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Overview of coralline red algal crusts and rhodolith beds (Corallinales, Rhodophyta) and their possible ecological importance in Greenland

Helle I. Ø. Jørgensbye[1] · Jochen Halfar[2]

Abstract Coralline red algae are a globally distributed and abundant group of shallow marine benthic calcifiers. They can form important ecosystems that provide a three-dimensional habitat to a large variety of marine organisms. While the study of coralline red algae has traditionally been focused on warm-water habitats, numerous recent reports have now described widespread coralline red algal ecosystems from high-latitude regions, particularly in the Northern Hemisphere. In fact, it is becoming increasingly evident that coralline red algae are likely the dominant marine calcifying organisms on the seafloor of the Arctic and subarctic photic zone. This article gives a first overview of the distribution of coralline red algal crusts and rhodolith (free-living coralline red algal nodules) grounds in Greenland and the first report of rhodoliths in East Greenland. Museum data and recent sampling information have been compiled to develop a distribution map of coralline genera and rhodolith communities. The depth range of coralline red algae in Greenland has been extended by 27 m, from 50 to 77 m depth. In addition, rhodoliths of the normally crust-forming species *Clathromorphum compactum* are described for the first time from a sheltered Greenland fjord. Based on the data compiled here, it becomes clear that rhodolith communities are a widespread feature of the Greenland shallow shelf areas. Gaining a better understanding of the distribution of these hitherto poorly understood high-latitude ecosystems is essential due to their function as spawning areas and nursery grounds for commercially important fish and invertebrates.

Keywords Coralline red algae · Rhodoliths · Greenland · *Clathromorphum compactum* · Maërl

Introduction

Coralline red algae exhibit a wide variety of growth forms from cushion like to branching or free-living forms, the latter called rhodoliths (Fig. 1a). In Europe, the open-branching rhodoliths are often known as maërl (Foster 2001). They are all grouped in the subclass Corallinophycidae and have hard tissue in the form of cells fortified with calcium carbonate (Le Gall and Saunders 2007; Adey et al. 2013, 2015). The Corallinophycidae are divided into two large groups of (1) geniculate (segmented) and (2) non-geniculate (non-segmented) algae, which can be further subdivided by growth form (Nelson 2009):
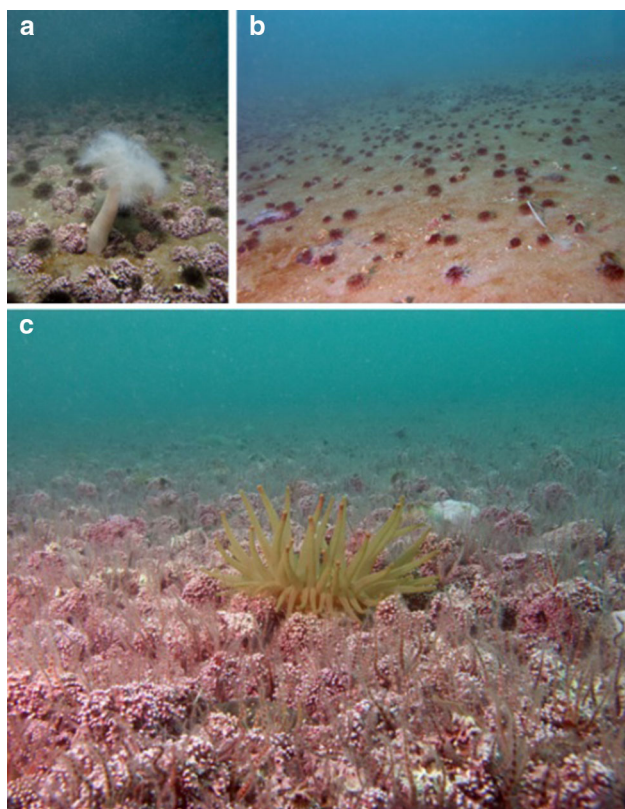
Non-geniculate corallines

a. Grow as calcified crusts on rocks or other hard substrates and can form extensive red crusts of algae or small build-ups.
b. Some of the species can also grow as free living, branched twigs, "balls" or nodules that are known as rhodoliths. Rhodoliths can accumulate over extensive areas known as rhodolith beds or maërl grounds.

Rhodoliths are free-living structures composed >50 % of coralline red algae (Bosence 1983; Fig. 1a, c). They develop when branches from encrusting corallines break, around a core (e.g. shell fragment and pebble) or through settlement of spores (Bosence 1983). The distribution of the coralline red algae is coastal at euphotic depths and

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Fig. 1 a Single large frilled anemone [*Metridium dianthus* (Ellis, 1768)] in field of scattered densely branched rhodoliths. Size of rhodoliths approximately 8–10 cm, sea urchins are seen grazing between rhodoliths. **b** Coralline red algae crust with dense cover of grazing sea urchins [probably *Strongylocentrotus droebachiensis* (O. F. Müller, 1776)] size of sea urchins approximately 8 cm. **c** Sea anemone in rhodolith bed. In and in-between rhodoliths arms of numerous brittle stars [*Ophiopholis aculeata* (Linnaeus, 1767)] are visible. All images from Disko Bay by Jonas Thormar

worldwide, from the tropics to the Arctic areas (Foster 2001). Already in 1852, Rink mentioned coralline red algae as undergrowth for the large kelp forests in West Greenland and noticed this habitats resemblance with tropical coral reefs (Rink 1852). In 1883, Kjellman pointed out that very extensive parts of the sublittoral zone of the Arctic sea (Northern Norway, Spitsbergen, Nova Zemlya and Kara Sea in Russia and Baffin Bay off Greenland) were overgrown by coralline crusts and specifically mentioned rhodoliths (described as coralline red algae growing as balls) from Spitsbergen (Kjellman 1883).

Coralline crust distribution is determined by physical conditions that favour growth such as light, temperature, salinity and seawater chemistry (Adey 1970a, b; Freiwald and Henrich 1994; Freiwald 1998; Teichert et al. 2012; Adey et al. 2013; Teichert et al. 2014; Adey et al. 2015). The substrate greatly influences where coralline red algal crusts can live as they only grow on hard bottom or other suitable hard substrate such as pebbles or shells (Adey

1970a; Konar and Iken 2005; Teichert 2014). Despite the widespread distribution, few surveys exist on the crust ecosystems in the Arctic and subarctic (e.g. Freiwald and Henrich 1994; Freiwald 1998; Adey et al. 2013; Teichert et al. 2014; Adey et al. 2015). Crustose coralline communities are among the highly diverse shallow marine bottoms of the Holarctic (Ojeda and Dearborn 1989; Himmelmann 1991; Chenelot et al. 2011; Adey et al. 2013). Adey et al. (2013) even consider coralline crusts to have coral reef-like species richness (with respect to the associated epi- and infauna). Despite that, the terms coralline sea urchin barrens or barren grounds are often used for crusts, resulting from removal of the large brown algae species by grazing sea urchins (Fig. 1b; Mathieson et al. 1991; Estes and Duggins 1995; Steneck et al. 2002; Wegeberg 2014). Sea urchins, chitons and other grazers are essential to the maintenance of the hard coralline surface by removing fast-growing algae and sedentary invertebrates (Freiwald 1993). Growth rates of corallines are generally low (10s–100s μm/year) relative to those of uncalcified macro algae, and the northernmost corallines can thrive under sea ice, in darkness for several months and at low temperatures (Foster 2001; Wilson et al. 2004; Teichert et al. 2012; Adey et al. 2013; Teichert and Freiwald 2014).

