Chapter 6
Phytoplankton Seasonal Dynamics in Kongsfjorden, Svalbard and the Adjacent Shelf

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Abstract Phytoplankton phenology is a key driver of biological and chemical processes in marine ecosystems because it directly affects cycling of nutrients, the strength of the biological carbon pump, and energy transfer to higher tropic levels. However, phytoplankton time-series from the Arctic are scant, thus limiting our ability to link phytoplankton phenology to environmental variability. Kongsfjorden on the west coast of Spitsbergen is an established coastal monitoring site at the entrance to the Arctic Ocean. In this review we have compiled previously published phytoplankton investigations, chlorophyll fluorescence time-series data and unpublished phytoplankton data covering the years 2002–2014 from Kongsfjorden and the shelf outside the fjord to elaborate the most pertinent environmental factors

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responsible for the seasonal and inter-annual variability in phytoplankton bloom dynamics, biomass and species composition. In general, phytoplankton dynamics in Kongsfjorden follow the classic spring-bloom paradigm, with the main biomass peak in April–May dominated by spore-forming diatom species and the colony-forming haptophyte *Phaeocystis pouchetii*, followed by a diverse, but low biomass community characterised by dinoflagellates and small flagellates and their protozoan grazers during summer. Despite this general trend, phytoplankton phenology is subject to large inter-annual variability with no clear long-term trend. This variability can be mainly attributed to variability in the magnitude and depth of Atlantic Water (AW) inflow, sea ice cover and glacier melt-water discharge. We have shown the impact of environmental variability on phytoplankton phenology, but high-resolution monitoring of annual cycles over many years is required to resolve the ephemeral variations of phytoplankton populations in space and time against the backdrop of climate change.

Keywords Arctic · Kongsfjorden · Phytoplankton · Svalbard · Time-series

6.1 Introduction

Kongsfjorden on the west coast of Spitsbergen is an established reference site for Arctic marine studies and one of the most extensively monitored marine ecosystems in the Arctic (Hop et al. 2002, 2006). This open fjord integrates oceanic signals related to advection of warm Atlantic Water (AW) masses within the West Spitsbergen Current, and cooler, fresher shelf waters originating from the more Arctic water masses found on the east side of Spitsbergen (Svendsen et al. 2002; Fig. 6.1). Kongsfjorden is characterized by large inter-annual differences in the timing, depth and magnitude of warm AW inflow (Tverberg et al., Chap. 3) and sea ice cover (Pavlova et al., Chap. 4). In addition, melt-water run-off from tidewater glaciers induces strong environmental gradients along the fjord axis during summer (Cottier et al. 2005a, 2010; Nilsen et al. 2008). Thus, Kongsfjorden lends itself to studying the effects of variability in the physical environment on its marine ecosystem on time scales ranging from diurnal to decadal.

Investigations of the phytoplankton community in Kongsfjorden date back to the early 1970s and sampling has been conducted from either ship-based oceanographic transects of fixed stations along the fjord axis and across the adjacent shelf, or shore-based studies carried out from the international research settlement of Ny-Ålesund (Fig. 6.1). The early studies noted the important roles of AW and glacier runoff in shaping phytoplankton dynamics in Kongsfjorden (Halldal and Halldal 1973). Evidence for the advection of AW into Kongsfjorden came from observations of Atlantic indicator species, in particular the coccolithophore *Coccolithus pelagicus* (Halldal and Halldal 1973; Hasle and Heimdal 1998). The majority of phytoplankton taxa this far identified in Kongsfjorden are of cosmopolitan or Atlantic origin (Hop et al. 2002). Indeed, the diatom

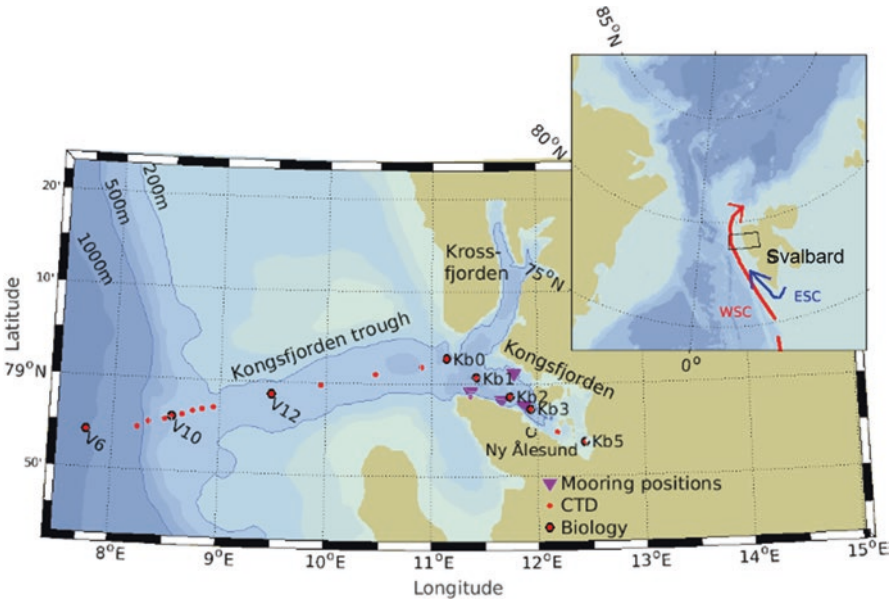

Fig. 6.1 Svalbard with the East Spitsbergen Current (ESC, blue) and West Spitsbergen Current (WSC, red). Enlarged insert with Kongsfjorden mooring locations, CTD and biology stations

Chaetoceros gelidus (formerly *Chaetoceros socialis*, Chamnansinp et al. 2013) and the haptophyte *Phaeocystis pouchetii* dominating the 1984 spring bloom (Eilertsen et al. 1989), and the diatom *Thalassiosira nordenskioeldii* dominating the 1996 spring bloom (Wiktor 1999) in Kongsfjorden are also prominent spring bloom species along the Atlantic dominated coast of Northern Norway (Degerlund and Eilertsen 2010).

During the pre-2000 investigations, fast-ice typically covered the inner basin, and drifting pack-ice was commonly found in the outer parts of the fjord during spring (Pavlova et al., Chap. 4). Bloom initiation started under the ice while the bloom culminated in late May, characterized by open water conditions with some drifting pack ice (Eilertsen et al. 1989; Wiktor 1999). It was also recognized that the heavily reduced submarine light field caused by glacier melt-water runoff in the inner fjord, and the gradually increasing penetration of light towards the mouth of the fjord plays an important role in structuring phytoplankton productivity, biomass and species composition during summer (Halldal and Halldal 1973; Eilertsen et al. 1989; Keck et al. 1999).

The post-bloom phase and the summer months were characterized by low phytoplankton biomass and the community shifted towards a flagellate-dominated system (Wiktor 1999), with few diatom species present and a large diversity of unidentified dinoflagellates (Eilertsen et al. 1989). Taxonomic scrutiny applied to concentrated net samples collected in summer 1988 revealed a total of 96 species

that were predominantly represented by diatoms (57) and dinoflagellates (26) (Hasle and Heimdal 1998). The remaining species belonged to several algal groups, including the numerically most abundant species *Phaeocystis pouchetii* and the chrysophyte *Dinobryon balticum.* Although species-rich, diatoms occurred at low abundances while dinoflagellates were a dominant component of the summer phytoplankton assemblage. A similar number of dinoflagellate species, and numerical dominance of *D. balticum,* was observed in summer 1996, while diatoms were represented by only nine species, most of which were in moribund condition (Keck 1999; Okolodkov et al. 2000).

Despite the 30 years of phytoplankton investigations in Kongsfjorden between 1970 and 2000, summarized in Hop et al. (2002), we still lack a mechanistic framework for phytoplankton phenology, and how it is controlled by variability in the physical environment and grazing pressure. This is primarily because most studies have been confined largely to snapshots of the plankton ecosystem during either spring or summer sampling campaigns. It was clear that more holistic studies were necessary to understand the bloom dynamics of this fjord, which were observed to be highly variable from year to year, and influenced by sea ice and oceanographic conditions. Furthermore, scarce information on crucial biological rates (in particular primary production, grazing rates and particle flux) and biomass estimates as well as the lack of information on heterotrophic microorganisms (bacteria and protozooplankton) were identified as knowledge gaps (Hop et al. 2002).

More recently, repeated phytoplankton sampling off Ny-Ålesund covering the spring and summer period (Leu et al. 2006a; Piquet et al. 2010, 2014; Hodal et al. 2012; Mayzaud et al. 2013) and nearly the entire annual cycle at a monthly resolution (Rokkan Iversen and Seuthe 2011; Seuthe et al. 2011) have helped to fill some of the identified knowledge gaps. Additionally, the apparent link between the timing and magnitude of the spring bloom and the magnitude and depth of AW inflow has been described (Hegseth and Tverberg 2013). Since 2000, the summer phytoplankton assemblage has been investigated in some years covering the period 2002–2010 during ship-based oceanographic transects (Kang et al. 2003; Wiktor and Wojciechowska 2005; Piwosz et al. 2009, 2015; Wang et al. 2009; Kubiszyn et al. 2014). More systematic investigations have been performed since 2009 during the annual Kongsfjorden "*Climate and Ecosystem-MOSJ*" cruises in July by the Norwegian Polar Institute. Additionally, since April 2002 an oceanographic mooring has been deployed in the outer basin of the fjord (Cottier et al. 2005a; Hop et al., Chap. 13). This has recorded continuous hydrographical data (temperature, salinity and current vectors), acoustic backscatter, fluorometry, photosynthetic active radiation (PAR) and export flux (sediment traps) – for example see Wallace et al. (2010). The fluorometer was added in September 2005, providing valuable information on seasonal bloom dynamics, which could not have been obtained by traditional sampling approaches.

Here we attempt to refine our understanding of phytoplankton seasonal dynamics in Kongsfjorden and the adjacent shelf by synthesizing the existing knowledge, particularly after publication of the last major review on the marine ecosystem in Kongsfjorden (Hop et al. 2002), but by also including unpublished

data obtained during recent years. We focus on phytoplankton bloom dynamics, biomass, primary production and species composition in relation to hydrographic conditions (AW inflow and glacier runoff), bottom-up (light and nutrients) and top-down factors (grazing). More specifically, we link shifts in spring bloom timing and magnitude with variability in hydrographic conditions. We also integrate the observations obtained during winter, spring, summer and autumn into an ecological framework of phytoplankton seasonal succession patterns and widen the scope of phytoplankton investigations by including information on photoprotective pigments and fatty acid composition. Genetic identification of previously understudied taxa such as phytoflagellates is included, and we evaluate the role of top-down control by zooplankton grazers in regulating phytoplankton biomass.

6.2 Sampling Stations and Physical Observations

Phytoplankton sampling in Kongsfjorden was either performed along a transect (Fig. 6.1) from the inner to the outer part of the fjord (stations Kb5-Kb0), over the shelf (stations V12-V10) and out to the shelf break (station V6), or on a more regular basis at station Kb3 outside Ny-Ålesund. Overview of sampling times, stations and parameters sampled, including references, for the different seasons is given in Table 6.1. A mooring, providing hydrographical data, was deployed in the fjord, first in 2002, and then from 2003 on a regular basis (Tverberg et al., Chap. 3). The mooring itself has been moved and redeployed in the fjord several times after the first positioning in 2003. Its position has been in the outer parts of the fjord, and along the southern coast except for the 2 years from September 2005 to September 2007 where the mooring was close to the middle of the fjord (see exact positions in Tverberg et al., Chap. 3). From 2006, the fluorescence (FL) sensor and the hydrographical data have provided information on water mass characteristics and bloom phenology during the entire year. Temperature measurements and FL data reveal large inter-annual variability (Fig. 6.2a). For better comparison of the various years, the average annual temperature structure, based on the period 2002–2014 (Fig. 6.2b), has been used to calculate the temperature anomaly for each year (Fig. 6.2c). Obviously, there are cold, average and warm years, and some years for which spring and summer behave differently compared to the average year (Fig. 6.2c). A further discussion of these results is included in the winter, spring and summer sections below.

Ice observations from the Norwegian Meteorological Institute (MET) have been used to evaluate pack ice conditions along the coast and in the fjord (http://polarview.met.no/index_HI.html), since no such ice data from Kongsfjorden have been published. Fast ice data for the period 2003–2005 were published by Gerland and Renner (2007), and here the authors divided the inner part of Kongsfjorden into four zones to describe the fast–ice cover. We have adopted this division (Fig. 6.3), and have estimated the fast ice cover area for the years from 2002 to 2014 at the end of

Table 6.1 Stations sampled and parameters measured, with seasons and dates, during the period 2002–2014 in Kongsfjorden, Svalbard

Season	Date	Stations sampled	Hydro-graphy	Light	Nutrients	Chl a	Phyto-plankton	Prim. prod.	References
Winter	18 March 2006, 2 December 2006	Kb3	X		X	X	X		Rokkan Iversen and Seuthe (2011) and Seuthe et al. (2011)
	19–22 January 2010	Kb3	X				X		Berge et al. (2012)
	18 January 2014	Kb3	X		X	X	X[1]		This work
Spring	15–18 April 2002	Kb3	X		X	X	X		Hodal et al. (2012)
	1–22 May 2002	Kb3	X		X	X	X	X	Hodal et al. (2012)
	11–17 April 2002	Kb5, Kb3, Kb2, Kb1, Kb0, V10, V6	X						Walkusz et al. (2009)
	17 April – 23 May 2003	Kb3	X	X	X	X	X		Leu et al. (2006a)
	8 May – 8 June 2004	Kb3	X	X	X	X	X		Leu et al. (2006a)
	25 April & 30 May, 2006	Kb3	X		X	X	X	X	Rokkan Iversen and Seuthe (2011)
	25–28 April 2006	Kb5, Kb4, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		Hegseth and Tverberg (2013)
	30 May – 1 June 2006	Kb5, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
	26 April – 30 May 2007	Kb3					X		Hegseth and Tverberg (2013)
	12–15 May 2007	Kb5, Kb4, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		Hegseth and Tverberg (2013)
	22 May – 25 June 2007	Kb4 (G), Kb3 (M)	X	X	X	X	X		Piquet et al. (2014)
	2–30 May 2007	Kb3	X		X	X	X		Mayzaud et al. (2013)
	18–22 April 2008	Kb5, Kb4, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		Hegseth and Tverberg (2013)
	9 April – 12 May 2008	Kb4 (G), Kb3 (M)	X	X	X	X	X		Piquet et al. (2014)
	17–18 April 2009	UNIS 116, 0042					X		This work
	22–29 May 2009	T05, A05, B09, B03, B01				X[2]	X	X	Ha et al. (2012)

	26 April – 7 May 2014	Kb3					X		This work
	9–10 May 2014	Kb5, Kb4, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
Summer	29–30 July 2002	Kb5 (P1), Kb4 (P2), Kb3 (K3), Kb1 (K1), Kb0 (K0)	X	X		X	X	X	Piwosz et al. (2009) and Wiktor and Wojciechowska (2005)
	27–28 July 2006	Kb4, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
	22 May – 25 June 2007	Kb4 (G), Kb3 (M)	X	X	X	X	X		Piquet et al. (2014)
	6 June – 22 August 2007	Kb3	X			X	X		Mayzaud et al. (2013)
	26–28 July 2007	Kb4, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
	2–3 August 2007	Kb5, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
	17–20 July 2009	Kb5, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
	13–18 July 2011	Kb5, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
	13–20 July 2012	Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
	23–25 July 2013	Kb 7, Kb6, Kb5, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
	23–24 July 2014	Kb7, Kb6, Kb5, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X		X	X	X		This work
Autumn	16 September 2006	Kb3	X		X	X	X		Rokkan Iversen and Seuthe (2011) and Seuthe et al. (2011)
	5–24 September 2007	Kb3	X			X	X		Mayzaud et al. (2013)
	3–6 October 2007	Kb5, Kb4, Kb3, Kb2, Kb1, Kb0, V12, V10, V6	X			X[3]			This work

Data are collected from the references given

[1]Data includes sediment samples [2]Chlorophyll data from satellite (MODIS) measurements only [3]Fluorescence measurements only

