

# Chapter 9

## Biodiversity of Benthic Macro- and Microalgae from Svalbard with Special Focus on Kongsfjorden



Stein Fredriksen, Ulf Karsten, Inka Bartsch, Jana Woelfel,  
Miriam Koblowsky, Rhena Schumann, Siri Røang Moy, Robert S. Steneck,  
Józef M. Wiktor, Haakon Hop, and Christian Wiencke

**Abstract** Several floristic studies on macroalgae of Svalbard have been published, but as access to the archipelago is difficult, these studies are scattered and often only cover single sites and habitats. Kongsfjorden, Isfjorden and Hornsund are the three most comprehensively investigated areas, and most of the species information comes from these three fjords. Quantitative and structured sublittoral sampling has been undertaken along depth transects and along the fjord only in Kongsfjorden. Clear dif-

---

S. Fredriksen (✉)

Section for Aquatic Biology and Toxicology, Department of Biosciences, University of Oslo, Oslo, Norway

e-mail: [stein.fredriksen@ibv.uio.no](mailto:stein.fredriksen@ibv.uio.no)

U. Karsten · M. Koblowsky · R. Schumann

Institute of Biological Sciences, Applied Ecology and Phycology, University of Rostock, Rostock, Germany

I. Bartsch · C. Wiencke

Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany

J. Woelfel

Department of Aquatic Ecology, Institute of Biological Sciences, University of Rostock, Rostock, Germany

S. R. Moy

Department of Biosciences, University of Oslo, Oslo, Norway

R. S. Steneck

Darling Marine Center, Walpole, ME, USA

J. M. Wiktor

Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland

H. Hop

Norwegian Polar Institute, Fram Centre, Tromsø, Norway

Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway

© Springer Nature Switzerland AG 2019

H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,

Advances in Polar Ecology 2, [https://doi.org/10.1007/978-3-319-46425-1\\_9](https://doi.org/10.1007/978-3-319-46425-1_9)

ferences are found from the outer to the inner parts of the fjord. Macroalgal biodiversity data from Kongsfjorden are presented in detail and compared to data for the whole archipelago. In total 197 species of macroalgae have been recorded for Svalbard; 84 of these occur in Kongsfjorden. The current taxonomic status of some species is discussed. Changes in the macroalgal flora during the last decades for Svalbard in general and in Kongsfjorden in particular, are summarised and possible causes discussed. Information on biodiversity of microphytobenthos is very scarce, and investigations in Kongsfjorden on benthic diatoms from soft bottom and biotic surfaces provide the first floristic information available. A total of 69 diatoms species have been identified and form a first baseline for a high-latitude fjord system. Biodiversity is relatively low compared to other sandy marine shallow water areas of temperate regions as indicated by the Shannon-Weaver index. Some data on epiphytic diatoms colonising seaweeds are available. Benthic diatoms colonise large parts of Kongsfjorden in high abundances and, in addition to macroalgae, are important as primary producers and therefore also for trophic relationships in the harsh Arctic environment.

**Keywords** Arctic · Svalbard · Kongsfjorden · Macroalgae · Microalgae · Species diversity

## 9.1 The Abiotic Environment of the Arctic

Plant life on land diminishes northwards, whereas this trend is less apparent for marine algae. The temperature and wind extremes that affect life on land in the Arctic are not so pronounced under water (Taylor 1954). In the marine realm a mean August and February oceanic sea-surface isotherm of 9–10 and 0 °C, respectively, has been used as a southern boundary of the marine Arctic phytogeographic region for many years (Lüning 1990; Bartsch et al. 2012). In the ocean, major currents transport warm water far north, such as in the West Spitsbergen current, so that the environmental conditions remain relatively constant for marine organisms much farther north, as compared to terrestrial systems.

Even though temperature is the most important factor for bio-geographical distribution of benthic algae (e.g. van den Hoek 1984), this abiotic factor does not seem to limit the northern distribution of benthic micro- and macroalgae in the Arctic. Kjellman (1883) stated that sites in the Arctic with richest macroalgal vegetation are subject to seawater temperatures that do not, in general, exceed 0 °C at any time of the year. The number of species of macroalgae, however, declines from the Norwegian mainland to the Svalbard archipelago i.e. from the cold-temperate to the Arctic region (Rueness 1977; Hansen and Jenneborg 1996; Hop et al. 2012).

Above the Arctic Circle (66°34'N) the sun does not set after the summer solstice and does not rise after the winter solstice. At the North Pole, the sun even rises and sets only once each year; as a consequence there are 6 months of continuous daylight and 6 months of continuous darkness. This extreme seasonal light situation has severe consequences for organisms that are dependent on light to photosynthesise and is perhaps the most striking factor for the benthic algae in the Arctic. The changing light

climate during the year is the main factor influencing the development of benthic macro- and microalgae (Pavlov et al., Chap. 5). Polar algae are usually low light adapted, but must also tolerate high light after the ice break up (Gómez et al. 2011; Zacher et al. 2011) and many adaptations exist to overcome the pronounced seasonality in light climate (Dunton 1985; Dunton and Schell 1986; Lüning 1990; Wiencke et al. 2007, 2011; Pavlov et al., Chap. 5). In Kongsfjorden (Svalbard), which is situated at 79° N, the incident light is continuous from April to September. Besides its obliquity, the available light for submerged algae is diminished by the temporal ice cover that may last until spring and the turbidity during summer due to glacier melting and river run-off (Hanelt et al. 2001; Pavlov et al. 2013; Pavlova et al., Chap. 4).

All classes and groups of both macroscopic and microscopic marine alga are present in the Arctic. Macroalgae are represented with brown-, green- and red algae (Kjellman 1883). Among microalgae, diatoms are considered to be the most abundant component of phytoplankton, ice algae and benthic microalgae in polar waters, both in terms of number of species and number of individuals (Wulff et al. 2011). Another very abundant pelagic microalga is the prymnesiophyte *Phaeocystis pouchetii* (Hariat) Lagerheim (Hasle and von Quillfeldt 1996).

## 9.1.1 Macroalgae

### 9.1.1.1 Ecological Importance

Benthic macroalgae are considered to play an important role in shallow water systems. They are primary producers and may serve as habitats for other species (Christie et al. 2009). The three-dimensional structure of such beds provides substrate, shelter, nursery grounds and feeding area for other algal species, diverse invertebrates or fish (see Christie et al. 2009 for an overview). Macroalgal beds and especially kelp forests are among the most productive ecosystems on the planet (Lüning 1990; Mann 2000; Abdullah and Fredriksen 2004), also in coastal areas of the Arctic (Borum et al. 2002; Krause-Jensen et al. 2007, 2012). Parts of the primary production may enter food webs by grazing from herbivores although most are transferred via detrital pathways (Duggins and Ekman 1997; Fredriksen 2003; Norderhaug et al. 2003) or released as DOM (Dissolved Organic Matter) into the water (Abdullah and Fredriksen 2004).

### 9.1.1.2 Historical Background

Investigations of benthic algae from Svalbard have a long but scattered history. The first study on macroalgae was done by Sommerfelt (1832), who received herbarium material from M. Keilhau. Sommerfelt described 5 different algal species from Svalbard, in addition to 1 species from Bear Island, the southernmost island of the Svalbard archipelago. Lindblom (1840) compiled literature from 5 earlier papers and counted a total of 16 marine and 3 freshwater macroalgae. Agardh (1862, 1868)

expanded previous species lists to 51 species. Agardh's findings were based on material received from different Swedish expeditions. He noted that the material arrived in good condition, both with respect to freshness and colour, owing to the preservation method of putting the algae in barrels with salt.

The only early comprehensive account of marine benthic algae and their circum-boreal distribution is *The Algae of the Arctic Sea* by Kjellman (1883). Kjellman had firsthand knowledge, since he participated in the *Vega* expeditions led by Nordenskjöld to Spitsbergen, Novaya Zemlya, and northern Siberia, between 1872 and 1880. Three ships left Sweden for the expedition in 1872/73, two of which were supposed to return home during the autumn with Kjellman on board. However, due to bad weather conditions, all three ships were forced into an unplanned overwintering in Mossel Bay on the northwestern part of Spitsbergen when wind pushed ice into the bay and the ships were stuck. This allowed Kjellman to perform the first Arctic winter study, observing how algae both grew and reproduced under the ice during the dark winter period (Kjellman 1875a, b, 1877a, b).

Kjellman (1883) opined on the marine algal flora of the Arctic very aptly: *The most prominent features in the general aspects of the Arctic marine flora are scarcity of individuals, monotony and luxuriance*. Scarcity of individuals refers to lack of substrata in most places, monotony to the dull brown colour of the kelp and other brown algae and luxuriance to the growth and size of kelp vegetation (according to Lüning 1990).

After a long period without activity on algal research, Svendsen (1957, 1959) carried out fieldwork for his thesis in the outermost part of Isfjorden during the years 1954 and 1955. He studied the algal vegetation at Kapp Linné on the southern side and Ymerbukta on the northern side of the fjord. Approximately 50 years later Fredriksen and Kile (2012) revisited Svendsen's localities and found a higher number of species compared to 1954/55 (83 versus 59 species).

In 1957 the Polish Polar Station Hornsund, called the *Polish house next to the North Pole*, was established, and environmental monitoring and studies of biodiversity were conducted for several decades. Many publications from these studies have added significant knowledge to the marine benthic algal vegetation around Svalbard, with particular focus on Hornsund (Florczyk and Latala 1989; Weslawski et al. 1993, 1997, 2010, 2011; Tatarek et al. 2012 and references therein).

In Ny-Ålesund nearby Kongsfjorden, various nations have operated many different research stations. However, only the German and Norwegian groups have focused on benthic algal diversity. In 1996 to 1998, for the first time with the aid of SCUBA diving, both quantitative and qualitative aspects of marine benthic algae at Hansneset in Kongsfjorden were studied but only published later (Wiencke et al. 2004; Hop et al. 2012, 2016). In 2012/2013 the site was revisited and the study repeated (Fredriksen et al. 2014; Bartsch et al. 2016).

Other methods, such as acoustics and remote sensing, have been used to study biomass and distribution of macroalgae in Kongsfjorden. Kruss et al. (2012, 2017) used an echosounder to map the distribution of macroalgae at depths of 0–30 m. They found macroalgal vegetation to be present in about half of the coast of inner Kongsfjorden. Kelp forests near Ny-Ålesund have also been surveyed by an airborne hyperspectral imager (Volent et al. 2007).

Algal checklists published for whole Svalbard covered benthic macroalgae (Vinogradova 1995a, b; Hansen and Jenneborg 1996), and planktonic microalgae (Wiktor and Okolodkov 1995; Hasle and von Quillfeldt 1996). The present publication provides an updated checklist for both benthic macro- and microalgae in Svalbard with a specific focus on Kongsfjorden considering all hitherto published evidence.

### 9.1.1.3 Time Series

Although no time series have been recorded exclusively for benthic macro- and microalgae, the documentation of the sublittoral hard bottom by means of photographic time series was initiated by the University of Tromsø in the 1980s commencing in Kongsfjorden and Smeerenburgfjorden and subsequently extending to Isfjorden and Hinlopen. The sites have been sampled nearly every year since commencement. Permanent transect locations at 15 m depth were selected at all sites, with bolts driven into the bedrock such that the same locations could be photographed periodically, i.e. sampled non-destructively. Nearby areas of hard substrate were cleared of organisms by scraping in order to test community-recovery trajectories. Photographed organisms were identified, counted and measured. Results from these studies include the observation that scraped substratum at the Kongsfjorden site took approximately 13 years to recover before resembling natural substratum (Beuchel et al. 2006; Beuchel and Gulliksen 2008). Biodiversity in this habitat has been shown to vary inversely with the state of the North Atlantic Oscillation (NAO) climatic index. A positive NAO, implying warmer conditions, resulted in lower biodiversity (Beuchel et al. 2006). Around 1995 and 2000 there were abrupt community shifts in both Kongsfjorden and Smeerenburgfjorden, respectively (Kortsch et al. 2012). In Kongsfjorden, filamentous brown algal cover was sparse (on average 8%) until 1995 and increased rapidly to 80% in 1996. After this period the macroalgal (brown algae) cover fluctuated around 40%. Simultaneously ascidian and anemone cover was reduced (Kortsch et al. 2012). At the surveyed location in Smeerenburgfjorden, the shift occurred in 2000, 5 years later than in Kongsfjorden, and resulted in an increase of macroalgal cover from on average 3% to 26%. According to Kortsch et al. (2012), the observed changes are likely a consequence of a regional warming trend, that via reduced ice cover increases the light availability and thereby promotes an increase in macroalgal biomass.

### 9.1.1.4 Macroalgae in Kongsfjorden

The checklists collated by Vinogradova (1995b) and Hansen and Jenneborg (1996) provide species information up to their published date. By examining later publications by Gulliksen et al. (1999), Kim et al. (2003), Athanasiadis (2006, 2008), Weslawski et al. (2010), Fredriksen and Kile (2012), Hop et al. (2012), Tatarek et al.

(2012) and Fredriksen et al. (2014, 2015), a total of 197 macroalgal species have been reported for Svalbard: 51 green, 76 brown and 70 red algae. By reviewing all available literature from Kongsfjorden, a total of 84 species have been recorded, composed of 19 green, 36 brown and 29 red algae which corresponds to 42% of the total number of species for Svalbard (Table 9.1, Fig. 9.1). Photos of macroalgae and macroalgal vegetation from Kongsfjorden are included in Fig. 9.2.

During a thorough survey of the entire fjord based on video and SCUBA diving in 1997 and 1998, macroalgae were found widely distributed in Kongsfjorden, from the outer coast to the inner basins (Hop et al. 2016). The communities vary with substratum (e.g. hard vs loose and soft) and location in the fjord. In hard-bottom locations with exposure to tidal and wind currents there are well established macroalgal communities with characteristic zonation, as observed at Hansneset (Wiencke et al. 2004; Hop et al. 2012; Fredriksen et al. 2014; Bartsch et al. 2016; Hop et al. 2016). Other hard-bottom localities with macroalgal vegetation include points and rocky islands in Kongsfjorden, such as the islands outside Kapp Mitra and Kapp Guisnez in the outer fjord, and Juttaholmen and Colletthøgda in the inner fjord, which have both been surveyed for macroalgae and benthic invertebrates (Voronkov et al. 2012; Hop et al. 2016). Extended hard-bottom areas with vertical drops from 15–30 m depth occur along the south coast of Kongsfjorden along Kvadehuken in the outer part of the fjord. Macroalgae also occur on gravel and softer substrata but are then often attached to dropstones left by melting glacial ice and may consequently drift with currents. In the inner part of Kongsfjorden, macroalgae tend to concentrate in depressions in soft sediments where they are often anchored to small pebbles by branched holdfasts (Hop et al. 2016). Because of heavy siltation in the inner basin of Kongsfjorden (Svendsen et al. 2002), the thalli of kelps, such as *Laminaria digitata* and *Alaria esculenta* may be covered by sediments, which may reduce photosynthesis (Roleda and Dethleff 2011). Hop et al. (2016) found that macroalgal biomass peaked between 5 and 10 m in the middle to outer parts of the fjord, whereas in the inner part it peaked <5 m depth.

