

Arctic rhodolith beds and their environmental controls (Spitsbergen, Norway)

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Abstract Coralline algae (Corallinales, Rhodophyta) that form rhodoliths are important ecosystem engineers and carbonate producers in many polar coastal habitats. This study deals with rhodolith communities from Floskjeret (78°18'N), Krossfjorden (79°08'N), and Mosselbukta (79°53'N), off Spitsbergen Island, Svalbard Archipelago, Norway. Strong seasonal variations in temperature, salinity, light regime, sea-ice coverage, and turbidity characterize these localities. The coralline algal flora consists of *Lithothamnion glaciale* and *Phymatolithon tenue*. Well-developed rhodoliths were recorded between 27 and 47 m water depth, while coralline algal encrustations on lithoclastic cobbles were detected down to 77 m water depth. At all sites, ambient waters were saturated with respect to both aragonite and calcite, and the rhodolith beds were located predominately at dysphotic water depths. The rhodolith-associated macrobenthic fauna included grazing organisms such as chitons and echinoids. With decreasing water depth, the rhodolith pavements were regularly overgrown by non-calcareous *Polysiphonia*-like red algae. The

corallines are thriving and are highly specialized in their adaptations to the physical environment as well as in their interaction with the associated benthic fauna, which is similar to other polar rhodolith communities. The marine environment of Spitsbergen is already affected by a climate-driven ecological regime shift and will lead to an increased borealization in the near future, with presently unpredictable consequences for coralline red algal communities.

Keywords Depth gradient · Environmental parameters · *Lithothamnion glaciale* · *Phymatolithon tenue* · Rhodolith community · Seasonality · Spitsbergen

Introduction

Rhodoliths are free-living structures composed mostly (>50 vol%) of non-geniculate coralline algae (Corallinales, Rhodophyta). As ecosystem engineers sensu Jones et al.

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(1994), they provide habitats for many organisms. Rhodolith beds are described as one of the ‘big four’ benthic communities dominated by macrophytes (Foster 2001) and can act as major-scale carbonate factories (Freiwald and Henrich 1994).

During the 2006 MSM 02/03 expedition of RV *Maria S. Merian*, the northernmost rhodolith communities known to date were discovered at 80°31′N at Nordkappbukta off Nordaustlandet, Svalbard Archipelago, Norway (Teichert et al. 2012). During that expedition (see Lherminier et al. 2009 for cruise report), major rhodolith communities were also investigated at three other localities on the neighboring island of Spitsbergen (Fig. 1): Floskjeret in Isfjorden, Krossfjorden in the Kongsfjorden-Krossfjorden system, and Mosselbukta on the eastern side of the mouth of Wijdefjorden. The Mosselbukta (Mosselbay) beds were first observed by Kjellman (1875a, b) during the Swedish Polar Expedition of 1872–1873. Together with beds from Isfjorden, Yttre Norskön (now Yttre Norskoya) and Treurenbergbay (Kjellman 1875b: 3–4), they were the first rhodolith communities reported from the Svalbard Archipelago.

Here, we report on the rhodolith communities at Floskjeret, Krossfjorden, and Mosselbukta in terms of species composition, vertical distribution under euphotic and dysphotic conditions, rhodolith development from crustose plants attached to lithoclastic cobbles, rhodolith shape and size, rhodolith distribution in relation to environmental characteristics (light, salinity, temperature, and carbonate system parameters), and the interactions between rhodoliths and associated benthic organisms. Comparisons with the Nordkappbukta communities and, to the extent data availability permits, with other Arctic rhodolith communities are provided, and the potential susceptibility of Svalbard Archipelago rhodolith communities to environmental changes is considered.

Study sites and local environmental conditions

Floskjeret (78°18′N, 14°32′E) (Fig. 1) is located at the mouth of Borebukta in Isfjorden, which is the largest fjord system on Spitsbergen (~100 km long and up to 425 m deep) and includes 13 tributary fjords and bays (Forwick and Vorren 2009).

The geology of Borebukta features Early Cretaceous sediments consisting mainly of sandstones from the Helvetiafjellet and Carolinefjellet formations (Harland 1997).

Water masses of internal and external origin affect the hydrography of this estuarine system. Inside Isfjorden, surface waters consist of glacial melt water and river runoff during summer; local waters are characterized by increased salinity due to sea ice formation; and winter-cooled waters

prevail (Forwick and Vorren 2009). Atlantic Water (AW) from the West Spitsbergen Current (WSC) and Arctic Water (ArW), which is an extension of the polar East Spitsbergen Current (ESC), enter through the mouth of Isfjorden (Nilsen et al. 2008).

Sea ice usually forms in December/January and starts to break up between April and July (Węslawski et al. 1995; Svendsen et al. 2002; Nilsen et al. 2008; data from AMSR-E Sea Ice Maps). Mean annual water temperatures are 2.1 °C at the surface and 1.5 °C at 50 m water depth. Mean annual salinities are 34.9 (PPS) at the surface and 35.0 (PPS) at 50 m water depth (data from LEVITUS 94).

Krossfjorden (79°08′N, 11°40′E) (Fig. 1) is oriented more or less north to south and features ten tributary fjords and bays (map in Svendsen et al. 2002). It consists of a submarine channel (~30 km long and up to 370 m deep), which converges with Kongsfjorden in the Kongsfjordrenna, a deep glacial basin (Sexton et al. 1992; Svendsen et al. 2002). North of the mouth of Krossfjorden is Mitragrunnen Bank, which is as shallow as 30 m and is separated from the main shelf area by a north-south oriented trough (Ottesen et al. 2007). The Kong Haakons Halvøya divides the inner fjord into two parts, Möllerfjorden and Lilliehöökfjorden.

The geology of Krossfjorden and Mitragrunnen features a Late Neoproterozoic basement consisting of pelites from the Signehamna Formation and granites from the Generalfjella Formation (Harland 1997).

Seasonal variations in freshwater input result in a stable stratification in summer, when upper-layer circulation is confined to a shallow surface layer, and in a very weak stratification in winter (Svendsen et al. 2002). Lilliehöökfjorden is strongly influenced by the tidewater glacier Lilliehöökfjorden (Svendsen et al. 2002). The coastal water is of WSC origin and contains AW with increased temperature and salinity. In the inner parts of Krossfjorden, low temperature (<1 °C) local water that derives from glacial melt water spreads mostly over the AW. The surface water is also characterized by a lower salinity, 30 (PPS) in the middle of the fjord and <28 (PPS) in the inner basin near the glaciers. This surface water occupies several meters of the upper water column with a decreasing thickness towards the fjord mouth (Svendsen et al. 2002).

Sea ice usually forms in January/February and starts to break up between April and July (Svendsen et al. 2002; Spreen et al. 2008; data from AMSR-E Sea Ice Maps). Mean annual water temperatures are 0.6 °C at the surface and 0.7 °C at 50 m water depth. Mean annual salinities are 33.6 (PPS) at the surface and 34.7 (PPS) at 50 m water depth (data from LEVITUS 94).

Mosselbukta (79°53′N, 15°55′E) (Fig. 1) is a bay 5 km long and up to 8 km wide located at the mouth of the Wijdefjorden along the west shore of Mosselhalvøya

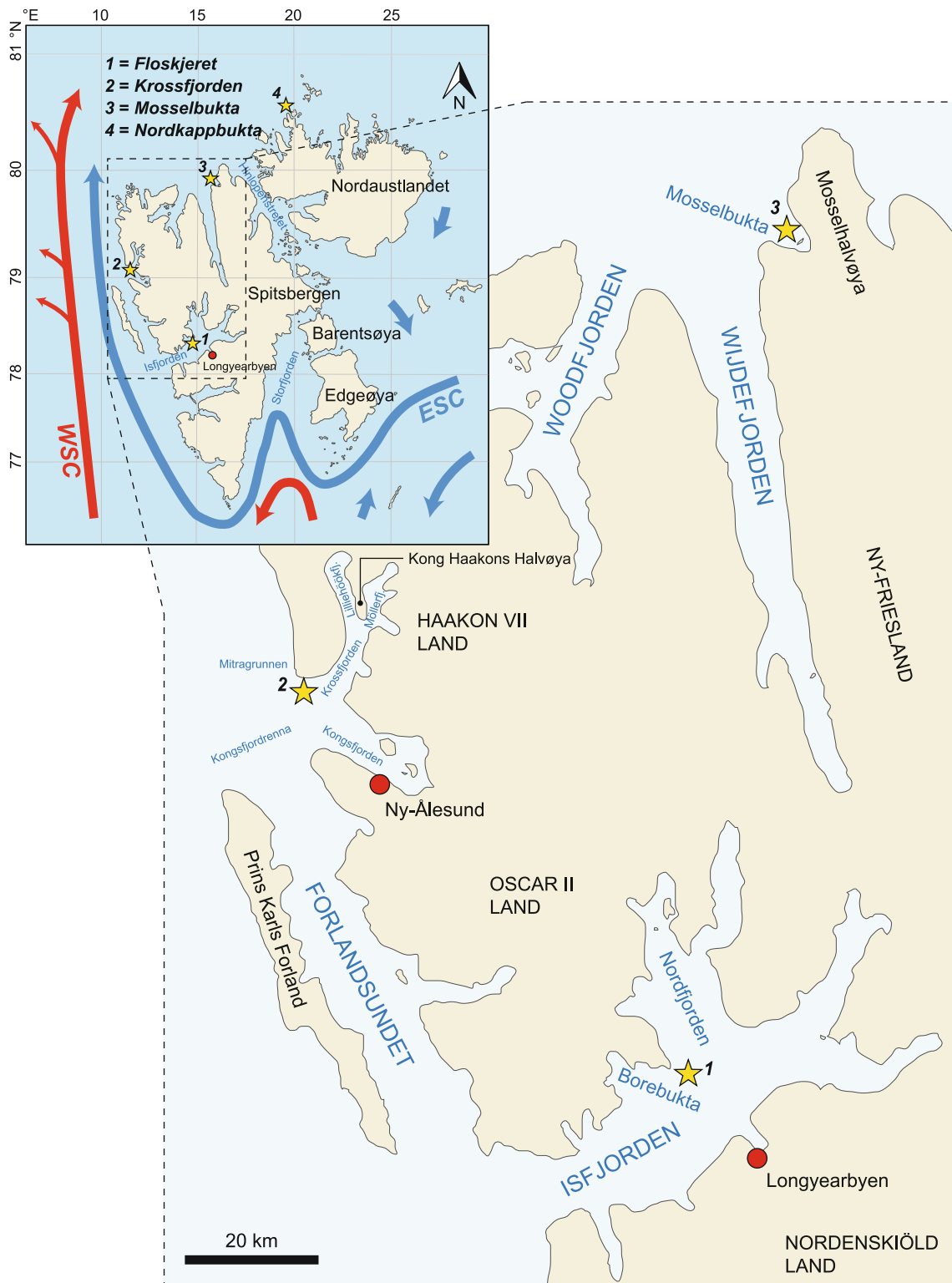


Fig. 1 Map of the Svalbard Archipelago (modified after Harland 1997) showing main islands, progressions of East (ESC, blue) and West Spitsbergen Current (WSC, red), and study sites; data for Nordkappbukta are presented in Teichert et al. (2012)

peninsula at the northern end of Ny-Friesland. It is a locality studied by Kjellman (1875a, b), who found rhodolith beds covering the whole seabed in some areas. The

geology features Late Paleoproterozoic basement of the Stubendorffbreen Supergroup, mainly consisting of psammites, quartzites, and amphibolites (Harland 1997).

In the area of Mosselbukta and Wijdefjorden, a mixing of AW and ArW occurs. The impact of AW is only pronounced during seasonally occurring WSC activity; the rest of the time, ArW prevails (Sapota et al. 2009). Sea ice usually forms in December/January and starts to break up between May and July (Spren et al. 2008; data from AMSR-E Sea Ice Maps). Mean annual water temperatures are 0.3 °C at the surface and 0.7 °C at 50 m water depth. Mean annual salinities are 33.3 (PPS) at the surface and 34.8 (PPS) at 50 m water depth (data from LEVITUS 94).

Materials and methods

Samples and data were obtained between July 31 and August 17, 2006 during the MSM 02/03 cruise of RV *Maria S. Merian* (Table 1).

Seafloor exploration

Seabed mapping was done using a KONGSBERG EM 1002 multibeam echo sounder (see Table 1 for start and end points of the multibeam surveys) that operated at a nominal sonar frequency of 95 kHz and was controlled with the software SIS (Seafloor Information System). NEPTUNE bathymetric post-processing software was used for correction and cleaning of multibeam raw data and for graphic description of the raw data to identify problems. CFLOOR software was used for chart production based on NEPTUNE data to generate digital terrain models.

The manned submersible JAGO was used for visual inspection and video documentation of the seafloor on dive tracks pre-selected in relation to the multi-beam data, and for rhodolith sampling with a hydraulic manipulator arm (see Table 1 for start and end points of JAGO dive tracks). The submersible was certified to a maximum operating depth of 400 m and accommodated two persons, the pilot and a scientific observer.

CTD measurements and seawater sampling

Altogether, seven CTD surveys were carried out (Table 1) and water samples for determining total alkalinity (TA) and dissolved inorganic carbon (DIC) were taken at the maximum water depth at each station using a SEA-BIRD SBE CTD mounted with a rosette of 24 water bottles (10 l capacity each). Additional near-bottom water samples were obtained by a 5-l Niskin bottle attached to the JAGO submersible.

Temperature was measured in °C and salinity was measured using the practical salinity scale (PSS). TA was determined by potentiometric titration (Gran 1952) using a METROHM BASIC TITRINO 794 system and DIC was

analyzed by means of a SEAL QUAATRO autoanalyzer, following the method of Stoll et al. (2001). TA and DIC results were corrected by parallel measurements of certified reference standards (Dickson et al. 2003). The carbonate system parameters pH, carbon dioxide partial pressure ($p\text{CO}_2$), calcite saturation (Ω_{Cal}), and aragonite saturation (Ω_{Arg}) were calculated from TA, DIC, temperature, and salinity.

Light measurements

Three profiles of the photosynthetic active radiation (PAR; unit = $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) in the water column were obtained with a LI-COR Spherical QUANTUM Sensor (LI-193SA) in combination with a LI-COR data logger (LI-1400) and a 100-m-long cable (see Table 1 for light survey points). In order to minimize potential bias due to shadows cast by the research vessel and to enable controlled measurements just below the water surface, the measurements were undertaken from the small rescue boat of RV *Maria S. Merian*.

