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# Hollow rhodoliths increase Svalbard's shelf biodiversity

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Rhodoliths are coralline red algal assemblages that commonly occur in marine habitats from the tropics to polar latitudes. They form rigid structures of high-magnesium calcite and have a good fossil record. Here I show that rhodoliths are ecosystem engineers in a high Arctic environment that increase local biodiversity by providing habitat. Gouged by boring mussels, originally solid rhodoliths become hollow ecospheres intensely colonised by benthic organisms. In the examined shelf areas, biodiversity in rhodolith-bearing habitats is significantly greater than in habitats without rhodoliths and hollow rhodoliths yield a greater biodiversity than solid ones. This biodiversity, however, is threatened because hollow rhodoliths take a long time to form and are susceptible to global change and anthropogenic impacts such as trawl net fisheries that can destroy hollow rhodoliths. Rhodoliths and other forms of coralline red algae play a key role in a plurality of environments and need improved management and protection plans.

Biodiversity in marine ecosystems depends on habitat heterogeneity<sup>1</sup>, which is often increased by so-called ecosystem engineers, i.e., organisms that modify, maintain or destroy habitats<sup>2</sup>. Ecosystem engineers can be divided into two main groups: allogenic engineers that change living or non-living materials from one form to another (e.g., beavers); and autogenic engineers that modify the environment as a consequence of being modified themselves (e.g., trees)<sup>2</sup>. In marine environments, rhodoliths (unattached coralline red algae) are globally<sup>3</sup> important autogenic engineers that develop rigid structures through calcified skeletal growth<sup>4</sup> and provide ecospace in the form of three dimensional habitat complexity<sup>2</sup>. One example are extensive maërl beds composed mainly of unattached twig-like and usually monospecific rhodoliths (sometimes termed nodules)<sup>5</sup>. Organisms living on complex substrata like maërl are better protected against predators<sup>6</sup>, and commercially important species like the queen scallop, *Aequipecten opercularis* (LINNAEUS, 1758) benefit from the existence of maërl<sup>6</sup>.

Here I report on the ecological role of rhodoliths at the Svalbard shelf (arctic Norway), which is dominated by moraine gravel deposits. In this environment, rhodoliths occur as solid (i.e., nucleated) structures and as hollow frameworks. Both impact the associated organisms, but hollow ones play a more significant ecological role. Hollow and partly hollow rhodoliths occur on coastal platforms (Northern Norway)<sup>7</sup>, summits of ocean sea-mounts (South-western Atlantic)<sup>8</sup>, deep-water reefs (Ryukyu Islands, south of Japan)<sup>9</sup>, volcanic arcs (South Pacific, personal observation), subarctic shallow-water environments<sup>10</sup>, the Arctic Sea<sup>11</sup>, and subarctic fjord and sound settings<sup>12</sup>. Hollow rhodoliths are also known from the Badenian (presently correlated with the Langhian and the Lower Serravallian, Middle Miocene) of southern Poland<sup>13</sup> and the lower Tortonian (Late Miocene) of Menorca<sup>14</sup>. Although hollow rhodoliths are common, knowledge of their formation and impact on the ecosystem is limited. One study<sup>10</sup> reported that hollow rhodoliths are utilised as breeding 'caves' for fish eggs and house echinoids, thus potentially favouring biodiversity, and a second<sup>12</sup> suggested that their formation may be caused by boring bivalves. While both points seem reasonable, an empirical demonstration of those circumstances is still lacking. In this study, I show how hollow rhodoliths develop from nucleated forms through the activity of boring bivalves and quantify their impact on local biodiversity by the provision of additional habitat space.

## Results

Data were obtained from five Svalbard sites during a 2006 expedition of the RV Maria S. Merian<sup>15</sup>; Krossfjorden in the Kongsfjorden-Krossfjorden fjord system (79°08' N, 11°40' E), Moflen island (79°59' N, 14°16' E), Mosselbukta (79°53' N, 15°55' E), Nordkappbukta (80°31' N, 19°52' E), and Lomfjorden (79°34' N, 17°52' E). The sites were similar in terms of temperature, light regime, salinity, pH, and calcite saturation of the seawater<sup>15,16,17</sup> but differed in the presence or absence of rhodolith pavements and the composition of the benthic community.