The depth distribution of macroalgae recorded in Kongsfjorden by Hop et al. (2016) varies depending on substrate and inclination, from large, relatively shallow areas of hard bottom on the outer coast, to steep and deep areas in the middle fjord to very limited hard-bottom regions in the inner fjord. At Kapp Mitra (slope angle 3.7°), the macroalgal belt was surveyed by diving to 17 m depth at a distance extending to 270 m from shore. At Kapp Guisnez (slope angle 7.6°), the survey was carried out to a depth of 30 m (max. diving depth) 230 m from shore and at Hansneset with a steep incline of 23.4° depths up to 30 m were surveyed 70 m from shore. In the inner bay, the surveys were only conducted to 15 m depth at Juttaholmen (slope angle 16.0°) and to 10 m depth at Colletthøgda (slope angle 7.4°). The macroalgal belts in these locations extended to the maximum depths surveyed at these locations, except at the Kapp Guisnez site, where no macroalgae occurred below 15 m depth and few macroalgae were found deeper than 5 m at Colletthøgda.

At sites where regular ice-scouring is prevalent, the Kongsfjorden littoral zone is typically deprived of algae and animal life, except in small crevices and cracks and in small rock pools. However, in upper-zone locations of the fjord that are sheltered

**Table 9.1** Macroalgal species recorded from various locations on Svalbard compared with species recorded from Kongsfjorden

Species	In Kongsfjorden
<b>Chlorophyta</b>	
<i>Acrochaete repens</i> N. Pringsheim	x
<i>Acrochaete viridis</i> (Reinke) R. Nilsen <sup>1</sup>	
<i>Acrosiphonia arcta</i> (Dillwyn) Gain	x
<i>Acrosiphonia flagellata</i> Kjellman	x
<i>Acrosiphonia incurva</i> Kjellman	x
<i>Acrosiphonia sonderi</i> (Kützing) Kornmann	x
<i>Blidingia marginata</i> (J.Agardh) P.J.L.Dangeard	
<i>Blidingia minima</i> (Nägeli ex Kützing) Kylin	x
<i>Blidingia subsalsa</i> (Kjellman) Kornmann & Sahling ex Scagel et al.	
<i>Bolbocoleon piliferum</i> N.Pringsheim	
<i>Chaetomorpha ligustica</i> (Kützing) Kützing	
<i>Chaetomorpha linum</i> (O.F. Müller) Kützing	
<i>Chaetomorpha melagonium</i> (F.Weber & Mohr) Kützing	x
<i>Characium marinum</i> Kjellman <sup>2</sup>	
<i>Cladophora fracta</i> (O.F. Müller ex Vahl) Kützing <sup>1</sup>	
<i>Cladophora hutchinsiae</i> (Dillwyn) Kützing	
<i>Cladophora laetevirens</i> (Dillwyn) Kützing	
<i>Cladophora pachyderma</i> (Kjellman) Brand	
<i>Cladophora sericea</i> (Hudson) Kützing <sup>2</sup>	
<i>Epicladia frustrae</i> Reinke	
<i>Kornmannia leptoderma</i> (Kjellman) Bliding	x
<i>Monostroma lubricum</i> Kjellman <sup>2</sup>	
<i>Ostreobium quekettii</i> Bornet & Flahault	
<i>Percursaria percurva</i> (C.Agardh) Rosenvinge	
<i>Pleurocladia lacustris</i> A.Braun <sup>2</sup>	
<i>Prasiola crispa</i> (Lightfoot) Kützing	x
<i>Prasiola fluviatilis</i> (Sommerfelt) Areschoug ex Lagersted <sup>2</sup>	
<i>Pseudendoclonium submarinum</i> Wille	
<i>Pseudopringsheimia confluens</i> (Rosenvinge) Wille <sup>2</sup>	
<i>Rhizoclonium riparium</i> (Roth) Harvey <sup>2</sup>	
<i>Rhizoclonium tortuosum</i> (Dillwyn) Kützing	
<i>Rosenvingiella polyrhiza</i> (Rosenvinge) P.C. Silva <sup>1</sup>	
<i>Spongomorpha aeruginosa</i> (Linnaeus) Hoek	x
<i>Syncoryne reinkei</i> R.Nielsen & P.M.Pedersen <sup>2</sup>	x
<i>Ulothrix discifera</i> Kjellman <sup>2</sup>	
<i>Ulothrix flacca</i> (Dillwyn) Thuret	x
<i>Ulothrix implexa</i> (Kützing) Kützing	x
<i>Ulothrix speciosa</i> (Carmichael) Kützing	
<i>Ulothrix subflaccida</i> Wille	
<i>Ulva compressa</i> Linnaeus <sup>2</sup>	

(continued)



**Table 9.1** (continued)

Species	In Kongsfjorden
<i>Ulva intestinalis</i> Linnaeus	
<i>Ulva lactuca</i> Linnaeus	
<i>Ulva linza</i> Linnaeus	x
<i>Ulva prolifera</i> O.F.Müller	x
<i>Ulvaria splendens</i> (Ruprecht) Vinogradova <sup>3</sup>	
<i>Ulvaria obscura</i> (Kützing) P.Gayral ex C.Bliding	x
<i>Ulvella lens</i> P.L. Crouan & H.M. Crouan <sup>1</sup>	
<i>Ulvella scutata</i> (Reinke) R.Nielsen, C.J.O' Kelly & B.Wysor	x
<i>Urospora elongata</i> (Rosenvinge) Hagem	x
<i>Urospora penicilliformis</i> (Roth) Areschoug	x
<i>Urospora wormskioldii</i> (Mertens ex Hornemann) Rosenvinge	
<b>Total: 51</b>	<b>19</b>
<b>Phaeophyta</b>	
<i>Alaria esculenta</i> (Linnaeus) Greville	x
<i>Alaria pylaiei</i> (Bory de Saint-Vincent) Greville <sup>2</sup>	
<i>Ascophyllum nodosum</i> (Linnaeus) Le Jolis <sup>4</sup>	
<i>Asperococcus compressus</i> A.W. Griffiths ex W.J. Hooker	x
<i>Battersia arctica</i> (Harvey) Draisma, Prud'homme & H.Kawai	x
<i>Botrytella micromora</i> Bory de Saint-Vincent	
<i>Botrytella reinboldii</i> (Reinke) Kornmann & Sahling	
<i>Chaetopteris plumosa</i> (Lyngbye) Kützing	x
<i>Chorda filum</i> (Linnaeus) Stackhouse	x
<i>Chordaria chordariformis</i> (Kjellman) Kawai et S.H. Kim <sup>5</sup>	
<i>Chordaria flagelliformis</i> (O.F.Müller) C.Agardh	x
<i>Climacosorus mediterraneus</i> Sauvageau	x
<i>Delamarea attenuata</i> (Kjellman) Rosenvinge	x
<i>Dermatocelis laminariae</i> Rosenvinge	
<i>Desmarestia aculeata</i> (Linnaeus) J.V.Lamouroux	x
<i>Desmarestia viridis</i> (O.F.Müller) J.V.Lamouroux	x
<i>Dictyosiphon chordaria</i> Areschoug	
<i>Dictyosiphon foeniculaceus</i> (Hudson) Greville	x
<i>Ectocarpus fasciculatus</i> Harvey <sup>6</sup>	x
<i>Ectocarpus confervoides</i> (Roth) Le Jolis <sup>2</sup>	
<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	x
<i>Elachista fucicola</i> (Vellay) Areschoug	x
<i>Elachista stellaris</i> Areschoug	
<i>Eudesme virescens</i> (Carmichael ex Berkeley) J.Agardh	
<i>Feldmannia irregularis</i> (Kützing) G.Hamel	
<i>Fucus bursigerus</i> J. Agardh <sup>5</sup>	
<i>Fucus ceranoides</i> Linnaeus	
<i>Fucus distichus</i> Linnaeus	x
<i>Fucus serratus</i> Linnaeus	

(continued)



**Table 9.1** (continued)

Species	In Kongsfjorden
<i>Fucus vesiculosus</i> Linnaeus	
<i>Halopteris scoparia</i> (Linnaeus) Sauvageau	
<i>Halosiphon tomentosus</i> (Lyngbye) Jaasund	x
<i>Haplospora globosa</i> Kjellman	x
<i>Hincksia ovata</i> (Kjellman) P.C.Silva	
<i>Isthmoplea sphaerophora</i> (Carmichael) Gobi	
<i>Laminaria digitata</i> (Hudson) J.V. Lamouroux	x
<i>Laminaria fissilis</i> J.Agardh <sup>2</sup>	
<i>Laminaria hyperborea</i> (Gunnerus) Foslie	
<i>Laminaria solidungula</i> J. Agardh	x
<i>Laminariocolax aecidioides</i> (Rosenvinge) A.F. Peters	x
<i>Laminariocolax tomentosoides</i> (Farlow) Kylin	x
<i>Leptonematella fasciculata</i> (Reinke) P.C. Silva	x
<i>Litosiphon laminariae</i> (Lyngbye) Harvey <sup>6</sup>	
<i>Mesogloia vermiculata</i> (Smith) S.F.Gray <sup>2</sup>	
<i>Microspongium alariae</i> (P.M.Pedersen) A.F.Peters	
<i>Mikrosyphar polysiphoniae</i> Kuckuck <sup>7</sup>	x
<i>Myrionema corunnae</i> Sauvageau	x
<i>Myrionema strangulans</i> Greville	
<i>Myriotrichia clavaeformis</i> Harvey <sup>1</sup>	
<i>Omphalophyllum ulvaceum</i> Rosenvinge	
<i>Petalonia fascia</i> (O.F.Müller) Kuntze	
<i>Petalonia zosterifolia</i> (Reinke) Kuntze	
<i>Petroderma maculiforme</i> (Wollny) Kuckuck	
<i>Phaeostroma parasiticum</i> Børgesen	
<i>Phaeostroma pustulosum</i> Kuckuck	
<i>Pleurocladia lacustris</i> A.Braun	
<i>Pogotrichum filiforme</i> Reinke <sup>7</sup>	x
<i>Protohalopteris radicans</i> (Dillwyn) Draisma, Prud'homme & H.Kawai	
<i>Pseudolithoderma extensum</i> (P.L.Crouan & H.M.Crouan) S.Lund	x
<i>Pseudolithoderma rosenvingei</i> (Waern) S.Lund	x
<i>Pseudothrix groenlandica</i> (J.Agardh) Hanic & S.C.Lindstrom <sup>8</sup>	
<i>Punctaria latifolia</i> Greville	
<i>Punctaria tenuissima</i> (C.Agardh) Greville	
<i>Pylaiella littoralis</i> (Linnaeus) Kjellman	x
<i>Pylaiella varia</i> Kjellman	x
<i>Ralfsia clavata</i> (Carmichael ex Harvey) P.L. Crouan & H.M. Crouan <sup>1</sup>	
<i>Ralfsia verrucosa</i> (Areschoug) Areschoug	
<i>Saccharina latissima</i> (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders	x
<i>Saccharina nigripes</i> (J. Agardh) C. Longtin et G.W. Saunders	x
<i>Saccorhiza dermatodea</i> (Bachelot de la Pylaie) J.Agardh	x
<i>Saundersella simplex</i> (De A.Saunders) Kylin	x

(continued)

**Table 9.1** (continued)

Species	In Kongsfjorden
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	x
<i>Sphaerotrichia divaricata</i> (C. Agardh) Kylin <sup>1</sup>	
<i>Sphacelorbis nanus</i> (Nägeli ex Kützing) Draisma, Prud'homme & H.Kawai <sup>9</sup>	x
<i>Stictyosiphon tortilis</i> (Gobi) Reinke	x
<i>Stragularia clavata</i> (Harvey) G.Hamel	
<b>Total 76</b>	<b>36</b>
<b>Rhodophyta</b>	
<i>Acrochaetium microscopicum</i> (Nägeli ex Kützing) Nägeli	
<i>Acrochaetium parvulum</i> (Kylin) Hoyt	x
<i>Ahnfeltia plicata</i> (Hudson) E.M.Fries	
<i>Antithamnionella floccosa</i> (O.F.Müller) Whittick <sup>6</sup>	
<i>Callocolax neglectus</i> F.Schmitz ex Batters	
<i>Ceramium circinatum</i> (Kützing) J.Agardh	
<i>Ceramium virgatum</i> Roth	
<i>Clathromorphum circumscriptum</i> (Strömfelt) Foslie	x
<i>Clathromorphum compactum</i> (Kjellman) Foslie	
<i>Coccotylus hartzii</i> (Rosenvinge) L.Le Gall & G.W.Saunders	
<i>Coccotylus truncatus</i> (Pallas) M.J.Wynne & J.N.Heine	x
<i>Colaconema hallandicum</i> (Kylin) Afonso-Carillo, Sanson, Sangil & Diaz-Villa	
<i>Cystoclonium purpureum</i> (Hudson) Batters	x
<i>Devaleraea ramentacea</i> (Linnaeus) Guiry	x
<i>Dilsea carnosae</i> (Schmidel) Kuntze	
<i>Dilsea socialis</i> (Postels & Ruprecht) Perestenko	
<i>Dumontia contorta</i> (S.G.Gmelin) Ruprecht	
<i>Euthora cristata</i> (C.Agardh) J.Agardh	x
<i>Fimbrifolium dichotomum</i> (Lepechin) G.I.Hansen	
<i>Furcellaria lumbricalis</i> (Hudson) J.V.Lamouroux	
<i>Grania efflorescens</i> (J.Agardh) Kylin	x
<i>Harveyella mirabilis</i> (Reinsch) F.Schmitz & Reinke <sup>2</sup>	
<i>Halisaccion arcticum</i> A.D. Zinova <sup>1</sup>	
<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini	x
<i>Leptophytum foecundum</i> (Kjellman) Adey <sup>2</sup>	x
<i>Leptophytum laeve</i> W.H. Adey	x
<i>Leptophytum jenneborgii</i> Athanasiadis <sup>5</sup>	
<i>Lithophyllum crouanii</i> Foslie <sup>1</sup>	
<i>Lithophyllum crouaniorum</i> Foslie	
<i>Lithophyllum fasciculatum</i> (Lamarck) Foslie <sup>2</sup>	
<i>Lithothamnion flavescens</i> Kjellman	
<i>Lithothamnion glaciale</i> Kjellman	x
<i>Lithothamnion tophiforme</i> (Esper) Unger	x
<i>Mastocarpus stellatus</i> (Stackhouse) Guiry	
<i>Meiodiscus spetsbergensis</i> (Kjellman) G.W.Saunders & McLachlan	x

(continued)

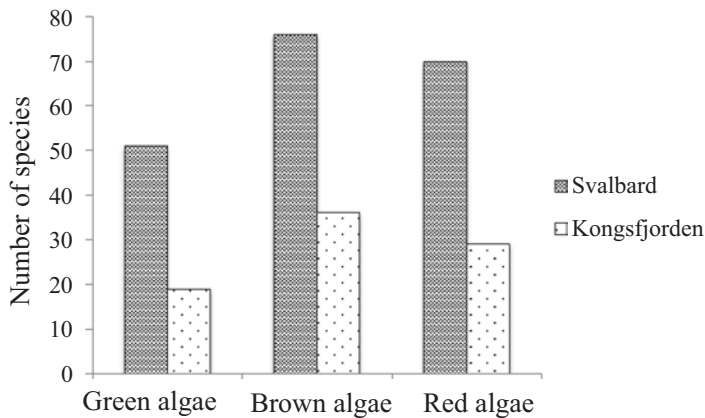
**Table 9.1** (continued)