In recent years, coralline crusts and build-ups have been shown to be important paleoenvironmental proxies (Adey et al. 2015). Due to their stratified growth patterns, chemistry of their complex skeleton and longevity, the term rhodochronology has been coined to define the field of coralline algal-based paleoreconstructions (Adey et al. 2013, 2015). For example, by analysing annual growth increments of long-lived thick crusts of *Clathromorphum compactum* (Kjellman) Foslie, 1898 it was possible to reconstruct annual changes in Arctic sea ice coverage for the last 646 years (Halfar et al. 2013). Kamenos et al. (2012) have developed a proxy that has enabled synchronous reconstruction of temperature in Kangerlussuaq Fjord and runoff from the Greenlandic ice sheet since 1939. This was done with samples of the rhodolith former *Lithothamnion glaciale* Kjellman 1883 (Kamenos et al. 2012). Estimated maximum ages of *Clathromorphum* sp. measured as thickness of carbonate build-ups are 1200 years in the North Pacific and 1600 years in the Labrador Sea (Adey et al. 2015). While icebergs can limit the age of coralline crusts due to their scraping action (Pugh and Davenport 1997; Pedersen 2011), no biological age limit is known for *Clathromorphum* sp. carbonate build-ups (Adey et al. 2015).

Rhodolith beds have received more attention than coralline crusts, and several studies exist from the wider Arctic and subarctic (Hall-Spencer and Moore 2000; Bosence and Wilson 2003; Gagnon et al. 2012; Teichert et al. 2012, 2014) and other areas in the North Atlantic

(review by Nelson 2009; Hall-Spencer et al. 2010). Rhodolith beds are described by Foster (2001) as one of the "big four" benthic communities that are dominated by marine macrophytes, ranking with coral reefs, kelp forests and seagrass meadows, which underlines the worldwide importance of these habitats. Rhodolith are well-known ecosystem engineers due to their three-dimensional structure where branches and cavities offer shelter for a range of animals, harbouring a high biodiversity, also in the Arctic (Penney 1992; Foster 2001; Gagnon et al. 2012; Teichert et al. 2012; Teichert 2014; Teichert et al. 2014). Besides functioning as habitat, they act as feeding, nursery and spawning grounds for various organisms from bivalves to fish (Hall-Spencer and Moore 2000; Kamenos et al. 2004; Steller et al. 2009; Riosmena-Rodriguez and Medina-López 2010; Gagnon et al. 2012). In a recent study from Svalbard, it was shown that hollow rhodoliths provide additional habitat and increase local biodiversity significantly (Teichert 2014).

A summary of the early exploration of the Greenlandic algal flora can be found in Rosenvinge (1898) and a more recent update in Pedersen (2011). While Greenlandic seaweeds have received considerable interest, both historically and recently (Pedersen 2011), the Greenlandic coralline red algae have only been treated taxonomically by Rosenvinge in the late 1800s (Rosenvinge 1893, 1898) and again in the 1990s (Düwel and Wegeberg 1996b). The distribution of coralline species and the extent of crusts and rhodolith beds in Greenland are poorly understood. Knowledge about rhodolith communities in Greenland is mostly anecdotal, and no formal habitat mapping has taken place. While a few studies have mentioned rhodoliths from various Greenlandic localities, most of the references are concentrated on corallines from Disko Bay on the west coast (Rosenvinge 1893, 1898; Thorsen et al. 1989; Düwel and Wegeberg 1992; Penney 1992; Düwel and Wegeberg 1996a; Thormar 2008; Pedersen 2011). In this paper, we have compiled known and newly discovered occurrences of coralline red algal crusts and rhodolith communities from throughout coastal Greenland to provide a basis for further studies of these poorly known, but widespread Arctic shallow marine habitats.

Materials and methods

Coralline crusts and rhodolith sites were studied using data from field observations, museum collections and existing literature. One benthic towed photograph transect (CON 129) was conducted near the coast north of Nuuk in an area closed for fishing in 2011. For this survey, the Natural Resources Canada (NRCan) digital drop camera system built by the Geological Survey of Canada in 2008 was

used. It houses a camera and two flashes enclosed inside an aluminium roll cage deployed from the Canadian Coast Guard Ship Hudson on 2 October 2012. The camera was submerged for 3.07 h., and the transect line was approximately 2.9 km. Three hundred and fifty-five photographs of good quality were taken (where at least 50 % of the picture were in focus). See Table 1 for details on this transect and the transects mentioned below. Two SCUBA dive transects perpendicular to the coast were conducted in Sana Fjord, outside Nuuk in September 2008. During both transects, a handheld camera was used for benthic observations as part of the survey of the Greenland Connect tele-cable. Transect one was 275 m long from 1.5 to 16 m depth, and transect two was 250 m long ranging from 3 to 17 m depth. In August 2012, rhodoliths were dredged from 6 localities in Nuuk Fjord (Fig. 2, insert) following drop camera observations at 36 localities to a depth of 20 m. In September 2015, *C. compactum* crusts were collected from one site near Ilulissat in West Greenland. Coralline red algae coverage was estimated, on all transects, from the photographs/video.
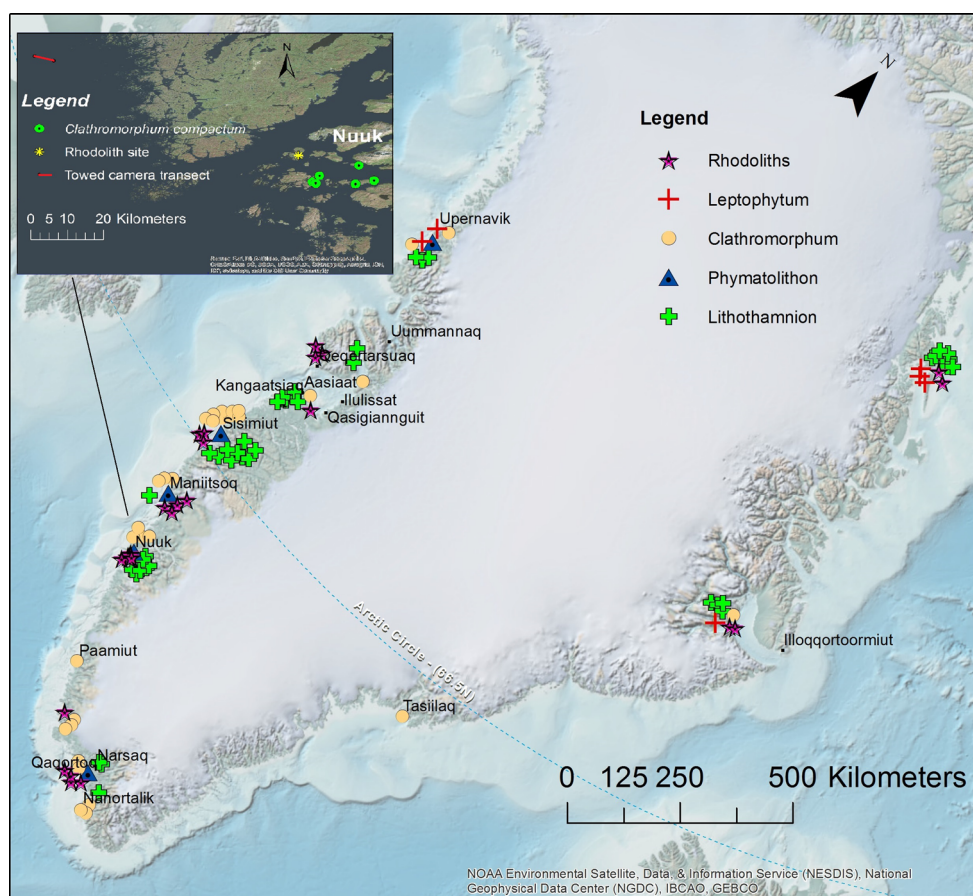
The Botanical Museum, part of the Natural History Museum of Denmark, contains the national collection of Greenlandic coralline red algae. The collection was visually inspected and samples were considered on genus level only, since the collection has not undergone recent taxonomic revision. Information available from the labels was entered into a database, and samples containing rhodoliths