Surface PAR was measured and used as a reference for various weather conditions. Raw data were transformed to percentages with respect to surface illumination to determine the photic zone boundaries at each study site.

Benthic community sampling

A dredge with an opening of 100 cm in width and 40 cm in height and a net of 0.5 cm mesh size was used to sample macro- and megabenthic epifauna at Krossfjorden (two hauls) and Mosselbukta (one haul) (see Table 1 for start and end points of hauls). No dredge samples were taken at Floskjeret. Net catches were sieved (1 mm), animal organisms were collected from the overall catch, and fixed in 70 % alcohol for later analysis in the laboratory using a ZEISS STEMI 2000 stereo microscope and a LEICA APOZOOM 1:6 M420 macroscope equipped with a LEICA DFC-320 Digicam. Specimens were determined to the lowest possible taxonomical level. Voucher specimens are housed at Senckenberg am Meer, Wilhelmshaven.

Rhodolith sampling

Rhodolith samples were collected using the hydraulic manipulator arm of the manned submersible JAGO during the six seafloor surveys (see Table 1 for the start and end points of the JAGO dive tracks) and by dredge (see previous section). Samples were collected from station 757 at Floskjeret, stations 637, 644, and 652 at Krossfjorden, and station 684 at Mosselbukta (Table 1). After collection, specimens were air dried and stored in air-tight containers. Voucher specimens are housed at Senckenberg am Meer, Wilhelmshaven.

Table 1 Station and gear list of RV *Maria S. Merian* MSM 02/03 expedition showing gear used and start and end points of tracks/scans

Station #	Gear	Location	Date	Start				End			
				Time (UTC)	Lat. [°N]	Long. [°E]	Depth [m]	Time (UTC)	Lat. [°N]	Long. [°E]	Depth [m]
616	CTD	Floskjeret	7/31/2006	10:18	78°09.29'	13°50.05'	424	10:55	78°09.29'	13°50.05'	424
632	CTD	Krossfjorden	8/1/2006	23:36	79°02.37'	10°46.99'	340	00:09	79°02.37'	10°46.99'	340
633-1	MB	Krossfjorden	8/2/2006	00:45	79°02.65'	10°45.57'	341	01:11	79°05.80'	10°43.26'	42
633-2	MB	Krossfjorden	8/2/2006	01:17	79°05.77'	10°44.31'	49	01:46	79°02.70'	10°50.48'	332
633-3	MB	Krossfjorden	8/2/2006	02:01	79°02.96'	10°54.97'	350	02:30	79°05.79'	10°44.91'	46
633-4	MB	Krossfjorden	8/2/2006	02:35	79°05.79'	10°45.88'	53	03:06	79°03.42'	10°59.14'	308
633-5	MB	Krossfjorden	8/2/2006	03:18	79°04.22'	11°01.06'	184	03:46	79°05.86'	10°46.47'	46
633-6	MB	Krossfjorden	8/2/2006	03:52	79°05.91'	10°47.86'	53	04:17	79°04.81'	11°03.29'	110
633-7	MB	Krossfjorden	8/2/2006	04:26	79°05.30'	11°04.03'	94	04:54	79°06.03'	10°48.37'	43
633-8	MB	Krossfjorden	8/2/2006	05:01	79°06.16'	10°50.65'	n.d.	05:21	79°05.69'	11°03.93'	93
633-9	MB	Krossfjorden	8/2/2006	05:28	79°06.08'	11°03.37'	115	06:05	79°06.42'	10°42.34'	36
633-10	MB	Krossfjorden	8/2/2006	06:05	79°06.42'	10°42.34'	36	06:38	79°06.37'	11°03.68'	130
634	JAGO	Krossfjorden	8/2/2006	08:19	79°04.50'	10°47.20'	261	10:49	79°04.99'	10°47.65'	140
636	DRG	Krossfjorden	8/2/2006	14:17	79°05.37'	10°47.22'	99	15:05	79°05.69'	10°49.44'	100
637	DRG	Krossfjorden	8/2/2006	15:34	79°05.94'	10°48.21'	51	16:11	79°05.84'	10°46.36'	49
638-1	MB	Krossfjorden	8/2/2006	17:27	79°04.66'	10°43.61'	213	19:53	79°05.92'	10°52.50'	136
638-2	MB	Krossfjorden	8/2/2006	20:28	79°05.11'	10°56.19'	127	21:35	79°04.23'	11°25.67'	n.d.
639	MB	Krossfjorden	8/2/2006	21:35	79°04.23'	11°25.67'	n.d.	08:00	79°05.69'	10°46.84'	70
640	CTD	Krossfjorden	8/2/2006	23:56	79°18.32'	11°36.69'	132	00:21	79°18.32'	11°36.69'	132
641	CTD	Krossfjorden	8/3/2006	01:32	79°12.99'	11°44.48'	243	01:46	79°12.99'	11°44.48'	243
642	CTD	Krossfjorden	8/3/2006	02:36	79°09.10'	11°46.73'	350	03:10	79°09.10'	11°46.73'	350
643	CTD	Krossfjorden	8/3/2006	04:05	79°05.55'	11°34.30'	283	04:33	79°05.54'	11°34.30'	284
644	JAGO	Krossfjorden	8/3/2006	06:39	79°05.70'	10°46.74'	71	09:29	79°05.95'	10°45.61'	41
651	MB	Krossfjorden	8/4/2006	01:46	79°12.87'	11°44.37'	234	05:40	79°03.64'	11°14.86'	106
652	JAGO	Krossfjorden	8/4/2006	06:56	79°03.52'	11°14.05'	99	09:29	79°04.35'	11°14.43'	47
654	PAR	Krossfjorden	8/4/2006	12:56	79°05.45'	10°48.20'	95	n.d.	n.d.	n.d.	n.d.
669	CTD	Mosselbukta	8/6/2006	03:51	79°55.33'	15°35'17"	156	04:08	79°55'33"	15°35.16'	156
670	MB	Mosselbukta	8/6/2006	06:28	79°54.20'	15°44.91'	81	10:33	79°53.40'	15°45.88'	42
671	JAGO	Mosselbukta	8/6/2006	11:40	79°54.64'	15°48.62'	44	14:09	79°54.51'	15°50.23'	27
672	PAR	Mosselbukta	8/6/2006	11:40	79°54.57'	15°49.72'	44	13:00	79°54.57'	15°49.72'	44
675	DRG	Mosselbukta	8/6/2006	20:57	79°54.21'	15°46.94'	61	21:59	79°53.52'	15°44.89'	72
684	JAGO	Mosselbukta	8/7/2006	16:43	79°53.72'	15°44.75'	80	19:24	79°53.54'	15°46.58'	44
685	PAR	Mosselbukta	8/7/2006	16:55	79°53.73'	15°44.62'	79	17:34	79°53.61'	15°45.65'	61
756	MB	Floskjeret	8/17/2006	08:17	78°18.30'	14°34.32'	127	08:58	78°18.86'	14°31.94'	54
757	JAGO	Floskjeret	8/17/2006	10:30	78°18.64'	14°32.00'	63	12:34	78°18.74'	14°31.22'	40

CTD conductivity, temperature and depth recorder, MB multibeam echosounder, JAGO manned submersible JAGO, PAR photosynthetic active radiation, DRG dredge, n.d. no data

Coralline algal taxonomy

Coralline species were determined using thin-sections (ZEISS STEMI 2000 stereo microscope, LEICA APO-ZOOM 1:6 M420 macroscope with Leica DFC-320 Digi-cam), histological slices (ZEISS AXIOPHOT), and samples for the scanning electron microscope (SEM, TESCAN VEGA \ XMU). For preparation of SEM samples,

longitudinal broken protuberances were attached to aluminium stubs using PONAL express wood glue and cleaned with compressed air after hardening. Samples were sputter-coated with gold for 4 min using a CRESSINGTON 108 auto sputter coater and were examined at an electron beam energy of 20–30 kV.

Identification of *Lithothamnion glaciale* Kjellman (1883) was based on Adey (1964, 1966b, 1970b, including

species keys), Adey et al. (2005), including comparisons of *L. glaciale* with *L. tophiforme* (Esper) Unger, 1858 and *L. lemoineae* Adey, 1970), Irvine and Chamberlain (1994, including species keys and accounts), and Kjellman (1883, 1885, containing the original account of *L. glaciale*).

Identification of *Phymatolithon tenue* (Rosenvinge) Düwel and Wegeberg was based on Rosenvinge (1893) and Düwel and Wegeberg (1996).¹ Teichert et al. (2012) provide additional information on Svalbard Archipelago specimens.

The JAGO video footage also showed occurrences of non-calcareous red algae that were mostly finely filamentous and resembled *Polysiphonia* Greville (Rhodomelaceae, Ceramiales; see also Womersley 1979). No specimens were collected during the cruise and they are referred to hereafter as “*Polysiphonia*-like red algae”.

Rhodolith description and classification

Rhodoliths were described and classified using specimens from Floskjeret (45 m water depth, $n = 37$), Krossfjorden (41–50 m water depth, $n = 122$), and Mosselbukta (44 m water depth, $n = 92$). Rhodolith shape was analyzed by measuring the specimens long (L), intermediate (I), and short (S) axes and applying the maximum projection sphericity formula ($\sqrt{\frac{S^2}{LI}}$) as described in Bosence (1983a). Results were plotted into a pebble-shape diagram (Sneed

and Folk 1958) using the MICROSOFT EXCEL sheet Triplot (Graham and Midgley 2000).

Rhodolith size was estimated by calculating the volume of an ellipsoid ($\sqrt{\frac{LIS}{4\pi}}$) as described in Bosence (1976).

Results

Seafloor and rhodolith bed properties

In this study, coralline red algae occur either as “coralline algal encrustations” or as “rhodoliths”. The term “coralline algal encrustation” means that the alga grows on hard substrate (e.g., a lithoclast) and contributes <50 vol% to the overall structure, while the term “rhodolith” indicates that the algal component is >50 vol% of the overall structure. Estimating the overall volume of coralline red algal material is essential, irrespective of species. A rhodolith can be monospecific (consisting of a single coralline species) or multispecific (consisting of several coralline species) (Bosence 1983a). Additionally, rhodoliths commonly have more highly developed protuberances in terms of size and number per unit surface area. At all study sites, bioclasts are of minor importance as a substrate for coralline red algal settlement, probably due to the poor stability of the bioclasts.

The Floskjeret site (78°18'N, 14°32'E) multibeam echosounder map (Fig. 2a) covers ~0.4 km² and includes dive track 757. Both *L. glaciale* and *P. tenue* occur.

Dive track 757 (60–40 m water depth) (Fig. 2a), which heads towards the inner part of Borebukta, shows a smooth seafloor covered with presumably glaciogenic lithoclasts of cobble size, and bioclasts mainly consisting of shells, barnacles, and sea urchin tests, covered with fine sediment. At 60 m water depth, coverage with coralline algal encrustations on hard substrate, which is free of fine sediments, is <5 % and limited to smooth crusts without protuberances (Fig. 3a). This coverage increases with decreasing water depth to up to 100 % in 47-m water depth, where coralline algal encrustations with well-developed protuberances (>5 mm length) and rhodoliths up to 20 cm in diameter occur (Fig. 3b). Coequally, fine sediment decreases. These conditions do not change up to 40 m water depth.

The Krossfjorden site (79°08'N, 11°40'E) multibeam echosounder map (Fig. 2b) covers ~176 km² and includes dive tracks 634, 644, 647, and 652. The only coralline detected was *L. glaciale*.

Dive track 634 (250–140-m water depth) (Fig. 2b), south of Mitragrunnen Bank, shows presumably glaciogenic pebbles and cobbles covered with fine sediment. The well-sorted lithoclastic pavement is regularly grooved by

¹ *Phymatolithon tenue* has incorrectly been associated with the name *Leptophytum laeve*, a heterotypic synonym of *Phymatolithon lenormandii*. Complex nomenclatural issues are involved. Düwel and Wegeberg (1996) concluded from a study of relevant type specimens and other material that *P. tenue* was a distinct species, that the designated epitype of *L. laeve* Adey (1966a) was conspecific with the type of *P. lenormandii*, and that Adey's (1966a) concept of *L. laeve* was in full accord with *P. tenue* (see also Woelkerling et al. 2002). The holotype of *L. laeve*, a Strömfelt specimen originally described as *L. laeve* (Strömfelt 1886), was considered by Düwel and Wegeberg (1996) to be demonstrably ambiguous and not critically identifiable for purposes of the precise application of a name to a taxon, necessitating designation of an epitype. The interpretation (Athanasidis 2007, p. 485) that *P. tenue* is a heterotypic synonym of *L. laeve* stems from the arguments (Adey et al. 2001) that the designated epitype and the holotype of *L. laeve* differ taxonomically and that the designated epitype is in serious conflict with the protologue. Based on these arguments, Athanasidis and Adey (2003) proposed the formal conservation of the name *L. laeve* Strömfelt with a conserved type. The nomenclatural Committee for Algae (Compère 2004), however, concluded that the arguments mentioned above were not substantiated, and the proposal was unanimously rejected. The Committee for Algae (Prud'homme van Reine 2011) also noted that subsequent arguments (Athanasidis and Adey 2006, p. 72; Athanasidis 2007, p. 485) that the epitypification of Düwel and Wegeberg was “non-effective” involve incorrect, unacceptable interpretations of the International Code of Nomenclature. The above statement is reproduced with the permission of Prof. M.D. Guiry from *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org>, searched on April 4, 2013.