Rhodolith pavements result from the colonisation of glaciogenic gravel and bioclasts (mostly shell fragments) by coralline red algae, mainly *Lithothamnion glaciale* KJELLMAN, 1883. Individuals of *L. glaciale* form a rigid calcium carbonate skeleton but grow very slowly (100.9–200.3 g  $[\text{CaCO}_3] \text{ m}^{-2} \text{ yr}^{-1}$ )<sup>18</sup>. The rhodoliths are turned regularly by currents and bioturbation, allowing the stony or bioclastic nucleus to become coated by the coralline in a concentric fashion. By definition, such coated nuclei are called rhodoliths as soon as the  $\text{CaCO}_3$  produced by the alga accounts for  $\geq 50\%$  of the overall structure<sup>19</sup>. This explains the occurrence of rhodoliths with a nucleus but not the existence of the frequent hollow forms.

I observed that Svalbard rhodoliths are often bored by the wrinkled rock boring bivalve, *Hiatella arctica* (LINNAEUS, 1767), capable of boring into calcified coralline red algal tissue and hard rock<sup>20,21</sup>. As a consequence, part of the rhodolith and the rhodolithic nucleus are degraded, and a hollow rhodolith results. In this coherence, the versatile composition of the glaciogenic debris, ranging from relatively soft sandstone to hard magmatic material, accounts for the coincidental existence of hollow and solid rhodoliths. Earlier studies of the boring habits of *H. arctica* indicate that the mean burrow volume is  $1.6 \text{ cm}^3 \text{ a}^{-1}$  and occupancy of the particular substrate is generally high with up to 2.5 borings  $\text{cm}^{-2}$ <sup>20</sup>, but based on a subset of rhodoliths ( $n = 9$ ), I observed considerably less (mean borings per surface [ $n \text{ cm}^{-2}$ ] =  $0.05 \pm 0.005 \text{ SE}$ ,  $A^2 = 0.44$ ,  $p(\text{normal}) = 0.22$ ). The other seafloor substrate at the Svalbard sites consists largely of glaciogenic debris and burrows of *H. arctica* have not been observed. Given the boring capacity of *H. arctica*, hollowing out a Svalbard rhodolith with a mean volume ( $n = 9$ ) of  $450 \text{ cm}^3$  ( $\pm 60.3 \text{ SE}$ ,  $A^2 = 0.51$ ,  $p(\text{normal}) = 0.14$ ) and a mean surface ( $n = 9$ ) of  $288 \text{ cm}^2$  ( $\pm 25.0 \text{ SE}$ ,  $A^2 = 0.45$ ,  $p(\text{normal}) = 0.21$ ) would take 19.6 years (see equations 1–5).

Hollow rhodoliths occur intermixed with solid forms (Fig. 1a). Although precise quantification of relative abundances proves to be difficult, I have estimated a mean percentage of 50% for each based on the JAGO video footage. The surface of both hollow and solid rhodoliths is occupied by grazing organisms (mainly polyplacophores and echinoids), but CT-scans show that the interior of the hollow forms is also intensely colonised by a variety of organisms (Fig. 1b–d). Accordingly, local biodiversity at sites where solid rhodoliths (SR) are present is significantly greater than at sites where rhodoliths are absent (NR) and the greatest biodiversity was found at sites with hollow rhodoliths (HR). Data from Margalef's richness index (see equation 6) and the Shannon index (see equation 7) are summarised in Table 1 and comparatively illustrated in Figure 2. The mean frequencies of distinct taxonomic groups in NR, SR, and HR environments are shown in Figure 3. Sites with hollow rhodoliths exhibit the highest mean numbers of taxa for bryozoans, polychaetes, molluscs, echinoderms, and the group of organisms summarised as "others". This pattern is less pronounced for cnidarians and fish but still visible when considering the standard errors of the organism counts. The highest mean number of crustacean taxa occurs at sites with solid rhodoliths, followed by sites with hollow rhodoliths. The overall frequency of the taxonomic groups resembles the biodiversity pattern calculated for the three (NR, SR, HR) environmental settings.

