

Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming

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Abstract Rocky littoral macroorganisms that live between the high and low water marks were sampled in the summers of 1988 and 2007–2008 in Hornsund Fjord and along the adjacent Sorkappland coast (76–77°N). The same sampling stations and methodology were used to collect the samples. Over the last 20 years, the study area has been exposed to well-documented increases in air and sea temperature, increased windiness, and marked decreases in both the duration and extent of sea ice cover. The study revealed a twofold increase in the number of species found intertidally, a threefold increase in the biomass of macrophytes, and an upward shift in algae occurrence on the coast. Subarctic boreal species occupied new areas, while arctic species retreated. There were no species new to the area in 2007–2008, and all newcomers to the intertidal zone were noted in 1988 in the sublittoral zone. The relative stability of intertidal flora and fauna after 20 years is explained by the fact that the warm Atlantic waters (the main warming agent) are distant from the Sorkappland coast. Current observations show a marked change in the coastal belt biocenosis.

Keywords Climate change · Arctic · Littoral · Benthos

Introduction

All global warming models indicate that the European arctic is the region with the highest and fastest temperature increase (ACIA 2005), and, consequently, the greatest biological

changes (Cheung et al. 2009). Coastal change (e.g., erosion, permafrost melt) is also a major problem linked to warming in the arctic (Ziaja 2001, Rachold et al. 2004). Littoral waters are the most susceptible to climate irregularities, ranging from overheating, UV radiation, and drying during low tide, to freezing, siltation, and abrasion. This is why intertidal ecosystems can be used as models for studying the biological effects of climate change (Hawkins et al. 2008; Jones et al. 2009). Intertidal waters are also most vulnerable to anthropogenic stress like oil spills (Weslawski et al. 1997a; Moe et al. 2000; Guenette et al. 2003). For many years, the arctic littoral zone was regarded as being devoid of life. This was due to ice scouring and the desert appearance of the arctic shores (Stephenson and Stephenson 1949; Ellis and Wilce 1961). Between 1988 and 1993, a number of littoral surveys were performed in the Svalbard intertidal zone (Ambrose and Leinaas 1989; Hansen and Haugen 1989; Weslawski et al. 1993a, b, 1997b; Szymelfenig et al. 1995). Not less than 60 species of macroorganisms and abundant meiofauna were reported at these high latitude intertidal sites (77–80°N). Increasing air and sea temperature on the west coast of Svalbard is well documented, and is linked to the strong, positive NAO indices of recent years (Walczowski and Piechura 2006, 2007; Marsz and Styszynska 2007). Recent decreases in sea ice thickness and range has been documented by satellite imagery data (ACIA 2005). On a local scale, the fast ice cover, duration, and thickness in the west Spitsbergen fjords is decreasing (personal observations at the Polish Polar Station in Hornsund, and communications from Norwegian settlements in Longyearbyen and Ny Alesund).

Most of the papers cited above, documenting climate change on Svalbard, indicate that rapid warming began in the 1980s (e.g., Weslawski and Adamski 1988). Several reports were made regarding biological changes associated with climate change on Svalbard, including distribution

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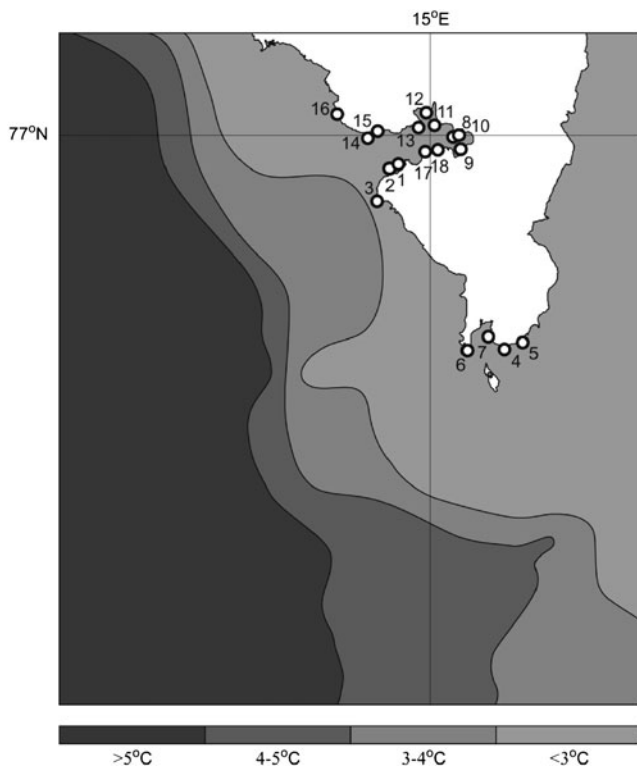


