



You have downloaded a document from
RE-BUŚ
repository of the University of Silesia in Katowice

Title: Primary producers and production in Hornsund and Kongsfjorden - Comparison of two fjord systems

Author: Zofia T. Smoła, Agnieszka Tatarek, Józef M. Wiktor, Józef M. W. Wiktor, Anna Kubiszyn, Jan M. Węsławski

Citation style: Smoła Zofia T., Tatarek Agnieszka, Wiktor Józef M., Wiktor Józef M. W., Kubiszyn Anna, Węsławski Jan M. (2017). Primary producers and production in Hornsund and Kongsfjorden - Comparison of two fjord systems. "Polish Polar Research" (Vol. 38, iss. 3 (2017), s. 351-373), doi 10.1515/popore-2017-0013



Uznanie autorstwa - Użycie niekomercyjne - Bez utworów zależnych Polska - Licencja ta zezwala na rozpowszechnianie, przedstawianie i wykonywanie utworu jedynie w celach niekomercyjnych oraz pod warunkiem zachowania go w oryginalnej postaci (nie tworzenia utworów zależnych).





Primary producers and production in Hornsund and Kongsfjorden – comparison of two fjord systems

Zofia T. SMOŁA^{1,2}, Agnieszka TATAREK¹, Józef M. WIKTOR¹,
Józef M.W. WIKTOR Jr.¹, Anna KUBISZYN¹ and Jan M. WĘŚLAWSKI^{1*}

¹ Institute of Oceanology Polish Academy of Science – Marine Ecology Department,
ul. Powstańców Warszawy 55, 81–712 Sopot, Poland
<zosiasmola@iopan.gda.pl>

² Centre for Polar Studies KNOW (Leading National Research Centre), Faculty of Earth Sciences,
University of Silesia, ul. Będzińska 60, 41-200 Sosnowiec, Poland

* corresponding author <weslaw@iopan.gda.pl>

Abstract: Hornsund and Kongsfjorden are two similar-sized Arctic fjords on the West coast of Spitsbergen. They are influenced by cold coastal Arctic water (Hornsund) and warmer Atlantic water (Kongsfjorden). Environmental conditions affect the timing, quantity, spatial distribution (horizontal and vertical) of spring and summer blooms of protists as well as the taxonomic composition of those assemblages. Here, we compile published data and unpublished own measurement from the past two decades to compare the environmental factors and primary production in two fjord systems. Kongsfjorden is characterized by a deeper euphotic zone, higher biomass and greater proportion of autotrophic species. Hornsund seems to obtain more nutrients due to the extensive seabird colonies and exhibits higher turbidity compared to Kongsfjorden. The annual primary production in the analysed fjords ranges from 48 g C m⁻² y⁻¹ in Kongsfjorden to 216 g C m⁻² y⁻¹ in Hornsund, with a dominant component of microplankton (90%) followed by macrophytes and microphytobenthos.

Key words: Arctic, Spitsbergen, primary production, environmental conditions, fjords.

Introduction

Arctic Ocean is surrounded by continents that partially extend over shelf areas, and these are the most productive parts of the Arctic. Arctic shelf areas are also much more productive than the terrestrial areas, so most of the fresh biogenic matter produced in the Arctic is of marine origin (6.4 Pg y⁻¹ versus 0.8 Pg y⁻¹, respectively; Geider *et al.* 2001).

The first broad assessment of the Arctic marine primary production was published by Subba Rao and Platt (1984). These authors demonstrated the productivity in the shelf waters *versus* the deep, oligotrophic Central Arctic Basin. Subba Rao and Platt estimates were followed by those of Gosselin *et al.* (1997) and Arrigo *et al.* (2008). More recent data were published by, Olli *et al.* (2007), Hill *et al.* (2013), Matrai *et al.* (2013) and Fernández–Méndez *et al.* (2015). Primary production in the Barents Sea shelf was studied by, Sakshaug (2004) and Loeng *et al.* (2005), and primary production across the entire Arctic shelf was studied by Pabi *et al.* (2008), whereas primary production in the Arctic Marginal Ice Zone (MIZ) has been reported by, Sakshaug and Skjoldal (1989), Falk-Petersen *et al.* (2000), Ratkova and Wassmann (2002) and Wassmann *et al.* (2006). Recently, the use of a modelling approach has been more common for the presentation of primary production in the Arctic (*e.g.*, Wassman *et al.* 2006; Popova *et al.* 2012). As the Arctic itself presents a huge logistical challenge, Arctic fjords are often suggested as a research option because they are more accessible and can be used as model areas (Syvitski *et al.* 1987). Hornsund and Kongsfjorden are fjords of West Spitsbergen, studied extensively with regard to the marine ecosystem over the past two decades (see reviews in Hop *et al.* (2002) and Svendsen *et al.* (2002)). Marine ecosystem studies in Kongsfjorden started in 1960, when Digby (1961) first published observations on the microplankton, while marine ecological observations in Hornsund started at the end of the 1970s (*e.g.*, Węśławski *et al.* 1988; Eilertsen *et al.* 1989). Further studies concerning primary production and phytoplankton communities in Kongsfjorden and Hornsund are shown in Table 1.

The aim of this study is to review the published (Table 1) and archival unpublished data on the primary production in Hornsund (77°N) and Kongsfjorden (79°N), which are known for their different levels of exposure to the increasing inflow of Atlantic Waters (AW) (Walczowski and Piechura 2011). We aim to demonstrate how the primary producers and their performance may differ in the two examined fjords.

Study area

Hydrological parameters. — The West Spitsbergen coast faces an overwhelming influence of Atlantic Waters (AW), as the West Spitsbergen Current (WSC) (Walczowski and Piechura 2011). AW brings from the south, relatively warm (2 to 4°C and even 10°C during summer) and saline (>34.65 PSU) waters (Svendsen *et al.* 2002; Cottier *et al.* 2005). This current follows the deeper part of the Fram Strait and often enters Kongsfjorden and warms its environment (Svendsen *et al.* 2002 ; Fig. 1). A recent increase in northward heat transport with AW ranges from 28 to 70 terawatts (Cisewski *et al.* 2003; Schauer *et al.*

Table 1
Factors measured during studies conducted in Hornsund (H) and Kongsfjorden (K).

Author	Fjord	Sampling period	Chl <i>a</i>	Biomass	Nutrients	Prim. prod.	Abundance	Taxonomy
Węślawski <i>et al.</i> 1988	H	1984–1985	x		x	x	x	
Eilertsen <i>et al.</i> 1989	H	1978–1985, selected months	x		x	x	x	x
	K	1978–1985, selected months	x		x	x	x	x
Yamaguchi <i>et al.</i> 1996	K	May, June 1993	x			x		
Wiktor 1999	H	May 1996		x			x	x
	K	April, May 1996	x	x			x	x
Hop <i>et al.</i> 2002	K	Summary	x	x		x	x	x
Leu <i>et al.</i> 2006	K	Bloom: 24 April–23 May 2003	x	x	x		x	x
		post-bloom: 8 May–8 June 2004						
Wängberg <i>et al.</i> 2006	K	June 2001	x			x	x	x
Piwoższ <i>et al.</i> 2009	K	29–30 July 2002	x	x		x	x	x
	H	23–27 July 2002	x	x		x	x	x
Iversen and Seuthe 2011	K	03–05,07,09 December 2006	x	x	x	x	x	x
		15,18 April 2002 1–22 May 2002	x	x	x	x	x	x
Hodal <i>et al.</i> 2012	K	25–28 April 2006	x		x		x	x
		12–15 May 2007	x		x		x	x
		18–22 May 2008	x		x		x	x
Piquet <i>et al.</i> 2014	K	22 May–25 June 2007	x		x			x
		9 April–12 May 2008	x		x			x
IOPAN unpubl. data	H	July 2005				x		x