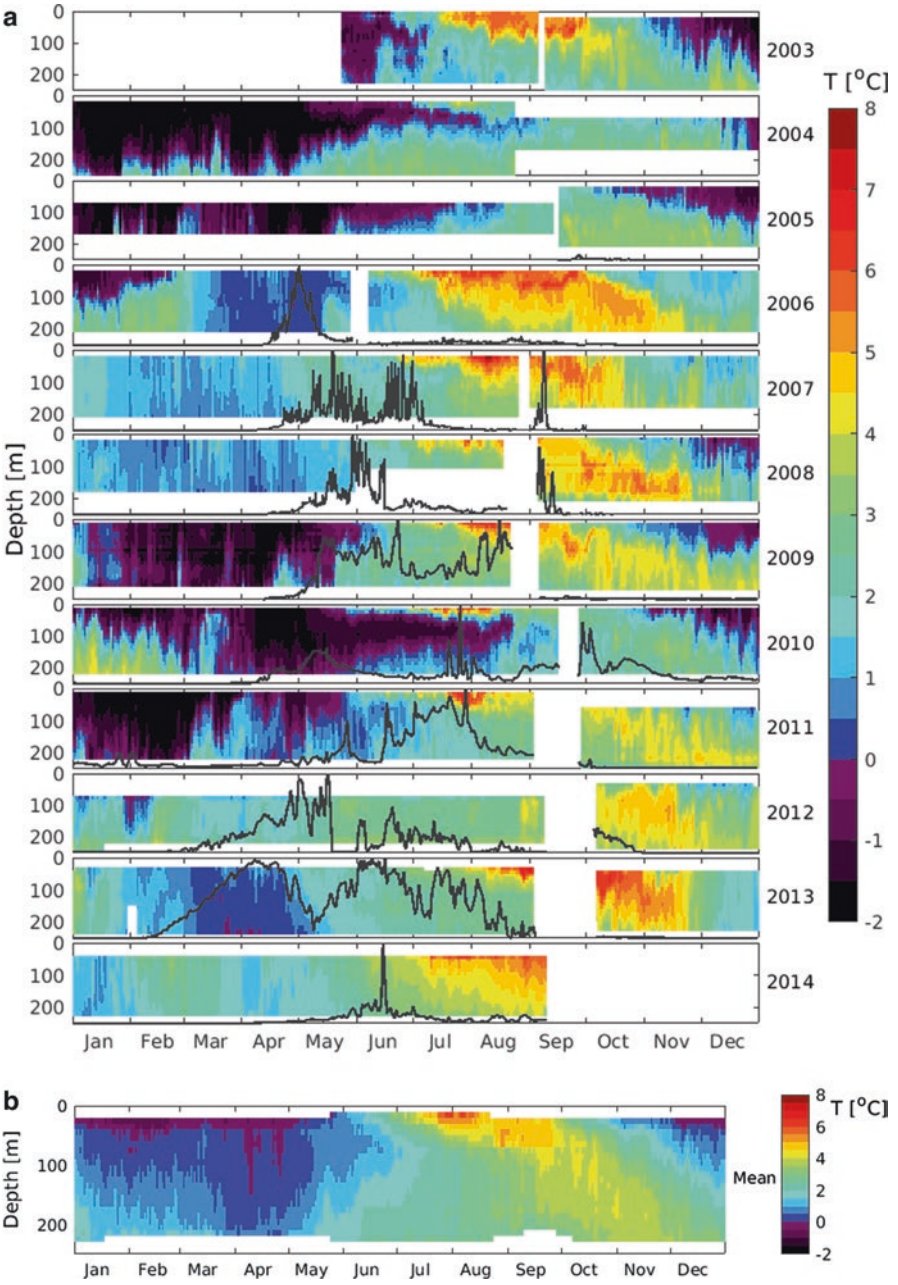

Fig. 6.2 (**a**) Temperature measurements (°C) from the Kongsfjorden Marine Observatory, May 2003 to September 2014. The superimposed black line depicts the normalized fluorescence units (measurements were normalized for each year). Note that the mooring location has been shifted over the years (see Fig. 6.1). But except for the 2 years from September 2005 to September 2007, where the mooring was close to the middle of the fjord, deployments have been on the southern shore; (**b**) Temperature during an average year in Kongsfjorden, based on data from the years 2003–2014; (**c**) Temperature anomalies in Kongsfjorden during the years 2003–2014, related to the average temperature during this period. (V. Tverberg, unpublished data)

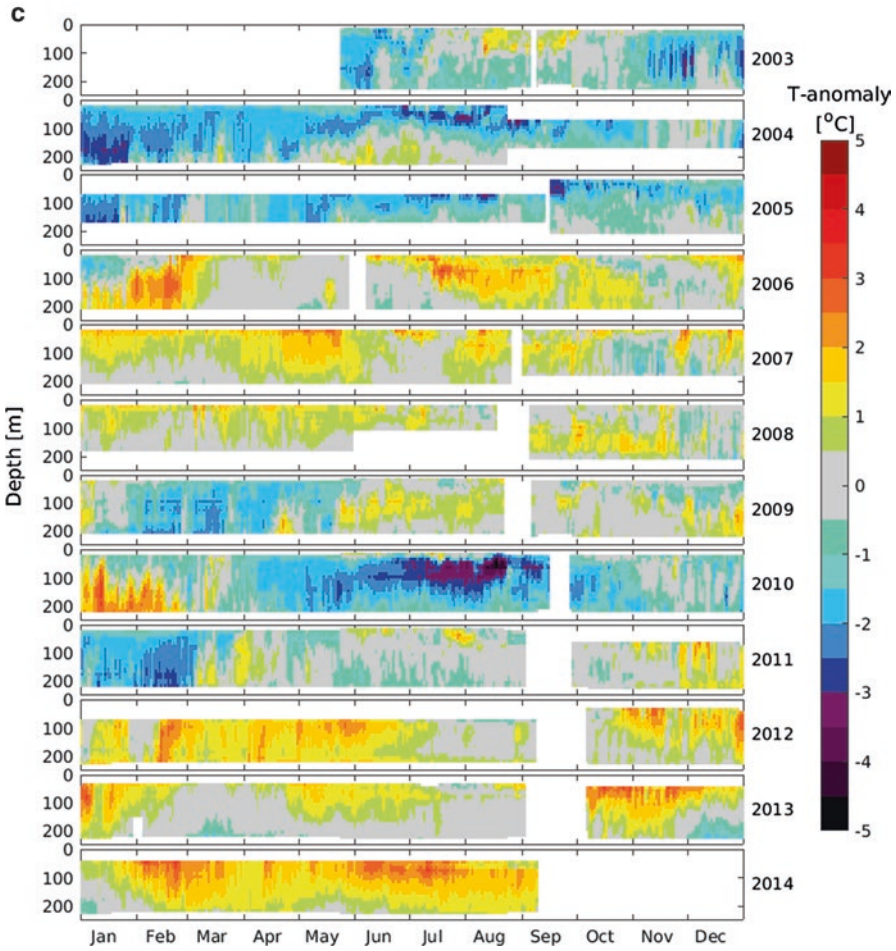

Fig. 6.2 (continued)

March each year (Table 6.2). Fast–ice data for the years 2006–2014 are from Pavlova et al. (Chap. 4). Both coast and fjord are characterized by variable sea ice conditions during winter. Pack ice may frequently be brought in and out of the fjord due to wind and currents. Some of the ice will come from broken fast ice in the inner part of the fjord, and the Spitsbergen Polar Current along the coast may bring pack ice from the Barents Sea to the coastal areas (Tverberg et al., Chap. 3). Accordingly, during most years, both the fjord and the coast have periods with ice cover of variable density, mixed with ice-free periods. An overview of ice conditions along the coast and in the fjord for the winter/early spring periods from 2002 to 2014 is given in Table 6.2.

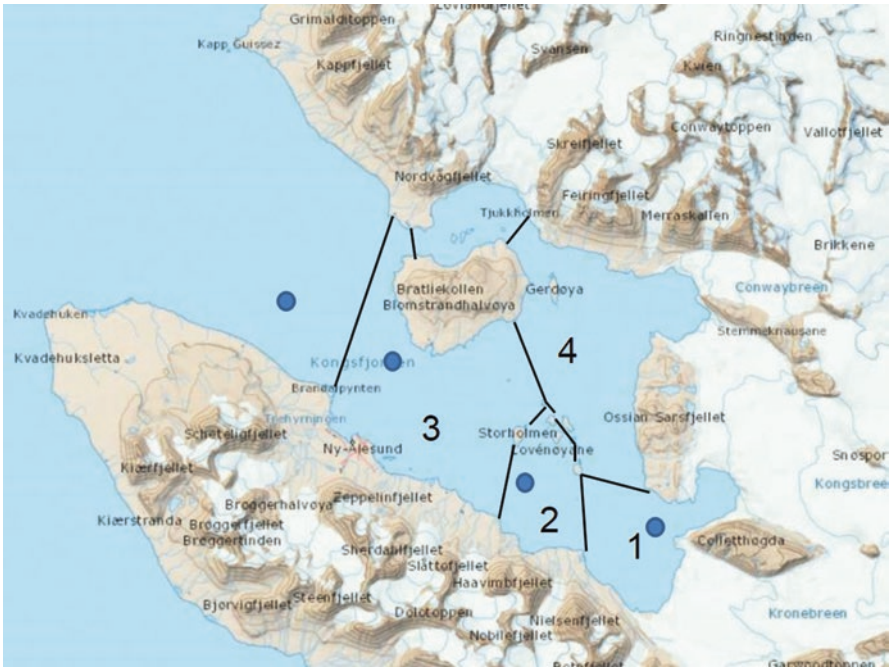

Fig. 6.3 Kongsfjorden showing sectors in the inner fjord related to fast–ice cover (see Table 6.2). Sectors based on Gerland and Renner (2007). Blue dots showing sampling stations in the fjord (Kb5-Kb2)

6.3 Winter in Kongsfjorden

The phytoplankton community in winter has received little attention in the past. In recent years, the diminishing ice cover has opened the fjord to winter sampling, revealing an unexpected high level of activity in the pelagic realm (Berge et al. 2015). Another earlier field study sampled station Kb3 outside Ny-Ålesund in March and December 2006 (Rokkan Iversen and Seuthe 2011; Seuthe et al. 2011), and more recently pelagic protists were identified in January 2010 (Berge et al. 2012) and 2014 (T.M. Gabrielsen, unpubl.; E.N. Hegseth, unpubl.).

6.3.1 Environmental Conditions

The polar night lasts from 24 October to 18 February at the latitude of Kongsfjorden (79 °N). During January the atmospheric light on a clear day at noon is about 1–1.5 × 10^{-5} µmol photons m^{-2} s^{-1} measured as PAR wavelengths (400–700 nm) (Cohen et al. 2015), compared to 1200 µmol photons m^{-2} s^{-1} on a clear day in May (Leu et al. 2006a). All measurements were performed with cosine-corrected sensors.

Table 6.2 Summary of data from spring and summer in Kongsfjorden 2002–2014

	Spring						Summer	
Year	Pack ice conditions along the coast and in the fjord	Fast-ice conditions in the inner fjord (sectors)	AW inflow in winter/spring	Cold or warm spring	Spring bloom peak	Spring phyto-plankton biomass (Chl *a* µg L^{-1})	Cold or warm summer	July phytoplankton biomass (Chl *a* µg L^{-1})
2002*	Coast mainly ice free from early April, fjord with pack ice until mid- April	No ice data before mid-May	No data, but probably no or little until summer	Cold	Late April	Low (2.0), but after the peak	Cold (probably)	No data
2003*	Coast mainly ice free from late April, fjord with pack ice until early May	1,2,3,4	No data until spring, but no surface inflow	Cold	Second week of May	Very high (> 10), peak	Cold	No data
2004*	Coast and fjord mainly free of ice most of April	1,2,3,4	Along the bottom	Cold	Late April	Low (2.0), post-bloom data	Cold	No data
2005	Coast mainly ice free from mid-April, fjord from early May	1,2,4	Along the bottom	Cold	No data	No data	Cold	No data
2006*	Ice along the coast in March, then ice free. Fjord ice free all winter	1,4	Along the bottom	Average	Late April	Very high (12.5)	Warm	High (1.7)
2007*	Coast and fjord ice free all winter	4	At the surface	Warm	Third week of May	Medium high (5.6)	Average/ warm	High (2.9)
2008*	Coast and fjord mainly ice free all winter	4	At the surface	Warm	Late May	Low (1.9), but before the peak	Average/ warm	No data
2009*	Ice along the coast and in the fjord until beginning of May	1,2,3 (50%), 4	Along the bottom	Cold	Mid May	Very low (0.8), but post-bloom phase	Average/ warm	High (2.1)
2010	Ice along the coast and in the fjord until beginning of May	1,4	Along the bottom	Cold	Mid May	No data	Cold	Low (0.6)

(continued)

Table 6.2 (continued)

	Spring						Summer	
Year	Pack ice conditions along the coast and in the fjord	Fast-ice conditions in the inner fjord (sectors)	AW inflow in winter/spring	Cold or warm spring	Spring bloom peak	Spring phyto-plankton biomass (Chl *a* µg L^{-1})	Cold or warm summer	July phytoplankton biomass (Chl *a* µg L^{-1})
2011	Ice along the coast mainly gone by end of April. Variable amounts in the fjord until mid-May	1,4	Along the bottom	Average/ cold	Late May	No data	Average	Low (0.7)
2012	Ice along the coast most of April. Fjord ice free most of winter	4 (50%)	Along the bottom	Warm	Mid-April	No data	Average/ warm	High (2.2)
2013	Ice along the coast until end of April. Fjord ice free most of winter	4	Along the bottom	Average/ warm	Mid-April	No data	Average/ warm	High (4.9)
2014*	Coast and fjord ice free all winter	4 (50%)	At the surface	Warm	Mid-June	Very low (0.1), pre-bloom phase	Warm	High (3.4)

Pack ice data from the Norwegian Meteorological Institute web page (http://polarview.met.no/index_HI.html). Fast ice data from Gerland and Renner (2007) and Pavlova et al. (Chap. 4), given as ice cover area in the innermost part of the fjord (divided into sectors 1–4, Fig. 6.3) during mid-April each year. *AW* Atlantic Water. Cold or warm spring/summer from Fig. 6.2c. Spring bloom peak timing estimated from the fluorescence (FL) in Fig. 6.2a and/or from years with measured chlorophyll data (*), either alone (2002, 2003, 2004) or as a supplement to the FL measurements. Spring and July phytoplankton biomass is based on measured chlorophyll data at stations Kb5 – Kb0. Low and high biomass in summer defined as having chlorophyll concentrations < and > 1 µg L^{-1}, respectively. Maximum chlorophyll concentration in µg L^{-1} for the respective years given in brackets. Note that spring sampling was not always during the peak of the bloom. Also note that 'high' and 'low' signifies different values in spring and summer

Table 6.3 Nutrient concentrations (μM) in Kongsfjorden and Fram Strait during winter 2014, Average concentrations for the water column surface-bottom in the fjord, and the upper 200 m in Fram Strait

	Nitrate μM	Phosphate μM	Silicate μM
Fram Strait (Atlantic waters)	13–15	0.7–0.9	4.5–6
Fjord sides (south and north sides)|	11–12.5	0.6–0.7	4.4–4.9
Mid-fjord (between inner part and mouth)	9.8–11	0.7–0.8	4.0–4.9

Data showing highest nitrate concentrations in the AW of Fram Strait, and lowest concentrations in the mid-fjord area (E.N. Hegseth, unpublished data)

The usual winter conditions in Kongsfjorden, describing most of the years since 2003, exhibit a gradual cooling of water masses in the fjord until the cooling has extended to the fjord bottom by the end of December or early January (Fig. 6.3 in Cottier et al. 2010). This deep mixing of the water column leads to relatively high nutrient concentrations in fjord waters during winter, although not quite as high as in the AW along the coast. An example of this can be seen in the pre-bloom concentrations in the winter of 2014, which were highest in AW at the shelf break (Station V6) and showed a small, but gradual decrease towards the fjord (Table 6.3). During many years, winter water temperatures stayed below −1 °C, and remained cold until June when a thermocline formed at about 20 m depth. However, pulses of warmer AW along the fjord bottom have been common during winter and early spring. The duration and magnitude of these inflows vary from short events lasting from a few days to inflows that are more persistent. In general, these inflows are restricted to depths below 150 m. Typically, the water column is often found to be unstratified in the periods between the inflows, indicating rather rapid convective overturning events – probably driven by periods of intense surface cooling.

However, in recent years (notably 2007, 2008 and 2012–2014) there has been a significant departure from this general picture. These were all "warm" years with surface water temperatures around 2 °C in winter and early spring and mean water column temperatures >0 °C (Table 6.2 and Fig. 6.2a). There was no significant pack ice cover in the fjord, and the fast ice cover in the inner fjord was very limited (Table 6.2).

The reason for this was a change in the AW inflow. In contrast to an inflow along the bottom as in most years, in these particular years the inflow occurred at the surface (Fig. 6.2a). The AW inflow into the fjord is much determined by the ice conditions along the coast and in the fjord, and has been more thoroughly described in Hegseth and Tverberg (2013). Further, Tverberg et al. (Chap. 3) have divided the winter conditions into three types based on AW advection and winter convection (their Table 3.6 and Figs. 3.23–3.25).

Type 1 winter has AW advected onto the shelf at intermediate depth, and limited AW inflow into the fjord. The convection inside the fjord is reaching the bottom. There is mainly ice in the fjord. Such winters occurred in 2002, 2003, 2006, 2009 and 2011.

Type 2 winter has AW advected over the shelf and into the fjord along the bottom, and the convection in the fjord extends to the AW bottom layer. There is mainly ice in the fjord. This happened in 2004, 2005 and 2010.

Type 3 winter has AW inflow at the surface, but the inflow is not always limited to the surface layers. There are two possible scenarios: Type 3a) AW in the West Spitsbergen Current (WSC) is lighter than the shelf/fjord water – the AW current will proceed in the upper part of the water column, and will spread out in the surface layers, like in 2007 and 2008, and there is no ice. Even if the convection is deep, periodically advected AW will act as a lid on up-stream water. The winter 2013/2014 never experienced AW bottom inflow. Instead, the inflow in the autumn of 2013 was concentrated between 100 and 200 m depth, spreading out to a homogeneous water column as early as December. Repeated surface inflow of AW, from December to May – and particularly in late February/early March – acted as a lid on the convection. This had a pronounced effect on the spring bloom, as shall be seen later.

Type 3b) AW in the WSC has nearly the same density as the shelf/fjord water – advection of AW will take place across the entire water column. Convection will extend from surface to bottom, bringing bottom water to the surface layers. This type of winter happened (more or less) in 2012 and 2013, which were both warm years with no ice in the fjord. In the winter of 2011/2012, there was a long-lasting AW inflow in the deep layers, stopped by a strong cooling down to 150 m in January/February. Then, a new AW inflow filled the entire water column in February/March, with ample possibilities of convection to the bottom. Minor AW inflow to the water column continued thereafter, keeping the fjord water warm until the April bloom observed in the mooring data this year. The winter of 2012/2013 resembled the previous winter, but the cooling of surface layers was not so pronounced. A homogeneous water column appeared in January/February, and together with a weak tendency of warmer surface layers the bloom in 2013 occurred slightly earlier in April than the previous year.

Winter ice conditions in the fjord since 2002 have shown great variability because of the changing AW inflow (Pavlova et al., Chap. 4). Warm years have virtually no ice due to the high surface water temperatures, while cold years have variable ice cover, both as fast ice and as pack ice (Table 6.2). The winter/early spring ice conditions is another factor strongly affecting the spring bloom.