Fig. 1 Sampling stations and sea surface temperature distribution at southern Spitsbergen (Sorkapland) in summer. Compilation from IOPAS Hydrographic Section measurements, July/August 2005–2009

shifts of zooplankton species (Hop et al. 2006) and sublittoral benthic fauna occurrence (Beuchel et al. 2006). The most conspicuous finding was the reappearance of the thermophilous blue shell *Mytilus edulis* on Bjornoya and Spitsbergen after an absence of a few thousand years (Weslawski et al. 1997b; Berge et al. 2009). Several intertidal stations that had been sampled in 1988 on South Spitsbergen (Weslawski et al. 1993a, b) were revisited 20 years later and resampled in 2007 and 2008. The aim of the current study is to present the extent and nature of

changes in arctic hard-bottom littoral marine life after two decades of warming.

Methods

Study area

Spitsbergen is the largest island of the Norwegian Svalbard archipelago. The southern tip of the island, Sorkapland and the Hornsund fjord (under protection as the South Spitsbergen National Park), was the research area where 21 randomly distributed sampling stations were located (Fig. 1). The area is influenced by two water masses: the Atlantic water of the West Spitsbergen Current from the west, and in the east by the cold waters of the East Svalbard Current (formed by coastal waters, freshened and loaded with glacial suspensions (Swerpel 1985; Weslawski et al. 1995). The coast consists mainly of low gravel and stony beaches, with several tidal glacier cliffs, moraine lagoons, and frequent rocky (mostly hard, metamorphic) peninsulas with half-submerged skjerra (Weslawski et al. 1993a, b). The semidiurnal, lunar M2 tides here have an amplitude that ranges maximally to 1.8 m (Swerpel 1985). Recent local climatic changes are summarized in data collected from the Polish Polar Station in Hornsund (increased wind patterns, air temperatures, decreases in the occurrence of fast ice; compilation of data from Marsz and Styszynska 2007) (Fig. 2). Data on changes in the hydrological situation, namely the northward advance of core Atlantic waters and the resulting rise in sea temperature, are presented in papers by Walczowski and Piechura (2006, 2007). Observations of sea surface temperature distribution in the investigated area show how warm Atlantic waters are separated from the shores by a belt of cool, local waters (data from r/v *Oceania* AREX cruises, IOPAS Data Center, courtesy of Dr. Walczowski) (Fig. 1).

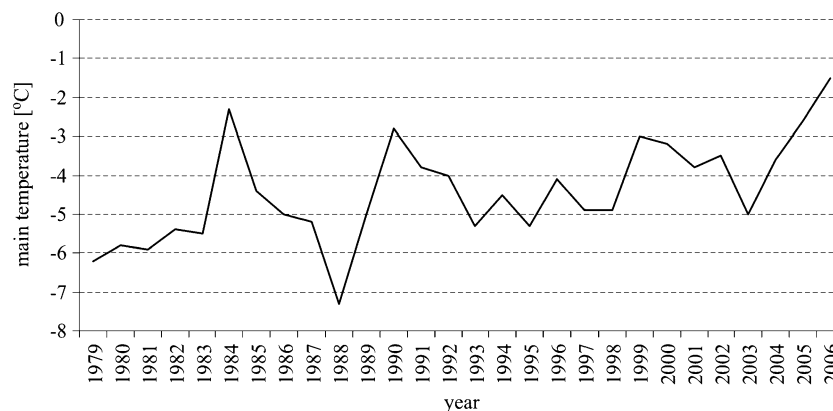


Fig. 2 Mean annual air temperature in Hornsund, between 1979 and 2006. Data compiled from Institute of Geophysics PAS and Marsz and Styszynska 2007

Table 1 Frequency of occurrence of macroorganisms species found intertidally in Hornsund and Sorkapland rocky shores during two surveys 20 years apart. Compilation of quantitative and qualitative samples from both periods