Species	In Kongsfjorden
<i>Membranoptera alata</i> (Hudson) Stackhouse	
<i>Mesophyllum lichenoides</i> (J.Ellis) Me.Lemoine	
<i>Odonthalia dentata</i> (Linnaeus) Lyngbye	x
<i>Palmaria palmata</i> (Linnaeus) Weber & Mohr	x
<i>Pantoneura fabriciana</i> (Lyngbye) M.J.Wynne	
<i>Phycodrys rossica</i> (E.S.Sinova) A.D.Zinova <sup>2</sup>	
<i>Phycodrys rubens</i> (Linnaeus) Batters	x
<i>Phymatolithon calcareum</i> (Pallas) W.H.Adey & D.L.McKibbin	
<i>Phymatolithon lenormandii</i> (Areschoug) W.H.Adey	
<i>Phymatolithon purpureum</i> (P.L.Crouan & H.M.Crouan) Woelkerling & L.M.Irvine	
<i>Pneophyllum fragile</i> Kützing	
<i>Polysiphonia arctica</i> J.Agardh	x
<i>Polysiphonia elongata</i> (Hudson) Sprengel	x
<i>Polysiphonia fucoides</i> (Hudson) Greville	x
<i>Polysiphonia nigra</i> (Hudson) Batters	
<i>Polysiphonia stricta</i> (Dillwyn) Greville	
<i>Porphyropsis coccinea</i> (J.Agardh ex Areschoug) Rosenvinge	
<i>Porphyrostromium boryanum</i> (Montagne) P.C.Silva	
<i>Pterothamnion plumula</i> (J.Ellis) Nägeli	
<i>Ptilota gunneri</i> P.C.Silva, Maggs & L.M.Irvine	x
<i>Ptilota serrata</i> Kützing	x
<i>Rhodochorton purpureum</i> (Lightfoot) Rosenvinge	x
<i>Rhodomela confervoides</i> (Hudson) P.C.Silva	x
<i>Rhodomela lycopodioides</i> (Linnaeus) C.Agardh	x
<i>Rhodophysema georgei</i> Batters	
<i>Rhodophysema kjellmanii</i> G.W. Saunders & Clayden	x
<i>Rubrointrusa membranacea</i> (Magnus) S.L.Clayden & G.W.Saunders	x
<i>Scagelothamnion pusillum</i> (Ruprecht) Athanasiadis <sup>5</sup>	
<i>Scagelia pylaisaei</i> (Montagne) M.J.Wynne	x
<i>Sparlingia pertusa</i> (Postels & Ruprecht) G.W.Saunders, I.M.Strachan & Kraft <sup>10</sup>	
<i>Titanoderma pustulatum</i> (J.V.Lamouroux) Nägeli	
<i>Turnerella pennyi</i> (Harvey) F.Schmitz	x
<i>Vertebrata lanosa</i> (Linnaeus) T.A.Christensen <sup>4</sup>	
<i>Wildemanian amplissima</i> (Kjellman) Foslie	
<i>Wildemanian miniata</i> (C.Agardh) Foslie	x
<b>Total: 70</b>	<b>29</b>
<b>Grand total: 197</b>	<b>84</b>
Notes	
1: From Gulliksen et al. (1999)	
2: Only in Vinogradova (1995a, b)	
3: From Fredriksen et al. (2015)	
4: Drift specimens	

(continued)

**Table 9.1** (continued)

Species	In Kongsfjorden
5: From Athanasiadis (2007)	
6: From Fredriksen and Kile (2012)	
7: From Hop et al. (2012)	
8: Siri Moy, pers. com.	
9: From Fredriksen et al. (2014)	
10: Most probably <i>Palmaria palmata</i>	



**Fig. 9.1** Total number of species of the three different algal groups of benthic macroalgae from Svalbard and in Kongsfjorden

from the outward-moving ice stream, brown seaweeds, such as *Fucus distichus* reside (Fig. 9.2). Other species in the littoral may include *Pylaiella littoralis* and *Chordaria flagelliformis*, as well as species of green algae (Hop et al. 2012; Fig. 9.2). For algae, scouring is not necessarily an impediment for occurrence and growth. Denuded substrata can be rapidly colonised by fast-growing green ephemeral species like *Urospora penicilliformis* and species of the genera *Ulothrix* and *Ulva* (Fig. 9.2). On a more general basis reduced ice scouring will lead to a richer littoral algal flora, both in terms of biomass and diversity (Fredriksen et al. 2014).

In the sublittoral zone in Kongsfjorden, the chlorophytes typically only extend to the upper few meters (Hop et al. 2012; Fredriksen et al. 2014), phaeophytes dominate down to 10–12 m depth and rhodophytes dominate below this depth at least to 60 m at some locations, such as Hansneset (C. Wiencke, unpubl. data). Biomass dominating species varied along the fjord axis (Hop et al. 2016). During 1996/1998 at the outer location of Kapp Mitra, *Alaria esculenta* and *Saccharina latissima* dominated the upper 5 m, *Laminaria digitata* and *Ptilota gunneri* were dominant between 5 and 10 m depth and patches of *Desmarestia viridis* and *Turnerella pennyi* were characteristic below this depth to 17 m. At Kapp Guisnez, the upper 5 m were



**Fig. 9.2** Macroalgae from Kongsfjorden (a) View of littoral at Hansneset in July 2012 with a dominant cover of fucoids; person: C. Wiencke (b) *Ulothrix* sp. and *Urospora* sp. in the upper littoral at Hansneset July 2012 (c) Tide pool at Hansneset July 2012 showing different brown algae (d) *Fucus distichus* from the littoral shore below Marine Lab in Ny-Ålesund July 2012 (e) Kelp plant with conspicuous sediment loads; photo: courtesy of M. Schwanitz (f) Sublittoral rock with calcareous crustose corallines, *Phycodrys rubens*, *Chaetomorpha melagonium*, and young kelp plants. (Photo: courtesy of M. Schwanitz)

dominated by *Chordaria flagelliformis*, *L. digitata* and *S. latissima*, whereas the deeper areas down to 10 m depth were dominated by *S. latissima*, *P. gunneri* and *A. esculenta*. Below 10 m, *Saccorhiza dermatodea* and patches of *D. viridis* and *D. aculeata* were most abundant. At Hansneset, in the middle of Kongsfjorden, the

dominance of *A. esculenta* was partly replaced by other kelp species with *L. digitata* as the most dominant species in addition to *S. dermatodea* in the upper 5 m. From 10–15 m depth *S. latissima* was dominant together with *D. viridis*, but *A. esculenta* still occurred. Below 15 m *Phycodrys rubens* was the dominant species down to 30 m depth. At Juttaholmen, in the inner fjord basin, *Fucus distichus* and *Pylaiella littoralis* dominated the upper 1–2 m, *S. latissima* below this depth down to 13 m and *L. digitata* below this depth to where the soft sediments began at about 15 m depth. In the inner bay, near the glaciers, hard substrata were only present in the upper 3 m, where *Chorda filum*, *P. littoralis* and *S. latissima* were dominant. The latter species extended down to 5 m depth and below that *L. digitata* and *D. aculeata* occurred in patches of soft sediments with holdfast on cobbles or small pebbles.

Kim et al. (2003) identified a total of 32 macroalgal species from four sites in Kongsfjorden. Some of these are most probably misidentified. With reference to photos provided in their publication it is almost certain that *Gracilaria gracilis* (Stackhouse) M. Stentoft, L.M. Irvine & W.F. Farnham is in fact *Devaleraea ramentacea*, *Rhodymenia pacifica* Kylin is in fact *Palmaria palmata* and *Schizochlaenion rhodotrichum* Wynne et Norris is in fact *Rhodomela confervoides*. Kim et al. (2003) also report *Hinksia secunda* (Kützinger) P.C. Silva in the running text but refer to *Hincksia ovata* in a summarizing table. It is postulated that *H. ovata* is the identified species, since this species has previously been recorded in Svalbard and we have therefore included this record also from Kongsfjorden (Table 9.1). Two new species identifications, *Asperococcus compressus* and *Ulva linza*, are new records for both Kongsfjorden and Svalbard (Kim et al. 2003).

### 9.1.1.5 Taxonomic Problems

Some taxa need a taxonomic revision. In a paper from Northern Baffin Island in Canada, Küpper et al. (2016) stress the importance to include molecular methods in order to unravel the total cryptic diversity. Before this has been performed, the published taxon names of valid species in earlier species lists have to be accepted. Important taxa or algal groups with high priority for further investigation are discussed below.

#### Small Green Algae

Genera like *Acrosiphonia*, *Cladophora*, *Ulothrix* and *Urospora* all contain species in need of a taxonomic revision. For example, there are 4 species of *Acrosiphonia* listed in Table 9.1. The two species described by Kjellman, *A. flagellata* and *A. incurva*, are currently considered valid species (Guiry and Guiry 2018). The diagnostic characteristics used to separate these from *A. arcta* and *A. sonderi* are doubtful. Both *Acrosiphonia flagellata* and *A. incurva* may reach a cell diameter of 150 µm (Kjellman 1893), which may overlap with *A. sonderi*, a species with cell



diameter > 120 µm (Pedersen 2011). *Acrosiphonia incurva* has the same type of hooked branches close to the base as *A. arcta*, but with some differences in chloroplast structure (Kjellman 1893). *Acrosiphonia flagellata* produces small mats with interwoven rhizoids, a description that also fits *A. arcta* (Brodie et al. 2007). According to Kjellman (1893) both *A. flagellata* and *A. incurva* are known from Northern Norway only, but they are included in the Svalbard checklists by Vinogradova (1995b) and Hansen and Jenneborg (1996) as well as for Kongsfjorden (Hop et al. 2012). *Acrosiphonia duriuscula* (Ruprecht) Yendo was recorded in Hornsund by Florczyk and Latala (1989) and in Isfjorden by Weslawski et al. (1993). This species is taxonomically valid but it is a Pacific species (Guiry and Guiry 2018). Florczyk and Latala (1989) noted that the species had a cell size of 90 to 150 µm, which could overlap with *A. sonderi*, so we consider *A. duriuscula* to be a misidentification, a conclusion also supported by Vinogradova (1995b). Similar taxonomic problems exist for the other genera mentioned, with overlapping cell diameters described for species of *Ulothrix* and *Urospora*. A variety of species described in the genus *Cladophora* only possess weak morphological characters for clear distinction (Pedersen 2011). New insight using both morphological and molecular markers is needed to resolve these taxonomic issues.

*Chaetomorpha ligustica* and *C. melagonium* are on the species list of macroalgae (Table 9.1). Hansen and Jenneborg (1996) recorded *Chaetomorpha ligustica* under the synonym *C. mediterranea* (Kützinger) Kützinger in their checklist from Svalbard. In our Table 9.4, *Chaetomorpha linum* (O.F. Müller) Kützinger is presented as a substrate for benthic diatoms. *Chaetomorpha linum* was recorded from Isfjorden, Svalbard by Fredriksen and Kile (2012), however, they concluded that further investigations are needed before a certain presence of this species on Svalbard can be deduced. In a later paper Fredriksen et al. (2015) recorded *C. linum* from Isfjorden based on cell size and unattached specimens. Vinogradova (1995b) gives *Chaetomorpha tortuosa* (Dillwyn) Kleen from Hornsund in her checklist. This is a valid species according to Guiry and Guiry (2018). However, *C. tortuosa* Kützinger is regarded as a taxonomic synonym of *C. ligustica*. The taxonomic status of *C. tortuosa* is discussed in Guiry and Guiry (2018), and this species is therefore not included in Table 9.1. According to Guiry and Guiry (2018) a complete revision of the genus *Chaetomorpha* is required, and Brodie et al. (2007) describe an extensive variability of morphological characters depending on environmental conditions that account for the taxonomic confusion.

A similar problem is ascertained for *Monostroma lubricum* Kjellman 1877 (Table 9.1) and *M. grevillei* var. *lubricum* (Kjellman) Collins 1909 (Table 9.4), however, they are the same taxon since they are based on the same type specimen (*Monostroma bullosum* (Roth) Thuret 1854). Guiry and Guiry (2018) recognize all these three taxa as valid species, so there clearly must be some taxonomic confusion. By nomenclature rules priority should be given to *Monostroma bullosum* (Roth) Thuret as a valid name. Following Vinogradova (1995a), *M. lubricum* is probably related to *M. grevillei* (Thuret) Wittrock. According to Brodie et al. (2007) the type species, *M. bullosum*, may lack a *Codiolum* – phase and as presently cir-



cumscribed *Monostroma* may not be monophyletic (O’Kelly et al. 2004). In a paper by Gordillo et al. (2016) they used *Monostroma arcticum* from Kongsfjorden as a test species to study effects of temperature and acidification on biochemical composition and photosynthetic performance. According to Guiry and Guiry (2018) *M. arcticum* is a variety of *M. grevillei*. Before any further studies are done on this genus *M. lubricum* is the only *Monostroma* species included in Table 9.1. Some previously described *Monostroma* species have been transferred to other genera like *Ulvaria*, *Gayralia* and *Protomonostroma* (Brodie et al. 2007).

Heesch et al. (2016) provide a revision of the green algal order Prasiolales. They also describe two new genera, *Prasionella* and *Prasionema*. These two genera and the other species mentioned in their paper are not included in this paper since these species are mostly terrestrial or live in fresh water. Heesch et al. (2016) also confirm the widespread presence of *Prasiola crispa* and *P. fluviatilis*, the two *Prasiola* species included in this paper.

## Fucales

The genus *Fucus* sometimes may be difficult to identify to species level since Arctic specimens are often found as dwarf growth forms. This may have led to misidentifications or even unnecessary establishment of new species. Six different *Fucus* species are listed in Table 9.1. As early as the mid nineteenth century species problems in the genus *Fucus* were discussed by Agardh (1868) and he was obviously aware of difficulties in separating the small and atypical specimens. *Fucus bursigerus* is a species described by Agardh (1868) based on material he received from Swedish expeditions to Svalbard in 1868. Agardh himself believed that this species might be identical to *F. microphyllus* De la Pylaie (1830), described from Newfoundland. According to Athanasiadis (2006), later authors (Rice and Chapman 1985) have associated *F. microphyllus* with *F. distichus*, but Svalbard material was not included in their studies. Guiry and Guiry (2018) suggest that *F. bursigerus* and *F. microphyllus* should be accepted as synonyms of *F. evanescens*, which has been widely recorded in the Svalbard region. *Fucus evanescens* is used to describe plants with a large (> 10 cm tall) and wide (1 cm) thallus that grows in sheltered localities while thalli of *F. distichus* are small (< 5 cm) and narrow (0.5 cm) and grow in more exposed sites (Fig. 9.2d) or in tidal pools (Powell 1957). Coyer et al. (2006) used mtDNA markers and concluded that *F. evanescens* should be included in *F. distichus*. Also Kucera and Saunders (2008) concluded that all subspecies of *Fucus distichus* from Canada should be subsumed into one species as little to no nucleotide divergence was found among them for both mtDNA and ITS. Later studies by Moy (2015) using mtDNA markers assigned all algae that looked similar to *Fucus evanescens* and *F. distichus* in the littoral around Spitsbergen to one taxonomic entity, *F. distichus*.

