RESEARCH/REVIEW ARTICLE

Benthic algal vegetation in Isfjorden, Svalbard

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Abstract

Benthic algal vegetation was investigated at 10 sites in Isfjorden, Svalbard. Five sites were visited during summer 2010 and five during summer 2012. Both the littoral and sublittoral vegetation were sampled, the littoral by hand-picking and use of a throwable rake and the sublittoral using a triangular dredge. A total of 88 different taxa were registered, comprising 17 Chlorophyta, 40 Ochrophyta, 30 Rhodophyta and the Xantophyceae *Vaucheria* sp. The green algae *Ulvaria splendens* (Ruprecht) Vinogradova was recorded in Svalbard for the first time. Most of the sites consisted of hard bottom substrate, but one site, Kapp Wijk, consisted of loose-lying calcareous red algae (rhodoliths) and had species not recorded elsewhere. The sublittoral at the other sites was dominated by kelp. Molecular analysis confirmed the presence of the red alga *Ceramium virgatum* and a dwarf form of the brown alga *Fucus vesiculosus*. This study provides a baseline for future studies investigating changes in the vegetation due to environmental changes.

To access the supplementary material for this article, please see supplementary files under Article Tools online.

The algal flora of Svalbard is generally composed of species also found in other regions of the North Atlantic Ocean (Wulff et al. 2009). Very few species found in Svalbard are absent from Norwegian mainland (e.g., *Laminaria solidungula* and *Saundersella simplex*). A flora similar to Svalbard's extends eastwards along the Russian Arctic coast. Studies of the marine benthic algal vegetation from Svalbard date back to studies by Sommerfelt (1832) and Lindblom (1840). Later, Agardh (1862, 1868) studied samples brought back from several Swedish expeditions and registered a total of 51 different benthic algal species from Svalbard. The major studies of Arctic benthic seaweeds include contributions from Kjellman (1883), Rosenvinge (1893) and Lund (1959a, b). Vinogradova (1995a) made the first checklist of marine benthic algae from Svalbard, and Hansen & Jenneborg (1996) made a checklist based on the literature and their own studies. Gulliksen et al. (1999) compiled a distribution list of marine macro-organisms from Svalbard that also included benthic algae. Fredriksen & Kile (2012) added two not previously recorded species (*Antithamnionella floccosa* and *Lithosiphon laminariae*) from the outer Isfjorden area to the list, and Hop et al. (2012) added two more from Kongsfjorden (*Pogotrichum filiforme* and *Mikrosyphar polysiphoniae*). Finally, Fredriksen et al. (2014) added one species from Kongsfjorden (*Sphacelorbus nanus*), bringing the total number of marine macroalgal species recorded in Svalbard to 193.

Littoral benthic organisms may serve as useful tools to detect environmental changes since they integrate the environmental factors over time. Sessile organisms will better reflect any prominent changes in the environment than planktonic organisms that may be flushed into a fjord area and may only have a limited residence time. Littoral species are directly exposed to changes in air and sea surface temperatures, as well as changes in ice cover and freshwater input and the littoral may thereby be considered as an "early warning habitat" of a shifting

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climate (Høglund et al. 2014). A good baseline understanding of species diversity is therefore important from a management perspective.

This article provides a baseline for benthic algae in the Isfjorden area, which has previously been studied only in the outermost sites (Svendsen 1959; Fredriksen & Kile 2012). Ten sites were studied in the fjord, and traditional morphological characters were used for most algal identification. To increase the precision level of difficult taxa, molecular markers were examined.

Study area

In total, we sampled 10 sites from Selmaneset, in the outer part of Isfjorden, to the innermost Kapp Ekholm in Billefjorden (Fig. 1 and Table 1). Maps were examined to identify areas with hard bottom, a prerequisite for benthic algal growth, and on this basis, the sampling sites were selected. Many areas in the fjord have sediment bottoms or are heavily influenced by run-off from glaciers, leading to high turbidity and reduced salinity, which in turn may cause low diversity. The sites were selected to cover a gradient from the outermost part of the fjord to some of the side branches and included both exposed and more sheltered sites on both north and south sides of the fjord (see Table 1).