Table 1 Geographical location of transects described in text and *C. compactum* sites. Depth is indicated in metres

Transect	Start position	End position	Depth in m
Towed transect	64°22′57″N	64°23′41″N	25–125
CON 129	52°22′52″W	52°25′43″W	
SCUBA 1	64°09′57N	64°09′51″N	1.5–16
	51°44′46W	51°45′02″W	
SCUBA 2	64°09′59N	64°09′52″N	3–17
	51°44′38W	51°44′48″W	
Dredge locality 1	64°2′45″N	NA	13
	51°44′23″W		
Dredge locality 2	64°2′34″N	NA	13
	51°43′53″W		
Dredge locality 3	64°3′48″N	NA	14
	51°43′20″W		
Dredge locality 4	64°2′27″	NA	20
	51°37′59″		
Dredge locality 5	64°2′596″	NA	21
	51°35′13″		
Dredge locality 6	64°5′32″	NA	13
	51°37′29″		

Fig. 2 Map of coralline red algae distribution. One hundred and forty-one samples are from the Botanical Museum of Copenhagen, one location was reported by Martin Schiøtz (marked as "rhodolith site" in insert map), three locations are from the literature (Seaman 2006; Thormar 2008; Kamenos et al. 2012) and the remaining from this study. Samples of coralline crusts cluster around settlements and research stations due to sampling bias. Rhodoliths from museum samples and other sources are plotted with a star signature. Points are slightly replaced to make it possible to see all genera on the map. Insert enlargement of Nuuk Fjord area with *C. compactum* rhodolith sites found during sampling in 2012. The location of rhodoliths reported by Martin Schiøtz and the towed camera transect is mapped

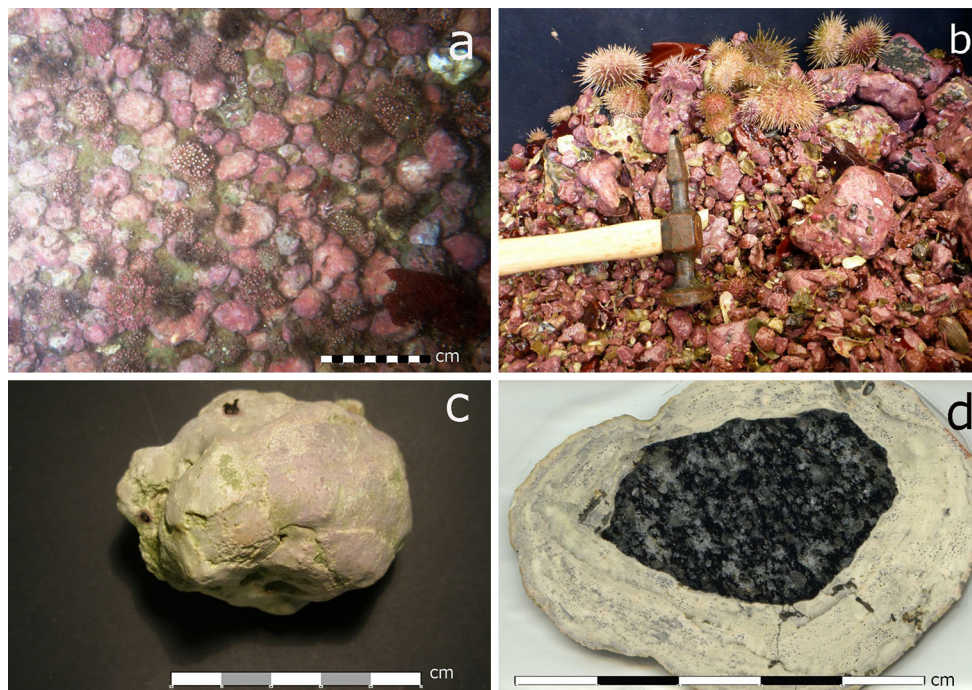were used to make a preliminary map of rhodolith communities in Greenland.

The sites found in the literature search have been mapped in ArcMap version 10.1. A few old sources mention coralline red algae (Kjellman 1883; Rosenvinge 1893, 1898), but accurate positioning is not possible based on these texts. Some of the sites mentioned by Rosenvinge (1893–1898) were sampled by him, and the samples are now found in the Botanical Museum in Copenhagen.