*Fucus ceranoides* Linnaeus, which thrives in river outlets or other areas that are influenced by fresh water, is listed for Svalbard by Hansen and Jenneborg (1996). They discuss the validity of this species that has not been reported there since

Kjellman (1883). Studies by Lein (1984) suggested that the northern limit of *F. ceranoides* lies in the Troms county, Norway, at approximately 70°N.

Fredriksen et al. (2015) reported a dwarf form of *F. vesiculosus* without air bladders from Isfjorden. Its identity was based on the presence of separate male and female plants and the identity was also confirmed by the use of molecular methods (mtDNA sequences). Thus we can confirm the occurrence of at least three species of *Fucus* on Svalbard, *Fucus distichus*, *F. serratus* and *F. vesiculosus* and that the presence of the other fucoids listed in Table 9.1 need further studies, preferably supported by molecular tools.

## Laminariales

Taxonomic reconsiderations are also needed in some Arctic kelp species. Digitate specimens recorded from Svalbard have mostly been designated to the widely distributed cold-temperate to Arctic species *Laminaria digitata*, or in some older papers to *L. nigripes* J. Agardh (Kjellman 1883; Vinogradova 1995b). McDevit and Saunders (2010) questioned the species concept of *L. digitata* for Arctic Canada as molecular markers revealed the presence of a second species that superficially looked similar to *L. digitata* and suggested the presence of *Saccharina groenlandica* (Rosenvinge) C.E. Lane, C. Mayes, Druehl & G.W. Saunders [= *Laminaria groenlandica* Rosenvinge and  $\neq$  *L. groenlandica* sensu Druehl 1968] but they were not able to include original material from Greenland for comparison. Rosenvinge's (1894) original description of *L. groenlandica* had a typical *Saccharina* morphology with a simple lamina, not digitate, and also the designated lectotype of *S. groenlandica* had a simple lamina (Longtin and Saunders 2015).

Agardh (1868) described a digitate species from Svalbard, *Laminaria nigripes*, based, amongst others, on the characteristic that it turns black when it dries (*nigripes* means black foot) but also differing from *L. digitata* by the presence of mucilage ducts in the stipe. Microscopic investigations on the presence of mucilage ducts in laminas and stipes of the type material of *L. nigripes* revealed the presence of two taxa: misidentified *L. digitata* and one specimen with mucilage ducts in the stipe but not in the lamina (Longtin and Saunders 2015) that matched the type description by Agardh (1868). Based on this fact, in addition to evidence from molecular analyses (not including type material however), they established the new combination *Saccharina nigripes* (J. Agardh) C. Longtin et G.W. Saunders. With the reduction of *Saccharina groenlandica* to synonymy with *S. latissima* (Longtin and Saunders 2015), all digitate specimens in the North Atlantic most probably belong to *Laminaria digitata*, *L. ochroleuca* Bachelot de al Pylaie, *L. hyperborea* or to *Saccharina nigripes* with *S. nigripes* probably confined to Arctic or sub-Arctic conditions. For Svalbard, investigations by Lund (2014) and Moy (2015) used the same molecular markers (COI-5 gene) and thereby also confirmed the presence of digitate *S. nigripes* [as *S. groenlandica*]. The investigated specimens were similar in external morphology to *L. digitata*, but different on the molecular level and prevailed at several sites around Spitsbergen. According to Pedersen (2011) all digitate

specimens of *Laminaria* in Greenland also belong to *L. nigripes*, but criteria for separation from *L. digitata* have not been given.

Moreover, the taxonomic status of *Laminaria fissilis*, a valid species according to Guiry and Guiry (2018) and listed for Svalbard by Vinogradova (1995b), also needs further study. The cold-temperate North-eastern Atlantic species *Laminaria hyperborea* has been reported from Isfjorden (Svalbard) by Vozzinskaja et al. 1992 (see Hansen and Jenneborg 1996) and Peltikhina (2002). Hop et al. (2016) registered *L. hyperborea* at 5 m depth at Kapp Guisnez in outer Kongsfjorden. However, no herbarium material exists that can be examined to verify the presence of this species. Kim et al. (2003) recorded *L. hyperborea* from Kongsfjorden as well and this is the only publication which depicts a photo but this does not show the typical morphology with its characteristic conical, round, stiff, rough and epiphytised stipe (Kain 1971). A recent quantitative investigation along the depth gradient at Hansneset revealed no evidence for the presence of *L. hyperborea* (Bartsch et al. 2016, Bartsch, unpubl.). Thus its presence still is under debate.

*Alaria esculenta* and *A. pylaiei* have both been recorded from Svalbard, the latter is only mentioned in the checklist by Vinogradova (1995b). Both are considered valid species by Guiry and Guiry (2018). The two species are separated by a two edged midrib in *A. pylaiei* and a 4 sided midrib in *A. esculenta*. According to Hansen and Jenneborg (1996) *A. grandifolia* is the most common *Alaria* species from Svalbard, but this species is now reduced to a synonym of *A. esculenta* (Kraan et al. 2001).

### Acrochaetiales

The small red algae previously belonging to genera like *Acrochaetium*, *Audouinella*, and *Rhodochorton* have undergone recent taxonomic revision (see Guiry and Guiry 2018). The names used in our list are updated according to the current nomenclature (Table 9.1), but one should treat these records with great care due to the lack of good diagnostic characteristics.

### Crustose Corallines

This group is very poorly studied in the Svalbard area and only two publications are available (Athanasiadis 2006, 2008). In the recent publications from Svalbard (Fredriksen and Kile 2012; Hop et al. 2012; Fredriksen et al. 2014, 2015) this group of algae is omitted mainly due to lack of competence. The corallines are an important group of algae that form the primary substratum for many other organisms, they may grow as epiphytes on other algal species, or they contribute to loose lying rhodolith communities that house a number of different animals (Chenelot et al. 2011; Teichert et al. 2012, 2014). All species listed for Kongsfjorden (Table 9.1) have been collected in 2012 at Hansneset and identified by R.S. Steneck.

### 9.1.1.6 Changes in Flora and Possible Causes

To date only four macroalgal investigations have included revisits to previously sampled sites. Weslawski et al. (2010) revisited some of their earlier sites after 20 years and found that the number of littoral species (algae and animals) had doubled in 20 years in the Hornsund and South Cape area. However, no species new to the area were discovered. Species previously found in the sublittoral were observed to have moved up to the littoral zone and during the same time the macrophyte biomass increased threefold. Fredriksen and Kile (2012) revisited Svendsen's (1959) sites in outer Isfjorden and recorded a higher number of species, particularly in the littoral zone, an increase from 25 to 39 species. In Kongsfjorden, Fredriksen et al. (2014) revisited the sampling site Hansneset in 2012/2013, 14–16 years after the study by Hop et al. (2012), which reports data from 1996–1998. The number of species found in these two studies was similar, although some differences in the species composition were noted. The most pronounced difference was the increase of species in the littoral zone, with more than twice as many species found in 2012/13 as compared to 1996/98. At the same site the macroalgal biomass increased considerably and the biomass had a significant peak at 2.5 m depth in 2012/13 (Bartsch et al. 2016) in contrast to the biomass peak at 5 m reported for 1996/98 (Hop et al. 2012). Moreover, the lower depth distribution limit of several kelp species shifted upwards by several meter except for *Alaria esculenta* (Bartsch et al. 2016). It is worth mentioning that in 1996/98 the fjord was covered by fast ice during winter and spring, while in 2012/2013 no ice was recorded. All four above-mentioned studies have pointed out the effect of reduced ice scouring due to increased temperature as a possible major factor explaining biodiversity increase in shallow sites. However, an increased turbidity due to higher run-off from land (Svendsen et al. 2002; Zajaczkowski 2008) may have caused the shift in the lower limit of kelp distribution and perhaps also the observed increase in the depth occurrence of the biomass peak. Bonsell and Dunton (2018) showed that reduced sea ice lead to increased fetch followed by higher sediment resuspension and thereby an increased turbidity and consequently a decreased critical depth for algal growth.

It has been recently proposed that the changing light conditions may lead to light driven tipping points in future polar systems (Clark et al. 2013). In the sublittoral, Kortsch et al. (2012) showed an increase in algal cover and explained their results by an increased temperature in the surface waters. This caused a rise in the number of ice-free days, which presumably ameliorated light availability to algae, but continuous measurements of underwater light to support this assumption are missing. According to Cottier et al. (2007) and Pavlov et al. (2013) the West Spitsbergen current has advected more warm Atlantic water to Kongsfjorden after 2005/2006 than previously, particularly during winter. This has led to an increased temperature both in the surface and in deeper water masses which influences the biota. For example, increased temperature has also led to a spawning krill population in Kongsfjorden (Buchholz et al. 2012). If temperatures continue to increase, one would expect that a number of more temperate species will become established. The rise in temperature also leads to an enhanced inflow of turbid melt water into the

fjord resulting in higher water turbidity, especially from July onwards (Pavlov et al. 2013). In addition, this melt water decreases salinity, especially in surface waters, and changes nutritional conditions (Rysgaard and Glud 2007). Low salinities in combination with exposure to ultraviolet radiation (UVR) inhibit germination of spores of e.g. *A. esculenta* and have the potential to limit the settlement of species in shallow waters (Fredersdorf et al. 2009), but all kelp species are still present at the upper sublittoral (Fredriksen et al. 2014; Bartsch et al. 2016). Various macroalgae inhabiting shallow water regions of Kongsfjorden, such as *Palmaria palmata* and *Saccharina latissima* amongst others, exhibit pronounced stenohaline features. Hence, under hyposaline conditions (15‰, melt water inflow) a strong loss of pigments (bleaching) or even high mortality can be observed (Karsten et al. 2003; Karsten 2007). On the other hand, increased water turbidity may have differential effects on kelps: while sediments may negatively influence the germination of spores and recruitment of juvenile sporophytes (Zacher et al. 2016), sediments may also protect seaweeds from the damaging effects of UVR (Roleda et al. 2008).

#### 9.1.1.7 Comparison to Other Arctic Sites

Wilce (1994) summarizes the Arctic by stating that the greatest portion of the Arctic intertidal and subtidal is unsuitable for macrobenthos development. This is true of immense coastal areas of Eurasia, much of northwestern and central Canada and northern Alaska. These areas are characterised by brackish water for much of the year and the bottom is mostly soft sediment, both environmental features that discourage attached algal colonization. Lantuit et al. (2012) state that 34% of the Arctic coastline is rocky ground so potentially suitable to be inhabited by macroalgae in the future.

Data from the Russian Arctic region are incomplete, but according to Zinova (1929), 120 macroalgal species have been found on Novaya Zemlya which stretches between 70° and 77°N. The algal vegetation is best developed on the western side of the island (Taylor 1954). Kjellman (1877b) described the algal vegetation on the eastern side of Novaya Zemlya to be very similar to what he found on Spitsbergen. Lein and Küfner (1998) obtained material from two areas on the eastern side of Novaya Zemlya area and recorded 31 species including some new species for the region, like *Devaleraea ramentacea*, *Rhodophysema kjellmanii*, *Harveyella mirabilis* and *Punctaria plantaginea* (Roth) Greville, the first three are also found at Spitsbergen (Table 9.1). The eastern side of Novaya Zemlya lies in the Kara Sea and this area as well as most of the northern Russian coastline is influenced by the great rivers, which discharge into this area affecting the algal vegetation (Taylor 1954). Reduced salinities and transport of sediment by the rivers make this area relatively uninhabitable for benthic algae due to suboptimal light conditions and reduced availability of stable substrate. In the Kara Sea three *Alaria* species different from those present in the rest of the Arctic region were described, namely *A. dolichorachis*, *A. elliptica* and *A. oblonga* (Taylor 1954). Of these, *A. dolichorachis* is considered a synonym to *A. esculenta*, while the other two are currently accepted species

(Guiry and Guiry 2018). According to Bolton (2010) five species of *Alaria* occur in the Arctic, but he does not specify which they are. So this genus also requires taxonomic reinvestigation in the Arctic. Along the eastern Siberian coast littoral algae appear to be nearly absent, and kelp in deeper waters is rare (Taylor 1954).

Franz Josef Land, another archipelago east of Svalbard is located mostly above 80°N. Marr (1927) showed the presence of different macroalgae like *Desmarestia viridis*, *Polysiphonia arctica*, *Laminaria* sp., and *Monostroma* sp. Later, Vinogradova and Schoschina (1993) reported a total of 63 species from the area. The permanent ice of the Arctic Ocean covers the northern waters around Franz Josef Land, which implies that these records document the northernmost limit of seaweed vegetation (Lüning 1990). Kelp forests are very extensive around Rossøya (80° 49.5 N), the northernmost island in the Svalbard archipelago (H. Hop, diving obs.).

Greenland which covers Arctic and subarctic habitats (Lund 1951) has a well-developed algal flora of approx. 200 species (Pedersen 2011) of which most species have been recorded at the subarctic south-western side, which is also the best investigated (Pedersen 1976, 2011). Cold-temperate species such as *Ascophyllum nodosum*, *Cladophora rupestris* and *Membranoptera alata* are commonly recorded there, but are not found in Svalbard. As these species are commonly found further south in Europe, this suggests that the flora of south-western Greenland is of a more temperate character than the Svalbard flora. The eastern side of Greenland is less hospitable to algae due to pack ice that scours the coast while being transported by the East Greenland current through Fram Strait. However, fucoids are well developed around 66°N (Taylor 1954), inhabiting the shallow sublittoral instead of the littoral zone and kelps are present below fucoids. Even in far northeastern Greenland, in Jörgen Brönlunds Fjord (82°10'N), Lund (1951) recorded 21 species, and he stated that *Coccotylus truncata* dominated, with other important species like *Rhodomela lycopodioides*, *Desmarestia aculeata*, *Pylaiella littoralis* and *Chaetopteris plumosa*.

The compilation of available literature has revealed a total of 197 species of macroalgae for Svalbard (Table 9.1). There are few so-called endemic Arctic macroalgal species. As stated in Hop et al. (2012), only 6.9% of the species found in Kongsfjorden can be considered to be Arctic endemic species. Arctic to cold temperate species in Kongsfjorden constituted 46.6% whereas the majority of the species are also present on the Norwegian mainland and even further south in the British Isles (Guiry and Guiry 2018). According to Adey and Steneck (2001) the flora of Kongsfjorden and western Svalbard may be considered as belonging to a subarctic bio-geographic region rather than a true Arctic region. Wilce (2016) claims that the High Arctic flora consists of a total of 161 species, including Cyanophytes, Dinophytes, Chrysophytes and Xanthophytes in addition the three groups of green, brown and red algae, and 21 of these are to be considered as Arctic endemics. Further, Wilce (2016) argues that many of the published papers dealing with Arctic biodiversity of macroalgae are not strictly Arctic, but contains flora elements of more cold temperate or subarctic areas. This last statement is fully correct, as we have seen from investigations in Svalbard in general and in Isfjorden and Kongsfjorden in particular. With the ongoing increase in temperature and the



reduction in sea ice the number of macroalgae moving northwards into the Arctic will most probably increase, however, currently true invasions have not yet been reported.