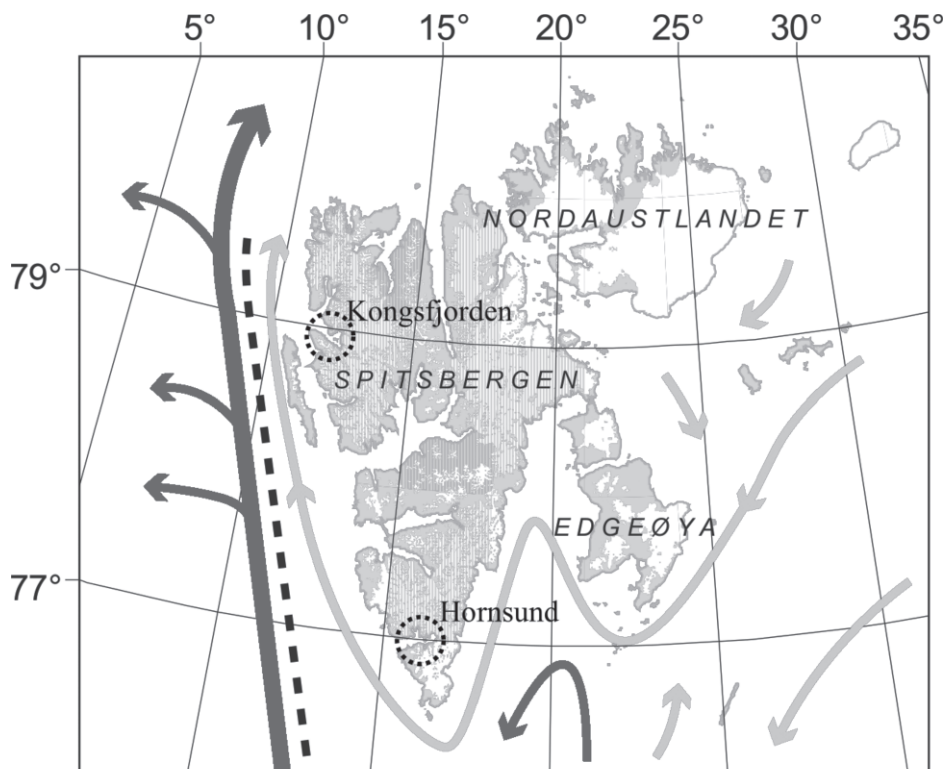


Fig. 1. Currents influencing the West Spitsbergen coast and locations of the fjords. Dark grey line marks the West Spitsbergen Current (Atlantic Water), light grey line marks the Sørkapp Current (coastal Arctic Water) and dotted line marks the Arctic Front (modified from Svendsen *et al.* 2002).

2004; Walczowski *et al.* 2005). This heat influx warms adjacent waters and land and increases vapour content, resulting in cloudiness that affects the light conditions during the growth season.

Hornsund is under the influence of cold, less saline coastal Arctic waters ($T < 0^{\circ}\text{C}$, $34.3 < S < 34.7$ PSU) of Barents Sea origin (Skagseth *et al.* 2008). These waters flow northward along the shelf of the southwest coast of Spitsbergen as the Sørkapp Current, temporarily entering the fjords of the southwest Spitsbergen coast (Swerpel 1985; Cottier *et al.* 2005). In some years, the Sørkapp Current carries remnants of pack ice from the Barents Sea together with ice-associated diatoms (Hegseth 1992). The simultaneous inflow of Atlantic or Arctic waters through the mouth of the fjord and runoff of fresh and turbid water from the glaciers result in strong horizontal gradients of temperature, salinity and light along the fjord's axis. All of these factors impact the phytoplankton assemblages (Keck *et al.* 1999; Piwosz *et al.* 2009). A summary of the relevant physical properties of the discussed fjords is provided in Table 2.

Table 2
 Characteristics of environmental and biological drivers in Hornsund
 and Kongsfjorden.

Driver	Hornsund	Kongsfjorden	Units	References
Fast ice	36% of the area (112 km ²)	3% of the area (6 km ²)		IO PAN unpublished data
Annual sea surface temperature range	-1.7 to 6	-1.4 to 12	°C	IO PAN data, Swerpel 1985; Walczowski and Piechura 2011
Salinity	34.2 (28–34.5)	34.4 (30–35)	PSU	IO PAN data
Spring incident PAR	18.1±17.8 to 30.7±19.0	21.4±14.0 to 29.9±7.0	Einstein·m ⁻² ·d ⁻¹	NASA GES DISC Mean for 2004–2014
Summer incident PAR	19.3±2.7 to 28.7±3.8	24.7±9.7 to 31.1±11.3	Einstein·m ⁻² ·d ⁻¹	NASA GES DISC Mean for 2004–2014
Euphotic zone (1% PAR)	9.56	16.21	m	IO PAN data, Sagan and Darecki unpublished data
Spring nutrient concentrations	Nitrates – no data Phosphates to 0.3 Silicate to 1.0	Nitrates to 11.3 Phosphates to 0.83 Silicate to 6.0	μmol·l ⁻¹	Hegseth and Tverberg 2013; Węśławski <i>et al.</i> 1988; Hodal <i>et al.</i> 2012
Summer nutrient concentrations	NO ₂ to 0.23 NO ₃ to 1.96 NH ₄ to 2.49 PO ₄ to 0.31 Silicate to 6.0	NO ₂ to 0.29 NO ₃ to 0.67 NH ₄ to 0.93 Silicate to 1.9	μmol·l ⁻¹	Eilertsen <i>et al.</i> 1989; Węśławski <i>et al.</i> 1988; Hodal <i>et al.</i> 2012; Zaborska <i>et al.</i> unpublished data
Pelagic euphotic zone (0–20 m depth)	277	188	km ²	www.iopan.gda.pl/game/visual
Volume of euphotic pelagic zone in summer	2.8	3	km ³	www.iopan.gda.pl/game/visual, Sagan and Darecki unpublished data
Area of seabed within euphotic zone (hard bottom %)	25(24%)	50 (30%)	km ²	www.iopan.gda.pl/game/visual

Sea ice. — Sea ice plays an important role in Arctic marine ecosystems during the formation of spring blooms of sea-ice associated algae (Hop *et al.* 2002; Arrigo *et al.* 2008; Leu *et al.* 2015). Through the melting period (late spring and summer), the margin of drifting ice pack with algae is an area of prolonged growth of sympagic autotrophs in areas of retreating sea ice. In autumn and winter, during the formation of fast ice in inner fjord basins, pelagic protists are incorporated into the ice; this, along with the advent of spring, initiates an ice algae bloom (Wiktor 2015).

In Hornsund, the fast ice starts to form in the innermost basins in late October and, with frequent breakups in the meantime, usually lasts until late May (Gorlich and Stepko 1992; Węśławski *et al.* 1993). Over the past decade, the fast ice extent has been limited to the innermost basins of Hornsund (personal observations). The sea ice pack, drifting with the Sørkapp Current from Storfjorden and the Barents Sea, occasionally enters Hornsund and may remain until July (Styszyńska and Kowalczyk 2007; Styszyńska and Rozwadowska 2008; Styszyńska 2009). The formation of fast ice was also a regular phenomenon in Kongsfjorden in the past, but in recent years, the fast ice has been forming only in the inner, most sheltered bay (Nicolaus *et al.* 2003; Hop *et al.* 2006; Gerland *et al.* 2008; Dieckmann *et al.* 2010; Berge *et al.* 2015), and compared to Hornsund, it covers a much smaller part of the fjord surface (Table 2).

Photosynthetically active radiation (PAR) and water transparency. — The total solar radiation at high latitudes due to the elevation angle of the Sun is negative for 104 days at 77°N (Hornsund) and 116 days at 79°N (Kongsfjorden), creating strong seasonality, with a few months of darkness (Fig. 2). Regarding the period from April to August, the photosynthetically active radiation doses are similar but slightly higher in Kongsfjorden (Table 2; Figs 3–4). Both fjords are characterized by strong underwater light gradients from the glacier fronts towards the fjord mouth. The substantial impact of glacier meltwater can result in high amounts of mineral suspension, restricting the depth of the euphotic zone in summer (Lydersen *et al.* 2014). During spring, when the glacier melt rate decreases, the main limiting factor is fast ice with snow on top. The snow has extremely high attenuation coefficients, causing a reduction in the irradiance in the top-most layer of water to 0.2–5% of incident PAR (Sakshaug *et al.* 1994). In summer, the euphotic zone thickness can range from 1 m to 35 m in both fjords (Halldal and Halldal 1973; Sagan *et al.* 1993; Bischof *et al.* 1998; Sagan and Darecki unpublished data; IOPAN data). On average, Hornsund has more turbid waters than Kongsfjorden in summer; hence, its euphotic zone is approximately 60% thinner (Table 2; Sagan and Darecki IOPAN data).

Nutrients. — The nutrients depleted during the spring bloom and summer are restored during the dark period through intensive vertical mixing, upwelling

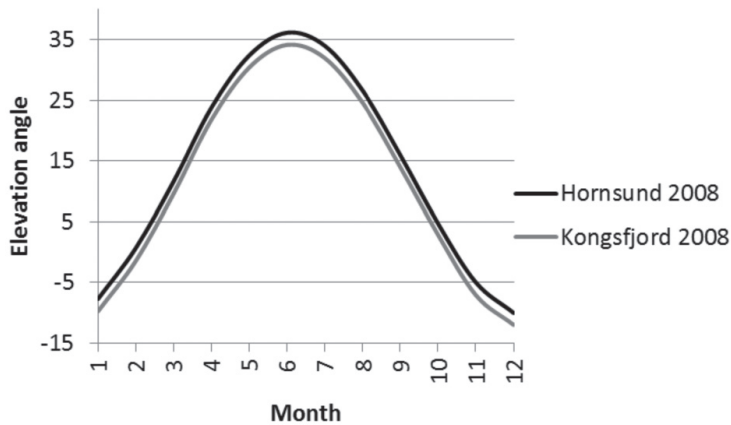


Fig. 2. Sun elevation angle for Hornsund and Kongsfjorden.