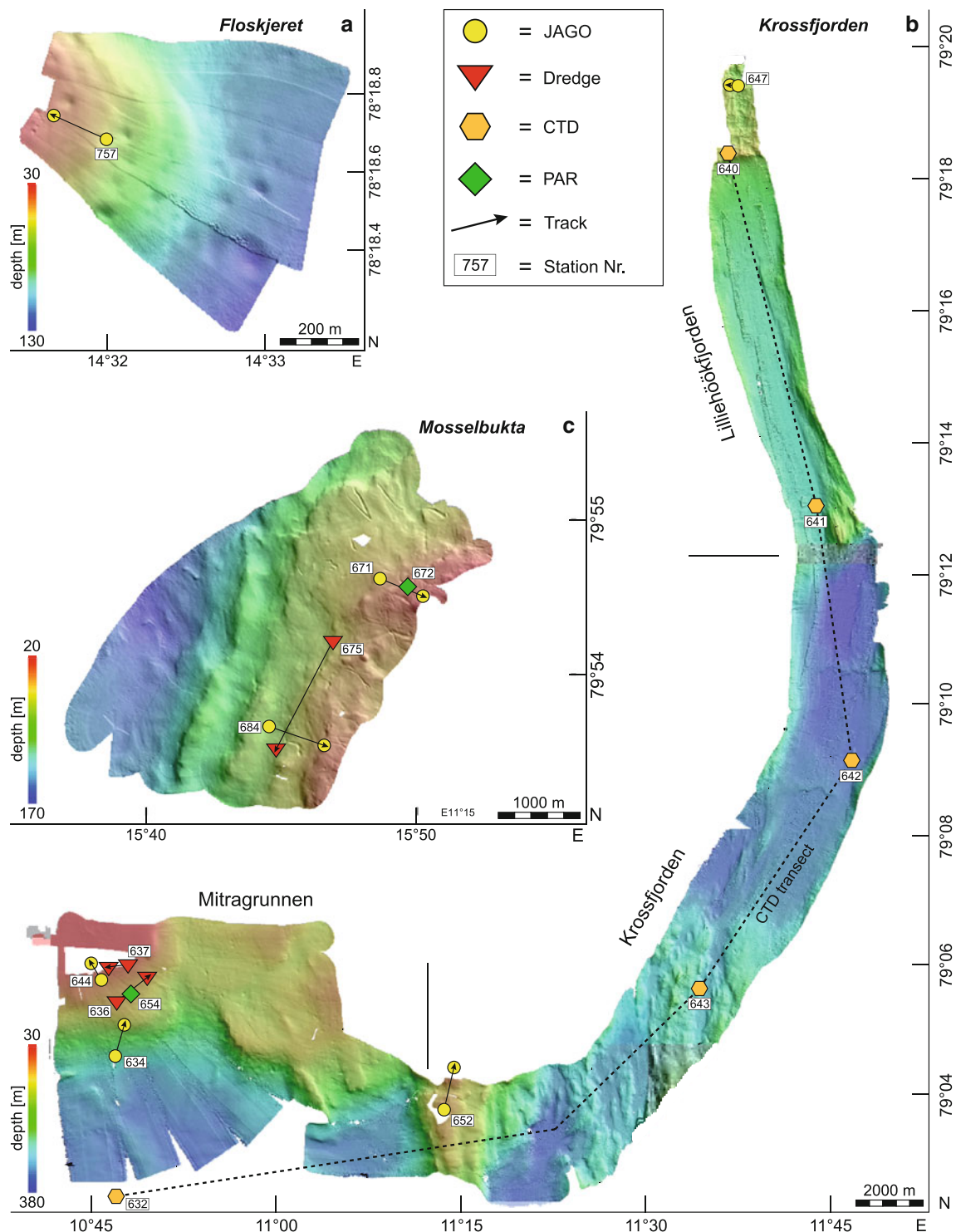


Fig. 2 Multibeam maps showing seafloor morphology, depth zonation, and positions of applied gear (see also Table 1); note different scales and depth ranges: **a** Floskjeret, with constantly rising seafloor from SE to NW and variably sized depressions presumably being iceberg grounding-marks; **b** Krossfjorden, consisting of Lilliehöökfjorden, Krossfjorden, and Mitragrunnen Bank at the mouth of Krossfjorden. The inner part of Lilliehöökfjorden begins with the steep glacier slope of Lilliehöökbrean in ~150 m water depth and leads into a narrow channel with smooth morphology and ~270 m

water depth. When the channel turns to the SW, it passes into Krossfjorden and the morphology changes to a steep moraine ridge in ~50 m water depth at the entrance of the fjord. Beyond this ridge, the seafloor rapidly rises into the Mitragrunnen Bank; **c** Mosselbukta with continuously rising seafloor from ~170 to ~20 m water depth towards the shore in the SE, showing a strong morphology with distinct ridges heading parallel to the shoreline. Iceberg scouring-marks are clearly visible and are perpendicular to the shoreline

sediment-trapping iceberg scouring-marks oriented parallel to the slope. With decreasing water depth, the amount of fine sediment decreases, coarse material becomes less sorted, and the quantity of shells increases. Coralline algal encrustations and rhodoliths are absent.

Along dive track 644 (60–41 m water depth) (Fig. 2b), situated at the margin of Mitragrunnen Bank, patches of pebbles and cobbles alternate with depressions up to 1 m in depth and up to 15 m in diameter. These depressions contain shell accumulations on fine sediment. Coralline algal encrustations appear at 58 m water depth ($\sim 5\%$ coverage) and $\sim 20\%$ of the crusts have protuberances. Coralline algal encrustations are restricted to pebbles and cobbles while fine sediment depressions and bioclasts are not colonized. From a water depth of 53 m upwards, coralline algal encrustation cover on hard substrate increases to 25–75 %, and up to 50 % of the corallines have well-developed protuberances. Rhodoliths are absent.

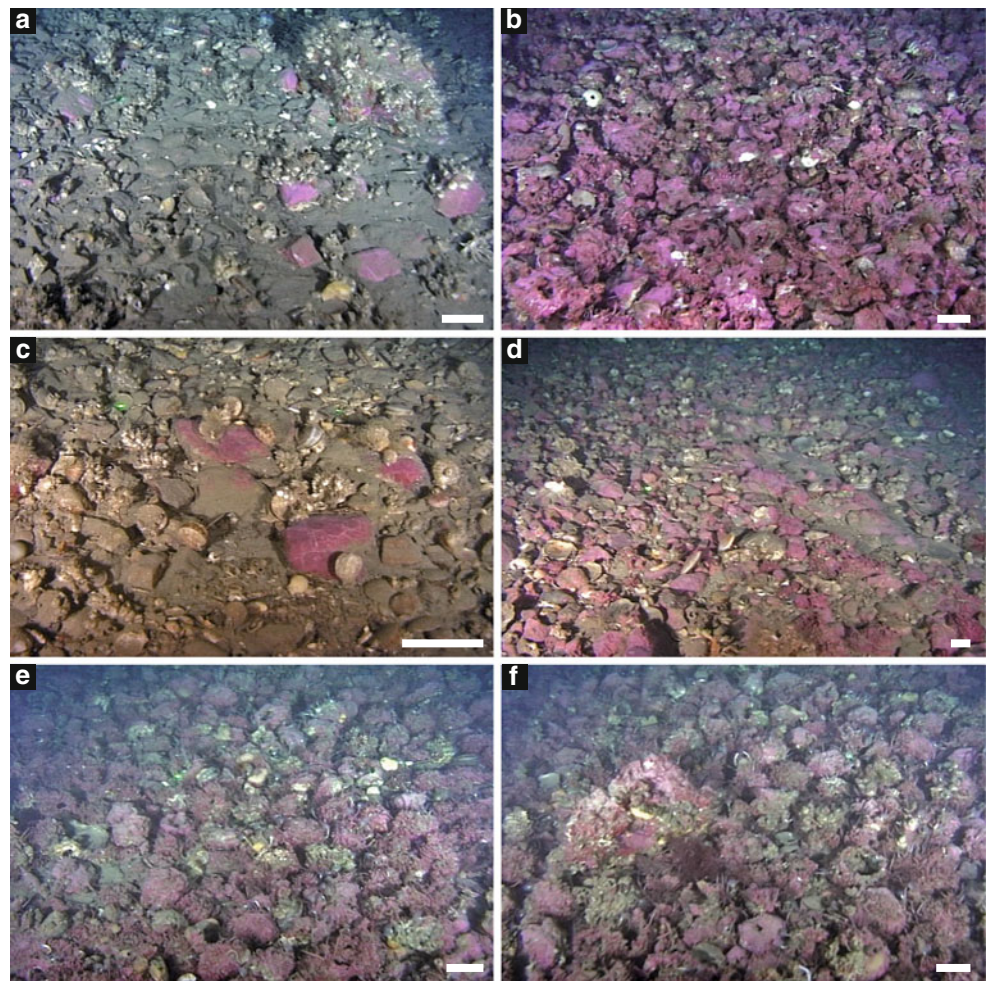
Dive track 647 (41–39-m water depth) (Fig. 2b), along the glacier slope of Lilliehöökreen, shows a fine sediment seafloor with distinct morphology. This sediment presumably originates directly from the melting glacier front, and

the general seafloor morphology appears to change regularly as a result of glacial dynamics. Lithoclastic hard substrate such as pebbles and cobbles, shell accumulations, coralline algal encrustations, and rhodoliths were not detected.

Dive track 652 (92–47 m water depth) (Fig. 2b), along the moraine ridge at the entrance of Krossfjorden, shows distinct iceberg scouring-marks perpendicular to the ridge. The seafloor features pebbles and cobbles, while boulders ($>1\text{ m}^3$) are rare. Accumulations of shells and fine sediment is limited to small depressions (up to 0.5 m in depth and up to 5 m in diameter) and to iceberg scouring-marks. Coralline algal encrustations appear at 77 m water depth ($<5\%$ surface coverage) and constantly increase in coverage and in development of protuberances (Fig. 3c). At 50 m water depth, $\sim 40\text{--}80\%$ of hard substrate is covered with coralline algal encrustations, generally with well-developed protuberances. Additionally, rhodoliths up to 15 cm in diameter occur but are rare (Fig. 3d).

The Mosselbukta site ($79^{\circ}53'\text{N}$, $15^{\circ}55'\text{E}$) multibeam echosounder map (Fig. 2c) covers $\sim 13\text{ km}^2$ includes dive tracks 671 and 684. Only *L. glaciale* was found.

Fig. 3 JAGO seafloor photographs. **a** Smooth coralline algal encrustations on lithoclastic cobbles free from fine sediment (Floskjeret, dive track 757, 60 m water depth). **b** Rhodoliths up to 20 cm in diameter (Floskjeret, dive track 757, 47 m water depth). **c** Coralline algal encrustations on lithoclastic cobbles above a distinctive size (Krossfjorden, dive track 652, 77 m water depth). **d** Rhodoliths up to 15 cm in diameter (Krossfjorden, dive track 652, 50 m water depth). **e**, **f** Rhodoliths up to 25 cm in diameter and some hollow specimens (Mosselbukta, dive track 671, 42 m water depth); note the connection between coralline algal development and water depth (scale bars 10 cm)