### **9.1.2 Marine Benthic Microalgae**

#### **9.1.2.1 Ecological Importance**

Benthic diatoms provide a major food source for benthic suspension- and deposit-feeders (Cahoon 1999). Due to their being photoautotrophic, they influence all elemental fluxes (e.g. oxygen, nutrients) especially at the sediment/water interface (Risgaard-Petersen et al. 1994). Furthermore, benthic diatoms stabilise sediment surfaces against hydrodynamic forces (e.g. erosion) by the excretion of sticky extracellular polymeric substances (De Brouwer et al. 2003). Consequently, microphyto-benthic diatom assemblages represent an important component of trophic webs in many coastal regions. While we have a good knowledge of species diversity in cold-temperate areas (Vyverman et al. 2007), the biodiversity in Arctic locations and especially in Svalbard is scarce (Stachura-Suchoples et al. 2016). Although the ecological importance of this group of algae is recognised, there are relatively few studies from the Arctic (e.g. see review of Glud et al. 2009 and references therein; Karsten et al., Chap. 8).

The main substratum affinities of microalgae have been characterized as epilithic (on rock substrata), epipellic/episammic (on mud and sand, respectively) and epiphytic/epizooic (on macrophytes and animals, respectively) (Round 1971). Although most benthic diatoms in Kongsfjorden grow on various hard and soft inorganic substrata, there are also various taxa living epiphytically on macroalgae.

#### **9.1.2.2 Historical Background**

The majority of studies on species composition and biodiversity of polar benthic diatoms have focussed on Antarctica (e.g. Leventer 1992; Tanimura 1992; Taylor et al. 1997; Longhi et al. 2003). Thus, until recently, only few studies existed on the occurrence and distribution of marine benthic and epiphytic diatom assemblages in both Polar Regions. Campeau et al. (1999) analysed sediment diatom composition from 0.4 to 14 m water depth along the Beaufort Sea coast, Arctic Canada. They showed a strong correlation between the diatom community and water depth controlled by the near-shore hydrodynamic conditions. Currents and turbulence affect the relative abundance of the epipsammon (on sand grains), epipelon (on sediments) and plankton species and thereby induce a water depth dependence. Cremer (1998) investigated diatom assemblages and their distribution patterns in the Laptev Sea on the basis of sediment and plankton samples, which resulted in classification of four diatom-provinces.



Even though Kongsfjorden has received a high degree of research attention, basic information about benthic microalgae is still fragmentary (Hop et al. 2002; Woelfel et al. 2009, 2010; Karsten et al. 2012; Stachura-Suchoples et al. 2016), although the basic structures of the pelagic and benthic food webs in Kongsfjorden have been described (Hop et al. 2002; Renaud et al. 2011). Kongsfjorden, however, does have exceptional characteristics for an Arctic region, due to the mild climate influenced by the warm West Spitsbergen Current. Hence, Kongsfjorden represents a border area between the cold-temperate Atlantic and Arctic biogeographic zones and the biodiversity is strongly structured by different physical factors that influence the fjord from both ends (Hop et al. 2002). The microphytobenthic studies have focussed on areal biomass (Chl *a*) and primary production (Woelfel et al. 2009, 2010, 2014) as well as on ecophysiological aspects of selected diatom taxa (Karsten et al. 2006, 2012, Chap. 8; Schlie et al. 2011). Qualitative and quantitative information on species composition of benthic diatoms in Kongsfjorden, however, is mostly lacking. Sevilgen et al. (2014) investigated oxygen budgets in a microphytobenthic community at one location in Kongsfjorden (Brandal) and provided the first species and abundance list for this assemblage. Stachura-Suchoples et al. (2016) published the first molecular-taxonomic study of some benthic diatoms from Kongsfjorden and Adventsfjorden with the description of three new taxa.

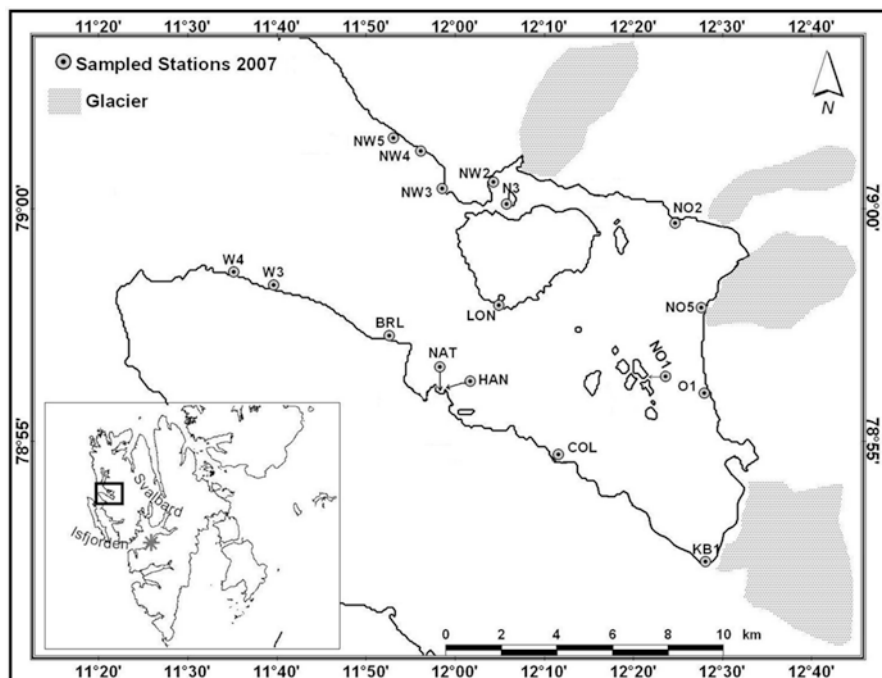
### 9.1.2.3 Production Aspects

Primary production of benthic diatoms in the Kongsfjorden has been studied by Woelfel et al. (2009, 2010, 2014), who estimated rates between 12 and 23 mg C m<sup>-2</sup> h<sup>-1</sup> down to 30 m water depth, with up to twofold higher rates compared to phytoplankton production values at the same stations. Generally, the structure and functioning of microphytobenthic communities remain poorly understood in Arctic waters (Glud et al. 2009).

### 9.1.2.4 Diversity of Benthic Diatoms

Species composition and abundances of marine benthic diatoms were studied for the first time in detail in Kongsfjorden in sediment surface cores collected at 17 stations around the coastline at 5 m water depth during summer 2007 (Fig. 9.3). As no sandy sediments were present at the fjord opening, which is characterized by rocky substrates, sediment traps installed at stations W3, W4 and NW5 were sampled. All other stations were more or less homogeneously distributed along the shore of Kongsfjorden and were characterised by muddy/sandy sediments (Table 9.2, station details in Woelfel et al. 2009).

A total of 47 diatoms species were identified from the top 5 mm of sediment cores (Table 9.2). Sevilgen et al. (2014) investigated sediment cores from 5 m water depth in June 2010 taken at the station Brandal (Fig. 9.3) and identified 29 benthic



**Fig. 9.3** Sampling stations for benthic microalgae in Kongsfjorden in 2007 (see Table 9.2; for details see Woelfel et al. 2009). Kongsfjorden on Svalbard is depicted on the insert

diatom species (Table 9.3). From both data sets a total of 69 benthic diatom species have been identified.

The maximum species number in individual samples in 2007 was 18 diatom taxa at station BRL (Fig. 9.3), whereas 9 to 10 species were found per station on average (range: 2–17 species; Fig. 9.4). Highest numbers of species were present near the southern shores of Kongsfjorden (stations BRL, NAT and HAN, Fig. 9.3), which are influenced by melt water from riverine input but not by glaciers. In contrast, the lowest species numbers occurred at stations NW2 and O1 along the northern shore as well as NO1 along the eastern shore of the island Blomstrandhalvøya, which are all near glaciers (Fig. 9.3).

Seven species dominated the samples in 2007 at most stations (Table 9.2): *Fossula arctica*, *Gyrosigma concilians*, *Navicula bipustulata*, *Navicula* sp., and *Pseudo-nitzschia granii*. The size and shape of the valves were similar: raphid pennates with ribs extending out from both sides of a longitudinal element (excl. *Fossula* and *Pseudo-nitzschia*). However, the community composition was highly variable from station to station (Table 9.2) pointing to a heterogeneous distribution of some taxa. At station NW2, for example, only *Pseudo-nitzschia granii* dominated the cell numbers, forming an almost mono-specific assemblage. In contrast, at station NAT 17 diatom taxa with visible chloroplasts occurred, of which *Fossula arctica* was one of the most abundant species (Table 9.2). Taxa such as *Cocconeis*

**Table 9.2** Relative abundance of benthic diatom species with visible chloroplasts from samples in Kongsfjorden at 5 m water depth in summer 2007

Station	Taxon	W4	W3	BRL	NAT	HAH	COL	KB1	O1	NO5	NO2	LON	N3	NW2	NW3	NW4	NW5
	<i>Amphora laevisissima</i> Gregory			+++													
	<i>Amphora</i> sp.			+++	++	++								+++	+++		++
	<i>Arthya decora</i> T. West	+++															
	<i>Arthya septentrionalis</i> (Østrup) Crawford	+++															
	<i>Caloneis crassa</i> (Gregory) R.Ross														+		
	<i>Cocconeis stauroneiformis</i> (W. Smith) Okuno				++												
	<i>Cylindrotheca closterium</i> (Ehrenberg) Reiman & Lewin				++		+++					+++			+++		
	<i>Cymatostira</i> sp.						+										
	<i>Diploneis bombus</i> (Ehrenberg) Cleve			+													
	<i>Diploneis litoralis</i> (Donkin) Cleve		+++	+++				+++				+++			+++	+++	+++
	<i>Entomoneis paludosa</i> (W. Smith) Reimer									+++							
	<i>Fallacia forcipata</i> (Grev.) Stickle & D.G. Mann			+													
	<i>Fallacia</i> sp.		++		++		+++										
	<i>Fossula arctica</i> G.R.Hasle, E.E.Syvertsen & C.H. von Quillfeldt		+++		+++	+++	++	+++									
	<i>Fragilariopsis cylindrus</i> (Grunow in Cleve & Möller) W. Krieger		++	+++		++				+++		++					++
	<i>Fragilariopsis oceanica</i> (P.T. Cleve) Hasle				+												
	<i>Fragilariopsis</i> sp.	+++															
	<i>Gyrosigma</i> cf <i>hudsonii</i> Poulin & Cardinal					++				+++							
	<i>Gyrosigma concilians</i> Cleve (Okolodkov)								+++								
	<i>Gyrosigma fasciola</i> (Ehrenberg) J.W. Griffith & Henfrey												+++				

(continued)





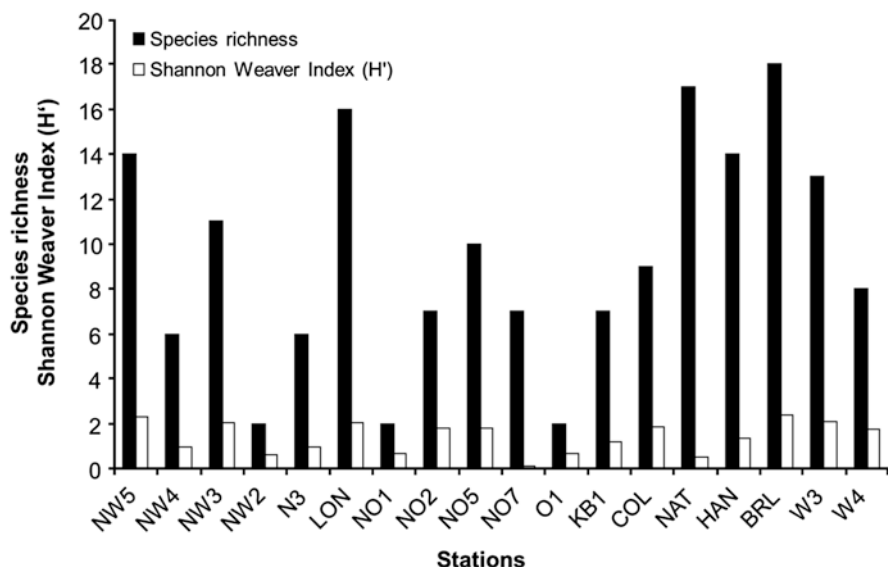
**Table 9.3** Relative abundance of benthic diatom species reported by Sevilgen et al. (2014) for the station Brandal (5 m water depth, June 2010), which is close to station BRL (Fig. 9.3)

Taxon	Abundance
<i>Achnanthes fimbriata</i> (Grunow) R.Ross	+
<i>Achnanthes</i> sp.	++
<i>Amphora acutiuscula</i> Kützing	++
<i>Amphora</i> cf. <i>arenaria</i>	++
<i>Amphora crassa</i> Gregory	+
<i>Amphora laevis</i> W.Gregory	++
<i>Amphora lineolata</i> Ehrenberg	++
<i>Amphora marina</i> W.Smith	+++
<i>Amphora</i> cf. <i>obtusa</i> Gregory	++
<i>Amphora sulcata</i> Gregory	+++
<i>Amphora</i> sp.	++
<i>Diploneis bomboides</i> (A.W.F.Schmidt) Cleve	++
<i>Diploneis</i> cf. <i>notabilis</i>	++
<i>Diploneis smithii</i> (Brébisson) Cleve	+++
<i>Diploneis</i> sp.	++
<i>Donkinia carinata</i> (Donkin) Ralfs	+++
<i>Fallacia forcipata</i> (Grev.) Stickle & D.G. Mann	++
<i>Navicula directa</i> (W.Smith) Ralfs	+++
<i>Navicula kariana</i> var. <i>frigida</i> (Grunow) Cleve	++
<i>Navicula</i> sp.	++
<i>Nitzschia hybrida</i> Grunow	++
<i>Nitzschia</i> sp.	++
<i>Odontella aurita</i> (Lyngbye) C.Agardh	++
<i>Petroneis marina</i> (Ralfs) D.G.Mann	++
<i>Pinnularia quadrata</i> Pankow	+
<i>Plagiotropis lepidoptera</i> (Gregory) Kuntze	+++
<i>Planorbulina delicatulum</i> (Kützing) Round & Bukhtiyarova	+++
<i>Pleurosigma normanii</i> Ralfs	++
<i>Seminavis</i> sp.	++

These authors quantified abundances as frequent (+++), rare (++), very rare (+)

*stauroneiformis* were documented as rare species at station NAT (Table 9.2). Most species exhibited a patchy distribution, whereas some taxa were widely distributed, e.g. *Navicula* sp. occurred at most of the investigated stations in 2007.