Results

Sampling

Sampling stations in Nuuk Fjord (Fig. 2, insert) revealed an extensive coverage of coralline crusts on hard substrate between depths of 18–25 m with coverages of up to 40 % of the seafloor. Crusts and individual small build-ups consist of *C. compactum*, which is a widely distributed species both in the North-western Atlantic, Arctic Ocean and North Pacific (Adey et al. 2013). *Clathromorphum compactum* in Nuuk Fjord can reach thicknesses of up to 4 cm, and crusts can cover rocky substrate on patches of

several 10 cm^2. The algal encrusted rocky substrate is densely covered by sea urchins and occasionally grades into *Agarum sp.* Dumortier, 1822 macroalgal habitats. Hence, the overall environment occupied by encrusting *C. compactum* can be described as a sea urchin barren, which is a common habitat throughout the subarctic/Arctic and despite its name a highly diverse ecosystem (Adey et al. 2013). In fact, dislodged *C. compactum* crusts house a dense array of invertebrates on their undersides. Out of the 36 sites surveyed at the mouth of Nuuk Fjord (Fig. 2), 27 sites can be defined as sea urchin barrens with *C. compactum* build-ups. Rocky substrate gives way to a soft bottom further offshore. This is either covered by bioclastic sediment, consists of almost 100 % of rhodoliths (Fig. 3a), or represents a mixture of both facies. Rhodoliths are almost exclusively made up of non-branching *C. compactum* and reach diameters of up to 8 cm often containing a pebble as a nucleus in their centre (Fig. 3b, c). *Clathromorphum compactum* has been extensively studied and mapped along the North-western Atlantic coastline ranging from Maine, USA, to northern Baffin Island, Canada (Adey et al. 2013, 2015), and at all locations it has been exclusively recorded as an encrusting species. Hence, the Nuuk Fjord is the only known location to date where *C.*

Fig. 3 Rhodoliths of C. *compactum* from Nuuk fjord. **a** Rhodolith bed with smooth C. *compactum* and branched *Lithothamnion glaciale*. **b** Dredge sample with C.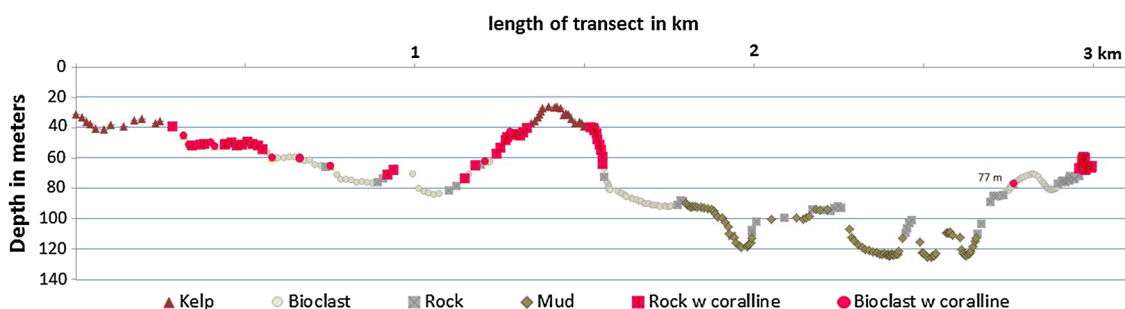 *compactum*. **c** Rhodolith of C. *compactum*, *scale bar* shows cm. **d** Sectioned rhodolith with black pebble as nucleus, *scale bar* shows cm. Picture credits: 3a M. Blicher, 3b A. Kronz

compactum occurs as a rhodolith former covering extensive areas of soft substrate. Contrary to widespread *Lithothamnion glaciale* dominated rhodolith beds along the Canadian North Atlantic (Adey et al. 2013) *L. glaciale* is estimated to play only a minor role in the Nuuk *C. compactum* rhodolith beds.

Transects

A towed still camera transect (Fig. 4) outside Nuuk (Fig. 2, 5a) showed red algae to 77 m depth, 27 m deeper than previously registered in Greenland, based on information from the museum collection. Extensive areas were covered
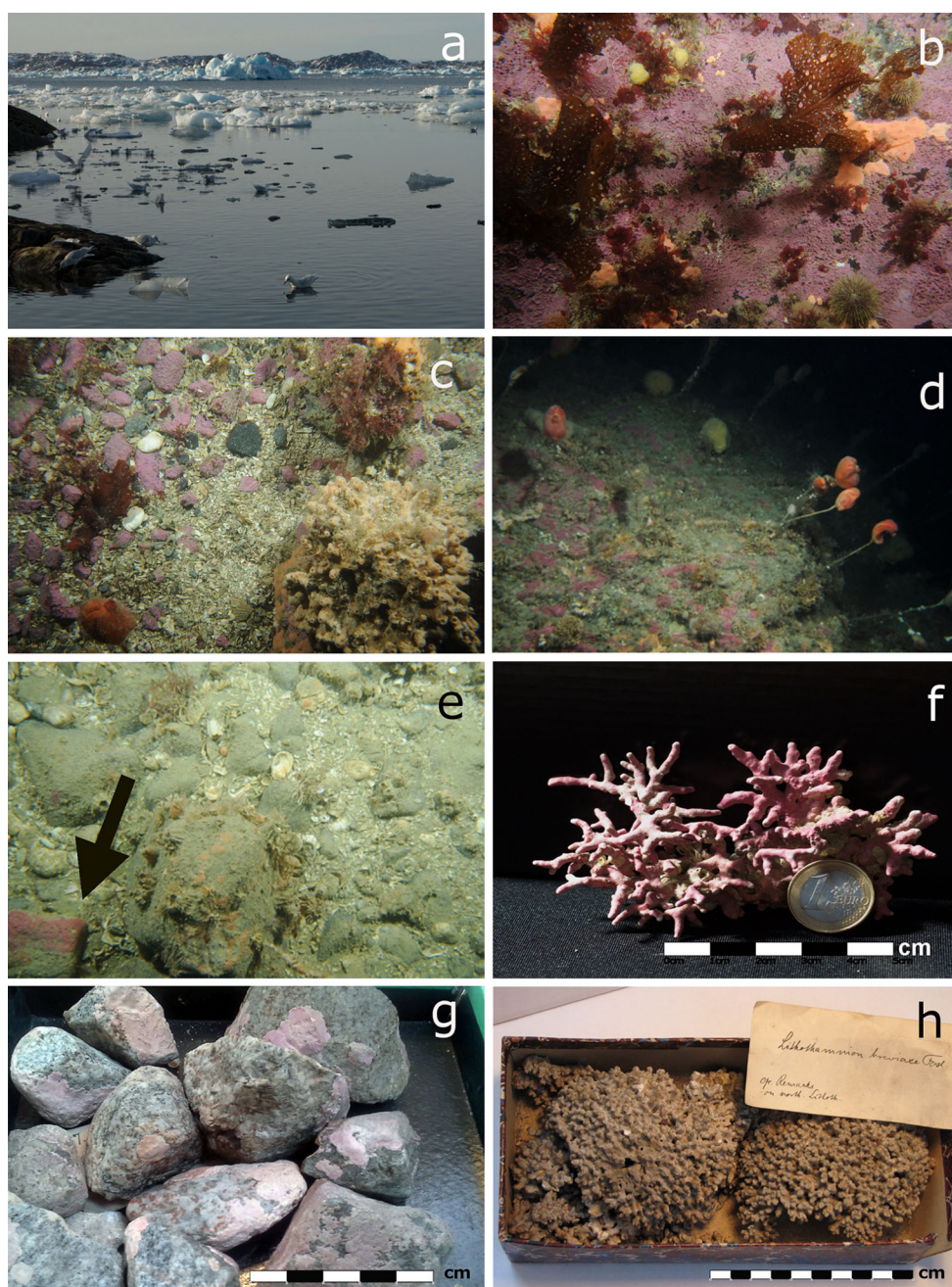
by coralline red algae growing on all suitable habitats (bedrock and stones) as a crust, in a belt spanning the interval from 25 m depth (the shallowest depth on the transect) to approximately 50–60 m depth (Fig. 4). From 25 m to approximately 40 m, the coralline red algae provided substrate for growth of *Agarum* sp. macroalgae and red foliose macroalgae (Fig. 5b). The coverage of foliose macroalgae increased with decreasing water depth, thinning markedly at around 40 m depth (Fig. 5c). From 40 m to approximately 60 m, suitable hard substrate was covered by a crust of coralline red algae and sessile invertebrates (mainly sponges, hydroids, tunicates, bryozoans and barnacles; Fig. 5d). In this depth range, extensive areas of