6.3.2 Winter Protists and Survival Strategies

The various algal groups have evolved different strategies to survive the polar night. Neritic diatoms of common spring bloom genera form resting spores or resting cells in response to nutrient depletion at the end of the bloom (Garrison 1981; Kuwata et al. 1993). The resting spores either survive in surface sediments (Gran 1912; Hegseth et al. 1995; Eilertsen et al. 1995) or persist in the water column for longer

or shorter time at low abundances (Hasle and Heimdal 1998) and serve as the main seeding stock for the next spring bloom (see below). This diatom seeding strategy is common for all shelf seas north of the Arctic Circle. Non-spore forming diatom species may survive the winter months as viable, vegetative cells at very dilute cell concentrations suspended in the water column (Berge et al. 2015; Marquardt et al. 2016). Viable cells of both phototrophic and heterotrophic dinoflagellates have also been found to persist in their vegetative stage at very low abundances in the water column in winter (Seuthe et al. 2011; Brown et al. 2015; Berge et al. 2012, 2015; Marquardt et al. 2016), while others probably survive as cysts on the seafloor. In addition to the dilute presence of dinoflagellates and diatoms, metabarcoding based on the 18S nrDNA hyper variable V4 region identified the presence of a number of different taxa of ciliates in addition to the parasitic Marine Alveolates (MALV) and Apicomplexa in January 2014 (T.M. Gabrielsen, unpubl.). Viable cells of the prasinophyte *Micromonas* sp. and the haptophyte *Phaeocystis pouchetii* were identified from surface to mesopelagic depths during the polar night based on their presence in RNA extracted from filtered seawater samples (Vader et al. 2014; Marquardt et al. 2016). Thus, *Phaeocystis pouchetii* may have a mixotrophic lifestyle similar to what was shown for *Micromonas pusilla* (McKie-Krisberg and Sanders 2014), allowing both species to survive the winter in the water column.

In March and December 2006, flagellates <10 μm and athecate (naked), heterotrophic dinoflagellates were the most abundant groups at station Kb3. No diatoms and only very few phototrophic species were recorded (Seuthe et al. 2011). Despite being the dominant groups, dinoflagellates and small flagellates contributed only 1–3.5% and 0.5–1.5%, respectively, to the low particulate organic carbon standing stocks of 2–4 mg C m^{-2} (Rokkan Iversen and Seuthe 2011). This example illustrates that most of the organic material in Kongsfjorden during winter-early spring consisted of detritus. Primary production during this period was close to zero with about 1% of the carbon biomass attributed to phototrophic species reflected in the very low chlorophyll values of 0.01–0.02 μg L^{-1}. The bulk (60–85%) of phytoplankton biomass was allocated in the <10 μm fraction (Rokkan Iversen and Seuthe 2011). These observations are consistent with similar investigations from Adventfjorden in winter 1996 (Wiktor 1999), and Rijpfjorden in winter 2012 (Brown et al. 2015; Błachowiak-Samołyk et al. 2015). Winter conditions seem to be quite comparable between different Svalbard fjords, and in summary, the winters are characterized by extremely low phytoplankton biomass, dominated by flagellates <10 μm and naked dinoflagellates, and very few diatoms. The *in situ* photosynthetic rates in winter are below detection limit, but phytoplankton cells in the water column may be primed to take advantage of the low light at the end of the polar night to induce growth (Berge et al. 2015). For resting stages primarily surviving on the seafloor, deep winter mixing is crucial for spring recruitment. However, both vegetative diatom cells as well as resting spores may still be present at very low abundances in the water column during winter (Berge et al. 2015).

6.3.3 Winter Growth Lab Experiments

To investigate the possibly very low cell/resting spore abundance in the water column and the much higher abundance in sediments, lab experiments have been performed in winter. When untreated fjord water, sampled in January, both from Rijpfjorden (Brown et al. 2015) and Balsfjorden in Northern Norway (E.N. Hegseth, unpubl.), with no extra nutrients added, was exposed to moderate light (30 µmol photons m^{-2} s^{-1}) and low temperature (3–4 °C), some spring diatoms (e.g. *Thalassiosira* sp.) appeared after about 3–4 weeks although their natural abundance was below the detection level in a 50 mL water sample counted under the microscope. Surface sediments seem to constitute the more important "seed bank" for the spring bloom. Growth experiments with sediments from Kongsfjorden in January 2014 (E.N. Hegseth, unpubl.) and from Rijpfjorden in January 2012 (Brown et al. 2015) resulted in the growth of several spring bloom species, like *Thalassiosira antarctica* var. *borealis, T. nordenskioeldii, T. hyalina, Chaetoceros gelidus, C. furcellatus, C. diadema, Fragilariopsis oceanica,* and *Attheya septentrionalis.* In these experiments, a small amount of sediment material was mixed with growth medium. The cultures were then exposed to the same moderate light and low temperature as the water samples. It is very difficult to see resting spores in sediments, partly because they are mixed with sediment particles, and partly because we do not always know what they look like. Vegetative cells have been spotted, but mainly in the period shortly after a spring bloom. Later in the year such cells are rarely seen, most likely the majority are eaten by benthic animals. Spores are also eaten, but they obviously survive the passage through the animal's digesting system. This was observed in the fecal pellets from a sea urchin in the northern Barents Sea, which was filled with seemingly intact spores from *Chaetoceros furcellatus* (E.N. Hegseth, unpubl.). Hence, diatom resting spores (and resting cells) in surface sediments are present and viable, and ready to be mixed to the surface layers and germinate after the vernal equinox.

6.4 The Spring Bloom

The spring season has been investigated several times since 2000, both as transects along the fjord and over the shelf during the years 2006–2008 and 2014, and at station Kb3 in 2002–2004 and 2006–2008 (Leu et al. 2006a; Hodal et al. 2012; Rokkan Iversen and Seuthe 2011; Seuthe et al. 2011; Hegseth and Tverberg 2013; Piquet et al. 2014). The fluorescence data from the mooring have given additional information about timing of the spring bloom, and temperature and salinity data have revealed the hydrographical conditions, helping to better understand the phytoplankton dynamics in the fjord.

6.4.1 Environmental Conditions

The most frequent hydrographical condition in Kongsfjorden in spring, except for a few years, has been a cold fjord with water temperatures similar to those in winter. Surface warming usually starts well after the spring bloom in the beginning of June, coinciding with the start of the melting and run-off season from the glaciers. But sometimes warmer water of Atlantic origin will enter the fjord, and during the last years the warm inflow seems to have increased and persisted. The winter/spring periods 2012–2014 have been warmer than average (Fig. 6.2b), and this was also observed in 2007 and 2008.

Another characteristic feature in spring has been the unstratified water masses during the bloom in cold years. This is similar to observations from Northern Norway (Eilertsen 1993), but it is by no means a phenomenon only from the Svalbard/northern Norwegian areas. It has frequently been observed offshore (Townsend et al. 1992, 1994). In a neutrally stable water column, blooms may commence if the vertical mixing does not produce light limitation by deep mixing (Townsend et al. 1994). This happens during the short period where the daily average heat flux across the air-sea interface tends to zero. In Northern Norway the spring bloom was observed to start when the heat flux switched from positive to negative values (warming of the sea). This minor warming, hardly visible on CTD profiles, was enough to trigger the bloom (Hegseth et al. 1995), probably by preventing deep mixing. Such a heat flux shift may also induce a bloom in Kongsfjorden even if there is no observable pycnocline. The late winter water is normally quite clear with deep light penetration (see below), and the rapidly increasing solar radiation and day length during spring in high latitude areas may lead to a phytoplankton bloom in the upper water column, despite the lack of vertical stratification, but not before the vernal equinox (see next chapter). During the warm years of 2007, 2008 and 2014, however, the AW in the surface layers stabilized the upper water column (Fig. 6.2a), which results in favourable condition for phytoplankton growth.

Ice cover in spring used to be the normal situation in Kongsfjorden (Svendsen et al. 2002; Pavlova et al., Chap. 4). But for many of the years after 2000 the ice conditions during spring have been variable, with ice melting and/or drifting in and out of the fjord in varying degree and times. Ice conditions can change within a day or two in the fjord because of ice drift. For years when ice cover was fairly stable during winter, it seemed to take 2–3 weeks from ice breakup until the spring bloom peaked, regardless of an April or May bloom, judged by the mooring and ice cover data (Table 6.2). Advection of ice into the fjord may delay the bloom peak due to light limitation of the incipient bloom.

Winter nutrient concentrations were sometimes reduced to values close to zero during the spring bloom, but not during all years (for nitrate, see Table 6.4). Blooms in April seemed to utilize all nutrients, while May blooms might not. This would partly depend on the size of the biomass produced during the spring bloom, and other factors may also influence the nutrient conditions (e.g. physical processes).

Table 6.4 Nitrate concentrations (μM) in the upper 10–20 m of station Kb3 in Kongsfjorden during the spring bloom period (before and after the peak)

Year	Date	Before the peak	After the peak	References
2002	18 April – 1 May	5.9	0.12	Hodal et al. (2012)
2003	27 April – 14 May	13.2	7.0	Leu et al. (2006a)
2006	18 March – 25 April	9.2	0.7	Rokkan Iversen and Seuthe (2011)
2008	09 April – 12 may	10.3	4.0	Piquet et al. (2014)

However, during May/early June most nutrients are depleted, so that the summer season normally starts in low-nutrient waters (Leu et al. 2006a; Hodal et al. 2012; Hegseth and Tverberg 2013; Piquet et al. 2014; Fig. 6.4).

The light situation is characterized by rapidly increasing day length at these high latitudes, with only 2 months separating the polar night and the midnight sun period (starting on 18 April). The water transparency in spring is normally high, as seen e.g. in 2008. This year had a deep euphotic zone (>70 m; Piquet et al. 2014) in the outer fjord prior to the phytoplankton spring bloom due to low particle content in the water. In contrast, close to the glacier, early run-off can modify the optical characteristics. During the phytoplankton bloom in 2006 the euphotic zone (calculated from Secchi disk measurements) was observed to be reduced to 10 m in the entire fjord (Fig. 6.5), even with a lower phytoplankton biomass at the innermost fjord station Kb5 (Hegseth and Tverberg 2013). The spring bloom in April 2006 was mainly confined within the fjord, but starting to spread out to the shelf. The bloom on the shelf was still going on in late May when the fjord bloom had ended, and in the Fram Strait a bloom was not observed until this time (Fig. 6.6). The euphotic zone in the outer fjord had then gradually increased towards 30 m during the post-bloom period, whilst at Kb5 (innermost fjord) there was no improvement in light conditions (Fig. 6.5). The next year (2007), however, with a smaller bloom occurring in May, the euphotic zone was 25–30 m throughout most of the fjord, including the innermost part (Hegseth and Tverberg 2013), where the light conditions were unaffected by the apparently low glacial runoff (Fig. 6.5). The runoff is obviously variable from year to year, adding to the variable light environment. The runoff must have been much higher in April 2008, reducing the euphotic zone to 10 m in the inner part of the fjord, but still 40 m in the outer fjord because the spring bloom was just about to start (Sperre 2010). Measurements (taken by a Li-Cor PAR sensor) from early April 2008 showed that the vertical light attenuation (K_d), normally low (0.10 m^{-1}) at this time, was enhanced to 0.15 m^{-1} in front of the Kongsbreen glacier. Melting and runoff from the glacier reduced the euphotic zone from about 10 m to 3–4 m by the end of spring (Piquet et al. 2014). Euphotic zone variability in Kongsfjorden mirrors both the glacier influence and the bloom magnitude and extent.

PAR intensities of 600–700 μmol m^{-2} s^{-1} (cosine-corrected sensors) have been measured at 5 m depth on a sunny day during the post-bloom period in late May, dropping to 200–300 on an overcast day (Leu et al. 2006a), corresponding to incoming PAR of 1200 and 700 μmol m^{-2} s^{-1}, respectively. Minimum values of incoming

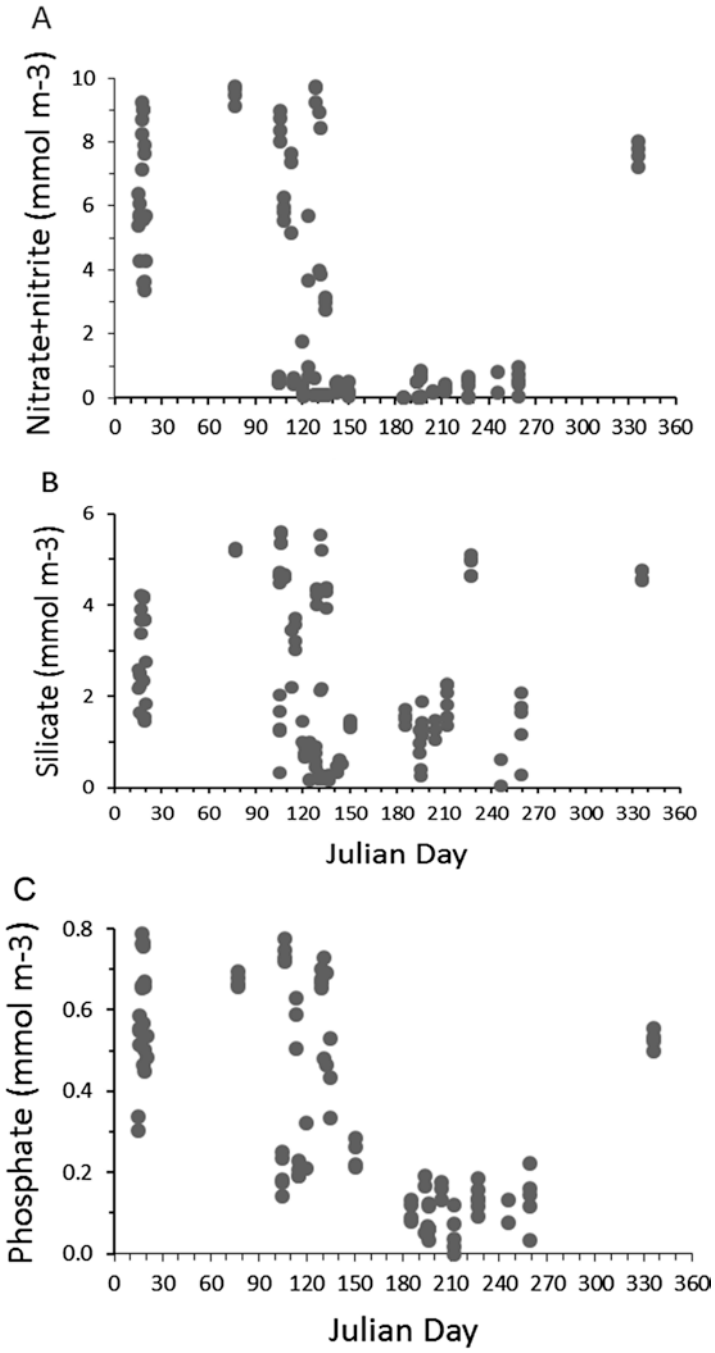

Fig. 6.4 Average concentrations of (**a**) nitrate+nitrite, (**b**) silicate and (**c**) phosphate in mmol m^{-3} in the upper 20 m at station Kb3 versus day of the year. N = 133, 136 and 97 respectively. (S. Kristiansen, unpublished data)

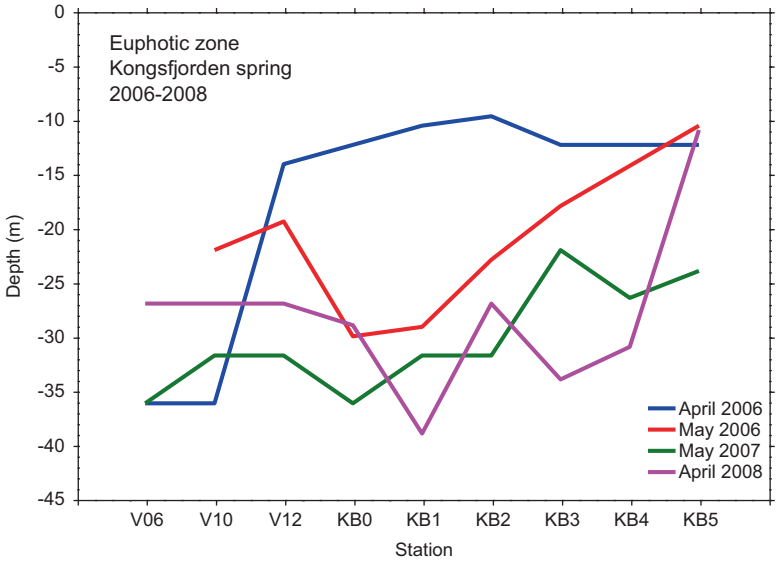

Fig. 6.5 Euphotic depth in Kongsfjorden measured during the spring bloom in 2006 and 2007, after the bloom in 2006 and at the beginning of the bloom in 2008. (Data from Hegseth and Tverberg 2013)

light during the midnight sun period were in the range of 100–300 µmol m^{-2} s^{-1} (Leu et al. 2006a), which illustrates that the phytoplankton will experience a pronounced day-night cycle during the entire productive season. More details about underwater light conditions in Kongsfjorden can be found in Pavlov et al. (Chap. 5).

6.4.2 Timing of the Spring Bloom

Sea–ice and hydrographic conditions in Kongsfjorden show great inter-annual variability, and so does the timing of the phytoplankton spring bloom. However, the controlling factors for the initiation of an algal bloom seem too complex to allow for a straightforward correlation between environmental conditions and bloom timing in a given year. Different spring scenarios that have been observed in Kongsfjorden are summarized below.

