Advances in Polar Ecology

Haakon Hop · Christian Wiencke *Editors*

The Ecosystem of Kongsfjorden, Svalbard

Springer

Advances in Polar Ecology

Volume 2

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Advances in Polar Ecology

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The Ecosystem of Kongsfjorden, Svalbard

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ISSN 2468-5712 ISSN 2468-5720 (electronic)
Advances in Polar Ecology
ISBN 978-3-319-46423-7 ISBN 978-3-319-46425-1 (eBook)
https://doi.org/10.1007/978-3-319-46425-1

Hop H, Wiencke C (eds) (2019) The Ecosystem of Kongsfjorden, Svalbard. Springer, Cham

Library of Congress Control Number: 2019935172

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The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

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Chapter 1
The Ecosystem of Kongsfjorden, Svalbard

Haakon Hop and Christian Wiencke

Abstract This book summarizes physical and biological aspects from Kongsfjorden (78° 59' N, 11–12° E), Svalbard. The contributions to this volume cover atmospheric conditions above Ny-Ålesund, as well as physical conditions in Kongsfjorden. The chapters about oceanographic dynamics and sea ice conditions are based on time-series observations of interannual variability, whereas the chapter about the underwater light regime focuses on seasonal dynamics. The pelagic system is covered by reviews of pelagic production, phytoplankton and zooplankton communities. Benthic flora studies address microphytobenthos and macroalgal biodiversity, as well as the physiology of kelp related to stress perception and responses. Benthic fauna communities are described with associated environmental drivers of change. An outline of an Arctic fjord ecosystem model for Kongsfjorden-Krossfjorden is presented. Data that go into models come from sampling at different stations in the marine environment, with an important contribution from long-term data series at stations. Some of the long-term data are based on recordings from autonomous underwater observatories. Finally, one summary presents Kongsfjorden as harbinger of the future Arctic.

Keywords Arctic marine ecosystem · Environmental drivers · Biodiversity · Advection · Climate change · Kongsfjorden · Arctic

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_1

1.1 Introduction

Kongsfjorden is a glacial fjord located in the European Arctic on the west Spitsbergen coast in Svalbard at 78° 59′ N, 11–12° E. Scenic mountains and calving glaciers surround the fjord (Figs. 1.1 and 1.2). It is an established reference site for marine ecological studies and monitoring, together with the atmospheric monitoring station at the Zeppelin Mountain. The establishment of the Marine Laboratory in Ny-Ålesund in 2005 allows for combining field research with controlled experiments in the laboratory (Fig. 1.3). Since 2007, the fjord has been protected against commercial trawling (Fig. 1.4), which has facilitated the establishment of automated marine observatories in this fjord (Hop et al., Chap. 13).

As Kongsfjorden is an open fjord, without a sill, it is strongly influenced by the inflow of warm Atlantic water from the West Spitsbergen Current, mixed with Arctic Water on the shelf (Cottier et al. 2005; Hop et al. 2006; Walczowski et al. 2012). The fjord is connected to Fram Strait, a gateway to the Arctic Ocean (Wassmann et al. 2015), through the trough Kongsfjordrenna, which extends from the fjord to the shelf break. Climate-driven physical and biological changes have been recorded in Fram Strait at the deep-sea long-term observatory HAUSGARTEN (Soltwedel et al. 2016). Advection of Transformed Atlantic Water (TAW) into the fjord is important for its seasonal oceanographic dynamics, as well as for its biological communities (Cottier et al. 2005, 2007; Hop et al. 2006; Willis et al. 2006, 2008; Dalpadado et al. 2016). Even though the Atlantic signal extends throughout the fjord, the inner fjord is considered mostly Arctic with regard to physical and biological characteristics (Hop et al. 2002; Lydersen et al. 2014). The inner fjord basin is largely influenced by run-off from tidal glaciers, which create gradients in freshwater influence and sediment load towards the middle of the fjord (Calleja et al. 2017; D'Angelo et al. 2018).

Because of the dual Atlantic and Arctic inputs, the fjord houses pelagic and benthic communities that comprise a mixture of boreal and Arctic flora and fauna (Hop et al. 2002, 2016; Walkusz et al. 2009; Voronkov et al. 2013). The spring bloom during April–May kick-starts the biological production (Hegseth et al., Chap. 6), which is utilized by zooplankton during the summer and autumn to build up lipid stores (Falk-Petersen et al. 2009; Walkusz et al. 2009). The biological communities in the fjord remain active during the dark winter season, although with changed composition and reduced abundance of zooplankton in the water column (Berge et al. 2015a, b; Grenvald et al. 2016; Geoffroy et al. 2018). Warming during wintertime and declining sea ice may influence seasonal ecosystem dynamics (Hop et al., Chap. 13; Pavlova et al., Chap. 4). Benthic fauna are relatively stable throughout the year (Wlodarska-Kowalczuk et al. 2016), with carnivores and opportunistic species increasing in numbers in shallow waters during winter (Kedra et al. 2011).

In the current era of climate change, documented and projected alterations in the physico-chemical environment in the Kongsfjorden system include: atmosphere and ocean warming (Maturilli et al., Chap. 2; Tverberg et al., Chap. 3), decrease of

Fig. 1.1 Kongsfjorden, in the background three prominent mountains (Tre Kroner): Svea (1225 m), Nora (1226 m), Dana (1175 m)

Fig. 1.2 Kronebreen tidal glacier in inner Kongsfjorden

Fig. 1.3 Kings Bay Marine Laboratory, Ny-Ålesund

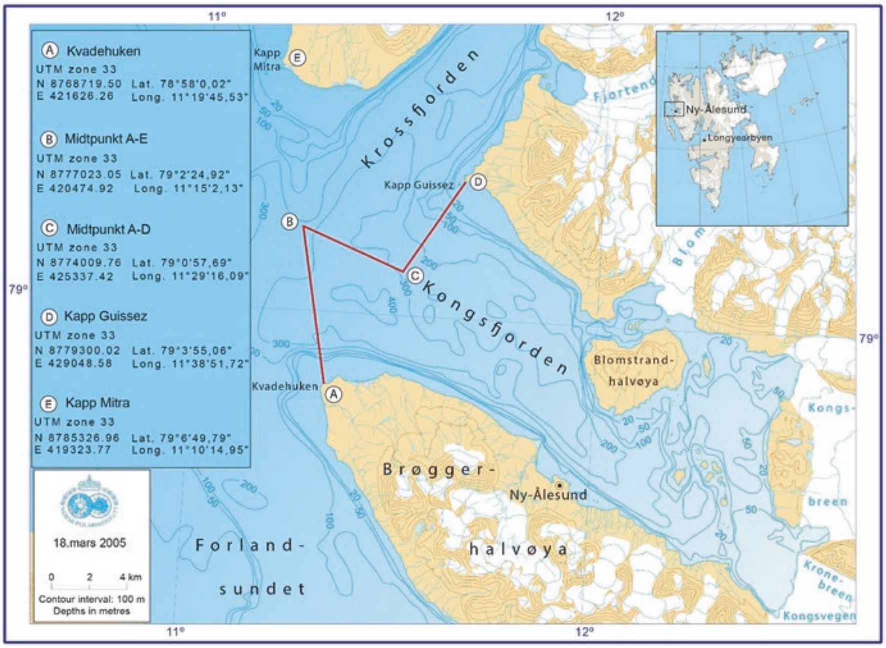

Fig. 1.4 Trawl protection zone in Kongsfjorden, 2005

winter sea-ice cover (Pavlova et al., Chap. 4), ocean acidification (Fransson et al. 2016), glacier retreat (Kohler et al. 2007; Blaszczyk et al. 2009), higher terrestrial run-off resulting in increasing nutrient, sediment and soil-associated contaminant loads (Granberg et al. 2017), and changes in light climate, particularly ultraviolet B exposure (due to stratospheric ozone depletion; Hanelt et al. 2001).

The marine communities in Kongsfjorden respond to the variability and changes in environmental conditions, as documented in seasonal and long-term studies. Long-term changes involve alterations of pelagic primary production and algal community composition (Hegseth and Tverberg 2013; Hegseth et al., Chap. 6), of benthic macroalgal biomass and production (Bartsch et al. 2016), and of community composition and production of benthic fauna (Beuchel et al. 2006; Kedra et al. 2010; Paar et al. 2016). Macro zooplankton is responding quite rapidly to changes in Arctic and Atlantic water masses (Kwasniewski et al. 2003; Willis et al. 2006, 2008; Ormanczyk et al. 2017), for instance in case of krill and amphipods in less than a decade (Buchholz et al. 2010; Dalpadado et al. 2016). Long-term changes in mesozooplankton were more difficult to detect over 20 years of monitoring in Kongsfjorden because of pronounced inter-annual variation and longer-term variability. However, the biomass of the boreal copepod *Calanus finmarchicus* has clearly increased, as well as the total biomass of zooplankton (Hop et al., Chap. 7). Moreover, strong changes in seaweed biomass and depth distribution have been detected over a time span of 20 years (Bartsch et al. 2016). In parallel, a drastic change in depth distribution of macrozoobenthic biomass and secondary production has been reported (Paar et al. 2016). Changes in the lower marine food web in Kongsfjorden have affected the middle and upper trophic levels, represented by fishes, seabirds and seals (Lydersen et al. 2014; Vihtakari et al. 2018). Such changes may involve abrupt regime shifts, rather than linear trends. Species-specific responses may result in new inter-specific interactions, such as competitive or trophic changes, and affect ecosystem functions (e.g. Russell et al. 2012; Pörtner 2014). Alternatively, because compartmentalized food webs tend to be resilient, marine ecosystems can adapt to ongoing climate change (Stouffer and Bascompte 2011).

Comparative studies of Svalbard fjords typically have involved Kongsfjorden, Isfjorden and Hornsund. These are all open fjords on the western coast of Spitsbergen that are influenced by Arctic and Atlantic water masses and tidal glaciers. They have their specific characteristics, however, since Isfjorden is much larger than Kongsfjorden, while Hornsund is shorter. Interestingly, Hornsund is colder than Kongsfjorden because of the inflow of Arctic Water of the South Cape Current, and future warming may result in Hornsund becoming more similar to Kongsfjorden with regard to hydrography and primary production (Piwosz et al. 2009). Comparative studies of Kongsfjorden and Hornsund have involved mostly physical and ecological aspects, which were published in a dedicated volume of *Oceanologia* (Weslawski 2017), adding further evidence to previously published comparative studies (e.g. Wlodarska-Kowalczuk et al. 1998; Gluchowska et al. 2016). Rijpfjorden on Nordaustlandet has become an Arctic comparison to Atlantic-influenced Kongsfjorden, particularly with regard to studies during the polar night on diurnal vertical migration (Berge et al. 2009, 2014, 2015a, b). According to modelling studies, the largest increase in temperature and primary production will occur on the north coast of Svalbard (Slagstad et al. 2011, 2015), which may cause Rijpfjorden to become more influenced by Atlantic Water and the ecosystem changes may project those that have already occurred in Kongsfjorden. Comparisons that are more distant can be done with glacial fjords in Greenland, such as Young Sound, although these fjords are much larger systems and influenced by cold water in the East Greenland Current (Rysgaard and Nielsen 2006).

The Kongsfjorden area has a rich history of research and monitoring activities, much of which are associated with the currently 11 research stations from 10 countries at Ny-Ålesund. Physical and ecological aspects of Kongsfjorden have been summarized in review papers (Hop et al. 2002, 2006; Svendsen et al. 2002), and research from the Kongsfjorden area have been collated in several special journal issues (Wiencke 2004; Weslawski 2017; Cappelletti et al. 2016). The 13 review chapters published in this volume of *Advances in Polar Ecology* complement the 34 research papers that were published in two issues of *Polar Biology* (Wiencke and Hop 2016). Both the book and the special issue were initiated during the Second Kongsfjorden Ecosystem Workshop held on 10–17 March 2014 at the conference facility *Hamn i Senja*, Skaland, Norway (Figs. 1.4, 1.5, 1.6, 1.7 and 1.8). The workshop involved 60 researchers from nine countries (Austria, France, Germany, Netherlands, Norway, Poland, Russia, Spain, and Sweden) (Fig. 1.9).

1.1.1 Reviews in this Volume

The contributions to this volume cover atmospheric conditions above Ny-Ålesund (Maturilli et al., Chap. 2), as well as physical conditions in Kongsfjorden. The chapters about oceanographic dynamics (Tverberg et al., Chap. 3) and sea ice conditions (Pavlova et al., Chap. 4) are based on time-series observations of interannual variability, whereas the chapter about the underwater light regime focuses on seasonal dynamics (Pavlov et al., Chap. 5). The pelagic system is covered by reviews of pelagic production, phytoplankton and zooplankton communities (Hegseth et al., Chap. 6; Hop et al., Chap. 7). Benthic flora studies address microphytobenthos (Karsten et al., Chap. 8) and macroalgal biodiversity (Fredriksen et al., Chap. 9), as well as the physiology of kelp related to stress perception and responses (Bischof et al., Chap. 10). Benthic fauna communities are described with associated environmental drivers of change (Molis et al., Chap. 11). Duarte et al. (Chap. 12) present an outline of an Arctic fjord ecosystem model for Kongsfjorden-Krossfjorden. Data that go into models come from sampling at different stations in the marine environment, with an important contribution from long-term data series at stations. Some of the long-term data are based on recordings from autonomous underwater observatories (Hop et al., Chap. 13). Finally, one summary presents Kongsfjorden as harbinger of the future Arctic (Bischof et al., Chap. 14). The main content and conclusions from these reviews and with novel presentations of long-term data are detailed below.

Fig. 1.5 Hamn i Senja hosted the Second Kongsfjorden Ecosystem Workshop, March 2014

Fig. 1.6 The Second Kongsfjorden Ecosystem Workshop in progress

Fig. 1.7 Michael Greenacre always ready to entertain with music or statistics

Fig. 1.8 Kongsfjord workshop organizers and Guest Editors: Christian Wiencke and Haakon Hop

1.1.1.1 Atmosphere

The Arctic region is considered as most sensitive to climate change, with warming occurring considerably faster than the global average due to several positive feedback mechanisms contributing to the "Arctic amplification" (Pithan and Mauritsen 2014). The study by Maturilli et al. (Chap. 2) focuses on the changes in atmospheric boundary conditions in the Kongsfjorden area and relates the long-term climate observations (1993–2017) from this area to a larger regional and hemispheric context. Temperatures have increased during the last century, primarily during winter (3.1 ± 2.2 K per decade). This winter warming is related to changes in the net longwave radiation, whereas changes in the net shortwave radiation during the summer period are attributed to the decrease in reflected radiation caused by less snow cover. Variability in synoptic cloud cover is the cause of the inter-annual variability in incoming solar radiation in summer, observed in the monthly mean global shortwave radiation, as well as in photosynthetically active radiation (PAR) and UV radiation. The marine system in Kongsfjorden is influenced by air temperature and atmospheric humidity. The hydrological cycle with seasonal run-off to Kongsfjorden is affected by atmospheric variability, and cloud formation determines incoming radiation at the surface.

1.1.1.2 Ocean Dynamics

Ocean dynamics have been monitored each year in Kongsfjorden since 1994. The transect covers the full length of the fjord, as well as the adjacent shelf and upper continental slope outside Kongsfjorden. Oceanographic data are also supplied from moorings in Kongsfjorden (Hop et al., Chap. 7). Tverberg et al. (Chap. 3) have shown that Atlantic Water (AW) from the West Spitsbergen Current enters Kongsfjorden every summer, although to a varying extent. The focus of their paper is on this variable content of AW in Kongsfjorden, the forcing mechanisms that may govern the inflow of this water mass, and its distribution in the fjord. In earlier years, the winter convection inside the fjord, combined with sea-ice formation, produced dense water that prevented AW from entering Kongsfjorden until the summer. However, since 2006, advection of AW occurred also during winter, either as water flowing along the bottom of Kongsfjordrenna or via advection near the surface. Some of the variation in advection is caused by the natural variability of wind and currents. However, the advection at the surface, which happens when open-water convection produces very dense shelf water, seems to be a consequence of the general trend of atmospheric and oceanic warming, and the decreasing sea-ice cover in the Arctic.

1.1.1.3 Sea Ice

Seasonal sea ice is an important feature of Svalbard fjords, with pronounced impact on both the physical environment and the ecosystem. Pavlova et al. (Chap. 4) present the results of systematic sea-ice monitoring in Kongsfjorden from 2003 to 2016.

Fig. 1.9 Group photo of the participants of the Second Kongsfjorden Ecosystem Workshop in March 2014. Registered participants were (in alphabetical order): Ragnhild Asmus, Philipp Assmy, Agnès Baltzer, Sebastien Barrault, Inka Bartsch, Jørgen Berge, Frank Beuchel, Kai Bischof, Markus Brand, Cornelia Buchholz, Friedrich Buchholz, Christian Buschbaum, Malin Daase, Sebastien Descamps, Pedro Duarte, Stig Falk-Petersen, Philipp Fischer, Stein Fredriksen, Geir Wing Gabrielsen, Marta Gluchowska, Francisco Gordillo, Martin Graeve, Michael John Greenacre, Svein Are Hanssen, Else Nøst Hegseth, Haakon Hop, Kim Huenerlage, Carlos Jiménez, Marianne Johansen, Ulf Karsten, Jack Kohler, Kit M. Kovacs, Svein Kristiansen, Slawek Kwasniewski, Jürgen Laudien, Benoit Lebreton, Eva Leu, Silke Lischka, Maarten J.J. Loonen, Cornelius Lütz, Christian Lydersen, Børge Moe, Markus Molis, Roland Neuber, Martin Paar, Alexey Pavlov, Vladimir Pavlov, Olga Pavlova, Paul E. Renaud, Marcus Rex, Joëlle Richard, Michael Y. Roleda, Vigidis Tverberg, Martine van den Heuvel-Greve, Jan Marcin Weslawski, Christian Wiencke, Józef M. Wiktor, Maria Wlodarska-Kowalczuk, Anette Wold and Angela Wulff

The inner Kongsfjorden is usually covered by seasonal fast ice, initially forming between December and March and persisting until April–June. Before 2006, sea ice typically extended into the central part of the fjord, but during the last decade, it has often been confined to the northern inner fjord, with a minimum extent in 2012. Only in 2009 and 2011, sea-ice extent was similar to earlier years. Maximum seasonal thickness of fast ice was around 0.6 m or more until 2006, since when it declined to about 0.2 m in recent years. The snow thickness on fjord fast ice declined from around 0.2 m in spring prior to 2006 to <0.05 m in recent years, which reflected the shorter duration of ice cover. Advection of warm Atlantic Water into Kongsfjorden, particularly during the winters of 2006 and 2007, contributed to reduced fast-ice formation. This inflow, in combination with relatively mild winters, can be regarded as the main factors for changing fast-ice conditions in Kongsfjorden during the last 10 years. The changes of the seasonal dynamics of sea-ice extent have important implications for the marine ecosystem in Kongsfjorden with regard to pelagic and benthic production, as well as for seabirds and marine mammals.

1.1.1.4 Underwater Light-Regime

Kongsfjorden at the high latitude of 79°N experiences a strong seasonality in light climate, changing from polar night in winter to midnight sun in summer. Sea ice conditions and the optical properties of seawater further modify the amount and the spectral composition of solar radiation penetrating into the water column, thus defining the underwater light climate in Kongsfjorden. Light represents one of the major drivers of the entire marine ecosystem. Pavlov et al. (Chap. 5) synthesize the fragmentary information available from the literature, as well as presenting some unpublished data, and discuss the underwater light regime and its main controlling factors in Kongsfjorden. They also provide a short synopsis about the relevance of light for different components of an Arctic marine ecosystem with regard to primary production, behavioural aspects and synchronization of growth and reproduction.

1.1.1.5 Phytoplankton

Phytoplankton phenology is a key driver of chemical and biological processes in marine ecosystems because it directly affects the cycling of nutrients, strength of the biological carbon pump, and energy transfer to higher trophic levels. However, phytoplankton time-series from the European Arctic are scant, thus limiting our ability to link phytoplankton phenology to environmental variability. Hegseth et al. (Chap. 6) compile 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 responsible for the seasonal and inter-annual variability in phytoplankton bloom dynamics, biomass and species composition.

Phytoplankton dynamics in Kongsfjorden generally 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, small flagellates and their protozoan grazers during summer. The long-term trend in phytoplankton phenology is not clear, as it is generally characterised by large inter-annual variability, which can be mainly attributed to variability in the magnitude of Atlantic Water inflow, sea-ice cover and glacier melt-water discharge.

1.1.1.6 Zooplankton

The zooplankton in Kongsfjorden is shaped by the irregular advection of water from the West Spitsbergen Current, as well as the input of freshwater of glacial and riverine origin. The zooplankton community reflects the varying contributions of Arctic and Atlantic water masses in the fjord, and changes with increasing temperature and declining sea ice. Hop et al. (Chap. 7) review zooplankton studies from Kongsfjorden and present new data from a 20-year time series (1996–2016) of zooplankton abundance/biomass in the fjord based on annual surveys during summer. During the last decade, the marine environment of the West Spitsbergen Shelf and adjacent fjords, including Kongsfjorden, has undergone changes in response to increasing temperatures and volumes of inflowing Atlantic Water, as well as to declining sea ice. Annual monitoring of mesozooplankton in the fjord since 1996 has shown high seasonal, spatial, and inter-annual variation in species abundance and biomass, as well as in the proportion of Atlantic and Arctic species. Inter-annual variations in species composition and abundance demonstrate fluctuating patterns related to changes in ocean dynamics. Long-term zooplankton data demonstrate that some Atlantic species have become more abundant in Kongsfjorden, suggesting that they may actually benefit from increasing temperatures. Moreover, the total biomass of zooplankton has increased in the fjord, implying potentially higher secondary production. There was no clear impact of changes in environmental factors on the abundance or biomass of the Arctic species *Calanus glacialis*, however, suggesting that these changes have not reached critical levels for this species.

1.1.1.7 Microphytobenthos

The seafloor of shallow waters is typically inhabited by microphytobenthic (MPB) communities, composed mainly of diatoms. Only sparse information is available on the MPB ecophysiology and acclimation processes from Arctic regions. Karsten et al. (Chap. 8) review the knowledge about the physico-chemical environment, ecology and ecophysiology of MPB diatoms in Kongsfjorden. They have high rates of primary production, stabilise sediment surfaces against erosion under hydrodynamic forces, and affect the exchange of oxygen and nutrients across the sediment-water interface. Additionally, this phototrophic community represents a key component in the functioning of the Kongsfjorden food web, particularly as a major food source for benthic suspension- or deposit-feeders. Microphytobenthos in Kongsfjorden is well adapted to pronounced seasonal variations in solar radiation, low temperatures, and hyposaline (meltwater) conditions in summer, as well as to long periods of ice and snow cover in winter. Enhanced knowledge of the molecular mechanisms involved in bioenergetics, resource allocation, metabolic fluxes and community composition are expected to improve our ability to understand the influence of polar benthic diatoms on biogeochemical processes and the responses to global-change scenarios.

1.1.1.8 Benthic Macro- and Microalgae

Several floristic studies on macroalgae of Svalbard have been published. Kongsfjorden, Isfjorden and Hornsund are the three best investigated Spitsbergen fjords, and most of the species information comes from these three fjords. However, quantitative sublittoral sampling along depth transects and along the fjord axis has been undertaken only in Kongsfjorden. Clear differences were found from the outer to the inner parts of the fjord. Fredriksen et al. (Chap. 9) present macroalgal biodiversity data from Kongsfjorden compared to data for the whole Svalbard archipelago. In total, 197 species of macroalgae have been recorded for Svalbard, and 84 of these occur in Kongsfjorden. The taxonomic status of some species is discussed. Changes in the macroalgal flora during the last decades in Svalbard in general and in Kongsfjorden in particular are related to increased temperature in combination with reduction in sea ice. Simultaneous changes in the sublittoral are due to an altered underwater light regime with both positive and negative consequences for the vertical species' distribution and productivity. Introductions of new species to Svalbard are expected from more temperate regions, especially from the North Atlantic. Although biodiversity of microbenthic diatoms is quite low, they colonise large parts of Kongsfjorden in high abundances and, in addition to macroalgae, are important as primary producers and therefore also for trophic relationships in the harsh Arctic environment.

1.1.1.9 Kelp and Environmental Changes

On rocky substrata along shallow-water cold-temperate and Arctic coastlines, large brown seaweeds ("kelps") form physically heterogeneous and biologically diverse habitats of high ecological significance. The distribution of these ecosystem engineers is largely controlled by the prevailing temperature, light regime (including UVB radiation) and substrate availability, but can also be influenced by biotic interactions within the kelp communities. Additional environmental factors in Kongsfjorden are alterations of current and wind patterns, resulting in the increased inflow of Atlantic Water into the fjord ('Atlantification'). Moreover, increased precipitation and higher terrestrial and glacial runoff have led to altered salinity regime and increased sediment discharge into the fjord, with the potential impact of reducing light availability to marine plants. Bischof et al. (Chap. 10) provide an overview on ecologically relevant abiotic and biotic factors influencing kelp distribution, and their potential to act as environmental stressors. They assess responses on different organisational levels of kelp by following the effects cascading from the initial sensing of the environment, signal transduction to gene expression, physiological reactions, to changes in cellular ultrastructure, and their consequences for growth, reproduction and population biology for the different kelp species in Kongsfjorden. Results synthesized from more than 20 years of seaweed research in Kongsfjorden suggest a generally high adaptability of most kelp species. An important exception is the Arctic-endemic species *Laminaria solidungula*, which will largely suffer from changing environmental conditions, primarily increase in temperature. Thus, changes in kelp community composition, but also overall system productivity, are to be expected.

1.1.1.10 Benthic Communities

Knowledge on the causes and consequences of benthic community change is essential to understand and conserve Arctic marine ecosystems. Molis et al. (Chap. 11) summarize the current knowledge about the effects of abiotic and biotic factors on benthic species interactions and community traits (diversity, structure, and functioning of Arctic coastal hard- and soft-bottom habitats), with emphasis on Kongsfjorden. Arctic hard- and soft-bottom communities show some fundamental differences in their ecology. For instance, the recovery in hard-bottom communities after disturbances takes exceptionally long (decades) due to slow growth and/or sporadic recruitment, while it is considerably shorter in soft-bottom communities. Arctic hard-bottom communities display strong competitive hierarchies that appear negligible in sediment communities. The authors suggest shifting the focus in Arctic benthos research from pattern to processes in future studies.

1.1.1.11 Arctic Fjord Ecosystem Model

Duarte et al. (Chap. 12) present a detailed outline of an Arctic fjord ecosystem model using Kongsfjorden-Krossfjorden as a case study. Marine ecosystem models are compared, with emphasis on fjord models, towards defining best available modelling technologies, based on an analysis of the differences in the variables and processes simulated by different models. The authors argue about the importance of (i) coupling Arctic fjord models with land and glacier drainage models, (ii) including thermodynamic, hydrodynamic and ice dynamic sub-models, and (iii) simulating biogeochemical processes in the water, ice and benthic environments for, at least, the macro-elements carbon, nitrogen and phosphorus. With regard to higher trophic levels, their energetic importance, predation and migration need to be considered in fjord ecosystem models, when developing these in direction of end-to-end models.

1.1.1.12 Autonomous Marine Observatories

Several moored autonomous marine observatories, with a variety of sensors and scientific instruments, have been installed in Kongsfjorden since 2002. They provide seasonal and inter-annual data on a number of physical, chemical and biological variables, which serve as important baselines for the gauging of seasonal variability vs. climate-induced changes in this fjord system. Environmental and ecological changes observed in Kongsfjorden are, to some extent, related to larger-scale changes in Fram Strait because of the advection of Atlantic Water into the open fjord. Hop et al. (Chap. 13) provide an account of the location of moored observatories in Kongsfjorden, with a list of parameters measured at the different moorings, and review the scientific advances that have been made through data collection from these marine observatories.

1.1.1.13 Kongsfjorden as Harbinger of the Future Arctic

Due to its year-round accessibility and excellent on-site infrastructure, Kongsfjorden and the Ny-Ålesund Research and Monitoring Facility have become a primary location to study the impact of environmental change on Arctic coastal ecosystems. As a result, Kongsfjorden is one of the best-studied Arctic fjord systems. Located at the interface of Arctic and Atlantic oceanic regimes, it is already experiencing large amplitudes of variability in physical and chemical conditions. Thus, Kongsfjorden may be considered as an early warning indicator of future changes, which can then be extrapolated to a pan-Arctic scale. Bischof et al. (Chap. 14) identify current knowledge gaps and research priorities, with respect to ecological and adaptive responses to Arctic ecosystem changes, and provide a stimulus for developing new international and interdisciplinary research initiatives.

1.1.1.14 Review Gaps

To further extend our understanding of the Kongsfjorden ecosystem, more physical and biological compartments need to be considered. Several of these were covered in presentations at the Second Kongsfjorden Ecosystem Workshop in 2014, but reviews are currently lacking on marine geology and palaeoceanography, hydrology and sedimentation processes, tidal glaciers, bacteria and the microbial loop, shrimps, fishes, seabirds, marine mammals, food-web aspects and pelagic-benthic coupling, environmental contaminants as well as other human impacts. Many of these topics have been dealt with in scientific publications of research conducted in the Kongsfjorden region. Since this extensive knowledge should also be summarized in reviews, there is certainly scope for a second Kongsfjord book, if somebody wishes to kick-start it.

Acknowledgements The initiative to assemble these review papers, including long-term data series, about the knowledge about the marine ecosystem of Kongsfjorden was taken during the Second Kongsfjorden Ecosystem Workshop in 2014. We are grateful for workshop funding from the Norwegian Polar Institute (NPI), Research Council of Norway, Svalbard Science Forum, Havet og kysten (Project no. 234347), Fram Centre Flagship, Fjord & Kyst (Project no. 2014–8), Alfred Wegener Institute, Kings Bay AS, and the Priority Programme on Antarctic Research of the German Science Foundation (DFG). Moreover, we appreciate the support from the Centre for Ice, Climate and Ecosystems (ICE) at NPI. We finally thank Roger Willy Hagerup (NPI) for assembling the map. We trust that this volume of *Advances in Polar Ecology* will set the stage for future work in Kongsfjorden and will strengthen the ongoing *Ny-Ålesund Research Flagship Programme*, where the *Kongsfjorden System* is one of the four flagships (http://nysmac.npolar.no/research/flagships/kongsfjorden.html). Photos are provided by Haakon Hop.