Taxon	Higher taxon	1988 n=24	2007–2008 n=51
Plants			
<i>Pilayella littoralis</i> (Linnaeus) Kjellman, 1872	Ochrophyta	8	78
<i>Fucus distychus</i> Linnaeus, 1767	Ochrophyta	41	74
<i>Acrosiphonia flagellata</i> Kjellman	Chlorophyta		62
<i>Chordaria flagelliformis</i> (O.F.Müller) C. Agardh, 1817	Ochrophyta		56
<i>Halosaccion ramentaceum</i> (L.)J.Ag.	Rhodophyta		22
<i>Urospora wormskioldii</i> Rosenvinge, 1893	Chlorophyta		19
<i>Desmarestia aculeata</i> (Linnaeus) J.V. Lamouroux, 1813	Ochrophyta		16
<i>Scytosiphon lomentaria</i> (Lyngbye) Link, 1833	Ochrophyta		15
<i>Elaschista fucicola</i> (Volley) Areschoug, 1842	Ochrophyta		11
<i>Sphacelaria plumosa</i> Lyngbye, 1819	Ochrophyta		10
<i>Rhodomela lycopodioides</i> (Linnaeus) C. Agardh, 1822	Rhodophyta		10
<i>Isthmoplea sphaerophora</i> (Carmichael) Kjellman, 1877	Ochrophyta		9
<i>Ulva lactuca</i> Linnaeus, 1753	Chlorophyta		7
<i>Dictyosiphon foeniculaceus</i> (Hudson) Greville, 1830	Ochrophyta		7
Animals			
<i>Gammarus oceanicus</i> Segerström, 1947	Amphipoda	23	62
<i>Lumbricillus</i> sp.	Oligochaeta	86	62
<i>Semibalanus balanoides</i> (Linnaeus, 1758)	Cirripedia	41	50
<i>Verrucaria</i> sp	Ascomycota	50	47
<i>Gammarus setosus</i> Dementieva, 1931	Amphipoda	68	26
<i>Spio filicornis</i> (Müller, 1776)	Polychaeta		26
<i>Onisimus littoralis</i> (Kroyer, 1845)	Amphipoda	32	21
Turbellaria	Platyhelminthes		21
<i>Ischyrocercus</i> sp.	Amphipoda	4	18
<i>Capitella capitata</i> (Fabricius, 1780)	Polychaeta		16
<i>Fabricia sabella</i> (Ehrenberg, 1836)	Polychaeta	4	16
<i>Syllis armillaris</i> (O.F. Müller, 1776)	Polychaeta		15
Polynoida n.det.	Polychaeta		14
<i>Harmothoe imbricata</i> (Linnaeus, 1767)	Polychaeta	4	13
<i>Margarites groenlandicus</i> (Gmelin, 1791)	Gastropoda	18	12
<i>Musculus</i> sp.	Bivalvia		9
<i>Liparis liparis</i> (Linnaeus, 1766)	Pisces	4	8
<i>Nymphon brevirostre</i> Hodge, 1863	Pycnogonida		8
<i>Eteone spetsbergensis</i> Malmgren, 1865	Polychaeta		7
<i>Eumidia arctica</i> (Annenkova, 1946)	Polychaeta		7
<i>Gammarus homari</i> (Fabricius 1779)	Amphipoda		6
<i>Calliopius laeviusculus</i> (Kroyer, 1838)	Amphipoda	4	4
<i>Linneus</i> sp.	Nemertina	8	4
<i>Palmaria palmata</i> (Linnaeus) Kuntze, 1891	Rhodophyta		4
<i>Boeckosimus edwardsi</i> (Kroyer, 1846)	Amphipoda	4	3
<i>Anonyx sarsi</i> Steele & Brunel, 1968	Amphipoda	4	2
<i>Harmeria scutulata</i> (Busk, 1855)	Bryozoa		2
Hydrozoa n.det	Hydrozoa		2
Tunicata n.det.	Tunicata		2
<i>Gammarus wilkitzkii</i> Birula, 1897	Amphipoda	4	
<i>Orchomenella minuta</i> (Kroyer, 1846)	Amphipoda	4	
Species count		19	43

Data collection

Sampling stations were chosen, using Norsk Polarinstitutt maps (scale 1:100,000) in 1988, and then revisited with GPS in 2007 and 2008. The samples were collected in late July, when neither fast ice nor sea ice were present on the shore. At each sampling site, the width of the intertidal zone (from the LW mark to the HW mark) was measured, and temperatures were noted. The salinity of tidal pools was measured with an electronic field reader. Salinity ranged between 33 and 34.5 PSU at all examined sites. There was no ice present in the littoral during sampling in 2007 and 2008 (save for small glacial ice chunks, growlers). Samples were collected from submerged rocks or large stones since these substrata are likely to be colonized by multi-annual organisms. Three frames measuring 20×20 cm were placed randomly on the seabed during low tide at the LW mark. All the organisms and the upper 5 cm of sediment within the frame were removed, placed into large jars, and fixed with 4% formalin. In the laboratory, the contents of each frame was gently washed on a screen with a mesh size of 0.5 mm. Additionally, 30–40 gammarid amphipods were collected from below the flat, loose rocks at the study sites. Data on gammarids collected in this way were presented as percent share of species in the sample (usually equivalent of 0.1 m^2). Large mobile organisms (like fish and hyperbenthic crustaceans) were collected qualitatively with a hand-held net in the tidal pools. Those organisms were marked as “present” or “absent” in the collection. A set of close-up and wider-angle photographs were made at each sampling site (<http://www.iopan.gda.pl/projects/SIP-2008/>). Overhead photographs were taken of areas 1 m^2 ; these were

scaled with 20-cm frames, and macrophyte coverage was assessed for each of 25 squares. Macrophyte coverage is presented as the mean value from all the photographs analyzed. Macrophyte and macrofauna biomass are presented as the actual sample weight (formaldehyde, wet weight).