Sediment samples were investigated again at the station Brandal by Sevilgen et al. (2014) in 2010 (Table 9.3), which resulted in 29 benthic diatom species, i.e. 11 more than in 2007. The species composition, however, was quite different. While in 2007, for example, only 2 *Amphora* species were reported, Sevilgen et al. (2014) described 9 taxa of this genus. Similarly, while *Diploneis bombus* and *Diploneis*



**Fig. 9.4** Number of benthic diatom species at 5 m water depth across Kongsfjorden in 2007 and Shannon Weaver Index ( $H'$ ) for benthic diatoms at 5 m water depth at different stations across Kongsfjorden. (For station details see Woelfel et al. 2009) (Koblowsky et al., unpublished data)

*litoralis* were abundant species in 2007, *Diploneis bomboides*, *Diploneis* cf. *notabilis*, *Diploneis smithii* (most abundant) and *Diploneis* sp. were recorded in 2010 (Tables 9.2, 9.3). These data suggest some variability in biodiversity at the same station which may be explained by community changes over time.

Microphytobenthic communities in Kongsfjorden are confronted with dynamic, seasonally changing environmental parameters, which act as strong structuring forces (Karsten et al. 2012, Chap. 8). Baseline data on biodiversity of benthic diatoms are lacking from Kongsfjorden, as well as other Arctic marine ecosystems, which makes it difficult to interpret community changes, because of e.g. global warming. Another explanation for the discrepancies in biodiversity of benthic diatoms at Brandal may be related to differences in the taxonomic identification skills and lack of comprehensive identification literature for benthic marine diatoms in Arctic regions. Proper molecular-taxonomic data on benthic Arctic diatoms do not yet exist, except for one recent study on a few isolates (Stachura-Suchoples et al. 2016). The same holds true for Antarctic benthic diatoms (Al-Handal and Wulff 2008). Consequently, the morphological and molecular taxonomy of these ecologically important microalgae need to be further addressed in order to prepare a reliable floristic list and, thus, expand our knowledge of their diversity.

In their paleoecological study on Arctic microphytobenthos off the south-eastern Arctic Beaufort Sea, Campeau et al. (1999) characterised four of the ten most abundant species as polar species or as typical of cold waters, whereas six species were



described as cosmopolitan taxa. Similarly, the ten most abundant species found at Svalbard in 2007 can be classified into four polar to cold temperate, five cosmopolitan species and one unidentified species of *Navicula*. It is difficult to distinguish between “polar water” and “sea-ice” species, since numerous benthic pennate diatoms contribute at least temporarily to sea-ice communities (von Quillfeldt 2004; Ratkova and Wassmann 2005). *Fossula arctica*, for example, was described by Hasle et al. (1996) and von Quillfeldt (2000) as a dominant species in Arctic waters. In addition, this species was associated with sea ice in the White Sea and Barents Sea (Ratkova and Wassmann 2005). The tychoplanktonic *Fragilariopsis cylindrus* was found in early phytoplankton spring blooms all over the Arctic Ocean (von Quillfeldt 2000) and is often associated with sea-ice (Gersonde and Zielinski 2000; Lizotte 2001; Mock and Thomas 2005). *Gyrosigma concilians* is characterised by Poulin (1991) as a sea-ice diatom from the Canadian Arctic, whereas *Navicula vanhoeffenii* has been documented as a cryopelagic species by Wiktor and Wojciechowska (2005). In the past, sea-ice diatoms received much more research attention as compared to their benthic counterparts in polar waters. Hence it is difficult to evaluate the available information about species-specific habitat preferences.

The five most abundant “cosmopolitan” species of the 2007 study are common taxa in coastal waters worldwide: *Cylindrotheca closterium* (Round et al. 1990), *Gyrosigma fasciola* (Hendey 1964), *Pseudo-nitzschia granii* (El-Sabaawi and Harrison 2006) and *Navicula directa* (Lee et al. 2006). *Navicula bipustulata* was also found in the Gulf of Riga (Vilbaste et al. 2000) and seems to be abundant in temperate regions. In Arctic regions, Campeau et al. (1999) identified *Fragilariopsis cylindrus*, *Navicula bipustulata* and *Navicula directa* as common species.

In contrast to the Arctic, the number of endemic benthic diatom species seems to be higher in Antarctica (Zacher et al. 2011). Karsten et al. (2006) argued that most Arctic algae, with an emphasis on benthic diatoms, have their main distribution in the temperate North Atlantic/Pacific due to the “young” geological cold-water history (3.5 Mio years). This low degree of endemism is also well documented for Arctic seaweeds (Wulff et al. 2011; Zacher et al. 2011; and references therein), which are generally characterised as eurythermal and/or psychrotolerant. In contrast, many Antarctic benthic micro- and macroalgae are stenothermal and psychrophilic, due to a much longer cold water history of this continent of 15–20 M years (Sabbe et al. 2003) and isolation as a result of the Antarctic Circumpolar Current. However, the degree of endemism even of Antarctic benthic diatoms seems to be rather small for marine and brackish water species despite the fact that they inhabit a very extreme habitat (Al-Handal and Wulff 2008).

Stations in Kongsfjorden influenced by glaciers (N3, NO1, NO2, NO5, O1, KB1; Fig. 9.3) always showed lower species richness than stations in the outer area of this fjord (NW5, NW3, LON, HAN, NAT, BRL, W3; Fig. 9.3), where an average of more than 10 species were identified per sample (Fig. 9.4). A possible explanation for the higher species richness in the outer fjord area might be the constant inflow of Atlantic water masses containing new “seed” organisms from the West Spitsbergen Current, which has been documented for the phytoplankton composition in Kongsfjorden by Wiktor and Wojciechowska (2005). An increased influx of

Atlantic water into the Kongsfjorden system might alter the species composition towards boreal species, whereas glacial input and distance from the coast would tend to make the inner part of the fjord more Arctic (Hop et al. 2002).

The Shannon biodiversity index ( $H'$ ) is different from species richness since it also shows community composition and takes into account the relative abundance of species that are present in the community. The  $H'$  varied between 0.5 at station NAT and 2.35 at BRL (Fig. 9.4), which is relatively low compared to other regions. Campeau et al. (1999) calculated indices of 2.7–3.7 for the coastal areas of the south-eastern Beaufort Sea, and higher indices (up to 4–5) are known from locations in Europe (Vilbaste et al. 2000; Sylvestre 2009).

### 9.1.2.5 Diversity of Epiphytic Diatoms

Macroalgae collected at different locations and depths in Kongsfjorden in 2002 revealed a low abundance of epiphytic diatoms (Table 9.4). While most kelps and larger seaweeds were almost free of any microalgal epiphytes, most filamentous macroalgae such as *Chaetomorpha linum* and *Ectocarpus siliculosus* exhibited high numbers of mainly stalked diatoms. In addition, particularly the shallow water filamentous macroalgae had the highest abundance of such diatoms pointing to enhanced light requirements of these benthic microalgae. An illustrative example is *Acrosiphonia arcta*. While a specimen from 10 m depth was free of epiphytic diatoms, an intertidal sample from the same location exhibited dark brown tips deriving from high cell numbers of Bacillariophyceae (Fig. 9.5). Although *Chorda filum* and *Chordaria flagelliformis* did not exhibit epiphytic diatoms on the thalli, their assimilation hairs were abundantly covered (Karsten et al. 2006). In addition, also the phaeophycean hairs of *Fucus distichus* exhibited many epiphytic diatoms, but they did not occur on the leathery thallus (Table 9.4). Most epiphytic diatoms found in Kongsfjorden were members of the araphid genus *Licmophora* C. Agardh, 1827 which has been described as a common and cosmopolitan component of epiphytic communities (Round et al. 1990; Woods and Fletcher 1991). *Licmophora* species usually form colonies, which are attached to branching polysaccharide stalks or mucilage pads (Fig. 9.6). In recent years, however, ecological field studies on kelp communities showed that particularly *Alaria esculenta*, but also other brown algae, carried a high load of micro- and macroalgal epiphytes (I. Bartsch, unpubl.). Whether the obviously changing environmental conditions in Kongsfjorden may also force a higher incidence of epiphytism is an open question (Karsten et al. 2015).

## 9.2 Conclusion

Benthic primary producers, both macro- and microalgae are abundant in Svalbard and a high number of species has been recorded in Kongsfjorden. While the diversity of the macroalgal flora is well described, information on benthic diatoms is only

**Table 9.4** Macroalgae (3 to 12 replicates) collected at different locations in Kongsfjorden during summer 2002 with epiphytic diatoms.

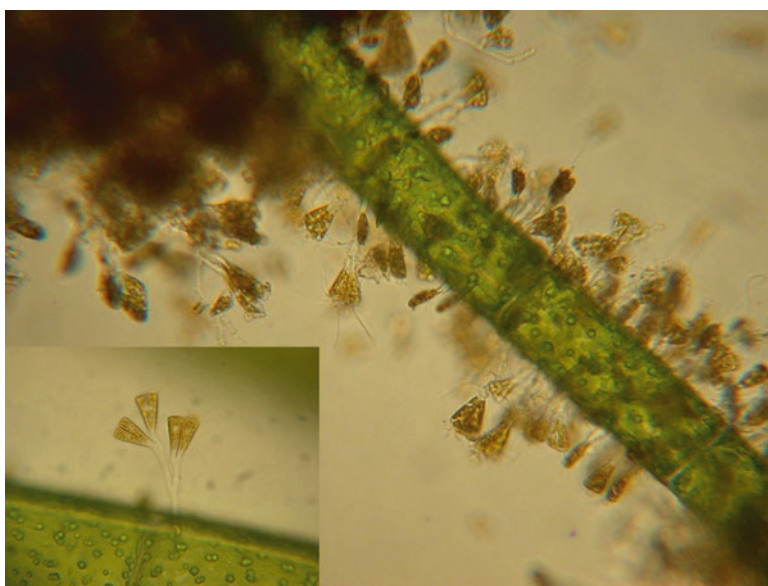
Species	Location	Depth (m)	Thallus (%)	Remarks
<i>Acrosiphonia arcta</i>	Hansneset	10	-	
<i>Acrosiphonia arcta</i>	Hansneset	0	+++	See Figures
<i>Alaria esculenta</i>	Hansneset	10	+	-
<i>Ceramium</i> sp.	Harbour	8	+	-
<i>Chaetomorpha linum</i>	Brandal	8	++	-
<i>Chaetomorpha melagonium</i>	Brandal	8	+	-
<i>Chorda filum</i>	Brandal	4.5	-	Assimilation hairs: +++
<i>Chordaria flagelliformis</i>	Brandal	4	-	Assimilation hairs: +++
<i>Coccotylus truncatus</i>	London	12	+	-
<i>Desmarestia aculeata</i>	Hansneset	6	-	-
<i>Devaleraea ramentacea</i>	Hansneset	2	+	-
<i>Dictyosiphon foeniculacens</i>	Hansneset	4	+	-
<i>Ectocarpus siliculosus</i>	Hansneset	2	+++	-
<i>Elachista fucicola</i>	Brandal	3	+++	-
<i>Fucus distichus</i>	Hansneset	0	+	Phaeophyceae hairs: +++
<i>Halosiphon tomentosus</i>	Brandal	10	+	-
<i>Laminaria digitata</i>	Hansneset	3	-	-
<i>Laminaria solidungula</i>	London	15	-	-
<i>Monostroma grevillei</i> var. <i>lubricum</i>	Brandal	10	-	-
<i>Odonthalia dentata</i>	Hansneset	15	+	-
<i>Palmaria palmata</i>	Brandal	8	+	-
<i>Phycodrys rubens</i>	Hansneset	15	+	-
<i>Polysiphonia arctica</i>	Hansneset	8	+	-
<i>Sacchorhiza dermatodea</i>	Hansneset	6	-	-
<i>Saccharina latissima</i>	Hansneset	6	-	-

Epiphytic diatoms were only present on thallus or in case of kelps on the blade. Diatom abundances according to Sevilgen et al. (2014) were determined. These authors quantified abundances as frequent (+ + +), rare (+ +), very rare (+), no (-) (Karsten, unpubl. data)

fragmentary due to a lack of comprehensive studies. In addition to their contribution to primary production, macroalgae create a three-dimensional habitat that harbours many other organisms, including several species of benthic microalgae. Increasing temperature in combination with a reduction in sea ice is expected to cause changes in the species composition of macro- and microalgae. Macroalgae are expected to increase in abundance and diversity in the littoral and make this zone hospitable for other organisms and we expect introductions of new species to Svalbard from more temperate regions such as the North Atlantic. Simultaneously, changes are expected in the sublittoral due to an altered underwater light regime with both positive and negative consequences for the vertical species' distribution and productivity. It is therefore important to obtain better baseline knowledge on these shallow water ecosystems and to study effects of climatic changes on both macro- and microalgal communities.



**Fig. 9.5** *Acrosiphonia arcta* collected at Hansneset (78°39'N, 17°57'E) at 10 m depth (left) and from the intertidal zone (0 m, right). While the deep-water sample was free of epiphytic diatoms, the intertidal one showed dark brown tips deriving from high cell numbers of Bacillariophyceae (Fig. 9.6). The diameter of the Petri dish is 94 mm



**Fig. 9.6** Shallow water *Acrosiphonia arcta* collected at Hansneset (78°39'N, 17°57'E) with high numbers of epiphytic diatoms of the stalked genus *Licmophora*

**Acknowledgements** The work on microphytobenthos has been performed at the Ny-Ålesund International Arctic Environmental Research and Monitoring Facility and under the agreement on scientific cooperation between the Alfred Wegener Institute and the University of Rostock. The authors thank the crew at the AWIPEV-base in Ny-Ålesund and the German dive team (Anita Flohr, Peter Leopold, Max Schwanitz) for assistance in the field, collecting samples and further support. Sediment tubes for sampling were manufactured by Peter Kumm (Institute of Chemistry, University of Rostock). We are grateful to Agnieszka Tatarek (Institute of Oceanology, Polish Academy of Sciences, Sopot) for counting and identifying diatom samples. Financing and logistic support of the microphytobenthic research was provided by the German Research Council (DFG, KA899/12 and KA899/15). Parts of the macroalgal sampling reported here were carried out by divers from the AWI; we are grateful for their contribution, especially to Max Schwanitz and Martin Paar. Line transects at different locations in Kongsfjorden, from inner to outer fjord, were carried out by divers from the Norwegian Polar Institute. The authors thank Joachim Bartsch for giving a final touch to the English and Sandra C. Lindstrom and Susse Wegeberg for valuable critique and comments during the review process.