Before 2000, fast ice in the inner part of the fjord and various amounts of pack ice in the outer fjord (Svendsen et al. 2002) limited available light, and the spring bloom. Even though the bloom could be initiated under the ice in April, it did not peak until the end of May (Eilertsen et al. 1989; Wiktor 1999). Since 2000, many changes from this general development have been observed and the variability of the spring bloom timing has increased (we refer to the peak of the bloom when we

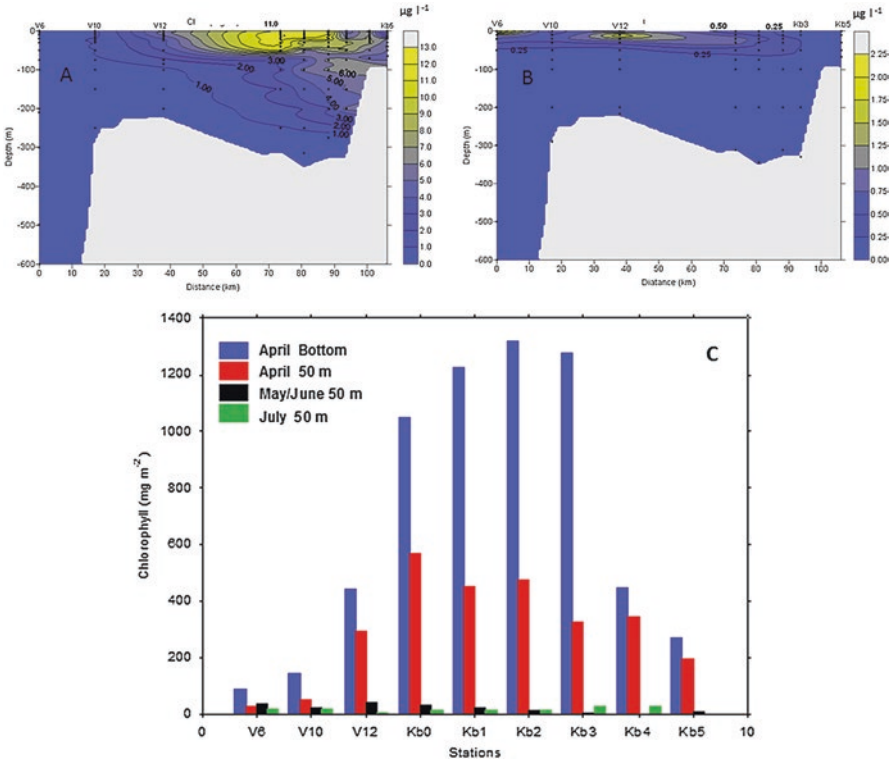

Fig. 6.6 Chlorophyll sections across Kongsfjorden and the adjacent shelf in 2006 during (**a**) the spring bloom in April and (**b**) in late May/early June, when high phytoplankton biomass was restricted to the outermost areas of the shelf and Fram Strait, while the bloom inside Kongsfjorden had terminated. (**c**) Integrated chlorophyll standing stocks in April (to bottom and to 50 m), late May (to 50 m) and July (to 50 m) for the same stations shown in the contour plots. (E.N. Hegseth, unpublished data)

discuss the concept of timing). During the period 2002–2014 an April bloom has occurred five times (in 2002, 2004, 2006, 2012, and 2013, Table 6.2), while a May bloom was observed in the remaining years (2003, 2007, 2008, 2009, 2010, 2011) except in 2014 when no bloom was observed until mid-June.

Mid-April seems to be the earliest period for a spring bloom to peak in Kongsfjorden. This is in accordance with findings that resting spores of several spring diatom species require 12 h day length to germinate and thus the majority of the biomass increase will not commence before the vernal equinox has been passed (Eilertsen et al. 1995). Early blooms are favoured during years with little or no pack-ice (but not necessarily with an observed pycnocline), and this has been the case for the first five years mentioned. The ice cover had either fragmented, melted, or drifted out of the fjord for a period of at least 2 weeks prior to bloom onset, or no ice had been present in the fjord during winter, except for the innermost part.

Accordingly, April blooms may occur both in cold and warm springs (Table 6.2), and do not seem to be related to the fast–ice cover in the inner part of the fjord (Fig. 6.2). No ice implies maximum light available to the growing cells, which is one of the requirements for an early bloom. However, another and equally important requirement is the presence of a suitable inoculum. In all the years with April blooms, the winter convection had reached the bottom during winter or early spring, illustrated by the 2006 bloom (Hegseth and Tverberg 2013), and provided spores to start the bloom. Hence, winter convection with mixing to the bottom layers is a prerequisite for a diatom spring bloom. The cold April springs (2002, 2004, 2006) were all of the winter type 1 or 2 by the definition of Tverberg et al. (Chap. 3), while 2012 and 2013 were warm years and belong to the 3a winter type.

However, timing of the spring bloom does not necessarily depend on a cold or warm spring (compared to a normal year, Table 6.2 and Fig. 6.2c). The important factors are the presence of sufficient light and inoculum. However, the years with May and June blooms may be divided into cold and warm years. The latter years had no ice, while cold years with May blooms (2003, 2009, 2010, and 2011, Table 6.2) are defined as years with variable amounts of drift ice in the fjord in spring until 2–3 weeks before the bloom. The ice cover had either melted or been transported out of the fjord by strong katabatic winds or water currents (Cottier et al. 2010), allowing a bloom to form. The spring bloom in 2003 was an example of a cold May bloom (Leu et al. 2006a). The long-lasting ice cover had delayed the bloom by reducing available light compared to an April bloom. But also for these blooms there is a requirement of deep winter convection to provide the bloom inoculum, and they are all either winter type 1 or 2 (Table 6.2).

During the warm years with a late bloom (2007, 2008, and 2014) the fjord had been open all spring with no or very little ice. Such conditions, often accompanied by a pronounced thermocline, should be favourable for an early spring bloom, but instead were characterized by blooms in late May or even June. In those years, the winter convection was severely reduced due to the AW surface inflow, acting as a lid on the fjord water (Hegseth and Tverberg 2013). They were examples of a hydrographical type 3a winter.

The delay of the blooms in these warm years had several other consequences, both for biomass and species composition. The spring bloom in April 2006 was massive and dominated by the typical spring diatoms and *Phaeocystis pouchetii*. The magnitude of the bloom in 2007 was reduced, and so was the number and abundance of diatoms species, while *Phaeocystis* was more dominant in 2007 than in 2006 (Hegseth and Tverberg 2013). This species, now found to have a pelagic winter stage, should consequently not be affected by changes in winter mixing. Nevertheless, no monospecific *Phaeocystis* blooms have been observed in the fjord prior to the diatoms, and a possible explanation for this is that this species needs to attach to a diatom cell before it is able to form colonies (Eilertsen et al. 1989; Jacobsen 2002; Nejstgaard et al. 2006). During the 2014 spring in Balsfjorden (Northern Norway), this process was observed to occur around the vernal equinox when the diatom cells started to become numerous. Cells of *Phaeocystis* attached themselves primarily to the setae of *Chaetoceros* cells (particularly *C. gelidus*), but

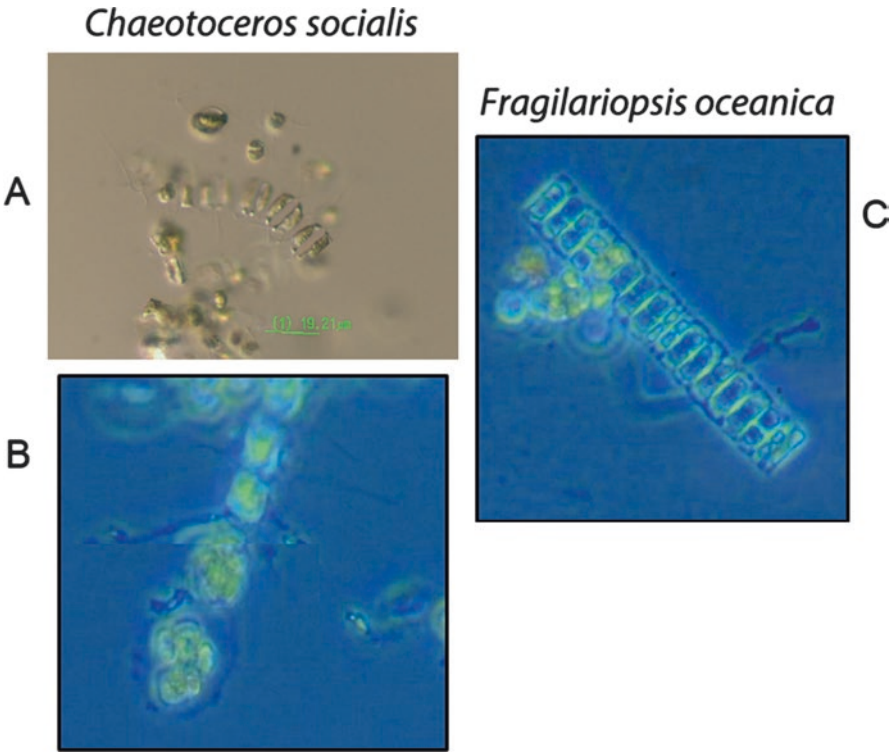

Fig. 6.7 Cells of *Phaeocystis pouchetii* attached to (**a**) and (**b**) chains of *Chaetoceros gelidus*, and (**c**) to a chain of *Fragilariopsis oceanica* at the start of the spring bloom in Balsfjorden, northern Norway. (J.M. Wiktor, unpublished data [A], E.N. Hegseth, unpublished data [B, C])

were also observed on chains of *Fragilariopsis oceanica* (Fig. 6.7). It seemed like one cell started to divide after attachment, and then, after a few divisions, developed the gel around the cells and acquired the look of a small colony (E.N. Hegseth, unpubl.). This process will undoubtedly be the same in Kongsfjorden, and, hence, low diatom abundance in the early bloom phase will most likely also have a negative effect on the *Phaeocystis* bloom.

The negative impact of the AW surface inflow on the Kongsfjorden spring bloom was particularly visible in 2008. When the bloom had barely started in Kongsfjorden in late April, a large, diatom-dominated bloom had already peaked in Isfjorden, which is another fjord on the western side of Svalbard, situated further south. In this fjord, AW did not penetrate into the fjord, but stopped at the entrance (Sperre 2010). Consequently, fjords along the west coast of Svalbard may simultaneously experience very different hydrographic conditions, leading to large differences in spring bloom timing and magnitude in the same year.

The extensive AW inflow in 2014 had a significant impact on the spring bloom. Very low phytoplankton biomass was registered in spring at least until mid-May,

and except for a small peak of 0.25 µg L^{-1} at 30 m at station Kb3, chlorophyll values in the rest of the fjord were < 0.1 µg L^{-1}. According to the mooring data, the bloom peaked in mid-June. Unfortunately, we do not have plankton samples from this June bloom and therefore cannot comment on its species composition. In any case, 2014 was an exceptional year in Kongsfjorden. The AW surface inflow all winter, particularly strong in November/December and February/March (Fig. 6.2a), probably prohibited extensive mixing to the bottom, so that almost nothing but small flagellates grew in cultures established from water collected in January (E.N. Hegseth, unpubl.). Viable cells of some dinoflagellates and diatoms, all with pigments, were observed in the surface waters. But like the cultured samples, they did not belong to the spring bloom species (Berge et al. 2015). Winter-water samples from earlier years and other Svalbard fjords (Adventfjorden, Billefjorden, E.N. Hegseth, unpubl.), as well as Rijpfjorden (Brown et al. 2015), always produced many of the spring diatom species when grown in the lab. Resting spores are normally present at abundances <10–20 spores L^{-1}, too low to be detected in microscope samples of 50–100 mL, but they can be detected when grown in lab cultures. As described earlier, the Kongsfjorden sediment samples from January resulted in the growth of several spring bloom diatoms in the lab. This shows that their resting spores were present and viable in the surface sediments. Despite the seemingly favourable growth conditions in 2014, with an early ice break up, high nutrient concentrations (Table 6.3), and with a well-developed thermocline, an early spring bloom did not develop. Obviously, in spring 2014 the diatom inoculum was lacking because AW surface inflow prevented deep winter convection and mixing, as postulated by Hegseth and Tverberg (2013). The lack of diatom resting spores in the water column in January supports this conclusion. The idea of resting spores acting as a seed population for the spring bloom was already suggested by Gran in 1912, and later his idea was tested and found valid for different areas (Garrison 1981, 1984). Resting spores of diatoms probably add to the seeding of the spring bloom in shelf areas in general, but it is north of the Arctic Circle that this process becomes crucial due to the long, dark winter. Vegetative cells in general do not survive there, and the over-wintering stage is a resting spore, or a resting cell (Sicko-Goad et al. 1989; Kuwata et al. 1993).

The timing of the spring bloom in Kongsfjorden is controlled by several environmental factors. To form a phytoplankton bloom, one needs an inoculum of cells. In Kongsfjorden, the diatom resting spores and the winter stage of *Phaeocystis* primarily form this inoculum. The spores are provided by the deep winter convection, which needs to reach the bottom layers. This may happen either in the cold fjord water unaffected by AW inflow, or by AW inflow along the bottom. A strong bottom current in the AW inflow will mix up sediments along its path, which may be a crucial factor for supplying diatom spores to the water column. Finally, convection to the bottom may also take place if the fjord is filled with AW and the water column is homogeneous. After germination the newly formed cells need sufficient light to grow, hence, no/little ice cover in the fjord is another factor that will govern an early bloom. A pronounced pycnocline is not necessary to start the growth after germination, but ongoing cooling of the water masses is a negative factor. But even with a

Table 6.5 Controlling factors of the spring bloom in Kongsfjorden in the period 2002–2014, and the timing of the bloom

	Convection		Ice cover		Bloom timing			
Year	Bottom	Surface	Early melt	Long lasting	April	Early May	Late May	June
2002	X		X					
2003	X			X		X		
2004	X		X		X			
2005	X							
2006	X		X		X			
2007		X	No ice				X	
2008		X	No ice				X	
2009	X			X		X		
2010	X			X		X		
2011	X			X			X	
2012	X	X	No ice		X			
2013	X	X	No ice		X			
2014		X	No ice					X

pycnocline and sufficient light a bloom will not develop if the inoculum is missing. The controlling factors and timing of the spring bloom in the years between 2002 and 2014 (Table 6.5) can be divided into three groups, depending on ice conditions and the winter/early spring convection. These are illustrated in Fig. 6.8, as a schematic of the processes and of the species development for diatoms and *Phaeocystis*.

(A) April bloom (mid or late; 2002, 2004, 2006, 2012, 2013) (Fig. 6.8a)

1. Convection to the bottom
2. Early melt of ice cover, or no ice

(B) May bloom (early or late; 2003, 2009, 2010, 2011) (Fig. 6.8b)

1. Convection to the bottom
2. Long lasting ice cover (May)

(C) May bloom (late) or June bloom (2007, 2008, 2014) (Fig. 6.8c)

1. Shallow mixing (surface layers)
2. No ice

For other Arctic fjords, like Godthåbsfjord in Greenland, hydrographic conditions and wind seem to be the crucial factor controlling the spring bloom (Meire et al. 2016). Strong upwelling in the inner part of the fjord, driven by out-fjord winds and inflow of coastal water (Meire et al. 2015), probably ensures the necessary inoculum. Although little information on the spring phytoplankton species is given, both diatoms and *Phaeocystis* are involved in the bloom (Juul-Pedersen et al. 2015). Hence, in this fjord wind strongly determines the timing of the bloom, and as such, Kongsfjorden and Godthåbsfjord are controlled by different environmental factors during spring.

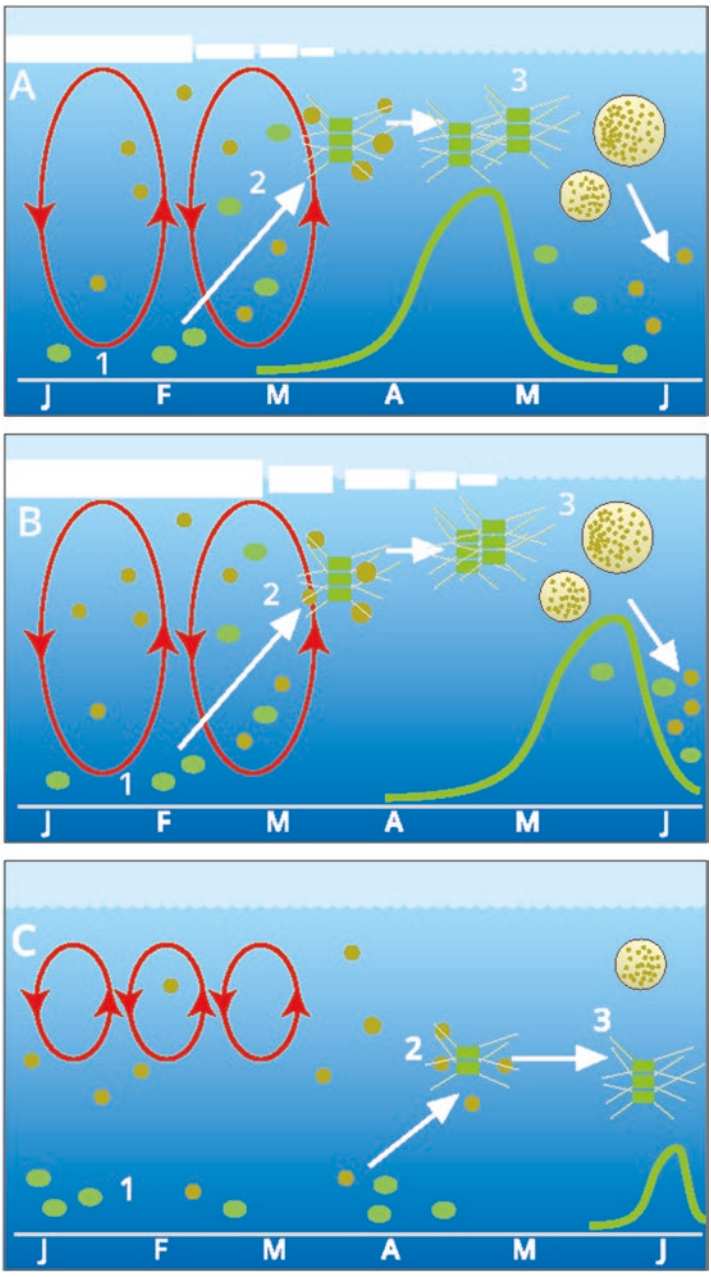

Fig. 6.8 Schemes of the spring bloom types in Kongsfjorden. (**a**) Group A spring bloom (deep convection, early ice melt, early bloom), (**b**) Group B spring bloom (deep convection, late ice melt, late bloom, (**c**) Group C spring bloom (shallow convection, no ice, very late bloom). Green dots = diatom resting spores, brown dots = *Phaeocystis* single cells, green squares = diatom (*Chaetoceros*) colony, circles with brown dots = *Phaeocystis* colonies. Green line = chlorophyll biomass during spring. The 3 phases of the bloom: 1.Winter with spores on the bottom, *Phaeocystis* cells in the water column; 2. Early spring (group A) or spring (group B or C) with spores germinated into cells and *Phaeocystis* single cells attached to diatom colonies; 3. Bloom with diatom colonies and *Phaeocystis* colonies

6.4.3 Spring Bloom Development: Spatial Patterns, Biomass, Production and Fate of the Bloom

The start and early development of the spring bloom seem to be geographically localized in the fjord. Svendsen et al. (2002) summarized the general current patterns in Kongsfjorden. Water masses are entering the fjord along its southern shore and leaving along its northern shore. This pattern is reflected in chlorophyll transects perpendicular to the fjord axis (Fig. 6.9a) that revealed higher phytoplankton biomass on the northern shore in different years with various spring conditions (Fig. 6.9b–e). Hence, this seems to be a recurrent phenomenon in the fjord. The standard transects along the mid-fjord axis presumably represent an average situation.