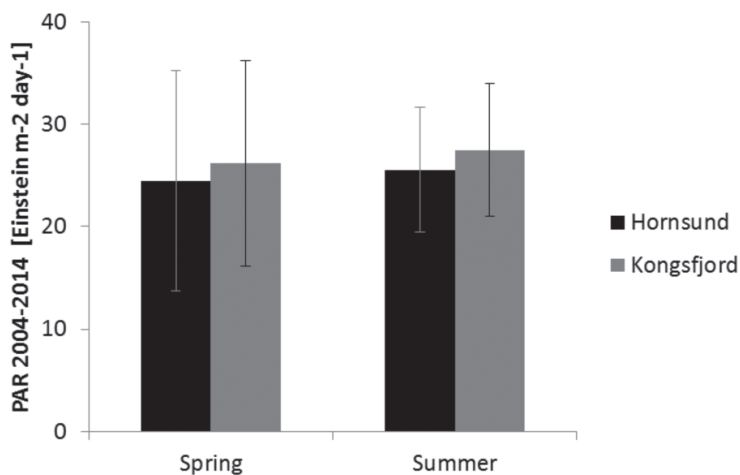


Fig. 3. Mean daily spring and summer PAR flux for the decade 2004–2014 in Hornsund and Kongsfjorden (NASA Goddard Earth Sciences Data and Information Services Center–GES DISC. Accessed data obtained 01 May 2015).

or convection at high latitudes (Olli *et al.* 2002). This process is magnified during winter because the pycnocline formed by glacier meltwater reduces the supply of nutrients from deeper water layers. There is apparently a strong local nutrient source — seabird colonies located by the seashore — as the biomass of seabirds in Hornsund is threefold higher compared to Kongsfjorden (Węśławski *et al.* 2009). This is reflected in the higher N content in Hornsund compared to Kongsfjorden (Table 2). Outside of ammonia, the nutrient concentrations are at similar levels in both fjords, with an apparent summer decrease. No depletion

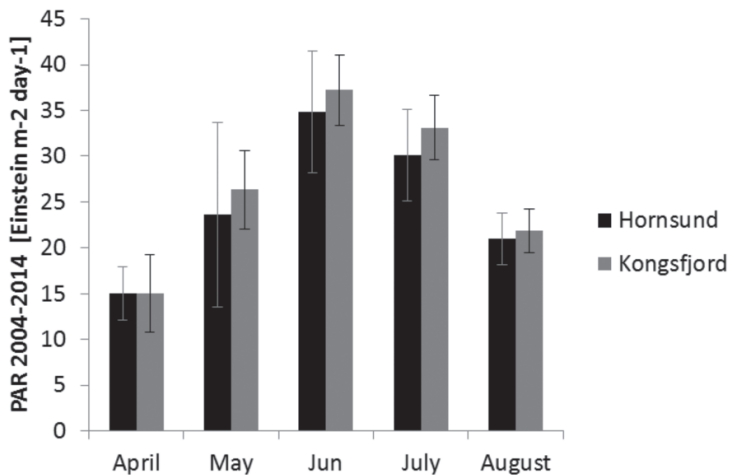


Fig. 4. Monthly average of PAR value for the decade 2004–2014 in Hornsund and Kongsfjorden (NASA Goddard Earth Sciences Data and Information Services Center–GES DISC. Accessed data obtained 1 August 2015).

of silicate in the fjords as a result of the strong freshwater runoff has been noted (Eilertsen *et al.* 1989; Wang *et al.* 2009; Hegseth and Tverberg 2013; IOPAN data; Table 2).

Primary producers

Microplankton. — Arctic planktonic protists account for over 2106 species (Poulin *et al.* 2011). Hop *et al.* (2006) reported a total of 148 taxa, of which Bacillariophyta (45%) and Dinophyta (11%) were the dominant groups in Kongsfjorden (Table 3). Protist biodiversity varies with the seasons, *e.g.*, for spring in Kongsfjorden, Hop *et al.* (2002) reported more than 60 microplankton taxa, most of which were diatoms, while Wiktor (1999) reported 35 taxa. Protist communities have been more frequently investigated during the summer season. Biodiversity seems to be higher in summer, and thus Keck *et al.* (1999) reported 50 taxa, Okolodkov *et al.* (2000) 40, Hop *et al.* (2002) more than 130, Wiktor and Wojciechowska (2005) 39, and Kubiszyn *et al.* (2014) 162. Most of the species are of Atlantic and cosmopolitan origin, whereas only 31 (21%) are considered to be Arctic or boreal-Arctic species (Hasle and von Quillfeldt 1996).

Common species in open water during May include the haptophyte *Phaeocystis pouchetii* (max. abundance 12^9 cells·m⁻³) and diatoms of the genera *Chaetoceros*, *Thalassiosira* and *Fragilariopsis* (Eilertsen *et al.* 1989; Hop *et al.* 2002; Hodal *et al.* 2012). Among the dinoflagellates, members of the genera

Table 3

Primary producers in Hornsund and Kongsfjorden. Range of microplankton biomass based on highest values recorded during reviewed studies.

Group/parameter	Hornsund	Kongsfjorden	References
Microplankton taxa number	84	148	Wiktor and Wojciechowska 2005; Okolodkov <i>et al.</i> 2000; Hop <i>et al.</i> 2002
Spring microplankton biomass range [mg C m ⁻³]	85.0	5–336	Wiktor 1999; Leu <i>et al.</i> 2006
Summer microplankton biomass range [mg C m ⁻³ , (mg C m ⁻²)]	100 (2100)	32 (1850–2770)	Piwosz <i>et al.</i> 2009; Iversen and Seuthe 2011
Ice algae species number	28*	23	* data from nearby Sassenfjord (Spitsbergen) Węśławski <i>et al.</i> 1993; Wiktor 1999
Microphytobenthos taxa number	no data	89	Woelfel <i>et al.</i> 2010
Microphytobenthos biomass [mg Chl <i>a</i> m ⁻²]	no data	317	Woelfel <i>et al.</i> 2010
Macroalgae biomass [tonne C]	1282	1936	calculated from Kruss <i>et al.</i> 2008; IOPAN unpublished data; hard bottom area after Duarte (unpublished data)
Macroalgae taxa number	49	76	Węśławski <i>et al.</i> 2010; Latała and Florczyk 1989; Hop <i>et al.</i> 2012; Fredriksen <i>et al.</i> 2014; Tatarek <i>et al.</i> 2012; http://www.iopan.gda.pl/~wiktor/macroalgae/index.html

Protoperidinium and *Gymnodinium* have been commonly found (Eilertsen *et al.* 1989; Wiktor 1999).

The dominance of microplankton species in summer assemblages in Kongsfjorden is variable across studies. Piwosz *et al.* (2009) reported a major contribution of diatoms to the phytoplankton biomass (especially *Pseudonitzschia seriata*), but Hop *et al.* (2002) and Okolodkov (2000) indicate the occasional occurrence of diatoms in Kongsfjorden summer assemblages and the domination of dinoflagellates (*Protoperidinium* spp., *Gymnodinium* spp. and *Gyrodinium* spp., max. cell no. $0.6 \cdot 10^9 \text{ m}^{-3}$), unidentified flagellates (<7 μm) and the chrysophyte *Dinobryon balticum* (max. $3.5 \cdot 10^9 \text{ cells m}^{-3}$). Further, in addition to the diatom

Pseudonitzschia seriata, Piwosz *et al.* (2009) indicated dinoflagellates as the second most important contributor to the total phytoplankton biomass in Kongsfjorden (autotrophic dinoflagellates, *e.g.*, *Scrippsiella trochoidea* and *Neoceratium arcticum*). They contributed over 60% of the biomass in the subsurface layers, in addition to *Gymnodinium arcticum* in some parts of the fjord. The maximal biomass values in Kongsfjorden vary from 15 g C m⁻² in spring to 7.9 g C m⁻² in summer (Table 3; Fig. 5).

In Hornsund, Wiktor and Wojciechowska (2005) identified 84 microplankton taxa (Table 3); however, Wiktor (1999) indicated poor assemblage composition in the water column under the fast ice and in adjacent areas. Eilertsen *et al.* (1989) recorded an overwhelming abundance of undetermined flagellates, *Phaeocystis puchetti* and diatoms (especially *Fragilariopsis* sp. and *Chaetoceros socialis*) in the spring community in Hornsund. In turn, Piwosz *et al.* (2009) recorded a great importance of diatom species in phytoplankton assemblages in summer, mostly *Chaetoceros socialis*, but also those from deeper water, below the euphotic zone, meaning that they were advected from other areas. Nanoflagellates were marked as the second most important contributor to the total phytoplankton biomass. Their contribution was >20% of the total phytoplankton biomass in some parts of the fjord and >80% of the total protist biomass. The biomass of autotrophic dinoflagellates contributed to no more than 22%, while Cryptomonads contributed up to 40% of the phytoplankton biomass. There is also a characteristic summer horizontal gradient in the microplankton distribution within the fjord, with flagellates and mixotrophs dominating the turbid waters of the inner basins, while the open outer fjord part is inhabited by larger-sized diatoms and dinoflagellates (Piwosz *et al.* 2009). The highest reported biomass of microplankton ranged from 2.3 g C m⁻² in spring (GAME project data) to 2.1 g C m⁻² in summer (Piwosz *et al.* 2009; Table 3) and dropped down to single cells observed during the winter dark season (Węśławski *et al.* 1990; Wiktor 1999; Berge *et al.* 2015; Błachowiak-Samołyk *et al.* 2015).