## References

- Abdullah M, Fredriksen S (2004) Production, respiration and exudation of dissolved organic matter by the kelp *Laminaria hyperborea* along the west coast of Norway. *J Mar Biol Assoc UK* 84:887–894
- Adey WH, Steneck RS (2001) Thermogeography over time creates biogeographic regions: a temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. *J Phycol* 37:677–698
- Agardh JG (1862) Om Spetsbergens alger. Akademisk program, Lund, 4 pp
- Agardh JG (1868) Bidrag til kännedomen af Spetsbergens alger. *K Sven Vetenskapsakad Handl* 7:1–49
- Al-Handal AY, Wulff A (2008) Marine benthic diatoms from Potter Cove, King George Island, Antarctica. *Bot Mar* 51:51–68
- Athanasiadis A (2006) The genus *Leptophytum* (Melobesioideae, Corallinales, Rhodophyta) in NW Spitsbergen. *Nord J Bot* 24:469–499
- Athanasiadis A (2008) Two endemic coralline red algae on the northern limits of the latest glaciation. *Taxon* 57:223–230
- Bartsch I, Wiencke C, Laepple T (2012) Global seaweed biogeography under a changing climate: the prospected effects of temperature. In: Wiencke C, Bischof K (eds) *Seaweed biology, ecological studies*, vol 219. Springer, Berlin/Heidelberg, pp 383–406
- Bartsch I, Paar M, Fredriksen S, Schwanitz M, Daniel C, Hop H, Wiencke C (2016) Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biol* 39:2021–2036
- Beuchel F, Gulliksen B (2008) Temporal patterns of benthic community development in an Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study. *Polar Biol* 31:913–924
- 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
- Bolton JJ (2010) The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. *Helgol Mar Res* 64:263–279
- Bonsell C, Duntun KH (2018) Long – term patterns of benthic irradiance and kelp production in the Central Beaufort Sea reveal implications of warming for Arctic inner shelves. *Prog Oceanogr* 162:160–170

- Borum J, Pedersen MF, Krause-Jensen D, Christensen PB, Nielsen K (2002) Biomass, photosynthesis and growth of *Laminaria saccharina* in a high-Arctic fjord, NE Greenland. *Mar Biol* 141:11–19
- Brodie J, Maggs CA, John DM (2007) The green seaweeds of Britain and Ireland. British Phycological Society, Dunmurry
- Buchholz F, Werner T, Buchholz C (2012) First observation of krill spawning in the high Arctic Kongsfjorden, West Spitsbergen. *Polar Biol* 35:1273–1279
- Cahoon LB (1999) The role of benthic microalgae in neritic ecosystems. *Oceanogr Mar Biol Ann Rev* 37:47–86
- Campeau S, Pienitz R, Héquette A (1999) Diatoms as quantitative paleodepth indicators in coastal areas of the southeastern Beaufort Sea, Arctic Ocean. *Palaeogeogr Palaeoclimatol Palaeoecol* 146:67–97
- Chenelot H, Jewett SC, Hoberg MK (2011) Macrobenthos of the nearshore Aleutian Archipelago, with emphasis on invertebrates associated with *Clathromorphum nereostratum* (Rhodophyta, Corallinaceae). *Mar Biodivers* 41:413–424
- Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. *Mar Ecol Prog Ser* 396:221–233
- Clark GF, Stark JS, Johnston EL, Runcie JW, Goldsworthy PM, Raymond B, Riddle MJ (2013) Light-driven tipping points in polar ecosystems. *Glob Chang Biol* 19:3749–3761. <https://doi.org/10.1111/gcb.12337>
- Cottier FR, Nilsen F, Inall ME, Gerland S, Tverberg V, Svendsen H (2007) Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. *Geophys Res Lett* 34:L10607. <https://doi.org/10.1029/2007GL029948>
- Coyer JA, Hoarau G, Oudot-Le Secq M-P, Stam WT, Olsen JL (2006) A mtDNA-base phylogeny of the brown algal genus *Fucus* (Heterokontophyta; Phaeophyta). *Mol Phylogenet Evol* 39:209–222
- Cremer H (1998) Die Diatomeen der Laptevsee (Arktischer Ozean): Taxonomie und biogeographische Verbreitung. *Ber Polarforsch* 260:1–205
- De Brouwer JFC, de Decker EMGT, Stal LJ (2003) Distribution of extracellular carbohydrates in three intertidal mudflats in Western Europe. *Estuar Coast Shelf Sci* 56:313–324
- Duggins DO, Ekman JE (1997) Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. *Mar Biol* 128:489–495
- Dunton KH (1985) Growth of dark-exposed *Laminaria saccharina* (L.) Lamour. and *Laminaria solidungula* J. Ag. (Laminariales, Phaeophyta) in the Alaskan Beaufort Sea. *J Exp Mar Biol Ecol* 94:181–189
- Dunton KH, Schell SH (1986) Seasonal carbon budget and growth of *Laminaria solidungula* in the Alaskan high Arctic. *Mar Ecol Prog Ser* 31:57–66
- El-Sabaawi R, Harrison PJ (2006) Interactive effects of irradiance and temperature on the photosynthetic physiology of the pennate diatom *Pseudo-nitzschia granii* (Bacillariophyceae) from the Northeast subarctic Pacific. *J Phycol* 42:778–885
- Florczyk I, Latala A (1989) The phytobenthos of the Hornsund fjord, SW Spitsbergen. *Polar Res* 7:29–41
- Fredersdorf J, Müller R, Becker S, Wiencke C, Bischof K (2009) Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp *Alaria esculenta* (Phaeophyceae). *Oecologia* 160:483–492
- Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analyses. *Mar Ecol Prog Ser* 260:71–81
- Fredriksen S, Kile MR (2012) The algal vegetation in the outer part of Isfjorden, Spitsbergen: revisiting Per Svendsen's sites 50 years later. *Polar Res* 31:17538. <https://doi.org/10.3402/polar.v31i0.17538>
- Fredriksen S, Bartsch I, Wiencke C (2014) New additions to the benthic marine flora of Kongsfjorden, western Svalbard, and comparison between 1996/1998 and 2012/2013. *Bot Mar* 57:203–216



- Fredriksen S, Gabrielsen TM, Kile MR, Sivertsen K (2015) Benthic algal vegetation in Isfjorden, Svalbard. A survey of the main fjord area. *Polar Res* 34:25994. <https://doi.org/10.3402/polar.v34.25994>
- Gersonde R, Zielinski U (2000) The reconstruction of late quaternary Antarctic sea-ice distribution – the use of diatoms as a proxy for sea-ice. *Palaeogeogr Palaeoclimatol Palaeoecol* 162:263–286
- Glud RN, Woelfel J, Karsten U, Kühl M, Rysgaard S (2009) Benthic microalgal production in the Arctic: applied methods and status of the current database. *Bot Mar* 52:559–571
- Gómez I, Wulff A, Roleda MY, Huovinen P, Karsten U, Quartino ML, Dunton K, Wiencke C (2011) Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. In: Wiencke C (ed) *Biology of polar benthic algae*. de Gruyter, Berlin, pp 195–220
- Gordillo FJL, Carmona R, Viñeola B, Wiencke C, Jiménez (2016) Effects of simultaneous increase in temperature and ocean acidification on biochemical composition and photosynthetic performance of common macroalgae from Kongsfjorden (Svalbard). *Polar Biol* 39:1993–2007
- Guiry MD, Guiry GM (2018) *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org>. Accessed 2 May 2018
- Gulliksen B, Palerud R, Brattgard T, Sneli J (1999) Distribution of marine benthic macroorganisms at Svalbard (including Bear Island) and Jan Mayen. Research Report for DN 1999-4. Directorate for Nature Management, 151 pp
- Hanelt D, Tüg GH, Bischof K, Gross C, Lippert H, Sawall T, Wiencke C (2001) Light regime in an Arctic fjord: a study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth. *Mar Biol* 138:649–658
- Hansen JR, Jenneborg JH (1996) Benthic marine algae and cyanobacteria. In: Elvebakk A, Presterud P (eds) *A catalogue of Svalbard plants, fungi, algae and cyanobacteria*, vol 198. Norsk Polarinst Skr, Oslo, pp 361–374
- Hasle GR, von Quillfeldt CH (1996) Marine microalgae. In: Elvebakk A, Presterud P (eds) *A catalogue of Svalbard plants, fungi, algae and cyanobacteria*, vol 198. Norsk Polarinst Skr, Oslo, pp 375–382
- Hasle GR, Syvertsen EE, von Quillfeldt CH (1996) *Fossula arctica* gen. nov., spec. nov., a marine Arctic araphid diatom. *Diatom Res* 11:261–272
- Heesch S, Pazoutova M, Moniz MBJ, Rindi F (2016) Prasiolales (Trebouxiophyceae, Chlorophyta) of the Svalbard Archipelago: diversity, biogeography and description of the new genera *Prasionella* and *Prasionema*. *Eur J Phycol* 51:171–187
- Hendey NI (1964) An introductory account of the smaller algae of British coastal waters. V. Bacillariophyceae (diatoms). HMSO, London
- Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalczuk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S-Å, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. *Polar Res* 21:167–208
- Hop H, Wiencke C, Vögele B, Kovaltchouk NA (2012) Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard. *Bot Mar* 55:399–414
- Hop H, Kovaltchouk NA, Wiencke C (2016) Distribution of macroalgae in Kongsfjord, Svalbard. *Polar Biol* 39:2037–2051
- Kain JM (1971) Synopsis of biological data on *Laminaria hyperborea*. FAO Fisheries Synopsis No. 87
- Karsten U (2007) Salinity tolerance of Arctic kelps from Spitsbergen. *Phycol Res* 55:257–262
- Karsten U, Dummermuth A, Hoyer K, Wiencke C (2003) Interactive effects of ultraviolet radiation and salinity on the ecophysiology of two Arctic red algae from shallow waters. *Polar Biol* 26:249–258
- Karsten U, Schumann R, Rothe S, Jung I, Medlin L (2006) Temperature and light requirements for growth of two diatom species (Bacillariophyceae) isolated from an Arctic macroalga. *Polar Biol* 29:476–486



- Karsten U, Schlie C, Woelfel J, Becker B (2012) Benthic diatoms in Arctic seas – ecological functions and adaptations. *Polarforsch* 81:77–84
- Karsten U, Schaub I, Woelfel J, Sevilgen D, Schlie C, Becker B, Wulff A, Graeve M, Wagner H (this volume-c) Chapter 8: Living on cold substrata – new insights and approaches to study microphytobenthos ecophysiology and ecology in Kongsfjorden. In: Hop H, Wiencke C (eds) *The ecosystem of Kongsfjorden, Svalbard, Advances in polar ecology 2*. Springer, Cham
- Kim JH, Chung H, Choi H-G, Kim Y (2003) Macroalgal flora of Kongsfjorden in Svalbard Islands, the Arctic. *Ocean and Polar Res* 25:569–591
- Kjellman FR (1875a) Förberedande anmärkningar om algvegetationen i Mossel Bay enligt iakttagelser under vinterdragningar anställda av Svenska polarexpeditionen 1972–1873. *Öfvers Kungl Svenska Vetensk-Akad Förhandl* 5:59–68
- Kjellman FR (1875b) Om Spetsbergens marina, klorofyllförande thallophyter I. *Bih Kungl Svenska Vetensk-Akad Handl* 3:1–34
- Kjellman FR (1877a) Om Spetsbergens marina, klorofyllförande thallophyter II. *Bih Kungl Svenska Vetensk-Akad Handl* 4:1–61
- Kjellman FR (1877b) Bidrag til kännedomen af Kariska hafvets algvegetation. *Öfversikt Kungl Vetensk-Akad Förhandl* 2:3–30
- Kjellman FR (1883) Norra Ishafvets algflora. *Vega-Exped Vetensk Iakttag* 3:1–431
- Kjellman FR (1893) Studier öfver Chlorophycésläktet *Acrosiphonia* JG Ag och dess skandinaviska arter. *Bih Kungl Svenska Vetensk-Akad Handl* 3:1–114
- Kortsch S, Primicerio R, Beuchel F, Renaud PE, Rodrigues J, Lønne OJ, Gulliksen B (2012) Climate-driven regime shifts in Arctic marine benthos. *PNAS* 109:14052–14057
- Kraan S, Rueness J, Guiry MD (2001) Are North Atlantic *Alaria esculenta* and *A. grandifolia* (Alariaceae, Phaeophyceae) conspecific? *Eur J Phycol* 39:35–42
- Krause-Jensen D, Kühl M, Christensen PB, Borum J (2007a) Benthic primary production in young sound, northeastern Greenland. In: Rysgaard S, Glud RN (eds) *Carbon cycling in Arctic marine ecosystems: case study young sound*. Medd Grønland. Bioscience 58:159–174
- Krause-Jensen D, Marbà N, Olesen B, Sejr MK, Christensen PB, Rodrigues J, Renaud PE, Blasby TJS, Rysgaard S (2012) Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. *Glob Chang Biol* 18:2981–2994
- Kruss A, Blondel P, Tegowski J (2012) Acoustic properties of macrophytes: Comparison of single-beam and multibeam imaging with modelling results. 11th European conference on underwater acoustics 2012. Institute of Acoustics, St Albans, pp 168–175
- Kruss A, Tegowski J, Tatarek A, Wiktor J, Blondel P (2017) Spatial distribution of macroalgae along the shores of Kongsfjorden (West Spitsbergen) using acoustic imaging. *Pol Polish Res* 38:205–229
- Kucera H, Saunders GW (2008) Assigning morphological variants of *Fucus* (Fucales, Phaeophyceae) in Canadian waters to recognized species using DNA barcoding. *Botany* 86:1065–1079
- Küpper FC, Peters AF, Shewring DM, Sayer MDJ, Mystikou A, Brown H, Azzopardi E, Dargent O, Strittmatter M, Brennan D, Asensi AO, van West P, Wilce RT (2016) Arctic marine phyto-benthos of Northern Baffin Island. *J Phycol* 52:532–549
- Lantuit H, Overduin PP, Couture N, Wetterich S, Aré F, Atkinson D, Brown J, Cherkashov G, Drozdov D, Forbes DL, Graves-Gaylord A, Grigoriev M, Hubberten H-W, Jordan J, Jorgenson T, Ødegård RS, Ogorodov S, Pollard WH, Rachold V, Sedenko S, Solomon S, Steenhuisen F, Streletskaia I, Vasiliev A (2012) The Arctic coastal dynamics database: a new classification scheme and statistics on Arctic permafrost coastlines. *Estuar Coasts* 35:383–400
- Lee JB, Hayashi K, Hirata M, Kuroda E, Suzuki E, Kubo Y, Hayashi T (2006) Antiviral sulphated polysaccharide from *Navicula directa*, a diatom collected from deep-sea water in Toyama Bay. *Biol Pharm Bull* 29:2135–2139
- Lein TE (1984) Distribution, reproduction, and ecology of *Fucus ceranoides* L. (Phaeophyceae) in Norway. *Sarsia* 69:75–81