Sampling

The littoral zone, the zone from the high-water mark at high tide to the lowest water at low tide, was sampled by random hand-picking, preferentially at low tide. Walking along the shore, the researcher sampled all visible species. A throwable rake was also used from the shores or from a rubber boat to sample shallow areas. In 2010 and at site 6 (Kapp Ekholm) in 2012, snorkelling was used to better sample between 0 and 1–2 m depth. A triangular dredge with 50-cm sides towed behind a 15-m-long vessel, the RV *Viking Explorer*, was used to sample depths between 5 and 30 m. The dredge was towed from the deep towards land. At site 1 (Selmaneset), the sublittoral was sampled by divers. Divers collected all visible algal species. Since hand-picking, snorkelling and use of the throwable rake were done simultaneously, we did not separate the littoral and sublittoral samples. After sampling, some of the materials were identified in situ before returning to the laboratory.

Processing samples

All samples to be identified in the laboratory were put into buckets or smaller flasks, with about 2% formalin. Some living specimens of selected genera, or parts of such, were dried on silica gel to be used for molecular analyses. In the laboratory, the formalin was washed out in several rinses and the algae left to soak in seawater for at least 24 h to get rid of any remaining formalin. Samples were identified to the lowest taxonomical level possible with the aid of the literature: Vinogradova (1995b), Dixon & Irvine (1977), Kornmann & Sahling (1977), Rueness (1977), Irvine (1983), Fletcher (1987), Maggs & Hommersand (1993), Brodie & Irvine (2003), Brodie et al. (2007) and Pedersen (2011). The current accepted nomenclature was checked against the work of Guiry & Guiry (2014).

Permanent slides were made by placing small pieces of specimens in a drop of a mixture of 10 ml corn syrup, 10 ml formalin, 20 ml distilled water and 1 ml 1% aniline. The slide collection was deposited at the University Centre in Svalbard.

Molecular species identification

Silica-dried material of *Fucus* spp. and *Ceramium* spp. (Table 2) was extracted using a modified Cetyl trimethylammonium bromide DNA extraction protocol as described by Gabrielsen et al. (2003) with an additional bead-beating step using a mixer mill (Retsch, Haan, Germany) for 2 × 1 min at 22 Hz. A region of the mitochondrial 23S subunit and a mitochondrial intergenic spacer (IGS) was amplified to confirm the identity of *Fucus* spp. from site 3 (Bohemanneset) utilizing three specimens of each of *F. vesiculosus* and *F. distichus* (Table 2). Polymerase chain reactions (PCRs) were run in volumes of 25 µl containing 1 × Hot Star Taq buffer (Qiagen, Germantown, MD, USA), 2.5 mM $MgCl_2$, 0.16 µM of each primer (designed by Coyer et al. 2006), 16 µM of each nucleotide, 0.4 µg BSA, 0.25 U HotStar Taq polymerase (Qiagen) and 2 µl of DNA. The PCRs were run on a Mastercycler ep Gradient S (Eppendorf, Hamburg, Germany) using an initial denaturation step of two min at 94°C followed by 35 or 40 cycles (for the 23S and the IGS, respectively) of denaturation at 94°C for 30 s, annealing at 48°C for 30 s, and elongation at 72°C for one min. After a final elongation step of five min at 72°C, the amplicons were stored at 4–10°C until they were checked on an agarose gel. The amplicons were cleaned using the E.Z.N.A Cycle Pure Kit (Omega Bio-Tek, Norcross, CA, USA) before Sanger sequencing using the forward primer at GATC Biotech (Constance, Germany).

The nrDNA 18S gene of three specimens of *Ceramium* spp. was amplified using the EukA and EukB primers (Medlin et al. 1988) in volumes of 25 µl containing 1 × Dream Taq