Grazing on microplankton in fjords increases from spring to summer, when the new generation of local herbivorous copepods grows (Kwaśniewski *et al.* 2010) and large herbivores, such as krill, are advected from the shelf area (Buchholz *et al.* 2010).

Ice algae. — The first algal bloom in Arctic ice-covered marine areas occurs in the bottom layer of the sea ice. This community develops through three distinct phases in the transition from winter to spring, which is described by Leu *et al.* (2015). A total of 1027 sympagic protist taxa have been reported from four Pan-Arctic regions (Syvertsen 1991; Poulin *et al.* 2011). The biomass of ice algae communities is almost exclusively dominated by the genera *Nitzschia*, *Navicula*, *Pauliella* and *Fragilariopsis* (Gosselin *et al.* 1997; Riedel *et al.* 2008; Leu *et al.*

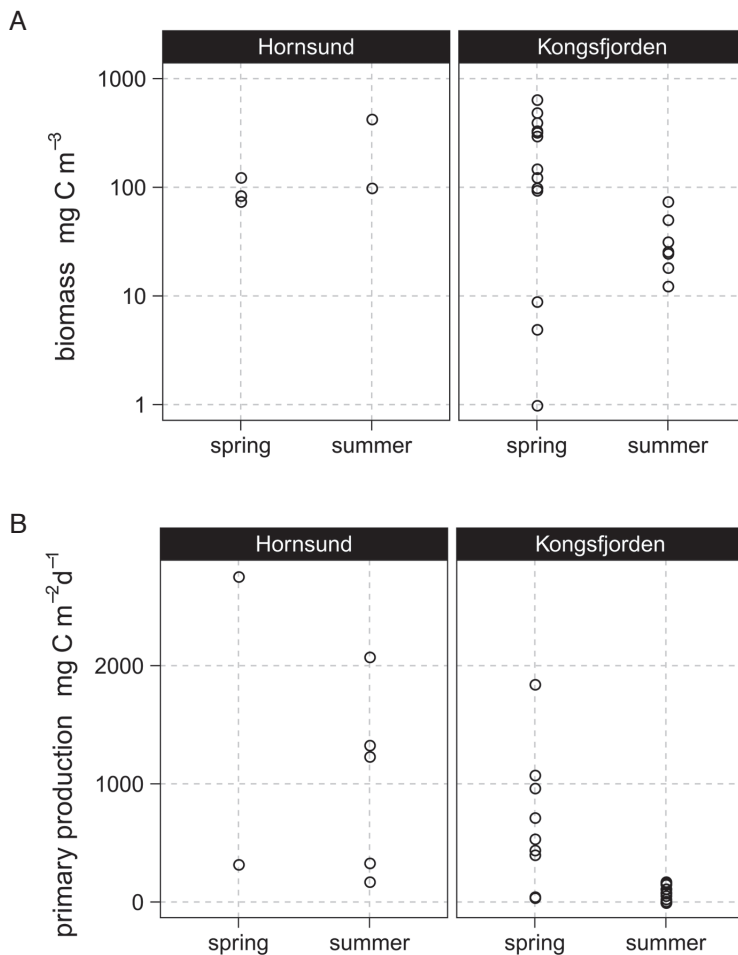


Fig. 5. Range of daily values of biomass (A) and primary production (B) reported across studies during spring and summer in Kongsfjorden and Hornsund (IO PAN data).

2015), which often account for >90% of the total algal cell abundance (Smith and Sakshaug 1990; von Quillfeldt 2000; Róžańska *et al.* 2009; Wiktor 2015). The occasional advection of true ice algae from the ice pack is possible in fjords (Wiktor 2015); however, both the diversity and biomass of ice-associated algae in the examined fjords are low. The fast ice contributes little to the diversity and biomass of ice algae; however, several typical ice-associated species have been noted for the Spitsbergen fjords (Węśławski *et al.* 1993; Wiktor 1999). There are no specific fast ice-related grazers in the fjords, and true sympagic fauna feeding on ice algae rarely enter the examined fjords (*op. cit.*).

Microphytobenthos. — Benthic microalgae occur from the upper littoral (splash zone) to the shallow sublittoral, on soft sediment and hard substrates and on large algae. They contribute to the coastal ecosystem not only as primary producers but also as sediment stabilizers (Decho 2000; Wiktor unpublished data). The microphytobenthos also has an important ecological role as a food source for ciliates, meiofauna (mainly Nematoda, Kinorhyncha and Harpacticoida) and some macrofauna (small species of gastropods and amphipods). Although the importance of benthic microalgae has been recognized and studied for decades around the globe, the role of the polar microphytobenthos, except that of Greenland (Rysgaard *et al.* 1999; Glud *et al.* 2007), has been given much less attention. Data from Spitsbergen were collected by Woelfel *et al.* (2010) and Wiktor (unpublished data); in Kongsfjorden, from 29 to 89 species were reported, with biomass attaining 317 mg Chl *a* m² (Woelfel *et al.* 2010; Sevilgen unpublished data).

Macroalgae. — Arctic macroalgae are abundant and diverse, with 194 species from Svalbard (Gulliksen *et al.* 1999) and 76 species from Kongsfjorden having been recorded (Fredriksen *et al.* 2014). In Hornsund, 49 species have been noted (Table 3). Their occurrence ranges from the upper littoral to the shallow sublittoral, limited by the euphotic zone (kelp to some 25 m and coralline algae to 50 m depth). There are reports of the deep occurrence of macrophytes in Kongsfjorden (Meyer and Sweetman 2015); however, this is likely to be the effect of the transport of stones with attached algae by sea currents and gravity rather than a natural phenomenon. There is also a consensus that macrophytes are increasing in biomass and vertical occurrence with diminishing ice cover and increasing temperature (Węśławski *et al.* 2010; Hop *et al.* 2012).

Tatarek *et al.* (2012) showed that macroalgae (mostly kelps) within a 0.65 km² area in the euphotic zone are potentially capable of reaching 988 T of biomass in Hornsund. A quite similar situation was found in Kongsfjorden, where Kruss *et al.* (2008) revealed that in a plot of 1.04 km² in the euphotic zone, brown algae are potentially capable of gaining 1825 T of biomass (Table 3). Duarte (unpublished data) assumes that macrophytes in Kongsfjorden occur on 30% of the bottom area restricted by the 5–25 m depth contour in the outer basin and 10% in the inner basin—these percentages reflect the share of hard bottom. The difference (20%) between these two fjords in biomass value may be explained by the physical conditions occurring in these fjords, such as less ice scouring and more extensive hard bottom shallow areas (Węśławski *et al.* 2010; Drewnik *et al.* 2016; Bartsch *et al.* 2016; Moy unpublished data).

Seaweeds are important not only as primary producers that supply a great amount of fixed carbon to fjords but also because they provide a substrate for benthic organisms (Lippert *et al.* 2001; Włodarska-Kowalczyk *et al.* 2009). Grazers living on macroalgae are rare in Spitsbergen, and the only confirmed

species is the sea urchin *Strongylocentrotus droebachiensis*. On the other hand, decaying macroalgal detritus is an important component of the sublittoral benthic food web in both fjords (Legeżyńska *et al.* 2014; Renaud *et al.* 2015).

Results

Primary production: measurements and estimates. — A summary of pelagic primary production can be found in Table 4. The data are presented as ranges of the highest values reported in the studies in Table 1. To standardize the pelagic biomass data as the biomass of organic carbon (Fig. 5a), a conversion from Chl *a* to C was applied (with the assumption of a 1:50 ratio of Chl *a* to C, adopted from Wiktor 1999). The annual pelagic primary production calculated

Table 4

Range of spring and summer Chl *a* and pelagic primary production and estimates of primary production in (H) Hornsund and (K) Kongsfjorden.