- Lein TE, Küfner R (1998) Marine benthosalger fra østsiden av Novaja Semlja, Karahavet 1993. IFM Report, Univ Bergen, Norway, No 10
- Leventer A (1992) Modern distribution of diatoms in sediments from the George V Coast, Antarctica. *Mar Micropaleontol* 19:315–332
- Lindblom AE (1840) Förteckning öfver de på Spetsbergen och Beeren Eiland anmärkta vexter. *Bot Notiser* 9:153–158
- Lizotte MP (2001) The contributions of sea-ice algae to Antarctic marine primary production. *Am Zool* 41:57–73
- Longhi ML, Schloss IR, Wiencke C (2003) Effect of irradiance and temperature on photosynthesis and growth of two Antarctic benthic diatoms, *Gyrosigma subsalinum* and *Odontella litigiosa*. *Bot Mar* 46:276–284
- Longtin CM, Saunders GW (2015) On the utility of mucilage ducts as a taxonomic character in *Laminaria* and *Saccharina* (Phaeophyceae) – the conundrum of *S. groenlandica*. *Phycologia* 54:440–450
- Lund S (1951) Marine algae from Jörgen Brönlunds Fjord in eastern north Greenland. *Medd Grønland* 128:1–26
- Lund L (2014) Morphological diversity in *Laminaria digitata*. MSc thesis in Marine Biology, NTNU, Trondheim, Norway, 65 pp
- Lüning K (1990) Seaweeds. Their environment, biogeography and ecophysiology. Wiley, New York
- Mann KH (2000) Ecology of coastal waters: with implications for management, 2nd edn. Blackwell Science, Malden, MA
- Marr JWS (1927) Plants collected during the British Arctic expedition, 1925. *J Bot* 65:272–277
- McDevitt DC, Saunders GW (2010) A DNA barcode examination of the Laminariaceae (Phaeophyceae) in Canada reveals novel biogeographical and evolutionary insights. *Phycologia* 49:235–248
- Mock T, Thomas DN (2005) Recent advances in sea ice microbiology. *Environ Microbiol* 7:605–619
- Moy SR (2015) Littoral and sublittoral macroalgal vegetation from 8 sites around Svalbard. MSc thesis in Marine Biology, University of Oslo, Norway, 120 pp
- Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. *Mar Ecol Prog Ser* 255:135–144
- O’Kelly CJ, Bellows WK, Wysor B (2004) Phylogenetic position of *Bolbocoleon piliferum* (Ulvoephyceae, Chlorophyta): evidence from reproduction, zoospore and gamete ultrastructure, and small subunit rRNA gene sequences. *J Phycol* 40:209–222
- Pavlov AK, Tverberg V, Ivanov BV, Nilsen F, Falk-Petersen S, Granskog MA (2013) Warming of Atlantic water in two West Spitsbergen fjords over the last century (1912–2009). *Polar Res* 32:11206
- Pavlov A, Leu E, Hanelt D, Bartsch I, Karsten U, Hudson SR, Gallet J-C, Cottier F, Cohen JH, Berge J, Johnsen G, Maturilli M, Kowalczyk P, Sagan S, Meler J, Granskog MA (this volume-e) Chapter 5: Underwater light regime in Kongsfjorden and its ecological implications. In: Hop H, Wiencke C (eds) The ecosystem of Kongsfjorden, Svalbard, *Advances in polar ecology* 2. Springer, Cham
- Pavlova O, Gerland S, Hop H (this volume-e) Chapter 4: Changes in sea-ice extent and thickness in Kongsfjorden, Svalbard (2003–2016). In: Hop H, Wiencke C (eds) The ecosystem of Kongsfjorden, Svalbard, *Advances in polar ecology* 2. Springer, Cham
- Pedersen PM (1976) Marine, benthic algae from southernmost Greenland. *Medd Grønland* 199:1–80
- Pedersen PM (2011) Grønlands Havalger. Epsilon, Copenhagen
- Peltikhina TS (2002) Distribution peculiarities and stocks of *Laminaria* algae in the area of Isfjord of the Spitsbergen Archipelago. In: Matishov GG, Tarasov GA (eds) The complex

- investigations of the Spitsbergen nature. Murmansk Biological Institute. In Russian (English Abstract), pp 168–174
- Poulin M (1991) Sea ice diatoms (Bacillariophyceae) of the Canadian Arctic. 2. A taxonomic, morphological and geographical study of *Gyrosigma concilians*. *Nor J Bot* 10:681–688
- Powell HT (1957) Studies in the genus *Fucus* L. I. *Fucus distichus* emend. Powell. *J Mar Biol Assoc UK* 36:407–432
- Ratkova TN, Wassmann P (2005) Sea ice algae in the White and Barents Seas: composition and origin. *Polar Res* 24:95–110
- Renaud PE, Tessmann M, Evensen A, Christensen GN (2011) Benthic food-web structure of an Arctic fjord (Kongsfjorden, Svalbard). *Mar Biol Res* 7:13–26
- Rice EL, Chapman ARO (1985) A numerical taxonomic study of *Fucus distichus* (Phaeophyta). *J Mar Biol Assoc UK* 65:433–459
- Risgaard-Petersen N, Rysgaard S, Nielsen LP, Revsbech NP (1994) Diurnal variation of denitrification and nitrification in sediments colonized by benthic microphytes. *Limnol Oceanogr* 39:573–579
- Roleda MY, Dethleff D (2011) Storm-generated sediment deposition on rocky shores: simulating burial effects on the physiology and morphology of *Saccharina latissima* sporophytes. *Mar Biol Res* 7:213–223
- Roleda MY, Dethleff D, Wiencke C (2008) Transient sediment load on blades of Arctic *Saccharina latissima* can mitigate UV radiation effect on photosynthesis. *Polar Biol* 31:765–769
- Round FE (1971) Benthic marine diatoms. *Oceanogr Mar Biol Annu Rev* 9:83–139
- Round FE, Crawford RM, Mann DG (1990) The diatoms: biology & morphology of the genera. Cambridge University Press, Cambridge
- Rueness J (1977) Norsk algeflora. Universitetsforlaget, Oslo
- Rysgaard S, Glud RN (2007) Carbon cycling in Arctic marine ecosystems: case study young sound. *Medd Grønland. Bioscience* 58
- Sabbe K, Verleyen E, Hodgson D, Vanhoutte K, Vyverman W (2003) Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. *Antarct Sci* 15:227–248
- Schlie C, Woelfel J, Rüdiger F, Schumann R, Karsten U (2011) Ecophysiological performance of benthic diatoms from arctic waters. In: Seckbach J, Kociolek P (eds) *COLE-Cellular Origin, Life in extreme Habitats and Astrobiology, The Diatom World*, vol 19, pp 425–436
- Sevilgen DS, de Beer D, Al-Handal AY, Brey T, Polerecky L (2014) Oxygen budgets in subtidal arctic (Kongsfjorden, Svalbard) and temperate (Helgoland, North Sea) microphytobenthic communities. *Mar Ecol Prog Ser* 504:27–42
- Sommerfelt C (1832) Bidrag til Spetsbergens og Beeren-Eilands flora efter herbarier, medbragt af M. Keilhau. *Mag Naturv* 11:232–245
- Stachura-Suchoples K, Enke N, Schlie C, Schaub I, Karsten U, Jahn R (2016) Contribution towards a morphological and molecular taxonomic reference library of benthic marine diatoms from two Arctic fjords on Svalbard (Norway). *Polar Biol* 39:1933–1956
- Svendsen P (1957) Om algevegetasjonen på Spitsbergen. En undersøkelse av den marine algefloren i den ytre del av Isfjorden. Cand. real thesis, University of Oslo
- Svendsen P (1959) The algal vegetation of Spitsbergen. A survey of the marine algal flora of the outer part of Isfjorden. *Nor Polarinst Skr* 116:1–49
- Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland OR, Wiencke C, Winther J-G, Dallmann W (2002) The physical environment of Kongsfjorden – Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res* 21:133–166
- Sylvestre F (2009) Modern diatom distribution in the Seine and Authie Estuaries. In: Amiard-Triquet C, Rainbow PS (eds) *Environmental assessment of estuarine ecosystems: a case study*. CRC, Boca Raton, pp 241–254

- Tanimura Y (1992) Distribution of diatom species in the surface sediments of Lützow-Holm Bay, Antarctica. In: Ishizaki K, Saito T (eds) Centenary of Japanese micropaleontology. Terra Scientific Publishing Co, Tokyo, pp 399–411
- Tatarek A, Wiktor J, Kendall MA (2012) The sublittoral macroflora of Hornsund. Polar Res 31:18900. <https://doi.org/10.3402/polar.v31i0.18900>
- Taylor WR (1954) The cryptogamic flora of the Arctic. II. Algae: non – planktonic. Bot Rev 20:363–399
- Taylor F, McMinn A, Franklin D (1997) Distribution of diatoms in surface sediments of Prydz Bay, Antarctica. Mar Micropaleo 32:209–229
- Teichert S, Wolkerling W, Rüggeberg A, Wisshak M, Piepenburg D, Meyerhöfer M, Form A, Büdenbender J, Freiwald A (2012) Rhodolith beds (Corallinales, Rhodophyta) and their physical and biological environment at 80°31'N in Nordkappbukta (Nordaustlandet, Svalbard archipelago, Norway). Phycologia 51:371–390
- Teichert S, Wolkerling W, Rüggeberg A, Wisshak M, Piepenburg D, Meyerhöfer M, Form A, Freiwald A (2014) Arctic rhodolith beds and their environment. Facies 60:15–37
- van den Hoek C (1984) World-wide longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of rhodophytan genera. Helgoländer Meeresun 38:227–257
- Vilbaste S, Sundbäck K, Nilsson C, Truu J (2000) Distribution of benthic diatoms in the littoral zone of the Gulf of Riga, the Baltic Sea. Eur J Phycol 35:373–385
- Vinogradova KL (1995a) Seaweeds. In: Klekowski RZ, Weslawski JM (eds) Atlas of marine flora of southern Spitsbergen. Polish Academy of Sciences, Gdansk
- Vinogradova KL (1995b) The checklist of the marine algae from Spitsbergen. Bot Z SSR 80:50–61
- Vinogradova KL, Schoschina EV (1993) Algae. In: Matishov GG, Galaktionov KV, Denisov VV, Drobysheva SS, Chinarina AD, Timofeeva SV (eds) Environment and ecosystems of Franz Josef Land (Archipelago and shelf). Kola Scientific Centre/Academy of Science of Russia, Murmanskaya Oblast/Moscow, pp 109–116
- Volent Z, Johnsen G, Sigernes F (2007) Kelp forest mapping by use of airborne hyperspectral imager. J Appl Remote Sens 1:011503. <https://doi.org/10.1117/1.2822611>
- von Quillfeldt CH (2000) Common diatom species in Arctic spring blooms: their distribution and abundance. Bot Mar 43:499–516
- von Quillfeldt CH (2004) The diatom *Fragilariopsis cylindrus* and its potential as an indicator species for cold water rather than for sea ice. Vie et Milieu 54:137–143
- Voronkov A, Hop H, Gulliksen B (2012) Diversity of hard-bottom fauna relative to environmental gradients in Kongsfjorden, Svalbard. Polar Res 32. <https://doi.org/10.30402/polar.v32i0.11208>. Suppl Table S1
- Vyverman W, Verleyen E, Sabbe K, Vanhoutte K, Sterken M, Hodgson DA, Mann DG, Juggins S, Van der Vijer B, Jones V, Flower R, Roberts D, Chepurnov VA, Kilroy C, Vanormelingen P, De Wever A (2007) Historical processes constrain patterns in global diatom diversity. Ecology 88:1924–1931
- Weslawski JM, Wiktor JM, Zajaczkowski M, Swerpel S (1993) Intertidal zone of Svalbard. 1. Macroorganisms distribution and biomass. Polar Biol 13:73–79
- Weslawski JM, Zajaczkowski M, Wiktor J, Szymelfenig M (1997) Intertidal zone of Svalbard. 3. Littoral of a subarctic, oceanic island: Bjornoya. Polar Biol 18:45–52
- Weslawski JM, Wiktor J Jr, Kotwicki L (2010) Increase in biodiversity in the arctic rocky littoral, Sorkapland, Svalbard, after 20 years of climate warming. Mar Biodivers 40:123–130
- Weslawski JM, Kendall MA, Włodarska-Kowalczyk M, Iken K, Kedra M, Legezynska J, Sejr MK (2011) Climate change effects on Arctic fjord and coastal macrobenthic diversity – observations and predictions. Mar Biodivers 41:71–85
- Wiencke C, Vögele B, Kovaltchouk NA, Hop H (2004) Species composition and zonation of marine benthic macroalgae at Hansneset in Kongsfjorden, Svalbard. Ber Polarforsch Meeresforsch 492:55–62

- Wiencke C, Clayton MN, Gómez I, Iken K, Lüder UH, Amsler CD, Karsten U, Hanelt D, Bischof K, Dunton K (2007) Life strategy, ecophysiology and ecology of seaweeds in polar waters. *Rev Environ Sci Biotechnol* 6:95–126
- Wiencke C, Gómez I, Dunton K (2011) Phenology and seasonal physiological performance of polar seaweeds. In: Wiencke C (ed) *Biology of polar benthic algae*. Walter de Gruyter GmbH & Co. KG, Berlin/New York, pp 181–194
- Wiktor JM, Okolodkov JB (1995) Phytoplankton. In: Klekowski RZ, Weslawski JM (eds) *Atlas of Southern Spitsbergen marine flora*. Institute of Oceanology, Sopot, pp 9–291
- Wiktor JM, Wojciechowska K (2005) Differences in taxonomic composition of summer phytoplankton in two fjords of West Spitsbergen, Svalbard. *Pol Polar Res* 26:259–268
- Wilce RT (1994) The Arctic subtidal as habitat for macrophytes. In: Lobban CS, Harrison PJ (eds) *Seaweed ecology and physiology*. Cambridge University Press, Cambridge/ New York/ Oakleigh, pp 89–92
- Wilce RT (2016) The “Arctic Stamp”, its imprint on an endangered marine flora – the Arctic benthic algal flora and its environment seen from 65 years of Arctic research. *Perspect Phycol* 3:155–180
- Woelfel J, Schumann R, Leopold P, Wiencke C, Karsten U (2009) Microphytobenthic biomass along gradients of physical conditions in Arctic Kongsfjorden, Svalbard. *Bot Mar* 52:573–583
- Woelfel J, Schumann R, Peine F, Flohr A, Flohr A, Kruss A, Tegowski J, Blondel P, Wiencke C, Karsten U (2010) Microphytobenthos of Arctic Kongsfjorden (Svalbard, Norway): biomass and potential primary production along the shore line. *Polar Biol* 33:1239–1253
- Woelfel J, Eggert A, Karsten U (2014) Marginal impacts of rising temperature on Arctic benthic microalgae production based on in situ measurements and modelled estimates. *Mar Ecol Prog Ser* 501:25–40
- Woods DC, Fletcher RL (1991) Studies on the strength of adhesion of some common marine fouling diatoms. *Biofouling* 3:287–303
- Wulff A, Iken K, Quartino ML, Al-Handal A, Wiencke C, Clayton MN (2011) Biodiversity, biogeography and zonation of marine benthic micro- and macroalgae in the Arctic and Antarctic. In: Wiencke C (ed) *Biology of polar benthic algae*. Walter de Gruyter GmbH & Co. KG, Berlin/ New York, pp 23–52
- Zacher K, Rautenberger R, Hanelt D, Wulff A, Wiencke C (2011) The abiotic environment of polar benthic algae. In: Wiencke C (ed) *Biology of polar benthic algae*. de Gruyter, Berlin, pp 9–22
- Zacher K, Bernard M, Bartsch I, Wiencke C (2016) Recruitment of Arctic kelp species under multifactorial global change scenarios. *Polar Biol* 39:2009–2020
- Zajaczkowski M (2008) Sediment supply and fluxes in glacial and outwash fjords, Kongsfjorden and Adventfjorden, Svalbard. *Polish Polar Res* 29:59–72
- Zinova ES (1929) Vodorosli Novoj Zemli. Gosudarstvenneyi godrologiceskij institut. Otdel nyj ottisk iz “Issledovanija Morej SSSR” Vyp 10:41–12