Results

Complete lists of the species found intertidally (macro-organisms only) in 1998 and 2007–2008 are presented in Table 1. Of the species found in 1988, only 2 were not noted in 2007–2008, while 22 more species were noted in 2007–2008. The missing species in 2008 were of arctic origin (e.g., *Gammarus wilkitzkii*), while most of the newcomers were boreal or arcto-boreal (e.g., *Fabricia sabella*). Most of the newly recorded species are macrophytes or small polychaetes, which are apparently associated with the muddy turf patches in rock crevices. The occurrence of twin *Gammarus* species changed clearly, with the boreal *G. oceanicus* advancing toward the inner part of the fjord, and the cold-water *G. setosus* retreating to the more brackish areas close to the glaciers (Fig. 3). The exception among subarctic species was the periwinkle, *Littorina saxatilis*, which was rather common in “warmer” (outer fjord and open coast) stations in 1988, and rare in 2007–2008. A single specimen was noted at one locality in Hornsund (station 13) and Sorkapp at Nesbukta (station 6).

The biomass and coverage of macroalgae is presented in Tables 2 and 3, while Fig. 4 presents the comparison of the two periods. A clear increase in biomass in 2007–2008 is noted (the mean for all the stations is threefold). The

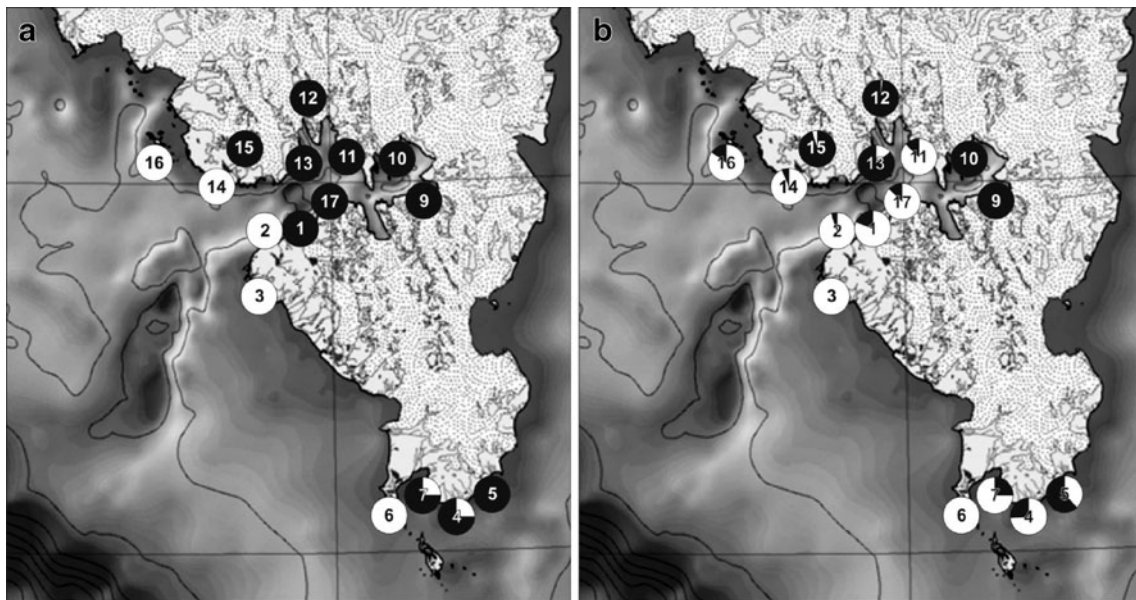


Fig. 3 Intertidal occurrence of boreal *Gammarus oceanicus* (light) and arctic *G. setosus* (dark) in 1988 (left) and 2008 (right)

Table 2 Biomass of macroorganisms found in Hornsund–Sorkapland in 1988 and 2007–2008