Even in spring 2014, when no bloom was recorded during a cruise in mid-May, there was a small, but distinct difference in the fluorescence profiles taken on either side of the fjord (Fig. 6.9c). Abundances averaged over the upper 20 m were almost fourfold higher at station M1 (175×10^3 cells L^{-1}) at the northern end of transect A (the innermost transect, Fig. 6.9a), compared to the central station Kb3 (46.5×10^3 cells L^{-1}), while 70×10^3 cells L^{-1} were counted at station M5 on the southern shore (E.N. Hegseth unpubl.). Diatoms at M1 were abundant with 62×10^3 cells L^{-1} at 10 m depth, which accounted for 27% of total phytoplankton abundances, while they (with some exceptions) were found in insignificant numbers ($<5 \times 10^3$ cells L^{-1}, or < 1% of phytoplankton abundances) at the other stations. Nutrient concentrations exhibited winter values in most parts of the fjord (Table 6.3), except for station M1. The cross-fjord transect A (Fig. 6.9a) was the only location where an incipient bloom could be traced, with average nitrate values slightly reduced in the upper 20 m: M1 (northern shore) 8.5 μM, Kb3 (middle of transect) 9.7 μM, M5 (southern shore) 10.4 μM. No cross-fjord transects were conducted closer to the inner fjord, but the innermost station Kb5 exhibited 10^4 diatoms L^{-1} at the surface, which amounted to 20% of total cell numbers. Hence, the inner and northern part of the fjord showed the highest diatom abundances, so it seems likely that the spring bloom in Kongsfjorden started at the innermost part and on the northern shore before spreading out to the rest of the fjord. Based on the distribution patterns from other years (Fig. 6.9b, d, e) we may conclude that this is the general spatial pattern of the spring bloom development. This is different from Godthåbsfjord in Greenland, where the spring bloom first developed in the mid- and outer fjord, and only moved to the inner part after the general wind direction changed to in-fjord wind in late May/early June (Meire et al. 2016).

The biomass of spring blooms, with maximum observed chlorophyll concentrations of 12.5–14.5 μg L^{-1} in 2006 (Table 6.2), was comparable to the 2008 measurements from Isfjorden (Sperre 2010). Maximum integrated chlorophyll biomass (down to bottom) in Kongsfjorden amounted to almost 1.4 g m^{-2} during the 2006 spring bloom, whereas peak chlorophyll biomass recorded in the upper 50 m was 565 mg m^{-2}, compared to <50 mg m^{-2} measured later in the summer (Fig. 6.6c). The spring biomass was a little higher than measured in Isfjorden in 2008 (385 mg m^{-2},

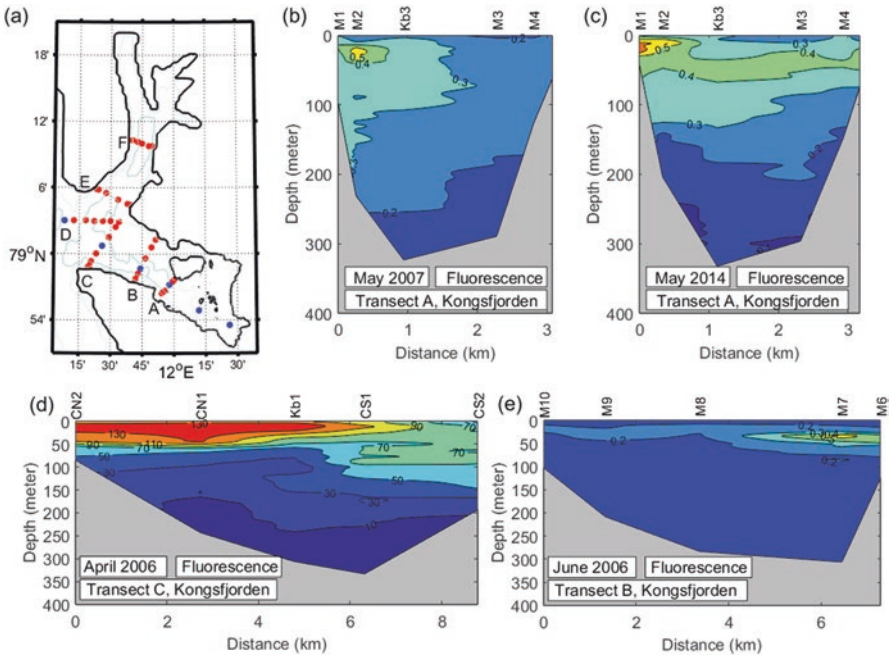

Fig. 6.9 Positions of cross-fjord transects in Kongsfjorden marked A, B, C on the map (**a**). Examples of cross-fjord transects in Kongsfjorden showing earlier bloom development on the northern side (to the left) of the fjord in (**b**) May 2007, (**c**) May 2014, and (**d**) April 2006. In June 2006 (**e**) the bloom had terminated on the northern side, but was still present on the southern side. Blue dots: Main stations (Kb5-Kb0); red dots: sampling stations along the cross-fjord transects. Transect A: May 2007 and 2014 with station M1 on northern side, M4 on southern side; transect B: June 2006 with station M10 on northern side, M6 on southern side; transect C: April 2006 with station CN2 on northern side, CS2 on southern side. (V. Tverberg, unpublished data)

Sperre 2010), but 5 times the biomass in Rijpfjorden on Nordaustlandet in spring 2007 (100 mg m^{-2}, Leu et al. 2011). Godhåbsfjord in Greenland seems to be in the same range as the western Svalbard fjords (Meire et al. 2016). In the middle and outer part of Kongsfjorden only 1/4 to 1/3 of the integrated chlorophyll biomass was located above 50 m, which indicated ongoing sinking (Fig. 6.6c). Station Kb2 had the highest biomass integrated to the bottom, whereas station Kb0 exhibited most chlorophyll above 50 m. The highest chlorophyll concentrations were located in the outer part of the fjord and over the inner shelf (stationV12). This was also the area with the highest cell numbers of 14×10^6 cells L^{-1} in 2006 (Hegseth and Tverberg 2013). During the spring bloom in 1984 even higher abundances of up to 17×10^6 cells L^{-1} were recorded (Eilertsen et al. 1989). For comparison, the Isfjorden bloom in 2008 exhibited only maximum abundances of 2×10^6 cells L^{-1}.

Kongsfjorden thus appears to be a highly productive fjord during spring, but primary production data from spring are scarce, only measurements from two seasons have been published (Rokkan Iversen and Seuthe 2011; Hodal et al. 2012).

Primary productivity of 0.4 g C m^{-2} d^{-1} during the 2006 bloom was fairly low (Rokkan Iversen and Seuthe 2011), compared to 1.5–1.9 g C m^{-2} d^{-1} during the 2002 bloom (Hodal et al. 2012). The latter is comparable to other bloom measurements from the Barents Sea and Svalbard waters (Hirche et al. 1991; Vernet et al. 1998; Hodal and Kristiansen 2008), and from Godthåbsfjord in Greenland (Juul-Pedersen et al. 2015), indicating that the 2006 data may have been taken in a post-bloom stage with reduced production rates.

During the 2006 spring bloom, diatoms made up 12% of the total cell numbers and *Phaeocystis* about 87% at station Kb3 (Hegseth and Tverberg 2013). Comparable numbers were found for the carbon biomass distribution (10% diatoms, 82% *Phaeocystis*, Rokkan Iversen and Seuthe 2011). Only 1% of the carbon biomass constituted heterotrophs (Rokkan Iversen and Seuthe 2011). This group, consisting of heterotrophic dinoflagellates (Table 6.6) and ciliates, probably imposed a heavy grazing pressure on the bacteria and small nanoplankton flagellates, and keeping the microbial food web active (Rokkan Iversen and Seuthe 2011), but not on diatoms and *Phaeocystis* colonies. The grazing pressure on the bloom-forming diatoms and *Phaeocystis* colonies is probably moderate since zooplankton abundance in spring is generally still low (Willis et al. 2008; Walkusz et al. 2009). Cirripedia larvae and small copepods like *Oithona similis* can be abundant in spring (Willis et al. 2006; Walkusz et al. 2009; Kwasniewski et al. 2013), but the former usually show a very patchy distribution and the latter are unlikely to substantially graze on the large colonies of the bloom-forming species. Thus, the bulk of the spring bloom is likely exported to the bottom ungrazed, as seen during the 2006 bloom (Fig. 6.6a, c), even though high abundances of *Calanus finmarchicus* was observed entering the fjord along with the AW inflow during winter (Willis et al. 2008). Sedimentation investigations from Kongsfjorden later than 2000 are not available, but from Adventfjorden, a side arm to Isfjorden, the main sedimentation peak of large cells (>20 μm), represented as chlorophyll, occurred during the spring bloom in 2007, and very little at other times of the year (Zajaczkowski et al. 2010). The same pattern was observed at the mouth of Adventfjorden in the early phase of the 2012 spring bloom, and the peak mainly consisted of diatoms (Wiedmann et al. 2016). Considerably lower vertical fluxes of chlorophyll were observed during the late spring, and this was interpreted both as a change into a *Phaeocystis*-society with less diatoms, and increased grazing (Wiedmann et al. 2016). A similar scenario may also take place in Kongsfjorden, and could explain low sedimentation rates measured in earlier years (Wiktor 1999).

6.4.4 Species Composition

During the spring bloom in Kongsfjorden, like in other Arctic areas, diatoms are a very important group with more than 60 species identified (Hop et al. 2002). In addition the haptophyte *Phaeocystis pouchetii* is always a major component (Eilertsen et al. 1989; Leu et al. 2006a; Hodal et al. 2012; Hegseth and Tverberg

Table 6.6 Phytoplankton species with maximum recorded cell numbers (× 10^3 L^{-1}) from the whole fjord in spring (years between 2003 and 2013) and in summer (July, between 2009 and 2013)

	Cells × 10^3 L^{-1}			
	Whole fjord		Station Kb3	
Species	Spring 2003–2013	July 2009–2013	25.04.06	July 2009–2013
Bacillariophyta				
Attheya septentrionalis	11		2.9	
Bacillaria paxilifer			9.8	
Berkeleya sp.			23	
Ceratoneis closterium	11	1.6	6.1	0.4
Bacterosira bathyomphala	55		14	
Chaetoceros ceratosporum			1.5	
Chaetoceros compressus	150			
Chaetoceros convolutus			15	
Chaetoceros curvisetus			4.3	
Chaetoceros debilis	440			
Chaetoceros decipiens	55			
Chaetoceros diadema	110			
Chaetoceros furcellatus	920		411	
Chaetoceros furcellatus resting spores	1.5			
Chaetoceros gelidus	800		165	
Chaetoceros karianus	290			
Chaetoceros simplex		3.9		3.9
Chaetoceros teres			0.3	
Chaetoceros wighamii	790		248	
Chaetoceros spp.	460	0.7	12	0.7
Detonula glomerata			24	
Entomoneis paludosa	33		5.9	
Eucampia groenlandica			11	
Fossula arctica	150			
Fragilariopsis cylindrus		11	28	
Fragilariopsis oceanica	880	2.8	115	2.8
Fragilariopsis pseudonana		1.1		
Fragilariopsis sp.	610	15		
Lennoxia faveolata		8.6		2.5
Licmophora gracilis		3.3		
Licmophora sp.		0.1		0.1
Navicula directa			1.5	
Navicula pelagica	200		66	
Navicula sp. ribbon			2.2	
Navicula septentrionalis			35	

(continued)

Table 6.6 (continued)

Species	Cells × 10^3 L^{-1}			
	Whole fjord		Station Kb3	
	Spring 2003–2013	July 2009–2013	25.04.06	July 2009–2013
Navicula transitans			35	
Navicula vanhoefenii			39	
Navicula sp.	77		2.2	
Nitzschia frigida			3.6	
Nitzschia polaris			5.2	
Nitzschia promare	160		0.7	
Nitzschia sp.		0.3		0.3
Odonthella aurita	22		2.7	
Pennales indet.	240	2.4		0.7
Porosira glacialis			3.0	
Pseudo-nitzschia granii		2.4	10	2.1
Pseudo-nitzschia pungens		2.0		2.0
Pseudo-nitzschia seriata			3.0	
Pleurosigma fasciculata			0.3	
Pleurosigma sp.	11		1.4	
Rhizosolenia hebetata f. *semispina*		0.1		
Skeletonema costatum			4.3	
Thalassiosira antarctica var. *borealis*	33	1.0	97	
Thalassiosira glomerata			17	
Thalassiosira hyalina	99		25	
Thalassiosira nordenskjoeldii	340	2.1	194	2.1
Thalassiosira spp.	340	3.3		3.3
Chlorophyta				
Chlamydomonas sp.		3.0		
Pyramimonas sp.		76	35	76
Pachysphaera pelagica		9.5		9.5
Chlorophyta not assigned		44		5.0
Chrysophyceae				
Dinobryon balticum		7.9		7.9
Dinobryon faculiferum		2.4		
Chrysophyceae indet.		86		29
Ciliophora				
Mesodinium rubrum		6.3		
Cryptophyta				
Cryptomonas sp.	54	98	32	
Leucocryptos marina		11		11
Plagioselmis prolonga		1.1	2.7	1.1
Teleaulax sp.		20		20
Telonema sp.		4.5		2.1

(continued)

Table 6.6 (continued)

Species	Cells × 10^3 L^{-1}			
	Whole fjord		Station Kb3	
	Spring 2003–2013	July 2009–2013	25.04.06	July 2009–2013
Cryptophyta indet		20		61
Dictyochophyceae				
Dictyochophyceae indet.		30		
Pseudopedinella pyriformis		2.7		
Dinophyceae				
Alexandrium minutum			4.0	
Alexandrium sp.		210	2.7	210
Amphidinium spp.		1.6		1.6
Amylax triacantha		0.4		0.4
Ceratium arcticum				
Cochlodinium sp.		3.2		3.2
Dinophyceae indet.		1.2		1.2
Dinophysis norvegica		5.8		5.8
Gonyaulax sp.		2.0		2.0
Gymnodiniales indet. *> 20 µm*	33			
Gymnodiniales indet. *10–20 µm*	77			
Gymnodiniales indet. *< 10 µm*	240			
Gymnodinium arcticum	38		72	
Gymnodinium galeatum		47		47
Gymnodinium gracilentum		44		44
Gymnodinium pulchellum			5.2	
Gymnodinium simplex		19		8.6
Gymnodinium wulffii		5.4	15	19
Gymnodinium spp.		47	0.9	5.4
Gyrodinium flagellare		6.2		4.9
Gyrodinium formosum		1.0		
Gyrodinium fusiforme		1.5	1.5	
*Gyrodinium grave**		0.1		
*Gyrodinium lachryma**			0.9	
*Gyrodinium spirale**		0.1		
Gyrodinium spp.		1.1	3.7	0.8
Heterocapsa minima		5.1		5.1
Heterocapsa rotundata		25		15
Heterocapsa sp.		2.2		2.2
Heterocapsa triquetra	5	4.2	15	4.2
*Katodinium glaucum**		4.9	2.0	1.9
Lessardia elongata		2.5		
*Micracanthodinium claytonia**		5.0		5.0
Nematopsides vigilans		0.1		0.1

(continued)

Table 6.6 (continued)

Species	Cells × 10^3 L^{-1}			
	Whole fjord		Station Kb3	
	Spring 2003–2013	July 2009–2013	25.04.06	July 2009–2013
Neoceratium arcticum		0.1		0.1
*Oxyrrhis marina**		25		6.3
Pentapharsodinium sp.		0.7		0.7
*Phalacroma rotundatum**		2.5		2.5
*Pronoctiluca pelagica**		2.1		2.1
Prorocentrum cordatum		2.4		
Prorocentrum spp.		38		34
*Protoperidinium brevipes**		7.4		7.4
*Protoperidinium cerasus**		5.9		5.9
*Protoperidinium pallidum**		2.0		1.0
*Protoperidinium pellucidum**		3.7	0.9	3.7
*Protoperidinium pyriforme**		0.1		0.1
Protoperidinium spp.*	11	0.2	3.1	0.2
*Protoperidinium bipes**	11	4.7	1.4	2.0
Scrippsiella sp.		9.2		9.2
Scrippsiella trochoidea		2.3	1.5	2.3
Torodinium robustum		1.5		
Euglenoidea				
Eutreptiella sp.		2.7		
Prymnesiophyceae				
Phaeocystis pouchetii	13,000	37	6313	2.1
Algirosphaera robusta		8.6		4.8
Emiliania huxleyi		28		28
Coccolithales indet		85		85
Prymnesium sp.		2.2		
Flagellates				
Flagellates indet. < 5 µm	3000	241	13	241
Xantophyceae				
Meringosphaera sp.		1.6		1.0

Included are also numbers from station Kb3 (outside Ny-Ålesund) from the spring bloom peak in 2006 and from summer (July, between 2009 and 2013). Dinoflagellates marked with an asterix (*) are heterotrophic species according to Tomas (1997) (J.M. Wiktor, unpublished data)

2013). Peak bloom abundances of phytoplankton in Kongsfjorden are listed in Table 6.6 for the decade between 2003 and 2013. One date with maximum numbers from station Kb3 during the 2006 bloom is also included, as a comparison. The most numerous diatom species, regardless of year and station, were *Chaetoceros gelidus, C. furcellatus, C. wighami, Thalassiosira nordenskioeldii* and *Fragilariopsis oceanica*, all of which are common species found in the fjords and along the coast of northern Norway and in the Barents Sea (Degerlund and Eilertsen 2010).