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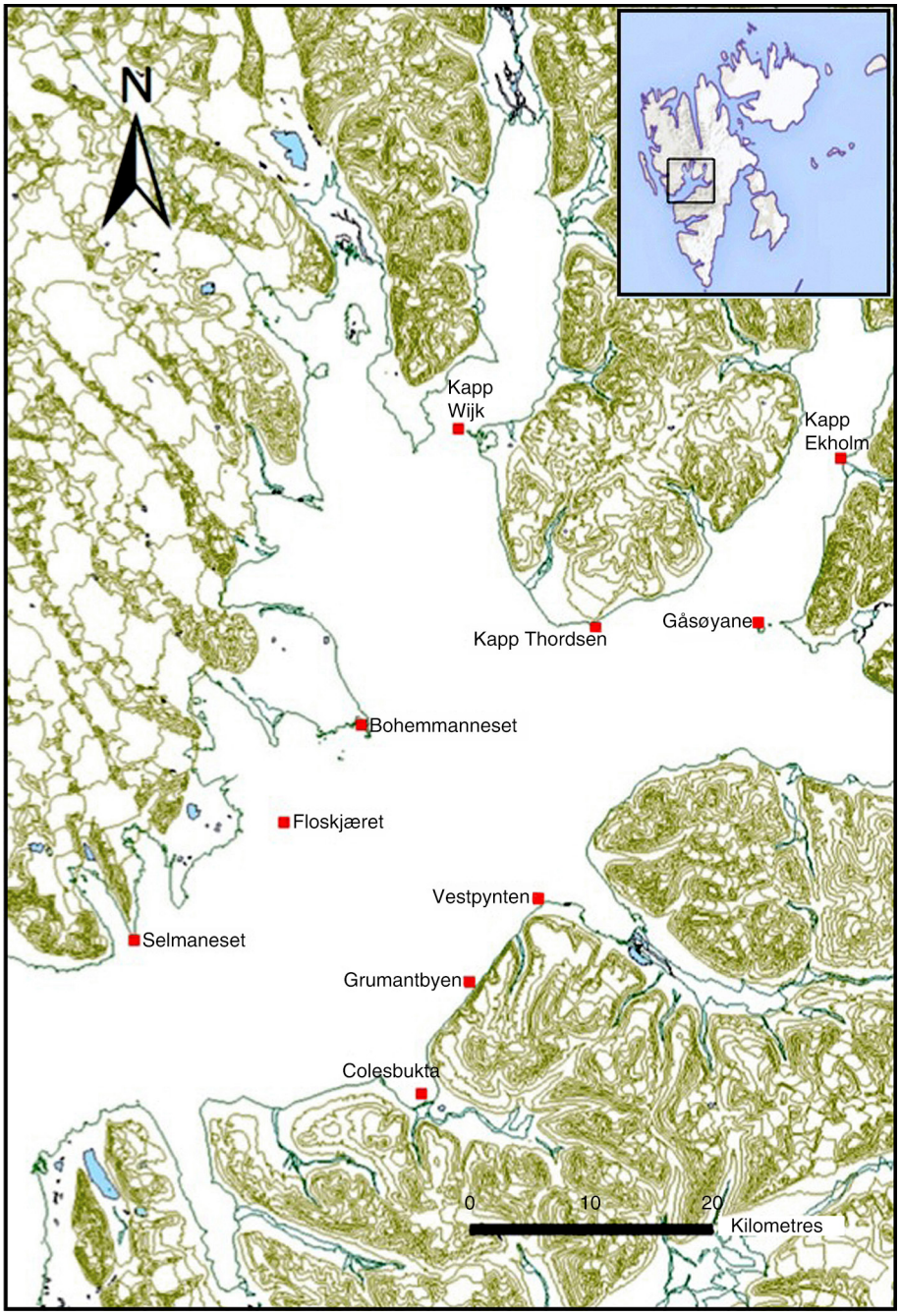

Fig. 1 Map of the sampling sites in Isfjorden. Numbers refer to sampling sites in Table 1. Inset shows Svalbard.

buffer (Thermo Fischer Scientific, Waltham, MA, USA), 200 µM of each nucleotide, 0.10 µM of each primer, 1 U Dream Taq polymerase (Thermo Fischer Scientific) and 2 µl DNA (10 × or 100 × dilutions). The PCRs were run using an initial denaturation step of three min at 94°C followed by 35 cycles of denaturation at 94°C for 45 s, annealing at 54°C for one min and elongation at 72°C for two min. After a final elongation step of 10 min at 72°C, the amplicons were stored at 4–10°C until they were checked on an agarose gel. The amplicons were cleaned using ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) before Sanger sequencing at GATC Biotech using the 528F primer (Elwood et al. 1985) and the EukB primer. The plastidic rubisco spacer region was amplified for seven specimens

Table 1 Collection data of the sampled stations in Isfjorden. See site number in Fig. 1; see also Supplementary Table S1.