## Discussion

The provision of additional habitat is the main reason for increased biodiversity in areas with hollow rhodoliths. Because the seafloor at all study sites consists mainly of glaciogenic gravel deposits of cobble size, appropriate niches and shelters for benthic organisms are rare. However, hollow rhodoliths serve as a kind of micro-cave that houses a variety of organisms, encompassing filter feeders like the Iceland scallop *Chlamys islandica* (MÜLLER, 1776) and predatory polychaetes. Different species of ophiurids also colonise the interior of the rhodoliths and protrude their arms outside the rhodoliths to collect food. Fish also benefit, as for example the Atlantic hookear

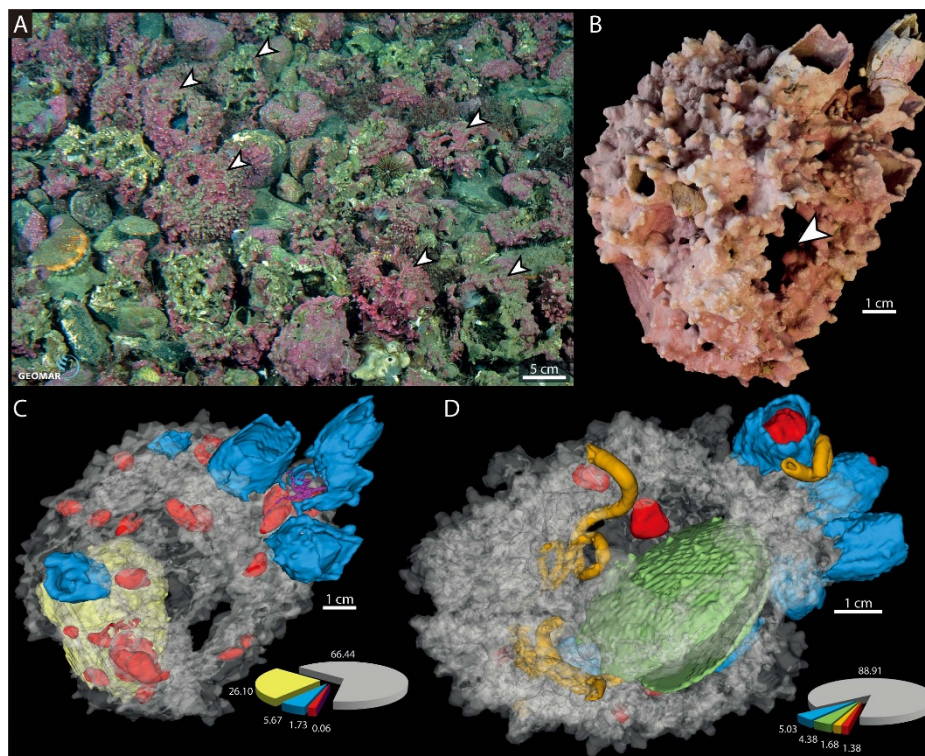
sculpin *Artedidellus atlanticus* JORDAN & EVERMANN, 1898, which feeds on the coexistent polychaetes, small molluscs, and crustaceans. Other taxa seen include the eelpouts (Zoarcidae SWAINSON, 1839) and the Atlantic snake pipefish (*Lumpenus lampretaeiformis* WAALBAUM, 1792), which was previously presumed to be confined to the waters south of Iceland<sup>22</sup>. Some fish may also use the hollow rhodoliths as breeding caves as occurs in subarctic shallow-water environments<sup>10</sup>.