Driver	Hornsund	Kongsfjorden	Units	References
Spring Chlorophyll <i>a</i> range	1.5–2.5	0.18–13.0	mg Chl <i>a</i> m ⁻³	H – Eilertsen <i>et al.</i> 1989; Węśławski <i>et al.</i> 1988 K – Iversen and Seuthe 2011; Hegseth and Tverberg 2013
Summer Chlorophyll <i>a</i> range	8.61	0.25–1.5	mg Chl <i>a</i> m ⁻³	H – Piwosz <i>et al.</i> 2009 K – Eilertsen <i>et al.</i> 1990; Piwosz <i>et al.</i> 2009
Pelagic spring primary production range	0.32–2.77 0.43–0.32*	9.72–44.40 2.23*	g C m ⁻² ·d ⁻¹ g C m ⁻³ ·d ⁻¹ *	H – Eilertsen <i>et al.</i> 1989; Eilertsen <i>et al.</i> 1989* K – Iversen and Seuthe 2011; Hodal <i>et al.</i> 2012; Hodal <i>et al.</i> 2012*
Pelagic summer primary production range	2.08 0.15*	0.03–0.169 0.003–0.019*	g C m ⁻² ·d ⁻¹ g C m ⁻³ ·d ⁻¹ *	H – Piwosz <i>et al.</i> 2009; Eilertsen <i>et al.</i> 1989*; K – Eilertsen <i>et al.</i> 1989; Eilertsen <i>et al.</i> 1989*; Piwosz <i>et al.</i> 2009*
Microplankton annual primary production range	48.07	216.43	g C m ⁻² ·y ⁻¹	calculated from reviewed data
Macroalgae annual primary production	2.0–20*	2.0–20	g C m ⁻² ·y ⁻¹	Gómez <i>et al.</i> 2009; adopted from Kongsfjorden*
Microphytobenthos	No data	2–14	g C m ⁻² ·y ⁻¹	Woelfel <i>et al.</i> 2012

basing on daily primary production values is shown in Fig. 5b, using data obtained from the investigations reported in Table 1. For this purpose, the data were standardized from hour⁻¹ to day⁻¹ (24 h). The annual carbon production was roughly estimated with the assumption of a 180-day growing season in the Arctic. The growth season begins in spring (April) and lasts until September (*e.g.*, Iversen *et al.* 2011). Thus, in calculations we assumed 60 days of spring and 120 days of summer (Table 4). Values were calculated for the euphotic layer of each fiord (Fig. 6). The mean euphotic zone (1% PAR) depth in summer was taken from Sagan and Darecki (unpublished data) as 9 m in Hornsund and 16 m in Kongsfjorden. According to this assumption, the total volume ranged from 2.8 to 3 km³, respectively. While these values were used for the estimates of annual primary production of the phytobenthos (macroalgae and microphytobenthos) specific to the surface of the bottom of the euphotic zone in each fjord, the euphotic area of the seabed (0–20 m depth) was taken as 25 km² in Hornsund and 50 km² in Kongsfjorden (Table 2). Values of microphytobenthic and macrophytobenthic primary production were adopted from the measurements and estimates shown below.

Microphytobenthos. — Woelfel *et al.* (2010) showed that the microalgae in a research area of 3.7 km² of sandy and muddy substrate in the euphotic zone are potentially capable of reaching 76–1900 kg C y⁻¹ of biomass and that

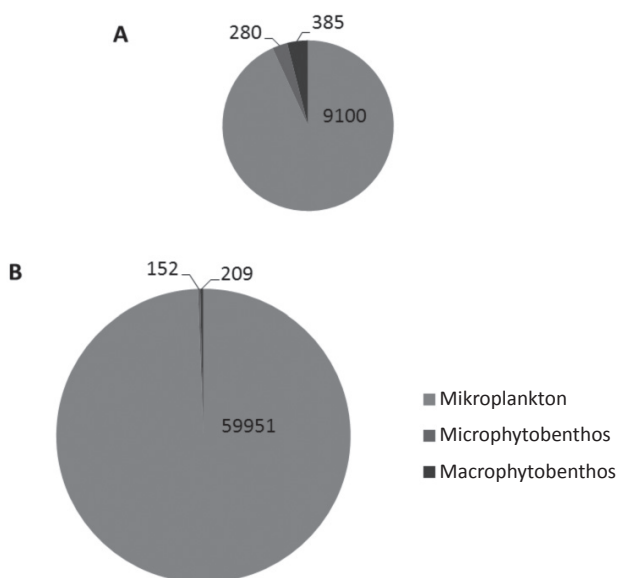


Fig. 6. Organic carbon production [tonne C y⁻¹] in the euphotic zone of Kongsfjorden (A) and Hornsund (B).

the summer period of primary production provides $19 \text{ g C m}^{-2}\cdot\text{y}^{-1}$ (Table 3). The estimates calculated by Glud and Rysgaard (2007) in Greenland during the summer season showed that the microbenthic community of Young Sound, which is dominated by diatoms, accounts for up to 40% of the total benthic primary productivity, with a mean production rate of $10 \text{ g C m}^{-2}\cdot\text{y}^{-1}$ (Rysgaard *et al.* 1999).

Macrophytes. — Seaweeds can reach high primary productivity in some areas, which can be comparable to or even higher than that of phytoplankton (Gómez *et al.* 2009). Arctic macroalgal primary productivity reaches up to $20 \text{ g C m}^{-2}\cdot\text{y}^{-1}$ (estimated for the brown algal species *Laminaria solidungula*). However, depending on the species, it may be only $1\text{--}2 \text{ g C m}^{-2}\cdot\text{y}^{-1}$ (for *Saccharina latissima*, Gómez *et al.* 2009). Benthic micro- and macroalgae in Arctic coastal areas may potentially provide 28% and 13% of the net primary production, respectively (Gómez *et al.* 2009).

Benthic macroalgae accounted for approximately 20% of the local net primary production in Greenland's Young Sound (Glud and Rysgaard 2007). For the purposes of this paper, we assume, following Gómez *et al.* (2009), that the macroalgal primary production in Hornsund and Kongsfjorden may range from 2.0 to $20 \text{ g C m}^{-2}\cdot\text{y}^{-1}$ and that the production rate depends on the surface of the seabed in the euphotic zone.

Microplankton. — With $48.07\text{--}216.43 \text{ g C m}^{-2}\cdot\text{y}^{-1}$ in Hornsund and Kongsfjorden (Table 4), the primary production and Chl *a* concentration of the microplankton seem to be higher than that in other Svalbard fjords, *e.g.*, Rijpfjorden (Leu *et al.* 2011), which is located further north ($>80^\circ\text{N}$) and is strongly influenced by the Arctic Ocean. Waters directly around the Svalbard archipelago are also less productive than those in the West Spitsbergen fjords. The estimated daily production in the examined fjords is similar to the daily production along the Barents Sea Polar Front (Owrid *et al.* 2000).

Production rates, biomass and Chl *a* concentrations in the High Arctic are restricted and inversely correlated to the ice cover, light attenuation, surface mixed layer depth and total mesozooplankton biomass (Gosselin *et al.* 1997; Owrid *et al.* 2000).

Production in the Bering Sea and Chukchi Sea estimating from 230 to $>400 \text{ g C m}^{-2}\cdot\text{y}^{-1}$ (Sakshaug 2004) or even $576\text{--}720 \text{ g C m}^{-2}\cdot\text{y}^{-1}$ (Hansell *et al.* 1993) is considered to be the highest in the Arctic and is significantly higher than in Hornsund and Kongsfjorden. The variation in primary production is well known in the Arctic and is mostly attributed to differences in water masses, ice presence, and nutrient concentrations (Hansell and Goering 1990; Springer and McRoy 1993; Springer unpublished data). The statement about

different annual primary production in the two fjords is supported by sediment data by Zaborska (unpublished data) and sediment trap data from Grzelak and Głuchowska (unpublished data), who demonstrate higher amounts of organic carbon falling to the Hornsund seabed compared to Kongsfjorden.

Discussion

The taxonomic structure of the phytoplankton assemblages in the two fjords demonstrated differences between the associations (Wiktor and Wojciechowska 2005), which may be an effect of the lower number of protist investigations in Hornsund. The expected number of taxa might be similar and slightly modified by macroscale hydrological conditions. Hasle and von Quillfeldt (1996) emphasized a high contribution of Atlantic species in Kongsfjorden phytoplankton assemblages. Phytoplankton communities inhabiting West Spitsbergen fjords appear to be more diverse in terms of taxonomic composition than those in open marine waters surrounding the archipelago (Owrid *et al.* 2000; Hegseth and Sundfjord 2008). Fjord associations are also substantially different from the diatom-dominated Margina Ice Zone (MIZ) blooming assemblages known in the Barents Sea (Olli *et al.* 2002; Ratkova and Wassmann 2002; Olli *et al.* 2007), other Arctic shelf areas (Sakshaug 2004), polynyas (Lovejoy *et al.* 2002), the Central Arctic Basin (where assemblages are dominated by relatively small and often unidentified flagellates), or the coastal waters of western Greenland (Nielsen and Hansen 1999). Kongsfjorden is more diverse in microplankton and macrophytobenthic species than Hornsund due to the advection of Atlantic Waters. The more extensive fast ice in Hornsund does not allow ice species to cope with the diversity of the warmer site.

There is a difference in the seasonal Chl *a* concentration between the two fjords (higher in spring and lower in summer in Hornsund compared to Kongsfjorden) (Fig. 5a). In general, Hornsund has higher microplankton primary production rates per unit area and over the whole year, despite the larger volume of the euphotic zone in Kongsfjorden (Fig. 5b). This can be caused by one or a combination of three reasons: lower grazing pressure in Hornsund, higher nutrient supply in Hornsund (seabird colonies, nutrient-rich coastal waters, shallower area with easy mixing), or low nutrient concentrations in the Atlantic Waters of Kongsfjorden (depleted on the way along the West Spitsbergen Currents, too deep to mix easily). In the present situation, the “warmer” fjord shows lower production compared to the colder coastal waters of Hornsund (Fig. 6). The different proportions of autotrophs in the net primary production show that Kongsfjorden experiences an important contribution from non-pelagic autotrophs, while in Hornsund, the share of benthic species is less visible (Fig. 6).