Locality	Position	Date	Description	Sampling depth	Comment
Site 1: Selmaneset	78°13′N 13°55′E	07.09.2012	Rocky shore; exposed	Littoral 0–10 m	Diving used as an additional sampling method
Site 2: Floskjæret	78°18′N 14°30′E	10.08.2010	Small pebbled skerry in the littoral; exposed	Littoral 0–10 m	Submerged on high tide; urchins in the sublittoral
Site 3: Bohemanneset	78°23′N 14°43′E	12.08.2010	Rocky shore with wide, shallow upper part of sublittoral; exposed, long shallow slope	Littoral 0–10 m	Sublittoral dredging both sheltered and exposed
Site 4: Kapp Thordsen	78°27′N 15°35′E	11.08.2010	Rocky shore; exposed	0–2 m	Very sparse vegetation in littoral
Site 5: Kapp Wijk	78°37′N 15°5′E	06.08.2012	Rhodolith area; sheltered	30–15 m	No littoral sampling
Site 6: Kapp Ekholm	78°34′N 16°35′E	04–05.08.2012	Littoral of small pebbled beach; sheltered	Littoral 0–2 m 6–20 m	Very sparse vegetation in littoral; urchins in the sublittoral
Site 7: Gåsøyane	78°27′N 15°15′E	13.08.2010	Exposed southern side of bird cliff; rocky shore and boulders	Littoral 8–15 m	Rich littoral; rich sublittoral kelp forest
Site 8: Vestpynten	78°15′N 15°25′E	05–06.08.2012	Littoral of small pebbled beach; exposed	Littoral 0–20 m	
Site 9: Grumantbyen	78°10′N 15°5′E	10.08.2010	Boulders; exposed	5–30 m	No littoral sampling
Site 10: Colesbukta	78°7′N 14°50′E	19.09.2012	Small pebbled shoreline; sheltered	Littoral 0–14 m	

using the primers designed by Goff et al. (1994), using the method of Gabrielsen et al. (2003), modified by using the Dream Taq polymerase and buffer (Thermo Fisher Scientific). The amplicons were cleaned using solid-phase reverse immobilization and Sanger sequenced in both directions at GATC Biotech.

The PRIMER computer package, version 5.2.1, was used to run a cluster analysis to identify similarity patterns between the different sampling sites. The Bray–Curtis similarity index was used on non-transformed data (Bray & Curtis 1957).

Results

In total, 88 taxa were registered during this survey, 17 green, 40 brown and 30 red algae, in addition to one Xanthophyceae, *Vaucheria* sp. (Supplementary Table S1). Site 3 (Bohemanneset) and site 7 (Gåsøyane) had the

Table 2 Samples of *Fucus* spp. and *Ceramium* spp. that were Sanger sequenced to confirm their taxonomic identity. Refer to Table 1 for localities.

Taxon	Locality	Pop. ID	Sample ID	Sequenced region	GenBank ID
F. distichus	Site 3	Fd2010-4	1	mt IGS, mt 23S	KP828760, [c]
F. distichus	Site 3	Fd2010-4	2	mt IGS, mt 23S	[c, d]
F. distichus	Site 3	Fd2010-4	3	mt IGS, mt 23S	KP828761, KP828758
F. vesiculosus	Site 3	Fv2010-4	1	mt IGS, mt 23S	[e, f]
F. vesiculosus	Site 3	Fv2010-4	2	mt IGS, mt 23S	[e], KP828756
F. vesiculosus	Site 3	Fv2010-4	3	mt IGS, mt 23S	KP828759, KP828757
C. virgatum	Site 3	2010-4	(*C.* cf. *strictum*)	Rubisco spacer	[b]
C. virgatum	Site 3	2010-4	1 (*C.* sp.)	Rubisco spacer	[b]
C. virgatum	Site 3	2010-4	2 (*C.* sp.)	18S/Rubisco spacer	[a, b]
C. virgatum	Site 4	2010-3	1 (*C.* sp.)	Rubisco spacer	KP828755
C. virgatum	Site 4	2010-3	2 (*C.* sp.)	18S/Rubisco spacer	[a, b]
C. virgatum	Site 4	2010-3	4 (*C.* sp.)	18S/Rubisco spacer	KP828754, [b]
C. virgatum	Site 7	2010-5	1 (*C.* cf. *virgatum*)	Rubisco spacer	[b]

[a]Samples with 18S partial sequences identical to KP828754. [b]Samples with Rubisco spacer sequences identical to KP828755. [c]Samples with partial 23S mtDNA sequence identical to KP828758. [d]Sample with mtDNA IGS sequence identical to KP828761. [e]Samples with mtDNA IGS sequence identical to KP828759. [f]Sample with partial 23S mtDNA sequence identical to KP828756.