Station name	Station no.	1988 Biomass (ww g/m ²)	2007 Biomass (ww g/m ²)	2008 Biomass (ww g/m ²)
Adriabukta	11a	354	728	
Amonitoya	10	7	250	435
Bauten	9	7		1
Gnalodden	13	546	919	1,435
Hofferpynten	1	1,907	326	1,660
Hyrneodden	11	12	2,363	63
Hyttevika	16	4		104
Isbjornhamna	15	3	38	
Kulmstranda	2	62		2,128
Lisbetelva	2a	8	728	
Luciapynnten	12	12	944	45
Moloen	5	525		739
Nesbukta	6	702		1,126
Olsokneset	6b	0,2		
Palffyodden	3	33		568
Petersbukta W	17a	12	18	
Samarinvagen	18	2		21
Sorneset	4	28		60
Stonehange	17	954		95
Treskelen	8	0		20
Wilczekodden	14	481	1,532	1,366
Mean		283	785	617
SD		480	726	706
Min		0	18	1
Max		1,907	2,363	2,128

Biomass in g wet formalin weight

occurrence of *Fucus distychnus* and barnacles was also wider in 2008 compared with that in 1988. The macrophyte colonization of the inner fjord basin was particularly apparent. This glacial bay with its long-lasting fast ice cover was devoid of any macrophytes in 1988, while in 2008, stable, perennial macrophytes (*Fucus*) were found in several places. In 2007 and 2008, only barren skjerra were found in Samarinvagen (station 8), Bauten (station 9), and Baranowskiodden (station 15). All these barren locations were situated close to the glacier cliffs, with the frequent occurrence of growlers and long-lasting fast ice cover. The barren skjerra in 2007–2008 were covered with thin layers of filamentous algae comprising *Pilayella* and *Ulothrix* (see photographs at www.iopan.gda.pl/projects/SIP-2008/). Another difference was that silt deposits among intertidal algae were common in the 2007–2008 samples, which permitted an abundance of minute, tube-building polychaete worms (genera *Fabricia*, *Polydora*, *Spio*; Table 1).

The length of *Fucus* fronds was also considered to be indicative of ice scouring activity; in 1988, fronds of 6–10 cm long were collected in the outer fjord only (stations 2, 13, 14). In 2007, fronds were not statistically different from 1988, yet specimens measuring more than 14 cm were

Table 3 Density, coverage and biomass of two key intertidal species from 2008 samples

Station name	Station no.	<i>Semibalanus balanoides</i> Mean number of ind/m ²	<i>Fucus</i> % m ²
Amonitoya	10	50	1
Bauten	9	0	0
Gnalodden	13	1,630	28
Hofferpynten	1	4,693	32
Hyrneodden	11	466	31
Hyttevika	16	350	10
Kulmstranda	2	1,800	42
Luciapynnten	12	133	0
Moloen	5	310	14
Nesbukta	6	167	21
Palffyodden	3	150	15
Samarinvagen	18	2,163	0
Sorneset	4	20	0
Stonehange	17	2,800	36
Treskelen	8	20,250	1
Wilczekodden	14	4,167	26

Station numbers refer to Fig. 2

Data from the count of 5–10 scaled photos from each site

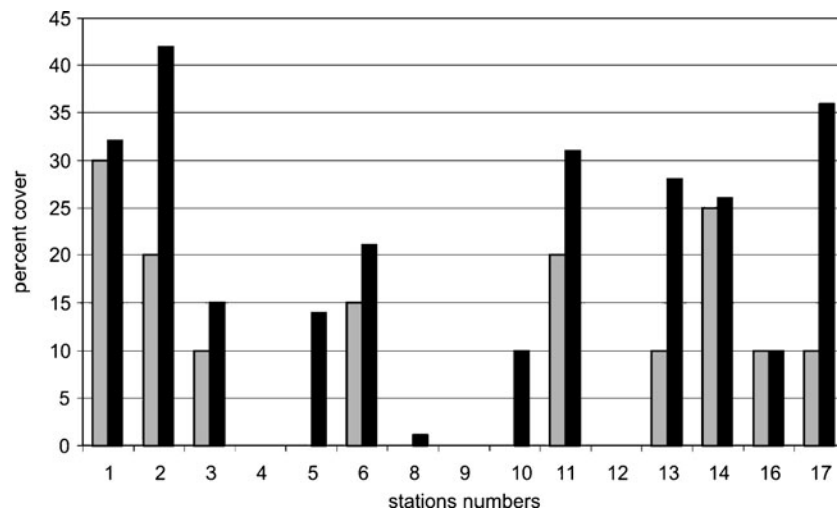


Fig. 4 Changes in the percentage cover of macrophytes in 1988 (light bars) and 2007/8 (dark bars). Sampling stations numbers (1–17) refer to Fig. 2. Zero values indicate lack of macrophytes on the rocks; algae film was not considered

found in the outer and middle parts of the fjord (stations 11 and 13, Fig. 5).