The presence of hollow rhodoliths on the Svalbard shelf has a significant influence on local biodiversity. The three-dimensionality of the hollow forms on the otherwise gravel-dominated seafloor appears to be a prerequisite for the functioning of this ecosystem. The long time required for formation of hollow rhodoliths, however, points out a vulnerability of this ecosystem. Because rhodoliths are calcifying organisms, the ongoing ocean acidification may hamper their future formation or result in the degradation of present specimens<sup>23,24</sup>. An increasing acidification of the seawater leads to a significant reduction in coralline red algal cover<sup>23</sup>, suggesting that lowered pH and reduction of carbonate saturation are important factors that may adversely affect the rhodolith beds. Coralline red algae induce a microenvironment suitable for carbonate precipitation and hence are quite independent of the conditions in the water column<sup>25,26</sup>, but this only holds as long as the water is least slightly saturated with respect to calcite. Additionally, if anthropogenic  $\text{CO}_2$  emissions follow the IPCC business as usual scenario (SRES A2)<sup>27</sup>, a decrease in rhodolith abundance and seafloor cover could occur because coralline algae are very sensitive to rising  $\text{CO}_2$  conditions and the coequally lowered pH<sup>23,24</sup>.

Another aspect of global change involves rising temperatures and concomitant global runoff increase<sup>28</sup>. A consequence generally implicated with this is the eutrophication of the seawater, something that possibly might enhance the thriving of coralline red algae. Although eutrophication may be expected in regions with high population density<sup>29</sup>, around the Svalbard archipelago, it will likely be of secondary relevance. Increased amounts of fine sediments in the water column and consequent light transmission reduction also would affect rhodolith productivity<sup>18</sup>. Experiments<sup>30</sup> have shown that smothering of coralline red algal thalli with fine sediments is likely to lead to a dieback. This is a possible outcome around the Svalbard archipelago, but for other regions, possible consequences of increased global runoff have to be evaluated separately.

Earlier studies<sup>31</sup> have shown that Svalbard archipelago rhodoliths grow very slowly, with an average increase of calcified tissue thickness of  $220 \mu\text{m} \text{ a}^{-1}$ . A meaningful conclusion on the age of the rhodoliths is not possible from this value as it does not consider growth discontinuities, but the slow growth and the findings above clearly show that hollow rhodoliths take a very long time to develop and thus can be thought of as a largely non-renewable resource. Although this has been recognised before<sup>32</sup>, coralline red algae in the form of maërl and rhodoliths are exploited for a variety of human wants, including usage as agricultural fertilizer, soil conditioner, and drinking water purifier<sup>33</sup>. Additionally, rhodolith and maërl beds are threatened by intensive aquaculture<sup>34</sup> and bottom fisheries<sup>32</sup>, which is of particular importance for polar and subpolar environments. Indeed, there has been some success in conserving rhodolith ecosystem engineers, e.g. in England<sup>35</sup>, but elsewhere, protection-plans are largely non-existent<sup>33</sup>.

Lack of more globalized protection or management is partly due to the as yet underestimated role of rhodoliths as ecosystem engineers compared to other habitat providing organisms such as corals. The importance of corals to local diversity is amply documented for tropical environments<sup>36</sup> and for cold water environments<sup>37</sup>. While "classic" photoautotrophic coral reefs extend on shallow, photic water layers of the tropics and subtropics<sup>36</sup>, cold-water corals occur world-wide, especially in deeper water layers and are heterotrophic<sup>37</sup>. Rhodoliths, as photoautotrophic organisms, however, fill the breach of shallow water, high latitudinal environments. Their impact on