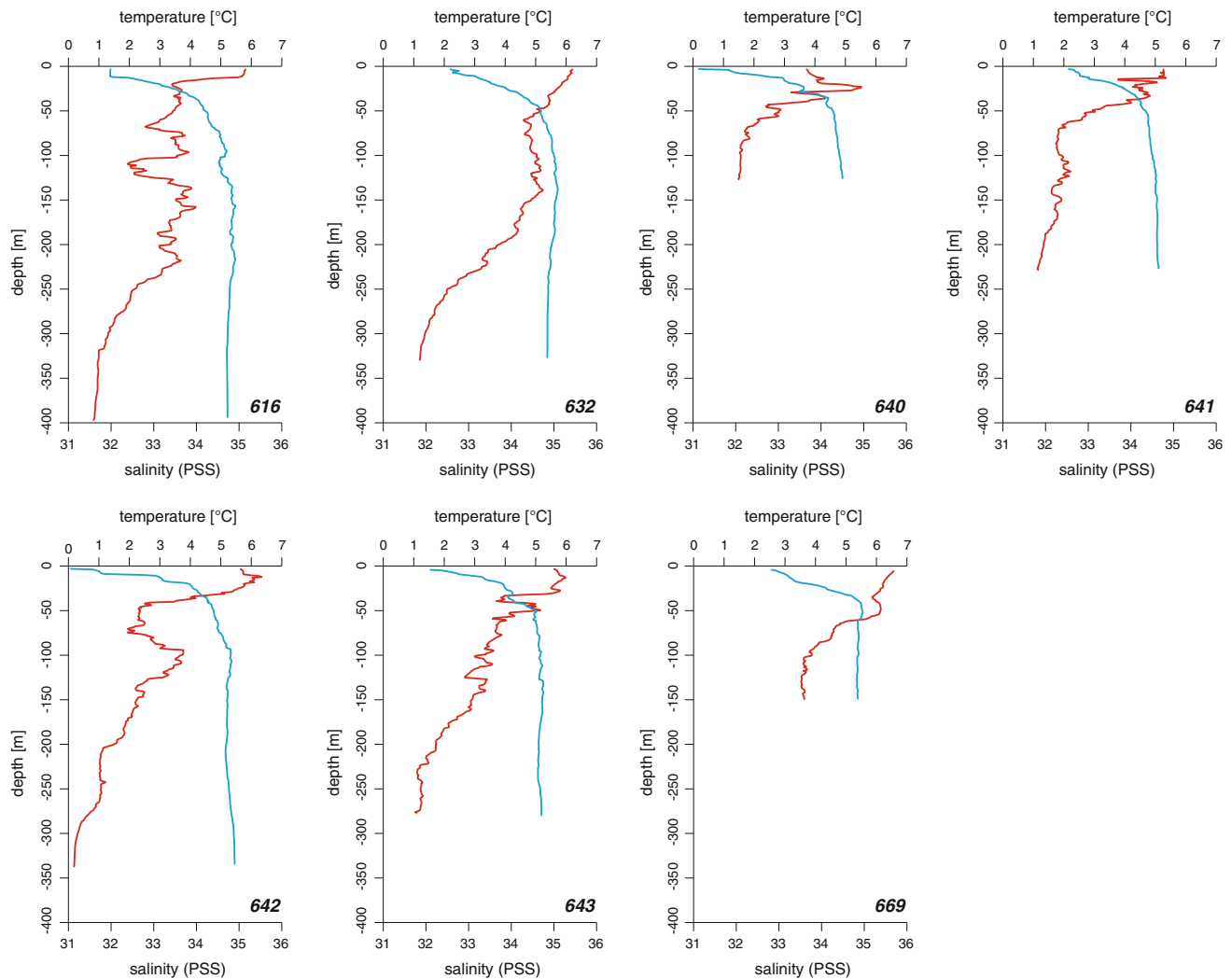


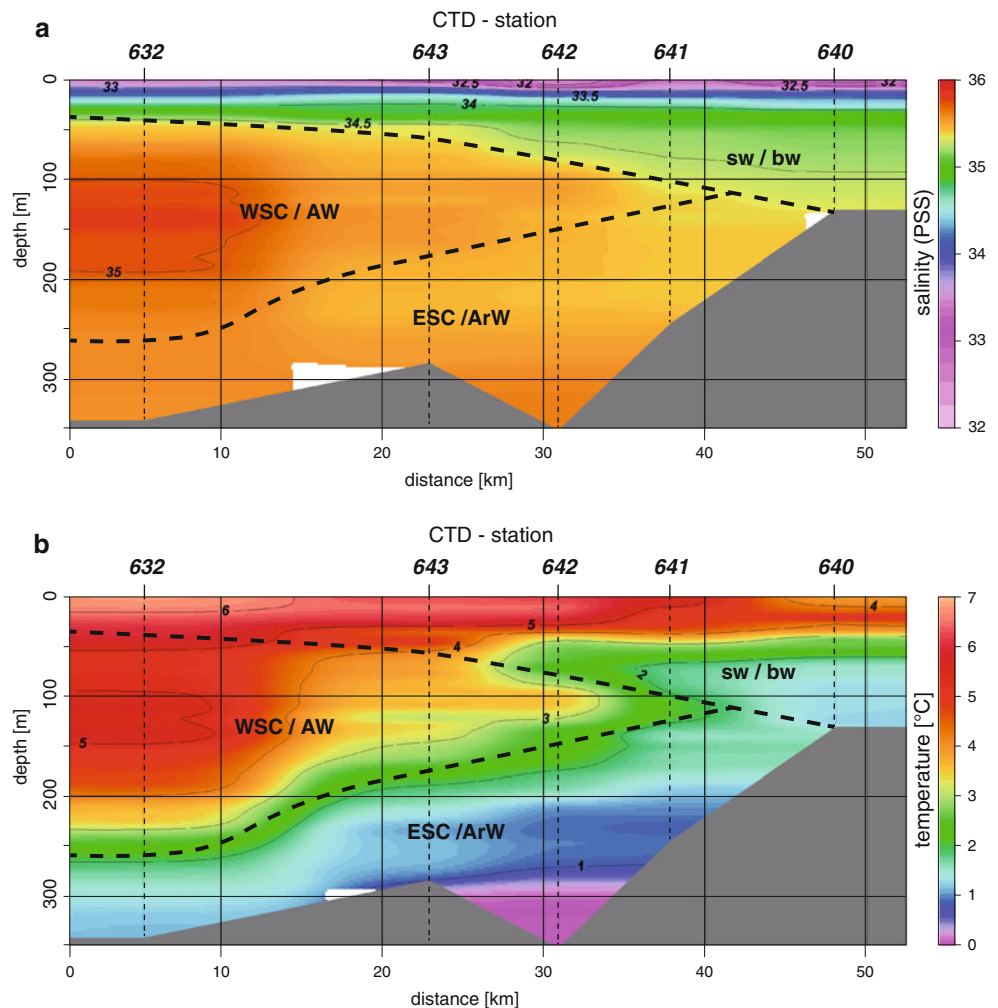
Fig. 4 CTD-profiles from stations 616 (Floskjeret), 632, 640, 641, 642, 643 (Krossfjorden), and 669 (Mosselbukta), showing similar patterns of increasing salinities and decreasing temperatures with increasing water depth

Along dive track 671 (42–27 m water depth) (Fig. 2c), 80–100 % of the seafloor at 42 m water depth is covered with coralline algae, partly in form of coralline algal encrustations, but mostly as rhodoliths (Fig. 3e, f). The rhodoliths are up to 25 cm in diameter, show well-developed protuberances, and some are hollow. At 37 m water depth, rhodolith coverage suddenly disappears. The coralline algae are reduced to thin encrustations attached to pebbles and cobbles, which lie on the fine sediment, and *Polysiphonia*-like red algae appear. The coverage with *Polysiphonia*-like red algae increases with further seafloor shallowing and coralline algal encrustations are reduced to growing on the upper parts of occasional boulders (>1 m³), which surmount the *Polysiphonia* fields. At 27-m water depth, two iceberg scouring-marks of ~50 m in length appear. Here, *Polysiphonia*-like red algae are absent and remaining coralline algal encrustations are bleached. Marks are carved into the seafloor and bleached, exhumed

coralline algal encrustations and rhodoliths of unknown age are present.

Dive track 684 (78–44 m water depth) (Fig. 2c) shows a presumably glaciogenic pebble and cobble pavement. At 78 m water depth, living barnacles are very common and coralline algal encrustations are absent. The size of the cobbles increases from 74 m water depth, and boulders (>1 m³) are visible. Coralline algal encrustations first appear in 70 m water depth but with <5 % coverage. At 64 m water depth, coralline algal encrustations on larger cobbles and boulders become more common (~10 % coverage) and the first protuberances are present. At 62 m water depth, a patch of pebbles and cobbles is covered with a fine sediment layer and coralline algal encrustations are not detectable. Development of protuberances markedly increases at a depth of 55 m, and coralline algal encrustation occurs on ~30 % of the larger cobbles. At 46 m water depth, rhodoliths up to 20 cm in diameter cover 60–80 % of

Fig. 5 CTD transects through Krossfjorden from Lilliehöökreen glacier slope to fjord mouth (see Fig. 2b for transect course). **a** Decreasing salinity to the inner fjord due to an incumbent brackish water layer. **b** Mixture of cold ESC and warm WSC water masses resulting in turbulence development. Transects were created using Ocean Data View 4 (Schlitzer 2012); WSC/AW West Spitsbergen Current/Atlantic Water, ESC/ArW East Spitsbergen Current/Arctic Water, sw/bw surface water/brackish water



the seafloor, and many of the specimens are hollow. A small field of *Polysiphonia*-like red algae occurs at 46 m water depth, and coralline algal encrustations and rhodoliths are absent in the areas where these filamentous red algae grow.

Temperature and salinity patterns

CTD records from stations 616 (Floskjeret), 632, 640, 641, 642, 643 (Krossfjorden), and 669 (Mosselbukta) show similar patterns of increasing salinities and decreasing temperatures with water depth (Fig. 4). This provides further evidence that stratified summer situations are characteristic for the coastal waters of Svalbard (Svendsen et al. 2002).

Stations from Floskjeret and Krossfjorden, both fjord localities, show distinct surface layers with reduced salinity (<34) present in the upper 10 m of the water column. This indicates an incumbent layer of less saline water originating from glaciers in the inner parts of the fjord system. The discharged melt water has a lower density and mixes only successively with underlying fully marine water masses. This is also the reason why the stratified pattern is very

distinctive in the inner part of the fjords and becomes less pronounced towards the fjord mouths. Underneath the incumbent water layer, salinity increases continuously (>34.5), probably representing AW deriving from the WSC. At station 669 (Mosselbukta), a non-fjord locality, this pattern is less developed and mixing with more saline waters occurs much faster. However, stratification is still visible on a smaller scale.

Decrease of temperature with depth is not continuous but fluctuates. This becomes particularly clear at station 616 at ~120 m water depth (fluctuation between 2.0 and 4.0 °C) and at station 641 at ~25-m water depth (fluctuation between 3.8 and 5.3 °C). This situation occurs because of the mixing of warm water masses deriving from the WSC with cold water masses from the ESC and holds for both Isfjorden and Krossfjorden (fjord localities) and for Mosselbukta (a non-fjord locality). The resulting turbulences lead in part to increasing temperatures with water depth (up to 2 °C from ~75 to ~100 m water depth in profile 642) where boundaries of different water masses are crossed by the CTD profile.

Fig. 6 PAR-measurements. **a** Exponentially decreasing surface illumination with increasing water depth. **b** Depth zonation of the photic zones at Krossfjorden and Mosselbukta

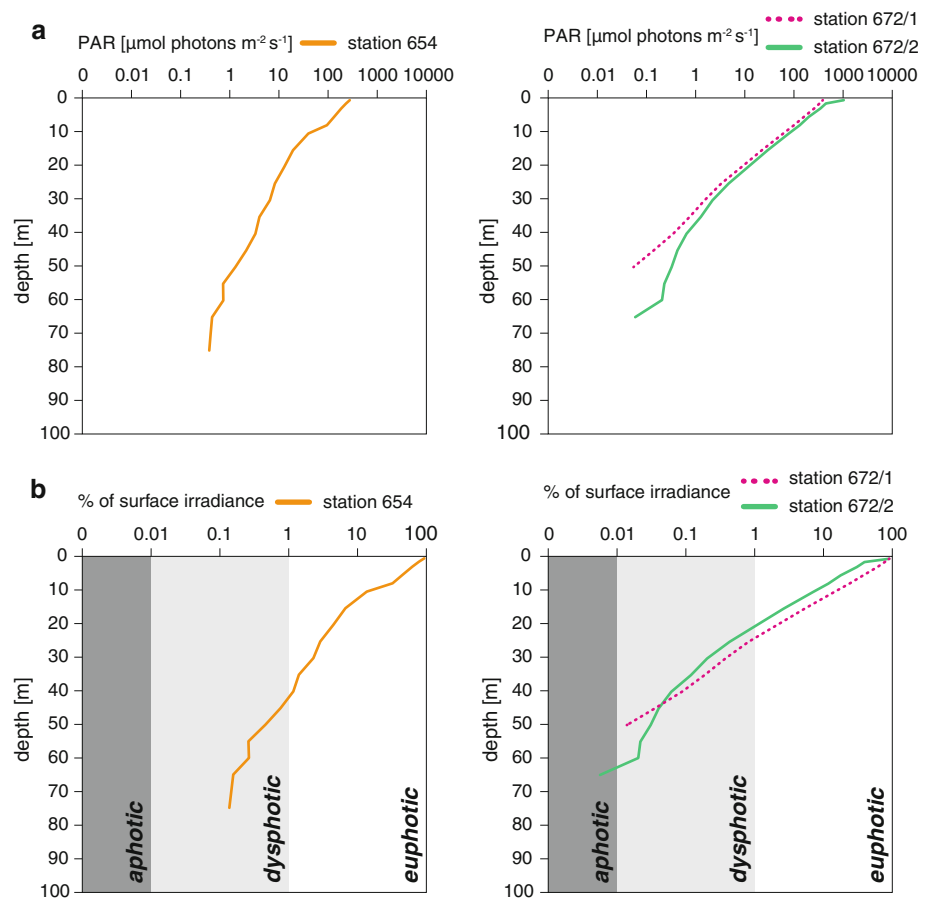


Table 2 Carbonate system parameters at selected stations

Station #	Measured					Computed			
	T [°C]	<i>p</i> [dbars]	Salinity (PSS)	TA [μmol/kg SW]	DIC [μmol/kg SW]	pH (total scale)	<i>p</i> CO ₂ [μatm]	Ω _{Cal}	Ω _{Arg}
616	0.8	417	34.8	2,292	2,227	7.85	593.5	1.44	0.91
632	1.3	332	34.8	2,244	2,178	7.85	589.1	1.45	0.92
640	1.4	132	34.5	2,288	2,125	8.14	297.9	2.76	1.74
641	1.1	231	34.7	2,274	2,144	8.06	363.0	2.26	1.42
642	0.2	341	34.9	2,312	2,215	7.96	458.4	1.81	1.14
643	1.3	283	34.8	2,288	2,148	8.07	348.0	2.36	1.49
652	3.0	47	35.0	2,252	2,098	8.09	336.4	2.67	1.68
669	2.8	147	34.9	2,276	2,218	7.79	716.8	1.47	0.93
684	3.0	44	35.0	2,283	2,136	8.07	360.4	2.59	1.64

T temperature, *p* pressure, *TA* total alkalinity, *DIC* dissolved inorganic carbon, *p*CO₂ carbon dioxide partial pressure, Ω_{Cal} calcite saturation, Ω_{Arg} aragonite saturation

Figure 5a, b show salinity and temperature transects through Krossfjorden (see Fig. 2b for transect course) computed by Ocean Data View 4 (Schlitzer 2012), using data from several CTD-profiles (stations 640, 641, 642, 643, and 632 from the inner fjord to the fjord mouth). The salinity transect shows the incumbent brackish water layer (sw/bw = surface water/brackish water)

derived from the glacier melt-water discharge becoming less pronounced towards the fjord mouth. The temperature transect shows cold ESC water masses in the inner fjord and warm WSC water masses at the fjord mouth. These water masses mix and develop turbulences that are particularly clear at station 642 (see Fig. 4 for the CTD profile).