Fig. 4 Seafloor substrate type and depth along towed photographic transect just north of Nuuk. Kelp habitat dominates in shallow parts of transect and is replaced with coralline crusts below 40 m. Below

approximately 70 m corallines give way to rock and bioclastic facies. Muddy facies is found in the deeper trenches

Fig. 5 a Coastline in Nuuk Fjord during winter showing growlers and icebergs coming from the glacier in the bottom of the fjord. Ice scour severely limits the possibility for algae to grow on the rocky sediment. **b** Bedrock with crust of coralline algae and *Agarum* sp. and rhodophyte foliose algae at approximately 30 m depth. One sea urchin of approximately 8 cm is seen to the right and several sponges (*orange* and *yellow*) are growing on or over the coralline *red* algae. **c** Bioclastic facies with pebbles and one larger boulder at approximately 40 m depth. Most of the pebbles are covered with encrusting corallines and a few rhodophyte macroalgae are seen. A stalked tunicate [*Boltenia ovifera* (Linnaeus, 1767)] of approximately 40 cm height is seen in the lower left corner and a sponge is covering the small boulder. **d** Rocky outcrop at approximately 60 m depth. In the foreground, coralline red algae are seen covering small areas of rock, encrusting invertebrates are covering the rest of the rocky surface. Two large sponges are seen in background and stalked tunicates (*Boltenia ovifera*) of approximately 40 cm height are seen on the right. **e** Bioclastic sediment with pebbles at approximately 70 m depth. Encrusting coralline algae (*arrow* at lower left corner), barnacles and sponges (*orange*) are attached to pebbles. **f** Rhodolith from Nuuk Fjord collected by Martin Schiøtz, showing open-branching growth, probably a *Lithothamnion* sp. **g** *C. compactum* collected near Aasiaat in 1890, Botanical Museum of Copenhagen. **h** *Lithothamnion breviaxe* Foslie, 1895 collected near Maniitsoq in 1895, Botanical Museum of Copenhagen (Museum nr 78719)Picture credits: **b**–**e** Bedford Institute of Oceanography

carbonate bioclasts were also seen. Bioclasts were composed of broken bivalve shells, barnacles, gastropod shells and broken urchin shells. No coralline red algae were seen on this type of substrate except on small pieces of hard substrate such as pebbles or large shells (Fig. 5c). Where pebbles graded into carbonate bioclasts it was obvious that substrate was the limiting factor for the coralline red algae, probably due to the poor stability of the shells that composed the carbonate bioclasts. From 60 m to approximately 77 m, few coralline algae were observed and they did not cover extensive areas (estimated <10 %), being confined to single pebbles or shells (Fig. 5e). The species of coralline red algae could not be determined from photographs as species identification requires samples. The specimens seen were encrusting or with small protuberances. No free-living corallines or rhodolith grounds were observed on this transect.

SCUBA transect one outside Nuuk from 1.5 to 10 m depth consisted of sandy bottom with pebbles, and a few boulders covered with *Agarum sp.* macroalgae. Pebbles were covered with thin crusts of coralline red algae and sessile organisms, mainly barnacles. Pebbles and boulders graded into sandy sediment at approximately 10 m depth, and the rest of the transect consisted of soft sediment. No corallines were seen on the sand substrate, due to the poor stability of this substrate. Large amounts of drifting *Agarum* sp. macroalgae were seen in depressions on sandy sediment, and most but not all drifts were heavily grazed by sea urchins. The last metres of the transect consisted of bioclastic facies at 14–16 m depth, where occasional pebbles and boulders were covered by coralline red algae. SCUBA transect two outside Nuuk from 1.5 m to approximately 17 m depth consisted of sandy substrate. No corallines were seen on the sand due to the poor stability of this substrate. Drifting seaweeds were common in depressions on sand, and most but not all seaweed drifts were heavily grazed by sea urchins. The sandy substrate abruptly changed to rocks with an extensive coverage of coralline crusts, and *Agarum* sp. macroalgae heavily grazed by sea urchins representing a sea urchin barren at around 7 m depth. The substrate gradually changed to pebbles and boulders with a more sparse vegetation of macrophytes at around 8 m depth. All available hard surfaces were covered with corallines and sessile organisms, mainly barnacles down to the end of the transect at 17 m depth. The sparsely distributed macrophytes (<5 %) consisted mainly of rhodophytes.

Museum data

The collection of the Botanical Museum of Copenhagen contains 141 samples of coralline red algae dating back to 1884 (see Table 2). Most samples were collected in the late 1800s to 1907 (Table 3; Fig. 5g, h). The taxonomy has been revised since then, and some of the designated species are taxonomic synonyms (Table 3). The samples have been acquired from various collectors visiting Greenland or local administrators who sent samples to the museum in Denmark. Many of the old samples were identified to species level by Mikael Foslie in the late 1800s. *Lithothamnion sp.* was the only rhodolith-forming genus. The distribution of the collected material reflects the population settlement pattern as most samples are from near a town, settlement or research station (Fig. 2). The general pattern indicates that coralline red algae are distributed along most of the Greenlandic coast, and the northernmost position is a *Lithothamnion* sp. (registered as *L. foecundum* Kjellman 1883) specimen found in 1907 at 76°46′N18°41′E at Danmarkshavn, Vestre Havnenæs in East Greenland. The deepest positions are specimens registered as *Lithothamnion laeve* Foslie, 1898 and *Lithothamnion glaciale* retrieved from 50 m depth. Twenty museum samples could be identified as rhodoliths. Of these, thirteen samples were collected from 1884 to 1907 (Table 3). Three samples were without any date but probably collected in the same time span as the previous samples. One sample was collected by C. Ryberg who sent other algal samples to the museum in 1890. The two other specimens were identified by K. Rosenvinge (1858–1939) and M. Foslie (1855–1909) who were active during the time span when the old samples were collected. Four samples were collected from 1990 to 1997, and three of these were from Disko Bay at a known rhodolith bed site (see Thormar 2008 for description). No rhodolith samples had been collected at depths deeper than 25 m, and all specimens belonged to *Lithothamnion* sp. Most of the material was collected more than 100 years ago, and the difficult logistics of collecting in Greenland defined that it was only possible to take a minimum of specimens in each sample. One further site in Nuuk Fjord was reported to the first author by Martin Schiøtz (pers. comm.; Fig. 2, insert and 5f).