However, there were large inter-annual variations in phytoplankton biomass (here measured as cell numbers), which also manifested itself in the specific-species abundances, as illustrated by the large difference in the *Chaetoceros gelidus* abundances in 1984 with almost five million cells L^{-1} (Eilertsen et al. 1989) and 2006 with only 800 × 10^3 cells L^{-1} (E.N. Hegseth, unpubl.). For *Phaeocystis*, the cell numbers were virtually the same in these 2 years. A succession of phytoplankton species is well-known for the spring bloom (von Quillfeldt 2000). This can explain some of the inter-annual differences in species-specific abundances, but abundance will also depend on sampling time in relation to the bloom peak.

Repeated sampling has mainly been restricted to the one station outside Ny-Ålesund (Kb3), but comprised several spring seasons. The 2002 bloom developed from a dominance of *Fragilariopsis oceanica* to one of several *Chaetoceros* species, followed by *Thalassiosira* species and finally *Phaeocystis* colonies (Hodal et al. 2012). Next year showed much of the same succession, with *Fragilariopsis oceanica* dominating at the start of the bloom, then with *Thalassiosira antarctica* var. *borealis*, followed by a mix of *Chaetoceros gelidus*, *C. furcellatus* and *T. nordenskioeldii* (Leu et al. 2006a). The bloom in 2007 was low in diatom abundance, as described earlier, and not all the common spring species were observed. The succession was slightly different, starting with a mixture of *C. gelidus, C. debilis, T. antarctica* var. *borealis* and *T. hyalina*. During the peak of the bloom *C. furcellatus, T. nordenskioeldii, F. oceanica, Bacterosira bathyomphala* occurred in addition, but *Phaeocystis* dominated in abundance. This dominance increased as diatoms sank out, so that by the end of the bloom there was mostly *Phaeocystis* left, while diatoms were represented by a few resting spores of *C. furcellatus* and a few sinking cells of *Thalassiosira* at 80 m (E.N. Hegseth, unpubl.). In the post-bloom period of 2007, smaller flagellates such as chlorophytes, cryptophytes, dinoflagellates and cyanobacteria were relatively abundant (Piquet et al. 2014). The rapid termination of the 2007 bloom probably was a result of spore formation and sedimentation of diatoms and sinking of *Phaeocystis* colonies. The spring diatom species are neritic, mostly from the Arctic neritic group and the rest from the Northern temperate neritic group according to Gran's definition of species (Gran 1912). *Phaeocystis* colonies have been observed to sink in high masses by the end of a bloom (Wassmann et al. 1990).

Even though diatoms and *Phaeocystis* dominated the spring bloom, there were dinoflagellates present. The most numerous groups were athecate (naked) species, most of which could not be identified to species level. They are normally divided into size classes, and species <10 µm dominated among the dinoflagellates (Table 6.6). Among the identified athecate genera, *Amphidinium, Gymnodinium* and *Gyrodinium* dominated, with *Gymnodinium arcticum* as the single most dominant species in 2006 with 38 × 10^3 cells L^{-1} as an average for the upper 50 m (Seuthe et al. 2011). Thecate (armoured) dinoflagellates were less abundant with 11 × 10^3 cells L^{-1} for *Protoperidinium bipes* (E.N. Hegseth, unpubl.), 5 × 10^3 cells L^{-1} for *Heterocapsa triquetra* (average upper 50 m), and 0.2 × 10^3 cells L^{-1} for *P. pellucidum* (Seuthe et al. 2011). Integrated biomass of dinoflagellates (0–50 m) during the 2006 spring bloom amounted to 1.7 g C m^{-2} (Seuthe et al. 2011). Unfortunately,

we do not have carbon biomass for the other groups during this bloom. In 2003, diatoms made up 72–87%, haptophytes maximally 15%, and dinoflagellates and small flagellates about 1% each of the carbon biomass. The total maximum carbon biomass recorded during the bloom was about 7–8 g C m^{-2}, hence, the fraction of dinoflagellate biomass may have been smaller this spring (Leu et al. 2006a). The pre-bloom conditions in spring 2014 were characterized by a large contribution of dinoflagellates to the phytoplankton community (E.N. Hegseth, unpubl.). Dinoflagellates were in general evenly distributed in the fjord, with average abundances of 20–30 × 10^3 cells L^{-1} (30–50% of total phytoplankton abundances), and maximum cell numbers of 40 × 10^3 cells L^{-1}. The most numerous species was *Gymnodinium arcticum* with maximum abundances of 15 × 10^3 cells L^{-1}. Except for diatoms, small flagellates made up the rest of the phytoplankton community.

After the spring bloom, a change in the species composition of the fjord marked the entrance to the summer season. One of the most striking features was the increase of dinoflagellates relative to the other groups, and the lack of spring diatom species and *Phaeocystis*, illustrated by the 2007 season at station Kb3 (Fig. 6.10). In 2006, the diatoms were replaced by dinoflagellate species like *Phalacroma rotundatum*, *Dinophysis acuminata*, *Gyrodinium* cf. *spirale* and *Amphidinium* sp. (E.N. Hegseth, unpubl.). Dinoflagellates became an increasingly more important group as the seasons progressed, together with *Emiliania huxleyi*, which entered the fjord at the end of May with 30 × 10^3 cells L^{-1}. On the shelf, however, the small

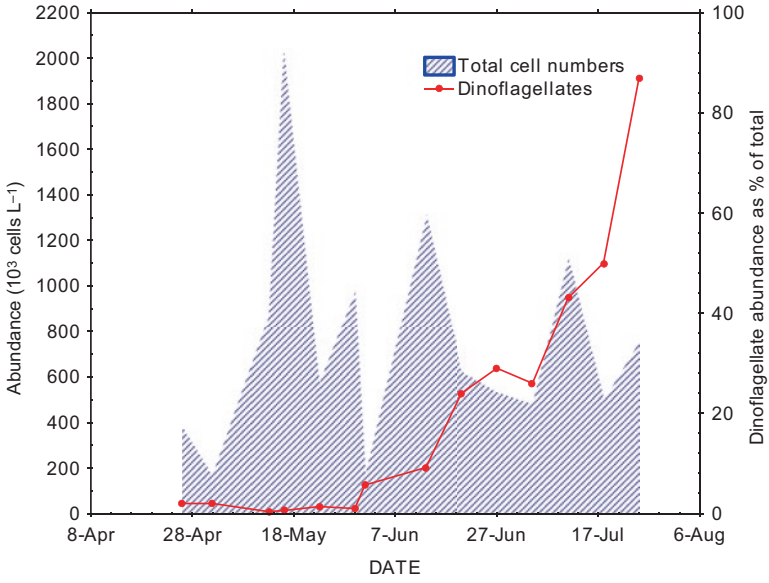

Fig. 6.10 Phytoplankton abundance at station Kb3 in spring and summer 2007. Hatched areas are total cell numbers L^{-1}, while red line represents the % contribution of dinoflagellates. (E.N. Hegseth, unpublished data)

bloom observed (Fig. 6.6b) had primarily the same diatoms that previously bloomed in the fjord. It is likely that fjord blooms continue over the shelf, but probably not into Fram Strait. The minor biomass located at the outermost station V6 at the same time was dominated by small flagellates, some dinoflagellates and very few diatoms, which belonged to other species than in the fjord (E.N. Hegseth, unpubl.). The fjord/shelf and Fram Strait seem to harbour distinct phytoplankton assemblages, with neritic species dominating in the former and oceanic species in the latter domain.

6.4.5 Fatty Acids and Photoprotective Pigments

Concomitantly with the description of the taxonomic and biomass development of the spring bloom in 2003 and the post-bloom period in 2004, the community fatty acid and pigment composition were studied with a high temporal resolution (sampling approximately once-twice a week in April–June). As fatty acids (and pigments) reflect to a great extent the functional groups of algae they are produced by, these variables showed a clear succession from a diatom-dominated state during early and peak-bloom conditions, to a post-bloom situation where flagellate markers were prevailing (Leu et al. 2006a; E. Leu, unpubl.). Long-chained polyunsaturated fatty acids (PUFAs) that are of great nutritional value, and efficiently enriched in higher trophic levels, were highest during the early phase of the bloom (up to 47% of total fatty acids), and considerably lower during the post-bloom period (only 20–25%). The dominance of diatoms was indicated by high percentages of 20:5(n-3) and 16:4(n-1) PUFAs, as well as the monounsaturated fatty acid (MUFA) 16:1(n-7), while increased levels of 18:3(n-3) and 22:6(n-3) reflected higher numbers of flagellates in the respective samples taken later in the season. In addition to changes in phytoplankton community composition, also the gradual decrease in nutrient availability during the bloom affected the phytoplankton fatty acid composition. Constrained multivariate analyses of the datasets proved furthermore a statistically significant correlation between higher irradiances and lower levels of PUFAs under stratified conditions during the post-bloom period in 2004. No such patterns were found during the bloom in 2003, where the water column was homogenous with respect to temperature and salinity. This negative impact of high irradiances on fatty acids was confirmed by outdoor and *in situ* experimental studies in Kongsfjorden during spring 2004 and 2008 (Leu et al. 2006b). Contrary to the working hypothesis of these studies, ultraviolet radiation (UVR, 280–400 nm) did not have a particularly detrimental effect on PUFAs, but led only to a moderate deterioration of the negative impact of high visible light (photosynthetically active radiation, PAR, 400–700 nm). Under stratified conditions, the ratio of photoprotective pigments (zeaxanthin and lutein) to Chl *a* were also significantly higher in the samples taken in the uppermost 10 m of the water column than in the samples taken between 10 and 50 m depth. This confirms the occurrence of light stress under *in situ* light conditions close to the surface.

6.5 The Stratified Summer Season

During summer, phytoplankton was either repeatedly sampled at a fixed location outside Ny-Ålesund at variable temporal resolution (Piquet et al. 2010; Seuthe et al. 2011; Rokkan Iversen and Seuthe 2011; Mayzaud et al. 2013) or during ship-based oceanographic transects along the fjord axis (Kang et al. 2003; Wiktor and Wojciechowska 2005; Piwosz et al. 2009, 2015; Wang et al. 2009; Kubiszyn et al. 2014; Lydersen et al. 2014). In addition, phytoplankton and chlorophyll have been sampled every July since 2009 and nutrients since 2011 (Table 6.1) during the annual Kongsfjorden "*Climate and Ecosystem-MOSJ*" cruises by the Norwegian Polar Institute, extending the standard Kongsfjorden transect (Kb stations) out onto the adjacent shelf (V stations).

6.5.1 Environmental Conditions

With the exception of drifting glacier ice, Kongsfjorden has been largely ice-free during recent summers (Pavlova et al., Chap. 4). The light climate experienced by phytoplankton is thus not negatively affected by light attenuation by sea ice and overlying snow (Pavlov et al., Chap. 5). At its head, Kongsfjorden is lined by predominantly tide-water glaciers, in particular Kongsvegen, Kongsbreen and Kronebreen, that terminate at the sea (Nuth et al. 2013) and introduce large volumes of melt-water, most significantly through in- or subglacial drainage, into the marine system during the summer melt season (Keck 1999; Keck et al. 1999; Lydersen et al. 2014). At the glacier front, melt-water thus enters the marine system at bottom to intermediate depth, as opposed to surface run-off in river estuaries, and subsequently rises to the surface due to its positive buoyancy relative to seawater. These melt-water plumes or "brown zones" (Fig. 6.11) carry large amounts of suspended sediments, mainly silt and clay minerals, and strongly reduce the submarine light field as evidenced by the strong reduction in beam transmission and underwater PAR transmission near the glacier front, exemplified for the summer 2011 (Fig. 6.11a, b). The euphotic zone can be reduced to 0.3 m near the glacier front (Keck et al. 1999), and as a consequence chlorophyll concentrations are very low (Fig. 6.11c), a persistent pattern found for all years during which the innermost Kongsfjorden station Kb5 has been sampled (Fig. 6.12). Although the effect of the sediment melt-water plume strongly declines down-fjord (Keck et al. 1999, Fig. 6.11a, b), it can still be recorded at outer locations in Kongsfjorden in some years (Hop et al. 2002). Thus, except in surface waters influenced by glacier run-off, phytoplankton growth rates are not light limited during the ice-free, midnight sun period, even on a cloudy day (Eilertsen et al. 1989; Kubiszyn et al. 2014). Indeed, high surface light intensities of up to 2500 µmol photons m^{-2} s^{-1} (scalar sensor) on a clear day can have a negative effect on phytoplankton growth through photoinhibition (Eilertsen et al. 1989, see also paragraph 6.4.5 on fatty acids and photoprotective pigments).

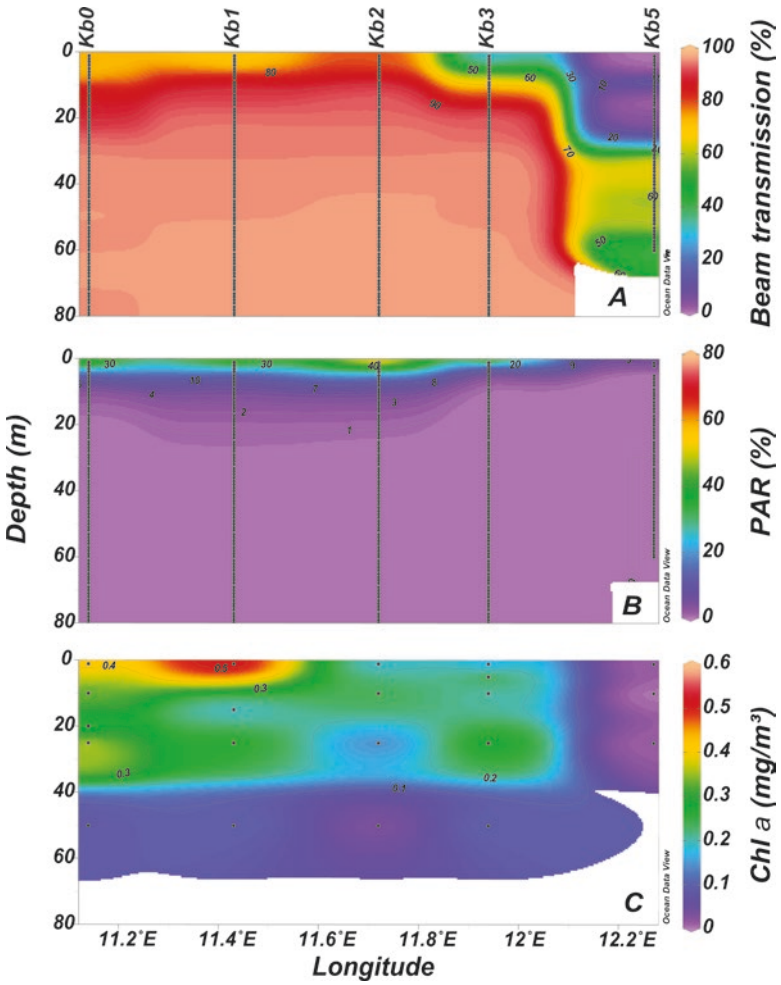

Fig. 6.11 Cross section of the upper 80 m of the water column. Measured from the inner basin (station Kb5, right hand side of plot), to the fjord mouth (station Kb0, left hand side of plot) on 15 July 2011: (**a**) Percentage beam transmission measured with the profiling transmissiometer (measure of turbidity), (**b**) Percent surface photosynthetically active radiation (PAR) and, (**c**) chlorophyll concentrations in μg L^{-1}. (NPI, unpublished data)

The prevailing down-fjord katabatic winds favour an outflow of the glacial meltwater at the surface, which can extend to the fjord mouth and onto the shelf. The lens of low salinity water is clearly depicted in the salinity sections from 2009 to 2014 (Fig. 6.13) and results in shallowing of the surface mixed layer by haline stratification. Stratification is further exaggerated by warming of the surface layer, which increases with distance from the glacier front and hence exposure time to insolation (Fig. 6.14). Although the moored CTD sensor was positioned 20 m below