Table 3 Presence and absence data of identified taxa at Krossfjorden, Mosselbukta, and Nordkappbukta (comprehensive presence/absence data are not available for Floskjeret); species are sorted alphabetically within taxa

Taxon	Site		
	Krossfjorden	Mosselbukta	Nordkappbukta ^a
Rhodophyta			
<i>Lithothamnion glaciale</i> Kjellman, 1883 ^b	×	×	×
<i>Phymatolithon tenue</i> (Rosenvinge) Düwel and Wegeberg, 1996 ^b			×
<i>Polysiphonia</i> -like red algae		×	×
Porifera			
<i>Geodia</i> sp.			×
Cnidaria			
<i>Actinia</i> sp.			×
<i>Gersemia rubiformis</i> (Ehrenberg, 1834)			×
<i>Hormathia nodosa</i> (Fabricius, 1780)			×
<i>Lucernaria quadricornis</i> Müller, 1776	×	×	
Mollusca			
<i>Astarte crenata</i> (Gray, 1824)			×
<i>Boreotrophon clathratus</i> (Linnaeus, 1767)		×	
<i>Boreotrophon truncatus</i> (Ström, 1768)		×	×
<i>Buccinum</i> sp.	×		
<i>Cadlina laevis</i> (Linnaeus, 1767)		×	
<i>Chlamys islandica</i> (Müller, 1776) ^b	×	×	×
<i>Hiatella arctica</i> (Linnaeus, 1767) ^b	×	×	×
<i>Musculus laevigatus</i> (Gray, 1824)			×
<i>Puncturella noachina</i> (Linnaeus, 1771)		×	×
<i>Tectura</i> sp.			×
<i>Tonicella rubra</i> (Linnaeus, 1767) ^a	×	×	×
<i>Tridonta montagui</i> (Dillwyn, 1817)			×
<i>Velutina</i> sp.		×	
Polychaeta			
<i>Brada</i> sp.		×	
<i>Eunoe nodosa</i> (Sars, 1861)		×	
<i>Flabelligera affinis</i> Sars, 1829		×	×
<i>Harmothoe imbricata</i> (Linnaeus, 1767)	×		
<i>Nephtys</i> sp.	×		×
<i>Nereis zonata</i> Malmgren, 1867		×	×
<i>Nothria conchylega</i> (Sars, 1835)	×		
<i>Terebellides stroemii</i> Sars, 1835		×	×
<i>Thelepus cincinnatus</i> (Fabricius, 1780)	×	×	×
Pantopoda			
<i>Nymphon</i> sp.		×	×
<i>Phoxichilidium femoratum</i> (Rathke, 1799)		×	
Crustacea			
<i>Anonyx laticoxae</i> Gurjanova, 1962	×		×
<i>Balanus</i> sp.	×	×	×
<i>Hyas araneus</i> (Linnaeus, 1758)	×	×	×
<i>Hyas coarctatus</i> Leach, 1816	×		
<i>Lebbeus polaris</i> (Sabine, 1824)	×	×	×
<i>Monoculodes borealis</i> Boeck, 1871	×		
<i>Mysis oculata</i> (Fabricius, 1780)	×		

Table 3 continued

Taxon	Site		
	Krossfjorden	Mosselbukta	Nordkappbukta ^a
<i>Pagurus pubescens</i> Krøyer, 1838 ^b	×	×	×
<i>Sabinea sarsii</i> Smith, 1879	×		
<i>Sabinea septemcarinata</i> (Sabine, 1824)	×		
<i>Sclerocrangon ferox</i> (Sars, 1877)	×	×	×
<i>Spirontocaris phippisii</i> (Krøyer, 1841)	×		
<i>Spirontocaris spinus</i> (Sowerby, 1805)	×	×	×
Bryozoa			
<i>Cellepora</i> sp.	×	×	
<i>Flustra foliacea</i> (Linnaeus, 1758)			×
<i>Myriapora coarctata</i> (Sars, 1863)	×	×	
Brachiopoda			
<i>Hemithiris psittacea</i> (Gmelin, 1790)		×	×
Echinodermata			
<i>Crossaster papposus</i> (Linnaeus, 1767)	×	×	
<i>Gorgonocephalus</i> sp. Leach, 1815	×		×
<i>Heliometra glacialis</i> (Owen, 1833)	×		×
<i>Henricia sanguinolenta</i> (Müller, 1776)		×	×
<i>Leptasterias</i> sp.	×		
<i>Ophiacantha bidentata</i> (Bruzelius, 1805) ^b	×	×	×
<i>Ophiocten sericeum</i> (Forbes, 1852)	×		×
<i>Ophiopholis aculeata</i> (Linnaeus, 1767)	×	×	×
<i>Ophiura robusta</i> (Ayres, 1854) ^b	×	×	×
<i>Ophiura sarsii</i> Lütken, 1855	×		
<i>Pteraster militaris</i> (Müller, 1776)		×	
<i>Solaster endeca</i> (Linnaeus, 1771)		×	
<i>Strongylocentrotus</i> sp.	×	×	×
<i>Strongylocentrotus pallidus</i> (Sars, 1871)	×		
Ascidiacea			
<i>Boltenia echinata</i> (Linnaeus, 1767)		×	×
<i>Styela</i> sp.		×	
<i>Styela rustica</i> Linnaeus, 1767		×	×
Pisces			
<i>Artediellus atlanticus</i> Jordan and Evermann, 1898		×	×
<i>Entelurus aequoreus</i> (Linnaeus, 1758)	×		
<i>Eumicrotremus spinosus</i> (Fabricius, 1776)	×		
<i>Gadus morhua</i> Linnaeus, 1758	×		
<i>Liparis</i> sp.	×	×	
<i>Lumpenus lampraeformis</i> (Walbaum, 1792)		×	
<i>Melanogrammus aeglefinus</i> (Linnaeus, 1758)	×		

^a Data from Teichert et al. (2012)

^b Taxa also identified at Floskjeret

These observations, although snapshots, clearly indicate the dynamic nature of the prevailing oceanographic regime, which depends both on the annual changing characteristics of ESC and WSC, and on the changing amounts of glacial melt water discharge.

Light regime

Surface illumination at stations 654 (Krossfjorden) and 672/1 and 672/2 (Mosselbukta) range from 276 to 1,052 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ just below the water surface;

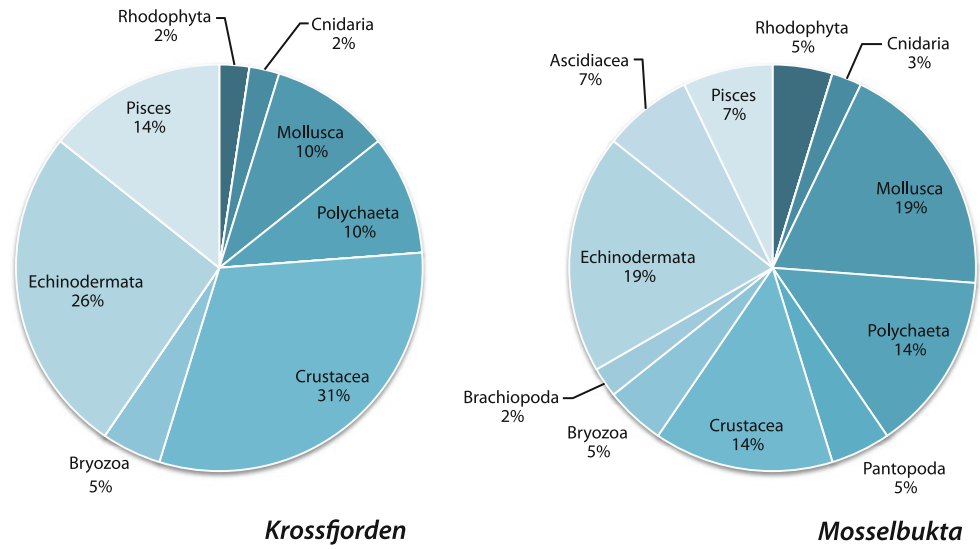


Fig. 7 Pie charts showing the percentages of taxa within higher taxonomic levels at Krossfjorden and Mosselbukta

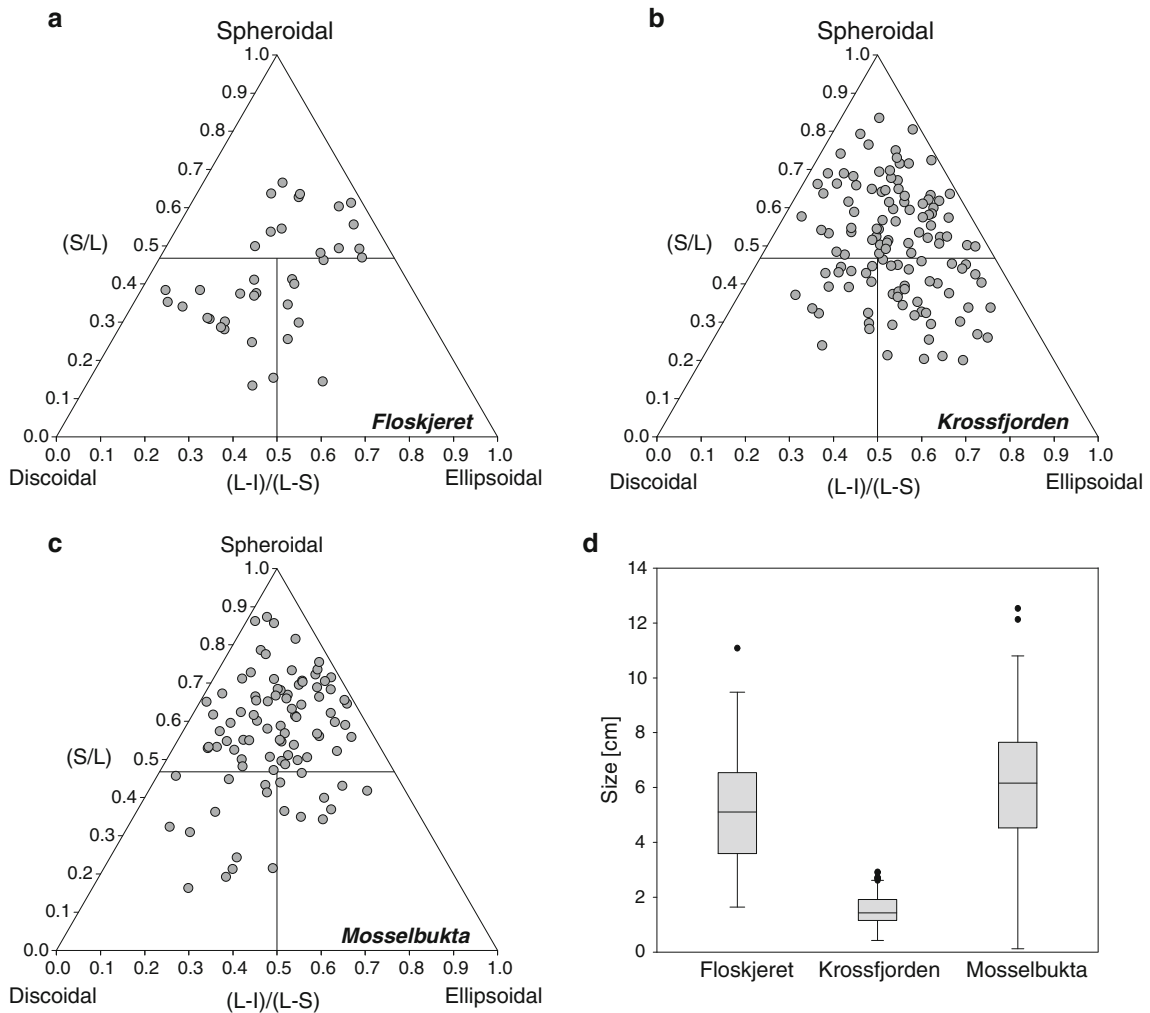


Fig. 8 Tri-plot diagrams showing rhodolith shapes. **a** Floskjeret ($n = 37$). **b** Krossfjorden ($n = 122$). **c** Mosselbukta ($n = 92$). **d** Box plot of rhodolith size ranges at the three sites

light levels decrease exponentially with water depth (Fig. 6a).

Euphotic zone (1 % surface illumination) boundaries are at ~45 m water depth at station 654 and at 20–25 m water depth at station 672/1 and 672/2. The lower dysphotic zone boundary (0.01 % surface illumination) is only reached in profile 672/2, at ~64 m water depth (Fig. 6b). Due to the considerable amount of melt water discharge by Lilliehöökreen, the PAR decreases much faster at Krossfjorden than at Mosselbukta.

Seawater chemistry

Bottom-water parameters are compiled in Table 2. Temperatures are relatively low, indicating that most stations are influenced by the ESC. Due to the particular water depth, salinities show no influence of incumbent water layers with reduced salinity but indicate fully marine conditions.

The pH is >8 for all water depths where rhodoliths occur, and Ω_{cal} is >1 and thus in the range of saturation at all stations. The same applies for Ω_{Arg} except for stations 616 and 632, which are slightly undersaturated with respect to aragonite but were measured in water depths where rhodoliths do not occur.

Benthic community composition

A total of 41 (Krossfjorden) and 42 (Mosselbukta) benthic species (or higher taxa) were identified in dredge samples and JAGO video footage (Table 3). No dredge samples were taken at Floskjeret. These numbers, especially those gained during JAGO dives, are conservative measures of overall species diversity, since more taxa can be found when more samples would be taken and/or a larger variety of sampling tools would be used (Hall-Spencer and Atkinson 1999). The general climate of Svalbard is arctic (Sapota et al. 2009; Svendsen et al. 2002), but due to the influence of the North Atlantic Current system, most benthic species are of Atlantic origin, i.e., they do also occur at boreal latitudes. Endemic Arctic species were not identified in our samples. The Atlantic snake pipefish (*Entelurus aequoreus*) that had hitherto been presumed to be confined to areas south of Iceland (Fleischer et al. 2007), was found at Krossfjorden.

The percentage fractions of higher taxonomic groups are shown in Fig. 7. The important grazers *Tonicella rubra* and *Strongylocentrotus* sp. are present on rhodoliths at all sites, including Floskjeret. Where rhodoliths are present, many benthic organisms can be found on their surfaces, in the interstices between them and inside hollow rhodoliths.

Krossfjorden exhibits the lowest benthic species diversity (Table 3). Crustacea dominate with 13 taxa (31 %), followed by Echinodermata with 11 taxa (26 %), and Pisces with six taxa (14 %). Mosselbukta features a more

balanced species assemblage, with Mollusca and Echinodermata exhibiting the highest diversity of taxa (both eight; 19 % each).

Interactions between animal taxa and rhodolith beds were manifold. The cnidarian *Lucernaria quadricornis* at Krossfjorden was fixed to rhodolith surfaces being a competitor for space. The Iceland scallop (*Chlamys islandica*) and the wrinkled rockborer (*Hiatella arctica*) were found at all sites, occurring inside hollow rhodoliths, and *H. arctica* also occurred in the calcitic matrix. Amongst grazing molluscs, the northern red chiton (*T. rubra*) was the most abundant and fed on rhodolith surfaces. This feeding behavior also holds for Noah's keyhole limpet (*Puncturella noachina*), found at Mosselbukta.

Nine taxa of polychaetes were identified, but only *Thelepus cincinnatus* was found at both Spitsbergen sites. Polychaetes were found inside hollow rhodoliths and also in interstices between them. Pantopoda occurred at Mosselbukta but no interactions with rhodoliths were detected. Crustaceans were abundant at both sites. The hermit crab *Pagurus pubescens* was commonly present in interstices between rhodoliths. Individuals of *Balanus* sp. growing on rhodolith surfaces act as a competitors for space. Many nektonic crustaceans (e.g., *Lebbeus polaris*, present at both sites) were visible just above the rhodolith beds, so interactions cannot be excluded.

The bryozoans *Cellepora* sp. and *Myriapora coarctata* occurred at both Spitsbergen sites, grew on rhodolith surfaces and functioned as space competitors. *Hemithiris psittacea*, the only brachiopod identified, occurred attached to rhodoliths in low numbers at Mosselbukta. Amongst echinoderms, the sea urchins *Strongylocentrotus* sp. (present at both Spitsbergen sites) and *Strongylocentrotus pallidus* (present at Krossfjorden), fed heavily on rhodolith surfaces and acted as bioeroders. Brittlestars, particularly *Ophiacantha bidentata* and *Ophiura robusta*, were very common and occurred at both sites. Brittlestars sheltered in interstices between rhodoliths and collected detritus. Starfish such as *Henricia sanguinolenta* (identified at Mosselbukta) also used the interstices between rhodoliths as shelter.

