence overlaps with areas of oil and gas mining, where exploitation activities represent a threat to these habitats (Araújo et al., 2021; Paiva et al., 2023; Santos et al., 2023).

6. Conclusions

Overall, we highlight here the serious mismatch between global rhodolith bed conservation needs and the knowledge required for their effective management, calling for scientific efforts to fill knowledge gaps and the development of specific strategies to ensure better conservation and management outcomes.

Although rhodolith beds have gained some recognition, as important and sensitive habitats at national/regional levels during the last decade, there is still a notable lack of specific conservation efforts. We reason that this situation is directly related to the lack of information about these habitats and their associated significant ecosystem services, as well as the conflict with economic (exploratory) activities. Thus, we urge for increased research initiatives to ‘level-up’ rhodolith-bed science to solve priority questions, regarding their (1) global distribution, (2) biodiversity, (3) demographic, ecological and genetic connectivity with other habitats, (4) contribution to ocean carbon fluxes and stocks, (5) vulnerability and resilience to anthropogenic, ocean warming and acidification impacts, and (6) existing degree of protection and conservation planning to delineate future priorities. In addition, initiatives to study and expand the public perception of these habitats should be increased to improve conservation success (Bennett, 2016; Bennett et al., 2017). Currently, the majority of the general population, including local stakeholders and others, such as policy makers, media, and school teachers, are widely unaware of the existence and importance of rhodolith beds.

Addressing these questions is essential for providing an empirical basis to inform conservation programs and management priorities for the protection of rhodolith bed habitats at local, regional and global scales. Importantly, addressing the imbalance in research effort, when compared to other coastal habitats, will directly contribute to the priority actions of global ocean sustainability programmes (including UN’s Ocean Decade 2030 Agenda for Sustainable Development) and emphasized in various initiatives (COP26–27), allowing us to fully realise the ecological and socio-economic benefits of coastal ecosystems.

CRedit authorship contribution statement

Fernando Tuya: Conceptualization, Visualization, Writing – original draft, Writing – review & editing. **Nadine Schubert:** Conceptualization, Visualization, Writing – original draft, Writing – review & editing. **Julio Aguirre:** Writing – review & editing. **Daniela Basso:** Writing – review & editing. **Eduardo O. Bastos:** Writing – review & editing. **Flávio Berchez:** Writing – review & editing. **Angelo F. Bernardino:** Writing – review & editing. **Néstor E. Bosch:** Writing – review & editing. **Heidi L. Burdett:**

Writing – review & editing. **Fernando Espino:** Writing – review & editing. **Cindy Fernández-García:** Writing – review & editing. **Ronaldo B. Francini-Filho:** Writing – review & editing. **Patrick Gagnon:** Writing – review & editing. **Jason M. Hall-Spencer:** Writing – review & editing. **Ricardo Haroun:** Writing – review & editing. **Laurie C. Hofmann:** Writing – review & editing. **Paulo A. Horta:** Writing – review & editing. **Nicholas A. Kamenos:** Writing – review & editing. **Line Le Gall:** Writing – review & editing. **Rafael A. Magris:** Writing – review & editing. **Sophie Martin:** Writing – review & editing. **Wendy A. Nelson:** Writing – review & editing. **Pedro Neves:** Writing – review & editing. **Irene Olivé:** Writing – review & editing. **Francisco Otero-Ferrer:** Writing – review & editing. **Viviana Peña:** Writing – review & editing. **Guilherme H. Pereira-Filho:** Writing – review & editing. **Federica Ragazzola:** Writing – review & editing. **Ana Cristina Rebelo:** Writing – review & editing. **Cláudia Ribeiro:** Writing – review & editing. **Eli Rinde:** Writing – review & editing. **Kathryn Schoenrock:** Writing – review & editing. **João Silva:** Writing – review & editing. **Marina N. Sissini:** Writing – review & editing. **Frederico T.S. Tâmega:** Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors 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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