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Part I
Atmospheric Conditions

Chapter 2
The Atmosphere Above Ny-Ålesund: Climate and Global Warming, Ozone and Surface UV Radiation

Marion Maturilli, Inger Hanssen-Bauer, Roland Neuber, Markus Rex, and Kåre Edvardsen

Abstract The Arctic region is considered to be most sensitive to climate change, with warming in the Arctic occurring considerably faster than the global average due to several positive feedback mechanisms contributing to the "Arctic amplification". Also the maritime and mountainous climate of Svalbard has undergone changes during the last decades. Here, the focus is set on the current atmospheric boundary conditions for the marine ecosystem in the Kongsfjord area, discussed in the frame of long-term climatic observations in the larger regional and hemispheric context.

During the last century, a general warming is found with temperature increases and precipitation changes varying in strength. During the last decades, a strong seasonality of the warming is observed in the Kongsfjord area, with the strongest temperature increase occurring during the winter season. The winter warming is related to observed changes in the net longwave radiation. Moreover, changes in the net shortwave radiation are observed during the summer period, attributed to the decrease in reflected radiation caused by the retreating snow cover.

Another related aspect of radiation is the intensity of solar ultra-violet radiation that is closely coupled to the abundance of ozone in the column of air overhead. The long-term evolution of ozone losses in the Arctic and their connection to climate change are discussed.

Keywords Arctic climate change · Surface temperature · Surface radiation budget · Stratospheric ozone

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_2

2.1 Introduction

Like anywhere else on the globe, the atmosphere in the Kongsfjord area, Svalbard, is affected by global climate change. Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia. The atmosphere and ocean have warmed, the amounts of snow and ice have diminished, sea level has risen, and the atmospheric concentrations of greenhouse gases have increased (IPCC 2013).

The Arctic region is considered to be most sensitive to climate change. Warming in the Arctic occurs considerably faster than the global average (IPCC 2007) due to various feedback mechanisms contributing to the "Arctic amplification". Climate model simulations suggest that the largest contribution can be attributed to temperature feedbacks (Pithan and Mauritsen 2014). Furthermore, the snow/sea ice – albedo feedback is a well-known concept (Curry et al. 1995; Lindsay and Zhang 2005; Screen and Simmonds 2010), which gains importance as climatic warming has caused a substantial decrease in the extent and thickness of Arctic sea ice (Cavalieri and Parkinson 2012). Over the last two decades, the Greenland ice sheet has been losing mass, glaciers have continued to shrink, and Arctic sea ice and Northern hemisphere springtime snow cover have continued to decrease in extent (IPCC 2013). Large parts of the excess energy absorbed by the climate system have been stored in the oceans, leading to an increase in upper ocean temperature and facilitating evaporation of water vapor to the atmosphere. Water vapor, clouds, and their radiative feedbacks are known as important factors in the Arctic climate system (Curry et al. 1996; Francis and Hunter 2007; Bennartz et al. 2013). Moreover, changes in the atmospheric circulation result in a strengthening of meridional heat transport to the high latitudes and further account for Arctic warming (Graversen et al. 2008; Zhang et al. 2008), along with the possibility that Arctic atmospheric circulation itself is modified by the strong warming (Francis et al. 2009; Overland and Wang 2010). In the upper atmosphere, stratospheric water vapor, ozone, and other greenhouse gases contribute with chemical and dynamical feedbacks in the coupled system on the global scale (e.g. Garcia and Randel 2008; Dessler et al. 2013).

Furthermore, the ozone layer is modulating the ultra-violet (UV) radiation reaching the surface. While radiative fluxes in both the shortwave and longwave range generally play a key role in the complex Arctic region, the incoming solar radiation determines the biological activity in the Arctic marine environment. Photoautotrophic organisms need sunlight for the process of photosynthesis, and e.g. the diel vertical migration of zooplankton is controlled by the incoming irradiance (Wallace et al. 2010), even in polar night conditions (Berge et al. 2009). The Kongsfjord marine environment and ecosystem structure are thus conditioned by the climatological situation and the available radiation at the surface. The following sections describe the climatological aspects of the Kongsfjord area, and emphasize on surface radiation observations to provide a setting for the biological aspects that are discussed in the chapters thereafter.

2.2 Recent Climate in Ny-Ålesund, Kongsfjorden, Svalbard

The Svalbard archipelago is located in the high Arctic, yet due to the North Atlantic Current moderating temperatures it has a significantly warmer climate than other environments at the same latitude. Situated North of the Arctic circle, the Svalbard archipelago experiences polar day in summer and polar night in winter. In Kongsfjorden at the west coast of Svalbard (Spitsbergen), atmospheric observations are centered in and around the settlement of Ny-Ålesund. Though generally, polar night (polar day) conditions in the Kongsfjord are given between 24 October and 18 February (18 April and 24 August), respectively, direct sunlight reaches Ny-Ålesund only between 8 March and 8 October due to mountains in the South. The complex orography of mountains and glaciers also affects atmospheric processes on the micro- and mesoscale. With both coastal and mountainous influences, Ny-Ålesund may not be a representative location for the general Arctic, but provides evidence for general Arctic variability and change when looking at synoptic time scales.

The Kongsfjord climate is characterized by the superposition of synoptic and mesoscale effects. Typically, Svalbard is situated along the main track of cyclones transporting warm and humid air from lower latitudes to the North. Generally, there are fewer shorter and stronger cyclones in winter, and more numerous longer-lived, but weaker, cyclones in summer in the Arctic region (Zhang et al. 2004). Monthly mean station-level pressure in Ny-Ålesund is generally above 1000 hPa, and above 1010 hPa during the sun-lit period (Maturilli et al. 2013). As the cyclonic activity is lower in summer, pressure change from day-to-day is lower than in spring or autumn. The maximum of day-to-day pressure variability occurs in winter when passing cyclones persist shorter but with larger amplitudes in pressure gradient (Maturilli et al. 2013).

The orography of the Kongsfjord area has a large impact on the local climate. The surrounding mountains frequently cause the generation of orographically induced clouds, and modify the wind field by channeling the air flow along the fjord axis within the lowermost kilometer of the atmosphere. Also the occurrence of sea breeze and katabatic outflow from glaciers act on the local meteorology. Thus, atmospheric parameters may be different from the Ny-Ålesund observations when looking at different locations along Kongsfjorden.

2.2.1 *Temperature*

During the year, the land surface around Ny-Ålesund changes considerably due to the presence or absence of the snow cover. In summer, the surface around Ny-Ålesund exhibits its tundra vegetation, as temperatures rise above the freezing point and the snow-cover vanishes. The melt-season starts around May–June, with the actual onset of melting depending on the individual synoptic situation of each year. The annual cycle of the monthly mean surface air temperature in Ny-Ålesund is shown

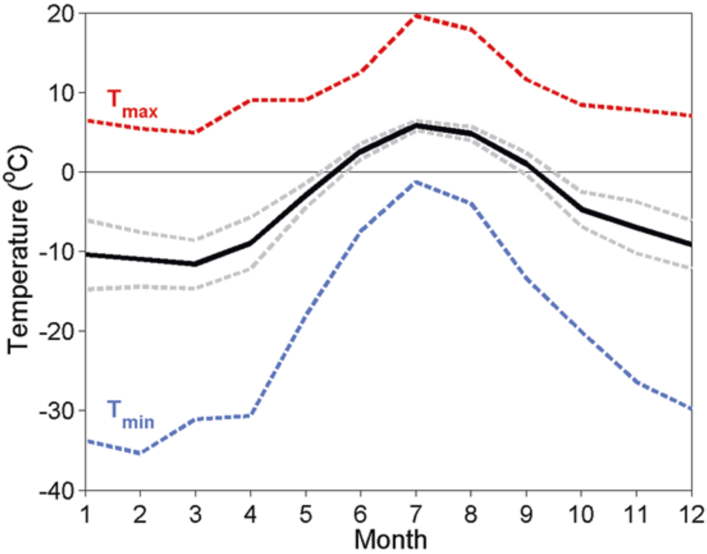

Fig. 2.1 Annual cycle of the monthly mean temperature (*black line*) ± 1 standard deviation (*grey lines*), and the daily minimum and maximum temperatures (*blue and red lines, respectively*) obtained from surface air temperature measurements between August 1993 and July 2014. (Update of Maturilli et al. 2013)

in Fig. 2.1, from temperature data measured at 2 m height on a meteorological tower operated by the Alfred Wegener Institute since August 1993. As indicated by the standard deviation, the inter-annual temperature variability is small during the summer months, but the minimum temperature still allows for single snow events. Usually, the snow cover remains stable only after October. During the polar night, the inter-annual temperature variability is much larger due to the dynamics and strength of the cyclonic systems. In winter, the air temperature is very sensitive to the synoptic wind direction as the large-scale temperature gradient is much stronger than in summer, so winters with common northerly-easterly winds are much colder than winters with common southerly winds. The Ny-Ålesund maximum temperature indicates the possibility of rain also during the winter months, and indeed during recent winters several periods with rain have occurred.

2.2.2 *Wind*

Throughout all seasons, the common wind direction in Ny-Ålesund is along the fjord axis from the inland to the coast (Førland et al. 1997a). While the synoptic wind field is present above roughly 800 m altitude, the Spitsbergen mountains modify the air flow in the lowest atmospheric kilometer, resulting in a complex wind field and causing a decoupling from the large scale synoptic flow (Maturilli and

Kayser 2017). In the surface layer, the prevailing wind direction in Ny-Ålesund is south-easterly, with the flow from 120° along Kongsfjorden due to drainage winds transporting cold air from the Kongsvegen glacier located about 10 km to the east-south-east of Ny-Ålesund (Beine et al. 2001). Furthermore, the channeled wind flow along the fjord is locally superimposed by mesoscale air flow along valleys or katabatic winds from glaciers (Burgemeister 2013). Thermal land-sea breeze circulation and mechanical wind channeling are the leading processes in the modulation of the local wind field (Esau and Repina 2012). Also the formation of a cold-pool over ice-covered parts of the fjord may play a role. In Ny-Ålesund, sea breeze from northern directions arrive on short time scales during the summer months (Maturilli et al. 2013). Overall, independent of the synoptic scale flow the wind flow in the lowermost atmosphere is mainly along the fjord axis, but local variations are likely to occur and will differ considerably for different locations along the fjord (e.g. Mazzola et al. 2016). Also, variations in the wind speed may lead to snow redistribution, with local differences in snow cover duration and according ecological impact. The wind speed also affects the generation of mechanical turbulence in a stably stratified atmospheric boundary layer, with impact on the surface fluxes.

2.2.3 Humidity and Precipitation

In the Svalbard fjord landscape, the combined effect of large-scale humidity advection and local processes result in a prevailing specific humidity inversion (Vihma et al. 2011) and also drive the amount of surface atmospheric humidity. Related to temperature, the summer months are more humid than the winter months. In relative humidity, the seasonal variation is small with monthly mean values between 60% and 85% (Maturilli et al. 2013). Yet, absolute values reveal the dryness of Arctic air, with the maximum in monthly average H_2O mixing ratio of about 4.7 g kg^{-1} in July, while the winter months (December/January/February) exhibit an average H_2O mixing ratio of about 1.4 g kg^{-1} (Maturilli et al. 2013).

The measurement of precipitation poses serious challenges in the Arctic environment due to drifting or blowing snow. While fake precipitation caused by solely blowing snow can be excluded through quality control, the combination of precipitation and blowing snow causes problems. Consequently, precipitation records from the Arctic are influenced by substantial measuring errors, e.g. caused by undercatch of the precipitation gauges (Førland and Hansen-Bauer 2003).

As evident from the annual cycle in temperature (Fig. 2.1), both rain and snow (mixed precipitation) may occur in Ny-Ålesund at any time of the year. The annual cycle of the monthly precipitation amount in Ny-Ålesund, as measured by the Norwegian Meteorological Institute, is shown in Fig. 2.2. In the Svalbard region, most of the precipitation occurs in connection with cyclones approaching from the Southwest-Northwest sector (Førland et al. 1997a). Generally, the mountain regions receive the greatest amounts of precipitation and the inner fjord region the least, but orography causes local differences (Førland et al. 1997a). Precipitation is usually

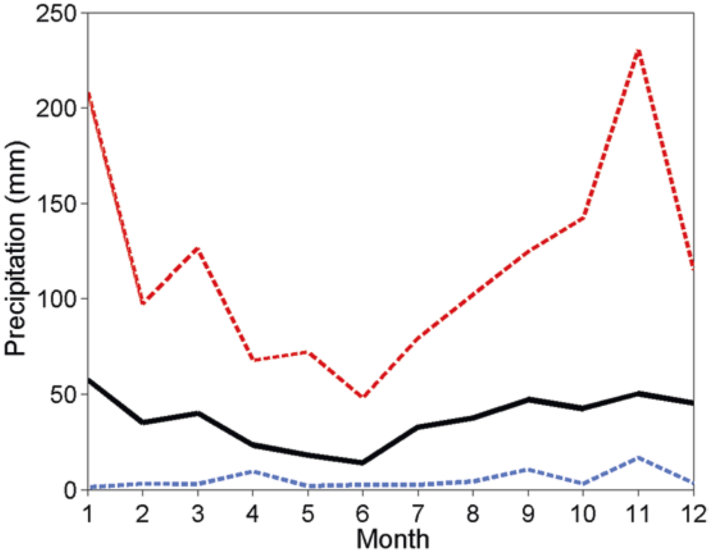

Fig. 2.2 Annual cycle of the monthly mean precipitation (*black line*), and the observed minimum and maximum monthly precipitation amount (*blue and red lines, respectively*), obtained between August 1993 and July 2014

increasing with increasing altitude due to the lifting and consequent cooling of air masses over hills and mountains (Førland 1979). Local precipitation also depends on the large-scale wind direction. Førland et al. (1997b) found that for large-scale winds from South and Southwest, the precipitation at the glacier Austre Broggerbreen was about 60% higher than in Ny-Ålesund, while for winds from northwest, Ny-Ålesund got more precipitation than the stations at the glacier.

2.2.4 Radiation

While the described meteorological parameters account for the climatological background of the Kongsfjord area, incoming radiation is particularly important for the biogeochemical activity of the ecosystem. With the increasing research activities in Ny-Ålesund in the late 1980s, surface radiation measurements have been set up by the Alfred Wegener Institute, contributing to the Baseline Surface Radiation Network (BSRN) since August 1992. The set-up includes the measurement of direct solar radiation by pyrheliometer, diffuse, global and reflected (downward and upward, respectively) shortwave radiation by pyranometers, as well as up- and downward longwave radiation by pyrgeometers (Maturilli et al. 2015). Here, longwave radiation refers to the spectral range 3.5–50 μm, while the broadband shortwave measurements cover the spectral range 200–3600 nm. In Ny-Ålesund, additional filtered shortwave radiation measurements are operated in the wavelength ranges 300–370 nm and 695–2800 nm.

The photosynthetically active radiation (PAR) refers to the spectral range that is effective in the process of photosynthesis, commonly defined from 400 to 700 nm. With the available BSRN measurements in Ny-Ålesund, it is possible to infer the PAR by subtracting the filtered radiation measurements from the broadband global radiation, as the energetic contribution of the remaining shortwave 200–300 nm and longwave 2800–3600 nm ranges to the broadband irradiances are negligible. The resulting BSRN-PAR refers to the spectral range 370–695 nm, and its annual mean cycle is shown in Fig. 2.3. The monthly mean noon values are listed in Pavlov et al. (Chap. 5). As a spectral subset, the BSRN-PAR closely follows the global radiation measurements. The main contribution to the large quantitative difference between global radiation and PAR is attributed to the subtracted longer wavelength range (695–2000 nm) which has 10 times larger irradiance values than the subtracted shorter wavelength range (300–370 nm). Examples for the daily PAR distribution on a clear and a cloud-covered day are given in Pavlov et al. (Chap. 5) in the context of resulting underwater radiation and its impact on the marine ecosystem.

Figure 2.4 shows the annual cycle of the various surface radiation parameters as measured by the BSRN station in the years 1993–2017. The global radiation basically depends on the solar elevation angle and the cloud cover. During the 25-year observation period, the monthly mean global shortwave radiation SW_{down} (Fig. 2.4a) reveals a large inter-annual variability during the summer months, caused primarily by the different occurrence of clouds. The reflected radiation (upward shortwave radiation, Fig. 2.4c) results from the incoming global radiation and the surface

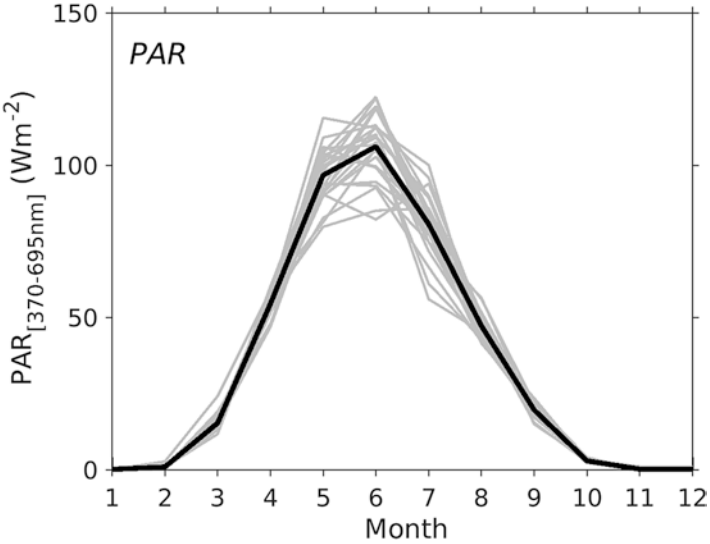

Fig. 2.3 Phytosynthetically active radiation (PAR) in the wavelength range 370–695 nm, as retrieved from BSRN pyranometer measurements in the years 1993–2017 (*grey lines for all years of observation, black line for overall mean*)

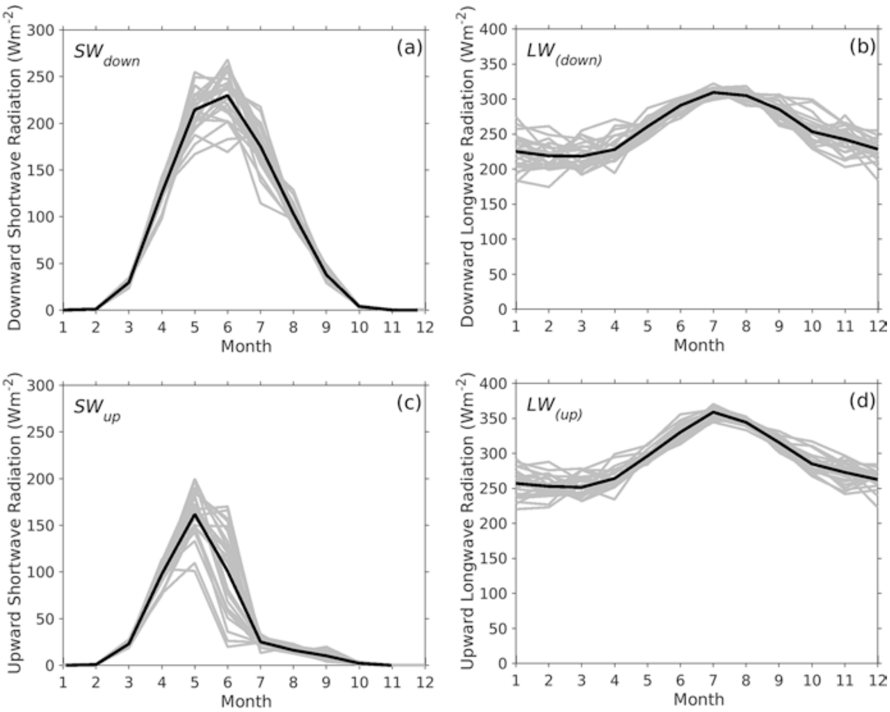

Fig. 2.4 Ny-Ålesund monthly mean values (*grey lines for single years 1993–2017, black line for overall mean*) for downward shortwave radiation SW_{down} (**a**), downward longwave radiation LW_{down} (**b**), upward shortwave radiation SW_{up} (**c**) and upward longwave radiation LW_{up} (**d**), respectively. (Update of Maturilli et al. 2015)

reflectivity. Here, the largest inter-annual variability is found for the snow melt months May, June and July, as the largest change in surface reflectivity occurs with the change from snow cover to tundra ground. Both shortwave components exhibit a distinct annual cycle related to the Earth's axial tilt.

As the thermal radiation components are temperature dependent, their annual cycle resembles very much the annual cycle of temperature. The amount of upward longwave radiation (Fig. 2.4d) is further controlled by the surface texture and state, while the downward longwave radiation (Fig. 2.4b) is additionally modified by the presence of radiative active components in the atmosphere, e.g. clouds, humidity, and greenhouse gases. Although the absolute values of the longwave radiation components are smaller during the dark period, the inter-annual and month-to-month variability is much larger due to the large winter variability in atmospheric temperature and humidity, as well as cloudiness and the related radiative effects.

The described surface radiation parameters add up to the surface net radiation budget $RAD_{net} = SW_{net} + LW_{net} = (SW_{down} - SW_{up}) + (LW_{down} - LW_{up})$ that describes the net flux of radiative energy at 2 meters above the terrestrial surface (Fig. 2.5). In the absence of shortwave radiation during the polar night period, net radiation

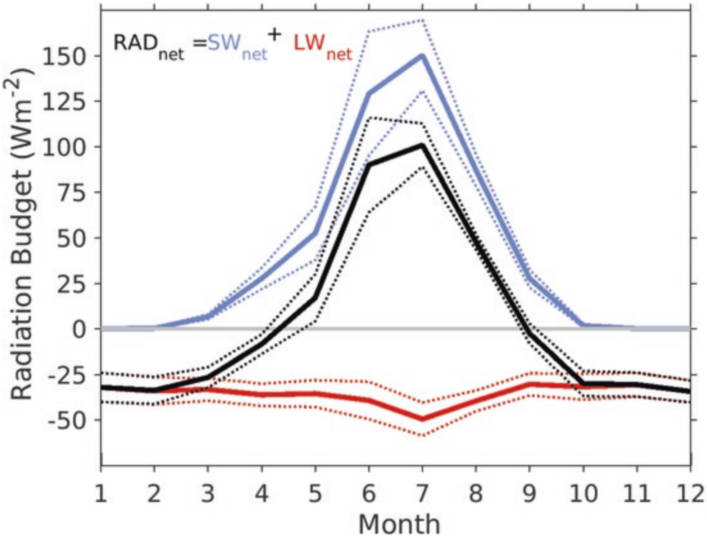

Fig. 2.5 Ny-Ålesund 25-year average monthly mean values of the shortwave net radiation [$SW_{net} = SW_{down} - SW_{up}$] (*blue line*), the longwave net radiation [$LW_{net} = LW_{down} - LW_{up}$] (*red line*), and the net radiation budget [$RAD_{net} = SW_{net} + LW_{net}$] (*black line*) +/− 1σ standard deviation of monthly means (*dotted lines, respectively*). (Update of Maturilli et al. 2015)

budget is given by the longwave net radiation only. Thus, the net radiation budget is negative during winter, as the upward thermal radiation overwhelms the downward thermal radiation. Only with the returning solar radiation during the sun-lit period and consequent positive shortwave net radiation, the net radiative budget increases and in the long-term mean is positive between April and August. The individual net radiation budget obviously depends on the persistence of the snow cover and on cloudiness. Overall, the annual mean net radiation budget in Ny-Ålesund has positive values for more than a decade, with a total average of 4.8 Wm^{-2} in the period 1993–2017. Together with sensible and latent heat fluxes, the net radiation budget contributes to the surface energy budget.

2.2.5 *Surface Energy Budget (SEB)*

Kongsfjorden is surrounded by mountainous terrain, characterized by tundra, glaciers, soil and rock fields, and local permafrost ground. Clearly, the formation and melting of a snow pack is the characteristic feature in the annual course of the Svalbard landscape. The snow cover has a considerable influence on the surface energy balance by changing the surface albedo and affecting the sensible and latent heat exchange between the surface and the atmosphere. For the terrestrial ecosystem, the surface energy balance is of crucial importance. Combined measurements of radiation, sensible and latent heat flux, as well as ground heat flux and other related parameters have been performed at several sites in the vicinity of Ny-Ålesund (e.g. Harding and Lloyd 1998; Boike et al. 2003, 2018). Analysing the annual cycle of the surface energy budget at the Bayelva site close to Ny-Ålesund, Westermann et al. (2009) found that during the summer months, the net shortwave radiation is the predominant energy source, while turbulent processes and the heat flux in the ground cause a cooling of the surface. For the months of July and August, they attributed 15% of the net radiation involved in the seasonal thawing of the soil active layer. During the dark winter period, the dominant energy loss of the surface is attributed to net longwave radiation, mainly compensated by the sensible heat flux and also by the ground heat flux originating from the refreezing of the active layer. While latent heat fluxes are found insignificant for the average surface energy budget when the surface is covered by snow, strong evaporation is observed during the snow melt and snow free period, leading to a compensation of the sensible heat fluxes by the latent heat fluxes when regarding the annual average (Westermann et al. 2009). Overall, the annual cycle of the surface energy budget at the Bayelva site is characterized by distinct features grouped in six seasons by Westermann et al. (2009), starting with summer season when the ground is snow free and the shortwave radiation dominates the SEB. In the following autumn season, the snow layer is formed and the shortwave-dominated SEB is in transition to the subsequent dark season which is dominated by the longwave radiation. With the returning sunlight after polar night, the shortwave radiation increases again during the light winter season, yet its influence on the SEB is small due to the high surface albedo of the remaining snow cover and the large zenith angles. After this period with the lowest soil and skin temperatures, the growing importance of the shortwave radiation and the increasing temperature define the premelt season, which is followed by the snow melt season when the bare tundra surface appears while the incoming shortwave radiation is largest.

Generally, the presence or absence of a snow layer and thus the timing of snow melt and resulting albedo changes are main factors for the surface energy budget. Horizontal heterogeneity of the terrain, the soil composition, the surface structure and also irregular snow accumulation patterns need to be taken into account when applying radiative, sensible or latent heat flux measurements for ecological studies.

2.3 Observed Climate Change in Ny-Ålesund and Svalbard

The above given climatological description elucidates the mean atmospheric state in Ny-Ålesund during the recent two decades. Yet, global change and the effect of Arctic amplification are detected also in the Svalbard region, affecting the current Kongsfjord climate.

Since 1901 almost the whole globe has experienced surface warming. However, the warming has not been linear, since most warming occurred in two periods:

around 1900 to around 1940 and around 1970 onwards (IPCC 2013). While the early twentieth century warming was mostly predominant in the Atlantic region (Overland et al. 2004), the more recent warming is global in nature, persisting over the whole Arctic. In Europe, the Svalbard Archipelago is the region that has experienced the greatest temperature increase during the past three decades (Nordli et al. 2014).

The detection of climate trends is a complex issue that strongly depends on measurement uncertainties and data homogeneity. Inhomogeneities in meteorological long-term series may be caused by e.g. relocations of sensors, changed environment (buildings etc) and instrumental improvements, (Førland et al. 1997a). In Ny-Ålesund, synoptic measurements of temperature have been performed at the same site since 1975, but by combining with earlier measurements at Isfjord Radio, homogenized, composite temperature series are established for Ny-Ålesund back to 1934 (Førland et al. 1997a, 2011). An even longer time series has been established known as the Svalbard Airport composite series, reaching back to 1898 by merging historical data from various Svalbard sites (Nordli et al. 2014).

Low-pass filtered updated composite temperature series for Ny-Ålesund and the Svalbard Airport are shown in Fig. 2.6. The series reveal long-term variability with a minimum in the 1910s. The early twentieth century warming from about 1920 to the middle of the century is obvious from the Svalbard Airport temperature recording, with a peak in the 1930s and another one following in the late 1950s detected in both time series. Since the late 1960s, temperature has increased rapidly, and the present regime of Spitsbergen temperatures, which covers the years 2005 to present, is the warmest one ever recorded (Nordli et al. 2014).

Despite the large variability, significant positive trends over the whole period were detected for annual as well as seasonal means. Regarding the annual mean, the

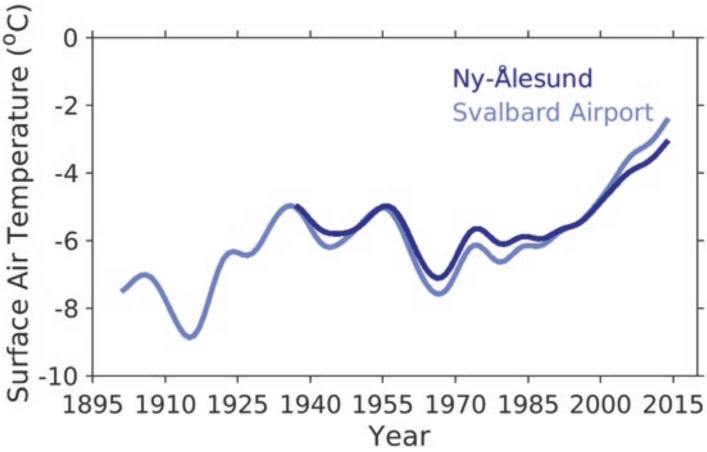

Fig. 2.6 Low-pass filtered annual mean surface air temperature for the composite series Ny-Ålesund (*dark blue line*) and Svalbard Airport (*light blue line*)

linear trend of the long-term Svalbard Airport composite series is 3.1 K per century, whereas the largest trend is in spring at 4.3 K per century.

However, climatic time series often have trends for which linear regression is not a good approximation (e.g. Seidel and Lanzante 2004). The residuals from a linear fit in time often do not follow a simple autoregressive or moving average process, and linear trend estimates are dependent on method and easily change when recalculated or when new data are added, especially for short time series. When linear trends for two parts of a longer time series are calculated separately, the trends calculated for the shorter periods may be very different (even in sign) from the trend in the full period, caused by decadal scale variability. Obviously, when considering the much shorter time frame of the Ny-Ålesund BSRN measurements during the last two decades, the annual mean temperature increase is much larger compared to other parts of the longer time series (Fig. 2.6). Yet, as polar ecological research in Kongsfjorden is mostly operated since 1993, the focus is now set on the last two decades when discussing temperature and radiation changes.