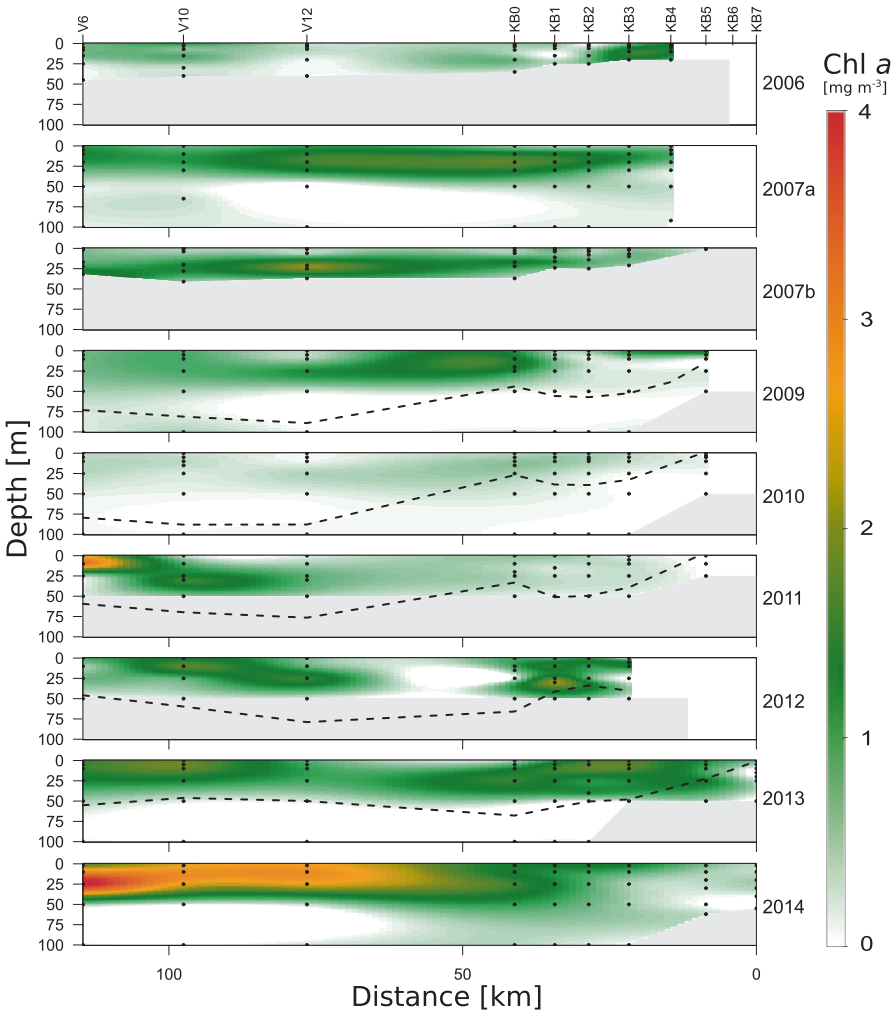

Fig. 6.12 Chlorophyll (in µg L^{-1}) sections from the inner bay (station Kb5) to the shelf break (station V6) during July for the years 2006, 2007 and 2009–2014. In 2007, a second chlorophyll section was obtained in early August during a cruise with RV *Oceania*. Note that the innermost station Kb5 has not been sampled in July 2006, 2007 and 2012, while in 2013 and 2014 two additional stations near the glacier front (Kb6 and Kb7) have been sampled. The dashed line indicates the 0.1 µmol photons m^{-2} s^{-1} light depth. The depth range without data points is depicted in grey. (NPI unpublished data)

the surface, the gradual warming of the surface layer can also be depicted in the temperature records of the mooring for most years (Fig. 6.2a). Glacier drainage and its impact on the adjacent marine ecosystem will vary from year to year as indicated by the inter-annual differences in the depth and spatial extension of the low salinity surface layer. Phytoplankton growth rates are therefore limited by low nutrient sur-

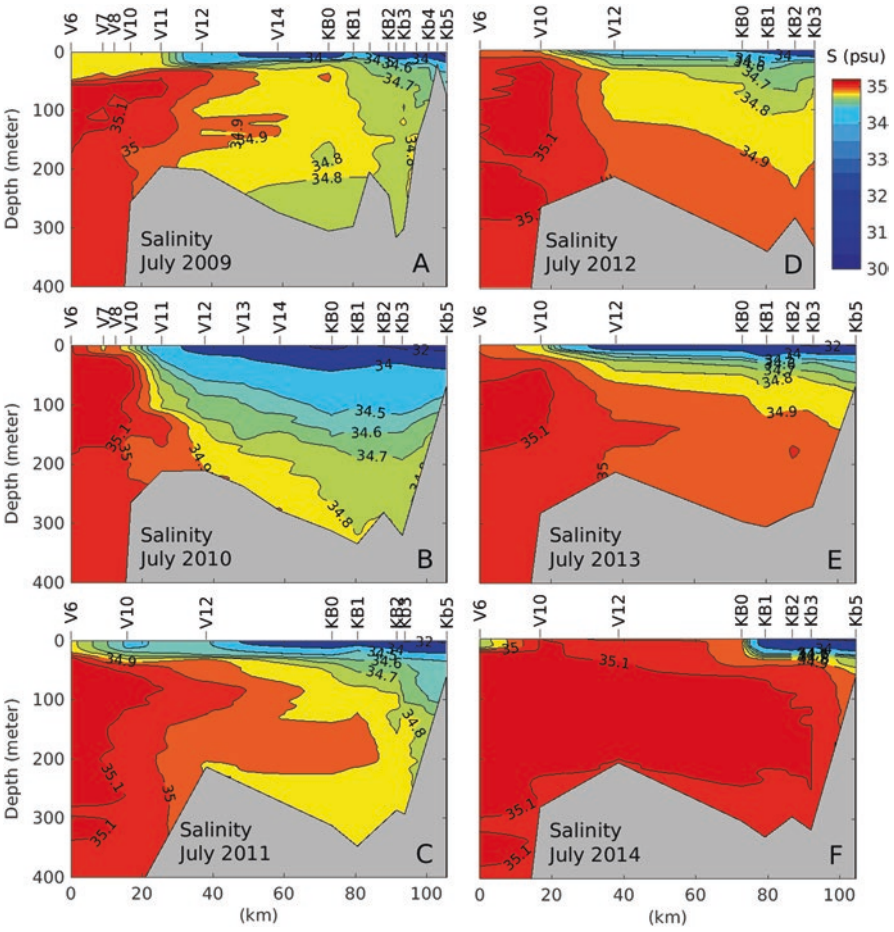

Fig. 6.13 Salinity sections (psu) across Kongsfjorden and the adjacent shelf from July for the years 2009–2014. (NPI, unpublished data)

face concentrations, especially nitrate (Table 6.7), during the stratified summer season (Fig. 6.15). As wind mixing across the strong halocline is limited, the main nutrient source into surface waters in summer is upwelling of AW through the above-described mixing of glacial meltwater with ambient fjord water.

Although fresh, compared to seawater, the surface water is salty relative to its source, because during the upwelling of glacial melt-water, large volumes of ambient fjord water are entrained. The subsequent outflow velocity will force additional entrainment, as illustrated by increasing surface salinities towards the fjord mouth (Fig. 6.13). Thus, it is the sum of buoyancy and momentum-driven entrainment (Mugford and Dowdeswell 2011), as well as the sinking velocity of the mineral

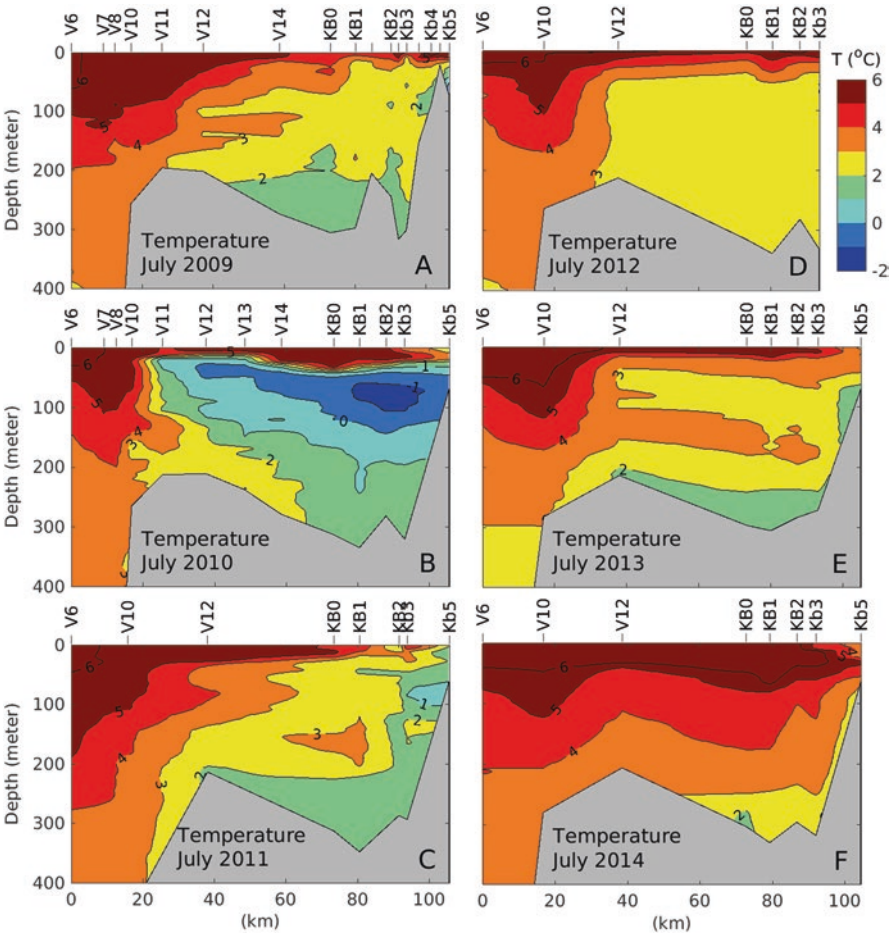

Fig. 6.14 Temperature sections (°C) across Kongsfjorden and the adjacent shelf from July for the years 2009–2014. (NPI, unpublished data)

particles and their coagulation with organic material, that determines the overall dilution and turbidity of the plume along the fjord axis. As rotational effects are more pronounced at high latitudes, the low salinity surface layer is advected outwards along Kongsfjorden's northern shore, which is compensated by the inflow of warmer and more saline AW at depth along its southern shore. This estuarine circulation is the characterizing hydrographical feature during summer.

Sequential frontal instabilities, first at the shelf break front and later at the mouth of the fjord, enable the inflow of AW into the fjord by mid-summer (Cottier et al. 2005a, b; Tverberg et al., Chap. 3). This inflow can proceed unhindered as Kongsfjorden lacks a sill at its mouth. Advection of AW into Kongsfjorden in summer is evident from the temperature and salinity sections (Figs. 6.13 and 6.14).

Table 6.7 Average concentrations of nitrate+nitrite, phosphate, silicate and ammonium in µM in Kongsfjorden (stations Kb5-Kb0), and over the shelf and out in Fram Strait (stations V12-V6) for the years 2002–2014

Period	Nitrate+nitrite	Phosphate	Silicate	Ammonium	N1 & N2
Kongsfjorden above 20 meters (Kb5-Kb0)					
Jun–Sep	0.4 ± 0.3	0.11 ± 0.09	2.09 ± 1.43	0.91 ± 0.85	126 & 70
Oct–May	4.7 ± 3.9	0.50 ± 0.22	2.96 ± 1.92	0.23 ± 0.09	194 & 11
Kongsfjorden below 20 meters (Kb5-Kb0)					
Jun–Sep	2.6 ± 2.1	0.35 ± 0.18	2.10 ± 1.21	2.14 ± 0.87	90 & 59
Oct–May	6.5 ± 3.1	0.57 ± 0.18	3.70 ± 1.75	0.33 ± 0.17	201 & 15
Off Kongsfjorden above 20 meter (V12-V6)					
Jun–Sep	0.6 ± 0.7	0.12 ± 0.09	2.24 ± 1.41	0.28 ± 0.18	66 & 35
Oct–May	8.7 ± 3.5	0.66 ± 0.19	5.38 ± 2.27	0.28 ± 0.10	60 & 6
Off Kongsfjorden below 20 meter (V12-V6)					
Jun–Sep	6.8 ± 4.2	0.51 ± 0.25	4.19 ± 2.13	0.68 ± 0.81	64 & 40
Oct–May	9.7 ± 2.4	0.69 ± 0.13	5.71 ± 2.74	0.28 ± 0.09	90 & 12

N1 is the number of nutrient samples except for ammonium. N2 is the number of ammonium samples (S. Kristiansen, unpublished data)

However, inter-annual differences exist, both in the magnitude and depth of AW inflow which have been attributed to the strength of northward advection of AW with the West Spitsbergen Current (Kubiszyn et al. 2014). While the inflow in 2010 was not very pronounced and largely restricted to the bottom (Figs. 6.13b and 6.14b), in all other years since 2009 AW penetrated much further into the fjord and filled most of the fjord basin. This inflow was particularly pronounced in 2014 when AW occupied the entire water column except for the surface melt-water lens (Figs. 6.13f and 6.14f). This is supported by the mooring data which show persistently high water temperatures (>3 °C) throughout the depth range covered by the mooring for the months of July and August except for the summer of 2010 (Fig. 6.3a). Based on the temperature and salinity sections for 2006–2014 and the temperature anomalies derived from the mooring data for 2003–2014, we define "cold" (2003–2005 and 2010), average (2011) and "warm" (2006–2009 and 2012–2014) summers. For a more detailed hydrographic characterization of cold and warm years see Tverberg et al. (Chap. 3). In the following we will mainly refer to the years 2009–2014 because we have the best data coverage for those years in summer.

6.5.2 Factors Controlling Summer Phytoplankton Biomass

Summer chlorophyll concentrations are generally <1 µg L^{-1}, but peak values can attain >4 µg L^{-1} (Table 6.2). Peak chlorophyll concentrations are usually associated with subsurface depths and found on the outer shelf (Fig. 6.12) because of the

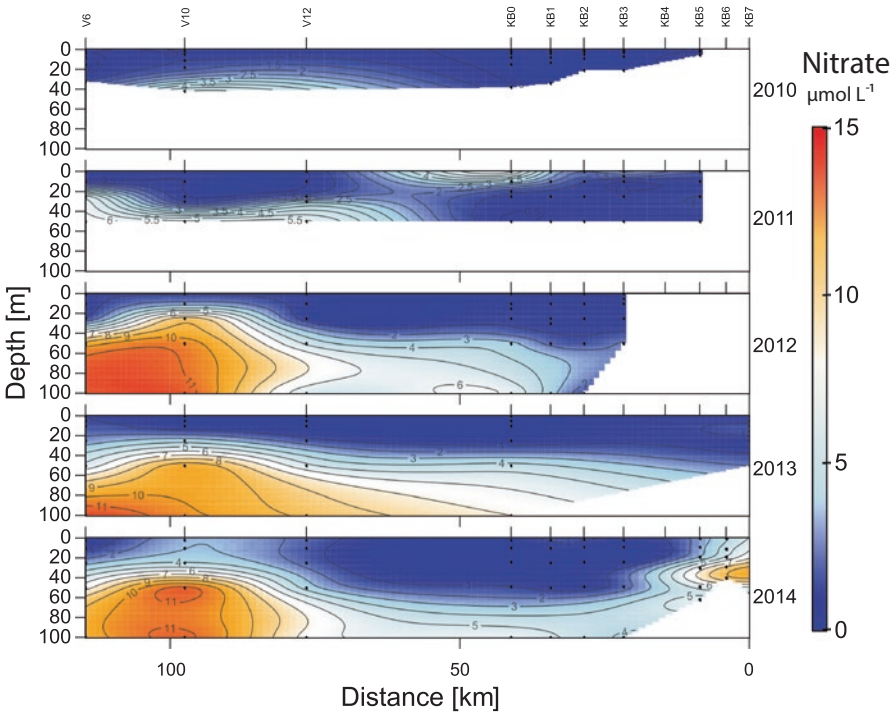

Fig. 6.15 Nitrate concentrations (in µM) in the upper 100 m of the water column across Kongsfjorden and the adjacent shelf in July 2010–2014. (NPI, unpublished data)

nutrient impoverishment of the surface layer (Table 6.7) that generally diminishes with distance from the glacier front (Fig. 6.15). Subsurface chlorophyll maxima (SCM) are a widespread phenomenon in the Arctic in summer (Arrigo et al. 2011; Ardyna et al. 2013). The oceanographic transects inside Kongsfjorden and across the shelf since 2009 show large inter-annual differences in chlorophyll concentrations in July (Fig. 6.12). Interestingly, summer chlorophyll concentrations are significantly higher during the "warm" years than during the "cold" years (including 2011) (Mann-Whitney Rank Sum Test: V10, $p < 0.014$; V12, $p < 0.024$; Kb1, $p < 0.003$; Kb2, $p < 0.007$; Kb3, $p < 0.001$; and Kb5, $p < 0.032$), with the exception of the two frontal stations at the shelf break (V6) and at the fjord mouth (Kb0). Although these chlorophyll sections represent merely snapshots during mid- or late July, similar changes in chlorophyll concentrations have been observed at coastal monitoring sites, with a large component of annual variability, and attributed to shifts or trends in climatic forcing (Cloern and Jassby 2010). The depth and spatial extent of the nutrient-impoverished, low-salinity surface layer seems to be an important factor in explaining the inter-annual variability. This becomes particularly evident when comparing the warmest (2014) and coldest (2010) year in the 2009–2014 summer time series. In 2014, when highest chlorophyll concentrations

were observed on the shelf (Fig. 6.12), the low salinity surface layer only extended to the fjord mouth (Fig. 6.13f). In contrast, the depth of the low-salinity layer was most pronounced in summer 2010 (Fig. 6.13b) when lowest chlorophyll levels were observed (Fig. 6.12). Interestingly, only the two frontal stations do not follow the general trend indicating that mixing of water masses at the fronts overrules the annual patterns seen at the other stations. The trends described above are particularly pronounced in the stratified surface layer, which unfortunately precludes a comparison of the measured chlorophyll sections and the pattern and amplitude measured by the moored fluorometer because it has been positioned at depths between 20 and 63 m. The fixed depth of the fluorometer also hampers inter-annual as well as within-year comparison during the stratified summer season when phytoplankton tends to be more layered compared to the more homogenously mixed spring situation. Thus in some years the instrument could have been located below the SCM while in other years temporal variability in normalized fluorescence could be mainly due to shifts in the depth of the SCM.