Discussion

Both coralline crusts and rhodolith communities are much more widespread in Greenland than previously reported, both in geographical distribution and depth range (Figs. 2, 4). The occurrence of coralline crusts on suitable substrate from the intertidal zone to approximately 60 m depth follows the general pattern seen in the North Atlantic (Freiwald and Henrich 1994; Freiwald 1998; Gagnon et al. 2012; Teichert et al. 2012; Adey et al. 2013; Teichert 2014). The deepest coralline observation in this study was at 77 m depth. Hitherto the deepest coralline recorded in

Table 2 Following genera of coralline red algae are found in the collection of Botanical Museum (Natural History Museum of Denmark)

Genera	Number of samples	Depth range (m)	Collected
Clathromorphum sp.	33 samples	0–36	1886–1899
Leptophytum sp.	27 samples	0–50	1886–1907
Lithothamnion sp.	75 samples	0–50	1884–1907 and 1990–1997
Phymatolithon sp.	6 samples	18–21	1884–1894

A number of samples are indicated, note that some samples can contain several specimens

museum samples from the Botanical Museum of Copenhagen was from 50-m water depth. Earlier results reporting corallines as deep as 90 m off Svalbard fit well with our Greenland depth data (Teichert et al. 2012; Sswat et al. 2015). The northernmost occurrences of corallines in Greenland were encrusting *Lithothamnion* sp. from 76°46′N collected in 1909. The northernmost report of Arctic coralline red algae is from Svalbard at 80°39′N (Sswat et al. 2015). This may indicate that corallines can be found further north than reported here, unless light limitation through perennial sea ice restricts their distribution in northernmost Greenland.

Crusts

This study found the sea urchin [likely *Strongylocentrotus droebachiensis* (O. F. Müller, 1776)] to be an overt species on Greenlandic crusts (Fig. 1b), an observation that is supported by other studies in Greenland (Christensen 1971; Thorsen et al. 1989; Düwel and Wegeberg 1996a; Thormar 2008). In the wider North Atlantic and North Pacific, the low-relief crustose community is a key habitat supporting a rich community by providing substrate, refuge and food to a wide variety of infaunal as well as epifaunal invertebrates (Ojeda and Dearborn 1989; Chenelot et al. 2011). The same pattern has been observed in Greenland in Disko Bay (see Table 4 for the literature compilation of fauna inhabiting coralline crusts in Greenland), where limpets (*Acmaea* sp.), chitons (*Tonicella* sp.), serpulid tubeworms, the wrinkled rock borer *Hiatella arctica* (Linnaeus, 1767) and the polychaete worm *Dodecaceria* sp. have been found to be common on or under crusts (Thorsen et al. 1989). Particularly, *H. arctica* can find ideal substrate by boring into the coralline red algal carbonate crusts (Adey et al. 2013). In 1988, four new species of Kinorhyncha (mud dragons), *Echinoderes peterseni* Higgins and Kristensen 1988 *E. tubilak* Higgins and Kristensen 1988, *E. angustus* Higgins and Kristensen 1988 and *Pycnophyes cryopygus* Higgins and Kristensen 1988 were described from or found in a habitat of stones encrusted with corallines (Higgins and Kristensen 1988). *Echinoderes peterseni* was also found inside densely branched hollow rhodoliths in Disko Bay (Thorsen et al. 1989). Besides the importance for biodiversity, the Greenlandic crustose corallines have a

stabilizing role for the unique submarine tufa columns forming over alkaline springs in Ikka Fjord (Düwel 1996; Buchardt et al. 1997; Sørensen and Kristensen 2000). The same stabilizing effect has been demonstrated from tropical reefs (Nelson 2009). The longevity and slow growth rate of these coralline crusts make them vulnerable to anthropogenic disturbances and ocean acidification (Steller et al. 2003; Büdenbender et al. 2011; Chenelot et al. 2011). While coralline crusts have been shown to harbour a rich biodiversity, little is known about the crust community and the importance it has as habitat and as feeding and breeding grounds. The Greenland coastline with numerous islets and coves provides ample opportunities for the growth of long-lived specimens, which could be used to reconstruct Greenland climate change throughout the last centuries.

Rhodoliths

The first finding of rhodolith-forming *C. compactum* which normally grows as crusts is presented here (Fig. 3). This unusual growth form must be influenced by local conditions as it has been shown that main factors regulating rhodolith formation are currents, tidal currents and wave action (Foster 2001) as well as epi- and endobenthic feeding activity of vertebrates and invertebrates (Marrack 1999). The above processes cause frequent overturning, which is a requirement for the concentric growth observed. The presence of an appropriate substrate of round stones is necessary for the formation as all *C. compactum* rhodoliths that were cut open had a small pebble at the nucleus. It must be assumed that relatively strong currents able to move the rhodoliths around are a necessity for *C. compactum* to form spherical rhodoliths in Nuuk Fjord. The presently known distribution of *C. compactum* rhodoliths is limited to Nuuk Fjord, but further investigations might reveal this unique ecosystem to be present at other localities.

Based on the museum samples, it seems likely that rhodolith communities can be found at numerous localities around Greenland except the most northern areas, where year-round sea ice cover does not allow the growth of the light-dependent coralline red algae. This widespread distribution follows the pattern from around the North Atlantic (Freiwald and Henrich 1994; Freiwald 1998;

Table 3 Rhodoliths identified in collection of Botanical Museum (Natural History Museum of Denmark)