Discussion

The warming of the European arctic brings Atlantic species farther north along the North Atlantic Current flow, as was demonstrated in the 1950s by Blacker (1957). New data show the northern advancement of some pelagic species (e.g., euphausiids; Buchholz et al. 2009) as well as benthic species (e.g., *Mytilus edulis*; Berge et al. 2005). The north Norwegian shore is a natural supply area for Svalbard littoral organisms, with over 350 species known from this habitat (Weslawski 2004). The present list of only 80 intertidal species from Svalbard indicates that increased littoral diversity can be anticipated since both areas have similar types of coastal geomorphology and water mass temperature and salinity. A major obstacle for colonization is the long

distance from the mainland shore to the archipelago (about 1,000 km). During field work, fronds of *Ascophyllum* (shipwrack, a common species in northern Norway) were noted drifting along the west coast of Spitsbergen; however, in the last 20 years, no settled specimens have been found. All the macrophyte species noted here as new for the littoral zone were noted previously on Svalbard and in Hornsund in the sublittoral (Svendsen 1959; Florczyk and Latała 1989). The changes observed were local shifts in species occurrence with the advance of macrophytes and boreal crustaceans into the cold inner fjord basins and toward the shore, and the retreat of cold-water arctic species. The local effects of climate change include increased wind and glacial melt, and the resulting increased siltation (Thrush et al. 2004; unpublished reports from IOPAS) leads to a reduction in the euphotic zone. This, in turn, creates an upward shift of macrophytobenthos as has been observed along Baltic shores (Bucas et al. 2007). The increased fine sediment captured by bushy, intertidal algae creates habitats for small sediment-

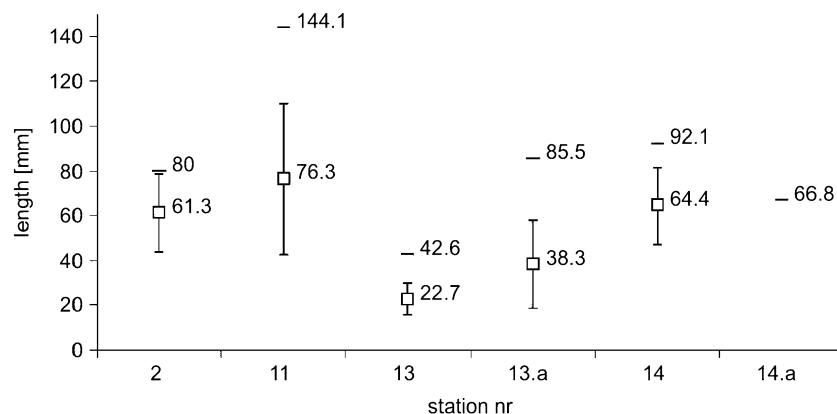


Fig. 5 Length of *Fucus* fronds (min, max, mean, and SD) in Hornsund littoral, summer 2007

dwelling organisms (like polychaetes and meiofauna). Another intertidal study performed at a 20-year time interval was that at Helgoland in 1984 and 2002. Pronounced changes were observed with 27 new species noted and 32 lost from the area (Reichert and Buchholz 2006). However, the overall diversity and species richness was similar in both of the periods compared. A limited number of long-term biological studies show that irregular cycles of abundance are typical for benthic and pelagic species (Blacker 1957; Dye 1998; Beuchel et al. 2006; Kedra et al. 2009). However, there are two surveys from Svalbard, performed over long time spans (at intervals of 20, 50, and 100 years) that show very stable patterns in species occurrence and zonation within the fjords (Renaud et al. 2007; Berge et al. 2009). The stability of the benthos might be linked to the semi-isolated character of the fjords, which are not heavily exposed to open seas. Studies of intertidal species distribution on open sea coasts were performed on UK shores, where changes between warm-water and cold-water barnacle species occurrence were documented over 50 years, yet a persistent boundary was observed (Herbert et al. 2009). On the other hand, models predict the disappearance of cold water barnacles from UK shores (Poloczanska et al. 2008). Icelandic intertidal studies reveal typical patterns of species richness associated positively with temperature, with 73 intertidal species on the warmer southern shore and 43 species on the colder northern shore (Ingolfsson 1996; Espinosa and Guerra-Garcia 2005). Weslawski (1994) demonstrated the indicative character of *Gammarus* species occurrence in Svalbard water masses. Present observations confirm the pattern of *G. oceanicus* expansion along with the warming of the Spitsbergen shores. A true arctic species, the ice-associated *G. wilkitzkii*, is found occasionally in the high arctic intertidal zone, and is the one that disappeared from Hornsund. The present situation likely creates isolated metapopulations of *G. setosus*, locked in the inner fjord basins, and separated by *G. oceanicus* populations that dominate the open oceanic shores.