Primary production in West Spitsbergen fjords is lower than in areas of high productivity, *e.g.*, the Barents Sea, and comparable to other high Arctic fjords. Of the two fjords compared, Hornsund is shallower, less connected with the Atlantic water inflow from the shelf and more ice covered compared to Kongsfjorden. The irradiance, sea surface temperature, and dynamics of the two fjords are comparable. Hornsund is poorer in autotrophic species number. Kongsfjorden on one hand receives more species and biomass from the Atlantic Waters inflow; on the other hand, increased glacial melt and increased turbidity in the inner basins reduce the performance of marine autotrophs. Hornsund will soon become a proper “sund” when the ice barrier bordering it from Storfjorden collapses (Głowacki pers. comm.). This shall increase the presence of coastal, cold water in Hornsund and cause consequent isolation from the warmer shelf waters. It is likely that Hornsund will remain more “local” and cold compared to the atlantification of Kongsfjorden.

Acknowledgements. — This publication was financed by funds from the Leading National Research Centre (KNOW) received by the Centre for Polar Studies for the period 2014–2018 and project NCN (National Research Center in Poland): GAME (Growing of the Arctic Marine Ecosystem) – DEC-2012/04/A/NZ8/00661. The research leading to these results has received funding from the Polish-Norwegian Research Programme operated by the National Centre for Research and Development under the Norwegian Financial Mechanism 2009–2014 in the frame of Project Contract No POL-NOR/199377/91/2014 (GLAERE).

References

- ARRIGO K.R., VAN DIJKEN G. and PABI S. 2008. Impact of a shrinking Arctic ice cover on marine primary production. *Geophysical Research Letters* 35: L19602.
- BARTSCH I., PAAR M., FREDRIKSEN S., SCHWANITZ M., DANIEL K., HOP H. and WIENCKE CH. 2016. Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biology* 39: 2021.
- BERGE J., RENAUD P.E., DARNIS G., COTTIER F., LAST K., GABRIELSEN T.M., JOHNSEN G., SEUTHE L., WĘSŁAWSKI J.M., LEU E., MOLINE M., NAHRGANG J., SØREIDE J.E., VARPE Ø., LØNNE O.J., DAASE M. and FALK-PETERSEN S. 2015. In the dark: A review of ecosystem processes during the Arctic polar Night. *Progress in Oceanography* 139: 258–271.
- BISCHOF K., HANELT D., TÜG H., KARSTEN U., BROUWER P.E. and WIENCKE C. 1998. Acclimation of brown algal photosynthesis to ultraviolet radiation in Arctic coastal waters (Spitsbergen, Norway). *Polar Biology* 20: 388–395.
- BŁACHOWIAK-SAMOŁYK K., WIKTOR J.M., HEGSETH E.N., WOLD A., FALK-PETERSEN S. and KUBISZYN A.M. 2015. Winter Tales: the dark side of planktonic life. *Polar Biology* 38: 23–36.
- BUCHHOLZ F., BUCHHOLZ C. and WĘSŁAWSKI J.M. 2010. Ten years after: krill as indicator of changes in the macro-zooplankton communities of two Arctic fjords. *Polar Biology* 33: 101–113.
- CISEWSKI B., BUDÉUS G. and KRAUSE G. 2003. Absolute transport estimates of total and individual water masses in the northern Greenland Sea derived from hydrographic and acoustic Dop-

- pler current profiler measurements. *Journal of Geophysical Research: Oceans* (1978–2012): 108(C9).
- COTTIER F., TVERBERG V., INALL M., SVENDSEN H., NIELSEN F. and GRIFFITHS C. 2005. Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. *Journal of Geophysical Research: Oceans* (1978–2012): 110(C12).
- DECHO A.W. 2000. Microbial biofilms in intertidal systems: an overview. *Coastal Shelf Research* 20: 1257–1273.
- DIECKMANN G., NEHRKE G., UHLIG C., GÖTTLICHER J., GERLAND S., GRANSKOG M.A., and THOMAS D.N. 2010. Ikaite ($\text{CaCO}_3 \cdot 6\text{H}_2\text{O}$) discovered in Arctic sea ice. *The Cryosphere* 4: 227–230.
- DIGBY P.S. 1961. The vertical distribution and movements of marine plankton under midnight-sun conditions in Spitsbergen. *The Journal of Animal Ecology* 30: 9–25.
- EILERTSEN H.C., TAASEN J.P. and WĘSŁAWSKI J.M. 1989. Phytoplankton studies in the fjords of West Spitsbergen: physical environment and production in spring and summer. *Journal of Plankton Research* 11: 1245–1260.
- FALK-PETERSEN S., HOP H., BUDGELL W.P., HEGSETH E.N., KORSNES R., LØYNING T.B., ØRBÆK J.B., KAWAMURA T. and SHIRASAWA K. 2000. Physical and ecological processes in the marginal ice zone of the northern Barents Sea during the summer melt period. *Journal of Marine Systems* 27: 131–159.
- FERNÁNDEZ-MÉNDEZ M., KATLEIN C., RABEL B., NICOLAUS M., PEEKEN I., BAKKER K., FLORE H. and BOETIUS H. 2015. Photosynthetic production in the Central Arctic during the record sea-ice minimum in 2012. *Biogeosciences Discussions* 12: 2897–2945.
- FLORCZYK I. and LATAŁA A. 1989. The phytobenthos of the Hornsund fjord, SW Spitsbergen. *Polar Research* 7: 29–41.
- FREDRIKSEN S., BARTSCH I. and WIENCKE CH. 2014. New additions to the benthic marine flora of Kongsfjorden, western Svalbard, and comparison between 1996/1998 and 2012/2013. *Botanica Marina* 57: 203–216.
- GEIDER R.J., DELUCIA E.H., FALKOWSKI P.G., FINZI A.C., GRIME J.P., GRACE J., KANA T.M., LA ROCHE J., LONG S.P., OSBORN B.A., PLATT T., PRENTICE I.C., RAVEN J.A., SCHLESINGER W.H., SMETACEK V., STUART V., SATHYENDRANATH S., THOMAS R.B., VOGELMANN T.C., WILLIAMS P. and WOODWARD F.I. 2001. Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biology* 7: 849–882.
- GERLAND S., RENNER A.H.H., GODTLIEBSEN F., DIVINE D. and LØYNING T.B. 2008. Decrease of sea ice thickness at Hopen, Barents Sea, during 1966–2007. *Geophysical Research Letters* 35: L06501.
- GLUD R. and RYSGAARD S. 2007. The annual carbon budget of Young Sound, NE Greenland. In: S. Rysgaard and R.N. Glud (eds), *Carbon Cycling in Arctic Marine Ecosystems: Case Study Young Sound*. Meddelelser om Grønland, Bioscience 58: 193–203.
- GÓMEZ I., WULF A., ROLEDA M.Y., HUOVINEN P., KARSTEN U., QUARTINO M.L., DUNTON K. and WIENCKE C. 2009. Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. *Botanica Marina* 52: 593–608.
- GORLICH K.A. and STEPKO W. 1992. Hydrological phenomena related to sea ice formation and presence in Hornsund, Spitsbergen. In: K.W. Opaliński and R.Z. Klekowski (eds), *Landscape, Life World and Man in High Arctic*. Instytut Ekologii, Polska Akademia Nauk, Warszawa: 83–92.
- GOSSELIN M., LEVASSEUR M., WHEELER P.A., HORNER R.A. and BOOTH B.C. 1997. New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep-Sea Research II* 44: 1623–1644.