The surface meteorological measurements at the BSRN site are operated since August 1993, and linear regression of the annual mean temperature for the years 1994–2017 gives a temperature increase for this period of 1.6 ± 0.7 K per decade (update of Maturilli et al. 2013). Yet, the observed warming is more complex when looking at the different seasons (Fig. 2.7), including data until 2017. While the considerable temperature increase in spring of about 1.0 ± 1.4 K per decade is statistically insignificant due to the large scatter of the data, the moderate summer warming of 0.6 ± 0.5 K per decade and the larger autumn warming of 1.4 ± 1.2 K

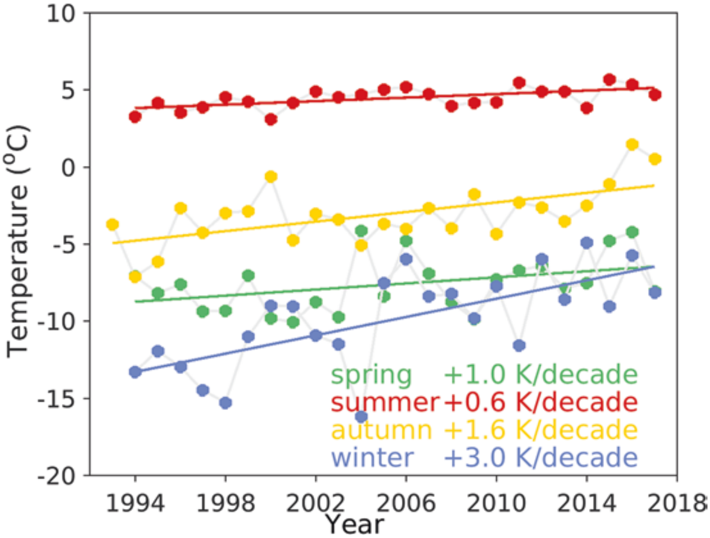

Fig. 2.7 Ny-Ålesund seasonal mean surface air temperature from BSRN site August 1993 to December 2017 for spring (*green dots*), summer (*red dots*), autumn (*yellow dots*), and winter (*blue dots*), with the linear regression (*colored lines, respectively*). (Update of Maturilli et al. 2015)

per decade are statistically more stable, respectively. By far the largest part of the annual mean temperature increase accounts for the winter period, showing a seasonal temperature increase of 3.0 ± 2.0 K per decade (update of Maturilli et al. 2015). Though featuring a large scatter of the data, the winter months obviously provide the main contribution to the observed warming during the recent 25 years. A very strong winter warming is also identified for the latest decades at other stations of the Svalbard region (Førland et al. 2011). Furthermore, different climate model simulations show a pronounced seasonality of polar warming amplification with largest polar surface warming in winter (Lu and Cai 2009).

The winter season is characterized by polar night conditions and, accordingly, the absence of solar radiation. Thus, radiative effects by shortwave radiation can be excluded during the winter months, while longwave radiation provides the only contribution to the net radiative budget. A major source is the terrestrial radiation emitted from the Earth's surface, detected as longwave upward radiation and dependent on the properties of the snow pack. On the other hand, the atmosphere absorbs and emits thermal radiation, detected on the surface as longwave downward radiation. In Ny-Ålesund, both longwave components have increased considerably during the winter seasons since 1993/1994 (Maturilli et al. 2015). The increase in terrestrial radiation is directly linked to the observed surface air temperature increase, while the even stronger increase in longwave downward radiation consequently is related to changes within the atmospheric column above Ny-Ålesund.

Such an increase of the atmospheric longwave radiation emission may be caused by various factors, like e.g. an increase in atmospheric humidity, changes in the cloud cover and properties, a general increase in atmospheric column temperatures, and of course a combination of those. Increasing greenhouse gases seem to be less relevant in this context as their effect should be present throughout all seasons.

The analysis of vertical humidity profiles measured by radiosondes that are launched daily from Ny-Ålesund since 1991 has shown a significant increase of the integrated tropospheric water vapor in the winter season (Maturilli and Kayser 2017). The observed increase in atmospheric humidity may be caused by more cyclonic systems reaching the Arctic, transporting moisture and cloud systems to the Svalbard region. Both the cyclone frequency and the winter cyclone intensity have increased in the high latitudes (McCabe et al. 2001; Sorteberg and Walsh 2008; Döscher et al. 2014 and references therein), and the advection of atmospheric energy into the Arctic region has been found to contribute to the vertical component of Arctic warming (Graversen et al. 2008; Dahlke and Maturilli 2017).

With future Arctic sea-ice retreat, the relative importance of local surface evaporation will increase, resulting in an amplified Arctic hydrological cycle (e.g. Bintanja and Selten 2014). Changing atmospheric moisture directly conditions the cloud cover. An increasing cloud amount and changes in vertical cloud distribution and cloud particle properties affect the radiation balance both in the longwave and shortwave range. With the longwave radiation dominating the polar night, radiative effects of low cloud cover are likely to contribute to the Arctic warming, introducing a positive climate feedback by potentially accelerating the melting of Arctic sea ice (Palm et al. 2010).

For the shortwave radiation, the presence of clouds yields a decrease in downward solar radiation. In Ny-Ålesund, there is no decrease in downward shortwave radiation found for the summer seasons (June, July, August) 1993–2014, rather a small but non-significant increase. For the spring seasons (March, April, May) 1993–2014, a small non-significant decrease in downward shortwave radiation is observed. Yet, for both seasons the shortwave net radiation $SW_{net} = SW_{down} - SW_{up}$ exhibits an increase that is caused by a robust decrease in upward shortwave radiation (Maturilli et al. 2015). This decrease in reflected radiation is due to the changing surface reflectivity related to the snow cover and changes in the timing of the snow-free period. As measure of surface reflectivity, the daily mean albedo SW_{up}/SW_{down} from 1993 to 2017 BSRN measurements is shown in Fig. 2.8, exhibiting a large inter-annual variability.

As dry, weakly metamorphosed snow reflects most of the shortwave downward radiation (Wiscombe and Warren 1980), the broadband shortwave albedo in the snow-covered period in Ny-Ålesund is about 0.8, dropping during the snow-melt season to about 0.1 for the snow-free tundra ground (Winther et al. 2002; Maturilli et al. 2015). The amount of snow and the duration of the snow-covered period are the results of the synoptic large-scale situation. Long-term changes in these snow-related parameters may be interpreted as indicators of climate change. While Winther et al. (2002) did not find any changes neither in the start of the snow melt period nor in the duration of the snow-free season for measurements performed 1981–1997 by the Norwegian Polar Institute in Ny-Ålesund, the BSRN dataset indi-

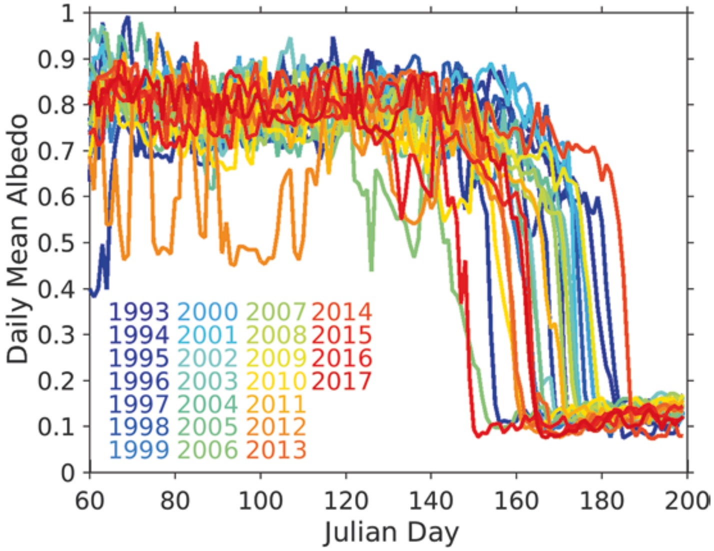

Fig. 2.8 Daily mean albedo SW_{up}/SW_{down} at the Ny-Ålesund BSRN radiation sensor set-up, on Julian days for all observation years from 1993 to 2017 (*color-coded*). (Update of Maturilli et al. 2015)

cates an insignificant temporal shift of the snow-free conditions in the time period 1993–2017. While the actual onset of melting processes is not clearly identifiable in the BSRN albedo data, the rapid drop to the low values of snow-free surface is evident. Here, we define the first snow-free day by daily mean albedo dropping below a value of 0.2. Figure 2.9 shows the Julian day of each year 1993–2017, when the first snow-free day has accordingly been detected below the BSRN instrumentation. Obviously, the local timing of snow melt can deviate considerably on small spatial distances as e.g. strong wind may accumulate snow banks or generally lead to snow redistribution.

Like other climate variables, the chosen parameter obviously does not vary linearly in time. Taking into account the years 1993–2017, linear regression suggests a non-significant earlier appearance of snow-free conditions by about 4 days per decade. Obviously, some years appear as outliers in the decline, like e.g. 2014 which was snow-free only after 5 July. Yet in 2014, the late melting was not related to lower than normal temperatures, but to the extraordinary large accumulated snow mass that was present due to heavy precipitation events in the weeks before. Obviously, changes in Arctic snow cover are not linearly dependent on changing surface temperatures, also precipitation patterns have a major influence. As precipitation varies locally on a smaller spatial scale than air temperature, individual long-term series in the Arctic may be diverse. Overall, an increase of annual precipitation is observed in the Svalbard region, with about 3–4% per decade in Ny-Ålesund (Førland et al. 2011). With the changing climate, changes in snow-cover persistence and thus in albedo are introduced to the Ny-Ålesund environment, leading to a decrease in the annual reflected radiation SW_{up}. Effectively, this is the main contribution to an observed significant increase in the annual net radiation budget RAD_{net} in the order of 3.1 Wm^{-2} per decade (Fig. 2.10).

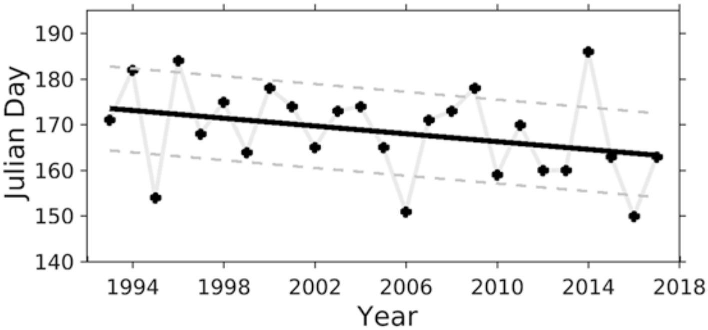

Fig. 2.9 First day of each year from 1993 to 2017 assumed to have a predominantly snow-free surface beneath the radiation sensor set-up because of a daily mean albedo <0.2, in Julian days (*black dots*) with linear regression (*black line*) and regression uncertainty (*grey dashed lines, respectively*)

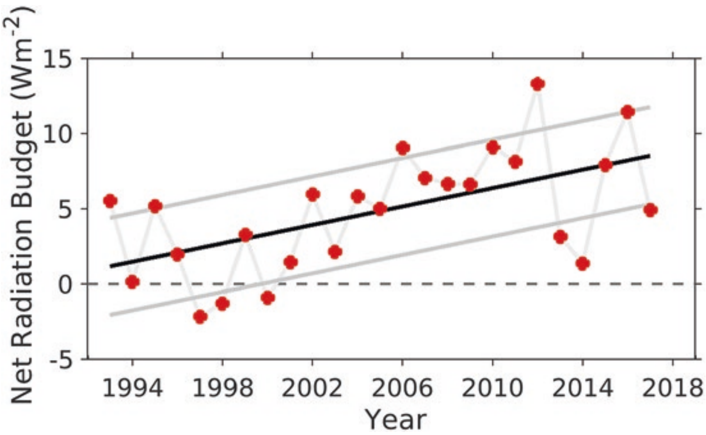

Fig. 2.10 Ny-Ålesund annual mean net radiation budget RAD_{net} (*red dots*), with the linear regression (*black line*) and regression uncertainty (*grey lines, respectively*) indicating an insignificant increase of +3.1 ± 2.7 Wm^{-2} per decade. (Update of Maturilli et al. 2015)

2.4 Surface UV Radiation and Stratospheric Ozone

The ultra-violet (UV) part of the solar spectrum reaching the earth's surface affects living organisms in various ways, which strongly depend on the exact distribution of the radiation intensity across the spectrum, the spectral irradiance. While the photosynthetically active radiation (PAR) described in Sect. 2.2.4 refers to the spectral wavelength range from 400 to 700 nm in the visible, the UV spectrum ranges from 100 to 400 nm and is separated into the UV-A (315–400 nm), UV-B (280–315), and UV-C (100–280) parts. Broadly speaking, the harmfulness of UV radiation increases from UV-A to UV-C, while at the same time the irradiance at the surface reduces strongly from UV-A to UV-C. The incoming solar UV light is strongly absorbed and scattered by the constituents of the atmosphere, like the column amount of ozone, clouds, and aerosols. The low elevation angle of the sun in polar regions results in much lower irradiances there than elsewhere on earth. In addition to cloudiness, also surface reflectivity (albedo) has a high influence on the irradiance. A snow covered surface of high reflectivity can lead to even higher irradiance than usual.

Due to the high variability within the daily and annual course, as well as the weather conditions, a good recording of the actual irradiance is mandatory in order to analyze the influence on the biota. In Ny-Ålesund, several stations perform spectral irradiance measurements with radiometers, but little data are readily available. A well conducted intercomparison campaign was performed in May and June 2009 according to the World Meteorological Organization (WMO) and Network for the Detection of Atmospheric Composition Changes (NDACC) standards, in order to assess the performance and intercomparability of the local spectroradiometers with a travelling standard (Groebner et al. 2010). In addition to the QUASUME reference spectroradiometer, four instruments where compared, including the

Brewer #50 instrument and a multi-filter ground-based UV-visible (GUV) radiometer from the Norwegian Institute for Air Research (Norsk institutt for luftforskning, NILU). The agreement between the instruments was usually better than 5% of the obtained UV-index, with deviations of up to 10% during low irradiance periods (midnight).

Data from the GUV radiometer is currently the only long term UV data available. Svendby et al. (2014) report not only the annual course of the monthly UV dose as observed in Ny-Ålesund, but present also the long-term development of the annually integrated UV doses from 1995 to 2013. Although potentially harmful peak values might not be reflected in the annual dose, it is interesting to note that the annual doses do not show any trend over the reported time span. Dahlback (2002) had extended the time series back to 1975 using a radiative transfer model and available ozone and cloudiness data from satellites and surface observations to derive UV doses. Despite the observed decrease in column ozone values during the later part of his time series, no trend in monthly integrated UV doses for the month of April could be detected.

Figure 2.11 shows the annual course of hourly measured UV dose rate at noon for Ny-Ålesund in 2013 as compared to the expected dose rate for clear sky days as calculated from a radiative transfer model. While during the first half of the year the curve roughly follows the model, it reaches the expected values on few days only in the second half. This reflects the increased cloudiness during summer, as compared to spring, when only very few days have low dose rates. The fact that sometimes the measured values are above the model curve can be attributed to multi–scattering of radiation between a high albedo surface (snow cover) and thin clouds, which

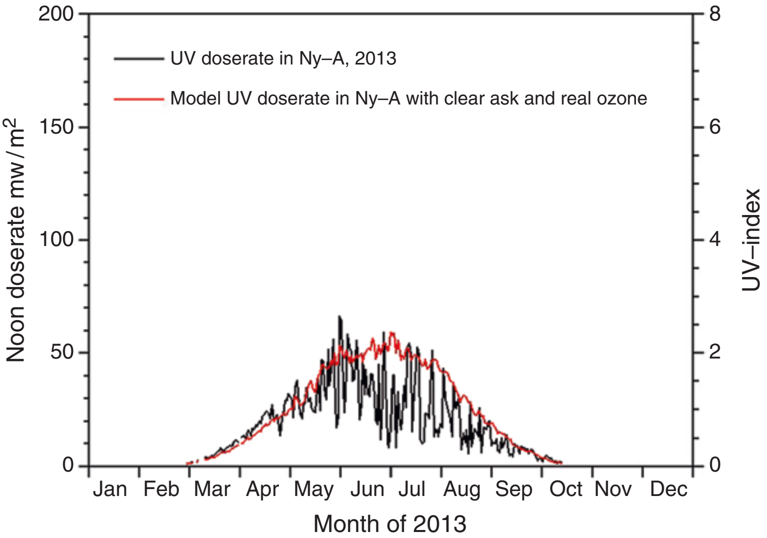

Fig. 2.11 Hourly averaged UV dose rate measured at noon (between 10:30 and 11:30 UTC) in 2013. (From Svendby et al. 2014)

provides a higher level of radiation as would be in a cloud-free atmosphere over a low albedo surface. It should be noted, that the noon dose rate in Ny-Ålesund is roughly a third of the dose rate modelled or measured for Oslo area.

Hanelt et al. (2004) had investigated how the UV light penetrates into the water column of Kongsfjorden in order to assess its influence on algae. They found that during spring months (like April) the highest UV levels can be found, due to reduced ozone values, little cloud cover, and little turbidity in the water column, allowing harmful UV radiation to reach as deep as 5–6 m below the surface.

Stratospheric ozone is the main absorber of UV radiation in earth atmosphere. Together with the scattering of UV radiation on aerosols and clouds and the reflection from the surface, the total amount of ozone above a given location largely determines the level of UV radiation at the surface. Anthropogenic reduction in stratospheric ozone has led to increasing UV levels particularly in polar latitudes (Brasseur and Solomon 1984; Kerr and McElroy 1993; McKenzie et al. 1999; Diaz et al. 2003; de Laat et al. 2010). Variable cloudiness and surface albedo can mask the effect of stratospheric ozone on surface UV at individual stations. Analysing polar cap averages based on many Arctic stations eliminates much of the noise introduced by these effects and can provide deeper insight into the general link between stratospheric ozone and UV and into the longer term evolution of surface UV driven by stratospheric ozone changes.

Anthropogenic loss of ozone above the Arctic is most pronounced in spring and is extremely variable from year to year (Fig. 2.12; Rex et al. 2006). The large degree of variability is driven by variable meteorological conditions during winter, with lower stratospheric temperatures during winter generally favoring larger springtime ozone losses. In Fig. 2.12, the years 1996, 2000, 2005 and 2011 stand out as the years with the largest springtime ozone depletion above the Arctic, leading to large

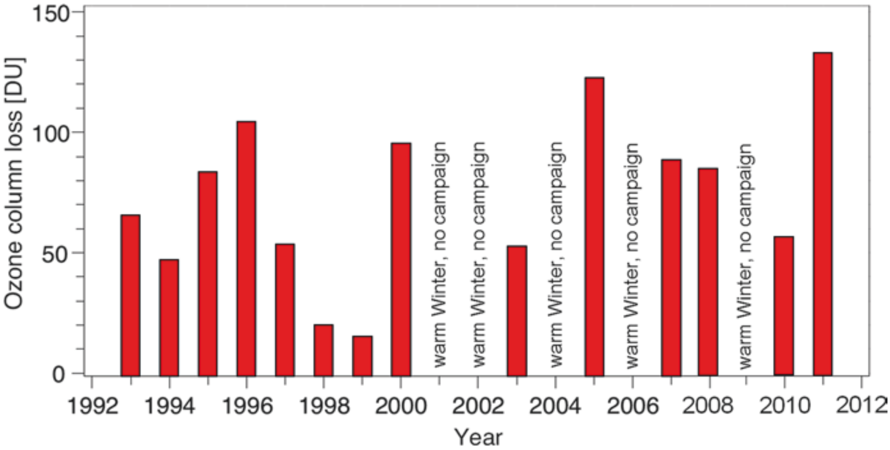

Fig. 2.12 Interannual variation of vertically integrated springtime chemical ozone loss in the Arctic stratosphere derived from measurements of the Match ozone sounding network. (Update of Rex et al. 2006)

negative anomalies of springtime total ozone (Fig. 2.13a). Figure 2.13a shows that 1997 was also characterized by very low total ozone in spring, which mostly resulted from anomalous transport processes during the preceding winter (Tegtmeier et al. 2008; Manney et al. 2011).

In the Arctic summer, stratospheric transport processes are weak and less important for the Arctic ozone budget. Hence, during summer springtime ozone anomalies slowly relax towards a photochemical equilibrium over several months. Figure 2.13a shows that anomalies in Arctic springtime total ozone tend to persist during summer and into fall (Karpechko et al. 2013; see also Fioletov and Shepherd 2003, 2005; Tegtmeier and Shepherd 2007).

Karpechko et al. (2013) showed that the persistence of ozone anomalies during summer results in corresponding polar cap wide anomalies of surface UV levels

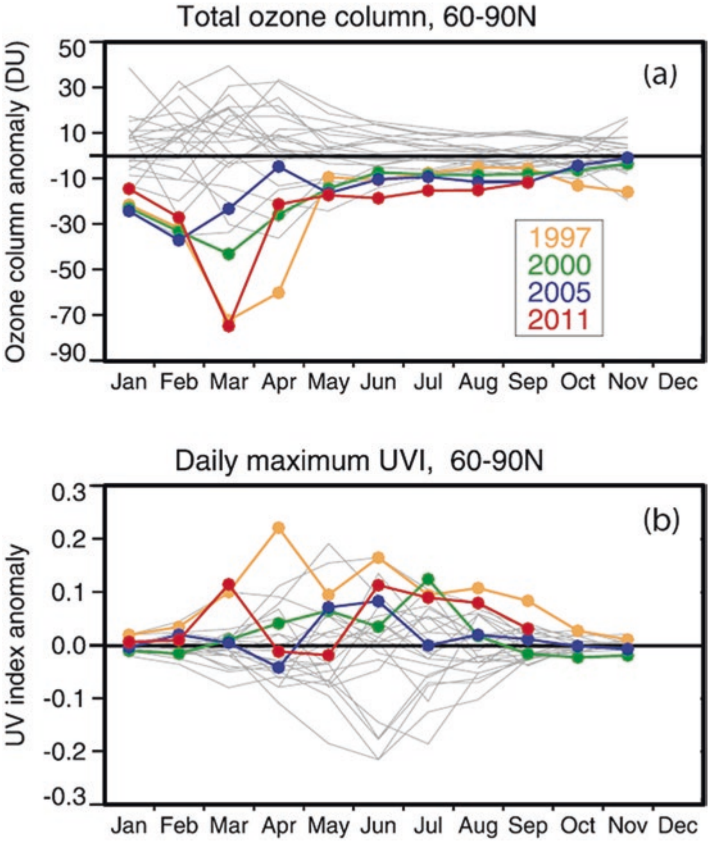

Fig. 2.13 (**a**) Seasonal evolution of TOMS/OMI satellite-derived monthly mean total ozone column anomalies averaged over 60°N–90°N for each year between 1979 and 2011 when the measurements were available, (**b**) Monthly mean cloud corrected noontime UV index anomaly for the same geographic region. Red, blue, green, and orange colors highlight the 2011, 2005, 2000, and 1997 years, respectively. (From Karpechko et al. 2013)

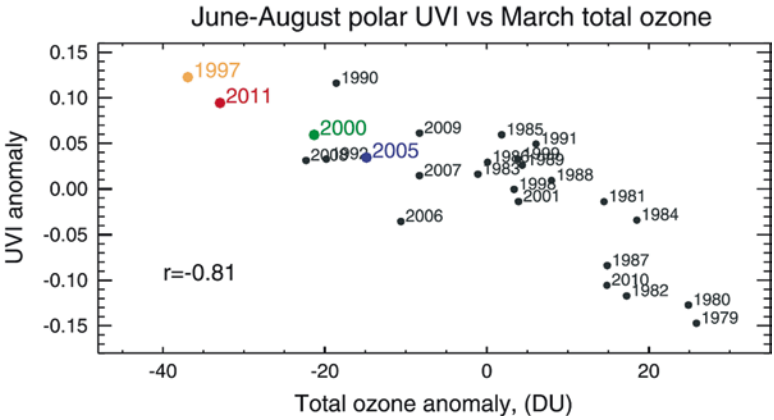

Fig. 2.14 Scatterplot of the June–August noontime UVI for polar latitudes versus March extra-tropical total ozone (TOMS/OMI data north of 35°N), with the correlation coefficient $r = -0.81$. (From Karpechko et al. 2013)

(Fig. 2.13b). Figure 2.14 shows the correlation between the March total ozone anomaly and June–August polar UV index anomaly, showing a correlation of −0.81. Record UV levels were measured at a number of Arctic stations in summer 2011, following record Arctic ozone depletion in spring 2011 and leading to unprecedented UV indices of 6–7 at some Arctic stations (Karpechko et al. 2013).

Overall, changes in the incoming radiation reaching the surface will affect the amount of available underwater radiation. The underwater light in Kongsfjorden and its ecological implications are described in Pavlov et al. (Chap. 5). Generally, the described processes impacting Arctic climate are important concerning local feedbacks with the underlying landmass, ice and ocean surface and consequently the ecosystem, but at the same time they induce a global feedback on the energy balance of the planet.

2.5 Conclusion

The sea surface layer of the Kongsfjord environment is in interaction with the above atmosphere as the exchange of latent and sensible heat affects both ambiences. Above, we described the climatological setting of the Kongsfjord area as a boundary condition for the marine ecosystem.

Though located in the high Arctic, summer air temperature in Ny-Ålesund rises above freezing point causing snow and ice melt. In the dark and colder wintertime, the inter-annual temperature variability is stronger, and though temperature generally remains well below freezing point even rain periods can be observed. Independent of the synoptic scale flow, the wind in the lowermost atmosphere is mainly along the fjord axis throughout the whole year due to channeling effects caused by orography. Orographic clouds may also add to the general cloud cover caused by synoptic systems. The variability in synoptic cloud cover is the cause of the inter-annual variability in incoming solar radiation in summer, observed in the monthly mean global shortwave radiation SW_{down} as well as in PAR and UV radiation. Quantitative changes in surface radiation parameters over the last two decades have been identified in relation to the changing climate. In the annual mean, the reflected radiation decreases since the period of high reflective snow cover shortens. During the winter months, an increase in thermal radiation is observed due to generally increasing temperatures at the surface and in the atmospheric column, increasing atmospheric moisture and potential changes in cloud cover. In fact, the winter period adds the largest contribution to the observed warming in Ny-Ålesund, with a winter season temperature increase of 3.1 ± 2.2 K per decade (update of Maturilli et al. 2015).

Though the air temperature and atmospheric humidity may not have a direct impact on the marine ecosystem, their relevance for the hydrological cycle and the formation of clouds as determining factors for the incoming radiation at the surface is unambiguous. The marine Kongsfjord ecosystem will be shaped by the changing ambient water conditions, but moreover will be affected by the changing atmosphere that holds the radiative boundary conditions to the system.

Acknowledgements The authors thank all technical and scientific staff at Ny-Ålesund who has been taking care of the atmospheric measurements described in this article, in particular the station staff of the Sverdrup and AWIPEV stations. The authors are grateful to the three reviewers for valuable comments and suggestions.

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Part II

Oceanography, Sea Ice and Underwater Light Regime

Chapter 3
The Kongsfjorden Transect: Seasonal and Inter-annual Variability in Hydrography

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Abstract The Kongsfjorden conductivity, temperature and depth (CTD) Transect has been monitored annually since 1994. It covers the full length of the fjord and the shelf, and the upper part of the shelf slope outside Kongsfjorden. In addition to CTD profiles, data from vessel-mounted Acoustic Doppler Current Profiler (ADCP) and moorings have been collected. Previous studies noted that Atlantic Water (AW) from the West Spitsbergen Current was observed in the fjord every summer, but to a varying extent. The prolonged monitoring provided by the Kongsfjorden Transect data set examined here reveals continuous variations in AW content and vertical distribution in the fjord, both on seasonal and inter-annual timescales. Our focus in

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_3

this paper is on this variable content of AW in Kongsfjorden, the forcing mechanisms that may govern the inflow of this water mass, and its distribution in the fjord. We classify three winter types linked to three characteristic scenarios for winter formation of water masses. During the historically typical winters of type “Winter Deep”, deep convection, often combined with sea ice formation, produces dense winter water that prevents AW from entering Kongsfjorden. Summer inflow of AW starts when density differences between fjord and shelf water allows for it, and occurs at some intermediate depth. During winters of type “Winter Intermediate”, AW advects into the fjord along the bottom via Kongsfjordrenna. Winter convection in Kongsfjorden will then be limited to intermediate depth, usually producing very cold intermediate water. Deep AW inflow continues during the following summer. A winter of type “Winter Open” seems to develop when open water convection produces very dense shelf water, and AW winter advection into Kongsfjorden occurs at the surface. Summer AW inflow is rather shallow after such winters. We find that variations between Winter Deep and Winter Intermediate winters are due to inherent natural variability. However, the Winter Open winters seem to be a consequence of the general trend of atmospheric and oceanic warming, and, more specifically, of the decreasing sea ice cover in the Arctic region. The Winter Open winters have all occurred after an unusual flooding of AW onto the West Spitsbergen shelf in February 2006.

Keywords Kongsfjorden · Atlantic Water · Hydrography · Water masses · Exchange

Abbreviations

ADCP	Acoustic Doppler Current Profiler
ArW	Arctic Water
AW	Atlantic Water
CTD	Conductivity Temperature Depth
ESC	East Spitsbergen Current
GSW	Gibbs SeaWater
IOPAN	Institute of Oceanology, Polish Academy of Sciences
IW	Intermediate Water
LW	Local Water
NPI	Norwegian Polar Institute
PSS78	Practical Salinity Scale 1978
SAMS	Scottish Association for Marine Science
SNR	Signal to Noise Ratio
SPC	Spitsbergen Polar Current
SW	Surface Water
TAW	Transformed Atlantic Water
TEOS-10	Thermodynamic Equation of SeaWater 2010

TS	Temperature-Salinity
UiB	University of Bergen
UNIS HD	UNIS Hydrographic Database
UNIS	The University Centre in Svalbard
WCW	Winter Cooled Water
WSC	West Spitsbergen Current

3.1 Introduction

The Kongsfjorden Transect is a set of CTD and biological stations distributed along a line from the head of Kongsfjorden to the continental slope west of Spitsbergen, and includes station locations that were identified and then commonly occupied after the Kongsfjorden workshop organized in Longyearbyen in 2000. The main outcome of this workshop was two review papers, one on the marine ecosystem (Hop et al. 2002) and one on the physical environment of Kongsfjorden (Svendsen et al. 2002). Subsequently, the number of hydrographic observations along the Kongsfjorden transect has expanded extensively, resulting in many publications. Here we review these publications, and introduce further unpublished data from the collection of observations. Summer observations of hydrography along the Kongsfjorden transect started in 1994 and continued every summer from 1997 to 2014. Winter observations from 13 of these years are also available, as well as time series from moorings inside Kongsfjorden. This expanded data set allows for deeper insight into the seasonal and inter-annual variations in oceanographic conditions in Kongsfjorden and also captures the interaction with the shelf and slope water masses.