Generally, the observed pattern of the lack of new littoral species, the upward movement of sublittoral species to the littoral zone, and an increase of intertidal biomass and cover are all caused by the isolation of Spitsbergen, which is 1,000 km from any potential source area (northern Norway). The Sorkapland coast itself is little influenced by the warm West Spitsbergen Current, which is the main vector of change (Karnovsky et al. 2003; Walczowski and Piechura 2006, 2007). In the studied area, colder coastal waters prevail, and major local hydrographic changes include sharp reductions in pack ice and fast ice and increased turbidity from melting glaciers. The well-documented and dramatic increase of the temperature of the West Spitsbergen Current and overall transport of Atlantic waters to the arctic (Walczowski and Piechura

2006, 2007) happened at a distance from the Sorkapland coast. It is likely that Atlantic coastal species will appear first in the Isfjorden–Kongsfjorden area since the West Spitsbergen Current flows closest to that shore, and it was there that the re-occurrence of the thermophilic *Mytilus edulis* was first noted (Berge et al. 2005).

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References

- ACIA (2005) Arctic climate impact assessment. Cambridge University Press, New York
- Ambrose WG, Leinaas HP (1989) Intertidal soft bottom communities on the west coast of Spitsbergen. *Polar Biol* 8:393–395
- Berge J, Johnsen G, Nilsen F, Gulliksen B, Slagstad D (2005) Ocean temperature oscillations enable reappearance of blue mussel *Mytilus edulis* in Svalbard after 1000 years of absence. *Mar Ecol Prog Ser* 303:167–175
- Berge J, Renaud PE, Eiane K, Gulliksen B, Cottier FR, Varpe O, Brattegard T (2009) Changes in the decapod fauna of an Arctic fjord during the last 100 years (1908–2007). *Polar Biol* 32:953–961
- Beuchel F, Gulliksen B, Carroll ML (2006) Long-term patterns of rocky bottom macrobenthic community structure in an Arctic fjord (Kongsfjorden, Svalbard) in relation to climate variability (1980–2003). *J Mar Syst* 63:35–48
- Blacker RW (1957) Benthic animals as indicators of hydrographic conditions and climate change in Svalbard waters. *Fish Invest Ser* 2:1–59
- Bucas M, Daunys D, Olenin S (2007) Overgrowth patterns of the red algae *Furcellaria umbilicaris* at an exposed Baltic sea coast. The result of a remote underwater video data analysis *Estuar Coast Shelf Sci* 75:308–316
- Buchholz F, Buchholz C, Węslowski JM (2009) Ten years after: krill as indicator of changes in the macro-zooplankton communities of two Arctic fjords. *Polar Biol* 33:101–113
- Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fisher* 10:235–251
- Dye AH (1998) Dynamics of rocky intertidal communities: analyses of long time series from South African shores. *Estuar Coast Shelf Sci* 46:287–305
- Ellis DV, Wilce RT (1961) Arctic and Subarctic examples of intertidal zonation. *Arctic* 14:224–235
- Espinosa F, Guerra-Garcia JM (2005) Algae, macrofaunal assemblages and temperature: a quantitative approach to intertidal ecosystems of Iceland. *Helgoland Mar Res* 59:273–285
- Florczyk I, Latała A (1989) The phytobenthos of the Hornsund fjord, SW Spitsbergen. *Polar Res* 7:29–41
- Guenette CC, Sergy GA, Owens EH et al (2003) Experimental design of the Svalbard shoreline field trials. *Spill Sci Techn Bull* 8:245–256
- Hansen JR, Haugen I (1989) Some observations of intertidal communities on Spitsbergen (79°N), Norwegian Arctic. *Polar Res* 7:23–27
- Hawkins SJ, Moore PJ, Burrows MT, Poloczanska E, Mieszkowska N, Herbert RJH, Jenkins SR, Thompson RC, Genner MJ,