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highest number of species, with 45 and 44, respectively. Both sites had a well-developed littoral zone with several species of algae and also barnacles, indicating limited ice scouring at least the last winter(s) prior to sampling. Fewer species were found in the inner branches of the fjord, as the sites in the main fjord basin in general had higher species richness than the innermost site 6 (Kapp Ekholm). Site 1 (Selmaneset), which was additionally sampled by divers, had the lowest number of species of all sites sampled in both littoral and sublittoral. The lowest number of species was found at site 5 (Kapp Wijk). This site was only sampled in the sublittoral using the triangular dredge. The bottom at Kapp Wijk consisted of loose-lying crustose coralline algae (rhodoliths).

A cluster diagram based on Bray–Curtis similarity showed that site 5 (Kapp Wijk) had the lowest similarity with the other sites, followed by site 1 (Selmaneset; Fig. 2). The two most similar sites were site 7 (Gåsøyane) and site 8 (Vestpynten), with site 3 (Bohemmanneset) in the same clade. These three last sites had the highest number of species. A similarity matrix is shown in Supplementary Table S2.

Some of the taxa could not be identified below the genus level on account of the small size of the specimens (*Cladophora* sp., *Ulva* sp. and *Porphyra* sp.) or the absence of good diagnostic characters (*Acrochaetium* sp.). Others were limited to groups like brown crusts and red crusts; both these groups probably contain several different species, but lack of sufficient material and fertile structures made identification of these uncertain. Figure 3 shows some of the taxa found, including *Ulvaria splendens*, a new species from Svalbard. See the Supplementary file for taxonomic notes pertaining to the identification of some species.

Discussion

Fjords are ecosystems with a complexity of habitats and, often, strong environmental gradients, such as exposure to wave action, salinity and turbidity. In this study, we registered a total of 88 different species of marine benthic macroalgae in Isfjorden. This is 45% of the total number recorded from Svalbard. In the outer part of Isfjorden, Fredriksen & Kile (2012) reported 83 taxa, based on collections from two sites in their revisit to Svendsen's sites 50 years earlier (Svendsen 1959). Fredriksen & Kile (2012) found 16 taxa (three green, eight brown and five red algae) that were not recorded during this study. The most plausible explanation may be the fact that one of the sites investigated by Fredriksen & Kile (2012) was at the opening of the fjord which may have been more strongly influenced by the Atlantic than further in the fjord. It is well known that diversity declines or species composition shifts from the outer to the innermost parts of fjords (Jorde & Klavestad 1963, Husa et al. 2014). Cluster analysis did not reveal any clear gradients in species composition in Isfjorden; the two most distant sites, site 6 (Kapp Ekholm) and site 10 (Colesbukta), clustered together. We did not, however, sample any sites in the innermost parts of any side branches to Isfjorden.

In general, all the sites were sampled in a similar way. Two sites were not sampled in the littoral: site 5 (Kapp Wijk) and site 9 (Grumantbyen). At site 1 (Selmaneset), the sublittoral was sampled by divers, who sampled all visible algal species from 14 m up to the surface; this yielded a surprisingly low species number (25), the lowest of all sites. Since we have no indications that diving is less efficient than dredging, we interpret this as a reflection of site 1's nature rather than an effect of the sampling method. Our study covered 10 sites in a large fjord system, and there are surely habitats that we missed.

Some of the species were only recorded once (see Supplementary Table S1). Some small epiphytic species are only visible using stereo- or compound microscopy and tend to be rare in samples such as those in our investigation. This does not mean that they are rare in nature; they are simply often overlooked in the samples.