- GULLIKSEN B., PALERUD R., BRATTEGARD T. and SNELI J. (eds) 1999. Distribution of marine benthic macro-organisms at Svalbard (including Bear Island) and Jan Mayen. *Research Report for Directorate for Nature Management* 4: 148.
- HALLDAL P. and HALLDAL K. 1973. Phytoplankton, chlorophyll, and submarine light conditions in Kings Bay, Spitsbergen, July 1971. *Norwegian Journal of Botany* 20: 99–108.
- HANSELL D.A. and GOERING J.J. 1990. Pelagic nitrogen flux in the northern Bering Sea. *Continental Shelf Research* 10: 501–519.
- HANSELL D.A., WHITLEDGE T.E. and GOERING J.J. 1993. Patterns of nitrate utilization and new production over the Bering-Chukchi shelf. *Continental Shelf Research* 13: 601–627.
- HASLE G.R. and VON QUILLFELDT C.H. 1996. A catalogue of Svalbard plants, fungi, algae and cyanobacteria. Part 8. Marine microalgae. *Skrifter–Norsk Polarinstitut* 198: 375–382.
- HEGSETH E.N. 1992. Sub-ice algal assemblages of the Barents Sea: species composition, chemical composition, and growth rates. *Polar Biology* 12: 485–496.
- HEGSETH E.N. and SUNDFJORD A. 2008. Intrusion and blooming of Atlantic phytoplankton species in the high Arctic. *Journal of Marine Systems* 74: 108–119.
- HEGSETH E.N. and TVERBERG V. 2013. Effect of Atlantic water inflow on timing of the phytoplankton spring bloom in a high Arctic fjord (Kongsfjorden, Svalbard). *Journal of Marine Systems* 113: 94–105.
- HILL V.J., MATRAI P.A., OLSON E., SUTTLES S., STEELE M., CODISPOTI L.A. and ZIMMERMAN R.C. 2013. Synthesis of integrated primary production in the Arctic Ocean: II. In situ and remotely sensed estimates. *Progress in Oceanography* 110: 107–125.
- HODAL H., FALK-PETERSEN S., HOP H., KRISTIANSEN S. and REIGSTAD M. 2012. Spring bloom dynamics in Kongsfjorden, Svalbard: nutrients, phytoplankton, protozoans and primary production. *Polar Biology* 35: 191–203.
- HOP H., PEARSON T., HEGSETH E.N., M. KOVACS K.M., WIENCKE C., KWAŚNIEWSKI S., EIANE K., MEHLUM F., GULLIKSEN B., WŁODARSKA-KOWALCZUK M., LYDERSEN C., WĘSŁAWSKI J.M., COCHRANE S., GABRIELSEN G.W., LEAKEY R.J.G., LØNNE O.J., ZAJĄCZKOWSKI M., FALK-PETERSEN S., KENDALL M., WÄNGBERG S-Å., KAI BISCHOF K., VORONKOV A.Y., KOVALTCHOUK N.A., WIKTOR J.M., POLTERMANN M., DI PRISCO G., PAPUCCI C. and GERLAND S. 2002. The marine ecosystem of Kongsfjorden, Svalbard. *Polar Research* 21: 167–208.
- HOP H., FALK-PETERSEN S., SVENDSEN H., KWAŚNIEWSKI S., PAVLOV V., PAVLOVA O. and SØREIDE J.E. 2006. Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. *Progress in Oceanography* 71: 182–231.
- HOP H., WIENCKE C., VÖGELE B. and KOVALTCHOUK N.A. 2012. Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard. *Botanica Marina* 55: 399–414.
- IVERSEN K.R. and SEUTHE L. 2011. Seasonal microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): I. Heterotrophic bacteria, picoplankton and nanoflagellates. *Polar Biology* 34: 731–749.
- KECK A. 1999. West Spitsbergen Fjords (Svalbard, Norwegian Arctic): Physical Settings and Sedimentation. *The Finnish Environment* 263: 58–68.
- KECK A., WIKTOR J.M., HAPTER R. and NILSEN R. 1999. Phytoplankton assemblages related to physical gradients in an Arctic glacier-fed fjord in summer. *ICES Journal of Marine Science* 56: 203–214.
- KRUSS A., BLONDEL P., TĘGOWSKI J., WIKTOR J.M. and TATAREK A. 2008. Estimation of macrophytes using single-beam and multibeam echosounding for environmental monitoring of Arctic fjords (Kongsfjord, West Svalbard Island). *Journal of the Acoustical Society of America* 123: 3213–3213.

- KUBISZYN A.M., PIWOSZ K. and WIKTOR J.M. 2014. The effect of inter-annual Atlantic water inflow variability on the planktonic protist community structure in the West Spitsbergen waters during the summer. *Journal of Plankton Research* 36: 1190–1203.
- KWAŚNIEWSKI S., GŁUCHOWSKA M., JAKUBAS D., WOJCZULANIS-JAKUBAS K., WALKUSZ W., KARNOWSKY N., BŁACHOWIAK-SAMOŁYK K., CIESEK M. and STEMPNIEWICZ L. 2010. The impact of different hydrographic conditions and zooplankton communities on provisioning Little Auks along the West coast of Spitsbergen. *Progress in Oceanography* 87: 72–82.
- LEGEZYŃSKA J., KĘDRA M. and WALKUSZ W. 2014. Identifying trophic relationships within the high Arctic benthic community: how much can fatty acids tell? *Marine Biology* 161: 821–836.
- LEU E., FALK-PETERSEN S., KWAŚNIEWSKI S., WULFF A., EDWARDSSEN K. and HESSEN D.O. 2006. Fatty acid dynamics during the spring bloom in a High Arctic fjord: importance of abiotic factors versus community changes. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 2760–2779.
- LEU E., MUNDY C.J., ASSMY P., CAMPBELL K., GABRIELSEN T.M., GOSSELIN M.T., JUUL-PEDERSEN T. and GRADINGER R. 2015. Arctic spring awakening – Steering principles behind the phenology of vernal ice algal blooms. *Progress in Oceanography* 139: 151–170.
- LEU E., SØREIDE J.E., HESSEN D.O., FALK-PETERSEN S. and BERGE J. 2011. Consequences of changing sea – ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. *Progress in Oceanography* 90: 18–32.
- LIPPERT H., IKEN K., RACHOR E. and WIENCKE CH. 2001. Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). *Polar Biology* 24: 512–522.
- LOENG H., BRANDER K., CARMACK K.E., DENISENKO S., DRINKWATER K., HANSEN B., KOVACS K., LIVINGSTON P., MCLAUGHLIN F. and SAKSHAUG E. 2005. Marine Systems: Arctic Climate Impact Assessment: An Assessment of Consequences of Climate Variability and Change and the Effects of Increased UV in the Arctic Region. *Arctic Climate Impact Assessment*: 439–538.
- LOVEJOY C., LEGENDRE L. and PRICE N.M. 2002. Prolonged diatom blooms and microbial food web dynamics: experimental results from an Arctic polynya. *Aquatic Microbial Ecology* 29: 267–278.
- LYDERSEN C., ASSMY P., FALK-PETERSEN S., KOHLER J., KOVACS K.M., REIGSTAD M., STEEN H., STRØM H., SUNDFJORD A., VARPE Ø., WALCZOWSKI W., WĘŚLAWSKI J.M. and ZAJĄCZKOWSKI M. 2014. The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. *Journal of Marine Systems* 129: 452–471.
- MATRAI P.A., OLSON E., SUTTLES S., HILL V., CODISPOTI L.A., LIGHT B. and STEELE M. 2013. Synthesis of primary production in the Arctic Ocean: I. Surface waters, 1954–2007. *Progress in Oceanography* 110: 93–106.
- MEYER K.S. and SWEETMAN A.K. 2015. Observation of a living macroalga at 166 m in a high Arctic fjord. *Marine Biodiversity Records* 8: e58–61.
- NICOLAUS M., HAAS C. and BAREISS J. 2003. Observations of superimposed ice formation at melt-onset on fast ice on Kongsfjorden, Svalbard. *Physics and Chemistry of the Earth* 28: 1241–1248.
- NIELSEN T.G. and HANSEN B.W. 1999. Plankton community structure and carbon cycling off the western coast of Greenland during stratified summer situation. I. Hydrography, phytoplankton and bacterioplankton. *Aquatic Microbial Ecology* 16: 205–216.
- OKOŁODKOV Y.B., HAPTER R. and SEMOVSKI S.V. 2000. Phytoplankton in Kongsfjorden, Spitsbergen, July 1996. *Sarsia* 85: 1–8.
- OLLI K., WASSMANN P., REIGSTAD M., RATKOVA T.N., ARASHKEVICH E., PASTERNAK A., MATRAI P.A., KNULST J., TRANVIK L., KLASIS R. and JACOBSEN A. 2007. The fate of production in the central Arctic Ocean—top—down regulation by zooplankton expatriates? *Progress in Oceanography* 72: 84–113.