In this review, we focus on the interaction between the fjord/shelf and the Atlantic Water (AW) from the West Spitsbergen Current (WSC). The WSC is topographically steered along the continental slope (Walczowski and Piechura 2007), and is a major source of warm and saline AW to the Arctic Ocean (Polyakov et al. 2005). The WSC is subject to cooling and freshening as it flows northward (Saloranta and Haugan 2004), and interactions with West Spitsbergen fjords such as Kongsfjorden can make a significant contribution to this modification. Understanding the mechanisms governing the interaction between the WSC and West Spitsbergen fjords (here represented by Kongsfjorden) is therefore important, not only for explaining environmental conditions inside the fjords, but also for explaining variability in the Arctic Ocean. Svendsen et al. (2002) and subsequent publications (Cottier et al. 2005; Nilsen et al. 2008) were able to observe that the volume and resulting influence from AW could change substantially from one summer to the next. This year-to-year variability in AW content in Kongsfjorden has been referred to as ‘warm’ and ‘cold’ years (Cottier et al. 2005) in line with earlier biological studies of West Spitsbergen fjords (Weslawski and Adamski 1987) as well as on a more regional scale (Furevik 2001). This review places these observations in a seasonal and inter-annual perspective. The West Spitsbergen fjords are separated from the WSC by a shallow shelf, along which there is a northward flowing coastal current advecting

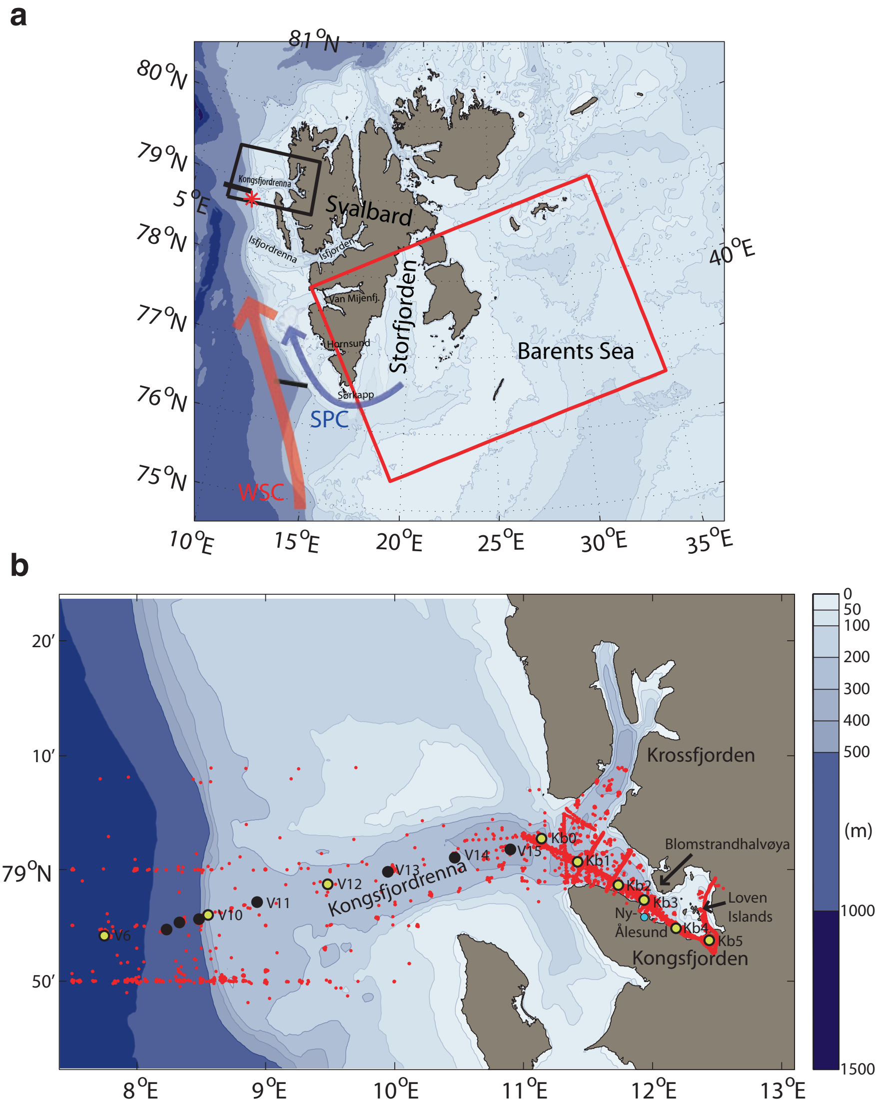

Fig. 3.1 (**a**) Map of Svalbard area. ERA Interim surface heat flux data extracted from red star position, and National Snow and Ice Data Center (NSIDC) monthly sea-ice data from within red box. Black transect lines show locations of CTD data used to produce data in Fig. 3.4. WSC West Spitsbergen Current, SPC Spitsbergen Polar Current (coastal current). Map inside black box shown in (**b**) Map of Kongsfjorden with adjacent shelf area. Red dots are all CTD positions included in this review. Black circles are positions of the CTD stations comprising the Kongsfjorden transect, also listed in Table 3.1. The black circles with yellow center are also biological stations. Ny-Ålesund is indicated with cyan dot

Arctic Water (ArW) and drift ice from Storfjorden and the Barents Sea (Fig. 3.1). This current was termed the Spitsbergen Polar Current (SPC) by Helland-Hansen and Nansen (1909), but is now sometimes termed the Sørkapp Current, or the continuation of the East Spitsbergen Current (ESC). Troughs cross the shelf from the shelf edge towards each fjord. In this paper we focus on the trough outside Kongsfjorden, called Kongsfjordrenna (Fig. 3.1). A substantial part of the AW inflow to the fjords is topographically steered along these troughs as modelled by Nilsen et al. (2016), where they named this flow the Spitsbergen Trough Current. Throughout this paper we use the term 'Kongsfjordrenna' when we specifically discuss the topographically-steered AW inflow to Kongsfjorden, while in most cases we use the term 'shelf' when we mean the area between the WSC and Kongsfjorden.

Mooring temperature data from within Kongsfjorden have revealed that unusually large volumes of AW entered the fjord during February 2006 (Cottier et al. 2007), increasing the annual mean temperature in Kongsfjorden by 2 °C in 2006. Substantial sea ice melting was also observed around Svalbard that winter, following a tendency of increased winter sea ice melting in the region (Onarheim et al. 2014). One particular question that the present review intends to answer is: Was the February 2006 AW event a tipping point for the environmental conditions and biological response in Kongsfjorden, or was it part of the natural variability? The 2 °C increase in yearly mean temperature in Kongsfjorden has not been permanent, and the degree of ice melting in the region has been observed to vary inter-annually. We use two decades of CTD observations along the Kongsfjorden Transect as well as a decade of mooring data from Kongsfjorden, a large portion of which have not been published previously, to shed light on the reasons for the observed inter-annual variations. The paper is organized with an overview of the data first, followed by an extensive presentation of the forcing mechanisms that determine water mass transformations in the Kongsfjorden Transect. We then proceed by showing how variability in the forcing mechanisms affects the seasonal cycle and is consequently leading to inter-annual variability in hydrography as well as AW content in Kongsfjorden. Detailed descriptions of yearly winter and summer versions of the Kongsfjorden Transect hydrography are given in Appendix A, while in the discussion we relate our findings to inter-annual variations in other environmental factors, especially the Arctic ice cover.

3.2 Observations

The Geophysical Institute at the University of Bergen (UiB) in Norway initiated monitoring of the physical oceanography of Kongsfjorden and the adjacent shelf during a September cruise in 1994. This initiative was soon supported by two additional Norwegian institutions, The University Centre in Svalbard (UNIS) and the Norwegian Polar Institute (NPI), with a joint cruise in December 1994. In 1996, Institute of Oceanology Polish Academy of Sciences (IOPAN) in Sopot, Poland, started their monitoring program with yearly summer cruises to the west coast of Spitsbergen and

Table 3.1 Station list of the section referred to as the Kongsfjorden Transect. Stations named with italic letters are CTD stations only, the other stations are also biological stations. The station locations are indicated in Fig. 3.1b

Location	Latitude	Longitude	Bottom depth (m)
Kb5	N78 53.70	E012 26.44	85
Kb4	N78 54.75	E012 11.00	110
Kb3	N78 57.30	E011 56.16	345
Kb2	N78 58.63	E011 44.19	300
Kb1	N79 00.70	E011 25.24	360
Kb0	N79 02.76	E011 8.50	325
V15	N79 01.78	E010 53.83	320
V14	N79 01.05	E010 27.99	290
V13	N78 59.79	E009 56.99	260
V12	N78 58.70	E009 28.95	225
V11	N78 57.10	E008 56.11	220
V10	N78 55.95	E008 33.28	280
V9	N78 55.58	E008 29.00	500
V8	N78 55.28	E008 20.00	750
V7	N78 54.65	E008 14.01	870
V6	N78 54.11	E007 44.99	1140

Kongsfjorden, undertaking both physical and biological sampling. In 2000, biologists at the Norwegian Polar Institute started biological sampling at stations initiated by IOPAN (Kb0–Kb5), and with additional CTD (V6–V15) and biological stations (V6, 10 and 12) on the adjacent shelf and slope. These sampling stations evolved into what is now called ‘the Kongsfjorden Transect’. The station positions in the Kongsfjorden Transect are listed in Table 3.1, and indicated in Fig. 3.1b.

The assemblages of CTD surveys that provide data for this review paper, are extracted from the UNIS Hydrographic Database (UNIS HD), a CTD database for the whole Svalbard region. Our subset of this database contains stations sampled during the period August 1906 – May 2015 (red dots in Fig. 3.1b), and it includes all data sampled over the period 1994–2014, as described in the previous paragraph. We here name our subset the Kongsfjorden Transect data. The Norwegian Polar Institute has provided a few additional data from July 2015 and July 2016. The CTD stations in the database do not all follow the defined positions of the Kongsfjorden Transect (see Fig. 3.1b). However, since biological data are associated with these stations, when we show section plots, we have chosen to interpolate all data onto a line approximately following the CTD transect listed in Table 3.1. Moreover, the transect stations follow Kongsfjorden and Kongsfjordrenna more or less along the central axis, while the expected path of geostrophic AW advection will be along the southern side of Kongsfjordrenna. At Kb3 the transect is close to the expected topographically steered AW advection inside Kongsfjorden, as the current tends to follow the 200 m isobath. Data coverage is best for summer months (July–September). However, there were quite a few surveys in the period January to May as well,

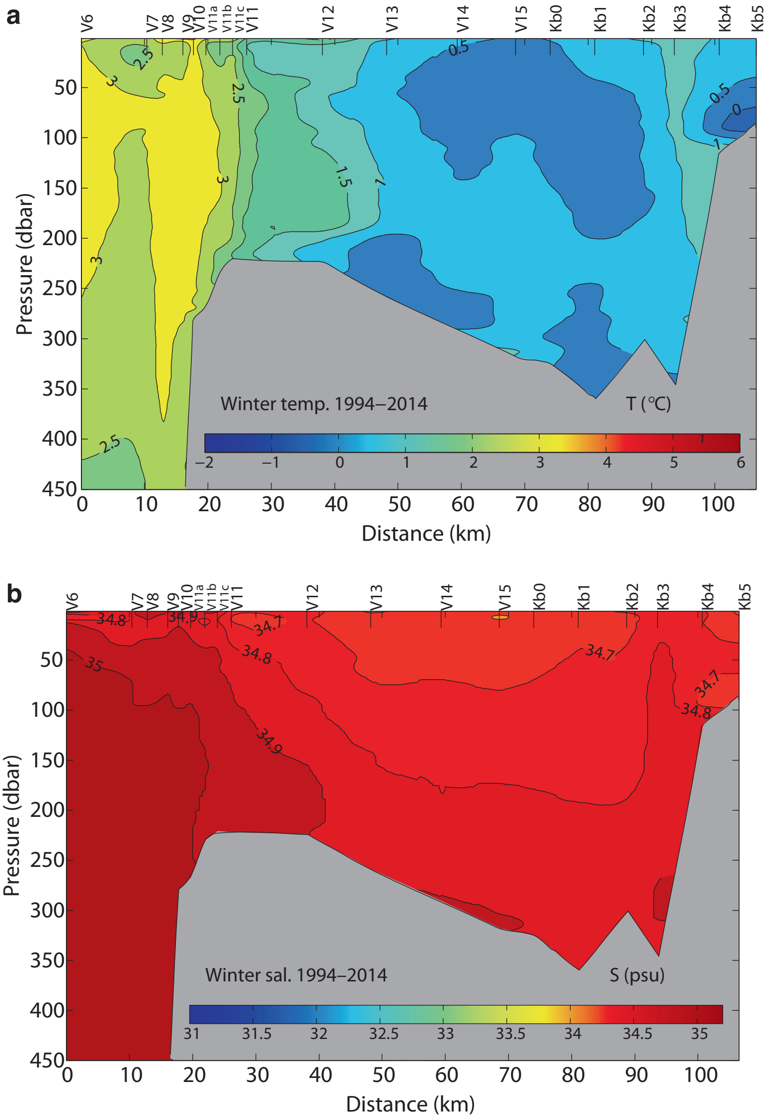

Fig. 3.2 Mean winter temperature and salinity along the Kongsfjorden transect, based on all available Kongsfjorden Transect data between 1994 and 2014. The entrance of the Kongsfjorden-Krossfjorden system is located between stations Kb0 and Kb1

making it possible to present winter (January–May) and summer (July–September) versions of the transect. The interpolation procedure is as follows. The data from the CTD stations are averaged into bins between the positions comprising the Kongsfjorden Transect (Table 3.1), then the non-uniform binaveraged temperature, salinity and density transects are interpolated onto a regular grid with 500 m horizontal resolution using the kriging interpolation method. The method interpolates between data points, and extrapolates beyond data points, similar to objective mapping (Emery and Thomson 2014). Regions with horizontal isolines in temperature, salinity and density can be indicative of bad data coverage. The two panels in Fig. 3.2 show mean winter (January–May) distribution of temperature and salinity in the Kongsfjorden Transect, based on all winter data collected during the bi-decadal period 1994–2014 (data from 13 of the possible 21 winters). The mean summer (July–September) distribution of temperature and salinity in the Kongsfjorden Transect during the two decades 1994–2014 (data from 19 of the possible 21 summers) are shown in the two panels in Fig. 3.3. The entrance of the Kongsfjorden-Krossfjorden system is located between stations Kb0 and Kb1, and the shelf edge at V10, separating the transect into three regions: the fjord, the SPC region on the shelf (Kongsfjordrenna) and the WSC over the continental slope. Throughout the paper, we use the old standard for salinity; Practical Salinity PSS78 as opposed to the new standard Absolute Salinity in TEOS-10 (Millero et al. 2008), mainly to avoid confusion in water mass characteristics.

Mooring data have been available from various locations in the central Kongsfjorden basin since April 2002, and nearly continuously since September 2003. The moorings have been well equipped with temperature sensors, an upward looking ADCP (often with both upward and downward looking instruments, since 2012), and two or three conductivity loggers. Over time, additional parameters have been added, including fluorescence and PAR loggers and 21-bottle sediment traps. These moorings were designed by Scottish Association for Marine Science (SAMS), and deployed in Kongsfjorden in a joint effort with different Norwegian institutions (NPI, UiB and UNIS). We refer to them as SAMS moorings in an overview of all moorings deployed in Kongsfjorden (Table 3.2). Time series of temperature and fluorescence from the SAMS moorings are presented in Hegseth et al. (Chap. 6), and we will refer to those Figs. later in the review. UNIS and UiB have had additional, more conventional moorings equipped with current meters with temperature, conductivity and pressure sensors at up to three depths. From September 2002 to September 2003 and from August 2004 to September 2005, this type of mooring was deployed on the southern side of the entrance of Kongsfjorden in the central basin (U1 in Table 3.2). Then it was redeployed each year from September 2005 to August 2015 further inwards in the fjord, close to Blomstrandhalvøya (H1 in Table 3.2; Fig. 3.1b). Table 3.2 contains observation periods and positions of moorings in Kongsfjorden. It is not a complete list, only the ones from which data have been used here for tidal analysis, and presented in Hegseth et al. (Chap. 6). A more complete presentation of SAMS mooring data can be found in Wallace et al. (2010).

3.3 Forcing Mechanisms

The seminal review by Svendsen et al. (2002) distinguished between internal and external forcing mechanisms contributing to water mass transformations in Kongsfjorden. The internal mechanisms act within the fjord, and comprise

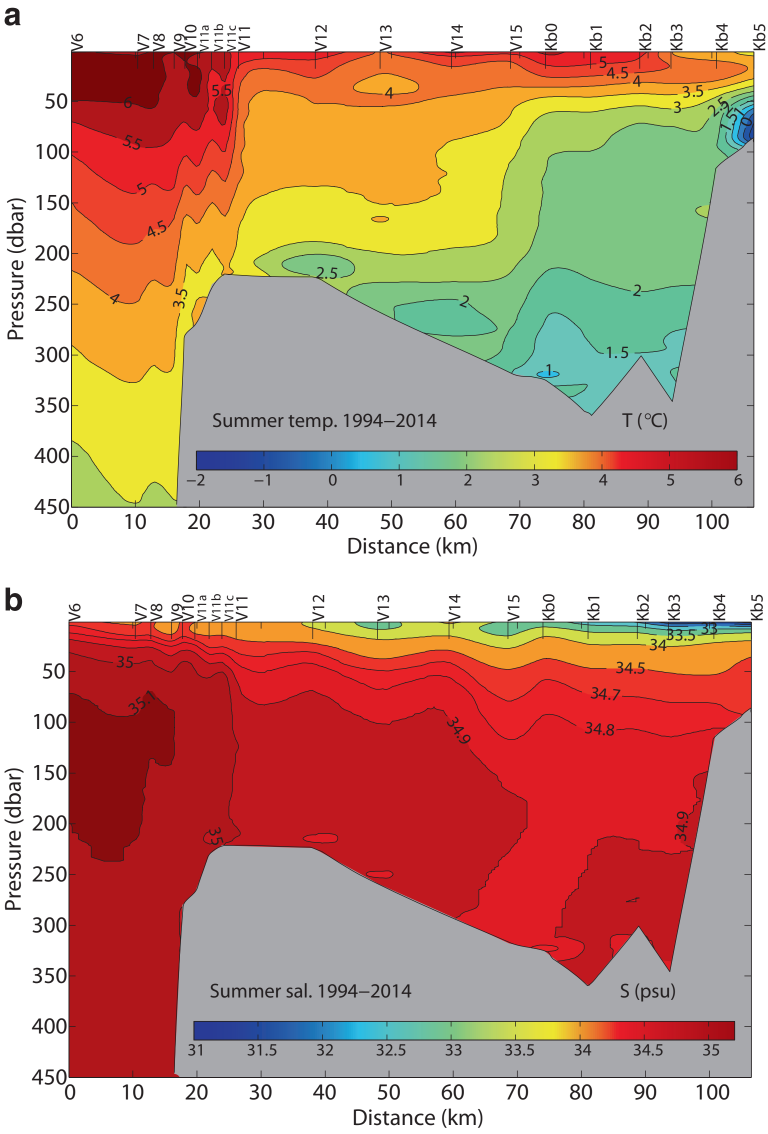

Fig. 3.3 Mean summer temperature and salinity along the Kongsfjorden transect, based on all available Kongsfjorden Transect data between 1994 and 2014. The entrance of the Kongsfjorden-Krossfjorden system is located between stations Kb0 and Kb1

freshwater runoff, solar heating, wind forcing, vertical mixing and sea ice formation, and modifications on internal circulation from the effects of the rotation of the earth. Svendsen et al. (2002) emphasized the upper layer circulation caused by freshwater runoff and wind forcing, and on rotational effects on the deep circulation. These physical processes were further reviewed by Cottier et al. (2010).

Table 3.2 Mooring positions in Kongsfjorden, including selected periods where tidal analysis were made for this review

Mooring	Date from	Date to	Latitude	Longitude	Bottom (m)	
D1	16 April 2002	23 June 2002	N79 03.25	E011 18.00	212	SAMS
	16 April 2002	23 June 2002				Tidal anal.
D2	3 July 2002	28 Sep 2002	N79 03.336	E011 17.24	213	SAMS
	3 July 2002	28 Sep 2002				Tidal anal.
D3	24 May 2003	6 Sep 2003	N78 58.307	E011 39.114	260	SAMS
	24 May 2003	6 Sep 2003				Tidal anal.
D4	9 Sep 2003	22 Aug 2004	N78 58.32	E011 38.75	270	SAMS
	9 Sep 2003	16 Oct 2003				Tidal anal.
D5	23 Aug 2004	14 Sep 2005	N78 57.443	E011 49.365	170	SAMS
D5–1	23 Aug 2004	10 Oct 2004	N78 57.443	E011 49.365	170	Tidal anal.
D5–2	11 Oct 2004	14 Sep 2005	N78 57.443	E011 49.365	170	Tidal anal.
D6	16 Sep 2005	30 May 2006	N79 01.21	E011 46.45	210	SAMS
D7	06 June 2006	25 August 2007	N79 01.20	E011 46.417	209	SAMS
D8	30 Aug 2007	19 Aug 2008	N78 57.44	E011 49.60	178	SAMS
D9	04 Sept 2008	22 Aug 2009	N78 59.18	E011 20.929	209	SAMS
D10	06 Sept 2009	16 Sept 2010	N78 57.75	E011 45.556	225	SAMS
D11	26 Sept 2010	02 Sept 2011	N78 57.75	E011 45.556	221	SAMS
D12	26 Sept 2011	08 Sept 2012	N78 57.75	E011 45.556	251	SAMS
D13	03 Oct 2012	03 Sept 2013	N78 57.73	E011 48.428	241	SAMS
D14	05 Oct 2013	09 Sept 2014	N78 57.75	E011 48.30	230	SAMS
U1	Sep 2002	Sep 2003	N78 58.681	E011 32.490	202	UNIS
U1–1	24 May 2003	6 Sep 2003				Tidal anal.
U1	Sep 2004	Sep 2005	N78 58.681	E011 32.490	202	UNIS
U1–2	11 Oct 2004	24 Jan 2005				Tidal anal.
H1	Sep 2005	Aug 2015	N78 58.382	E011 58.613	218	UNIS
	27 Mar 2015	26 Aug 2015				Tidal anal.

External mechanisms are acting outside of the fjord itself, and they are important in determining the volume and timing of AW present on the shelf (Cottier et al. 2005). Svendsen et al. (2002) briefly touched on this issue, suggesting wind-driven upwelling and downwelling associated with offshore and onshore Ekman transport combined with ageostrophic processes at the shelf-edge front between AW in the WSC and the shelf water as the governing mechanisms. Since then, different mechanisms that can lead to exchange of AW across this shelf-edge front have been suggested (Nilsen et al. 2006; Cottier et al. 2007; Tverberg and Nøst 2009; Teigen et al. 2010, 2011; Tverberg et al. 2014; Inall et al. 2015; Nilsen et al. 2016), involving both ageostrophic and geostrophic processes. These studies illustrate the variety of aspects connected to the exchange mechanisms, which in combination determine how the AW inflow to Kongsfjorden behaves. In this section we first present the WSC and the SPC, then discuss the different aspects of the exchange across the front between these two currents, and the resulting advection of AW towards Kongsfjorden, and why the AW does not always enter Kongsfjorden. Some updates on internal mechanisms are given at the end of the section.

3.3.1 West Spitsbergen Current

Two branches of AW (western and eastern) converge in the region of western Spitsbergen. The western, offshore branch flows along the deep underwater ridges, the eastern branch (core of the WSC) flows along the Barents Sea shelf-break and slope and continues along the western Spitsbergen coast (Walczowski and Piechura 2007). Properties of the eastern, alongshore branch are analyzed more closely here, as it is water from this branch that may flow into the western Svalbard fjords. This current is topographically steered, and the center of the flow is generally situated over the 800 m isobath. Properties of AW vary between successive summers according to the upstream conditions. Moreover, continuing along the Spitsbergen coast, AW in the WSC core becomes colder and fresher due to mixing with ambient waters and exchange with the atmosphere (Boyd and D'Asaro 1994; Saloranta and Haugan 2004). To determine the AW lower limits of temperature and salinity, the AW characteristics (S > 34.90, T > 3 °C) from Svendsen et al. (2002) were used herein.

We present variability of AW calculated on the basis of the IOPAN summer data for two regions of the WSC (Fig. 3.4). The longest time series in the IOPAN database is for the section along N76°30′. This section is representative of the general

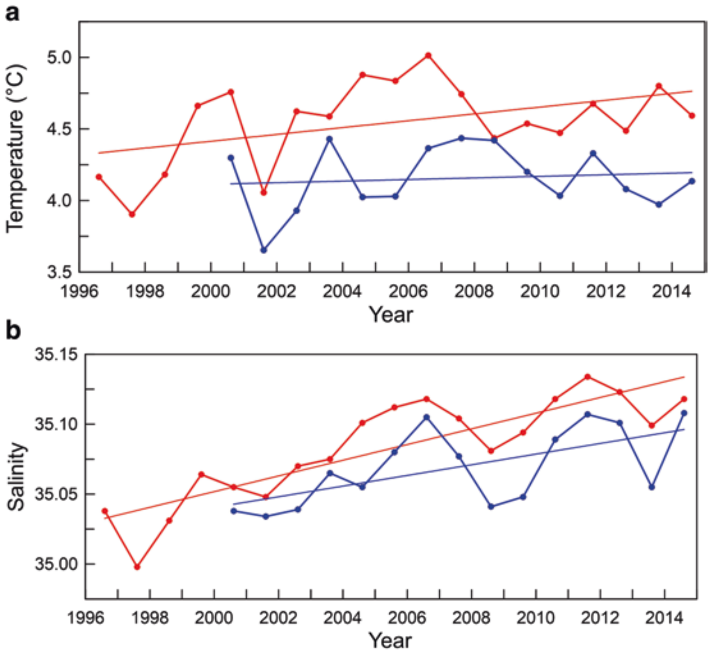

Fig. 3.4 Time series of (**a**) temperature and (**b**) salinity of Atlantic Water (AW) (T > 3 °C. S > 34.9) in the core of the West Spitsbergen Current at latitude N76°30′, between longitudes E012°30′ and E014°30′ (red lines) and at latitude N78°50′, between longitudes E007° and E009° (blue lines). Locations of transects are show in Fig. 3.1a

variability of AW in the WSC (Walczowski 2014). A positive trend of AW temperature and salinity in summer during the period 1996–2014 is evident (Fig. 3.4). The temperature maximum at N76°30′ occurs in 2006. Salinity has a more continuous trend, however, with maxima in 2006 and 2011. At the section along N78°50′ (close to Kongsfjorden) the salinity variability is very similar to that from N76°30′, with values about 0.03 lower. The pattern of temperature variability is somewhat different compared to N76°30′, but values are generally lower than at the southern section. AW shows high temperatures in the vicinity of Kongsfjorden in 2003 and during the 2006–2008 period. The summers 2001, 2004, 2005, 2010 and 2013 were relatively cold at the 78°50′N section.

3.3.2 Spitsbergen Polar Current

In their review, Svendsen et al. (2002) stated that the West Spitsbergen shelf is occupied by a cold and relatively fresh Arctic type coastal water originating from Storfjorden and the Barents Sea, and carried northwards by a coastal current. As mentioned in the introduction, we adapt the name Spitsbergen Polar Current (SPC) for this coastal current, from Helland-Hansen and Nansen (1909). The water mass transported by the SPC is often called Arctic Water (ArW) with somewhat varying characteristics. In this review, we adapt the characteristics (-1.5 °C < T < 1.0 °C and 34.30 < S < 34.80) suggested by Cottier et al. (2005), which have a salinity range similar to that by Loeng (1991), but with a wider temperature range than suggested by both Loeng (1991) and Helland-Hansen and Nansen (1909). The mean winter characteristics of shelf water (Fig. 3.2) fits into the upper range of our adapted ArW definition. However, our inter-annual comparison of the Kongsfjorden Transect will reveal that the characteristics of the water mass transported by the SPC are even more variable than previously anticipated and do not always fit into the ArW classification.

The general assumption has been that ArW is a version of the Arctic halocline layer, formed by sea ice formation during winter (Rudels et al. 1996). However, some studies (Steele et al. 1995; Cokelet et al. 2008; Tverberg et al. 2014) indicate that drift ice melting in warm water, combined with strong heat loss to the atmosphere, can form a halocline layer similar to that formed by brine release, except that it is possible for the temperature of the layer to be higher than the freezing point. The SPC normally carries drift ice northwards, and ice charts show that this drift ice gradually disappears as it flows northwards, so Tverberg et al. (2014) suggested that interaction with AW in the WSC supplies heat for the melting, indicating that melting can occur even during the winter season, and ensures that the shelf water stays fresh and cold. The combination of ice melting and heat loss to the atmosphere will produce denser melt water than ice melting alone does, implying that a winter melt layer will be thicker than a summer melt layer. Cokelet et al. (2008) even suggested that such a combination; AW losing heat to the atmosphere (90%) and ice melting (10%) forms the Arctic Intermediate Water, found down to

1000 m in the Greenland Sea. When drift ice is not present in the SPC, or north of where it has melted, continuous AW exchange will make the shelf water gradually warmer and more saline, as also Helland-Hansen and Nansen (1909) suggested. This can explain why the northern part of the west Spitsbergen shelf is more of an Atlantic type and less of an Arctic type than further south on the shelf, and that it can be a contribution to the large variability in water mass properties in the SPC. The structure and variability of water mass properties in the SPC have, to our knowledge, never been studied in detail. However, it can be an important factor in the dynamics of the fjord-shelf exchange and interaction with the AW advection towards Kongsfjorden.

3.3.3 Shelf-Edge Front

A classic upwelling mechanism was likely important during the event in February 2006 (Cottier et al. 2007) where it led to deep inflow of AW towards Kongsfjorden. Conservation of volume can be used as a simplified explanation for such a relationship; winds from the north will move water away from the coast in the surface Ekman layer, and this water has to be replaced by ocean water from a deeper level. Northerly winds occurred between 24 January and 27 February. The strong northerly winds were preceded by a period with unusually strong southerly winds (18 December to 24 January). These periods are indicated in Fig. 3.5, showing observations of temperature from within Kongsfjorden. The figure reveals that during winter, episodes of warm AW appeared in the deep part of the fjord basin. During the period with strong northerly winds, AW extended vertically up until it filled the whole water column. After this, a period with unusually strong heat loss to the atmosphere started, along with melting of local sea ice in the fjord or drift ice on the shelf. The end result in late April was a water column that was homogeneous in temperature and slightly stratified in salinity, very similar to the formation of ArW suggested in the previous subsection.