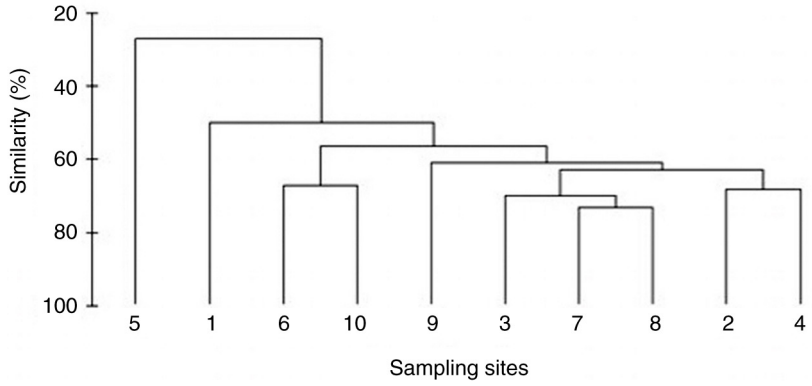

Fig. 2 Cluster diagram showing the similarity between the different sites.

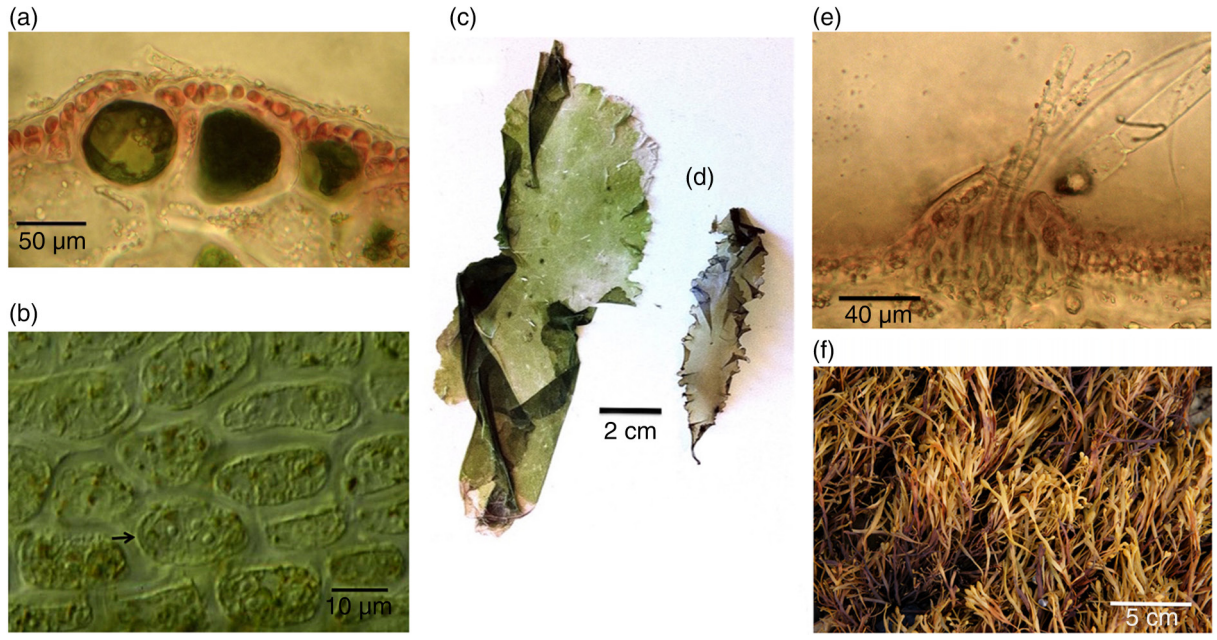

Fig. 3 (a) Photograph of the green endophyte *Chlorocythrium inclusum* in the red alga *Euthora cristata* from Kapp Wijk, Isfjorden. *C. inclusum* represents the diploid phase in the life cycle of *Spongomorpha aeruginosa*. (b) Microscopic view of cells in *Ulvaria splendens*. The arrow is pointing at a cell with three visible pyrenoids. This species is found in Svalbard for the first time. Herbarium specimens of (c) *U. splendens* from Vestpynten and (d) *Ulvaria obscura* (right) from Colesbukta. Note the difference in colour. (e) *Laminariocolax aecidioides* growing inside *Saccharina latissima* from Vestpynten, Isfjorden, in 2012. (f) *Fucus vesiculosus* from site Bohemanneset, Isfjorden, in 2010. Identified by both morphology (it was dioecious) and molecular methods.

