Rhodolith beds (Corallinales, Rhodophyta) and their physical and biological environment at 80°31′N in Nordkappbukta (Nordaustlandet, Svalbard Archipelago, Norway)

SEBASTIAN TEICHERT[1]*, WILLIAM WOELKERLING[2], ANDRES RÜGGEBERG[3], MAX WISSHAK[1], DIETER PIEPENBURG[4], MICHAEL MEYERHÖFER[5], ARMIN FORM[5], JAN BÜDENBENDER[5] AND ANDRÉ FREIWALD[1,6]

[1]*Senckenberg am Meer, Abteilung Meeresforschung, Südstrand 40, D-26282 Wilhelmshaven, Germany*
[2]*La Trobe University, Department of Botany, Kingsbury Drive, AUS-3086 Bundoora, Victoria, Australia*
[3]*Renard Centre of Marine Geology, Gent University, Krijgslaan 281–S8, B-9000 Gent, Belgium*
[4]*Akademie der Wissenschaften und der Literatur Mainz, c/o Institut für Polarökologie, Universität Kiel, Wischhofstraße 1–3, D-24148 Kiel, Germany*
[5]*Helmholtz-Zentrum für Ozeanforschung Kiel (GEOMAR), Düsternbrooker Weg 20, D-24105 Kiel, Germany*
[6]*MARUM, Zentrum für Marine Umweltwissenschaften, Leobener Straße 2, D-28359 Bremen, Germany*

Polar coralline red algae (Corallinales, Rhodophyta) that form rhodoliths have received little attention concerning their potential as ecosystem engineers and carbonate factories; although, recent findings revealed that they are much more widespread in polar waters than previously thought. The present study deals with the northernmost rhodolith communities currently known, discovered in 2006 at 80°31′N in Nordkappbukta (North Cape Bay) at Nordaustlandet, Svalbard. These perennial coralline algae must be adapted to extreme seasonality in terms of light regime (*c.* 4 months winter darkness), sea ice coverage, nutrient supply, turbidity of the water column, temperature and salinity. The rhodolith communities and their environment were investigated using multibeam swath bathymetry, CTD measurements, recordings of the photosynthetic active radiation (PAR) and determination of the water chemistry, seabed imaging and targeted sampling by means of the manned submersible JAGO as well as benthic collections with a dredge. The coralline flora was composed mainly of *Lithothamnion glaciale*, with a lesser amount of *Phymatolithon tenue*. Based on their distribution and development at different depth levels, a facies model was developed. Rhodoliths occurred between 30 and 51 m, while coralline algae attached to cobbles were present as deep as 78 m. Measurements of the PAR indicated their adaptation to extreme low light levels. Ambient waters were always saturated with reference to calcite and aragonite for the whole area. The rhodolith-associated macrobenthic fauna samples yielded 59 species, only one of which was typically Arctic, and the concomitant appearance of corallines and grazers kept the corallines free from epiphytes and coequally provided feeding grounds for the grazers. Overall, *L. glaciale* and *P. tenue* appeared to be well adapted to the extreme environment of the Arctic.

KEY WORDS: *Lithothamnion glaciale*, Nordkappbukta, *Phymatolithon tenue*, Polar carbonate factory, Rhodolith community, Svalbard

INTRODUCTION

In polar regions, major physical oceanographic, chemical and biological parameters are affected by the strong seasonality in solar radiation. At 80° northern latitude, the polar night lasts for *c.* 4 months, and the annual solar radiation is 30–50% less than in temperate to tropical regions (Lüning 1990). This dark period is prolonged by sea ice covered by snow for several additional months. Multiyear sea ice can scour the seabed down to depths of 40 m (Gutt 2001). After the melting of the sea ice in coastal waters, the development of phytoplankton blooms and the inflow of turbid meltwater also affect the light transmission in the water column. Therefore, even under full-illuminated conditions during the polar summer, low irradiances often

prevail (Wiencke *et al.* 2007). Under calm weather conditions, the meltwater generates a freshwater surface layer. At times when this stratification is disturbed by storms, the mixing of freshwater affects the upper 20-m water depth (Hanelt *et al.* 2001). Furthermore, biolimited macronutrients, such as nitrogen and phosphorus, follow a pronounced seasonal fluctuation. In Svalbard waters, macronutrients are abundant during the winter months but become rapidly depleted along with the development of the short-lived phytoplankton blooms in summer (Aguilera *et al.* 2002). All these environmental fluctuations led to the evolution of specific life strategies and ecophysiological adaptations amongst perennial polar algae to cope not only with low temperatures but also with depletion or absence of light and nutrients (see review in Wiencke *et al.* 2007). This study focuses on the environment of the northernmost known coralline algal rhodolith bed off the northern coast of Nordaustlandet, Svalbard, Norway.

* Corresponding author (sebastian.teichert@senckenberg.de).

Rhodoliths are free-living structures composed mostly (> 50%) of nongeniculate (i.e. lacking uncalcified joints) coralline red algae (Rhodophyta; Foster 2001). They are abundant from tropical to polar latitudes and from the lower intertidal zone to water depths of 150 m, where they provide a habitat for numerous animals and plants. Foster (2001) described rhodolith beds as one of the 'big four' benthic communities dominated by macrophytes in terms of area covered, ranking alongside kelp beds and forests, seagrass meadows and nongeniculate coralline reefs. Coralline algae are well adapted to a variety of environmental disturbances and hence are slow growing and probably long lived (Foster 2001). Many exhibit distinct banding patterns (Freiwald & Henrich 1994; Freiwald 1998; Foster 2001) and were successfully used in studies on climatic conditions (Kamenos *et al.* 2007; Halfar *et al.* 2008, 2010, 2011; Kamenos & Law 2010).

North of the Arctic Circle (66°33.73′N), rhodoliths have been reported to occur off Devon Island northern Canada (*c.* 75°N), northern mainland Norway (*c.* 70°N), Spitsbergen (Svalbard; including Treurenberg Bay, 79°56′N; see Kjellman 1883, 1885) and Novaya Zemlya (Russia; *c.* 75°N; see Kjellman 1883, 1885; maps in Bosence 1983b; Foster 2001). South of the Arctic Circle but still under Arctic climatic conditions, rhodolith beds are known from Herring Bay, Prince William Sound, Alaska (*c.* 60°N; Konar *et al.* 2006), and from Belle Isle Strait, Newfoundland (Halfar *et al.* 2000). Information on the environmental conditions of these high-latitude rhodolith beds are provided by Freiwald (1998) and Freiwald & Henrich (1994) for the northern Norwegian region and by Konar *et al.* (2006) for the Alaskan area. Examples for other well-investigated rhodolith beds at lower latitudes are the Sound of Arizaig, Scotland (*c.* 57°N; Davies & Hall-Spencer 1996); the Ryukyu Islands, Japan (*c.* 27°N; Matsuda & Iryu 2011), the southwestern Gulf of California, Mexico (*c.* 24°N; Hetzinger *et al.* 2006); the Gulf of Panama and the Gulf of Chiriquí, Panama (*c.* 8°N; Fortunato & Schäfer 2009; Schäfer *et al.* 2011); the coast of the State of Paraíba, Brazil (*c.* 7°S; Riul *et al.* 2004), Inhaca Island, Mozambique (*c.* 26°S; Perry 2005); and Arvoredo Island, Brazil (*c.* 27°S; Gherardi 2004).

In 2006, during the MSM 02/03 cruise of RV *Maria S. Merian*, the northernmost rhodolith communities currently known were discovered at 80°31′N in Nordkappbukta (North Cape Bay) off Nordaustlandet Island, Svalbard, Norway. The sites were intensively documented and sampled, thus providing an opportunity to determine the biological composition of and interactions within these rhodolith communities and to elucidate the physical and chemical conditions under which these apparently thriving communities were growing. This study of currently living rhodolith communities provides a basis for interpreting the geography, climatology and ecology associated with fossil rhodolith communities.

The study site is located on the Svalbard archipelago, which is situated about halfway between the Norwegian mainland and the North Pole and includes all islands in the region between 74°–81°N and 10°–35°E. Nordkappbukta (North Cape Bay; 80°31′N, 19°52′E; Figs 1–3), the focus of the present study, is located at the northern tip of the Laponiahalvøya, Nordaustlandet, and features the Early Neoproterozoic Laponiafjellet Granite (Harland 1997). Beverlysundet (Beverly Sound) extends 4.8 km SSE, separating the Nordaustlandet mainland from a disembarkation area around Nordkapp.

Nordkappbukta is currently the most northern known locality where well-developed coralline red algal rhodolith communities occur. The area is regularly exposed to sea ice formation for several months during winter, but ice cover often lasts into the summer, occurring mostly as open drift ice (Falk-Petersen *et al.* 2000; Spreen *et al.* 2008). The prevailing Arctic Ocean water is influenced by the West Spitsbergen Current (WSC), which is the northernmost extension of the Norwegian Atlantic Current, a relatively warm (> 3°C) and saline [>34.9 practical salinity scale (pss)] water mass (Orvik & Niiler 2002). These Atlantic waters mix with the Arctic Ocean water, but the impact of the Atlantic waters is pronounced only in periods of strong WSC activity; whereas, at other times the area is under the influence of Arctic Ocean water (Sapota *et al.* 2009).

Seasonally changing freshwater input from melting glaciers additionally contributes to the local attributes of the water column. The mean temperatures are 0.20°C and 0.46°C at the sea surface and at 50-m water depth, respectively. The mean salinities are 33.13 at the sea surface and 34.77 at 50-m water depth (data from NODC_WOA94).

MATERIAL AND METHODS

Samples and data were obtained on 9–10 August 2006 during the MSM 02/03 expedition of RV *Maria S. Merian* (Table 1, Figs 1–3; Lherminier *et al.* 2006). Seabed mapping was carried out with a Kongsberg EM 1002 multibeam echo sounder, operating at a nominal sonar frequency of 95 kHz and controlled with the software Seafloor Information System. Multibeam raw data were processed using the software packages Neptune and Cfloor. The Neptune bathymetric postprocessing software brought raw multibeam data through a data correction and cleaning process and was designed for graphical description of the raw data to identify problems. It also provided tools to correct or remove errors in navigation data, depth soundings or sound speed profiles. The Cfloor software was used for chart production starting with Neptune output data from which digital terrain models were generated.