Wind events along the WSC can lead to geostrophic advection of AW towards Kongsfjorden as well, and Nilsen et al. (2016) published an idealized model study of this mechanism. A brief description of the mechanism is as follows: a wind curl (horizontal wind shear) adds relative vorticity to the WSC, forcing the current up or down the slope due to conservation of potential vorticity. In the case when the WSC is forced up the slope (during southerly wind events), topographic steering leads to geostrophic advection of AW into troughs on the shelf, and in some extreme situations onto the shelf itself. Results from this model study are shown in Fig. 3.6. This effect has not been tested against observations in Kongsfjordrenna. In Kongsfjorden, Inall et al. (2015) reported the mean flow in current meter data to be 4 cm s^{-1}, but with episodic events of stronger currents (see next paragraph).

Upwelling events along the WSC will in practice involve instabilities at the shelf-edge front, and will then be the ageostrophic process that Svendsen et al. (2002) mentioned. Instabilities at the shelf-edge front are laterally meandering

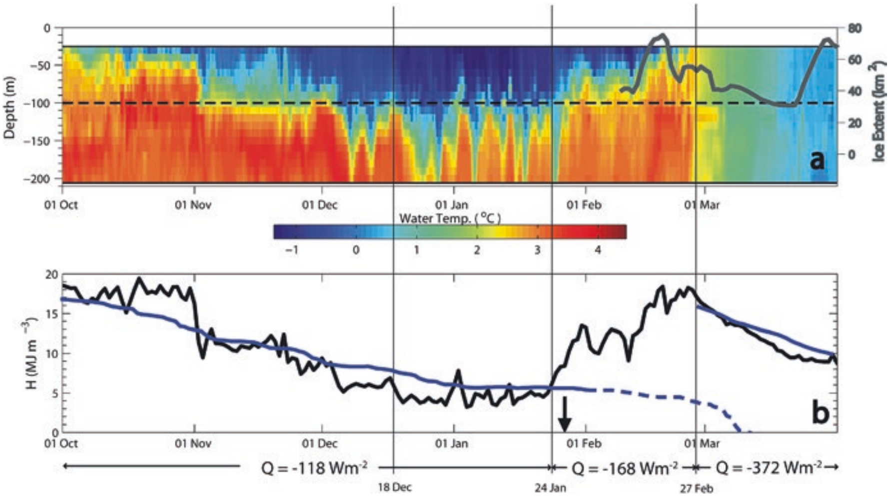

Fig. 3.5 (**a**) Temperature observations at Kongsfjorden mooring (N79°3.250′, E011°18.00′) between 30 m and 200 m with H (mean heat content) calculated over the interval 30–100 m (dashed line). The 7-day running mean of fast ice extent in Kongsfjorden is overlaid (grey). (**b**) Mean heat content (H) from Kongsfjorden mooring (black) and from the 1-D model (blue line – dashed when the model diverges from observations) with mean surface heat flux (Q). The model is reinitialized on 27 February 2006 and the arrow marks when the model predicts freezing. (Figure adapted from Cottier et al. (2007), their Fig. 4)

waves along the front that turn unstable and break off from the WSC in the form of eddies and filaments. The laterally meandering waves can generally be called topographic waves, and they do not always become unstable. However, even when the topographic waves are stable, they are associated with lateral exchange of heat (Nilsen et al. 2006). Moreover, stable topographic waves, generated by wind events at the shelf-edge front, can create signals that propagate along the southern side of Kongsfjordrenna towards Kongsfjorden as coastal-trapped waves with strong along-isobath currents moving back and forth over typically 2–3 days. Inall et al. (2015) detected episodes of such waves from mooring data inside Kongsfjorden (Table 3.2) with current speeds of 20–30 cm s^{-1}, and having a two-layer (baroclinic) structure with along-shore inflow in one layer concurrently with outflow in the other layer. They estimated that 100 m was a typical separation depth between the two layers. Coastal-trapped waves are trapped to steep sloping bottom, and the width of the slope and the level of stratification determine the width of their associated current. Such wave currents are in geostrophic balance and can easily be interpreted as topographically steered flow, which means that rotational constraints (Coriolis) force the flow to follow bathymetric contours. If an assumption is made that some level of mixing takes place during the inward and outward directed currents associated with these topographic waves, then the waves also contribute to the exchange of water properties between the shelf and inner fjord. Inall et al. (2015) estimated that trapped waves contribute more to exchange than either tidal

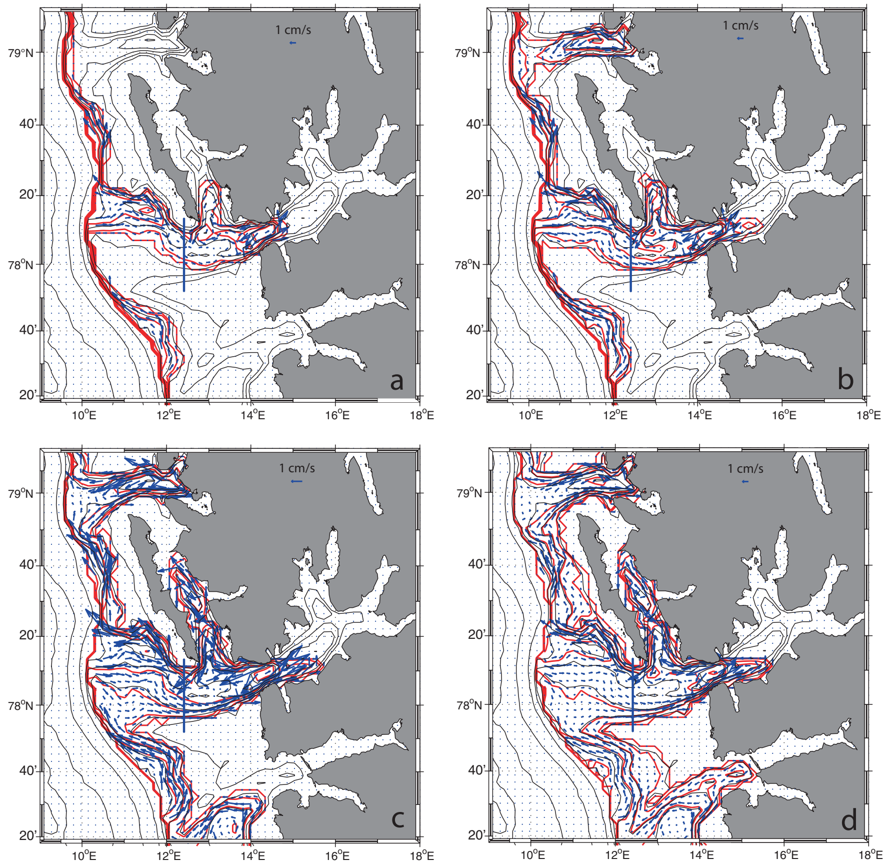

Fig. 3.6 Topographic steering of AW from the WSC in cases when the position of the West Spitsbergen Current (WSC) is shifted eastwards a distance (a) 2 km, (b) 3 km, (c) 8 km and (d) 14 km. Contoured streamlines/circulation pattern ψ (red lines) are plotted on top of the bottom topography (black lines). The blue arrows are the geostrophic velocity vectors and a velocity scale is given in the upper right corner. (Figure adapted from Nilsen et al. (2016), their Fig. 11)

or estuarine processes. The two-layer structure appearing during winter 2006 (Fig. 3.5), with layers separated at 100 m depth level, and the episodic occurrence of AW, may possibly be associated with these coastal-trapped waves. Inflow episodes of similar duration were reproduced in a recent high-resolution model study of Kongsfjorden (Sundfjord et al. 2017).

When the topographic waves along the shelf-edge front become unstable, there are two extreme versions of instabilities. The instabilities are: (1) barotropic instability (Collings and Grimshaw 1980) due to a horizontal current shear with no horizontal density gradients across the shelf-edge front, and (2) baroclinic instability (Mysak and Schott 1977) due to horizontal density gradients across a front. In practice, instabilities are likely caused by a combination of barotropic and baroclinic instabilities, and other factors, like bottom features and wind, can be involved. The above mentioned upwelling situation is an example of the latter, and may actually lead to baroclinic instability at the front because deep water in the WSC is lifted upwards in the water column, altering the horizontal density gradients across the front. Instabilities in the WSC have been investigated by Teigen et al. (2010, 2011), based on current-meter time series in the WSC, linking them to generation of topographic waves in the current. As these waves are undulations of the current, they contain a strong horizontal component to the WSC, leading to transport of heat and salt across the current and shelf-edge front as the undulations develop into eddies and filaments. Typically, during a winter, there are 8–10 barotropic instability events lasting between 1 day and up to several days where interaction with surrounding local water masses occurs.

Barotropic eddies extend through the whole water column whilst baroclinic eddies extend through only part of the water column. In some cases this can imply that eddies formed by baroclinic instabilities in the relatively deep slope current (WSC) appear as barotropic eddies when they advect onto the shallower shelf. The vortex circulation of an eddy is approximately in geostrophic balance due to the large horizontal scale of these eddies (of order 10 km), in the same way as the WSC is a geostrophic current. However, their slightly ageostrophic quality determines the fate of eddies generated by the unstable topographic waves. This quality means that the eddies and filaments spread water laterally, predominantly along similar density (isopycnal diffusion), but in such a way that lighter water is eventually laid over denser water, over time leading to flattened or terrain-following isopycnals across the front (Adcock and Marshall 2000). This long-term effect is called eddy overturning, which always exchanges water perpendicular to a mean geostrophic current, and can transform a baroclinic front into a barotropic front. A barotropic front is the typical summer situation along the shelf-edge front outside Kongsfjorden (Saloranta and Svendsen 2001), perhaps leading to the misunderstanding that barotropic instability is the dominating process at the shelf-edge front. During winter, heat loss to the atmosphere is constantly increasing the density of surface water. This occurs more efficiently on the shallower shelf side of the shelf-edge front than in the deeper WSC. Continuous heat loss to the atmosphere can thus help maintain an eddy overturning because it changes the density of the water column to a different extent on each side of the front, and eddies along the front are then never able to flatten the isopycnals. Other processes that change the density of the water column, like sea ice formation and melting, can also be drivers of eddy overturning. The combined effect of wind-driven Ekman transport and eddy overturning is generally called residual-mean overturning (Marshall and Radko 2003). Tverberg et al. (2014) used such theory to explain winter evolution of the water mass on the shelf just south of Kongsfjorden.

The eddy and residual-mean overturning are not measurable circulations since eddy overturning is a slow response over weeks, as opposed to Ekman transport, which responds to the wind on a timescale of hours, and can be estimated. Evidence of eddy and residual-mean overturning is hard to specify in general circulation models, even if they have high enough resolution to resolve eddies. The method used to quantify residual-mean overturning requires that modeled currents can be averaged both in time and along some distance of uniform bottom profile, the latter normally requiring an idealized model set up. In such an idealized model study by Tverberg and Nøst (2009), eddy activity was the only process leading to water exchange across a shelf-edge front between a shelf with water column temperature and salinity characteristics of Kongsfjorden, and a slope current with WSC characteristics. The evolvement of three situations were simulated for 100 days each. Model results from an April 2002 situation, with shelf water lighter than WSC water at every depth level, had an eddy field evolving after 20 days, with eddy overturning that brought AW onto the shelf in the deep sector of the water column. An April 2007 situation, with shelf water denser than WSC water at every depth level, had an eddy field evolving after 4 days, with eddy overturning that brought AW onto the shelf at the surface. A September 2000 situation, with lighter upper shelf water and denser deepest shelf water than water at similar depth levels in the WSC, had eddies forming already the first day, with eddy overturning that brought AW onto the shelf at intermediate depth where the density across the front was the same. The eddy overturning thus appeared like a purely density-driven flow (ageostrophic). However, one should have in mind that eddy overturning is a secondary effect of the eddy activity. In the initial phase, the baroclinic eddies and filaments have a stirring effect, meaning they are stretched laterally into complex shapes, substantially increasing the area of the front between AW from the WSC and shelf water. The integrated effect of turbulent diffusion along this enlarged area, leads to an effective diffusion that can be orders of magnitude greater than the turbulent diffusion itself, depending on the degree of stretching (Marshall et al. 2006).

The shelf-edge front processes described above are summarized for a winter situation with heat loss through the ocean surface (Fig. 3.7). The surface heat loss will then drive a residual mean overturning (eddy overturning) across the shelf-edge front that will try to put light water on top of dense water. Wind forcing that will lead to Ekman transport in similar direction as eddy overturning is indicated (Fig. 3.7). During some periods, Ekman transport may of course oppose the eddy overturning. In these cases, the Ekman transport (wind) will likely lead to enhanced baroclinic instabilities, and a resulting stronger eddy overturning. Ekman and eddy overturning are the ageostrophic processes, while topographic steering governs the geostrophic advection, which involves larger volumes and will be important in all cases. The classical situation, with shelf water being less dense that the WSC, will lead to topographically-steered geostrophic advection in the deep part of the water column, while when the WSC is noticeably less dense than shelf water, the vertical extent of the geostrophic advection might be from the surface to some limited depth. Our observations indicate that when density differences across the shelf-edge front are weak, the topographic steering may involve the whole water column, and topographic steering of advected AW is pronounced. In cases when the shelf and fjord water columns are stratified, with AW occupying upper or lower part of the water column, the AW advection may also be associated with coastal-trapped wave episodes (Inall et al. 2015). Fig. 3.7 refers to three winter types, which we will define in Sect. 3.4 "Seasonal Cycle". They are closely connected to the depth level where winter advection of AW towards Kongsfjorden occurs, and whether it enters the fjord basin.

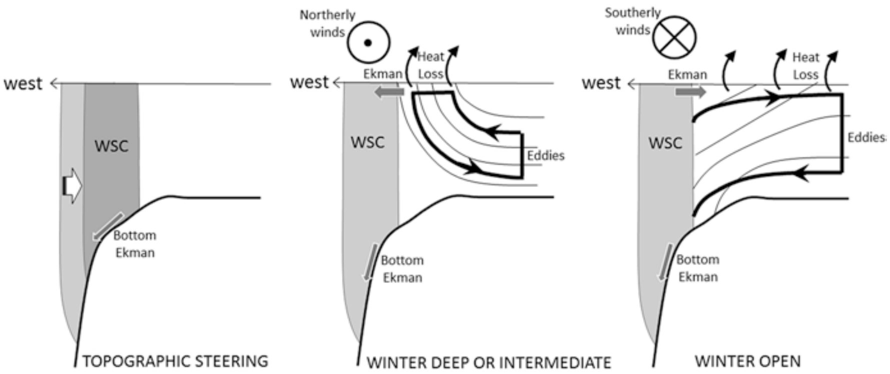

Fig. 3.7 Shelf edge processes that leads to advection of Atlantic Water (AW) towards Kongsfjorden, from the West Spitsbergen Current (WSC), inspired by Fig. 2 in Tverberg et al. (2014). Ekman refers to surface Ekman drift towards the fjord due to southerly winds or surface Ekman drift towards the ocean due to northerly winds. Thick lines (tagged with 'Eddies') superimposed on thin lines (isopycnals) refer to a long-term mean overturning resulting from eddy activity along the shelf-edge front, acting to put light water on top of dense water. If special wind conditions lift the WSC higher up on the shelf slope, AW will be topographically steered towards Kongsfjorden along the southern side of Kongsfjordrenna

3.3.4 Geostrophic Control

The Cottier et al. (2005) study suggests that geostrophic control at the fjord entrance prevents AW from entering the fjord during the winter season because the water column inside the fjord basin is denser than the water column on the shelf. This concept of geostrophic control was introduced by Klinck et al. (1981) to explain how a coastal current can be prevented from entering the adjacent fjord, and instead passes by the mouth of the fjord. The underlying principle is that density differences between the fjord water column and the adjacent shelf has a thermal-wind effect on the geostrophic coastal current. Thermal wind makes the geostrophic current speed decrease or increase with depth depending on the density difference on both sides of the current. If the water is lighter on the right side of the current, when facing the current direction, the current speed will decrease with increasing depth. If the situation is opposite (denser water to the right), the current speed will increase with increasing depth. The implication of this for the coastal current outside the fjord entrance is that during a winter with strong winter convection in the fjord, and the deep fjord water being denser than shelf water, the speed of the coastal current will be enhanced towards the bottom. This blocks the advection of AW into the fjord, and instead the advected AW will join the coastal current and make a detour in the mouth region. After the onset of the summer season, the density of the fjord water column gradually decreases, altering the density differences between the fjord and the shelf. When there is density matching inside and outside the fjord the geostrophic control breaks down and AW can enter the fjord at depth. Atlantic Water entering the fjord may happen during the winter as well, if the water column in the fjord has lower density than the shelf. The speed of the coastal current will then decrease with depth, and it is possible in these situations that the coastal current is confined to an upper layer. There may then be no geostrophic control at the mouth in the deep layer, and AW can enter the fjord in that deeper part of the water column.

Klinck et al. (1981) assumed that the fjord entrance is narrow compared to the internal Rossby radius of deformation. This is normally not the case for Kongsfjorden, which should allow for baroclinic flow through the fjord entrance. Kongsfjorden is about 10 km wide, while a typical summer internal Rossby radius is 3–4 km (Svendsen et al. 2002). However, Cottier et al. (2005) observed in a numerical modeling experiment, that a geostrophic control mechanism took place at the common entrance of Kongsfjorden and Krossfjorden. Atlantic Water was advected towards the fjord along the southern side of Kongsfjordrenna, but was forced to make a detour at this entrance. Geostrophic control has also been used to explain why AW does not enter Isfjorden because it is blocked by the coastal current passing very close to the mouth of the fjord (Nilsen et al. 2008). We are not aware of any study that has focused on the path of the coastal current as it flows past Kongsfjorden, and due to the fact that the coastal current continuously interacts with the WSC and has to pass the island Forlandet along its path between Isfjorden and Kongsfjorden, the situation may be more complicated for Kongsfjorden than for the case of Isfjorden. Nevertheless, we here make the assumption that Kongsfjorden behaves somewhat similar to Isfjorden, and geostrophic control applies. Our hydrographic data indicate that the geostrophic control may happen either at the common mouth of Kongsfjorden-Krossfjorden (Kb0) or at the entrance of Kongsfjorden (Kb1).

3.3.5 Internal Circulation

Along the West Spitsbergen coast, the tide travels as a transient Kelvin wave (Gjevik and Straume 1989), and the tide inside the Kongsfjorden-Krossfjorden system is a response to this tidal elevation of the ocean surface outside the fjord (Svendsen et al. 2002). Tidal analysis of mooring data reveals that the tide in Kongsfjorden is dominated by three semidiurnal constituents, M2, S2, and N2, and one diurnal constituent, K1. All other constituents are very small compared to these. M2 is the most significant tidal component (Table 3.3), with the largest amplitude in both sea level elevation and in current, and the highest Signal to Noise Ratio (SNR) of all the constituents. The tidal current is however very weak and not strong enough to dominate the flow pattern. Very little of the total variance in the velocity time series is of tidal origin. Inall et al. (2015) found that these four constituents only captured 1.2% of the total velocity time series variance. Harmonic tidal analysis on the data from the three current meters in Table 3.3 showed that the tide was responsible for only 1.3%, 1.2%, and 1.2%, respectively for the three depths, of the total variance of the velocity, which is consistent with the result of Inall et al. (2015).

M2 has an amplitude of nearly 0.5 m while S2 and N2 together have an amplitude half this. The diurnal component K1 gives only a minor contribution. This

Table 3.3 Harmonic tidal analyses made from both current (left side) and pressure (right side) data from instruments at 37, 121, and 216 m at Mooring H1 for the period Sep 2014-Aug 2015

37 m	Frequency	Major (cm s^{-1})	Minor (cm s^{-1})	SNR	37 m	Amplitude (dbar)	SNR
M2	0.0805	0.814	0.024	15	M2	0.48	2900
S2	0.0833	0.307	−0.014	2.6	S2	0.16	290
N2	0.0790	0.08	0.029	0.33	N2	0.09	84
K1	0.0418	0.127	−0.037	0.34	K1	0.06	180
121 m					121 m		
M2	0.0805	0.518	0.11	5	M2	0.48	2700
S2	0.0833	0.133	0.043	0.42	S2	0.16	290
N2	0.0790	0.074	−0.054	0.29	N2	0.09	89
K1	0.0418	0.2	0.028	1	K1	0.04	140
216 m					216 m		
M2	0.0805	0.443	0.03	11	M2	0.45	470
S2	0.0833	0.143	−0.027	2.4	S2	0.14	49
N2	0.0790	0.08	−0.018	0.63	N2	0.07	10
K1	0.0418	0.094	−0.02	0.72	K1	0.05	13

The mooring's position was N78°58′ and E011°58′
SNR signal to noise ratio

explains why the tide is semidiurnal in Kongsfjorden. The solar component (S2) causes the amplitudes to vary considerably during a fortnightly spring-neap period. The average difference between high tide and low tide in Kongsfjorden is about 1 m. The resulting M2 tidal ellipses from the different moorings are shown in Fig. 3.8a. The ellipses closest to land (U1, D3-D5 and H1) are nearly unidirectional, and more open away from the coast (D1/D2). In the mouth area (D1/D2), the tidal signal is stronger than further into the fjord (see Table 3.4). Mean currents from the same mooring data are shown in Fig. 3.8b. Based on topographic steering (Nilsen et al. 2016), and a relatively small internal Rossby deformation radius (3–4 km during summer, according to Svendsen et al. (2002), one would expect the circulation in Kongsfjorden to describe exactly this inflow along the southern shore that turns northwards along Blomstrandhalvøya (Fig. 3.1b) and outflow along the northern shore. The coastal-trapped waves (Inall et al. 2015) will periodically constitute a similar circulation and the reverse, similar to the tidal currents in the fjord as well, but with longer periods (2–3 days) and stronger velocity (20–30 cm s^{-1}).

Unpublished shipboard ADCP observations as well as model results sometimes reveal a semi-permanent closed eddy in this central basin of Kongsfjorden. ADCP observations during the April 2002 cruise indicated that the semi-permanent eddy was present (Cottier et al. 2003), superposed on the temperature field at 30 m depth. This particular occurrence appeared to have an eddy confined to the upper layer, and might represent a situation with restricted exchange with the shelf due to geostrophic control at the fjord entrance. A somewhat similar example of modeled circulation is shown in Fig. 3.9b. Sundfjord et al. (2017) found that such eddy patterns

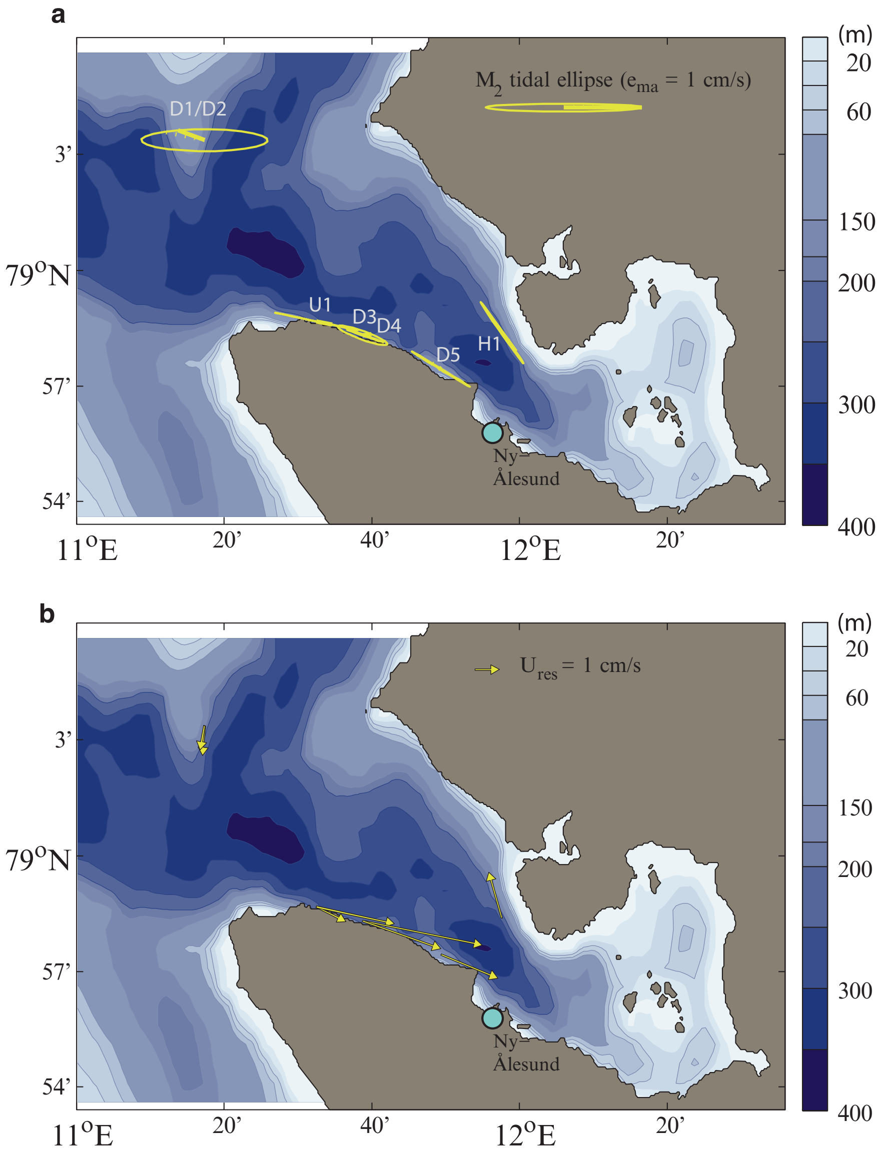

Fig. 3.8 (**a**) The M2 tidal ellipses and (**b**) residual mean currents in Kongsfjorden from different current meter moorings as indicated in (**a**) and listed in Table 3.2. The mean residual current vectors at the U1 mooring are shown for both 44 m (~1.5 cm s^{-1}) and 97 m (~3.5 cm s^{-1}) depths, while the others show the depth-averaged residual currents. The time means of the residual currents are over the measuring period for each mooring

Table 3.4 Percent total variance predicted, from the tidal analyses from SAMS moorings (D1 to D5) and UNIS/GFI moorings (U1 and H1)

Mooring	Depth (m)	Total var.	Pred var.	%
D1	145–29 in 4 m bins	25.70	1.67	6.5
D2	145–29 in 4 m bins	14.99	1.76	11.7
D3	120–50 in 4 m bins	25.04	0.26	1
D4	126–62 in 4 m bins	42.86	0.89	2.1
D5	132–20 in 4 m bins	33.72	0.46	1.4
U1–1	44	25.89	0.74	2.9
U1–1	94	68.98	2.20	3.2
U1–2	94	45.69	0.93	2.5
H1	37	28.27	0.34	1.3
H1	121	11.27	0.14	1.2
H1	216	9.19	0.11	1.2

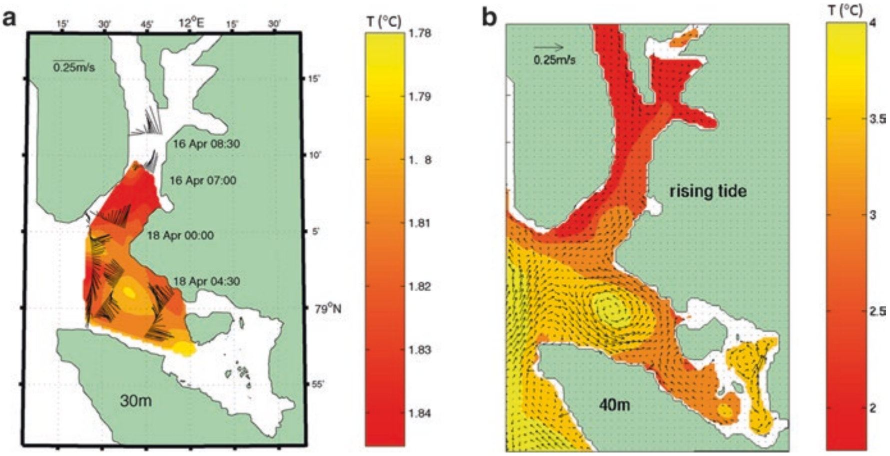

Fig. 3.9 (**a**) Observed and (**b**) modeled snap shots of typical circulation in Kongsfjorden. (Figure adapted from Cottier et al. 2003)

in the fjord could be associated with inflow of AW as well, with periodicity similar to the coastal-trapped waves (Inall et al. 2015).

3.3.6 *Fjord Ice*

The extent of the sea ice cover in Kongsfjorden varies significantly between years, and the inter-seasonal evolution is highly variable (Pavlova et al., Chap. 4). Systematic mapping of sea ice cover in Kongsfjorden was established in 2003 (Gerland and Renner 2007), based on observations from the mountain Zeppelinfjellet near Ny-Ålesund at the southern shore of the fjord (Fig. 3.1b). From 2004 onwards, there were sufficient observations to represent the inter-annual variability by e.g. the average ice covered area from all observations done within one particular month. The area is calculated from digitized maps using ArcGIS tools. The area of landfast ice in Kongsfjorden for each March during 2004–2015 show a variable but declining sea ice coverage (Fig. 3.10). The total surface area of Kongsfjorden (east of 11°12′E and south of 79°5′N) is in comparison about 275 km^2, and the surface area inside of the Lovénøyane (Fig. 3.1b) is 60–70 km^2. This implies that only in 2004, 2009 and 2011, did the ice cover extend beyond the area inside of Lovénøyane. These islands in the inner part of Kongsfjorden restrict the local circulation to such a degree that there may be distinctly more Arctic water masses inside them, than in the central Kongsfjorden basin, due to glacial runoff and ocean-glacier front interaction. The more regular fast ice cover inside Lovénøyane is an indication of this (see e.g. MacLachlan et al. (2007)).

Brine release during ice formation can be a potential contribution to the production of dense winter water. The release is strongest during the early phases of ice freezing (Notz and Worster 2008). Under land-fast ice, the ice growth becomes slower as the ice thickness increases, since ice and snow insulates the water column from the cold air above. The areal extent of open water at freezing temperatures, leading to newly formed ice, thus determines to a large degree how much brine is added to the water column (Nilsen et al. 2008). The smallest salt increase estimated for Isfjorden was in 2004 (Nilsen et al. 2008), analogous to the maximum seen in Kongsfjorden that year (Fig. 3.10), and we note that this was related to the reduced polynya area and a maximum in fast ice area.