At site 5 (Kapp Wijk), rhodoliths dominated the bottom. These are loose-lying corallines of the species *Litothamnion glaciale*, with a lesser amount of *Phymatolithon tenue* (Teichert et al. 2012; Teichert et al. 2014). We recorded species of algae here that were not found at any of the other sites (see Supplementary Table S1), and this was also the site that differed most from the other sites according to the cluster analysis. Teichert and co-workers (2012, 2014) investigated rhodolith beds at four sites in Svalbard, including Floskjæret, which was also studied in our investigation. They recorded only one genus of, as they put it, *Polysiphonia*-like alga. The low number of concomitant alga may be explained by the depth—exceeding 30 m—that they investigated. In total, we recorded 16 algal species from the rhodolith bed in Kapp Wijk. Peña et al. (2014) found a total of 349 macroalgal species on loose-lying corallines in the north-east Atlantic, a remarkable 30% of the total seaweed diversity in this region. This shows the importance of this type of habitat for benthic algae.

We observed the rhodoliths to be an important habitat for the sea urchin *Strongylocentrotus droebachiensis*, mostly smaller than 2 cm in diameter. Some sites showed clear signs of grazing by *S. droebachiensis*. In particular, this was the case when approaching site 2 (Floskjæret) and site 6 (Kapp Ekholm), as the bottom shifted from being covered by kelp to barren patches dominated by sea urchins. When the dredge was deployed at these sites, numerous urchins came up together with kelp and other algae. The grazing of urchins has been reported from the Norwegian mainland (Hagen 1983; Sivertsen 1997, 2006), and Norderhaug & Christie (2009) have reviewed grazing and re-vegetation in the north-east Atlantic. If urchins graze down most of the sublittoral kelp vegetation, it could have severe effects on the sublittoral community. On barren areas where urchins dominate, there is a significant reduction in both the number and diversity of other organisms (Norderhaug & Christie 2009). Grazed areas in Isfjorden should be monitored for changes in urchin distribution.

Warming temperatures are particularly notable in polar areas (Stocker et al. 2013). The presence of non-indigenous species (blue mussels [*Mytilus edulis*] in Isfjorden; Berge et al. 2005) or the increased number of warm-water species (Beuchel & Gulliksen 2008; Müller et al. 2009) will reflect environmental changes. In Kongsfjorden, Cottier et al. (2007) showed that advective processes with the West Spitsbergen current led to a greater inflow of warmer water to the fjord. Kortsch et al. (2012) showed that in the same fjord temperature and the number of ice-free days had increased in the period from 1980 to 2010. Inflow of Atlantic water masses to Isfjorden and a subsequent increase in temperature has also been shown by Nilsen et al. (2008) and by Pavlov

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et al. (2013). Pavlov et al. (2013) compiled data from the last century (1912–2009) and showed an increase of 1.9°C in the maximum temperature in Isfjorden during autumn and a recent warming event at the beginning of the 21st century to be more than 1°C higher than the second warmest period in the time series.

Marine benthic algae may be a useful group of organisms to study the effects of climate change (light and temperature in particular) on biota since they are primary producers as well as foundation species that create habitats for many animals (Christie et al. 2009). Algal vegetation in the littoral zone will reflect the degree of ice scouring there. Fredriksen & Kile (2012) recorded an increased number of littoral algal species (from 25 to 39) in the Kapp Linné area in the outermost part of Isfjorden compared to the number recorded by Svendsen (1959) 50 years earlier. Similarly, Weslawski et al. (2010) revisited several littoral sites in Hornsund and around Sørkapp in 2007–08 and found twice as many species and a threefold increase in macrophyte biomass compared to 20 years earlier. Species in the littoral had previously been recorded only from the sublittoral. According to Weslawski et al. (2010), the explanation was an increase in sea temperature, leading to reduced ice scouring. In Kongsfjorden, Fredriksen et al. (2014) showed an increase in the number of littoral species from 46 recorded in 2012–13 compared to 20 species recorded in 1996–98 (Hop et al. 2012). Warmer water and reduced ice cover will lead to an increased diversity in benthic algae, a phenomenon visible in the littoral zone in particular.

In their survey from the outer most part of Isfjorden, Fredriksen & Kile (2012) recorded 16 taxa not found during our investigation in Isfjorden. A total of 104 taxa are now recorded for Isfjorden and its side branches. With the finding of *Ulvaria splendens* in this investigation, a total of 194 marine macroalgal species have now been recorded in Svalbard.

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