For the measurements of physical and chemical variables in the water column, a Sea Bird CTD was mounted with a rosette of 24 water bottles with a capacity of 10 litres each. At the maximum water depth at each station, water samples were taken for total alkalinity (TA) and dissolved inorganic carbon (DIC). Additional near-bottom water samples were obtained by a 5-litre Niskin bottle attached to the submersible JAGO. The carbonate system parameters pH, carbon dioxide partial pressure (pCO$_2$), calcite (cal) saturation (Ω_{cal}) and aragonite (arg) saturation (Ω_{arg}) were calculated from TA, DIC, temperature and salinity.
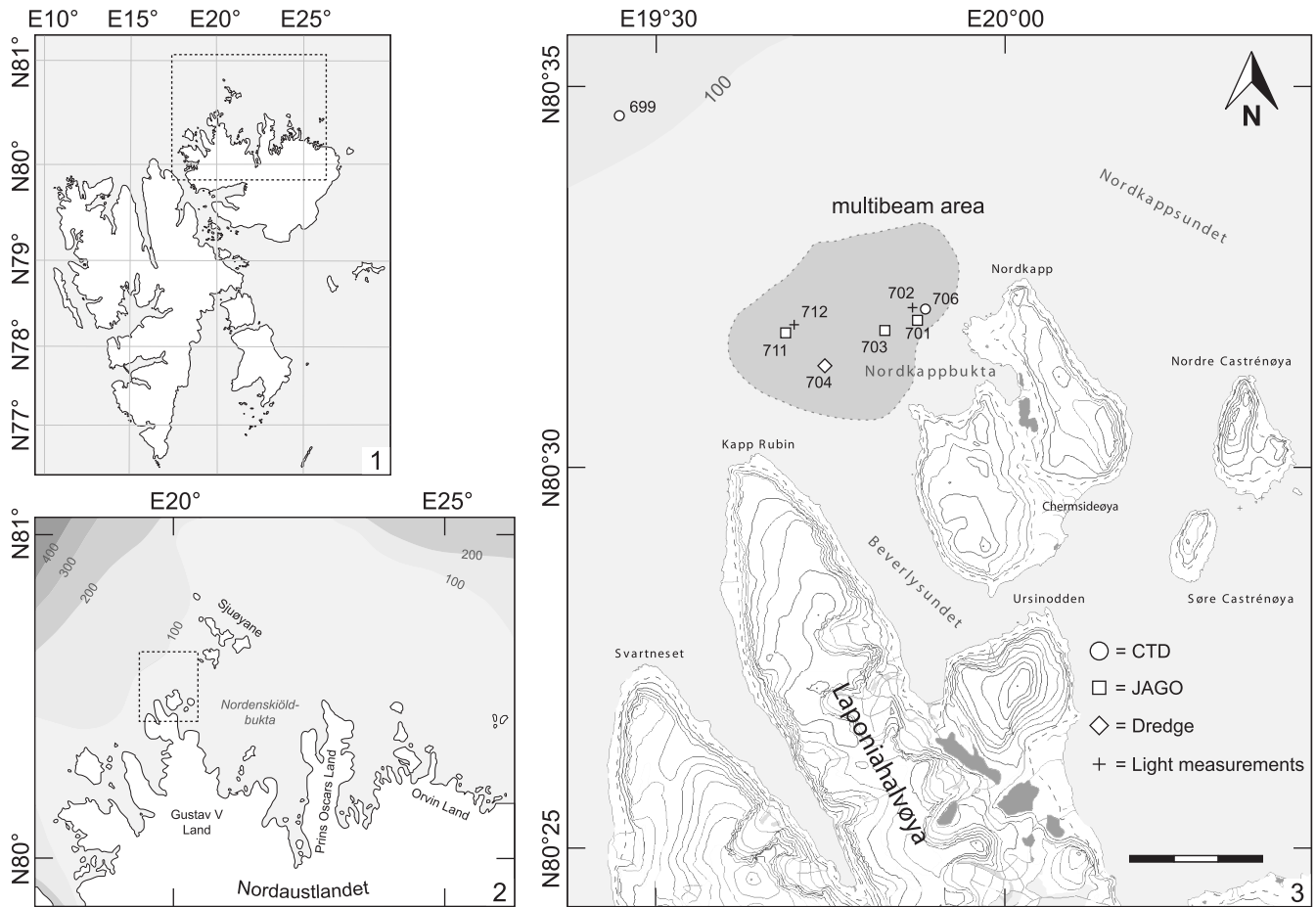
Figs 1–3. Maps of the study site and surrounding regions.
   Fig. 1. Svalbard Archipelago, north of mainland Norway. Area enclosed in rectangle enlarged in Fig. 2.
   Fig. 2. Northern part of Nordaustlandet Island where the study site is situated. Area enclosed in rectangle contains study site and is enlarged in Fig. 3.
   Fig. 3. Study site and neighbouring regions showing the area mapped by multibeam echosounder (*c.* 16 km^2). Symbols denote sampling and measuring gear used. A detailed list of the applied gear is given in Table 1. Scale bar = 3 km, showing 1-km divisions.

Two light measurements were carried out with a LICOR Spherical Quantum Sensor (LI-193SA) in combination with a data logger (LI-1400) and a 100-m-long cable. The measured wavelength spectrum (400–700 nm) corresponds to the photosynthetic active radiation (PAR). Measurements were undertaken from the rescue boat of RV *Maria S. Merian* in order to minimise potential bias due to shadows cast by the research vessel and to enable controlled

Table 1. Station list and associated data.[1]

Station no.	Gear	Date	Start				End			
			Time UTC	Lat. °N	Long. °E	Depth (m)	Time UTC	Lat. °N	Long. °E	Depth (m)
699	CTD	9 Aug. 2006	07:09	80°35.01′	19°27.62′	142	07:15	80°35.03′	19°27.48′	144
700	MB	9 Aug. 2006	07:59	80°31.62′	19°39.45′	n.d.	11:34	80°31.00′	19°44.09′	41
701	JAGO	9 Aug. 2006	12:15	80°32.01′	19°50.77′	78	15:24	80°31.95′	19°51.30′	30
702	LS	9 Aug. 2006	12:46	80°32.00′	19°50.74′	75	12:46	80°32.00′	19°50.74′	75
703	JAGO	9 Aug. 2006	15:59	80°31.77′	19°48.70′	99	16:43	80°31.77′	19°48.42′	95
704	DRG	9 Aug. 2006	18:12	80°31.22′	19°44.23′	45	18:29	80°31.44′	19°43.02′	44
706	CTD	9 Aug. 2006	20:17	80°32.02′	19°50.78′	61	20:22	80°32.02′	19°50.77′	81
707	MB	9 Aug. 2006	20:39	80°31.76′	19°49.34′	87	21:16	80°32.23′	19°36.74′	84
710	MB	10 Aug. 2006	01:54	80°31.72′	19°39.79′	69	07:55	80°31.83′	19°39.40′	41
711	JAGO	10 Aug. 2006	09:03	80°31.76′	19°40.04′	70	11:54	80°31.86′	19°41.47′	30
712	LS	10 Aug. 2006	09:22	80°31.77′	19°40.32′	69	09:22	80°31.77′	19°40.32′	69
713	MB	10 Aug. 2006	12:36	80°32.09′	19°43.49′	112	16:16	80°31.76′	19°44.06′	60

[1] CTD, conductivity, temperature and depth measurements; MB, multibeam echosounder; JAGO, JAGO dive track; LS, light measurement; DRG, dredge; n.d., no data.

shallow measurements just below the water surface. Raw data were translated to percentages with respect to surface illumination to determine the water depth of the boundaries of the photic zoning at various study sites (see below). In addition to subaquatic measurements, the surface PAR was used as a reference for various weather conditions.

To gain information about the composition and diversity of the benthic community at the study site, a dredge (100-cm width, 40-cm height, 0.5-cm mesh size) was used to sample macro- and megabenthic epifauna. The samples were gently washed through a 1-mm sieve, and the organisms collected from the sieve residue were fixed in 70% alcohol for later
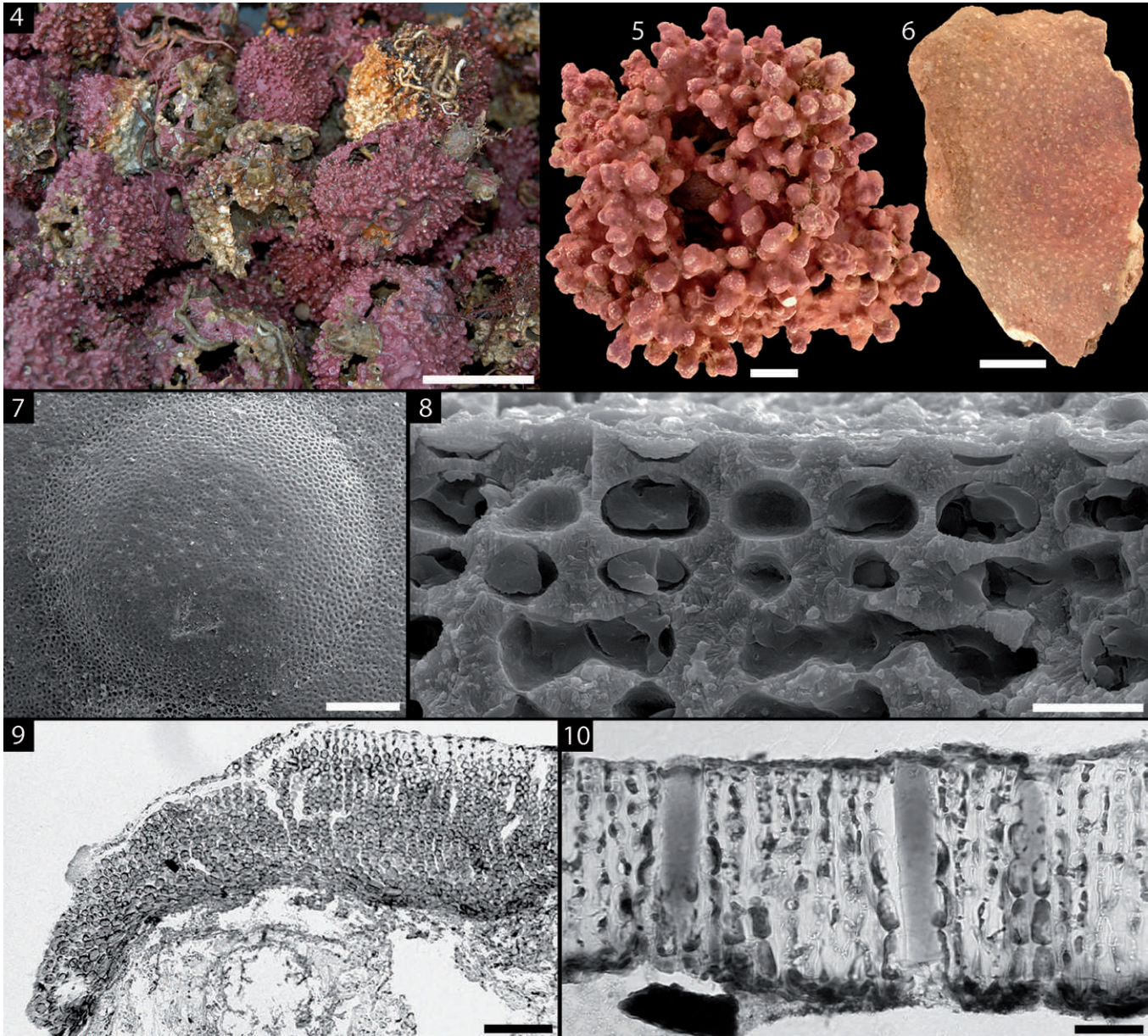
Figs 4–10. Principal species of coralline red algae in Nordkappbukta.
  Fig. 4. Group of living rhodoliths of *Lithothamnion glaciale*, most of which are hollow. Scale bar = 10 cm.
  Fig. 5. Individual living rhodolith of *Lithothamnion glaciale* (R_711_36). Scale bar = 1 cm.
  Fig. 6. Part of a living plant of *Phymatolithon tenue* (R_704_3). White dots on upper surface denote positions of individual sporangial conceptacles. Scale bar = 1 cm.
  Fig. 7. Tetrasporangial conceptacle of *Lithothamnion glaciale* in surface view (R_711_36_1). Note conceptacle pores on flattened part of roof. Scale bar = 100 μm.
  Fig. 8. Section of thallus of *Lithothamnion glaciale* showing calcified filaments terminating in flattened and flared epithallial cells (R_711_36_4). Note fusions between some cells of adjacent filaments. Scale bar = 10 μm.
  Fig. 9. Longitudinal section of edge of thallus of *Phymatolithon tenue* showing a ventral core of filaments portions of which curve upwards to the dorsal thallus surface (R_704_3_3). Scale bar = 100 μm.
  Fig. 10. Part of a tetrasporangial conceptacle roof of *Phymatolithon tenue* showing three pore canals still blocked by sporangial plugs (R_711_31_1). Note that cells lining the pore canals characteristically are somewhat swollen compared with other roof cells. Scale bar = 25 μm.

analysis. Voucher specimens currently are housed at Senckenberg am Meer, Wilhelmshaven.