**Figure 1 | Hollow rhodoliths are an important feature at the shelves of the Svalbard archipelago.** (A), Seafloor at Mosselbukta in 42 m water depth showing the great abundance of solid and hollow (arrows) rhodoliths (image taken from the JAGO video footage). (B), Hollow rhodolith with its surface colonised by barnacles and with several centimetres wide opening to its interior (arrow). (C), CT scan of a hollow rhodolith in an early stage of development. The rhodolith (semi-transparent grey) is partly gouged by the numerous wrinkled rock boring bivalves, *Hiattella arctica* (red), but the residue of nucleus (yellow) is still visible. The outer surface of the rhodolith is colonised with barnacles (blue) and ophiurids (purple). The pie-chart indicates the relative volumes of the main components. (D), CT scan of a completely gouged rhodolith (semi-transparent grey) whose outer surface is colonised mainly by barnacles (blue). Wrinkled rock boring bivalves (red) are less frequent and the hollow interior of the rhodolith provides shelter for an adult Iceland scallop (green) and numerous polychaetes (yellow). The scallop does not fit through the rhodoliths opening, so a colonisation during the larval stage is obvious. The pie-chart indicates the relative volumes of the main components.

local biodiversity needs to be the focus of future research to determine their ecological (and economic) importance globally. Such research also could lead to potentially increasing human-induced protection and management efforts.

## Methods

Samples were collected during the RV Maria S. Merian expedition to the near-shore of Svalbard. Rhodoliths and benthos were collected with the JAGO submersible and with a dredge. Net catches were sieved (1 mm), organisms were gathered from the overall catch, and fixed in 70% alcohol. Seafloor video footage was recorded during JAGO dives. The organism censuses together with the calculated diversity indices (see below) are compiled in Supplementary Table 1.

The mean volume  $V_R$  of a rhodolith was calculated on the base of a subset of rhodoliths ( $n = 9$ ) using the equation<sup>38</sup>

$$V_R = \frac{4}{3} \pi * abc \quad (1)$$

where  $a$ ,  $b$ ,  $c$  represent the semi-axes of the rhodolith.

The mean surface  $S_R$  of a rhodolith was calculated on the base of a subset of rhodoliths ( $n = 9$ ) using the equation<sup>39</sup>

$$S_R \approx 4\pi \left[ \frac{(ab)^{1.6} + (ac)^{1.6} + (bc)^{1.6}}{3} \right]^{0.625} \quad (2)$$

where  $a$ ,  $b$ ,  $c$  represent the semi-axes of the rhodolith.

Normal distribution of the samples was tested with the Anderson-Darling test using the equation<sup>40</sup>

$$A^2 = -n - \frac{1}{n} \sum_{i=1}^n (2i-1) [\ln F(Y_i) + \ln(1-F(Y_{n+1-k}))] \quad (3)$$

where  $F$  is the normal cumulative distribution function (CDF) and  $Y_i$  represents the data  $X_i$  sorted in ascending sequence, using the equation<sup>40</sup>

$$Y_i = \frac{X_i - \hat{\mu}}{\hat{\sigma}} \quad (4)$$

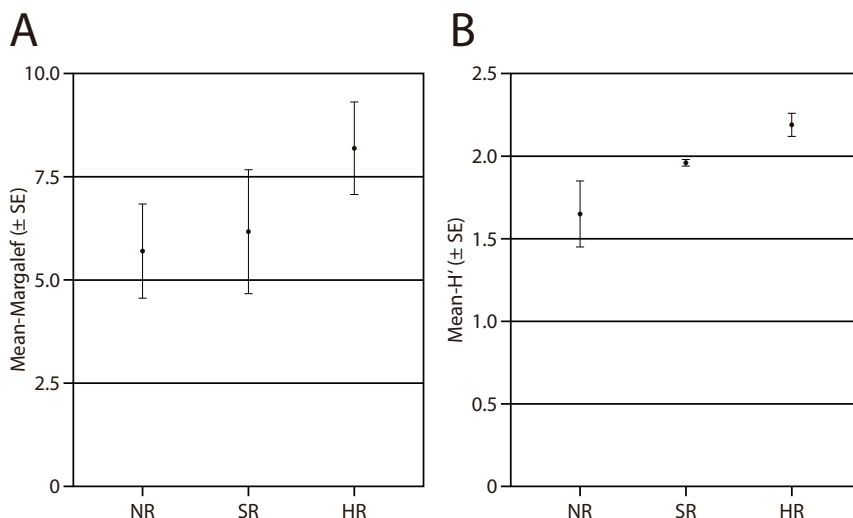
**Table 1 | Diversity indices**

Site	M(MR)	SE(MR)	A <sup>2</sup> (MR)	p(normal)A <sup>2</sup> (MR)	M(H')	SE(H')	A <sup>2</sup> (H')	p(normal)A <sup>2</sup> (H')
NR	5.70	1.14	0.32	0.43	1.65	0.20	0.64	0.06
SR	6.17	1.50	0.48	0.06	1.96	0.02	0.38	0.14
HR	8.19	1.12	0.36	0.28	2.19	0.07	0.39	0.23