The fixosessile sea squirts *Boltenia echinata* and *Styela rustica* (Ascidiacea) grew on rhodolith surfaces at Mosselbukta but were not very common. Fish were numerous, but except for the Atlantic hookear sculpin (*Arctediellus atlanticus*) and the snake blenny (*Lumpenus lamprettaeformis*), which use interstices between rhodoliths as shelter, no interactions were detected.

Coralline algal and rhodolith characteristics

Living thalli of *L. glaciale*, collected from all three Spitsbergen localities, are dull in texture and reddish to dull pink in color, and tetrasporangial conceptacles have up to 50

pores in the roof. Like other species of *Lithothamnion*, vegetative filaments of *L. glaciale* are terminated by epithallial cells with flared outer corners. The thalli produce short warty or knobby protuberances up to 19 mm long and of varying diameter from a crustose base.

Phymatolithon tenue, collected at Floskjeret but not at Krossfjorden or Mosselbukta, has a thin encrusting thallus (usually up to 200 µm thick) that does not produce protuberances and has sporangial conceptacles that appear as white dots on the upper thallus surface. Pore canals of the sporangial conceptacles are lined with cells that are mostly somewhat larger than other cells in the conceptacle roof. These features were described and illustrated by Düwel and Wegeberg (1996, p. 478, figs. 29–33) in the type material and are clearly evident in specimens from Floskjeret, where thalli of *P. tenue* grow attached to cobbles and occur intermixed with *L. glaciale*.

Rhodoliths from Floskjeret ($n = 37$) show a slight concentration on discoidal (43 %) and spheroidal (38 %) shapes, while ellipsoidal (19 %) shapes are less abundant (Fig. 8a). Rhodoliths from Krossfjorden ($n = 122$) are dominated by spheroidal (58 %) and ellipsoidal (29 %) shapes (Fig. 8b), while rhodoliths from Mosselbukta ($n = 92$) are mostly (79 %) of spheroidal shape (Fig. 8c).

Box plots of the rhodolith sizes indicate that specimens from Floskjeret and Mosselbukta have a much larger range of size than the rhodoliths from Krossfjorden (Fig. 8d).

The Floskjeret rhodolith community is composed of 86 % monospecific and 14 % multispecific rhodoliths. Monospecific rhodoliths consist either of *L. glaciale* or *P. tenue*, while both species provide ~50 % of the overall seabed coverage. Krossfjorden and Mosselbukta rhodoliths are monospecific and consist of *L. glaciale* only.

Rhodoliths from Floskjeret contain a lithoclastic nucleus or appear as isolated, partly hollow crusts of mostly discoidal shape. Rhodoliths from Krossfjorden always contain a lithoclastic nucleus. Rhodoliths from Mosselbukta contain a lithoclastic nucleus or appear as hollow structures with a central-open space that forms a microhabitat for internal colonization and settlement.

Discussion

Environmental controls

Hydrodynamic regime

The morphology of non-nucleated rhodoliths directly reflects the hydrodynamic regime (Bosence 1983b; Steneck 1986). Ellipsoidal rhodoliths are more easily transported than spheroidal ones, and discoidal rhodoliths are most resistant against displacement through water currents

(Bosence 1983b). The shape of nucleated rhodoliths with lithoclasts, however, is widely predetermined by the shape of the lithoclastic nucleus (Freiwald 1995). The majority of rhodoliths from Floskjeret, Krossfjorden, and Mosselbukta are nucleated and thus cannot be used as indicators for the prevailing hydrodynamic regime. The hollow rhodoliths from Floskjeret and Mosselbukta might have possessed a nucleus that was lost at an earlier growth stage, so they also cannot be used as indicators for the hydrodynamic regime.

Substrate

Although light is the most limiting factor for the development of coralline algae (Kain and Norton 1990), coralline algal abundance only increases with decreasing water depth if adequate substrate is available. The substrate has to be stable and free of fine sediment that decreases the photosynthetic efficiency of the coralline algae (Wilson et al. 2004).

In Svalbard, this results in a patchy distribution of rhodolith beds and hence in spatially separated communities. Most commonly, coralline algae are attached to lithoclasts, and even if corallines can also occur as epiphytes growing on the surface of other organisms (Kain and Norton 1990), shell accumulations (mainly consisting of *C. islandica* and *H. arctica*) are of much lesser importance. The light-weight shells, as well as cobbles below a certain size, do not provide enough stability, so storm waves and strong currents would intensely affect coralline algal encrustations (Adey 1970a).

In addition, the colonized substratum also has to be free of fine sediment, which regularly occurs at the Svalbard sites due to glacial melt-water input (Svendsen et al. 2002; Forwick and Vorren 2009). Since there is always at least some slight water movement throughout the year (Svendsen et al. 2002; Sapota et al. 2009), and because the topography of the seafloor is mostly flat, deposition of fine sediment is limited to depressions, which are generally devoid of living rhodoliths.

The successive development of the coralline algae from an initial stadium of encrustation to well-developed rhodoliths is clearly visible along single dive tracks. From a water depth where irradiance was sufficient (~78 m, averaged for all stations), most boulders >1 m³ and larger lithoclasts become colonized by encrusting coralline algae. With decreasing water depth, coralline crusts tend to develop small protuberances, which grow longer and thicker and become increasingly denser on the coralline surface with further flattening of the seafloor. This development continues until the coralline crust constitutes >50 vol% of a nodule (consisting of the lithoclast itself and the epilithic coralline algal skeleton), at which point it is considered a rhodolith by definition (Adey and Macintyre

1973; Bosence 1983a, b). Thus, the development of rhodoliths follows a multi-step process being advanced at different rates at the Svalbard sites, ranging from poorly developed specimens at Krossfjorden to well-developed communities at Floskjeret, Mosselbukta, and Nordkappbukta as described by Teichert et al. (2012).

Temperature

Temperature influences respiration, photosynthesis, and growth rates of coralline algae (Kain and Norton 1990; Wilson et al. 2004). Because growth rates usually increase with temperature to a maximum near the top of the tolerance range, temperature primarily determines the geographic species distribution. Therefore, biogeographic boundaries are usually associated with isotherms (Lüning 1990; Kain and Norton 1990). Parallel to this, Adey and Adey (1973) provided evidence that distribution patterns of coralline algae may be correlated with temperature patterns.

The maximum coralline cover at different sites were recorded at ~45 m water depth, at which mean temperatures vary from 0.5 °C at Nordkappbukta to 1.5 °C at Floskjeret (data from LEVITUS 94). These relatively high temperatures result from mixing of warm AW deriving from the WSC and colder ArW deriving from the ESC (Orvik and Niiler 2002; Sapota et al. 2009). However, temperatures are low compared to boreal localities (Lüning 1990), and at the Svalbard sites our data show that *L. glaciale* is adapted to lower temperatures than *Lithothamnion corallioides* (Crouan and Crouan) Crouan and Crouan, which has a minimum survival temperature of 5 °C (Adey and McKibbin 1970). Temperature also seems to limit the southward distribution of *L. glaciale*, whose production of conceptacles is limited to water temperatures <9 °C (Hall-Spencer 1994). Because the CTD records were taken during summertime and under ice-free conditions, it is possible that the values are close to the maxima of the annual range. The water temperatures in ~45 m water depth, where coverage and development of rhodoliths reach their maxima, are far below the 9 °C limit, so formation of conceptacles is presumably possible throughout summer. This enables *L. glaciale*, whose reproductive frequency is annually protracted (Jackson 2003), to produce conceptacles under improved light conditions. Our rhodolith samples from all sites (including Nordkappbukta, see Teichert et al. 2012:374, Fig. 7) had many conceptacles at the thallus surface. The temperature range at Svalbard seems to be both warm enough for sufficient growth and cold enough to enable conceptacle production during summertime.

The conspecificity of southern hemisphere material identified by Henriques et al. (2012) as *L. glaciale* from 54 to 55 m depth along the continental shelf of Espirito Santo State, Brazil (19°49'S to 20°45'S), where water

temperatures vary seasonally from 6 to 20 °C, with material examined from Spitsbergen and Nordaustlandet (78°18'N to 80°31'N) during our research, requires further investigation, a task beyond the scope of the present study. The designated lectotype of *L. glaciale* (Irvine and Chamberlain 1994, p. 183; Woelkerling et al. 2005, p. 291) was collected from Spitsbergen.

Salinity

Rhodophyta are known to be more susceptible to changes in salinity than Phaeophyta and Chlorophyta, and heavy fluctuations may cause stress with respect to osmosis, ionic balance, and availability of essential metabolites (Coutinho and Seelinger 1984; Kain and Norton 1990).

The CTD records indicate a thin incumbent layer of less saline water, resulting from strong freshwater input by glaciers (e.g., at Lilliehöökreen in the Krossfjorden transect). Because of the lower density, the less saline water does not fully mix with the ESC and WSC water masses, which are fully marine (Svendsen et al. 2002). Thus, conditions in the water depths where well-developed rhodoliths occur (~45 m) remain fully marine even in times of increased melt-water input. These conditions are suitable to *L. glaciale*, which is also able to tolerate both low (<18, Wilson et al. 2004) and strongly fluctuating salinities (18–40 in sea lochs off the west coast of Scotland, Jackson 2003) but is best adapted to fully marine conditions. This also is supported by Adey (1970b) and Wilson et al. (2004, p. 283), who found that *L. glaciale* survives very low salinities but with greatly decreased photosynthetic capacities. However, adaptation to varying salinities is an important attribute of *L. glaciale* that contributes to its persistence in various environments and may also partly explain its predominance over *P. tenue*, whose salinity tolerances are unknown.

Irradiance

Tolerance to a wide range of light levels and the general adaptation to low light conditions of coralline and other red algae are well known (Kain and Norton 1990). The non-calcareous red alga *Palmaria decipiens* (Reinsch) Ricker, for example, is able to survive several months of complete darkness. After that, respiration suddenly drops but rapidly recovers after exposure to illumination (Lüder et al. 2002). Elsewhere, Adey (1970b) stated that coralline algae of the high Arctic may require only 1 month of photosynthesis at low light levels for three-fourths of each day to be able to live in the dark for the remainder of the year. This enables sufficient growth even at high latitudes like in Svalbard, where the polar night lasts for up to 126 days in Nordkappbukta (data from USNO Sun Rise Tables).

Although there are slight variations among the different dive tracks, the rhodolith bed properties show the same overall pattern, starting with initial growth of encrusting coralline algae at ~ 78 m water depth. That deep, the average PAR for all stations is $0.1 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, being in the range of 0.01–1 % of the surface illumination and hence in the dysphotic zone. The average PAR for all stations at 45 m water depth is only $2.1 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, but rhodoliths cover nearly 100 % of the available substrate and specimens of *L. glaciale* have well-developed protuberances. This clearly shows the adaptation of *L. glaciale* to low light conditions and may also explain its greater prevalence compared to *P. tenue*. Experiments by Roberts et al. (2002) have shown that *P. tenue* has no significant net photosynthesis under those conditions ($2 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ at a PAR of $2.1 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$). The decrease in coralline cover with further topographic flattening (<30 m water depth) seems to be directly linked to increasing abundance of *Polysiphonia*-like red algae, which do not calcify, grow much faster than coralline algae, and have sufficient light in shallow waters.

Carbonate saturation

Coralline algae are heavily calcified and precipitate calcite and Mg-calcite within their cell walls (Bosence 1991). For *L. glaciale*, the direct association of the Mg with the calcite lattice has been shown by Kamenos et al. (2009) using Synchrotron Mg-X-ray absorbance near edge structure (XANES). The concentration of calcium in the water column is critical for coralline algae (King and Schramm 1982), and the maintenance of potassium in algal cells, transported by the ion pumps in the cell membrane, depends on the presence of adequate quantities of calcium ions (Kain and Norton 1990). Martin et al. (2008) showed that an increasing acidification of seawater leads to a significant reduction in coralline algal cover, indicating that a lowered pH and reduction of carbonate saturation are important factors that may affect rhodolith beds.

The water chemistry measured at all sites (Table 2) shows carbonate saturation (Ω_{Cal} and $\Omega_{\text{Arg}} \geq 1$) and pH ≥ 7.85 for the whole area, which is an important factor for the thriving of the rhodolith beds. The only stations slightly undersaturated regarding aragonite were sampled in water depths of 417 m (station 616, $\Omega_{\text{Arg}} = 0.91$), 332 m (station 632, $\Omega_{\text{Arg}} = 0.92$), and 147 m (station 669, $\Omega_{\text{Arg}} = 0.93$) and hence are negligible with respect to the growth conditions of the coralline algae.

Interactions with the vagile benthic community

Many studies have shown that coralline algae and prevailing benthic organisms interact in various ways (Milliken and

Steneck 1981; Steneck 1983, 1986). This holds for both coralline algae that grow as encrustations and those that form rhodoliths. Biofilms covering rhodolith surfaces represent a major source of food for many organisms including gastropods, crustaceans, and sea urchins (Kain and Norton 1990). At the same time, grazing activity exerted by benthic organisms is beneficial to rhodoliths because it keeps them largely free of epiphytes (Adey and Macintyre 1973).

To test if the corallines really depend on the grazing, suitable removal experiments as described by Steneck (1990) would be necessary; and because epithallial sloughing by coralline algae also can result in removal of epibionts (Johnson and Mann 1986b), the exact importance of grazing at the Spitsbergen sites has not yet been conclusively determined. However, numerous grazers are present and they feed on coralline surfaces. The most effective physical defense against intensive grazing is the calcareous thallus of corallines, which is much tougher than thalli of most other algae (Steneck 1983; Littler et al. 1983; Watson and Norton 1985). At the Svalbard sites, *L. glaciale* and *P. tenue* are grazer-resistant against *T. rubra* and *Strongylocentrotus* sp. which are very common in the rhodolith beds. Molluscs such as *T. rubra* exert a relatively low grazing pressure, while the impact of the larger and more effective sea urchin *Strongylocentrotus* sp. is higher. The abundance of *Strongylocentrotus* sp. may partially account for the greater number of *L. glaciale* individuals, most of which are intensively branched, as compared to the smooth, encrusting *P. tenue*. The reason is, as Milliken and Steneck (1981) and Steneck (1983) have shown, that intensively branched corallines are better protected against deep-grazing sea urchins than smooth specimens, because the sea urchins cannot reach between the protuberances.