The manned submersible JAGO was used for visual inspection and video documentation of shallow-water slopes as well as for water sampling just above the seabed and for selective sampling of rhodoliths and their associated fauna. Video material was additionally used to analyse the distribution of rhodoliths and megafauna in a spatial context and to assess the sedimentary facies. The dredged material helps to identify major species. The video footage also included noncalcareous red algae that were mostly finely filamentous and resembled *Polysiphonia* (Rhodomelaceae, Ceramiales), but no specimens were collected during the 2006 cruise. Consequently, unequivocal identification was not possible, and these organisms are referred to hereafter as '*Polysiphonia*-like red algae'.

RESULTS

Coralline red algal flora

The Nordkappbukta coralline red algal rhodolith community was mainly composed of *Lithothamnion glaciale* Kjellman (Figs 4, 5), with a lesser amount of *Phymatolithon tenue* (Rosenvinge) Düwel & Wegeberg (Fig. 6). Identification of thalli of *L. glaciale* was based on data in Adey (1964, 1966, 1970; includes species keys), Adey *et al.* [2005; includes comparisons of *L. glaciale* with *L. tophiforme* (Esper) Unger and *L. lemoineae* Adey], Irvine & Chamberlain (1994; includes species keys and accounts) and Kjellman (1883; contains the original account of *L. glaciale*). Living thalli (Figs 4, 5) were dull in texture and reddish to dull pink in colour, and tetrasporangial conceptacles had up to 50 pores in the roof (Fig. 7). This contrasts with another Arctic species, *L. tophiforme* (not identified in our samples), which is characterised by a glossy texture, an orange-red colour and tetrasporangial conceptacles with up to 85 pores in the roof (Adey *et al.* 2005). Like other species of *Lithothamnion*, the vegetative filaments of *L. glaciale* were terminated by epithallial cells with flared outer corners (Fig. 8). *Lithothamnion tophiforme* is said to be primarily an Arctic species that extends only into the deeper and colder parts of the subarctic Atlantic (Adey *et al.* 2005), while *L. glaciale* is said to be the dominant subarctic species of *Lithothamnion*. Elsewhere, Adey & Adey (1973) state that *L. glaciale* is the primary subarctic rhodolith builder, partly being replaced by *L. tophiforme* in Arctic waters. It should be remembered, however, that the type specimen of *L. glaciale* comes from Spitsbergen Island, Svalbard, and in the original account of the species (Kjellman 1883), *L. glaciale* is said to be common and plentiful on the west and north coasts of Spitsbergen Island and to occur as far north as Treurenberg Bay (79°56′N). According to Hansen & Jenneborg (1996, p. 372), *L. glaciale* is the dominant non-geniculate coralline at Spitsbergen Island. In Nordkappbukta, *L. glaciale* grew as unattached rhodoliths and also attached to cobbles or bedrock. Rhodoliths were more or less spherical to ovoidal to more irregular in form, consisted largely of knobby protuberances (branches) and were solid or hollow (see below). Attached thalli produced short (up to 19 mm) warty
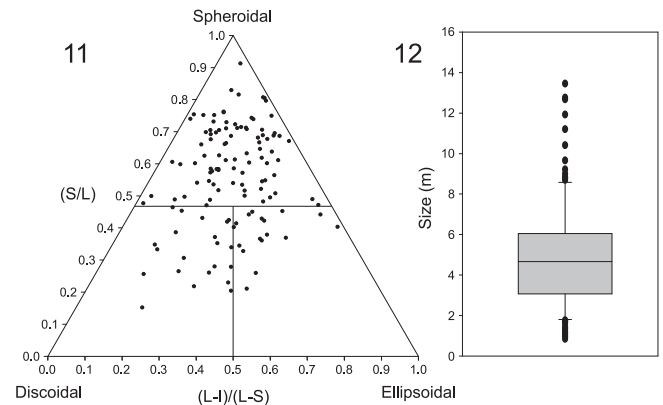
Figs 11, 12. Graphic analyses of rhodolith shape and size.
Fig. 11. Triplot shape distribution of rhodoliths based on measurements of long, intermediate and short axes as described in Bosence (1983a). $n = 128$.
Fig. 12. Box plot showing size range of rhodoliths based on measurements using the volume of an ellipsoid as described in Bosence (1976). $n = 128$.

or knobby protuberances of varying diameter from a crustose base.

Identification of specimens of *P. tenue* was based on Düwel & Wegeberg (1996) and Rosenvinge (1893). *P. tenue* was originally described under the name *Lithothamnion tenue* by Rosenvinge (1893), but a modern examination of the lectotype specimen by Düwel & Wegeberg (1996) showed that the species belongs to *Phymatolithon*. The type specimen comes from Holsteinborg, Greenland. *Phymatolithon tenue* characteristically had a thin encrusting thallus (usually up to 200 μm thick; Figs 6, 9) that did not produce protuberances and had sporangial conceptacles that appeared as white dots on the upper thallus surface (Fig. 6). Pore canals of sporangial conceptacles were lined with cells that were mostly somewhat larger than other cells in the conceptacle roof (Fig. 10). These features were described and illustrated by Düwel & Wegeberg (1996, p. 478, figs 29–33) in the type and were clearly evident in algae from Nordkappbukta. In Nordkappbukta, thalli of *P. tenue* grew attached to cobbles or bedrock and occurred intermixed with *L. glaciale* but never produced protuberant branches.

Rhodolith morphology

The rhodoliths measured were collected from 45-m water depth. The shape of the rhodoliths was analysed as described in Bosence (1983a) by measuring the long (L), intermediate (I) and short (S) axes of all rhodoliths ($n = 128$), and the results were plotted in Sneed & Folk's (1958) pebble shape diagram using Tri-plot (Graham & Midgley 2000) (Fig. 11). The plot showed a majority of spheroidal shapes and the remaining rhodoliths dispersed on discoidal and ellipsoidal shapes in approximately equal parts.