- OWRID G., SOCAL G., CIVITARESE G., LUCHETTA A., WIKTOR J.M., NÖTHIG E.M., ANDREASSEN I., SCHAUER U. and STRASS V. 2000. Spatial variability of phytoplankton, nutrients and new production estimates in the waters around Svalbard. *Polar Research* 19: 155–171.
- PABI S., VAN DIJKEN G.L. and ARRIGO K.R. 2008. Primary production in the Arctic Ocean, 1998–2006. *Journal of Geophysical Research* 113: C08005.
- PIWOSZ K., WALKUSZ W., HAPTER R., WIECZOREK P., HOP H. and WIKTOR J.M. 2009. Comparison of productivity and phytoplankton in a warm (Kongsfjorden) and a cold (Hornsund) Spitsbergen fjord in mid–summer 2002. *Polar Biology* 32: 549–559.
- POPOVA E.E., YOOL A., COWARD A.C., DUPONT F., DEAL C., ELLIOTT S., HUNKE E., JIN M., STEELE M. and ZHANG J. 2012. What controls primary production in the Arctic Ocean? Results from an intercomparison of five general circulation models with biogeochemistry. *Journal of Geophysical Research: Oceans (1978–2012)*: 117(C8).
- POULIN M., DAUGBJERG N., GRADINGER R., ILYASH L., RATKOVA T. and VON QUILLFELDT C. 2011. The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: A first-attempt assessment. *Marine Biodiversity* 41: 13–28.
- RATKOVA T.N. and WASSMANN P. 2002. Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea. *Journal of Marine Systems* 38: 47–75.
- RENAUD P., LOKKEN T.S., JORGENSEN L.L., BERGE J. and JOHNSON B.J. 2015. Macroalgal detritus and food–web subsidies along an Arctic fjord depth–gradient. *Frontiers in Marine Science* 2: 31.
- RIEDEL A., MICHEL C., GOSSELIN M. and LEBLANC B. 2008. Winter–spring dynamics in sea ice carbon cycling in the coastal Arctic Ocean. *Journal of Marine Systems* 74: 918–932.
- RÓZAŃSKA M., GOSSELIN M., POULIN M., WIKTOR J.M. and MICHEL C. 2009. Influence of environmental factors on the development of bottom ice protist communities during the winter–spring transition. *Marine Ecology Progress Series* 386: 43–59.
- RYSGAARD S., NIELSEN T.G. and HANSEN B.W. 1999. Seasonal variation in nutrients, pelagic primary production and grazing in a high–Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. *Marine Ecology Progress Series* 179: 13–25.
- SAGAN S., KOWALCZUK P. and ZAJĄCZKOWSKI M. 1993. Optical properties of waters around Svalbard and Franz Josef Land. *International Society for Optics and Photonics* 2048: 64–72.
- SAKSHAUG E. 2004. Primary and Secondary Production in the Arctic Seas. In: R. Stein and R.W. Macdonald (eds) *The organic carbon cycle in the Arctic Ocean*. Springer, Berlin, Heidelberg: 57–81.
- SAKSHAUG E. and SKJOLDAL H.R. 1989. Life at the ice edge. *Ambio* 18: 60–67.
- SAKSHAUG E., BJØRGE A., GULLIKSEN B., LOENG H. and MEHLUM F. 1994. Structure, biomass distribution, and energetics of the pelagic ecosystem in the Barents Sea: a synopsis. *Polar Biology* 14: 405–411.
- SCHAUER U., AHRBACH E.F., ØSTERHUS S. and ROHARDT G. 2004. Arctic warming through the Fram Strait: Oceanic heat transport from 3 years of measurements. *Journal of Geophysical Research: Oceans (1978–2012)*: 109(C6).
- SKAGSETH Ø., FUREVIK T., INGVALDSEN R., LOENG H., MORK K.A., ORVIK K.A. and OZHIGIN V. 2008. Volume and heat transports to the Arctic Ocean via the Norwegian and Barents Seas. In: B. Dickson, J. Meincke and P. Rhines (eds), *Arctic–subarctic ocean fluxes: defining the role of the northern seas in climate*. Springer, Netherlands: 45–64.
- SMITH W.O.Jr and SAKSHAUG E. 1990. Polar phytoplankton. In: W.O. Smith Jr. (ed.), *Polar Oceanography, Part B Chemistry, Biology and Geology*. Academic Press, San Diego: 477–525.
- SPRINGER A.M. and MCROY C.P. 1993. The paradox of pelagic food webs in the northern Bering Sea–III. Patterns of primary production. *Continental Shelf Research* 13: 575–599.

- STYSZYŃSKA A. and KOWALCZYK M. 2007. Zlodzenie Hornsundu i jego przedpola (SW Spitsbergen) w sezonie zimowym 2005–2006. *Problemy Klimatologii Polarnej* 17: 147–158.
- STYSZYŃSKA A. and ROZWADOWSKA A. 2008. Zlodzenie Hornsundu i jego przedpola (SW Spitsbergen) w sezonie zimowym 2006/2007. *Problemy Klimatologii Polarnej* 18: 141–160.
- STYSZYŃSKA A. 2009. Zlodzenie Hornsundu i jego przedpola (SW Spitsbergen) w sezonie zimowym 2007/2008. *Problemy Klimatologii Polarnej* 19: 247–267.
- SUBBA RAO D.V. and PLATT T. 1984. Primary production of Arctic waters. *Polar Biology* 3: 191–210.
- SVENDSEN H., BESZCZYŃSKA-MÖLLER A., HAGEN J.O., LEFAUCONNIER B., TVERBERG V., GERLAND S., ØRBÆK J.B., BISCHOF K., PAPUCCI C., ZAJĄCZKOWSKI M., AZZOLINI R., BRULAND O., WINCKE C., WINTHER J.G. and DALLMANN W. 2002. The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar Research* 21: 133–166.
- SWERPEL S. 1985. The Hornsund fjord: Water Masses. *Polish Polar Research* 6: 475–496.
- SYVERTSEN E.E. 1991. Ice algae in the Barents Sea – types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. *Polar Research* 10: 277–287.
- SYVITSKI J.P.M., BURRELL D.C. and SKEI J.M. 1987. *Fjords: Processes and Products*. Springer Science & Business Media: 379 pp.
- TATAREK A., WIKTOR J.M. and KENDALL M.A. 2012. The sublittoral macroflora of Hornsund. *Polar Research* 31: 18900.
- VON QUILLFELDT C.H. 2000. Common diatom species in arctic spring blooms: their distribution and abundance. *Botanica Marina* 43: 499–516.
- WALCZOWSKI W. and PIECHURA J. 2011. Influence of the West Spitsbergen Current on the local climate. *International Journal of Climatology* 31: 1088–1093.
- WALCZOWSKI W., PIECHURA J., OSINSKI R. and WIECZOREK P. 2005. The West Spitsbergen Current volume and heat transport from synoptic observations in summer. *Deep-Sea Research I* 52: 1374–1391.
- WANG G., CHAOYING G., WEI L.C., CAI M. and HE J. 2009. The distribution of picoplankton and nanoplankton in Kongsfjorden, Svalbard during late summer. *Polar Biology* 32: 1233–1238.
- WÄNGBERG S.Å., ANDREASSON K.I., GARDE K., GUSTAVSON K., HENRIKSEN P. and REINTHALER T. 2006. Inhibition of primary production by UV–B radiation in an arctic bay—model calculations. *Aquatic Sciences-Research Across Boundaries* 68: 117–128.
- WASSMANN P., SLAGSTAD D., RISER C.W. and REIGSTAD M. 2006. Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone: II. Carbon flux and interannual variability. *Journal of Marine Systems* 59: 1–24.
- WĘSŁAWSKI J.M., WIKTOR J.JR. and KOTWICKI L. 2010. Increase in biodiversity in the arctic rocky littoral, Sorkapland, Svalbard, after 20 years of climate warming. *Marine Biodiversity* 40: 123–130.
- WĘSŁAWSKI J.M., KWAŚNIEWSKI S. and WIKTOR J.M. 1990. Winter in a Svalbard fjord ecosystem. *Arctic* 44: 115–123.
- WĘSŁAWSKI J.M., KWAŚNIEWSKI S., JEZERSKI J., MOSKAL W. and ZAJĄCZKOWSKI M. 1988. Seasonality in an arctic fjord ecosystem, Hornsund, Spitsbergen. *Polar Research* 6: 185–189.
- WĘSŁAWSKI J.M., KWAŚNIEWSKI S., STEMPNIEWICZ L. and BŁACHOWIAK-SAMOŁYK K. 2006. Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. *Polish Polar Research* 27: 259–278.
- WĘSŁAWSKI J.M., KWAŚNIEWSKI S., WIKTOR J.M. and ZAJĄCZKOWSKI M. 1993. Observations on the fast ice biota in the fjords of Spitsbergen. *Polish Polar Research* 14: 331–343.
- WIKTOR J.M. 1999. Early spring microplankton development under fast ice covered fjords of Svalbard, Arctic. *Oceanologia* 41: 51–72.
- WIKTOR J.M. 2015. Morskie pierwotniaki Arktyki. *Rozprawy i monografie IO PAN* 24: 178 pp.

- WIKTOR J.M. and WOJCIECHOWSKA K. 2005. Differences in taxonomic composition of summer phytoplankton in two fjords of West Spitsbergen, Svalbard. *Polish Polar Research* 26: 259–268.
- WŁODARSKA-KOWALCZUK M., KUKLIŃSKI P., RONOWICZ M., LEGEŻYŃSKA J. and GROMISZ S. 2009. Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). *Polar Biology* 32: 897–905.
- WOELFEL J., SCHUMANN R., PEINE F., FLOHR A., KRUSS A., TĘGOWSKI J., BLONDEL P., WIENCKE C. and KARSTEN U. 2010. Microphytobenthos of Arctic Kongsfjorden (Svalbard, Norway): biomass and potential primary production along the shore line. *Polar Biology* 33: 1239–1253.
- YAMAGUCHI Y., MIYAHARA T., MATSUDA O. and KUDOH S. 1996. Primary production of phytoplankton in high Arctic Kongsfjorden, Svalbard. *Memoirs of National Institute of Polar Research. Special Issue* 51: 143–151.

Received 23 February 2016

Accepted 2 May 2017