Latitude	Longitude	Locality	Depth (m)	Species name as recorded at the museum	Present name based on AlgaeBase	Year of collection	Museum No.	Identified by
65°25′N	52°55′W	Sukkertoppen	NA	*Lithothamnion soriferum* Kjellman, 1883	*Lithothamnion tophiforme* (Esper) Unger, 1858	NA	78774	K. Rosenvinge
65°28′N	52°48′W	Sukkertoppen	10	*Lithothamnion tophiforme* (Esper) Unger, 1858	*Lithothamnion tophiforme* (Esper) Unger, 1858	NA	78842	M. Foslie
60°43′N	46°03′W	Julianehaab	NA	*Lithothamnion soriferum* Kjellman, 1883	*Lithothamnion tophiforme* (Esper) Unger, 1858	NA	78839	M. Foslie
65°25′N	52°55′W	Sukkertoppen	NA	*Lithothamnion glaciale* Kjellman, 1883	*Lithothamnion glaciale* Kjellman, 1883	1884	78809	M. Foslie
66°51′N	53°36′W	Umanarssuk	20	*Lithothamnion glaciale* Kjellman, 1883	*Lithothamnion glaciale* Kjellman, 1883	1886	78836	M. Foslie
68°38′N	51°50′W	Ikamiut	NA	*Lithothamnion glaciale* Kjellman, 1883	*Lithothamnion glaciale* Kjellman, 1883	1888	78810	M. Foslie
68°38′N	51°50′W	Ikamiut	NA	*Lithothamnion glaciale f. boreale* (Foslie) Foslie, 1909	*Lithothamnion glaciale f. boreale* (Foslie) Foslie, 1909	1888	78835	M. Foslie
60°43′N	46°03′W	Julianehaab	NA	*Lithothamnion breviaxe* Foslie, 1895	*Lithothamnion breviaxe* Foslie, 1895	1890	78717	K. Rosenvinge
66°56′N	53°40′W	Holsteinsborg	20	*Lithothamnion glaciale* Kjellman, 1883	*Lithothamnion glaciale* Kjellman, 1883	1890	78814	M. Foslie
60°43′N	46°03′W	Julianehaab	NA	*Lithothamnion flabellatum* Rosenvinge, 1893	*Lithothamnion tophiforme* (Esper) Unger, 1858	1890	78775	K. Rosenvinge
60°43′N	46°03′W	Julianehaab	NA	*Lithothamnion soriferum* Kjellman, 1883	*Lithothamnion tophiforme tophiforme* (Esper) Unger, 1858	1890	78834	K. Rosenvinge
70°27′N	26°16′W	Danmarks Ø	18	*Lithothamnion tophiforme* (Esper) Unger, 1858	*Lithothamnion tophiforme* (Esper) Unger, 1858	1892	78768	M. Foslie
70°27′N	26°16′W	Danmarks Ø	18	*Lithothamnion flabellatum* Rosenvinge, 1893	*Lithothamnion tophiforme* (Esper) Unger, 1858	1892	78767	M. Foslie
65°25′N	52°54′W	Sukkertoppen	0	*Lithothamnion breviaxe* Foslie, 1895	*Lithothamnion breviaxe* Foslie, 1895	1895	78719	M. Foslie
76°46′N	18°41′W	Danmarkshavn	0	*Lithothamnion glaciale* Kjellman, 1883	*Lithothamnion glaciale* Kjellman, 1883	1907	78820	M. Foslie
76°46′N	18°41′W	Danmarkshavn	0	*Lithothamnion glaciale* Kjellman, 1883	*Lithothamnion glaciale* Kjellman, 1883	1907	78822	M. Foslie
69°29′N	53°57′W	Disko Fjord	9	*Lithothamnion glaciale* Kjellman, 1883	*Lithothamnion glaciale* Kjellman, 1883	1990	38887	L. Düvel & S. Wegeberg
61°11′N	48°27′W	Arsuk Fjord	0, 5	*Lithothamnion* sp.	*Lithothamnion* sp.	1992	78644	(probably S. Wegeberg)
69°27′N	53°55′W	Disko Fjord	8	*Lithothamnion glaciale* Kjellman, 1883	*Lithothamnion glaciale* Kjellman, 1883	1997	75982	S. Wegeberg
69°27′N	53°55′W	Disko Fjord	20	*Lithothamnion tophiforme* (Esper) Unger, 1858	*Lithothamnion tophiforme* (Esper) Unger, 1858	1997	75983	S. Wegeberg

The species names designated have been included even though the collection has not undergone recent taxonomic revision, and the old names have been used to identify recent nomenclature based on AlgaeBase. Note that geographical positions for samples from 1800s are approximate

Table 4 Literature compilation of animals found on coralline red algae crusts and in rhodolith beds in Greenland, mainly Disko Bay

Taxonomic unit	Crusts	Rhodoliths
Seaweeds		
Several species	x	
Bacillariophyceae		
Several species		x
Foraminifera		
Several species		x
Porifera		
Several species of small sponges	x	x
Nematoda		
Greeffiella sp.		x
Desmoscolex sp.		x
Draconema sp.		x
Gastrotricha		
Several species		x
Rotifera		
Several species		x
Kinorhyncha		
Echinoderes peterseni Higgins and Kristensen 1988	x	x
E. tubilak Higgins and Kristensen 1988	x	
E. angustus Higgins and Kristensen 1988	x	x
Pycnophyes cryopygus Higgins and Kristensen 1988	x	
Ciliophora		
Tintinnina and others		x
Hydrozoa		
Several species		x
Actiniaria		
Urticina sp.		x
Metridium dianthus (Ellis, 1768)		x
Mollusca		
Larvae		x
Juveniles		x
Emarginula fissura (Linnaeus, 1758)		x
Puncturella noachina (Linnaeus, 1771)		x
Margarites groenlandicus (Gmelin, 1791)		x
Hiatella arctica (Linnaeus, 1767)	x	x
Tonicella rubra (Linnaeus, 1767)	x	x
T. marmorea (O. Fabricius, 1780)	x	x
Testudinalia testudinalis (O. F. Müller, 1776)	x	
Solenogastres (undetermined)		x
Sipuncula		
Golfingia sp.		x
Phascolion sp. (2 species)		x
Nemertea		
Nemertea (undetermined)		x
Polychaeta		
Larvae (undetermined)		x
Spirorbis sp.	x	
Serpulidae	x	
Dodecaceria sp.	x	
Pholoe sp.		x

Table 4 continued

Taxonomic unit	Crusts	Rhodoliths
Pholoe minuta (Fabricius, 1780)	x	x
Harmothoe sp.		x
Sabellidae		x
Dodecaceria sp.		x
Cirratulus sp.		x
Nerellidium sp.		x
Paranerilla sp.		x
Meganerilla sp.		x
Echinodermata		
Ophiopholis aculeata (Linnaeus, 1767)	x	x
Leptasterias polaris (Müller and Troschel, 1842)	x	x
*Crossaster papposus (*Linnaeus, 1767)	x	x
Strongylocentrotus droebachiensis (O.F. Müller, 1776)	x	x
S. pallidus Sars (G.O., 1872)	x	x
Psolus fabricii (Düben and Koren, 1846)	x	
Crustacea		
Balanus spp.	x	
Halacaridae (Nine species)		x
Akanthophoreus gracilis (Krøyer, 1842)		x
Harpacticoida (Several species)		x
Munnidae spp.		x
Uromunna petiti (*Amar, 1948*)		x
Gnathiidae		
Gnathiidae		x
Ostracoda		
Philomedes globosus (Lilljeborg, 1853) Sars, 1869		x
Baffinicythere howei (Hazel, 1967) Hazel, 1967		x
Cythere lutea Mueller, 1785[†]		x
Cytherois sp.		x
Cytheromorpha cf. macchesneyi		x
Cytheropteron nodosoalatum Neale and Howe, 1973		x
Cytheropteron pyramidale Brady, 1868		x
Elofsonella concinna (Jones, 1857)[†]		x
Baffinicythere emarginata (Sars, 1866) Hazel, 1967		x
Microcythere bahusiensis Elofson, 1944		x
Paracytherois cf. arcuata		x
P. cf. flexuosa		x
Polycope orbicularis Sars, 1866		x
Pseudocythere cf. norvegica		x
Robertsonites tuberculatus (Sars, 1866) Hazel, 1967		x
Sarsicytheridea punctillata (Brady, 1865)[†]		x
Sclerochilus spp.		x
Semicytherura affinis[†]		x
S. undata (Sars, 1866) Wagner, 1957		x
Xestoleberis depressa Sars, 1866		x
Decapoda		
Hyas araneus (Linnaeus, 1758)		x
Amphipoda		
Several species		x