The size of all rhodoliths ($n = 128$) was measured using the volume of an ellipsoid [$(L*I*S/4\pi)^{-2}$] as shown in Bosence (1976). Plotting these values in a box plot showed that most rhodoliths ranged 3–6 cm in size but could also grow much bigger (Fig. 12).
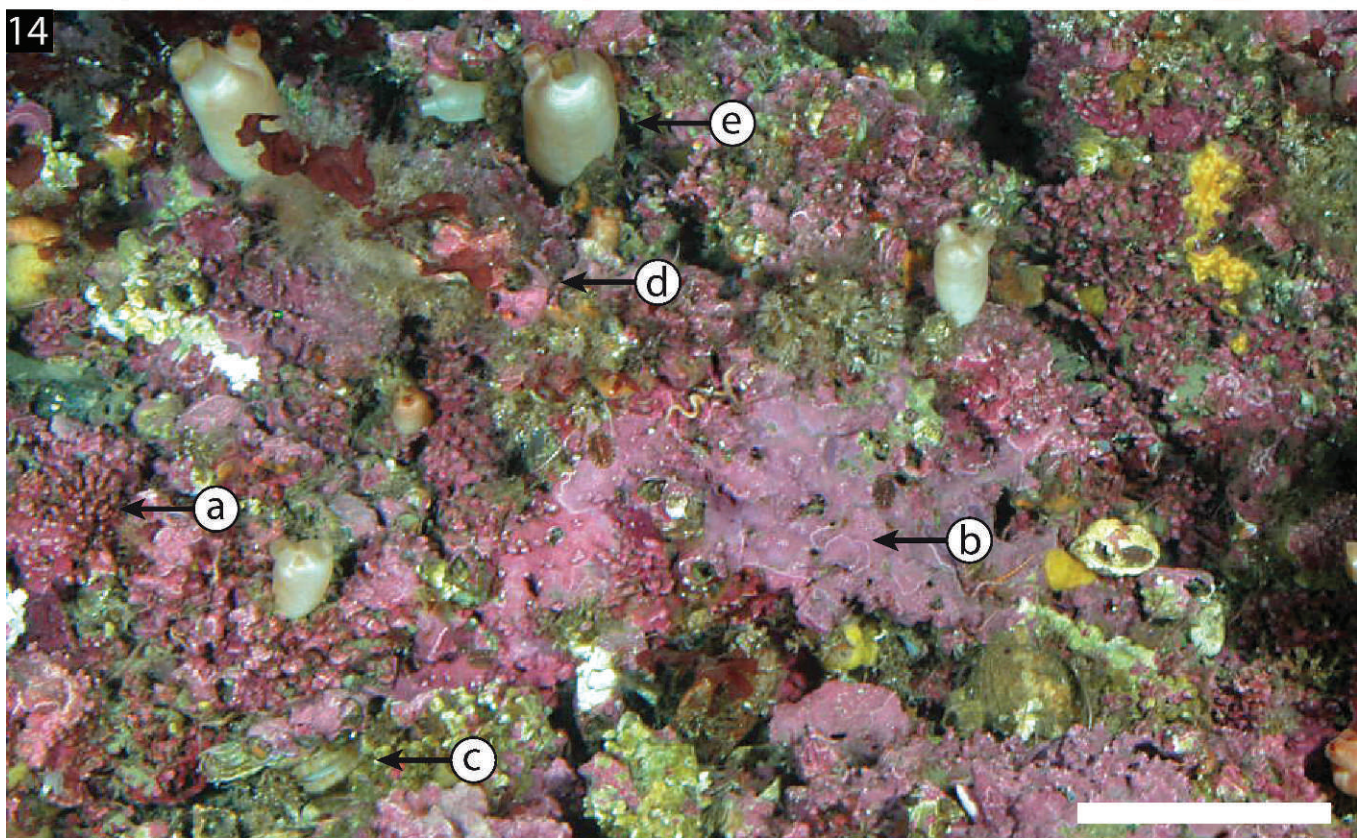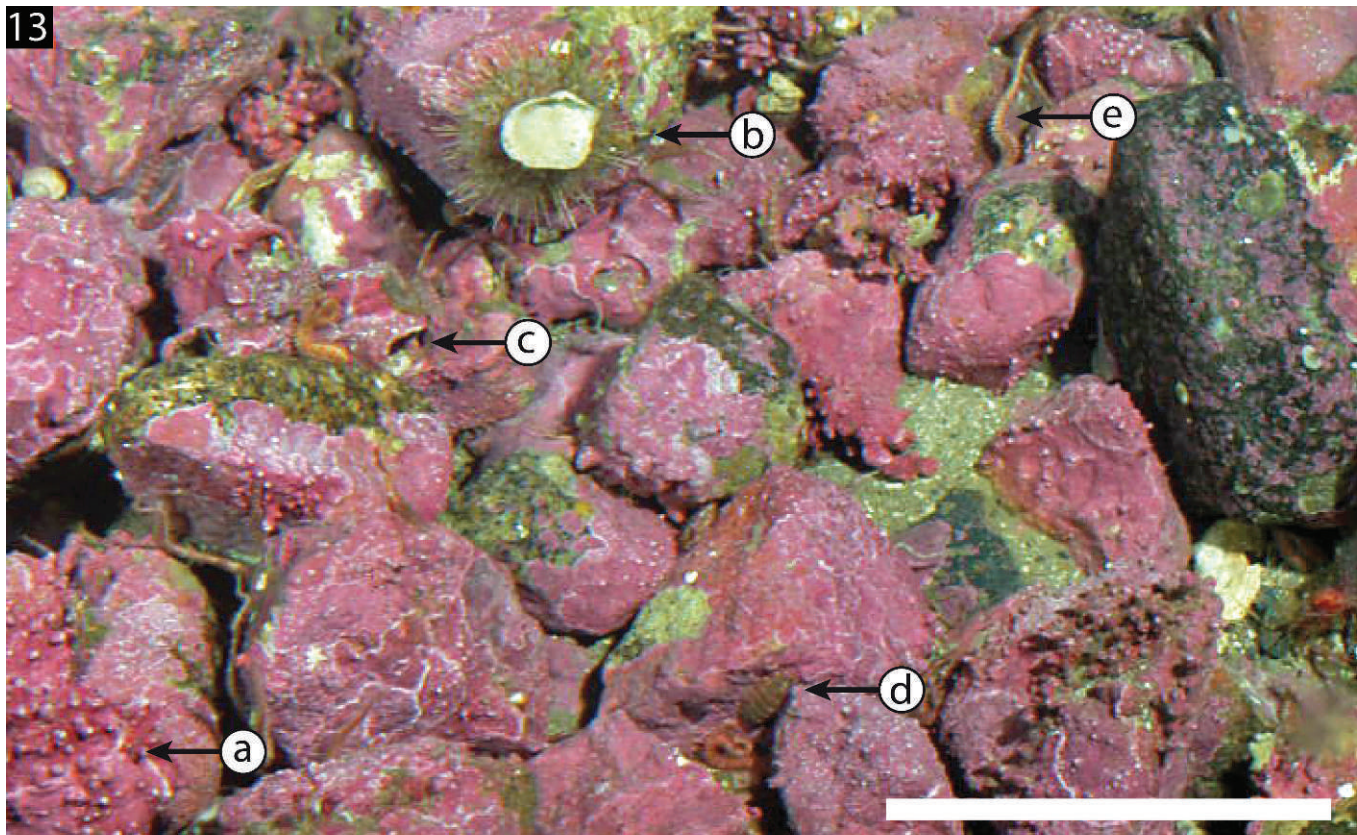
Figs 13–14. Examples of cobble communities and bedrock communities dominated by coralline red algae.
Fig. 13. Coralline red algal crusts of different stages of development and associated benthos covering cobbles on a glaciogenic gravel flat at 70-m water depth. a, *Lithothamnion glaciale*; b, *Strongylocentrotus* sp.; c, *Balanus* sp.; d, *Tonicella rubra*; e, *Terebellides stroemi*. Scale bar = 10 cm.
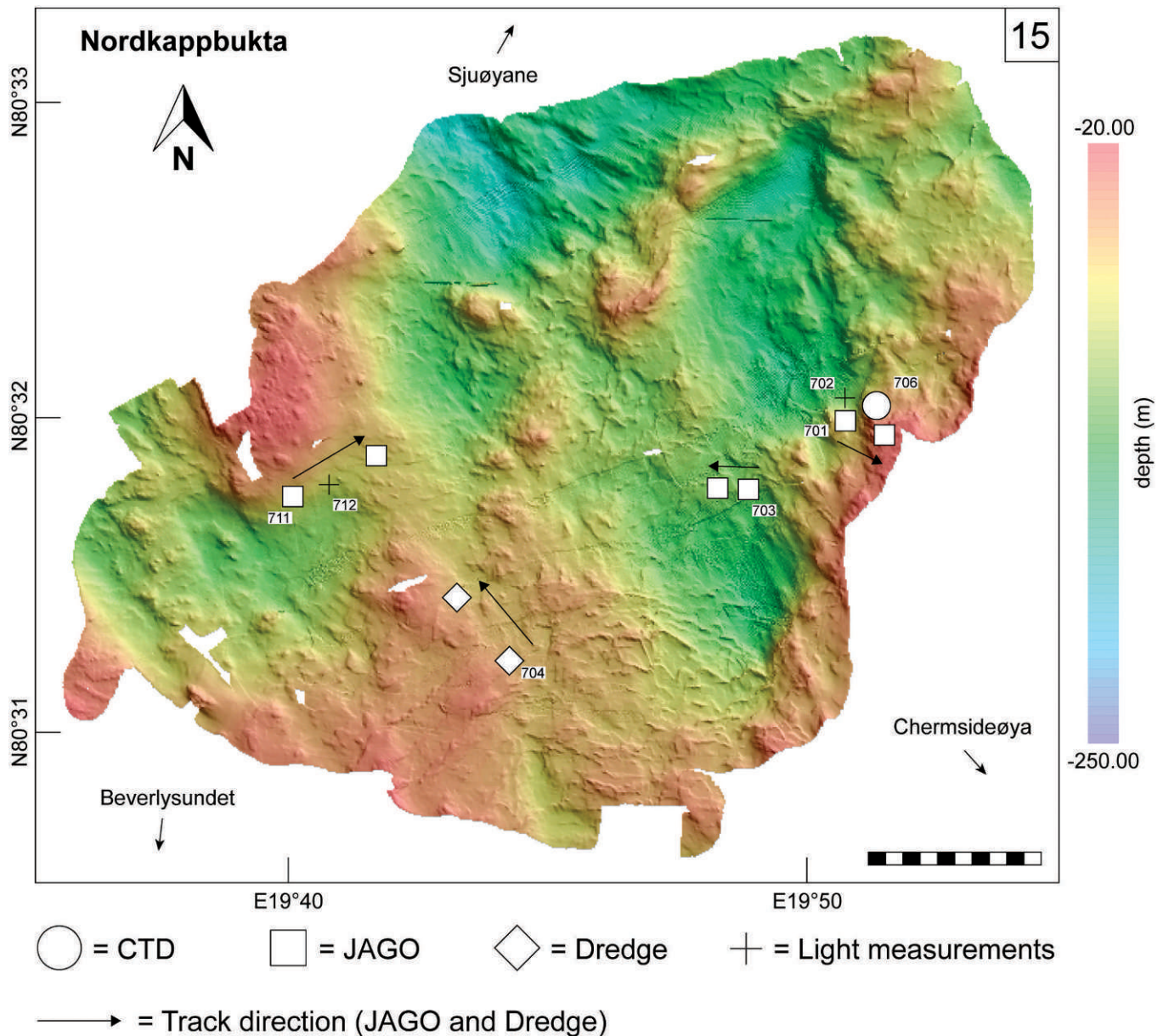
Fig. 15. Multibeam map of Nordkappbukta showing depth, morphology and positions of the applied gear. A detailed list of the applied gear is given in Table 1. Scale bar = 1 km, showing 100-m divisions.

Most rhodoliths were monospecific and consisted of *L. glaciale*. Some were multispecific, and both *L. glaciale* and *P. tenue* were present and overgrew each other. Overall, *L. glaciale* provided about 90% of the surface coverage. The coralline red algae settled on hard substratum (clastic or biogenic) above a distinctive size that provided enough stability (Fig. 13). If bedrock was present, it was also covered mainly by coralline red algae (Fig. 14). The fully developed rhodoliths generally contained a lithoclastic core and occurred both mixed with cobble communities and as distinct accumulations. Hollow rhodoliths with a wide-open

space for internal colonisation and settlement to form a specific cryptic microhabitat also occurred. Although not yet fully understood, we believe that hollow rhodoliths have lost their lithoclastic nucleus at an earlier growth stage.

Seafloor and rhodolith bed features

The area mapped by the multibeam echosounder covered *c.* 16 km². The seafloor had a distinct morphology that featured zones of relatively flat depressions and plateaus alternating with steep ridges, ribs and slopes,

←

Fig. 14. Fully developed coralline red algal crusts and associated benthos nearly entirely covering the bedrock granite at 45-m water depth. a, *Lithothamnion glaciale*; b, *Phymatolithon tenue*; c, *Chlamys islandica*; d, *Balanus* sp.; e, *Actinia* sp. Scale bar = 10 cm.

while large iceberg scouring marks were not detected (Fig. 15).

Dive track 701 (78–30-m water depth; see Fig. 16 for facies profile) showed a bumpy, heavily structured seafloor and headed along a slope with a total inclination of *c.* 32°. The track started on a gravel pavement of poorly sorted material partly covered with a thin silty sediment layer, and some of the larger stones (> 10 cm) were covered with initial crusts of coralline algae. Crusts appeared only if the substratum was clean and were absent if it was smothered with soft sediment. At 75-m water depth, additionally large boulders occurred and were mostly completely covered with coralline algae crusts (Fig. 17). This boulder facies stopped at 70-m water depth and skipped to the same facies as in 78-m water depth and showed some shell accumulations of *Chlamys islandica* (O.F. Müller) and *Hiatella arctica*