NR = sites without rhodoliths; SR = sites with solid rhodoliths; HR = sites with hollow rhodoliths; MR = Margalef's richness index; H' = Shannon index; M = mean; SE = standard error; A<sup>2</sup> = Anderson-Darling test value.

The mean indices indicate the highest diversity for sites with hollow rhodoliths present, while site without rhodoliths have the lowest diversity levels and sites with only solid rhodoliths show intermediate values. All samples are normally distributed according to the Anderson-Darling test.





**Figure 2 | Biodiversity is directly linked to presence and shape of rhodoliths.** (A), The mean Margalef's richness indices ( $\pm$  SE) indicate that biodiversity is slightly higher at sites where solid rhodoliths (SR) are present than at sites without rhodoliths (NR), and that sites with hollow rhodoliths (HR) expose the highest biodiversity. (B), The mean Shannon indices ( $\pm$  SE) indicate that biodiversity is higher at sites where solid rhodoliths (SR) are present than at sites without rhodoliths (NR), and that sites with hollow rhodoliths (HR) expose the highest biodiversity.

The time necessary to hollow out a standard rhodolith was calculated on the base of a subset of rhodoliths ( $n = 9$ ) using the equation

$$\text{Time}[a] = \frac{\frac{1}{C_B} * V_R}{M_B * S_R} \quad (5)$$

where  $C_B$  is the mean boring capacity of *H. arctica* retrieved from former studies<sup>20</sup>, being  $1.6 \text{ cm}^3 \text{ a}^{-1}$ ,  $V_R$  is the mean volume of a rhodolith, being  $450 \text{ cm}^3 (\pm 60.3 \text{ SE}, A^2 = 0.51, p(\text{normal}) = 0.14, \text{ see calculations above})$ ,  $M_B$  is the mean number of borings observed in the used rhodolith subset ( $n = 9$ ), being  $0.05 \text{ n cm}^{-2} (\pm 0.005 \text{ SE}, A^2 = 0.44, p(\text{normal}) = 0.22, \text{ see calculation above})$ , and  $S_R$  is the mean surface of a rhodolith, being  $288 \text{ cm}^2 (\pm 25.0 \text{ SE}, A^2 = 0.45, p(\text{normal}) = 0.21, \text{ see calculations above})$ .