3.3.7 Runoff and Freshwater from Glaciers and Land

During summer, freshwater and sediment discharges at the base of the glaciers can be significant and provide a driving mechanism for exchange of water masses with the central basin (Salcedo-Castro et al. 2013; Kimura et al. 2014; Lydersen et al. 2014). More than 80% of the land area drainage into Kongsfjorden is covered by glaciers, and therefore glacier runoff accounts for the majority of the freshwater entering the fjord. Arctic river runoff has a strong seasonality; similarly, the onset of glacier surface melt typically occurs in late spring, with peak discharges as late as July and August. This is due to the internal hydrology of the glaciers, where the initial pulse of surface melt first refreezes in the cold snow and firn until temperatures are brought to the melting point, after which the meltwater finds its way to the base of the glacier and down toward the glacier front. There it typically enters the fjord through one or a few large tunnels at or near the base of the glacier front, i.e. some 10s of meters below the sea surface. Radar measurements of ice thickness reveal that the tidewater glacier fronts in the inner part of Kongsfjorden are ca. 50–100 m deep (J. Kohler, NPI, unpubl. data.). The glacial discharge released at depth is very buoyant with respect to the ambient water, and quickly rises,

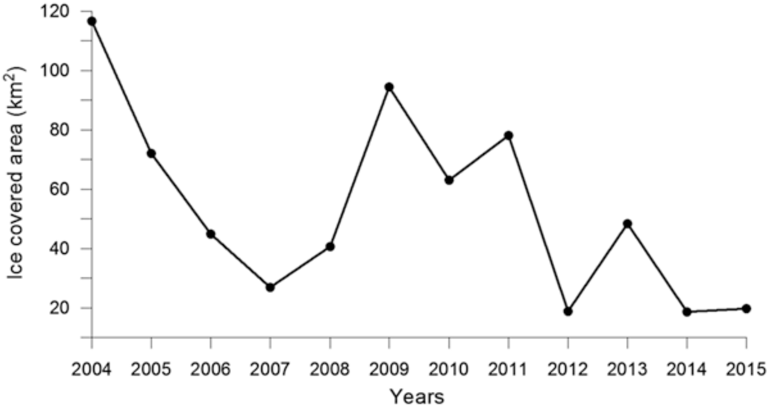

Fig. 3.10 Average fast-ice covered area in Kongsfjorden during March 2004–2015, based on photographic observations from the mountain Zeppelinfjellet, Ny-Ålesund

entraining and mixing with large volumes of surrounding water. The effects of subglacial discharge on local circulation can be profound, with large volumes of water drawn from intermediate depths and a thick, brackish outflow layer at the surface (Urbanski et al. 2017). This process is different from typical surface river runoff, which occurs in the surface layer and does not entail large conversion of potential energy into mechanical mixing. In Kongsfjorden, studies show that the modification of such a subsurface plume through mixing occurs very close to the glacier face so that its signature is not seen in the ambient water within 2 km of the glacier (MacLachlan et al. 2007). In addition to melt water drainage, the glaciers also contribute freshwater via icebergs (mostly in summer) and through frontal melt (potentially the whole year) (Luckman et al. 2015). Frontal melt will be strongly related to the heat content of the surface and intermediate layers; in years where AW protrudes deep into the fjord and relatively high in the water column, frontal melting is likely to be largest (Luckman et al. 2015).

Local winds, usually blowing along the fjord axis move the surface layer, typically so that wind blowing out of the fjord forces freshwater to concentrate along the northern shore and flow out of the fjord (Ingvaldsen et al. 2001). Such outflow would be compensated by inflow of more saline, warmer AW over the bottom, along the southern shore (Moffat 2014). This wind-driven circulation may enhance glacier melting, increase freshwater discharge thus generating a feedback that will force more intensive water exchange. A high-resolution model study by Sundfjord et al. (2017) shows significant transport of water towards the glacier fronts in the inner part of the fjord, throughout the annual cycle. In that study, wind appears to be the primary driver of variability for this circulation. It has been shown that Van Mijenfjorden (Fig. 3.1a), which has similar width to Kongsfjorden, responds rapidly to changes in wind forcing; a shift from down-fjord to up-fjord wind can move the thickest segment of the fresh surface layer from the northern to the southern side in a matter of hours (Skarðhamar and Svendsen 2010).

3.3.8 Vertical Structure and Mixing

We have argued that the vertical density structure and the density difference between the water column in the fjord and on the shelf controls the depth of inflow of AW to the fjord. However, we have also noted that topographically-steered advection along the southern shore, combined with bursts of intensified flow due to coastal trapped waves, are likely to be responsible for the largest volumes of inflow of AW. The apparent advection of AW at particular depth levels can then be explained by the eddy stirring effect spreading water along isopycnals away from the core of a geostrophic flow, which can either be the flow along the shore inside Kongsfjorden or the WSC, or a combination of these. The stirring effect of eddies and filaments behave like isopycnal diffusion, or simplified, like horizontal diffusion. Vertical or diapycnal diffusion adds to this by changing the stratification (vertical stability) of the water column and may be essential in the slow process of reducing the density of the Kongsfjorden water masses after the winter.

The most striking feature in terms of vertical stability is the seasonal pycnocline, which for all practical purposes isolates the deeper layers from the otherwise efficient wind mixing. Wind energy will be able to deepen the mixed layer during strong wind events, but it will not erode further into the seasonal pycnocline as the density difference is too large between surface and deeper waters. During autumn and winter, wind driven mixing will more efficiently aid in breaking down stratification as the water column is cooled from the surface and the freshwater content decreases with the cessation of melt water supply. Tides and other persistent currents may contribute to vertical mixing if they are sufficiently strong, especially over shallow or steep topography and in interaction with significant density gradients. In Kongsfjorden, we have observed that tidal currents are weak (Fig. 3.8a), and the mean internal circulation in the fjord as well (Fig. 3.8b). We see a need for more investigation of the temporally and spatially varying rates of diapycnal mixing in the fjord, especially during periods where the geostrophic control prevents advection of AW into the fjord. Knowledge of diapycnal mixing rates inside the fjord can indicate how fast the internal fjord processes can contribute to the preconditioning of the water column that is required to initiate exchange of AW with the shelf and slope.

3.4 Seasonal Cycle

Svendsen et al. (2002) deduced a scenario for the mechanisms governing the production of water masses in Kongsfjorden, solely based on summer temperature-salinity (TS) characteristics. The established scenario is as follows: In autumn and winter, the fjord water is strongly cooled at the surface through heat loss to the atmosphere, leading to densification of the surface water and convection; producing Local Water (LW). Sea ice will begin to form and brine is released when the surface layer reaches the freezing point. The combination of cooling and ensuing increase

Table 3.5 Definitions of water masses found in Kongsfjorden

Water mass	Abbreviation	T (°C)	S_P (psu)	S_A (g kg^{-1})
Atlantic water	AW	3.0–7.0	34.9–35.2	35.1–35.4
Transformed Atlantic water	TAW	1.0–7.0	34.7–34.9	34.9–35.1
Surface water	SW	1.0–7.0	30.0–34.0	30.1–34.2
Intermediate water	IW	1.0–7.0	34.0–34.7	34.2–34.9
Local water	LW	−0.5 – 1.0		
Winter-cooled water	WCW	−1.9 – −0.5	34.4–35.0	34.6–35.2

Adapted from Svendsen et al. (2002)
S_P is in practical salinity units (psu), S_A is in absolute salinity (g kg^{-1})

in salinity can lead to deep convection, which reaches the bottom in the fjord interior in periods with sufficient freezing; producing Winter Cooled Water (WCW). In spring, when sea ice begins to melt and the surface water is heated by solar radiation, a low-density surface layer forms. This layer ranges from a few cm when melting occurs without wind-driven mixing, to typically 10–20 m after a longer period of melt and with wind-driven down-mixing of the fresh water, or entrainment of saltier LW into the faster moving surface layer. Freshwater from glaciers and rivers will further increase the freshwater content, forming low salinity and warm Surface Water (SW). This low-density SW will increase vertical stability and will tend to flow out of the fjord. In response, and as partial compensation for this outflow, there are seasonally varying influxes of intermediate and deep AW from the WSC and coastal water (normally ArW) of intermediate salinity, typically following the southern shore into the fjord. AW and ArW will mix along their path; forming Transformed Atlantic Water (TAW); the predominant Atlantic water mass found in Kongsfjorden. Below the SW layer, there will be a transition layer called Intermediate Water (IW) that is formed through mixing with whichever water mass resides below SW in the water column (usually TAW or LW/WCW).

This seasonal cycle is typical of Arctic fjords in general (Cottier et al. 2010), where advection of water from the open ocean into the fjord is expected to be important only during summer (their Fig. 3). However, the Kongsfjorden Transect reveals that advection of AW from the WSC can be significant also during winter. Moreover, Svendsen et al. (2002) did not expect to find pure AW inside Kongsfjorden, only TAW. In recent years, such AW from the core of the WSC has indeed been observed inside the fjord during summer. We adapt the water mass classifications from Svendsen et al. (2002), as defined in Table 3.5, with AW having the characteristics of water in the WSC, as defined by Swift (1986) and Hopkins (1991). Note that we are using the old standard Practical Salinity (PSS78) in our water mass classifications, but show in Table 3.5 corresponding water mass limits in the new TEOS-10 standard; Absolute Salinity (Millero et al. 2008), calculated by the Gibbs Seawater (GSW) toolbox (McDougall and Barker 2011). Water mass salinity limits are around 0.16 psu higher in Absolute Salinity than in Practical Salinity. Cottier et al. (2005) applied a slightly different classification of water masses, adapted to conditions north of Svalbard, involving more influence from melting sea ice (Rudels et al.

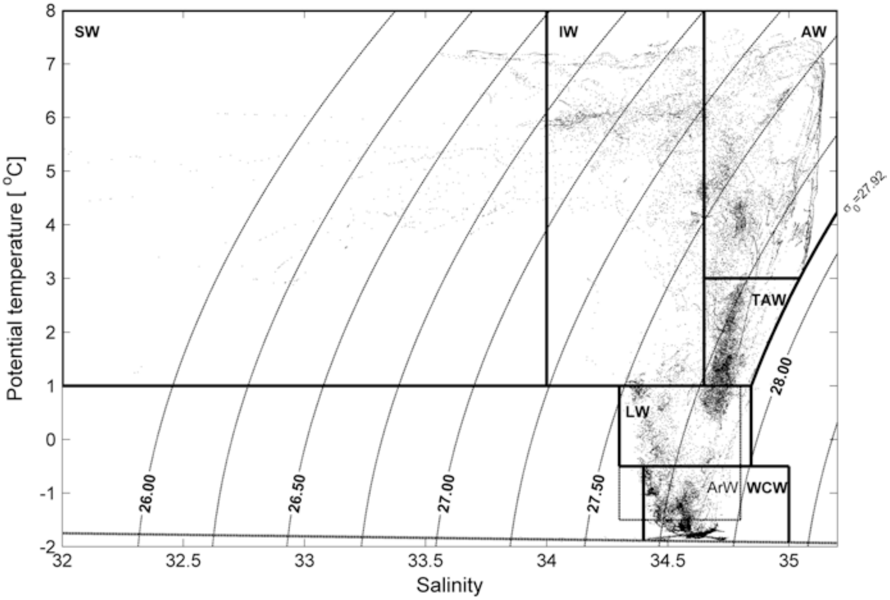

Fig. 3.11 Temperature-salinity observations from Kongsfjorden in April, June, July and September 2002, as well as September 2000, 2001 and August and September 2003. Water mass classifications differ slightly from Table 3.5. Isopycnals are at 0.25 intervals, and the dotted line indicates the freezing point. (Figure adapted from Cottier et al. (2005), their Fig. 2)

2000). Their water masses were the same as in Table 3.5, except for lower salinity limit (34.65) in both AW and TAW, as well as an upper density limit ($\sigma_\theta < 27.92\ \mathrm{kg\ m^{-3}}$) for both these water masses. This limit corresponds to the density at the bottom of the AW layer in the WSC. Their notion was that water masses inside Kongsfjorden would never be denser than this unless significant sea ice formation was involved, producing denser WCW, and this implied that LW would have an upper salinity level. Our data will prove this notion to be wrong, as surface cooling of AW can produce denser winter water than the WCW classification. However, observations from the summers 2000–2003 and April 2002 all fitted well into those classifications, as can be seen in Fig. 3.11, adapted from Fig. 2 in Cottier et al. (2005).

The seasonal cycle in 2002 in the Kongsfjorden water masses, as observed by Cottier et al. (2005), agrees well with the cycle suggested by Svendsen et al. (2002). Based on mooring data, they observe that AW/TAW became present in the fjord from a certain time during summer. With limited data available, they also observed that both the timing and depth of this AW inflow could vary between summers, and proposed that the consequent ‘warm’ and ‘cold’ years are really a result of early or late onset of this AW inflow. The summer 2003 is then a good example of a late onset of AW inflow, as can be seen in Cottier et al. (2005) their Fig. 10. They linked the timing of the inflow to the breakdown of geostrophic control at the fjord entrance, and discussed that it would most likely depend on mechanisms internal to the fjord, like freshwater runoff, surface heating, vertical mixing and wind forcing. We propose that it would also depend on the density of the Kongsfjorden water column at the start of the summer season, i.e. affected by the type of dense winter water production.

In our data, there are 11 years with what we regard as late winter observations (April–May) in the central basin of Kongsfjorden (between stations Kb2 and Kb3; Table 3.1; Fig. 3.1b). TS data from these years reveal large interannual variability in winter production of water masses in Kongsfjorden (Fig. 3.12). A typical winter production with heat loss to the atmosphere and brine release through varying rates of sea ice formation, will form a water column having close to freezing temperature through the entire column, but salinity slightly increasing with depth; a mini version of a cold halocline layer in the Arctic (Rudels et al. 1996). Only in 2002, our observations show a water column structured like this, containing WCW from surface to bottom. In April 2006 a halocline layer filled the fjord, with relatively warm temperatures in the range 0–0.5 °C, and we have suggested that this water mass may have been formed by sea ice melting combined with strong surface heat loss (see Sect. 3.3.2 "Forcing Mechanisms/Spitsbergen Polar Current"). The whole water column fits into the LW definition. The Kongsfjorden water mass in April 2006 was perhaps not formed locally, but advected into the fjord from the shelf by the coastal current. Other than in 2002, only in 2001 we observe WCW in the deepest part of Kongsfjorden, while the rest of the water column was rather warm.

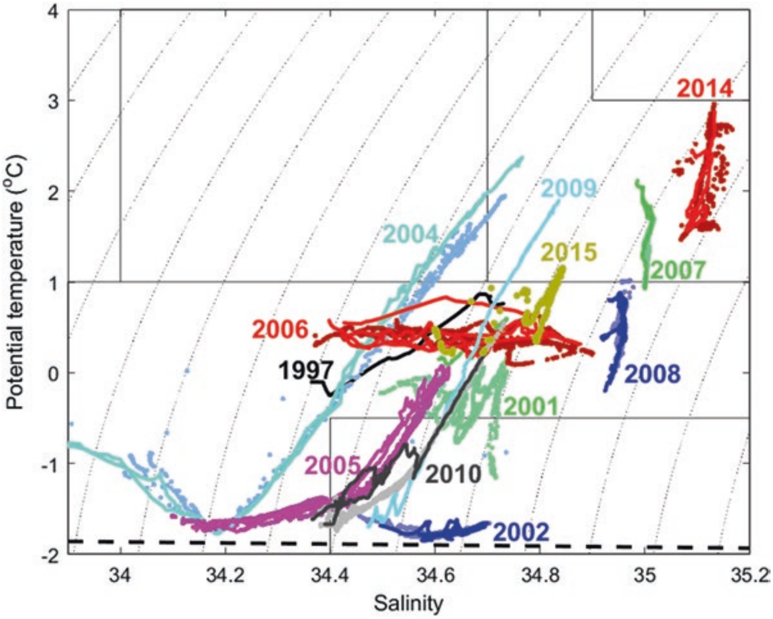

Fig. 3.12 CTD data from April or May from years indicated in plot. Solid lines are from locations in vicinity of Kb1, dots from locations in vicinity of Kb2 and Kb3. Thick dashed black graph is freezing line. Black thin lines indicate water mass classifications from Table 3.5

Section plots shown in Appendix A reveal that the rather warm water in winter 2001 was due to advection of AW across the shelf at an intermediate level.

In April 2001 (and also in April 2002), AW influence is more pronounced in the vicinity of Kb1 (Kongsfjorden entrance) than in the central basin (Kb2–Kb3). The winters 2001 and 2002 may thus be influenced by situations when AW advection is blocked at the fjord entrance due to geostrophic control and recirculates back across the shelf. These winters produce winter water that seem to involve convection to the bottom, and very limited amounts of AW entered the fjord. However, the remaining winter observations give the impression that it is common for advected AW to enter the fjord basin through the fjord entrance. This can be a significant factor that determines the water properties in late winter. The winters 2004 and 2005 were examples of this (Fig. 3.12). Atlantic Water inflow was apparent in the deepest part of the water column, while it seems that a halocline was formed down to some intermediate depth. In contrast, the AW inflows in 2007, 2008 and 2014 were pronounced at surface level. The strength and depth level of the AW advection is indicated in Table 3.6 determined by both CTD data and from mooring data (time series shown in Hegseth et al., Chap. 6).

We select 3 years, 2002, 2004 and 2007, representing the most distinct versions of the three characteristically different winter scenarios we just described. The mean winter hydrography of the Kongsfjorden Transect from each of these 3 years is shown in Fig. 3.13, as well as the summer mean hydrography from the same years. All these three winter transects are noticeably different from the winter mean calculated from the total data set (Fig. 3.2). The winter temperature mean from the total dataset has perhaps the closest resemblance to winter 2002, but is warmer. The winter salinity mean from the total data set, however, has closer resemblance to the winter 2004, but is more saline. A comparison between the single year summer means and the summer mean calculated from the total dataset (Fig. 3.3) shows discrepancies as well.

Summer observations are much more numerous and available from every year in our dataset. We observe advection of AW into the fjord every summer, where AW gradually mixes with the winter-produced water masses present in the fjord. This implies that the AW content gradually increases during the summer, while winter-water content decreases. However, the winter water mixed with AW is still detectable even late in the summer season. Based on all available summer data and comparison with the winter data (Fig. 3.12), we suggest that summer hydrographic profiles in Kongsfjorden form three different characteristic shapes in the TS diagram, depending on which type of winter production has been dominating. In the following, we point to some characteristic differences between three types of seasonal cycles in hydrography of the Kongsfjorden Transect.

Winter Deep winters (resulting in summer profiles shown in TS diagrams in Fig. 3.14) is characterized by winter convection in Kongsfjorden that extends all the way to the bottom, with either no winter AW advection or limited AW advection into the fjord at some intermediate depth. Convection to the bottom as well as AW advection limited to the shelf area, are indicated in the winter 2002 section plots (Fig. 3.13). The winter profiles from 2001, 2002 and 2006 (Fig. 3.12) are examples of

Table 3.6 Number of winter stations in vicinity of Kb1 and between Kb2-Kb3 selected for plotting in Fig. 3.12, together with observation date and likely AW advection type into Kongsfjorden, preceding the observation date, and observed winter AW advection from Kongsfjorden mooring data

Year	Kb1 #	Date	Kb2-Kb3 #	Date	Likely winter AW advection	Mooring observed winter AW advection	Kb2-Kb3 #	Date	Suggested winter convection depth
1994							3	18 Sep	Intermediate
1995							4	18 Aug	Intermediate
1996							2	16 July	Intermediate
1997	1	31 May	–	–	Deep		5	16 Aug	Bottom
1998							1	14 July	Intermediate
1999							2	12 July	Intermediate
2000							8	10–12 Sep	Bottom
2001	1	19 May	4	19 May	Interm.		5	3 Sep	Bottom
2002	8	15 April	9	15 April	Weak interm.		5	27 Sep	Bottom
2003							16	2 Aug	Bottom
2004	2	4 May	3	4 May	Strong deep	Deep	7	22–23 Aug	Intermediate
2005	4	24 April	5	25 April	Deep	Deep	3	13 Sep	Intermediate
2006	4	27 April	5	25, 30 April	Interm. and melting?	Deep – no	6	20 Sep	Bottom
2007	2	29 April	3	29 April	Surface	Surface	5	9–10 Sep	Bottom AW
2008	5	19 April	3	18, 22 April	Surface	Surface	4	12–13 Sep	Bottom AW
2009	1	26 April	–	–	Strong deep	Weak – strong deep	6	12–13 Sep	Bottom
2010	2	27 April	3	28 April	Deep	Strong – weak deep	3	11–12 Sep	Intermediate
2011						Weak – strong deep	4	10 Sep	Bottom
2012						All depth	8	8–9 Sep	Bottom AW
2013						Weak surface	6	29, 31 Aug	Bottom AW
2014	2	9 May	3	10 May	Surface	Weak surface	3	30 Aug	Bottom AW
2015			1	8 May	Interm		3	15 July	Bottom
2016							3	26 July	

Number of selected summer stations in the central basin together with suggested preceding dominant winter vertical convection types; Bottom (Winter Deep, Fig. 3.14) Intermediate (Winter Intermediate, Fig. 3.15) or bottom convection of AW (Winter Open, Fig. 3.16). The selected stations are subsamples from the Kongsfjorden Transect data, with additional data provided by the Norwegian Polar Institute from July 2015 and 2016 this type, indicating that the convection can be a result of either sea ice formation (2002), or heat loss to the atmosphere, possibly combined with some sea ice melting (2006; after the massive AW advection into Kongsfjorden). The deep convection leads to dense bottom water in the fjord, forcing the summer advection of AW to occur at some intermediate depth. The depth level of AW advection, as well as location of old winter water, are indicated in the summer 2002 section plots (Fig. 3.13). Vertical mixing of this AW layer with solar-heated surface water above it leads to formation of relatively warm and saline IW.

Winter Intermediate winters (resulting in summer profiles shown in TS diagrams in Fig. 3.15) are characterized by winter convection that is limited to some intermediate depth, with winter advection of AW into the deepest part of the water column. The location of AW advection and convection for winter 2004 are indicated in the section plots in Fig. 3.13. The winter profiles from 2004, 2005 and 2010 (Fig. 3.12) are typical examples of this type, while 1997 and 2009 might be examples of years when the geostrophic control prevented AW advection in winter to enter the central basin (winter observations made only close to Kb1; see Table 3.6). The advection of AW continued to be located very deep also in summer, resulting in relatively cold water at intermediate level. The cold water was the remnant of winter water, as indicated in the section plots in Fig. 3.13 for summer 2004, together with deep inflow of AW. As can be seen in Fig. 3.15, both IW and SW were generally colder than in the Winter Deep profiles (Fig. 3.14).

Winter Open winters (resulting in summer profiles shown in TS diagrams in Fig. 3.16) are characterized by AW advecting into the fjord over depths that include the surface layer, and winter convection of this AW all the way to the bottom of Kongsfjorden. Location of AW advection, and convection for winter 2007 are indicated in the section plots in Fig. 3.13. This scenario is typical during winters with very little sea ice present in the area, and the winter profiles from 2007, 2008 and 2014 (Fig. 3.12) are examples of this type. The summer situation is then quite similar to that after Winter Deep, except that the advection of AW may be exceptionally shallow due to the very dense winter water that this type of winter production forms. In the section plots from summer 2007 (Fig. 3.13), we have indicated large amounts of old winter water, and shallow inflow of AW.

There are two additional characteristic differences between the hydrographic winter transects in Fig. 3.13, which seem to be associated with the three winter types. During a Winter Deep (2002), the WSC is narrow and confined to the shelf-edge region. Typically, the upper part of the shelf water column is less dense, while the deep part of the shelf water column is denser than the WSC, and we observe little exchange across the front. During a Winter Intermediate winter (2004), the WSC tends to be isolated from the surface, meaning that shelf water spreads westward on top of the WSC. We have indicated this westward spreading of shelf water in Fig. 3.13. The advection of AW from the WSC onto the deep part of the shelf water column is extensive, and the WSC is clearly denser than the shelf water at all depths. During a Winter Open winter (2007), the WSC reaches the surface and is generally less dense than the shelf water in the whole water column, and we observe a pronounced advection of AW in the upper part of the water column. These frontal

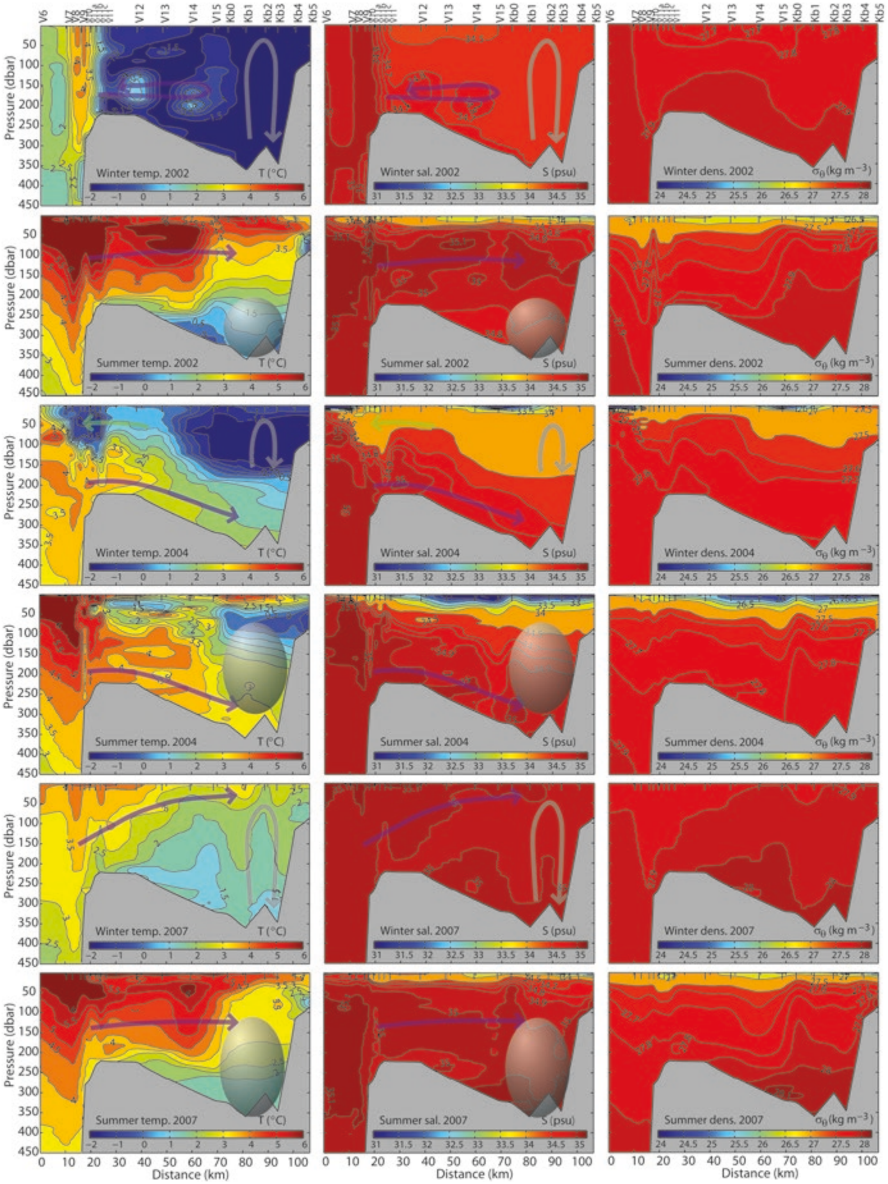

Fig. 3.13 Mean winter and summer temperature, salinity and potential density along the Kongsfjorden transect, based on all available Kongsfjorden Transect data in 2002 (having "Winter Deep" winter), 2004 (having "Winter Intermediate" winter) and 2007 (having "Winter Open" winter). Purple arrows indicate path of main inflow of AW. Green arrow indicate surface off-shelf flow of shelf water. Gray arrows indicate winter convection depth in Kongsfjorden, and spheres indicate location of old winter water

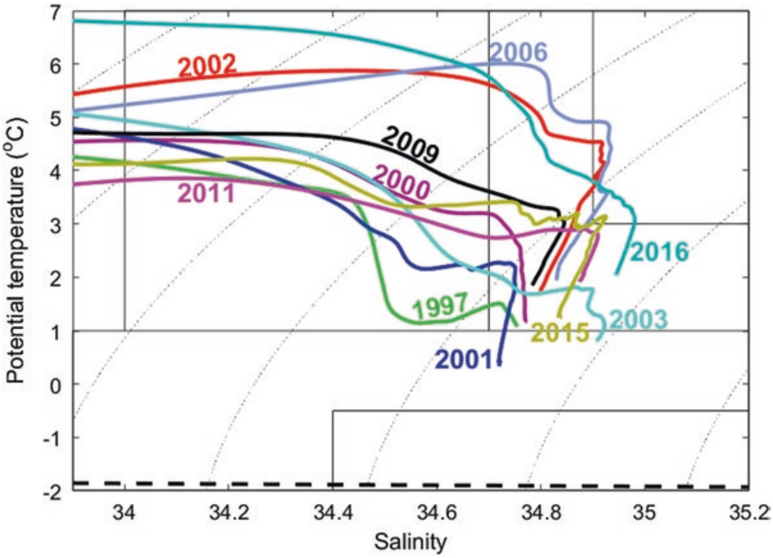

Fig. 3.14 Examples of summer mean temperature-salinity-profiles from Kongsfjorden central basin (between Kb2 and Kb3) after what we suggest is a "Winter Deep" winter with convection all the way to the bottom and no advection of AW into the central basin. Refer to Table 3.6 for dates of and number of observations

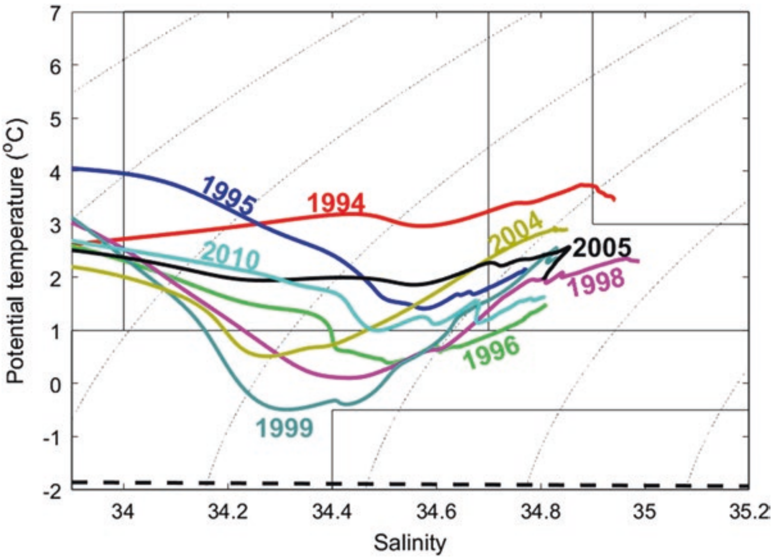

Fig. 3.15 Examples of summer mean temperature-salinity-profiles from Kongsfjorden central basin (between Kb2 and Kb3) after what we suggest is a "Winter Intermediate" winter with convection only to some intermediate depth, and advection of AW into the central basin in the bottom layer. Refer to Table 3.6 for dates of and number of observations

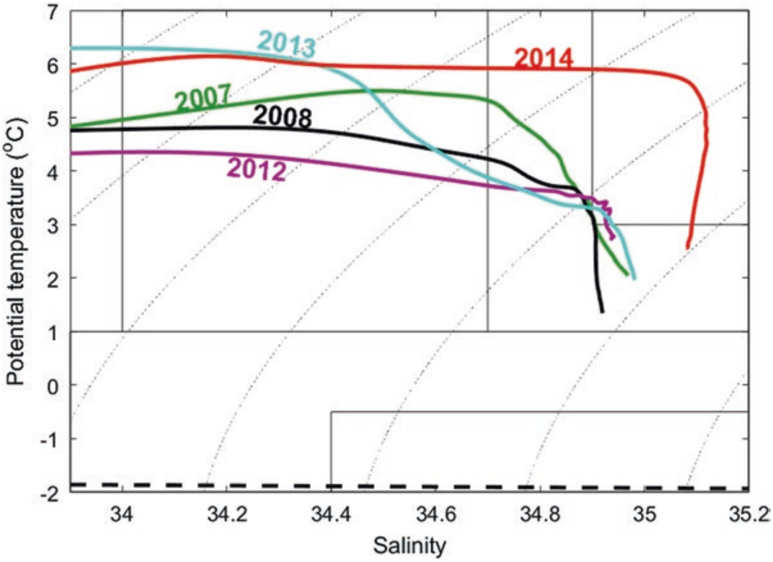

Fig. 3.16 Examples of summer mean temperature-salinity -profiles from Kongsfjorden central basin (between Kb2 and Kb3) after what we suggest is a "Winter Open" winter with advection of Atlantic Water (AW) into the central basin in, or including, the surface layer, and convection all the way to the bottom. Refer to Table 3.6 for dates of and number of observations

exchange behaviors all agree with expected eddy overturning (Tverberg and Nøst 2009). However, topographically-steered geostrophic advection of AW is an additional factor, which may be particularly strong in situations when density differences across the shelf-edge front are weak. The winter 2014 was an example of such a situation, resulting in a winter water column in Kongsfjorden where we observed TS characteristics closest to the AW type (see Fig. 3.12).