(Linnaeus) valves, which were restricted to patches. In 60-m water depth, shell beds were absent, and a boulder and gravel facies dominated again, while the degree of coralline algal encrustation and protuberance development increased. A steep slope at 51-m water depth made up of bedrock showed lots of encrustations of coralline red algae with fully developed protuberances, and the first individual rhodoliths accumulated in cracks (Fig. 18). The surface flattened again at 45 m, and nearly the whole substratum was covered with encrusting corallines, corallines with short protuberant branches and rhodoliths. Additional shell beds in this area were restricted to patches again. At 31-m water depth, a flat gravel pavement dominated, and coverage with *Polysiphonia*-like red algae increased, while rhodolith coverage decreased. Iceberg plough marks were absent, and epibenthos was very frequent along the entire track.
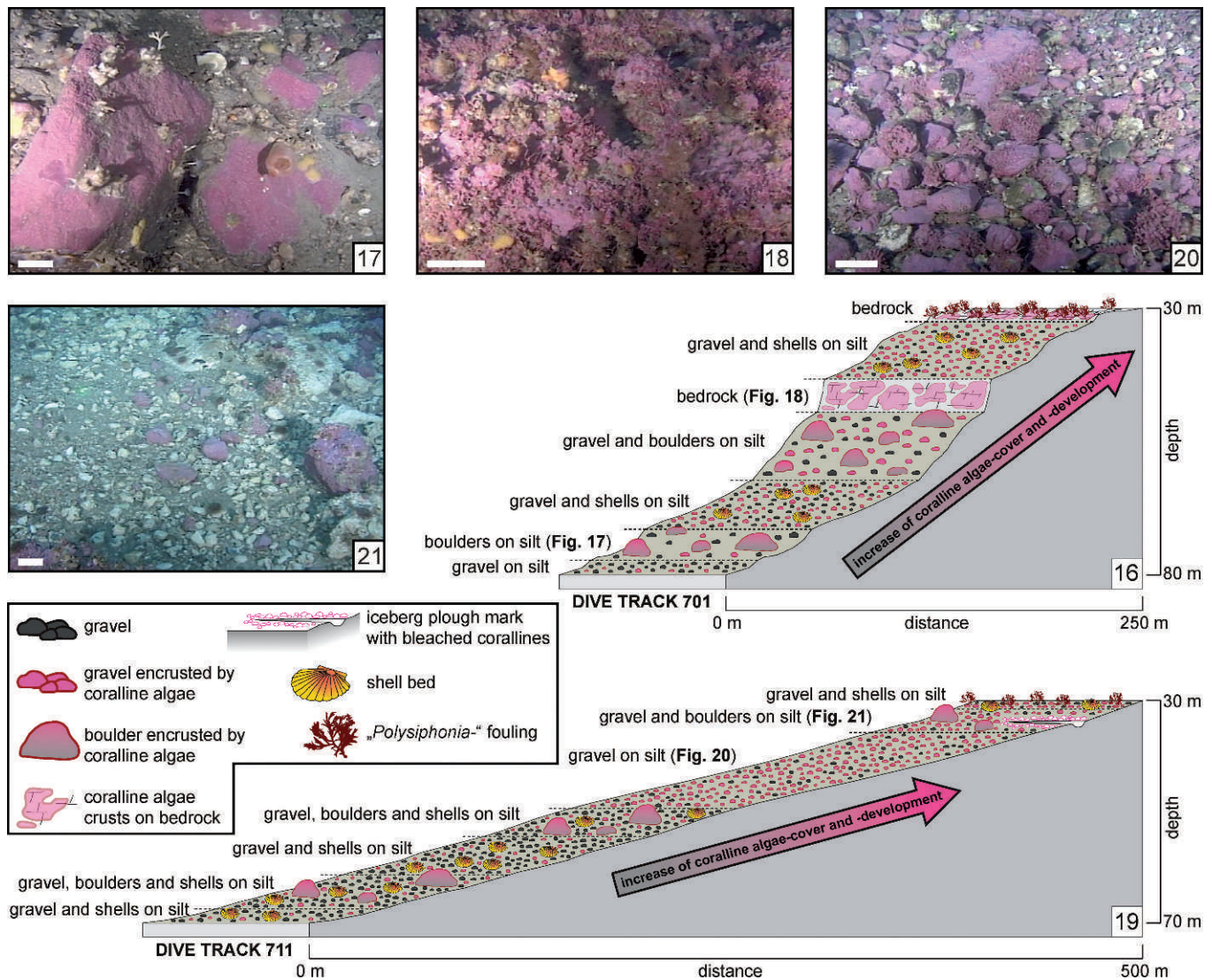
**Figs 16–21.** Facies profiles and associated sea floor pictures.

Fig. 16. Facies profile of dive track 701 showing the increase of coralline algae coverage with flattening and the prevailing substratum.

Fig. 17. Boulders with initial crusts in 75-m water depth (dive track 701). Scale bar = 10 cm.

Fig. 18. Fully developed protuberances attached to bedrock in 51-m water depth (dive track 701). Scale bar = 10 cm.

Fig. 19. Facies profiles of dive track 711 showing the increase of coralline algae coverage with flattening and the prevailing substratum.

Fig. 20. Rhodoliths in an intermediate stage of development on a gravel bottom in 45-m water depth (dive track 711). Scale bar =10 cm.
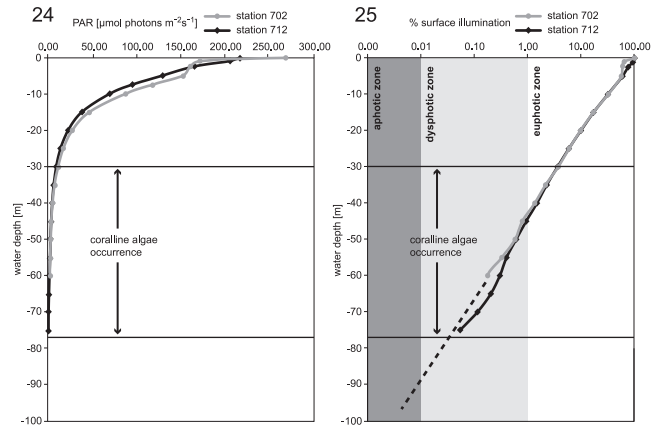
Fig. 21. Bleached crusts in an iceberg plough mark in 36-m water depth (dive track 711). Scale bar = 10 cm.
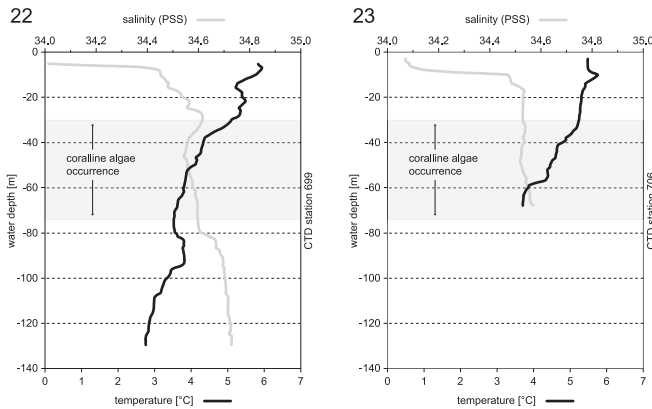
Figs 22, 23. CTD diagrams from stations 699 (Fig. 22) and 706 (Fig. 23) showing a similar pattern. Temperature decreases continuously with increasing water depth. Salinity strongly increases in the upper water column and stabilises at *c.* 20-m water depth. The coralline algae occurrence extends from 78- to 30-m water depth.

Figs 24, 25. Light measurements from stations 702 and 712 showing exponentially decreasing surface illumination toward deeper waters. The coralline algae occurrence extends from 78- to 30-m water depth.

Dive track 703 (95–110-m water depth) was very short and showed a partly washed-out pebble and cobble pavement with many large boulders on a smooth slope with *c.* 6° inclination. Epibenthos and shell accumulations were sparse and limited to depressions, where the pavement was also covered with a thin silty sediment layer. Coralline red algae were completely absent.

The seafloor at dive track 711 (70–30-m water depth; see Fig. 19 for facies profile) mainly conformed to the observations from dive track 701, but the morphology was less pronounced, the total inclination of the slope was *c.* 15° and bedrock was absent. The track started on a gravel pavement with shell accumulations that were restricted to patches. Thin coralline crusts appeared on individual larger cobbles at 70-m water depth, and the frequency and thickness of corallines increased with decreasing water depth. Occasionally, large boulders occurred, and the upper parts were completely covered with encrusting coralline algae. In 50-m water depth, shell beds and boulders were absent, and a flat gravel pavement dominated, while the bulk of the material was covered with encrusting coralline algae. Rhodoliths successively displaced the coralline-encrusted cobble community at 45-m water depth and partly covered the seafloor (Fig. 20). In 36-m water depth, encrusted boulders occurred again, and a small area was affected by an iceberg plough mark, and the affected rhodoliths and coralline crusts were bleached (Fig. 21). *Polysiphonia*-like red algae appeared and increasingly covered the seafloor at 32-m water depth, so that the rhodoliths and encrusting coralline algae were successively displaced.

Appearance and properties of the rhodolith beds slightly varied along the different dive tracks but showed the same overall pattern. Initial growth of encrusting algae started at *c.* 78-m water depth. With further flattening, thickness of crusts and development of protuberances increased. Coralline red algal coverage amounted to 30% below *c.* 45-m water depth. With further flattening, crust coverage strongly increased up to 100% if adequate substratum was available, and the coralline algae were not shaded and displaced by *Polysiphonia*-like red algae.

Environmental characteristics

The CTD records from stations 699 and 706 (Figs 22, 23) indicated a stratified summer situation characteristic for coastal Svalbardian waters. Temperatures decreased continuously with water depth from 5.8°C (surface) to 2.8°C (130-m water depth) at station 699 and from 5.5°C (surface) to 3.7°C (68-m water depth) at station 706. A surface layer with reduced salinity (*c.* 34) is developed in the upper 10 m of the water column at both stations. Underneath, more saline (> 34.5) waters, probably representing Atlantic-type water of the West Spitsbergen Current, prevail.

At stations 702 and 712 (Figs 24, 25), the ambient light levels decreased exponentially with water depth. The lower boundary of the euphotic zone (1% surface illumination) was at *c.* 45-m water depth at both stations. The lower boundary of the dysphotic zone (0.01% surface illumination) was not determined in the profiles, but extrapolation indicated a water depth of *c.* 90 m.

The bottom-near water parameters obtained by CTD and JAGO samples are compiled in Table 2. Despite the

Table 2. Water parameters obtained by CTD and JAGO.[1]

Station	T (°C)	p (dbars)	Salinity (PSS)	TA (µmol/kgSW)	DIC (µmol/kgSW)	pH	$p\text{CO}_2$ (µmatm)	Ω(cal)	Ω(arq)
699	3.0	131	35.0	2285	2106	8.15	294.10	2.97	1.88
703	3.0	30	35.0	2262	2096	8.12	314.78	2.84	1.79
706	3.7	62	34.6	2276	2110	8.11	323.70	2.86	1.80
714	3.0	50	35.0	2266	2084	8.16	285.17	3.06	1.93

[1] T, temperature; p, pressure; TA, total alkalinity; DIC, dissolved inorganic carbon; $p\text{CO}_2$, carbon dioxide partial pressure; Ω(cal), calcite saturation; Ω(arq), aragonite saturation.
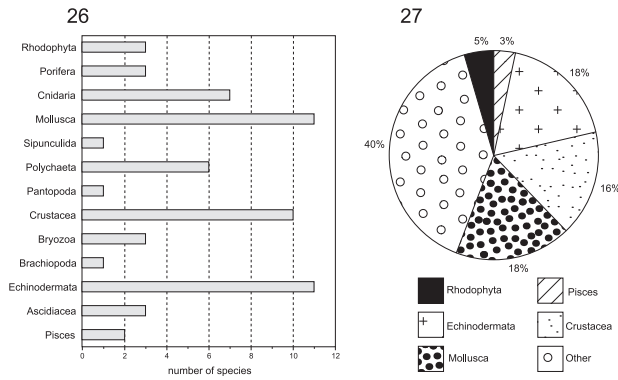
Table 3. List of identified benthos.