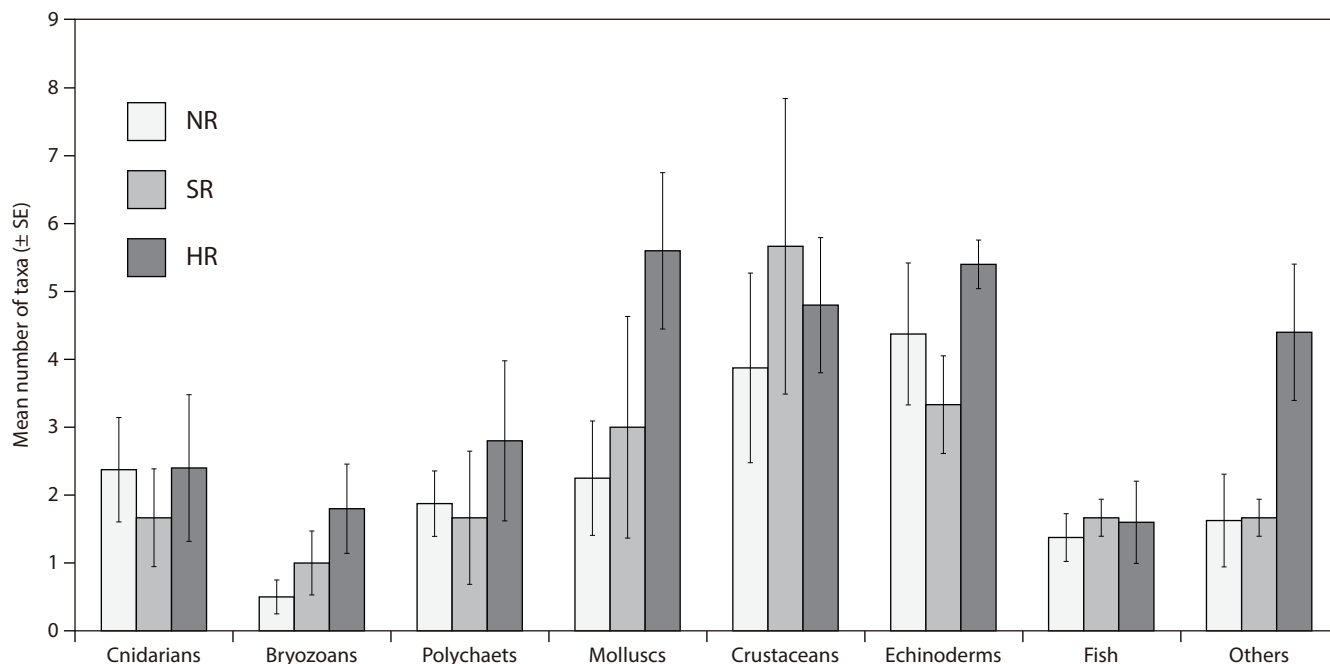
CT-scans were carried out with a SIEMENS SOMATOM Sensation 16. Data acquisition was carried out with 90 mA at 120 kV and 2.0 mm slice width with a collimation of  $16 \times 0.75 \text{ mm}$ . Data were saved to DICOM-format and reconstructions were performed with the software SPIERS 2.20<sup>41</sup>.

To compile species numbers, observations on benthic organisms were extracted from the cruise report<sup>15</sup> for each investigated site (Supplementary Table 1). The censuses were assigned to three groups, being sites without rhodoliths (NR), sites with solid rhodoliths (SR), and sites with hollow rhodoliths (HR). From these data, the Margalef's richness indices<sup>42</sup> were calculated for each site ( $n_{NR} = 8, n_{SR} = 3, n_{HR} = 5$ ), using the equation

$$MR = (S - 1) / \ln(n) \quad (6)$$

where  $S$  represents the number of taxa and  $n$  represents the number of individuals. For each group, the mean Margalef's richness index and the standard error were calculated and normal distribution of the samples was tested with the Anderson-Darling test, using the equation above.

The species numbers were then assigned to groups and the species per group were added. The censuses were again assigned to the three groups (NR, SR, HR). From these data, the Shannon indices<sup>43</sup> were calculated for each site ( $n_{NR} = 8, n_{SR} = 3, n_{HR} = 5$ ), using the equation



**Figure 3 | Most taxonomic groups favour sites with hollow rhodoliths.** For most taxonomic groups, bars ( $\pm$  SE) indicate the lowest mean numbers of taxa at sites without rhodoliths (NR), followed by sites with solid rhodoliths (SR) and led by sites with hollow rhodoliths.



$$H' = - \sum_i \frac{n_i}{n} \ln \frac{n_i}{n} \quad (7)$$

where  $n$  represents the number of taxa (here: groups) and  $n_i$  the number of individuals of the taxon  $i$  (here: Number of taxa in each group). For each group, the mean Shannon index and the standard error were calculated and normal distribution of the samples was tested with the Anderson-Darling test, using the equation above.

All calculations were carried out with the software PAST<sup>44</sup>, except for the time necessary to hollow out a rhodolith, which was calculated in Microsoft Excel 2010.

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## Additional information

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