The second characteristic difference between the hydrographic winter transects in Fig. 3.13 were associated with our assumption that geostrophic control at the fjord entrance prevents AW from entering the fjord only when the fjord water is denser than the shelf water. The Winter Deep type of winter somewhat confirms this, as it seems to have a less dense water on the shelf just outside the fjord entrance, which might be associated with geostrophic AW advection making a detour at the fjord entrance. Winter Intermediate winters seem to be associated with a water column in Kongsfjorden interior that has lower density than the shelf, and free entrance of AW in the deep part of the water column. Observations from Winter Open winters are few, but density differences across the fjord entrance seem to be weak in those available, apparently leading to strong topographically-steered geostrophic advection of AW into Kongsfjorden. We do not expect that the density differences between the fjord and shelf water columns are stationary throughout each winter, so we may for instance expect that geostrophic control break down during segments of Winter Deep winters.

The standard view of the seasonal cycle of stratification in an Arctic fjord includes the Winter Deep, with sea ice formation as an important process, as illustrated in a review on Arctic fjords by Cottier et al. (2010). In light of the varying mechanisms involved during winter formation of water masses in Kongsfjorden in particular, we include here an updated version of their illustration of the seasonal cycle (Fig. 3.17). We propose that the main impact of the three different winter types on the summer water mass situation is that the core of summer AW advection will occur at varying depth levels. However, every summer we see remnants of winter water in the fjord (old winter water in Fig. 3.17) that is more or less influenced by winter AW advection. The depth level of the summer AW advection will depend largely on the density of this old winter water; the denser it is, the shallower is the summer AW advection. To a large degree, we may expect that Winter Open winters will produce the densest winter water, while Winter Intermediate winters will produce the least dense. However, there are large variations, and the depth level of AW advection at all times in the seasonal cycle will depend on external forcing mechanisms as well; on the shelf, in Kongsfjordrenna and at the shelf-edge front inshore of the WSC, in addition to the geostrophic control that can limit exchange at the fjord entrance. Given the large variations, both seasonally and between years, it is important to study each year separately when trying to interpret which forcing mechanisms have been important for shaping the hydrography of the Kongsfjorden Transect that particular year. We have sufficient data coverage to form 32 annual versions of winter or summer hydrography of the Kongsfjorden

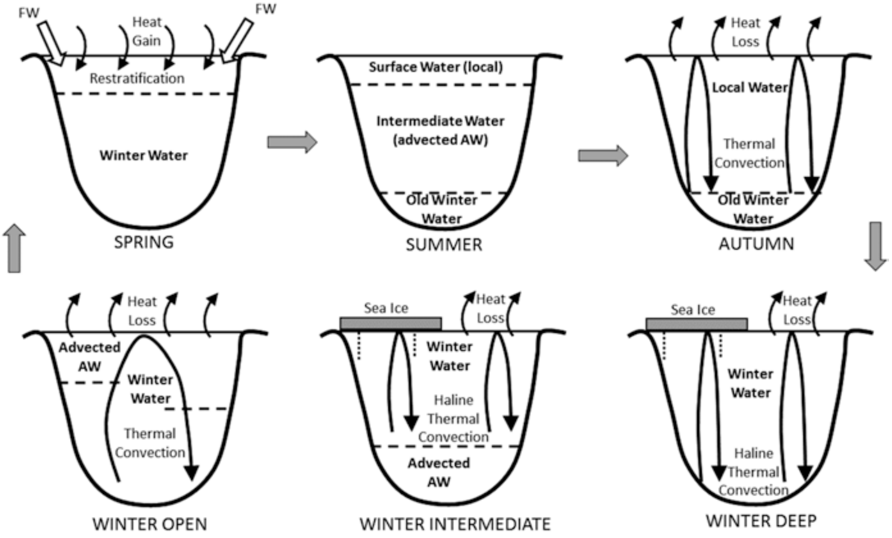

Fig. 3.17 Illustration of the seasonal cycle of stratification in Kongsfjorden, modified from Fig. 3 in Cottier et al. (2010). See text for explanation of types of winters. Sea ice influence can be extracting (during freezing) or adding (during melting) freshwater, in addition to freshening due to the seasonal ice melt in spring

Transect; the 13 winters averaging into Fig. 3.2 and the 19 summers averaging into Fig. 3.3. All are shown in Appendix A, grouped into which types they are most likely associated with.

3.5 Inter-annual Variability of AW in Kongsfjorden

We have shown that both the seasonal and inter-annual variability in the Kongsfjorden water masses can be substantial, and that this is largely due to the varying influence of AW from the WSC. Mooring data uniquely provide a continuous annual measure of water temperatures and we use these to construct an index that quantifies the relative proportion of AW present in the system. The index is based on the temperature from all loggers located in the depth range 70 m to the bottom (to reduce bias by any surface heating). Data are restricted to the 3-month period of August to October, which typically shows the greatest occupation of the fjord by AW. Atlantic Water was identified in the data as having a temperature >3 °C and the index is calculated by multiplying the mean temperature of AW by the % occupation determined from the depth distribution of water >3 °C. The index anomaly (based on the full period of mooring observations) illustrates the variability among years (Fig. 3.18). The AW

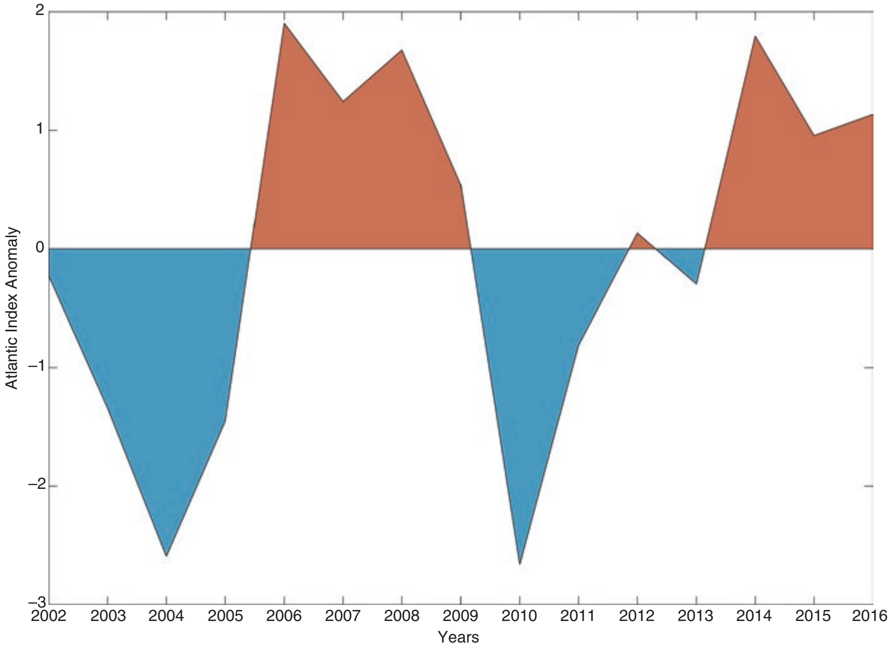

Fig. 3.18 Atlantic Water Index Anomaly for 2003–2012, based on temperature loggers between 70 m and ca 200 m depth on the Kongsfjorden mooring. Each year represents the mean temperature from these loggers during three summer months; July–September

index potentially provides a tool for systematic comparison (e.g. correlations) between oceanographic, meteorological, glacial and biological time series.

Our Kongsfjorden Transect data set provides salinity data in addition to temperature data. Moreover, since AW is normally both the most saline and warmest water mass in the region (disregarding solar heating of surface water), examining inter-annual variations in temperature and salinity may be an alternative way to express the AW influence. Average temperatures and salinities based on this data set are presented in Fig. 3.19, with additional data from July 2015 and July 2016. We present both available winter (January–May) and summer (July–September) averages, and expand the time series backwards to 1980, to better detect trends. The values are based on stations with bottom depth deeper than 100 meters, and the averaging is made as a weighted average, where the value for each depth level is multiplied by

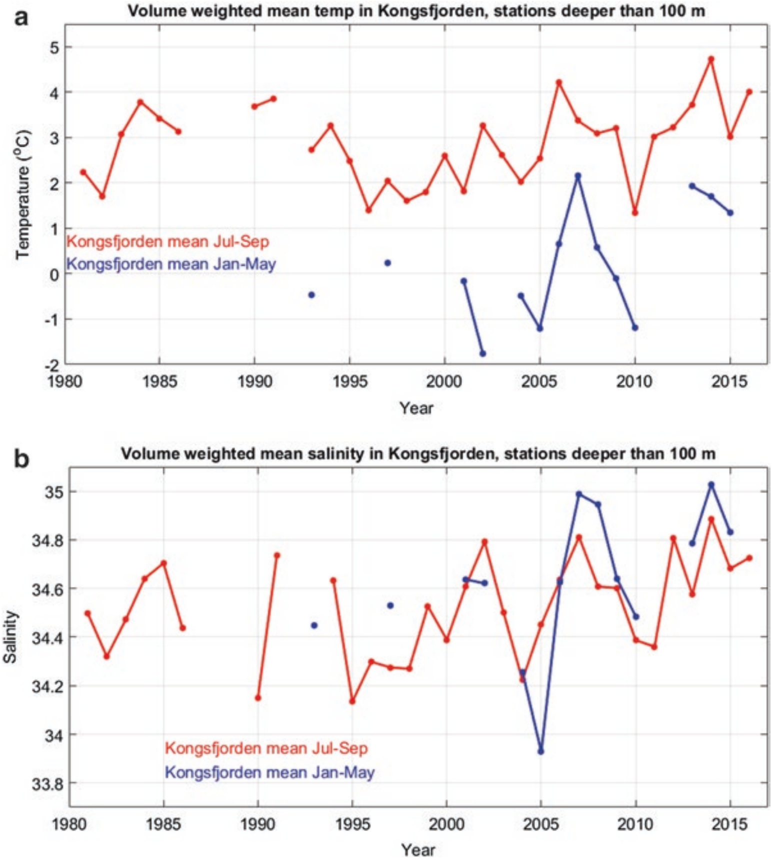

Fig. 3.19 (**a**) Time series of volume-weighted mean temperature (i.e. temperature value for every meter in the water column is weighted with horizontal fjord areal extent at that depth). Only CTD stations sampled in Kongsfjorden with bottom depth >100 m have been included in the averaging. (**b**) Similarly for salinity

the area of Kongsfjorden at that depth level, and the sum of all these is divided by the total volume of the fjord. This method makes the values represent the total heat and salt content in the fjord, and in that sense differ from the simple averaging method for the AW index (Fig. 3.18), as well as in an earlier version of temperature and salinity time series from Kongsfjorden, published in Tverberg et al. (2008).

The Atlantic Index derived from the mooring data (Fig. 3.18) gives a more robust measure of AW content since it is based on data collected continuously throughout the summer, while the CTD temperature means (Fig. 3.19a) would be biased by cold water appearing in the water column, as well as the varying timing of the CTD surveys on which they are based. We deduce from the extended CTD time series (Fig. 3.19) that we cannot extract a definite trend in summer values. Although we can say that 2006–2007 and 2014 had the warmest and most saline summer water masses in the fjord, we note that during the 1980s and around 1990 there were almost equally warm and saline summer water masses in the fjord. The winter values however, appear to be extremely high in 2007 and 2014 (temperature and salinity combined), which coincides with winters with very little drift ice on the West Spitsbergen Shelf. The mean AW core temperature in the WSC outside of Kongsfjorden varies from 3.6 °C to 4.4 °C in summer (Fig. 3.4a) and is always higher than the mean summer temperature in Kongsfjorden (Fig. 3.19a). However, the difference varies from year to year, as we would expect since the amount of AW advecting into the fjord depends on several factors, as we describe under Sect. 3.3 “Forcing Mechanisms”.

Based on the same Kongsfjorden Transect data that we used to calculate the averages in Fig. 3.19, we have constructed the vertical distribution of summer water masses in the total volume of Kongsfjorden, as a time series (water masses as defined in Table 3.5; Fig. 3.20). The interaction between winter and summer that we proposed when we defined the winter types, can be used to explain the inter-annual variations in vertical distribution of water masses. The last half of the 1990s was generally characterized by Winter Intermediate winters (Fig. 3.15) leading to deep summer inflow of AW and cold upper layer, with 1997 as a possible exception. The early part of the 2000 decade was generally associated with Winter Deep (Fig. 3.14) leading to cold deep water and shallower summer AW advection. The typical summer distribution after a Winter Open winter (Fig. 3.16) is also clearly apparent with AW and TAW influence in most of the water column and rather shallow summer AW advection (years 2007–2008 and 2012–2014). We include also the volume fraction of AW+TAW present in the fjord each summer. During the overlapping period, the AW+TAW fraction variation (Fig. 3.20) matches the CTD mean variations (Fig. 3.19). The largest volume fraction among our data occurred in 1991. However, this was purely TAW, and apart from that year, the highest volume fractions were in 2006, 2012 and 2014, and then combined with rather high fraction of AW. We conclude that summer AW presence has been strong in earlier years, however, never as strong as in 2012–2014, which were all classified as Winter Open years.

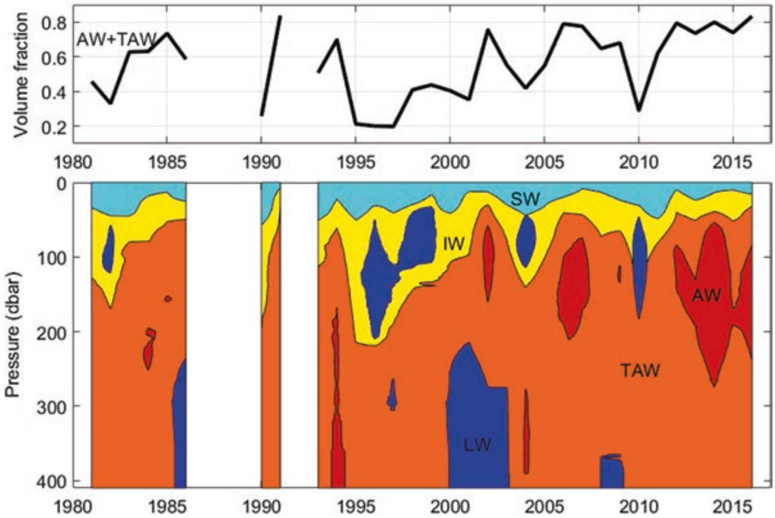

Fig. 3.20 Lower panel: Time series of summer water masses in Kongsfjorden, as defined in Table 3.5, based on the Kongsfjorden transect data. Upper panel: Fraction of total volume of Kongsfjorden that was occupied with Transformed Atlantic Water (TAW) or Atlantic Water (AW). SW Surface Water, IW Intermediate Water, LW Local Water

3.6 Discussion

3.6.1 Seasonal Temperature – Salinity Characteristics

Our main finding from the Kongsfjorden Transect is that inflow of AW during winter is more common than described in the established scenario; that dense water formation inside the fjord prevents AW from entering the fjord basin during the winter season. We have named that established scenario Winter Deep. We call it Winter Intermediate if AW enters the fjord in the deep part of the water column, and Winter Open if the AW inflow includes the surface layer. It appears that the vertical distribution of horizontal density differences across the shelf-edge front determines at which depth the inflowing AW settles on the shelf, and this seems to agree with the behavior of eddy overturning across the front, as argued by Tverberg and Nøst (2009), and illustrated schematically by the sketches of shelf-edge processes (Fig. 3.7). We might see indications that pure topographic steering of AW from the WSC into Kongsfjordrenna, as explained by Nilsen et al. (2016) and illustrated in Fig. 3.7, is most pronounced if density differences across the shelf-edge front are weak. This was the case during winter 2014, leading to the warmest and most saline Kongsfjorden winter water in our database (Fig. 3.12). We also find indications that whether or not the AW in Kongsfjordrenna enters the fjord, depends on density differences between the fjord and shelf, providing a geostrophic control at the fjord entrance that prevents AW from entering the fjord when fjord water is denser than shelf water. The latter can lead to Winter Deep condition in the fjord. The winter transects of this type (Figs. 3.13 and 3.23) may suggest that Winter Deep is associated with limited AW exchange across the shelf-edge front with AW settling at some intermediate depth in Kongsfjordrenna.

According to our simplified classification, winter inflow of AW at intermediate depth level (Winter Deep) is normally associated with vertical convection to the bottom inside Kongsfjorden. Deep winter inflow of AW (Winter Intermediate) should be associated with vertical convection to intermediate depth, while winter inflow of AW over depths that include the surface (Winter Open) is associated with vertical convection to the bottom of this cooled AW. The only years that do not fit our classifications of winter convections types (Table 3.6) are 1997 and 2009, and possibly 2011, all of them suggested by us to be Winter Deep (see Fig. 3.14), while deep AW inflow is observed (associated with Winter Intermediate). None of these years actually has winter CTD observations from within the fjord basin. However, there are mooring observations from 2009 and 2011. A detailed look at those time series (Fig. 6.2 in Hegseth et al., Chap. 6) reveals that the deep AW advection in 2009 was a single event in April, while before that, deep convection producing LW or WCW was dominating. A somewhat similar development happened in spring 2011, with deep inflow of AW evident in both March and April, but strong convection of LW and WCW prior to that. If the production of WCW has been strong enough, a short period with deep AW advection at the end of the winter may not be sufficient to replace all the deep winter water produced by convection.

The three winter scenarios are followed by summers with distinctly different distributions of water masses in the Kongsfjorden water column (Fig. 3.20). During a summer after a Winter Deep winter, one normally finds remnants of the coldest winter water in the deepest part of the water column, and summer inflow of AW at intermediate depth. After Winter Intermediate winters, remnants of the coldest winter water is normally found at some intermediate depth, and summer inflow of AW below that. The summers after Winter Open winters have similar characteristic water column as summers after Winter Deep winters, except that the winter water is rather warm. One implication of these interannual variations is that, constructing a mean picture from the whole Kongsfjorden Transect data set, will not reflect a realistic seasonal cycle. We refer to the Appendix for a comparison between hydrographic transects from individual years and the overall winter and summer means (Figs. 3.2 and 3.3).

3.6.2 Environmental Forcing

Here we seek to link the changes and variability we see in the water masses in Kongsfjorden to associated environmental changes and variability. So far in the discussion we have focused on how strong and at what depth level is the advection of AW into the fjord. This, we have seen, is closely linked to processes leading to overturning across the shelf-edge front. The strength of eddy overturning can depend on how large is the heat loss to the atmosphere (Tverberg et al. 2014) and on wind conditions (Cottier et al. 2007). Wind conditions at the shelf-edge front governs surface Ekman transport and can affect topographic steering of AW into Kongsfjordrenna (Nilsen et al. 2016). However, the Kongsfjorden Transect data set best illustrates how much the shelf-edge processes depend on the density of the shelf water column, and we propose that this is mainly governed by how much fresh water and drift ice the SPC contains. Earlier, we have looked into how much sea ice forms locally, while the presence of drift ice in the SPC is rather associated with melting of sea ice.

First, we investigate heat loss to the atmosphere, through analysis of surface heat fluxes from reanalysis ERA Interim model data from a position located at the shelf edge; the time series shown in Fig. 3.21. The data are low-pass filtered with a long window of 90 days, so they reveal only the overall seasonal cycle and its deviation from the mean seasonal cycle over 35 years (1980–2014). It appears the winters in the 1990s were relatively cold, while the period from spring 2002 to winter 2009 was warm during both winters and summers. Since 2009, some winters have been cold while others have been warm, and summers have been generally cold. The

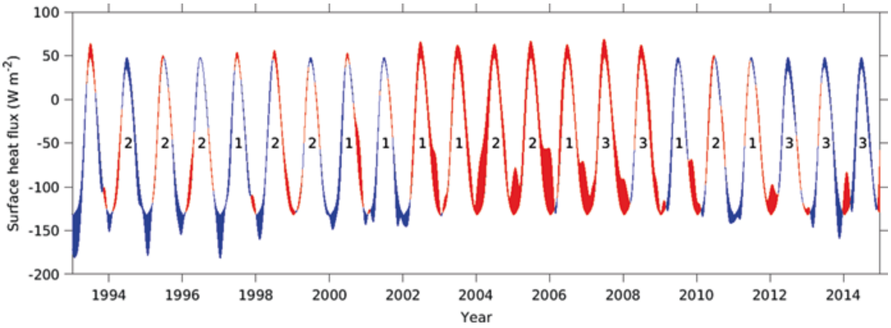

Fig. 3.21 Surface heat flux at position 78°45′N and 009°E, extracted from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA Interim reanalysis database. The time series has been low-pass filtered with a 90 days window and are shown as deviations from a seasonal mean over 35 years, from 1980 to 2014. Blue indicates negative anomalies ('colder') and red positive anomalies ('warmer'). Numbers indicate winter type associated with each year; 1 indicates "Winter Deep" winters, 2 to "Winter Intermediate" winters and 3 to "Winter Open" winters

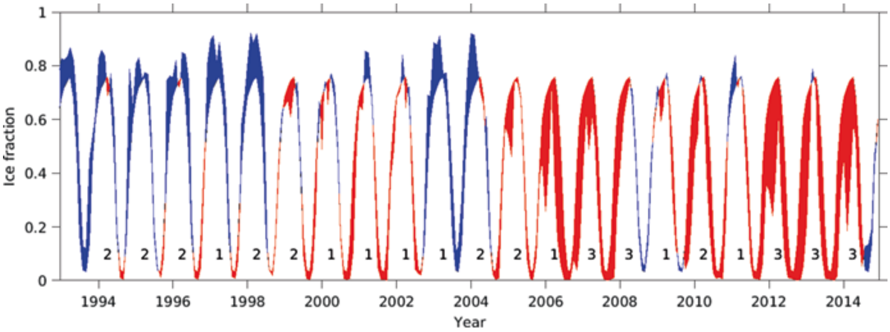

Fig. 3.22 Average sea ice cover fraction in a part of the northern Barents Sea (inside the red rectangle indicated in Fig. 3.1). Data are extracted from monthly means from the National Snow and Ice Data Center (NSIDC) database. The data are shown as deviations from a seasonal mean over 35 years; from 1980 to 2014. Blue indicates positive anomalies (more sea ice) and red negative anomalies (less sea ice). Numbers indicates winter type associated with each year; 1 indicates "Winter Deep" winters, 2 to "Winter Intermediate" winters and 3 to "Winter Open" winters

warm period coincides in time with a period of warm summer AW in the southern part of the WSC (Fig. 3.4). The WSC outside Kongsfjorden is, however, not particularly warm during this period, especially after the Winter Intermediate winters in 2004 and 2005. This can indicate that lateral heat loss (eddies and geostrophic advection) from the WSC is particularly strong during and after Winter Intermediate winters. Other than this, we find no clear effect from varying surface heat flux alone.

We seek information on the potential for drift ice occurring in the SPC on the shelf, by analyzing data on average sea ice cover inside a region of the Barents Sea just east of Svalbard, including Storfjorden (Fig. 3.1). This area is likely to feed drift ice into the coastal current (SPC). We may even suggest that the ice cover there has a direct effect on water mass conditions in the SPC, so a diminishing Arctic ice cap will affect those water mass conditions. The average sea ice cover in this box is shown in Fig. 3.22 as time series of deviations from the mean seasonal cycle, similar to the method applied in Fig. 3.21. Our Kongsfjorden Transect data set indicates that between 1994 and 1999, all winters except for 1997 were Winter Intermediate winters, and they were indeed associated with much sea ice. Even though the Winter Deep winter of 1997 was a winter with much sea ice east of Svalbard, there was an anomalously long period with less sea ice than normal the preceding summer and autumn. After 2000, there have been only two winters with extensive sea ice cover in that region, and one of these winters (2004) was indeed a Winter Intermediate winter. The Winter Open winters are all associated with very low sea ice cover east of Svalbard during the preceding summer and autumn. In such a situation, the SPC will be unusually saline already before the winter, and will easily become denser than the WSC even during relatively warm winters. The Winter Deep winters have mixed ice conditions as well as varying surface heat loss, and some of the Winter

Intermediate winters as well. Summing up our findings, we may suggest that heavy drift ice conditions in the SPC are usually associated with Winter Intermediate winters, while very low sea ice coverage reflects Winter Open winters.

3.6.3 'Cold' and 'Warm' Years

Winter Intermediate winters are usually followed by cold summer water masses in the fjord because of remnants of winter convection to intermediate depth (Fig. 3.17). Winter Deep winters on the other hand, can sometimes be followed by warm summers, because of rather shallow and strong AW inflow. The Winter Open winters have generally warm water masses in the fjord, however, they are not consistently followed by particularly warm summers, because the very dense Winter Open winter water can delay summer inflow of AW. The three winter types we have defined are thus not directly linked to 'warm' or 'cold' years. Hegseth et al. (Chap. 6) refer to the periods 2003–2005 and 2009–2011 as 'cold' and the periods 2006–2008 and 2012–2014 as 'warm'. All these 'warm' years we associate with strong AW advection, and all, except 2006, had Winter Open winters. Three of the 'cold' years, we have associated with Winter Intermediate winters (2004, 2005, 2010) and two with Winter Deep winters (2003, 2011). These particular Winter Deep winters produced unusually dense winter water (see Fig. 3.14), which may have suppressed AW inflow during the following summer. Year 2009 (Winter Deep) has also been classified as a 'cold' year, but only the winter/spring period. Extensive sea ice cover inside Kongsfjorden can be indications of a 'cold' year and provide a cold source for the summer water column (due to melting). In fact, the 5 years with most extensive sea ice cover in Kongsfjorden (Fig. 3.10), are all suggested to be 'cold' years. The most extensive sea ice cover was observed in March 2004, which, however, had melted by April (Hegseth et al., Chap. 6). Isfjorden had a large fast ice cover in 2004 as well, while there was substantial sea ice production in 2002, 2003 and 2005 (Nilsen et al. 2008). We may assume that somewhat similar conditions apply to Kongsfjorden, although conditions in Isfjorden do not automatically apply to Kongsfjorden. For instance, a study comparing Isfjorden and Kongsfjorden during 2007 (Ledang 2009) showed that Isfjorden was much less influenced by AW advection than Kongsfjorden that year, with Isfjorden containing distinctly fresher water masses. This may be an influence from drift ice in the coastal current, because solely considering the effect of AW advection one would expect the contrary, since Isfjordrenna (Fig. 3.1a) is more easily connected to WSC than any of the other troughs along the West Spitsbergen Shelf (Nilsen et al. 2016). All the 'warm' years are associated with least extensive ice cover inside Kongsfjorden (Fig. 3.10). As mentioned before, the warm years are also associated with extremely little sea ice east of Svalbard (except the rather special year 2006), and consequently very little or no drift ice in the coastal current (SPC).

3.6.4 Tipping Point

The 2 °C increase in annual mean temperature in Kongsfjorden that suddenly occurred after the massive AW inflow event in February 2006, ‘recovered’ after a few years, followed by three relatively cold years in 2009–2011. However, the period 2012–2016 reveals prevailing large volumes of Atlantic water masses in the fjord during summer, although TS profiles suggest they have followed Winter Deep winters as well as Winter Open winters (Figs. 3.14 and 3.16). Similar inter-annual variations are seen in the Arctic ice cover, explained by climatic feedback mechanisms (Stroeve et al. 2012). Glacier run off during winter appears to mainly affect the inner part of Kongsfjorden; inside the Lovénøyane. The Kongsfjorden Transect data set has indicated to us that the behavior of the AW inflow to Kongsfjorden is very much depending on the density of the shelf water column, thus indirectly being affected by a diminishing Arctic ice cap. Our data suggest that heavy drift ice in the SPC is usually associated with Winter Intermediate winters (Fig. 3.22). We might suggest that the impact of reduced drift ice in the SPC can be, down to a certain threshold, a colder shelf water, either due to increased heat loss to the atmosphere, or somewhat contradictory, more melting by AW from the WSC (in combination leading to Winter Deep winters). In this situation, all the factors we have mentioned in this paper, act together in a delicate balance, making it very hard to relate the strength of one single factor to the density of the shelf water. Only when drift ice extent is below some undetermined threshold, will the temperature and salinity of the shelf water increase due to exchange with AW in the WSC (in combination with heat loss to the atmosphere, leading to very dense shelf water and Winter Open winters). If the Arctic ice cap continues the diminishing trend it has had since 1980 (Xia et al. 2014), the Winter Open winters are likely to become the normal situation in Kongsfjorden, resulting in AW filling the fjord both in winter and summer. In that case, the February 2006 event was a tipping point for the Kongsfjorden environment. A better understanding of the coastal current (SPC) is needed to improve our knowledge of what determines the density of the shelf water column, and should be the focus for future studies. We have not investigated wind effects on shelf-edge processes in this paper, and we feel that the geostrophic control at the fjord entrance is not explained properly as well. Thus, we leave these topics for future studies.