- Southward AJ (2008) Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. *Climate Res* 37:123–133
- Herbert RJH, Southward AJ, Clarke RT, Sheader M, Hawkins SJ (2009) Persistent border: an analysis of the geographic boundary of an intertidal species. *Mar Ecol Prog Ser* 379:135–150
- Hop H, Falk Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Soreide J (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. *Prog Oceanogr* 71:182–231
- Ingolfsson A (1996) The distribution of intertidal macrofauna on the coasts of Iceland in relation to temperature. *Sarsia* 81:29–44
- Jones SJ, Mieszowska N, Wetthey DS (2009) Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the east coast of the United States. *Biol Bull* 1:73–85
- Karnovsky NJ, Kwasniewski S, Weslawski JM, Walkusz W, Beszczynska-Möller A (2003) Foraging behavior of little auks in a heterogeneous environment. *Mar Ecol Prog Ser* 253:289–303
- Kedra M, Włodarska-Kowalczyk M, Weslawski JM (2009) Decadal change in macrobenthic soft-bottom community structure in a high Arctic fjord (Kongsfjorden, Svalbard). *Polar Biol* 33:1–11
- Marsz A, Styszynska A (eds) (2007) *Klimat rejonu Polskiej Stacji Polarnej w Hornundzie (Climate of the Polish Polar Station in Hornsund)*. Wyd. AM w Gdyni, ISBN 978-83-7421-0287 (in Polish)
- Moe KA, Skeie GM, Brude OW, Lovas CM, Nedrebo M, Weslawski JM (2000) The Svalbard intertidal zone: a concept for the use of GIS in applied oil sensitivity, vulnerability and impact analyses. *Spill Sci Techn Bull* 6:187–206
- Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (2008) Modelling the response of populations of competing species to climate change. *Ecology* 89:3138–3149
- Rachold V, Are FE, Atkinson DE, Cherkasov G, Solomon SM (2004) Arctic coastal dynamics – an introduction. *Geoph Mar Lett* 25:63–68
- Reichert K, Buchholz F (2006) Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. *Helgoland Mar Res* 60:213–223
- Renaud PE, Włodarska-Kowalczyk M, Trannum H, Holte B, Weslawski JM, Cochrane S, Dahle S, Gulliksen B (2007) Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (van Mijenfjord, Spitsbergen). *Polar Biol* 30:295–305
- Stephenson TA, Stephenson A (1949) The universal features of zonation between tide-marks on rocky coasts. *Ecology* 37:289–305
- Svendsen P (1959) The algal vegetation of Spitsbergen. *Norsk Polarinst Skr* 116
- Swerpel S (1985) The Hornsund fjord: water masses. *Pol Polar Res* 4:475–469
- Szymelfenig M, Kwasniewski S, Weslawski JM (1995) Intertidal zone of Svalbard 2. Meiobenthos density and occurrence *Polar Biol* 15:137–141
- Thrush SF, Hewitt JE, Cummings VJ, Ellis JI, Hatton C, Lohrer A, Norkko A (2004) Muddy waters: elevating sediment input to coastal and estuarine habitats. *Front Ecol Env* 2:299–306
- Walczowski W, Piechura J (2006) New evidence of warming propagating toward the Arctic Ocean. *Geoph Res Lett* 33: L1 2601
- Walczowski W, Piechura J (2007) Pathways of the Greenland Sea warming. *Geoph Res Lett* 34: L1 0608
- Weslawski JM (1994) Genus *Gammarus* (Crustacea, Amphipoda) from Svalbard and Franz Josef Land. Distribution and density. *Sarsia* 79:145–150
- Weslawski JM (2004) The marine fauna of Arctic islands as bioindicators. In: S. Skreslet (ed) *Jan Mayen Island in scientific focus*. Kluwer, Dordrecht, pp 173–180
- Weslawski JM, Adamski P (1988) Cold and warm years in South Spitsbergen coastal marine ecosystem. *Pol Polar Res* 8:95–106
- Weslawski JM, Kwasniewski S, Wiktor J, Zajaczkowski M (1993a) Observations on the fast ice biota in the fjords of Spitsbergen. *Pol Polar Res* 14:331–343
- Weslawski JM, Wiktor J, Zajaczkowski M, Swerpel S (1993b) Intertidal zone of Svalbard. 1 Macroorganisms distribution and biomass. *Polar Biol* 13:73–108
- Weslawski JM, Koszteyn J, Zajaczkowski M, Wiktor J, Kwasniewski S (1995) Fresh water in Svalbard fjord ecosystems. In: Skjoldal HR, Hopkins CC, Erikstad KE, Leinaas HP (eds) *Ecology of fjords and coastal waters*. Elsevier, New York, pp 229–241
- Weslawski JM, Wiktor J, Zajaczkowski M, Futsaeter G, Moe KA (1997a) Vulnerability assesment of Svalbard intertidal zone for oil spills. *Estuar Coast Shelf Sci* 44: Supplement A: 33–41
- Weslawski JM, Zajaczkowski M, Wiktor J, Szymelfenig M (1997b) Intertidal zone of Svalbard. 3 Littoral of a subarctic, oceanic island: Bjornoya. *Polar Biol* 18:45–52.
- Ziaja W (2001) Glacial recession in Sorkapland and Central Norden-skioldland, Spitsbergen, Svalbard, during the 20th century. *Arct Antarct Alp Res* 33:36–41