Species	No observations	Interrelation to rhodoliths						
		Living on the surface of the rhodoliths	Attached to the surface of the rhodoliths	Living inside of hollow rhodoliths	Attached to the inside of hollow rhodoliths	Feeding on the surface of the rhodoliths	Living between the rhodoliths	Overgrowing rhodoliths and coralline crusts
Rhodophyta								
Lithothamnion glaciale								X
Phymatolithon tenue								X
Polysiphonia-like red algae								X
Porifera								
Calcaronea indet.	X							
Geodia sp.	X							
Porifera indet.								X
Cnidaria								
Alcyoniidae indet.	X							
Actinia sp.			X					
Gersemia rubiformis	X							
Gorgoniidae indet.			X					
Hormathia nodosa			X					
Hydrozoa indet.	X							
Lafeiodae indet.	X							
Mollusca								
Astarte crenata	X							
Chlamys islandica				X			X	
Hiatella arctica			X	X	X		X	
Musculus laevigatus	X							
Tridonta montagui	X							
Boreotrophon truncatus	X							
Lepeta caeca						X		
Margarites sp.	X							
Naticidae indet.	X							
Tectura sp.						X		
Tonicella rubra						X		
Sipunculida								
Golfingiidae indet.				X			X	
Polychaeta								
Flabelligera affinis				X			X	
Nephtys sp.				X			X	
Nereis zonata				X			X	
Sabellidea indet.			X			X		
Terebellides stroemi				X			X	
Thelepus cincinnatus				X			X	
Pantopoda								
Nymphon sp.	X							
Crustacea								
Anonyx laticoxae	X							
Balanus sp.			X					X
Hyas araneus	X							

Table 3. Continued

Species	No observations	Living on the surface of the rhodoliths	Attached to the surface of the rhodoliths	Living inside of hollow rhodoliths	Attached to the inside of hollow rhodoliths	Feeding on the surface of the rhodoliths	Living between the rhodoliths	Overgrowing rhodoliths and coralline crusts
Lebbeus polaris	X							
Pagurus pubescens	X							
Pagurus sp.	X							
*Sclerocrangon ferox**	X							
Spirontocaris spinus	X							
Spirontocaris turgida	X							
Bryozoa								
Bryozoa indet.			X					X
Flustra foliacea			X					
Flustridae indet.			X					
Brachiopoda								
Hemithiris psittacea			X					
Echinodermata								
Cucumariidae indet.		X						
Gorgonocephalus sp.	X							
Heliometra glacialis	X	X						
Henricia sanguinolenta								
Ophiacantha bidentata							X	
Ophiocten sericeum							X	
Ophiopholis aculeata							X	
Ophiura robusta							X	
Ophiuridae indet.								
Solasteridae indet.	X							
Strongylocentrotus sp.						X		
Ascidiacea								
Ascidiacea indet.	X							
Boltenia echinata	X							
Styela rustica			X					
Pisces								
Artediellus atlanticus							X	
Cottidae indet.							X	

*Endemic Arctic species.

Figs 26, 27. Number and ratio of benthic species identified.
  Fig. 26. Number of species in each major taxonomic group identified during present study.
  Fig. 27. Pie chart showing percentage of species belonging to each major taxonomic group identified during present study. The Porifera, Cnidaria, Sipunculida, Polychaeta, Bryozoa, Brachiopoda and Ascidiacea have been collectively grouped under 'Other'.

low temperatures prevailing in the whole area, Ω_{Cal} and Ω_{Arg} were > 1 and thus in the range of saturation at any water depth in the study area.

Benthic community composition

A total of 61 benthic species were identified in the dredge sample and the video footage during the present study (Table 3; Figs 26, 27). However, this number, especially for taxa identified during the JAGO dives, probably will be an underestimate regarding the higher biodiversity that can be found when a larger variety of sampling tools is used (Hall-Spencer & Atkinson 1999). Mollusca and Echinodermata were richest in species (11 each), followed by Crustacea (10). The most prominent animal species are shown in Figs 28–36 and Figs 37–43. A clear depth zonation was evident in the distribution of the benthic fauna, with abundance and diversity decreasing with water depth. When rhodoliths were present, many species could be found on the surfaces of the rhodoliths, in gaps between them and even inside hollow rhodoliths (see Table 3 for the way of interrelation between benthos and rhodoliths).

DISCUSSION

Situated more than 1500 km north of the Arctic Circle, Nordkappbukta is an extreme environment in terms of water temperature, ice cover dynamics, light regime and salinity variability in response to meltwater formation. It is exposed both to cold Arctic Ocean water and, depending on seasonal activity, to the warmer Atlantic water of the West Spitsbergen Current. The mixing of the different water masses leads to a temperature range between the relatively warm (average 2°C; data from NODC_WOA94) upper-layer waters off western Spitsbergen (strongly influenced by the WSC) and the cold waters (average −1°C; data from NODC_WOA94) at the Barents Sea off eastern Nordaustlandet. All these characteristics exert high demands on the coralline red algae.

**Comparisons with other rhodolith communities**

Other polar and subpolar rhodolith communities occur, for example, in Alaska (Konar *et al.* 2006) and mainland Norway (Freiwald & Henrich 1994). The Alaskan community, situated in Herring Bay (Prince William Sound) at 60°28′N and 47°45′W, is the most northern known in the Pacific Ocean. In contrast to Nordkappbukta, Herring Bay features a monospecific rhodolith community composed of *Phymatolithon calcareum* (Pallas) W.H. Adey & D.L. McKibbin 1970 residing on a soft-bottom facies at 12–18-m water depth. The Alaskan rhodoliths have a similar ecological function as those in Nordkappbukta in providing a habitat for benthic organisms. Their branches are inhabited by specialized cryptofauna. This causes a strong increase in diversity of micro- and macrobenthos, a feature that seems to characterise many rhodolith communities (Foster 2001). At Herring Bay, the most abundant organisms are chitons (Konar *et al.* 2006), and thus the Herring Bay community seems to show the same interaction of coralline red algae and bioeroders as in Nordkappbukta and other localities (Steneck 1986).

In Norway, the Storvoll Plateau (Freiwald & Henrich 1994) situated in the Troms district at the southern tip of Rebbenesøy (69°59′N, 18°40′E) consists of rhodolith communities that fringe a rigid, *in situ* red algal buildup (14–15-m water depth). The community is multispecific, consisting of *Lithothamnion* cf. *glaciale*, *Lithothamnion* sp. and *Phymatolithon* sp., but the proportion of the two genera is much more balanced than in Nordkappbukta. However, the major sources for rhodolith production are detached heads from *Lithothamnion* branches, so most of the rhodoliths are not nucleated as they are in Nordkappbukta. The benthos is similarly diverse to that in Nordkappbukta, and many species [e.g. *C. islandica*, *H. arctica*

$\rightarrow$

Figs 28–36. Prominent epibenthic animals at Nordkappbukta. All scale bars = 0.5 cm.
  Fig. 28. *Flustra foliacea*.
  Fig. 29. *Hemithiris psittacea*.
  Fig. 30. *Astarte crenata*.
  Fig. 31. *Chlamys islandica*.
  Fig. 32. *Hiatella arctica*.
  Fig. 33. *Lepeta caeca*.
  Fig. 34. *Tonicella rubra*.
  Fig. 35. Polychaete (suborder Terebellomorpha).
  Fig. 36. *Balanus* sp.
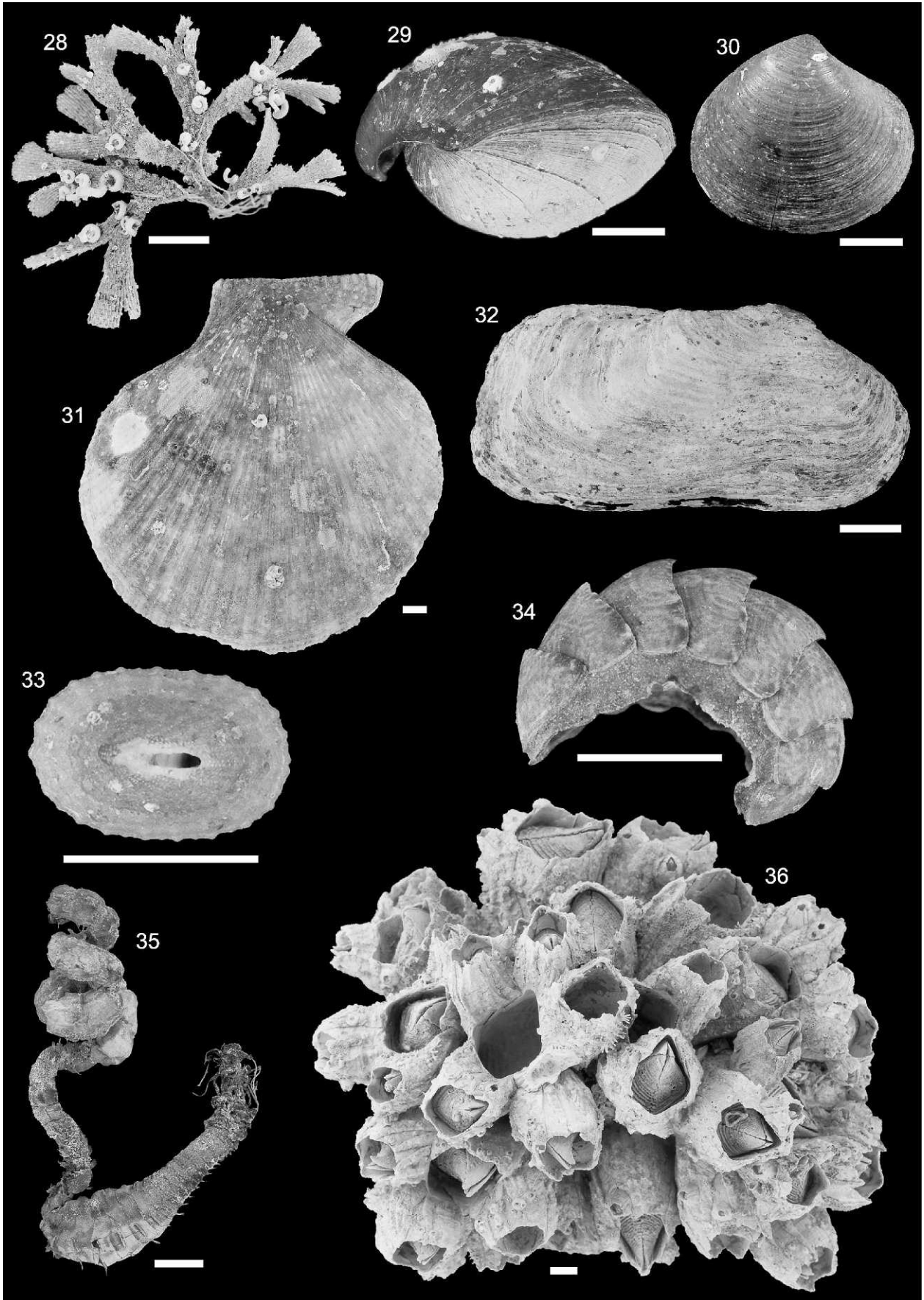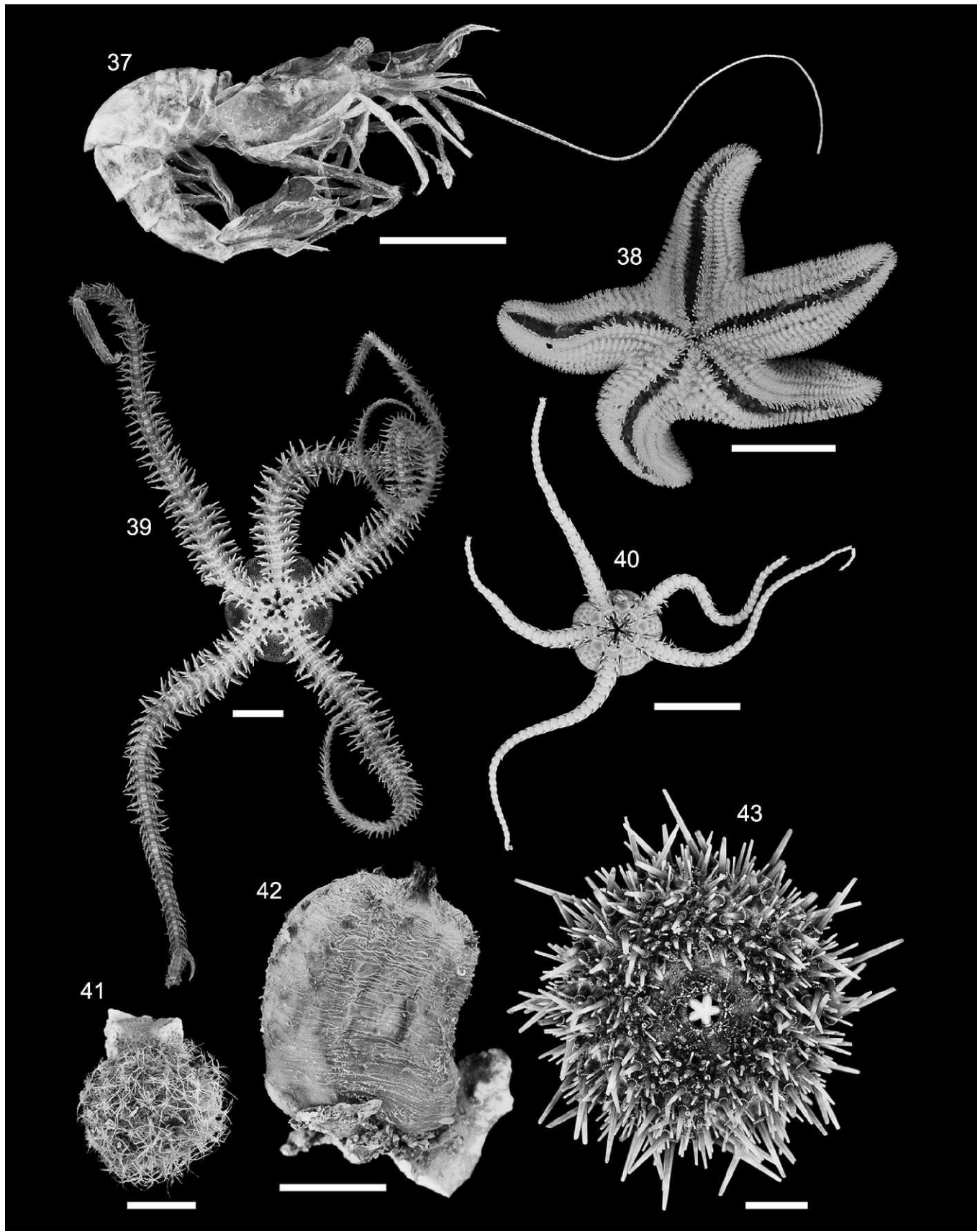
Figs 37–43. Prominent epibenthic animals at Nordkappbukta. All scale-bars = 0.5 cm.
   Fig. 37. *Lebbeus polaris.*