Table 4 continued

Taxonomic unit	Crusts	Rhodoliths
Bryozoa		
Bryozoan spp.	x	x
Rhamphostomella ussowi (Kluge, 1908)	x	
Oncousoecia diastoporides (Norman, 1869)	x	
Tubulipora flabellaris (O. Fabricius, 1780)	x	
Lepraliella contigua (Smitt, 1868)		x
Tegella arctica (d'Orbigny, 1853)		x
Tardigrada		
Styraconyx qivitoq (Kristensen and Higgins, 1984)		x
S. nanoqsunguak (Kristensen and Higgins, 1984)		x
Tunicata		
Solitary species of ascidia		x
Pisces		
Gadus morhua (over rhodolith bed)		x
Hippoglossus hippoglossus (over rhodolith bed)		x
Pholis cf. gunnelus (inside rhodolith)		x
Eggs		
Different phyla, invertebrates and fish		x

Taxa are to the lowest rank possible

Available data on organisms found on/in coralline crusts or rhodoliths in Disko Bay (Higgins and Kristensen 1988; Thorsen et al. 1989; Penney 1992; Thormar 2008)

[†] Only dead specimens found

Gagnon et al. 2012; Teichert et al. 2012; Adey et al. 2013; Teichert 2014). It is, however, not possible at this point to provide information on the extent of these rhodolith communities based on the museum collections. The only two places where rhodolith beds are mentioned in the literature are the rhodolith bed outside the Disko Bay settlement at approximately 69°29′N 53°56′W (Thorsen et al. 1989; Düwel and Wegeberg 1992; Penney 1992; Thormar 2008) and near the town of Qaqortoq at approximately 60°42′N 46°02′W (Thormar 2008). The rhodolith bed near Qaqortoq (formerly Julianehåb) is probably the same place where three museum-housed rhodoliths were collected between 1875 and 1890. In Greenland, no two settlements are connected by road and all travel is done by boat or plane, and this made and still makes the logistics of collecting specimens quite challenging (see, e.g. Rasmussen 1932). The rhodolith sites found in this study are all located near settlements or research stations, a pattern that is also found in other studies carried out in remote areas (Tobler et al. 2007). It must be expected that the number of rhodolith sites reported here inevitably is an underestimate based on the above assumptions.

Several studies have reported rhodolith grounds globally to be vulnerable to disturbances due to physical breakage or burial of plants (Hall-Spencer and Moore 2000; Riosmena-Rodríguez et al. 2012). Hall-Spencer and Moore (2000) reported significant negative effects on the algae in the short term (weeks) after trawling but also found extensive long-term damage on the order of years, following a first trawling of a pristine rhodolith bed. The integrity of rhodolith beds depends upon the survival of a surface layer of slow-growing algae. These algae are unable to withstand prolonged burial owing to lack of light, and so they are easily killed by trawling or dredging (Wilson et al. 2004). This damage is further increased when rhodolith beds are relatively restricted in size, such as small beds that have spatial coverages on the order of hectares rather than square kilometres (Riosmena-Rodríguez et al. 2012). A sound knowledge of the distribution and extent is a fundamental requirement for their successful conservation and management (Donnan and Moore 2003). The size of the only rhodolith bed in Greenland that has been sampled (Disko Bay) is (probably) measured in hectares based on diving observations (Thormar 2008; Fig. 1). It can be assumed that many Greenlandic rhodolith beds are in an undisturbed state as the main trawling operations for cod *Gadus morhua* Linnaeus, 1758, Greenland halibut *Reinhardtius hippoglossoides* (Walbaum,

1792) and northern shrimp *Pandalus borealis* Krøyer, 1838, take place below the depth of rhodolith occurrence. Iceland scallop *Chlamys islandica* (O. F. Müller, 1776) dredging is carried out in the depths where rhodoliths are found but the fishery is not widespread, and the dredging footprint is documented and limited to distinct fishing grounds (Garcia et al. 2006; Jørgensbye 2009). Near-shore-based fishing nets (gillnets and fish traps) can entangle and damage rhodoliths, but the damage is spatially less extensive than trawling (pers. obs. by first author).

Considering their role as ecosystem engineers, the destruction of rhodolith beds has severe impacts on the diverse benthic community that lives on/in rhodolith beds. In Greenland, only a few observations from Disko Fjord are published, but those report a rich macrofauna with 80 species or species groups (see Table 4 for the literature compilation of fauna inhabiting rhodoliths in Disko Bay Greenland). For example, sponges are common inside rhodoliths (Thormar 2008; ForBio 2013). Penney (1992) found four new ostracod species for Greenland at Disko Bay living inside rhodoliths and found this habitat to be richer in number of individuals and number of species than samples from the intertidal zone, algal holdfasts and stones. Eggs from various animal groups have been found inside Disko Bay rhodoliths, and carnivorous fish have been observed to utilize this habitat (Thorsen et al. 1989; Thormar 2008). Rhodolith beds globally have been documented to be spawning grounds and nursery areas for fish (Kamenos et al. 2004; Steller et al. 2009; Gagnon et al. 2012). In West Greenland, local breeding stocks of the cod *G. morhua* have recently been documented (Therkildsen et al. 2013). These stocks are caught along the coast and play an increasing role for the economy as catches of shrimp are diminishing (Jørgensbye 2010; Råd 2014). Rhodolith beds might play an important but hitherto unknown role in the maintenance of these local stocks in Greenland.

The Greenlandic rhodolith beds can be categorized as vulnerable marine ecosystems (VME) based on the "International Guidelines for the Management of Deep-sea Fisheries in the High Seas" (FAO 2009). The inclusion of rhodolith beds is based on the following traits:

- Functional significance of the habitat.
- Structural complexity (ecosystem engineers).
- Long-lived.
- Vulnerability based on the slow recovery after disturbance (such as trawling).

The high biodiversity living in/on coralline crusts and the role rhodoliths play as ecosystem engineers are underestimated but with growing knowledge it must be hoped that this unique ecosystem will merit a status as protected areas as is possible under Greenlandic law. The discovery of a new species of rhodolith former, only found in one fjord in Greenland, makes this ecosystem quite unique. The newly discovered role of *C. compactum* as long-lived climate archive adds to the importance for rhodolith bed conservation.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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