Coralline algae also compete among themselves, especially if substrate is limited. Individuals can collectively occlude the whole substrate and become conjoined with neighboring individuals, forming a continuous sheet (Littler and Kauker 1984; Johnson and Mann 1986a). This competition for space occurs at the Svalbard sites, where cobbles above a distinctive size are the only available substrate and are encrusted completely by the coralline algae. Here, coralline algal crusts, primarily of *L. glaciale*, compete with each other, resulting in white meristematic margins that raise between individual crusts when there is no more free space left on a particular lithoclast. Coralline algae depend on sufficient substrate for settlement and since this substrate is limited, competition for space is a common feature at the Svalbard sites. Additionally, corallines also have to compete with serpulids, barnacles, and bryozoans.

Most well-developed rhodoliths as well as initial coralline algal crusts contain a lithoclastic core. Secondarily, completely hollow rhodoliths are common at Mosselbukta and act as kind of microenvironment for benthic animals.

The mechanism of formation of hollow rhodoliths is not fully understood, but rhodoliths from Svalbard may start as coralline algal crusts and lose their lithoclastic nucleus at some stage of development. Hollow rhodoliths are commonly inhabited by various organisms, including bivalves (usually *C. islandica* and *H. arctica*), ophiuroids, and serpulids. Since most of the animals were still living at the time of sample collection, it is obvious that animals really use hollow rhodoliths as microenvironments. The presumably glaciogenic gravel flats at the four sites are quite bare of protective cavities, so hollow rhodolith structures, as well as the interstices between rhodoliths, provide valuable shelter for many organisms. In this way, rhodoliths act as ecosystem engineers (Nelson 2009), providing a highly diverse habitat on the otherwise unprotected glaciogenic flats, even favoring the reproduction of many organisms. Similarly, rhodolith beds can serve as refugia for scallops (Kamenos et al. 2004a) and as a habitat for juvenile cod (Kamenos et al. 2004b). Rhodoliths provide habitat for numerous organisms and hence can increase the biodiversity not only in polar latitudes but on a worldwide scale (e.g., Foster 2001; Steller et al. 2003; Fortunato and Schäfer 2009).

Comparison with other rhodolith communities

Arctic and subarctic rhodolith communities occur also in Alaska (Konar and Iken 2005; Konar et al. 2006), mainland Norway (Freiwald 1993; Freiwald and Henrich 1994), and Nordaustlandet (Teichert et al. 2012), the latter including the northernmost rhodolith communities known to date.

The northernmost known rhodolith community in the Pacific Ocean is situated in Herring Bay (Prince William Sound, Alaska, 60°28'N; 47°45'W). This community (Konar et al. 2006) consists of a species of *Lithothamnion*, unfortunately misidentified² as *Phymatolithon calcareum* (Pallas) Adey and McKibbin. While the seafloor at the Svalbard sites consists almost completely of presumed glaciogenic pebbles, cobbles, and boulders with fine sediments restricted to patches, 60 % of the seafloor at Herring

Bay was hard boulders and 40 % fine sediment (Konar and Iken 2005). Like at Svalbard, coralline algae were restricted to hard substrate. Konar and Iken (2005) showed that coralline algae are the major space occupiers (>60 %) but are not the competitive dominants against many other sessile organisms. This may be due to the high abundance of bioeroding chitons (Konar et al. 2006) that have a stronger impact on other sessile organisms such as sponges, bryozoans and tunicates (Konar and Iken 2005) than on coralline algae, which possess various adaptations against bioerosion (Steneck 1986). The Herring Bay community seems to show the same interaction of coralline algae and bioeroders as in Svalbard and other locations (Steneck 1986). Konar and Iken (2005) also showed that Alaskan rhodoliths have a similar ecological function to those in Svalbard in providing a habitat for benthic organisms, and their branches are inhabited by a specialized crypto fauna. This results in an increase in diversity of the micro- and macrobenthos, an attribute that seems to characterize many rhodolith communities (Foster 2001).

Elsewhere in Arctic Norway, rhodoliths in the Storvoll Plateau community in the Troms district (69°59'N; 18°40'E) fringe a rigid in situ coralline algal buildup in 14–15 m water depth. The community consists of *Lithothamnion* cf. *glaciale*, *Lithothamnion* sp., and *Phymatolithon* sp., with more or less balanced proportions of individuals of each species (Freiwald 1993; Freiwald and Henrich 1994). In contrast to the Svalbard communities, most individuals are not nucleated because detached heads of *Lithothamnion* branches from the in situ algal build-up are the major mode of propagation. Thus, the shape of rhodoliths can be used as an indicator for the hydrodynamic regime. Freiwald (1993) reported 88 % spheroidal rhodoliths at Straumensund south of the Storvoll Plateau, indicating high-energy hydrodynamics (Bosence 1983a; Freiwald 1993). Benthic organisms inhabiting mainland Norwegian rhodolith communities are similar to those at the Svalbard sites, and many species (e.g., *C. islandica*, *H. arctica*, and *H. psittacea*) occur in both areas. Bioeroders such as *Strongylocentrotus droebachiensis* and *Lepidopleurus asellus* are common and occupy the same ecological niche as grazers in Herring Bay and Svalbard. This further supports the conclusion of Steneck (1986) that coralline algae require bioeroding organisms to keep clean and healthy, as otherwise they would become overgrown by competitive fixosessile invertebrates (Steneck 1986; Konar and Iken 2005), which would lead to coralline dieback.

The rhodolith communities from Nordkappbukta (Teichert et al. 2012) are also multi-specific and consist of *L. glaciale* (~90 % coverage) and *P. tenue* (~10 % coverage), residing in 30–75 m water depth. Most rhodoliths bear a lithoclastic nucleus and some are hollow as some Mosselbukta specimens. Only lithoclasts above a distinct

² Figures 2–4 in Konar et al. (2006) clearly show that the Alaskan thalli belong to *Lithothamnion*, which is characterized by flared epithallial cells and subepithallial initials as long as or longer than subtending cells, and not *Phymatolithon*, which is characterized by rounded epithallial cells and subepithallial cells as short or shorter than subtending cells. The Alaskan thalli also have multiporate tetrasporangial conceptacles with protruding roofs and no surrounding rim, which is characteristic of some species of *Lithothamnion*. *Phymatolithon calcareum*, by contrast, has multiporate conceptacles in which the roofs are surrounded by a rim or are sunken below the surrounding thallus surface. Further comparisons and synoptic descriptions of *Lithothamnion* and *Phymatolithon* are found in Woelkerling (1988) and Harvey et al. (2003); Woelkerling and Irvine (1986) provide a detailed account of *P. calcareum*.

size and free of fine sediments are colonized, and the succession at Nordkappbukta resembles the pattern observed in this study, starting with thin, smooth crusts in ~75 m water depth and grading into larger rhodoliths with well-developed protuberances from ~45 m water depth onwards (Teichert et al. 2012). The rhodoliths act as bioengineers and hollow specimens house many benthic species including grazers such as *Strongylocentrotus* sp. and *T. rubra*. Overall, the Nordkappbukta communities closely resemble those from Spitsbergen.

The ecological importance of the Svalbard rhodolith communities is based primarily on their function as substrate and shelter for benthic organisms and as a food source for grazers. The communities, including the Nordkappbukta site (Teichert et al. 2012), vary slightly in species composition but show the same overall structure. The presence of rhodoliths can greatly increase the diversity by providing a microenvironment (Steller et al. 2003; Konar and Iken 2005), although rhodoliths might also depend on the activity of grazing organisms that keep them free from excessive epiphyte covering (Steneck 1986).

Implications for future developments

The Svalbard rhodolith communities are highly specialized in their adaptations to the physical environment as well as in their interactions with the fauna, thus showing parallels to other polar rhodolith communities (Freiwald 1993; Freiwald and Henrich 1994; Konar and Iken 2005; Konar et al. 2006). Climatic change will likely result in shifts in light conditions, temperature and sedimentation processes, as well as in ocean acidification and, hence, carbonate undersaturation. These multiple environmental shifts will have substantial impacts on rhodolith communities.

At the Svalbard sites, *L. glaciale* and *P. tenue* appear dependent on water temperature; if winter mean temperatures would decrease, vital processes may be disrupted (Kain and Norton 1990), and this could lead to a delayed start of the growing season, or even to a complete dieback of the thalli. In contrast, mean temperatures >9 °C (as projected by the IPCC 2007 A2 scenario) would presumably affect formation of conceptacles during the growing season (Hall-Spencer 1994).

Higher fluctuations in salinity may cause osmotic stress, unfavorable ionic balances and a shortage of essential metabolites (Kain and Norton 1990). *L. glaciale* tolerates low and fluctuating salinities but is best adapted to fully marine conditions (Wilson et al. 2004). This implies that permanently decreased salinities, which are predicted to develop also in deeper water layers, as a consequence of changing hydrography (Svendsen et al. 2002; Clarke and Harris 2003), will negatively affect the rhodolith beds because of impaired growth conditions.

Irradiance also limits the occurrence of coralline algae to a distinct depth range at the Svalbard localities. A major problem arising from increasing annual mean temperatures is the simultaneous glacial meltdown, resulting in the transport of huge amounts of fine sediments into the water column (Konar and Iken 2005). This would strongly impair the growth conditions for coralline algae due to a reduced PAR and burial with fine sediment. Higher water turbidity could thus result in an increased dieback level of corallines (Wilson et al. 2004). Moreover, increased melt water and sediment runoff would also foster the development of fine sediment layers on lithoclastic substrates, leading to significantly impaired settling conditions for coralline algae.

The concomitant appearance of coralline algae and prominent grazers is of mutual benefit for both sides: on the one hand, it decreases the fouling pressure on coralline algae (i.e., the likelihood of being overgrown by epiphytes and epizoans), and on the other hand, it provides feeding grounds for grazers utilizing the rhodolith-surface biofilms (Steneck 1986). Additionally, rhodolith accumulations act as bioengineers and represent sheltered microenvironments on the otherwise non-protected glaciogenic flats, with hollow rhodoliths being of particular significance as providers of microhabitats for associated benthic fauna. A regression in rhodolith stock due to the dieback of coralline algae would very likely result in more unfavorable conditions for many benthic organisms due to the loss of habitat and food resources.

The importance of carbonate saturation levels for coralline algae is well known, and observations by Hall-Spencer et al. (2008) showed that decreased pH values and ensuing carbonate undersaturation can result in the rapid decline of calcareous algae. Additionally, the abundance of gastropods and sea urchins, whose function as surface grazers is often essential for the thriving of coralline algae (Steneck 1985, 1986), may be negatively affected by lower pH levels (Hall-Spencer et al. 2008). The current state of the seawater carbonate system is suitable for rhodolith communities. However, high-latitude oceans will very likely be the first to become undersaturated with respect to calcite and aragonite (Orr et al. 2005), and modeling studies predict the onset of mean carbonate undersaturation by 2032 (Steinacher et al. 2009). This development will surely have a massive impact on the rhodoliths and many associated benthic organisms.

Conclusions

The findings of this study and those of Teichert et al. (2012) have led to various conclusions concerning rhodolith communities in the Svalbard Archipelago:

- Shapes of the rhodoliths cannot be used as indicators for the prevailing hydrodynamic regime because all rhodoliths are nucleated or presumably contained a lithoclastic nucleus at an earlier growth stage.
- The presence of an appropriate substrate is essential for the thriving of coralline algae. The substrate has to offer a minimum stability and must not be smothered by fine sediment. It is one of the main controls susceptible to environmental changes.
- Present-day temperatures and salinities are suitable for *L. glaciale*. Ongoing and predicted environmental changes, especially increasing temperatures and decreasing salinities, will presumably lead to impaired conditions for *L. glaciale* rhodolith communities.
- Irradiance is the most important control on the coralline algae and limits their occurrence to a distinct depth range, principally in the dysphotic zone.
- Coralline algae can cope with shifts of carbonate saturation in the water column, as long as the water is saturated with respect to calcite. However, increasing ocean acidification will likely have a strong impact on rhodolith communities.
- Rhodolith beds are an important part of the prevailing coastal ecosystem. Rhodoliths act as ecosystem engineers. Moreover, the biofilms on their surface represent a major source of food for many grazing organisms, but the exact importance of grazing at the Spitsbergen study sites has yet to be tested with suitable removal experiments (see Steneck 1990).