and *Hemithiris psittacea* (Gmelin)] occur at both localities. Even bioeroders like *Strongylocentrotus droebachiensis* (O.F. Müller) and *Lepidopleurus asellus* (Gmelin) are common and take the same ecological niche as other grazers do in Herring Bay and Nordkappbukta.

Growth forms comparable to the hollow rhodoliths from Nordkappbukta are reported from the Storvoll Plateau but not from Herring Bay. Moreover, the Storvoll Plateau community (14–15-m water depth) and the Herring Bay community (12–18-m water depth) occur in considerably shallower water than the Nordkappbukta communities (mostly 30–75-m water depth).

Overall, these rhodolith assemblages seem to be ecologically very important, especially in providing substratum and protection for many benthic organisms. This system works similarly at different sites, even when the communities are composed of different species. If rhodoliths are present in a biocenosis like Nordkappbukta, which consists mainly of flat gravel pavements, they can greatly increase the diversity by providing a kind of microenvironment for cryptofauna between their branches (Steller *et al.* 2003) and in their partly hollow bodies. Coevally, several species present between and on the rhodoliths (e.g. polyplacophores) act as grazers and keep the corallines free from epiphytes (Steneck 1986).

Substratum and water movement

Most commonly, coralline red algae are attached to stable rock, but under suitable conditions of water depth and water movement, cobbles can also be colonized and rhodoliths can develop. If the substratum is disturbed seasonally, annual plants may predominate (Lieberman *et al.* 1979; Sousa 1979). Corallines can also occur as epiphytes, growing on the surface of other organisms (Kain & Norton 1990). Visible bedrock is very rare in Nordkappbukta, and the substratum is made up of a few larger (> 1 m³) boulders and mainly by glaciogenic pebbles and cobbles appearing as gravel pavements. In a depth of 78 m, only cobbles above a distinctive size (> 10 cm) were colonized, but the minimum size of colonized cobbles and pebbles decreased with further seafloor flattening. Shell accumulations (mainly *Chlamys islandica* and *Hiatella arctica*) are of much lesser importance. The light shells as well as cobbles below a distinctive size do not provide enough stability, so storm waves and strong currents would intensely affect the coralline algal crusts. The reason why the minimum size of colonized material decreases with further flattening may be that other limiting factors, like irradiance, advance. Hence, the parts of the encrusted cobbles, which are currently buried, could be maintained sufficiently by the light-exposed part of the crust through secondary pits and cell fusions (Steneck 1986).

Another key factor for sufficient growth is water movement. Extensive beds of rhodoliths and maerl are found in areas with moderate to strong seabed currents that are relatively open yet sheltered (Bosence 1979). It has been suggested that these beds require both shelter from wave action to prevent burial of the thalli and enough water movement to prevent smothering with fine sediment (Hall-Spencer 1998); although, burial in coarse sediments has less severe effects on the algae (Wilson *et al.* 2004). Prevailing currents keep the exposed surfaces free from fine sediments due to the mostly flat topography in the Nordkappbukta coralline beds. Silt sedimentation, which is probably of seasonal origin due to meltwater transport, is limited to depressions. These depressions are generally devoid of living rhodoliths. The area, however, seems to be sufficiently protected from stronger wave and current action to enable the growth of large coralline crusts and rhodoliths. Shallower than *c.* 30-m water depth, crust and rhodolith coverage decreases and coralline algae are progressively replaced mostly by *Polysiphonia*-like red algae that shade the coralline red algae and inhibit further development. This change in algal cover could be caused mainly by increasing PAR (see below) and due to increasing wave action, which probably adversely affects *L. glaciale* and *P. tenue* more than the *Polysiphonia*-like red algae.

The action of waves and currents has a strong influence on the thriving of *L. glaciale* and *P. tenue* and is conducive to limit their main occurrence to a certain depth gradient between 70 and 30 m. Additionally, adequate substratum above a distinctive size has to be available to enable the development of initial encrustation. Hence, the bulk of the developed rhodoliths are nucleated or hollow, while rhodoliths with a core made up of coralline algae are rare. This also implies that the shape of the rhodoliths is controlled mainly by the shape of the encrusted material. Smothering of encrusted cobbles with soft sediment also seems to be harmful to the coralline algae. Signs of fresh-looking iceberg scour marks were not detected. Scouring of icebergs exerts a strong ecological disturbance to benthic ecosystems in polar waters (Heine 1989; Gerdes *et al.* 2003).

Temperature

Temperature has great effects on respiration, photosynthesis and growth rates of coralline red algae. The optimum temperature clearly varies geographically and with species, but the general pattern usually shows an increase in growth rate to a maximum that is near the top of the tolerated range (Kain & Norton 1990). Hence, temperature is the primary determinant of geographical distribution, and the boundaries of biogeographical regions are associated with isotherms (Lüning 1990). Adey & Adey (1973) showed that

←

Fig. 38. *Henricia sanguinolenta.*
Fig. 39. *Ophiopholis aculeata.*
Fig. 40. *Ophiura robusta.*
Fig. 41. *Boltenia echinata.*
Fig. 42. *Styela rustica.*
Fig. 43. *Strongylocentrotus* sp.

the distribution patterns of coralline red algae may be correlated with temperature boundaries.

In Nordkappbukta, the deepest occurrence starts at 78-m water depth, where the potential mean temperature is 0.7°C (data from NODC_WOA94). The maximum coverage appears at 45-m water depth, where the potential mean temperature is 0.4°C (data from NODC_WOA94). These relatively high temperatures result from mixtures of the warm Atlantic water with the colder Arctic Ocean water (Orvik & Niiler 2002; Sapota *et al.* 2009). However, this shows that *L. glaciale* is adapted to low temperatures compared to, for example, *Lithothamnion corallioides* (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan, which has a minimum survival temperature of 5°C (Adey & McKibbin 1970). On the other hand, it is also temperature that seems to limit the southward distribution of *L. glaciale*, possibly because reproductive conceptacles are produced only when water temperatures are < 9°C (Hall-Spencer 1994). The Nordkappbukta CTD records (Figs 22, 23) show only snapshot conditions, but they were taken during summertime and under ice-free conditions. Hence, one can assume that they may show values close to the possible maxima. With values of 3.5°C in 78-m water depth, where coralline algae encrustation starts, and 4.2°C in 45-m water depth, where coralline algae development reaches its maximum, the water temperature is far below the 9°C limit, so conceptacle formation should be possible during summertime. This is a great advantage since the reproductive frequency of *L. glaciale* is annually protracted (Jackson 2003) and reproduction during summer implies sufficient light conditions, while it may fail during winter darkness.

Altogether, *L. glaciale* occupies a distinctive temperature range in Nordkappbukta, which is coequally warm enough to enable sufficient growth and cold enough to enable reproduction during summer.

Salinity

Fluctuations in salinity may cause osmotic stress, unfavourable ionic balances and shortage of essential metabolites (Kain & Norton 1990). Passing down a salinity gradient, the number of species of Rhodophyta commonly declines sooner than that of the Phaeophyta; whereas, that of the Chlorophyta may actually increase (Coutinho & Seeliger 1984). Despite this, *L. glaciale* favours full marine conditions but is also presumed to be tolerant to varying salinities (18–40 pss; Jackson 2003). Experiments by Wilson *et al.* (2004) also showed that *L. glaciale* appears to be not very sensitive to low salinities (< 18 PSS).