Summer chlorophyll standing stocks for the upper 25 m exhibit a large range with minimum stocks of 2 mg m^{-2} near the glacier front and maximum stocks of 76 mg m^{-2} at the shelf break (Fig. 6.16) and are much lower compared to the spring bloom, particularly inside Kongsfjorden (Fig. 6.6a, c) in spite of the different depth-ranges the stocks were integrated over. Despite the large inter-annual variability, an increase towards the shelf is also evident in chlorophyll standing stocks during summer. Clearly light limitation near the glacier front and low nutrient levels in the stratified surface layer set an upper limit for buildup of phytoplankton biomass in Kongsfjorden. This is supported by the few primary production measurements conducted in Kongsfjorden during summer (Eilertsen et al. 1989; Hop et al. 2002; Rokkan Iversen and Seuthe 2011), which show low assimilation rates compared to spring (Rokkan Iversen and Seuthe 2011; Hodal et al. 2012). However, the reported

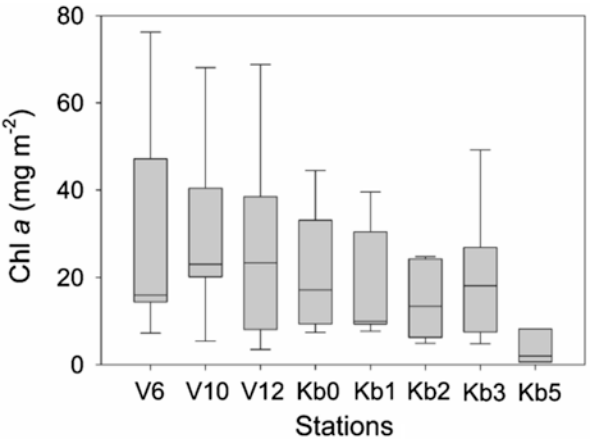

Fig. 6.16 Box-Whisker plot of depth-integrated (upper 25 m) summer chlorophyll *a* standing stocks (mg m^{-2}) for all years depicted in Fig. 6.12 (2006, 2007, 2009–2014)

range 0.024–1.4 g C m^{-2} d^{-1} of the few measurements made in July (Hop et al. 2002) is large and reflects the large variability described above. Extrapolation of these single point measurements to the entire year thus explains the large spread of previous annual production estimates (Hop et al. 2002) and illustrates the need for seasonally-resolved measurements of primary production (Hodal et al. 2012). Low phytoplankton biomass despite high and elevated primary production in late spring and summer respectively (Rokkan Iversen and Seuthe 2011), as well as residual nutrient concentrations persisting through summer (Eilertsen et al. 1989), indicate that zooplankton grazing is controlling phytoplankton biomass in the late and post-bloom period. While zooplankton stocks are low in spring (Leu et al. 2006a; Walkusz et al. 2009; Hodal et al. 2012; Seuthe et al. 2011) and play a minor role in regulation of the spring bloom (Eilertsen et al. 1989; Hodal et al. 2012), zooplankton biomass, particular of *Calanus* copepods, peaks in summer (Walkusz et al. 2009). Advection of AW during summer has been identified as the major conduit of zooplankton into the fjord where they seem to accumulate because their net inflow exceeds outflow (Basedow et al. 2004). As a result, *Calanus* standing stocks in summer 2009 inside Kongsfjorden by far exceed those of the protistan plankton (Fig. 6.17). The high production-to-biomass ratio during the post-bloom period (Rokkan Iversen and Seuthe 2011) and generally low sedimentation rates during the nutrient-impoverished summer months suggest that top-down regulation by zooplankton is the main control of phytoplankton biomass during summer.

6.5.3 Species Composition

The summer phytoplankton community in Kongsfjorden is quite diverse with >130 taxa recorded (Hop et al. 2002). The majority of taxa recorded were affiliated with cosmopolitan or Atlantic species and only 21% with Arctic or boreal species (Hop et al. 2002) which is not surprising given the strong advection of AW into Kongsfjorden in summer. Indeed, high abundances of coccolithophores during summer (Table 6.6) have been used as indicators of strong AW advection (Halldal and Halldal 1973). Taxonomic studies revealed dinoflagellates and flagellates to dominate the summer phytoplankton community in terms of abundance (Table 6.6), a finding supported by studies using molecular approaches (Piquet et al. 2010). Indeed, dinoflagellates, cryptophytes, prymnesiophytes (mainly coccolithophores and *Phaeocystis pouchetii*) and unidentified flagellates always accounted for well above 50% of the total protist abundance at station Kb3 for the summers 2009–2013, but their relative proportions varied substantially between years (Fig. 6.18). However, due to their much larger size compared to flagellates, dinoflagellates and ciliates dominate in terms of biomass (Seuthe et al. 2011; Mayzaud et al. 2013; Fig. 6.17).

Dinoflagellates are a heterogeneous group comprising autotrophic, mixotrophic and heterotrophic modes of nutrition across a wide range of shapes and sizes (Assmy and Smetacek 2009), reflected in the varying proportions of the three nutritional

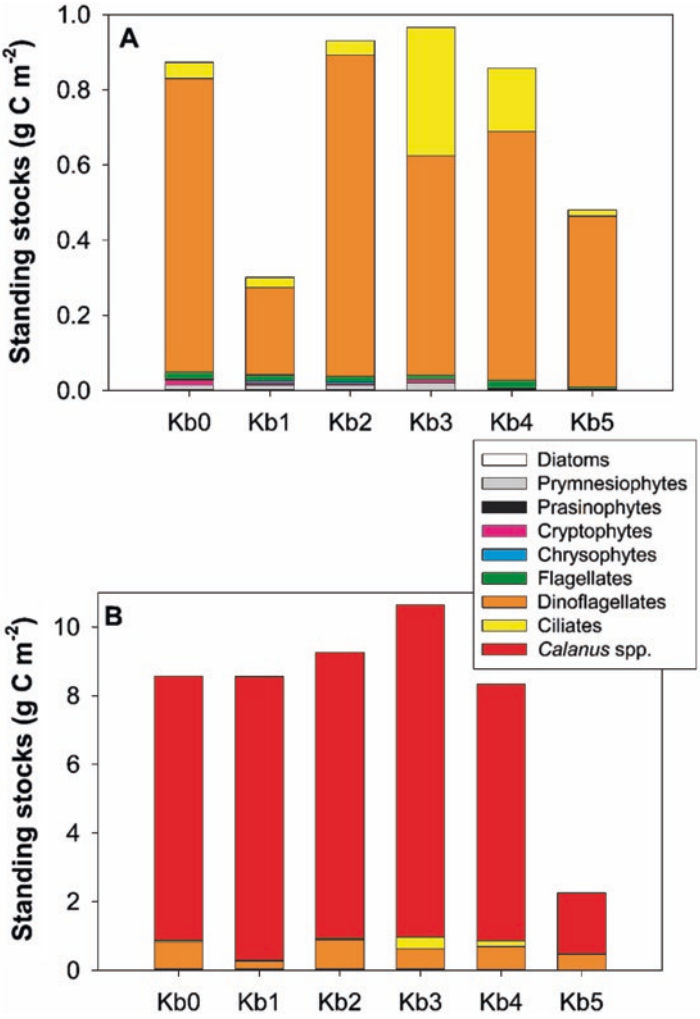

Fig. 6.17 Depth-integrated (upper 50 m) standing stocks (g C m^{-2}) of (**a**) protist plankton and (**b**) protist plankton and *Calanus* copepods in July 2009. Protist plankton was collected in water samples and copepods with Multinet. (NPI, unpublished data)

modes represented within the dinoflagellates at station Kb3 (Fig. 6.18). In summer 2006 athecate (naked) species of the genera *Gymnodinium* and *Gyrodinium* numerically dominated dinoflagellates, but thecate (armoured) species of the genus *Protoperidinium* dominated in terms of biomass (Seuthe et al. 2011). While all nutritional modes are represented in species of the former two genera, species of the latter genus are obligate heterotrophs and employ a special feeding mode (pallium-feeding) that enables them to graze on prey organisms much larger than themselves (Jacobson 1999). Mixotrophes are prominently represented within the dinoflagel-

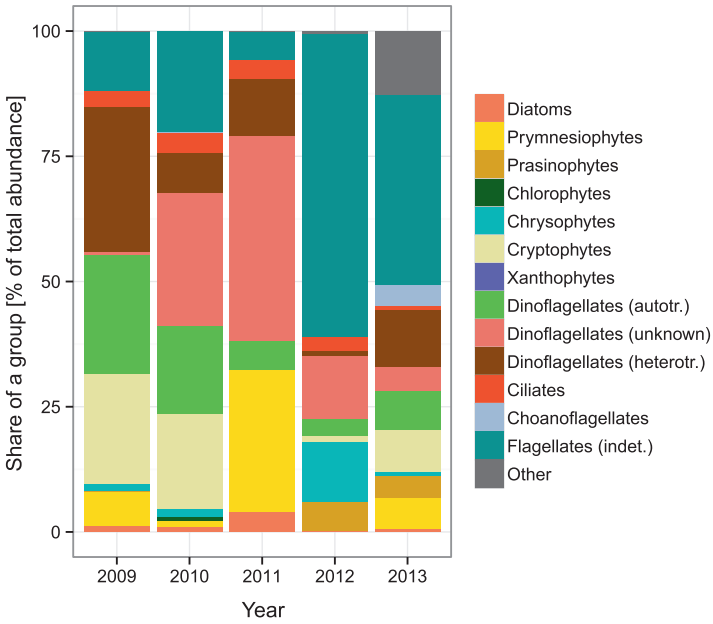

Fig. 6.18 Relative contribution (in terms of abundance) of the major taxonomic groups to total protist plankton at station Kb3 in July 2009–2013. Identification of taxonomic groups is based on microscopy. (NPI, unpublished data)

lates (Flynn et al. 2013). This is supported by the large fraction of the mixotrophic dinoflagellate species, *Heterocapsa triquetra*, *Scripsiella trochoidea*, and *Gymnodinium arcticum*, to the total dinoflagellate biomass in July 2006 (Seuthe et al. 2011). In addition, some autotrophic and mixotrophic dinoflagellates can migrate vertically to take up nutrients below the nutrient-impoverished surface layer due to their motility and comparatively large size. The ability to switch nutritional modes and vertically migrate between the surface and the nutricline constitutes a competitive advantage during the nutrient poor summer season.

The same basic principles apply to the ciliates, which are represented by both mixotrophic and heterotrophic species in summer (Seuthe et al. 2011). In summer 2006, aloricate (naked) species numerically dominated over loricate (tintinnid) species (Seuthe et al. 2011). The mixotrophic ciliates *Myrionecta rubra* (*Mesodinium rubrum*), *Laboea strobila*, and *Strombidium conicum* dominated total ciliate biomass in July (Seuthe et al. 2011). Furthermore, ciliates are efficient grazers of bacteria and autotropic and heterotrophic pico- and nanoflagellates that constitute an important component of the summer microbial community in Kongsfjorden (Wang et al. 2009; Piwosz et al. 2015). Due to their filter-feeding mode, ciliates are likely deterred by the high suspended sediment concentrations near the glacier front while dinoflagellates and flagellates with a more selective feeding mode are likely less affected (Keck et al. 1999).

Flagellates have been either neglected, or grouped into size classes during earlier taxonomic studies in Kongsfjorden, due to their small size and delicate cell structures. The few studies available have so far focused on the summer period (but see Piquet et al. 2014), and have shown that the taxa superficially grouped under flagellates harbour a large diversity of species and phylogenetic lineages. These are particularly important during summer as revealed by more recent molecular studies (Luo et al. 2009; Piquet et al. 2010, 2014; Piwosz et al. 2015). Small size, and thus a large surface-to-volume ratio, constitutes a competitive advantage under nutrient poor conditions consistent with the high abundances of small flagellates in summer. Despite their advantage in the growth environment, flagellates usually do not dominate in terms of biomass (Fig. 6.17) due to their small size and top-down control by the above-mentioned protozoa. Nevertheless, they can be important primary producers in summer due to their high production-to-biomass ratio (Rokkan Iversen and Seuthe 2011). Among the small flagellates, single taxa that dominate are the prasinophyte *Micromonas pusilla* and the haptophyte *Phaeocystis pouchetii* (Piwosz et al. 2015). Both species are ubiquitous and dominant (both in terms of abundance and biomass) members of the Arctic phytoplankton (Wassmann et al. 2005; Lovejoy 2014). The former is identified as the single most important member of the Arctic picophytoplankton (Lovejoy et al. 2007), and the colonial stage of the latter can contribute substantially to spring bloom biomass (Eilertsen et al. 1989; Leu et al. 2006a; Hodal et al. 2012; Hegseth and Tverberg 2013). A recent molecular study has identified *Phaeocystis* as being mainly associated with warm Atlantic water masses, while *Micromonas* sp. dominated the abundant biosphere in the Arctic halocline (Metfies et al. 2016). Alveolates, cryptophytes and Cercozoa have furthermore been identified as prominent members of the summer flagellate community of Kongsfjorden (Luo et al. 2009; Piquet et al. 2010; Piwosz et al. 2015).

In terms of abundance the chrysophyte *Dinobryon balticum* was the dominant component of the phytoplankton assemblage during the summers 1988, 1996 and 1997 (Hasle and Heimdal 1998; Keck et al. 1999; Okolodkov et al. 2000). This species occurred at high abundances in the outer and intermediate parts of the fjord while it was rare to absent in the inner bay (Keck et al. 1999). Low abundances in the inner bay can be explained by its ecological predilections. The high suspended loads of fine sediments near the glacier front might directly deter this filter-feeding species (Lydersen et al. 2014), as seems to be the case for ciliates, and its tendency to form large arborescent colonies facilitates coagulation with mineral particles and subsequent sedimentation (Keck et al. 1999). On the other hand, the ability of *D. balticum* to supplement autotrophy by ingesting particles (McKenrie et al. 1995) could explain its prevalence in the intermediate and outer parts of the fjord during the nutrient-limited summer months.

During summer, diatoms do not play such a prominent role both in terms of abundance and biomass as in spring (Table 6.6, Fig. 6.17a), but can be represented by many species (Hasle and Heimdal 1998; Wiktor and Wojciechowska 2005). They are usually restricted to subsurface depths or the outer parts of Kongsfjorden and the shelf (Hasle and Heimdal 1998; Keck et al. 1999; Piwosz et al. 2009), which is

consistent with the nutrient distribution outlined above. Hence, diatoms were found at low abundance in the low nutrient, low salinity surface layer (Hasle and Heimdal 1998). Resting spores of bloom-forming *Chaetoceros* and *Thalassiosira* species are frequently observed at subsurface depths during summer (Hasle and Heimdal 1998; Wiktor and Wojciechowska 2005; Piwosz et al. 2009) and represent remnants of the spring bloom. The high proportion of empty frustules in July 1996 (Okolodkov et al. 2000) indicated that the majority of diatoms was in a senescent state or represented dead cells advected into Kongsfjorden.

6.6 Significance of Autumn Blooms

Autumn blooms are a prominent and recurrent phenomenon in the seasonal plankton cycle of temperate seas (Assmy and Smetacek 2009) and have been reported to increase in the Arctic Ocean with declining ice cover (Ardyna et al. 2014). Little can be said about the significance of autumn blooms in Kongsfjorden because phytoplankton investigations from autumn are sparse. The limited information available suggests a secondary peak of diatoms in September accompanied by dinoflagellates and cryptophytes (Seuthe et al. 2011; Mayzaud et al. 2013). This finding is supported by the mooring data which show a fluorescence peak of variable magnitude for most years were data are available for September and early October (Fig. 6.3a). The magnitude of this "bloom" seems minor, however, compared to the spring bloom, as surface stratification persists well into autumn (Cottier et al. 2005a) and the low salinity layer can be even more pronounced than during summer (Rokkan Iversen and Seuthe 2011).

6.7 Summary of Annual Phytoplankton Phenology and Directions for Future Phytoplankton Research in Kongsfjorden

Winters conditions in Kongsfjorden are characterized by extremely low phytoplankton biomass, dominated by flagellates <10 μm and naked dinoflagellates while most diatoms survive the winter months as resting spores in the sediments. Although *in situ* photosynthetic rates in winter are below detection limit, phytoplankton cells in the water column are photosynthetically active and can resume growth at the low light levels by the end of the polar night. For resting stages primarily surviving on the seafloor, deep winter mixing is crucial for spring recruitment.

The timing and magnitude of the phytoplankton spring bloom showed considerable inter-annual variability over the observational period which could be largely attributed to difference in the strength and depth of AW inflow and persistence of the ice cover. Surface AW inflow (nutrients) and open water conditions (favorable light

climate) should favor an early spring bloom, but instead the opposite is observed which points to the fact that the ecological underpinnings of the dominant species are more important than light levels or nutrient ratios. The crucial factor seems to be the gearing of diatom life cycle patterns and winter mixing of the water column. Most of the dominant spring bloom diatom species, e.g. *Fragilariopsis oceanica*, *Thalassiosira hyalina*, *T. nordenskioldii*, *T. antarctica* var. *borealis*, and *Chaetoceros gelidus* (von Quillfeldt 2000), form resting spores as part of their life cycle (von Quillfeldt 2001). Since the bulk of resting spores overwinters in surface sediments, seeding of the spring bloom is dependent on deep convective mixing in winter and early spring and subsequent re-suspension of resting spores in the water column. Thus, any factor inhibiting or preventing inoculation of the spring water column with resting spores will delay or prevent the bloom of these species, as the size of the seeding population determines the timing and magnitude of a bloom (Assmy et al. 2007). It will also influence the occurrence of *Phaeocystis pouchetii* since this species seems to be depending on diatom cells/colonies in spring to form its own colonies. So even if this species does not have a bottom/resting stage, a delayed diatom bloom could also delay the *Phaeocystis* bloom despite favorable environmental conditions.

During summer, glacial melt-water run-off at the head of the fjord and advection of AW masses at its mouth create an estuarine circulation with pronounced physical-chemical gradients along the fjord axis. The production and transfer of organic material as well as plankton community composition varies along these gradients. Variability in glacier melt-water run-off and the extent of the associated sediment plume has a strong influence on nutrient availability and the light regime experienced by phytoplankton through glacier-induced nutrient upwelling, surface stratification and light attenuation by suspended sediments, respectively. Phytoplankton biomass build-up in summer is further constrained by heavy zooplankton grazing. Protist taxa with a flexible nutritional mode and those that are able to exploit the steep environmental gradients in the stratified surface layer dominate during the nutrient-poor summer months while diatoms are predominantly found in the subsurface chlorophyll maximum or as resting spores in surface sediments.

Phytoplankton studies during the autumn months are scant, but the few available data suggest that there is a secondary phytoplankton peak, that is small in magnitude, however, compared to the spring bloom. Further investigations are necessary to evaluate the persistency, magnitude and phytoplankton composition of the autumn bloom in Kongsfjorden.

Although we were able to identify the most pertinent environmental factors driving phytoplankton phenology in Kongsfjorden, identification of any long-term trends is hampered by the large inter-annual variability and the limited temporal resolution of phytoplankton observations. Thus, our understanding of phytoplankton phenology in Kongsfjorden would greatly benefit from a coordinated plankton time-series with high-resolution monitoring of annual cycles over many years in order to resolve the ephemeral variations of phytoplankton populations in space and time against the backdrop of climate change.

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