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References

- Adey WH (1964) The genus *Phymatolithon* in the Gulf of Maine. *Hydrobiologia* 24:377–420
- Adey WH (1966a) The genera *Lithothamnium*, *Leptophytum* (nov. gen.) and *Phymatolithon* in the Gulf of Maine. *Hydrobiologia* 28:321–370
- Adey WH (1966b) Distribution of saxicolous crustose corallines in the northwestern North Atlantic. *J Phycol* 2:49–54
- Adey WH (1970a) Some relationships between crustose corallines and their substrate. *Sci Isl* 2:21–25
- Adey WH (1970b) The effects of light and temperature on growth rates in boreal-subarctic crustose corallines. *J Phycol* 6:269–276
- Adey WH, Adey P (1973) Studies on the biosystematics and ecology of the epilithic crustose Corallinales of the British Isles. *Br Phycol J* 8:1–60
- Adey WH, Macintyre IG (1973) Crustose coralline algae: a re-evaluation in the geological sciences. *Geol Soc Am Bull* 84:883–904
- Adey WH, McKibbin DL (1970) Studies on the maerl species *Phymatolithon calcareum* (Pallas) nov. comb. and *Lithothamnion corallioides* Crouan in the Ria de Vigo. *Bot Mar* 13:100–106
- Adey WH, Athanasiadis A, Lebednik PA (2001) Re-instatement of *Leptophytum* and its type *Leptophytum laeve*: taxonomy and biogeography of the genera *Leptophytum* and *Phymatolithon* (Corallinales, Rhodophyta). *Eur J Phycol* 36:191–203
- Adey WH, Chamberlain YM, Irvine LM (2005) An SEM-based analysis of the morphology, anatomy, and reproduction of *Lithothamnion tophiforme* (Esper) Unger (Corallinales, Rhodophyta), with a comparative study of associated North Atlantic arctic/subarctic Melobesioideae. *J Phycol* 41:1010–1024
- Athanasiadis A (2007) The genus *Leptophytum* (Melobesioideae, Corallinales, Rhodophyta) in NW Spitsbergen. *Nord J Bot* 24:469–499
- Athanasiadis A, Adey WH (2003) Proposal to conserve the name *Lithophyllum laeve* Strömfelt against *L. laeve* Kützing (Corallinales, Rhodophyta) with a conserved type. *Taxon* 52:342–350
- Athanasiadis A, Adey WH (2006) The genus *Leptophytum* (Melobesioideae, Corallinales, Rhodophyta) on the Pacific coast of North America. *Phycologia* 45:71–115
- Bosence DWJ (1976) Ecological studies on two carbonate sediment producing coralline algae from western Ireland. *Palaeontology* 19:365–395
- Bosence DWJ (1983a) Description and classification of rhodoliths (rhodoids, rhodolites). In: Peryt TM (ed) *Coated grains*. Springer, Berlin Heidelberg New York, pp 217–224
- Bosence DWJ (1983b) The occurrence and ecology of recent rhodoliths—a review. In: Peryt TM (ed) *Coated grains*. Springer, Berlin Heidelberg New York, pp 225–242
- Bosence DWJ (1991) Coralline algae: mineralization, taxonomy, and palaeoecology. In: Riding R (ed) *Calcareous algae and stromatolites*. Springer, Berlin Heidelberg New York, pp 98–113
- Clarke A, Harris CM (2003) Polar marine ecosystems: major threats and future change. *Environ Conserv* 30:1–25
- Compère P (2004) Report of the Committee for Algae: 8. *Taxon* 53:1065–1067
- Coutinho R, Seelinger U (1984) The horizontal distribution of the benthic algal flora in the Patos Lagoon estuary, Brazil, in relation to salinity, substratum and wave exposure. *J Exp Mar Biol Ecol* 80:247–257
- Dickson AG, Afghan JD, Anderson GC (2003) Reference materials for oceanic CO₂ analysis: a method for the certification of total alkalinity. *Mar Chem* 80:185–197
- Düwel L, Wegeberg S (1996) The typification and status of *Leptophytum* (Corallinales, Rhodophyta). *Phycologia* 35:470–483
- Fleischer D, Schaber M, Piepenburg D (2007) Atlantic snake pipefish (*Entelurus aequoreus*) extends its northward distribution range to Svalbard. *Polar Biol* 30:1359–1362
- Fortunato H, Schäfer P (2009) Coralline algae as carbonate producers and habitat providers on the Eastern Pacific coast of Panamá: preliminary assessment. *N Jb Geol Paläont Abh* 253:145–161
- Forwick M, Vorren TO (2009) Late Weichselian and Holocene sedimentary environments and ice rafting in Isfjorden, Spitsbergen. *Palaeogeogr Palaeoclimatol Palaeoecol* 280:258–274
- Foster MS (2001) Rhodoliths: between rocks and soft places. *J Phycol* 37:659–667

- Freiwald A (1993) Subarktische Kalkalgenriffe im Spiegel hochfrequenter Meeresspiegelschwankungen und interner biologischer Steuerungsprozesse. PhD Thesis, University of Kiel, Kiel
- Freiwald A (1995) Sedimentological and biological aspects in the formation of branched rhodoliths in northern Norway. *Beitr Paläont* 20:7–19
- Freiwald A, Henrich R (1994) Reefal coralline algal build-ups within the Arctic Circle: morphology and sedimentary dynamics under extreme environmental seasonality. *Sedimentology* 41:963–984
- Graham DJ, Midgley NG (2000) Graphical representation of particle shape using triangular diagrams: an Excel spreadsheet method. *Earth Surf Proc Land* 25:1473–1477
- Gran G (1952) Determination of the equivalence point in potentiometric titrations of seawater with hydrochloric acid. *Oceanol Acta* 5:209–218
- Hall-Spencer JM (1994) Biological studies on non-geniculate Corallinaceae. PhD Thesis, University of London, London
- Hall-Spencer JM, Atkinson RJA (1999) *Upogebia deltaura* (Crustacea: Thalassinidea) in Clyde Sea maerl beds, Scotland. *J Mar Biol Assoc UK* 79:871–880
- Hall-Spencer J, Rodolfo-Metalpa R, Martin S, Ransome E, Fine M, Turner SM, Rowley S, Tedesco D, Buia M-C (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454:96–99
- Harland WB (1997) The geology of Svalbard. The Geological Society, London 521 p
- Harvey A, Woelkerling WJ, Millar AJK (2003) An account of the Hapalidiaceae (Corallinales, Rhodophyta) in south-eastern Australia. *Aust Syst Bot* 16:647–698
- Henriques MC, Villas-Boas A, Riosmena-Rodriguez R, Figueiredo MAO (2012) New records of rhodolith-forming species (Corallinales, Rhodophyta) from deep water Espírito State, Brazil. *Helgol Mar Res* 66:219–231
- IPCC (2007) The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Irvine LM, Chamberlain YM (1994) Rhodophyta Part 2B Corallinales, Hildenbrandiales. The Natural History Museum, London
- Jackson A (2003) *Lithothamnion glaciale*. Maerl. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme (online). Marine Biological Association of the United Kingdom, Plymouth. <http://www.marlin.ac.uk/reproduction.php?speciesID=3711> (Accessed 15 May 2011)
- Johnson CR, Mann KH (1986a) The crustose coralline alga *Phymatolithon* Foslie inhibits the overgrowth of seaweeds without relying on herbivores. *J Exp Mar Biol Ecol* 96:127–146
- Johnson CR, Mann KH (1986b) The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicuris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. *J Exp Mar Biol Ecol* 97:231–267
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Kain JM, Norton TA (1990) Marine ecology. In: Cole KM, Sheath RG (eds) *Biology of the red algae*. Cambridge University Press, New York, pp 377–422
- Kamenos NA, Moore PG, Hall-Spencer JM (2004a) Attachment of the juvenile queen scallop (*Aequipecten opercularis* (L.)) to maerl in mesocosm conditions; juvenile habitat selection. *J Exp Mar Biol Ecol* 306:139–155
- Kamenos NA, Moore PG, Hall-Spencer JM (2004b) Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play? *ICES J Mar Sci* 61:422–429
- Kamenos NA, Cusack M, Huthwelker T, Lagarde P, Scheibling RE (2009) Mg-lattice associations in red coralline algae. *Geochim Cosmochim Acta* 73:1901–1907
- King RJ, Schramm W (1982) Calcification in the maerl coralline alga *Phymatolithon calcareum*, effects of salinity and temperature. *Mar Biol* 70:197–204
- Kjellman FR (1875a) Förberedande anmärkningar om algvegetationen i Mosselbay enligt iakttagelser under vinterdragningar anställda af Svenska palarexpeditionen 1872–1873. Öfvers Kong Vetensk-Akad Förhandl 1875:59–68
- Kjellman FR (1875b) Om Spetsbergens marina, klorofullförande thallophyter I. Bih Till Kung Svenska Vetensk Handl 3:1–34
- Kjellman FR (1883) Norra Ishafvets Algflora. Vega-expeditionens Vetensk Iakt 3:1–431 [Note: subsequently published in English (Kjellman 1885)]
- Kjellman FR (1885) The algae of the Arctic Sea. Kong Svenska Vetensk Akad Handl 20:1–350 [Note: dated 1885 but first published in 1883. The original version (Kjellman 1883) is written in Swedish]
- Konar B, Iken K (2005) Competitive dominance among sessile marine organisms in a high Arctic boulder community. *Polar Biol* 29:61–64
- Konar B, Riosmena-Rodriguez R, Iken K (2006) Rhodolith bed: a newly discovered habitat in the North Pacific Ocean. *Bot Mar* 49:355–359
- Lherminier P, Meincke J, Freiwald A, Schauer J (2009) Circulation and ecosystems in the Subpolar and Polar North Atlantic, Cruise No. 2, May 23–September 16, 2006. *MARIA S. MERIAN-Berichte* 9(1), Universität Hamburg
- Littler MM, Kauker BJ (1984) Heterotrichy and survival strategies in the red alga *Corallina officinalis*. *Bot Mar* 27:37–44
- Littler MM, Littler DS, Taylor PR (1983) Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J Phycol* 19:229–237
- Lüder UH, Wiencke C, Knoetzel J (2002) Acclimation of photosynthesis and pigments during and after six months of darkness in *Palmaria decipiens* (Rhodophyta): a study to simulate Antarctic winter sea ice cover. *J Phycol* 38:904–913
- Lüning K (1990) Seaweeds. Their environment, biogeography and ecophysiology. Wiley Interscience, New York
- Martin S, Rodolfo-Metalpa R, Ransome E, Rowley S, Buia MC, Gattuso JP, Hall-Spencer J (2008) Effects of naturally acidified seawater on seagrass calcareous epibionts. *Biol Lett* 4:689–692
- Milliken B, Steneck RS (1981) The branching morphology of crustose corallines as a structural defence against herbivores and a refuge for filamentous algae. In: Abstracts of papers and posters to be presented at the 20th Northeast Algal Symposium April 11–12, 1981. Marine Biological Laboratory, Woods Hole, p 16
- Nelson WA (2009) Calcified macroalgae—critical to coastal ecosystems and vulnerable to change: a review. *Mar Freshw Res* 60:787–801
- Nilsen F, Cottier F, Skogseth R, Mattsson S (2008) Fjord-shelf exchanges controlled by ice and brine production: the interannual variation of Atlantic Waters in Isfjorden, Svalbard. *Cont Shelf Res* 28:1838–1853
- Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RM, Gnanadesikan A, Gruber N, Ishida A, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner GK, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig MF, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–686
- Orvik KA, Niiler P (2002) Major pathways of Atlantic water in the northern North Atlantic and Nordic Seas towards Arctic. *Geophys Res Lett* 29:1896–1899
- Ottesen D, Dowdeswell JA, Landvik JY, Mienert J (2007) Dynamics of the Late Weichselian ice sheet on Svalbard inferred from high-resolution sea-floor morphology. *Boreas* 36:286–306

- Prud'homme van Reine WF (2011) Report of the Nomenclature Committee for Algae: 10. *Taxon* 60:585–587
- Roberts RD, Kühl M, Glud RN, Rysgaard S (2002) Primary production of crustose coralline algae in a high Arctic fjord. *J Phycol* 38:273–283
- Rosenvinge LK (1893) Grønlands Havalger. *Med Grønland* 3:765–981
- Sapota G, Wojtasik B, Burska D, Nowiński K (2009) Persistent organic pollutants (POPs) and polycyclic aromatic hydrocarbons (PAHs) in surface sediments from selected fjords, tidal plains and lakes of the north Spitsbergen. *Polar Res* 30:59–76
- Schlitzer R (2012) Ocean data view. <http://odv.awi.de>
- Sexton DJ, Dowdeswell JA, Solheim A, Elverhøi A (1992) Seismic architecture and sedimentation in north-west Spitsbergen fjords. *Mar Geol* 103:53–68
- Sneed ED, Folk RL (1958) Pebbles in the lower Colorado River, Texas. A study in particle morphogenesis. *J Geol* 66:114–150
- Spreen G, Kaleschke L, Heygster G (2008) AMSR-E ASI 6.25 km Sea ice concentration data, V5.4. Institute of Oceanography, University of Hamburg, Germany, digital media. <ftp://ftp-projects.zmaw.de/seaice/> (Accessed 21 April 2011)
- Steinacher M, Joos F, Frölicher TL, Plattner G-K, Doney SC (2009) Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle-climate model. *Biogeosciences* 6:515–533
- Steller DL, Riosmena-Rodriguez R, Foster MS, Roberts CA (2003) Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. *Aquat Conserv* 13:5–20
- Steneck RS (1983) Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* 9:44–61
- Steneck RS (1985) Adaptations of crustose coralline algae to herbivory: Patterns in space and time. In: Toomey DF, Nitecki MH (eds) *Paleoalgology*. Springer, Berlin Heidelberg New York, pp 352–366
- Steneck RS (1986) The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annu Rev Ecol Syst* 17:273–303
- Steneck RS (1990) Herbivory and the evolution of nongeniculate coralline algae (Rhodophyta, Corallinales) in the North Atlantic and North Pacific. In: Garbary DJ, South GR (eds) *Evolutionary biogeography of the marine algae of the North Atlantic*. Springer, Berlin Heidelberg New York, pp 107–129
- Stoll MHC, Bakker K, Nobbe GH, Haese RR (2001) Continuous-flow analysis of dissolved inorganic carbon content in seawater. *Anal Chem* 73:4111–4116
- Strömfelt HFG (1886) Om Algevegetationen vid Islands Kuster. D.F. Bonniers, Göteborg
- Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther JG, Dallmann W (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res* 21:133–166
- Teichert S, Woelkerling W, Rüggeberg A, Wisshak M, Piepenburg D, Meyerhöfer M, Form A, Büdenbender J, Freiwald A (2012) Rhodolith beds (Corallinales, Rhodophyta) and their physical and biological environment at 80°31'N in Nordkappbukta (Nordaustlandet, Svalbard Archipelago). *Phycologia* 51:371–390
- Watson DC, Norton TA (1985) The physical characteristics of seaweed thalli as deterrents to littorine grazers. *Bot Mar* 28:383–387
- Węslawski JM, Kosztejn J, Zajaczkowski M, Wiktor J, Kwaśniewski S (1995) Fresh water in Svalbard fjord ecosystems. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaa HP (eds) *Ecology of fjords and coastal waters*. Elsevier Science, Amsterdam, pp 229–241
- Wilson S, Blake C, Berges JA, Maggs CA (2004) Environmental tolerances of free-living coralline algae (maerl): implications for European marine conservation. *Biol Conserv* 120:279–289
- Woelkerling WJ (1988) The Coralline red algae: An analysis of the genera and subfamilies of nongeniculate Corallinaceae. British Museum (Natural History)/Oxford University Press, London/Oxford
- Woelkerling WJ, Irvine LM (1986) The neotypification and status of *Phymatolithon* (Corallinaceae, Rhodophyta). *Br Phycol J* 21:55–80
- Woelkerling WJ, Furnari G, Cormaci M (2002) *Leptophytum* (Corallinaceae, Rhodophyta): to be or not to be? That is the question, but what is the answer? *Aust Syst Bot* 15:597–618
- Woelkerling WJ, Gustavsen G, Myklebost HE, Prestø T, Sæstad S (2005) The Coralline Red Algal Herbarium of Mikael Foslie: revised Catalogue with Analyses. *Gunneria* 77:1–625
- Womersley HBS (1979) Southern Australian species of *Polysiphonia* Greville (Rhodophyta). *Aust J Bot* 27:459–528