The salinity gradient in Nordkappbukta (Figs. 22, 23) seems to be quite stable except for the upper 10 m, which is subject to a thin incumbent freshwater lens deriving from terrestrial input (glacial meltwater, fluvial discharge). But this stable condition is only a snapshot and can change during times of melting sea ice or pronounced shifts of ocean currents and the coherent mixture of Atlantic water and Arctic Ocean water. Hence, it is an important attribute of *L. glaciale* to be suitably adapted to changing salinities. It may also be a reason why most of the red algal coverage in Nordkappbukta is made up of *L. glaciale*.

Irradiance

Coralline and other red algae can tolerate a wider range of light levels than any other group of photosynthetic plants, and many are low-light adapted (Kain & Norton 1990). This holds both for geniculate (jointed) corallines (Hader *et al.* 1996) and nongeniculate corallines (Kühl *et al.* 2001; Roberts *et al.* 2002), and such species often show an effective adaptation to low irradiance in polar latitudes and which is prolonged under sea ice conditions. Lüder *et al.* (2002) reported that the noncalcareous red alga *Palmaria decipiens* (Reinsch) R.W. Ricker could cope with complete darkness for several months before respiration suddenly drops, while photosynthetic capacity recovers rapidly after exposure to illumination. This enables sufficient growth even at high latitudes, such as in Nordkappbukta, where the polar night lasts for 120 days, and thus *L. glaciale* and *P. tenue* seem to be adapted very well to long-term dark periods.

Appearance and properties of the rhodolith beds slightly varied along different dive tracks but showed the same overall pattern. Initial growth of encrusting coralline algae started at *c.* 78-m water depth in the dysphotic zone (0.01–1% surface illumination), where the measured PAR was 0.1 μmol photons m^{-2} s^{-1} on average for both stations (Figs 24, 25). Roberts *et al.* (2002) showed that individuals of *P. tenue* have no significant net photosynthesis at such low irradiance. At 45-m water depth (2.1 μmol photons m^{-2} s^{-1}, averaged for both stations), coralline red algae cover nearly 100% of hard substratum, and protuberances of *L. glaciale* are fully developed. The relative abundance of *P. tenue* is 10% at most, and data from Roberts *et al.* (2002) show a net photosynthesis of only 2 mmol O_2 m^{-2} d^{-1} for individuals of this species at such irradiance conditions. Hence, the initial appearance of *L. glaciale* at > 75-m water depth shows that these algae can cope with very low light conditions and are able to colonise a large range of the dysphotic zone. It could also be one reason why there is such a disequilibrium between the abundance of *L. glaciale* and *P. tenue*.

Wilson *et al.* (2004) showed that coralline red algae might lack the ability to perform additional photochemistry under high-irradiance conditions. The decrease in coverage with further topographic flattening (< 30-m water depth) seems to be directly linked to the increasing coverage of *Polysiphonia*-like red algae, which do not calcify, grow much faster than the coralline red algae and find sufficient light conditions in the shallow waters. However, this seaweed cover seems not to be dense enough to enable the development of a shaded coralline algal understorey at shallow depths (see Irving *et al.* 2005). Irradiance is another factor that limits the appearance of coralline red algae at Nordkappbukta to a distinct depth gradient since light conditions seem not be sufficient in depths > 78 m, while in a depth of < 30 m, irradiance is high enough to favour other plants that displace the coralline red algae. The nearly 50-m-wide depth range for *L. glaciale* is much larger than characteristic depth ranges for algae in temperate and tropical environments. This observation indicates a very high degree of shade adaptation as has been demonstrated for coralline algae from the Ross Sea, Antarctica (Schwarz *et al.* 2005).

Overcoming nutrient and carbon depletions

Although not analysed by us, the ecophysiological adaptation of coralline algae to overcome the summer depletion of macronutrients (nitrogen, phosphorus) deserves some consideration. As stated before, these macronutrients are available during the dark winter period in Svalbardian waters and thus can be utilised by long-living algae instantaneously. Such an ecophysiological adaptation has been experimentally proven for some polar phaeophytes (see Wiencke *et al.* 2007 and further references therein). The carbon needed to maintain metabolism, biomass and even growth during the dark period derives from carbohydrates as storage products. Such carbohydrate products occur as starch grains in coralline algae, which are formed photosynthetically during the illuminated period and deposited within the vegetative cell compartments. During the dark period, the carbohydrates can be remobilised and may act as carbon source. A similar pathway has been detected by Lüning *et al.* (1973) for some polar laminarian phaeophytes.

Water chemistry

The concentration of calcium is critical for calcification in coralline red algae (King & Schramm 1982), and the maintenance of potassium in algal cells, relative to seawater, depends on the presence of adequate quantities of calcium ions (Kain & Norton 1990). The seawater carbon content, associated with its pH, has a marked effect on photosynthesis at the low salinities (Kain & Norton 1990) that can occur particularly during times of intense meltwater input, and hence carbonate saturation is an important factor for coralline growth at high latitudes. Martin *et al.* (2008) showed that an increasing acidification of seawater leads to a significant reduction in coralline algal cover, so a lowered pH and the reduction of carbonate saturation are important factors affecting rhodolith beds.

The water chemistry measured at four sites in Nordkappbukta (Table 2) shows carbonate saturation (cal and arq) and a pH > 8 for the whole area, which could be a very important factor for the thriving of the rhodolith beds. This is remarkable because high-latitude oceans should be the first to become unsaturated with respect to calcite and aragonite (Orr *et al.* 2005). Hence, it is one of the main factors that may be affected by the ongoing ocean acidification resulting in impaired conditions for the growth of coralline red algae. Modeling studies projected annual mean carbonate subsaturation as early as 2032 for the Arctic surface ocean if anthropogenic CO_2 emissions follow the Intergovernmental Panel on Climate Change's business-as-usual scenario (SRES A2; Steinacher *et al.* 2009). This could also imply that a possible acidification could lead to a decrease in rhodolith abundance and hence to more unfavourable conditions for many benthic organisms due to the loss of habitat.

Interactions between coralline red algae and other benthos

Distribution, composition and abundance of the benthos (excluding rhodophyceans) in Nordkappbukta seem to be controlled mainly by light penetration and the kinetic energy regime (waves, currents and tides). As these factors depend very much on water depth, depth zonation is the most pronounced pattern in the distribution of the benthic assemblages. If fully developed coralline crusts and rhodoliths are present, up to 55% of the observed organisms use them as a habitat, as they live in gaps between the rhodoliths, grow attached to their surface or even live inside hollow rhodoliths (see Table 3). Thus, rhodolith accumulations act as bioengineers and represent microenvironments for the otherwise nonprotected glaciogenic flats. Similarly, other studies report on rhodolith beds as refugia for scallops (Kamenos *et al.* 2004a) and as a habitat for juvenile cod (Kamenos *et al.* 2004b). Because of the influence of the WSC, most benthic species are of Atlantic origin and also occur at boreal latitudes. The only endemic Arctic species identified at Nordkappbukta is the shrimp *Sclerocrangon ferox* (Sars). Hence, the proportion of endemic Arctic fauna amounts to only 1.7%.

The surfaces of coralline algae represent a major source of food for a variety of herbivores like molluscs, crustaceans, sea urchins and fishes (Kain & Norton 1990). The grazing seems to be beneficial to the corallines, especially because fleshy algae are removed or limited (Adey & Macintyre 1973), so herbivory is often identified as the source of disturbance that keeps corallines clean and healthy (Steneck 1982, 1986). The most effective physical defence is seen in the calcareous thalli of the Corallinaceae, which are much tougher than those of most algae (Littler *et al.* 1983; Watson & Norton 1985). Such calcareous forms are among the most grazer-resistant algae; although, even these are not immune (Clokie & Norton 1974; Adey & Vassar 1975; Steneck 1982; Padilla 1984). Many calcareous crustose species seem to be dependent in some circumstances upon browsing animals to remove epiphytes or competitors that might otherwise swamp the algae (Brawley & Adey 1981; Steneck 1982). Both *L. glaciale* and *P. tenue* are among these grazer-resistant calcareous forms, and prominent grazers like *Tonicella rubra* (Linnaeus) and *Strongylocentrotus* sp. are very common in the coralline beds. The higher frequency of the intensely branched *L. glaciale* compared to the relatively smooth-surfaced *P. tenue* may be caused by the high abundance of *Strongylocentrotus* sp. because ecological studies have shown that branches in some nongeniculate corallines are an effective defence against deep-grazing sea urchins (Milliken & Steneck 1981). Competition for space is also important, and many red algae monopolise or virtually occlude the substratum by abutting with neighbours to form a continuous sheet (Littler & Kauker 1984; Johnson & Mann 1986). This also happens in Nordkappbukta, where many pebbles and cobbles are encrusted as a whole and appear completely pinkish red. Secondary to the encrusted stones, completely hollow rhodoliths are common and act as kind of microenvironment for benthic animals such as *Flustra foliacea* (Linnaeus), *C. islandica*, *H. arctica* and *Ophiura robusta* (Ayres). Not much is known about the formation of hollow rhodoliths, and this will be in the focus of another study, but their importance for the present ecosystem is clearly evident.

The environment of Nordkappbukta enables coralline red algal rhodolith formation if sufficient substratum is present and bottom currents are strong enough to prevent smothering of the corallines with fine sediments. *L. glaciale* occupies a distinctive temperature range in Nordkappbukta, which is warm enough to enable sufficient growth and does not exceed 9°C, so formation of reproductive conceptacles in *L. glaciale* is possible throughout the summer.

Nordkappbukta is exposed to strong seasonality, so changes in salinity due to changing currents and meltwater input are common. Hence, the occurrence of *L. glaciale* provides evidence of its adaptation to changing salinities.

The prevailing light conditions seem to be the main reason why the coralline algae are limited to a distinctive depth gradient since irradiance is too low in water depths > 80 m to enable sufficient photosynthesis. On the other hand, in water depths < 30 m, irradiance is high enough to favour faster-growing plants, which outcompete the coralline red algae, or is too high for the low-light-adapted corallines.

Carbonate saturation is of particular importance to maintain skeletal growth. Hence, the measured carbonate saturation in Nordkappbukta is another important factor that makes substantial rhodolith development possible. Coequally, it is the most sensitive parameter in view of possible ocean acidification.

The concomitant appearance of corallines and prominent grazers, such as *T. rubra* and *Strongylocentrotus* sp., keeps the corallines free from epiphytes and coequally provides feeding grounds for the grazers. Additionally, the rhodolith accumulations act as bioengineers and represent microenvironments for the otherwise nonprotected glaciogenic flats, with hollow rhodoliths being of particular significance as providers of microhabitats for the associated benthic fauna.

Overall, *L. glaciale* and *P. tenue* appear to be well adapted to the extreme environment of the Arctic. But like all ecosystems with highly specialised organisms present, even this environment is vulnerable to global change. The findings reveal that polar coralline algae are much more widespread in polar waters than previously thought, thus representing a unique polar carbonate factory. This will lead to further investigations using the collected material to estimate a budget for the carbonate production of these polar rhodolith communities and to assess their value as a recorder for historic environmental change.

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