Acknowledgements Ragnheid Skogseth (RS) prepared and shared CTD data from the UNIS Hydrographic database (UNIS HD) with data collected by NPI, UNIS, IOPAN and SAMS or extracted from public databases like The Norwegian Marine Data Centre (NMDC at the imr.no), the PANGAEA database (AWI) and ICES. Funding for RS and the construction of the UNIS HD merits REOCIRC (Remote Sensing of Ocean Circulation and Environmental Mass Changes, a Research Council of Norway project no. 222696/F50). The Norwegian Polar Institute provided CTD data from July 2015 and July 2016 through the MOSJ program. The work contributes as well to the project FjoCon 225218/E40, financed by the Norwegian Research Council. We thank Colin Griffiths for overseeing the SAMS mooring programme supported by the UK Natural Environment Research Council (Oceans 2025 and Northern Sea Program) and the Research Council of Norway (projects Cleopatra: 178766, Cleopatra II: 216537, and Circa: 214271/F20). Contribution by FC and MEI was undertaken through the Scottish Alliance for Geoscience Environment and Society (SAGES).

Appendix A: The Kongsfjorden Transect Hydrography from Individual Years

Here we show temperature, salinity and density distribution for each year with enough available data to construct the Kongsfjorden Transect, separated in Winter Deep, Winter Intermediate and Winter Open winter data (January–May) and their respective following summers (July–September).

The five Winter Deep winters with sufficient CTD data available to grid the transects are shown in Fig. 3.23, although in two of them, 1997 and 2009, the data coverage is poor in the central basin of Kongsfjorden. In 1997, the data coverage is also poor across the shelf-edge front. Focusing on those transects with good data coverage, all these years the WSC had a narrow warm core confined to the shelf-edge region, and reaching the surface. The surface shelf water had similar or lower density than the surface-layer part of the WSC core. The deepest part of the shelf water column was, however, generally denser than the water at the same depth in the WSC core, and the density differences across the front were weak at intermediate depth level.

Such a density distribution favors eddy overturning with AW exchange across the front dominating at the depth level where the density differences vanish, that is intermediate depth (Tverberg and Nøst 2009). This is indeed what can be observed over the shelf. The overturning cell indicated in the principle sketch (Fig. 3.17) of shelf-edge processes, would in such cases apply to the upper part of the water column only. In 2009, AW was found both at intermediate and deep water level, and cross-frontal density differences were weak at both levels. In the transects from the 3 years with good data coverage, it can be seen that Kongsfjorden interior was less influenced by AW than the shelf. We also note that in the mouth region of Kongsfjorden, a depression of the deepest isopycnals is visible each of these years. It may be possible that these depressions are associated with the coastal current at the mouth region of Kongsfjorden forcing the path of AW advection to be modified there (geostrophic control). The exact location of the depressions varies among the years, which may confirm that the location of the geostrophic control is located at the common mouth of Kongsfjorden-Krossfjorden (Kb0) in some years and at the mouth of the Kongsfjorden central basin (Kb1) in others. This is in line with the typical situation during a Winter Deep winter; denser water in the fjord in the deepest part of the water column enhances the bottom speed of the coastal current on the shelf, past the fjord.

Mooring data add valuable information from two of these years; 2006 and 2009. Most of the winter in 2006 was actually a Winter Intermediate winter with exceptionally strong deep AW advection, culminating in a rather short period with strong convection and mixing (see Fig. 3.5), and it must have been during this final part of the winter that the largest volumes of winter water were produced. The winter 2009 was opposite; during most of the winter the mooring data reveal deep convection and only weak indications of AW advection, except from a short period in late April with deep AW inflow (see Fig. 6.2 in Hegseth et al. this volume). That inflow was evidently not strong enough to replace all the winter water produced earlier that winter.

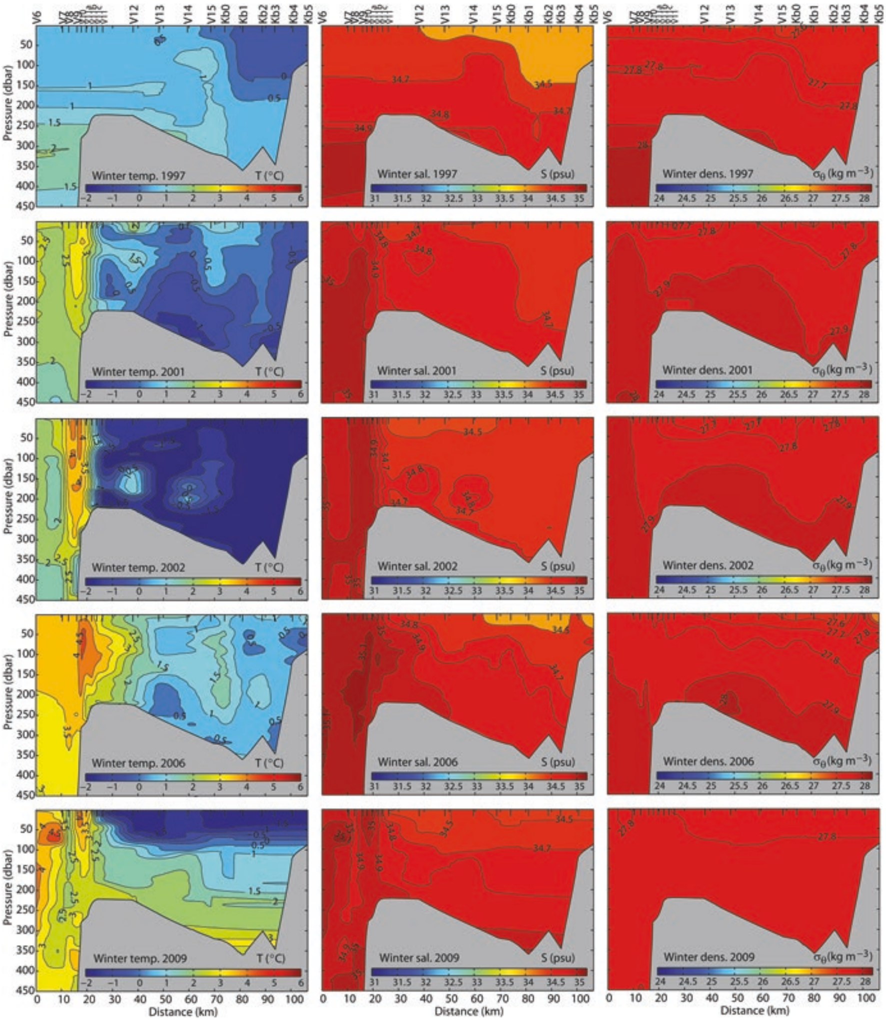

Fig. 3.23 Mean winter temperature, salinity and potential density along the Kongsfjorden transect, based on all available Kongsfjorden Transect data from winters 1997, 2001, 2002, 2006 and 2009, defined as "Winter Deep"

The five Winter Intermediate winters with sufficient CTD data available to grid the transects are shown in Fig. 3.24, although two of them have limited data coverage (1998 and 1999). The data coverage in the WSC, however, is good for all 5 years, revealing a WSC that tends to be isolated from the surface. Shelf water spreads westwards on top of the WSC, and AW from the WSC tends to enter the shelf in the deep water and more pronounced than during the Winter Deep winters. The WSC was clearly denser than shelf water at all depths. This leads to a weakening of the WSC with depth (thermal wind effect), perhaps contributing to enhanced

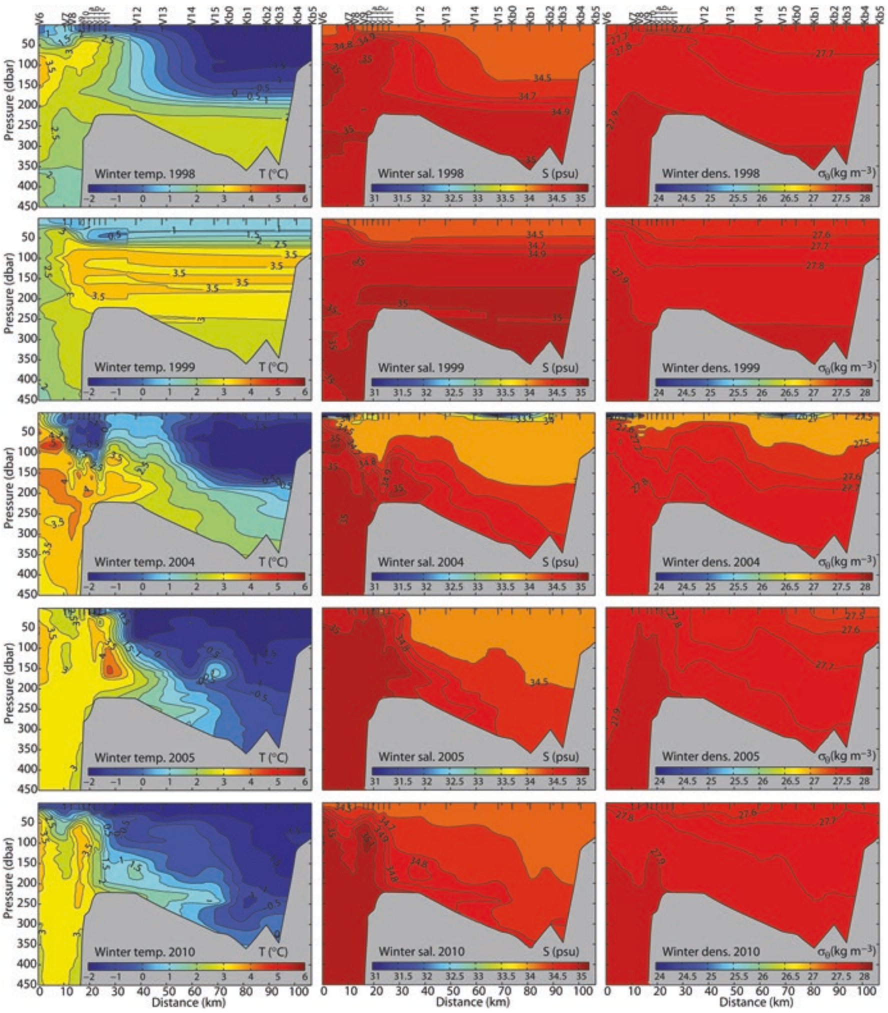

Fig. 3.24 Mean winter temperature, salinity and potential density along the Kongsfjorden transect, based on all available Kongsfjorden Transect data from winters 1998, 1999, 2004, 2005, and 2010, defined as "Winter Intermediate"

baroclinic instabilities at the shelf-edge front. The resulting eddy overturning will bring AW onto the shelf in the deep and shelf water off-shelf in the surface. The water column in Kongsfjorden interior had lower density than the shelf, meaning no geostrophic control at the entrance. Mooring data confirm deep AW advection inside Kongsfjorden during three of these winters (2004, 2005 and 2010), combined with homogeneously cold water above the AW inflow. In 2010, the AW advection reached rather shallow depths in January–March, while it almost disappeared in April–May and was replaced by a thick layer of homogeneously cold water, reaching almost 200 m depth (see Fig. 6.2 in Hegseth et al., Chap. 6).

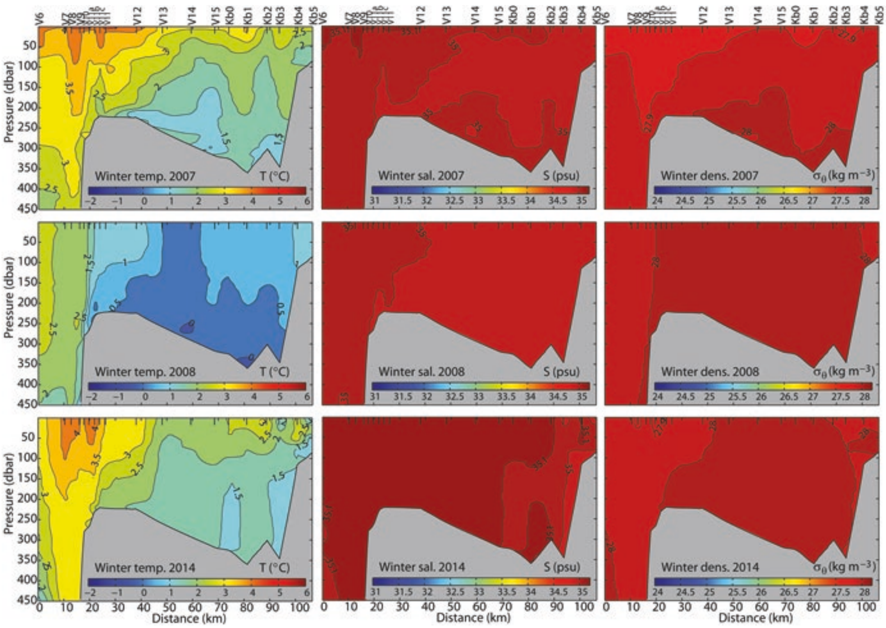

Fig. 3.25 Mean winter temperature, salinity and potential density along the Kongsfjorden transect, based on all available Kongsfjorden Transect data from winters 2007, 2008 and 2014, defined as "Winter Open"

The three Winter Open winters with sufficient CTD data available to make transects (2007, 2008 and 2014) are shown in Fig. 3.25. The WSC reaches the surface, is less dense than shelf water in the whole water column, and tends to spread onto the shelf, being most pronounced in the surface. The thermal wind effect on the WSC in such a situation will enhance the current speed with increasing depth. This might guide the WSC northwards past Kongsfjordrenna at depth, while the eddy overturning will spread AW onto the shelf in the surface layer. However, except for 2007, the density differences were weak, so topographic steering of geostrophic AW advection in Kongsfjordrenna can be significant, with AW advection in the whole water column. In 2007 it looks like the AW might not be passing Kb1 in the deep part of the water column (due to geostrophic control?). In the surface, however, AW entered the fjord freely. The mooring data inside Kongsfjorden indicated a rather homogeneously warm water column, but with a tendency of warmest temperatures in the surface (see Fig. 6.2 in Hegseth et al., Chap. 6). The homogeneously warm water column is particularly evident in the 2012 and 2014 time series, which may indicate no horizontal density differences across the shelf-edge front that year, meaning weak eddy overturning, but substantial geostrophic AW advection, with horizontal eddy diffusion spreading water masses laterally.

The eight summer transects after Winter Deep winters are shown in Fig. 3.26. Inside Kongsfjorden, they are characterized by remnants of cold winter water in the

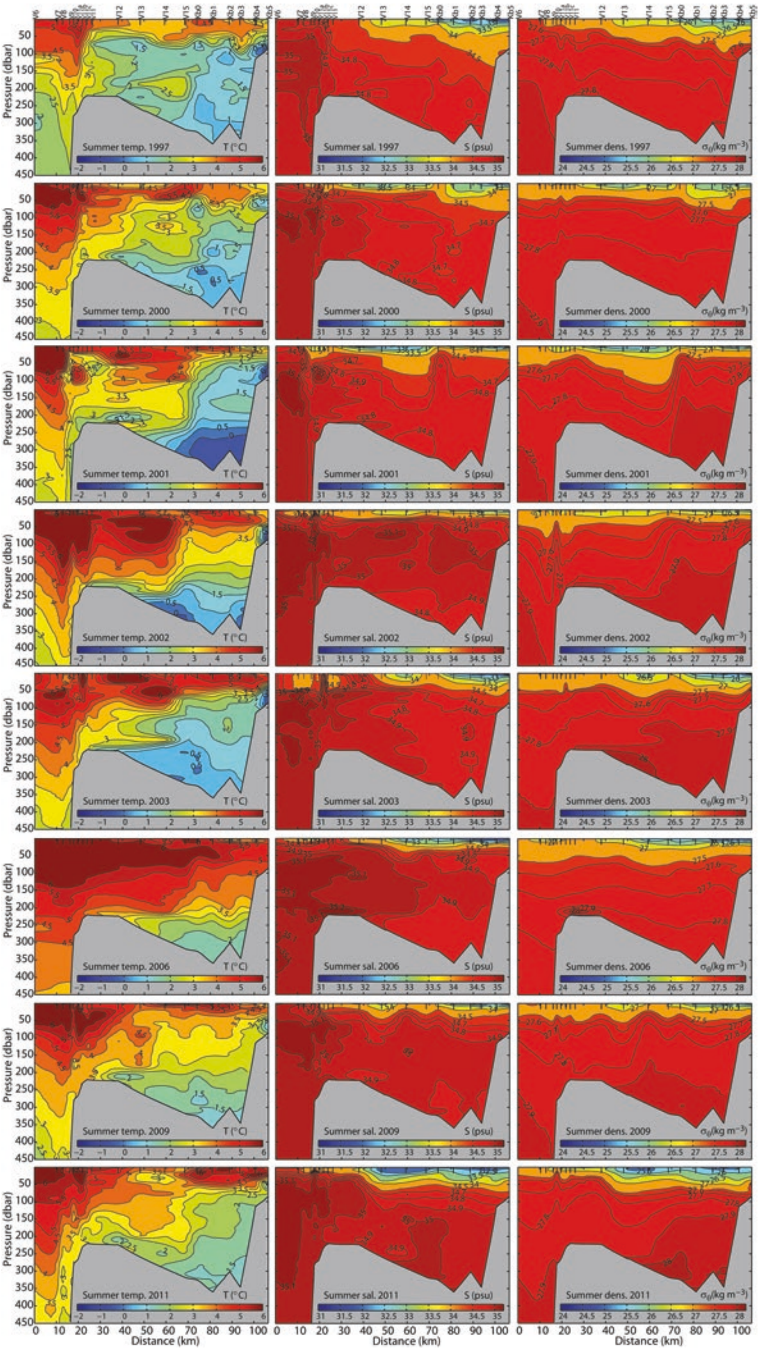

Fig. 3.26 Mean summer temperature, salinity and potential density along the Kongsfjorden transect, based on all available Kongsfjorden Transect data from summers 1997, 2000, 2001, 2002, 2003, 2006, 2009 and 2011, after "Winter Deep" winters

deep, and a core of warm and saline AW or TAW at some intermediate depth. The shelf has in principle the same distribution, however with more pronounced presence of AW or TAW. Some years (e.g., 2001), the deep fjord water was clearly denser than the deep water in Kongsfjordrenna, which indicates that the geostrophic control in the fjord entrance can be in effect throughout long parts of the summer. The AW exchange was extensive across the shelf-edge front, with no pronounced density front. The mooring data confirm rather cold water in the deep in summer 2003 and 2011, while in 2006 and 2009 the cold water resided below the mooring depth (see Fig. 6.2 in Hegseth et al., Chap. 6).

The six summer transects after Winter Intermediate winters are shown in Fig. 3.27 (in 1995 and 1996, the data coverage was too poor to form transects). They are characterized by remnants of cold winter water at intermediate depth level, while AW or TAW were found in the deep. The deep water can comprise remnants of deep AW inflow during the winter, or summer advection of AW. We would expect the summer transects in 2004 and 2010 to be examples of the first situation, because deep fjord water is denser than shelf water, possibly implying geostrophic control at work in the mouth. Mooring data, however, indicate that there was a distinct increase in AW in 2010, similar to 2005 (see Fig. 6.2 in Hegseth et al., Chap. 6), indicating summer advection of AW. Some years the AW exchange across the shelf-edge front appeared to be restricted (e.g. 1998), but in other years it was pronounced (e.g. 2004, 2005, 2010). The shelf-edge front is not a pronounced density front; rather the isopycnals tend to often be terrain following, which can be a long-term effect of eddy exchange across the shelf-edge front (Adcock and Marshall 2000).

The five summer transects after Winter Open winters are shown in Fig. 3.28. They show that large volumes of old winter water were present in the fjord and on the shelf during these summers (winter water from Winter Open winters is relatively warm). The density at intermediate and deep depth levels were generally higher than in the WSC, with two summers (2007 and 2013) being more pronounced in the fjord than on the shelf. Temperature and salinity were generally higher on the shelf than in the fjord. Mooring data confirm a rather warm water column during these summers and only in 2014 there was a pronounced increase in AW content throughout the summer (see Fig. 6.2 in Hegseth et al., Chap. 6). This indicates that there may be rather little water renewal in the fjord during a summer after a Winter Open winter. Our explanation is stronger geostrophic control at the mouth due to the high-density water inside the fjord.

The overall winter mean transects of temperature and salinity (Fig. 3.2) seem dominated by the Winter Deep type of winter, with a water mass close to LW definitions filling most of the shelf and fjord. However, they are strongly influenced by Winter Intermediate and Winter Open winters as well; the shelf-edge front has an overturning leading AW onto the shelf in the deep and shelf water over the WSC (Winter Intermediate), rather high bottom salinity on the shelf and in the fjord (Winter Intermediate), and TAW-type water mass close to Kb3 (Winter Open). Kb3 is the only CTD station in the transect that is placed within the path of the topographic steering of the geostrophic AW advection in the fjord. The influence from the Winter Open (AW) winters will thus likely be strongest there. The overall sum-

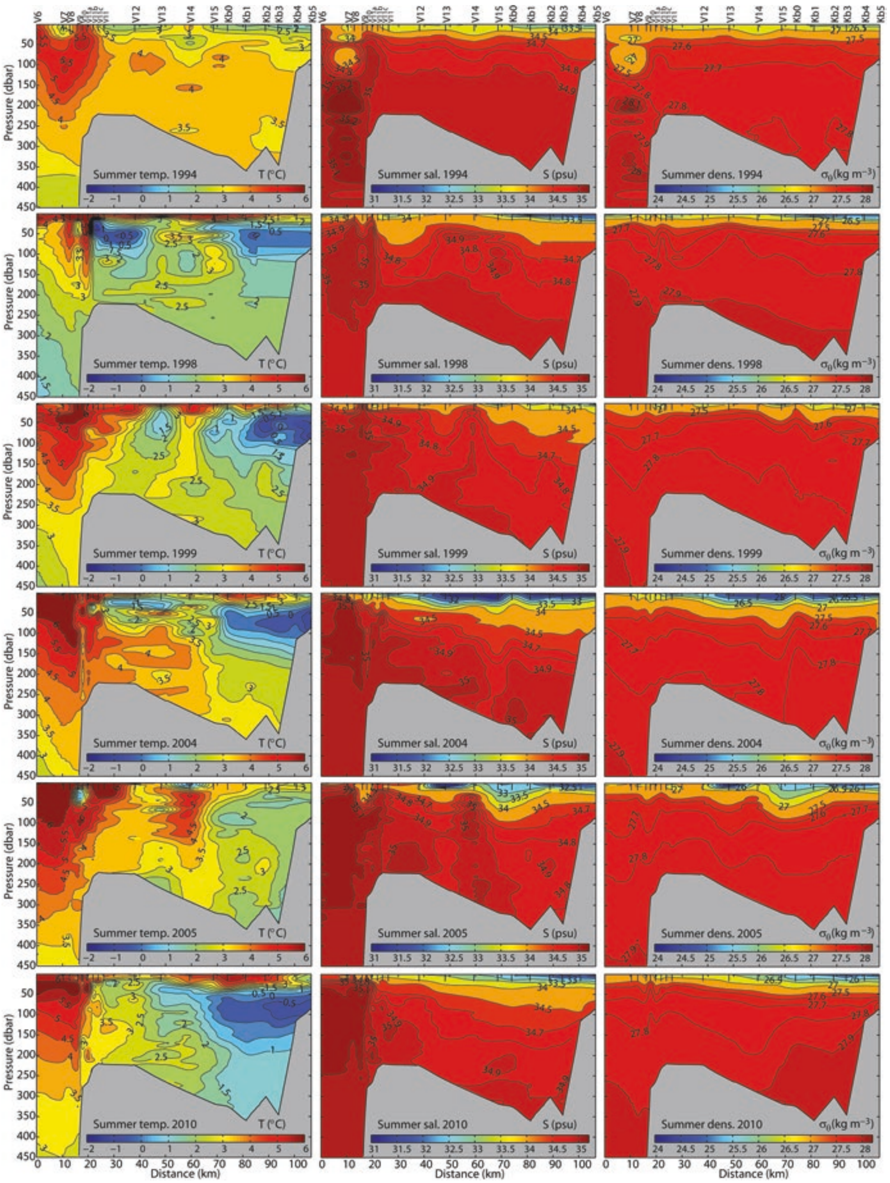

Fig. 3.27 Mean summer temperature, salinity and potential density along the Kongsfjorden transect, based on all available Kongsfjorden Transect data from summers 1994, 1998, 1999, 2004, 2005 and 2010, after "Winter Intermediate" winters

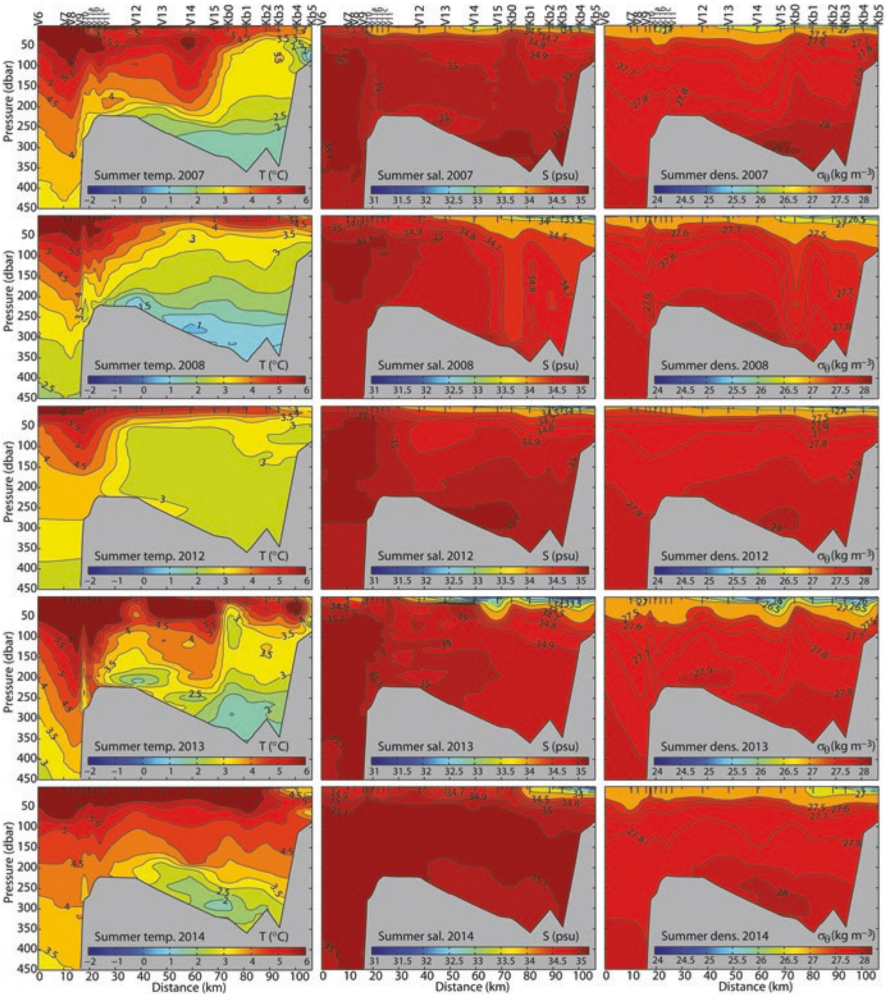

Fig. 3.28 Mean summer temperature, salinity and potential density along the Kongsfjorden transect, based on all available Kongsfjorden Transect data from summers 2007, 2008, 2012, 2013 and 2014, after "Winter Open" winters

mer mean transects of temperature and salinity (Fig. 3.3), display a clear discrepancy between the shelf and fjord regions, which in reality is only seen after some Winter Open winters (Fig. 3.28). The water mass distribution inside the fjord seems like a mixture of summers after a Winter Deep and a Winter Open winter. TAW fills most of the water column below thin layers of SW and IW, and LW is only found at the head of the fjord, reflecting the glacier influence in the basin inside the Lovénøyane (see Table 3.5 for water mass definitions). A summer after a Winter Deep winter would have had LW in the deepest part of the water column, while a summer after a Winter Open winter would have pure AW instead of TAW filling part of the water column. Comparing these mean summer sections with the time series of water mass distribution in Kongsfjorden (Fig. 3.20), we see that such a distribution has been the most common after 2006, more specifically the two periods 2006–2008 and 2012–2014.

- Data Availability: doi:10.21334/npolar.2019.074a215c.

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Chapter 4
Changes in Sea-Ice Extent and Thickness in Kongsfjorden, Svalbard (2003–2016)

Olga Pavlova, Sebastian Gerland, and Haakon Hop

Abstract Seasonal sea ice is an important feature in Svalbard fjords for both the physical environment and the ecosystem. Systematic sea-ice monitoring in Kongsfjorden, Svalbard, as a part of a long-term project conducted by the Norwegian Polar Institute (NPI), was started in 2003. The inner part of Kongsfjorden is usually covered by seasonal fast ice initially forming between December and March and persisting until April–June. Before 2006, the sea ice typically extended into the central part of the fjord, but during the last decade the sea-ice extent has often been reduced to the northern part of the inner bay. Two exceptions were 2009 and 2011, when the ice extent was similar to earlier years. The minimum record for spring ice extent within the observed period was in 2012, when sea ice was only present in the northern part of the inner bay. Maximum seasonal thickness of fast ice was around 0.6 m or more prior to 2006, declining to about 0.2 m in recent years. The snow thickness on fjord fast ice declined from around 0.2 m in spring prior to 2006 to <0.05 m in recent years, which reflected the shorter duration of ice cover. Advection of Atlantic water into Kongsfjorden, particularly during the winters of 2006–2007, contributed to reduced fast-ice formation. This, in combination with relatively mild winters, can be seen as main factors for changing fast-ice conditions in Kongsfjorden during the last 10 years. Sea-ice extent and seasonal duration have important implications for the marine ecosystem in Kongsfjorden with regard to pelagic and benthic production as well as selected species of seabirds and marine mammals.

Keywords Kongsfjorden · Svalbard · Sea ice · Time series · Ecosystem effects · Climate change

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_4

4.1 Introduction and Motivation

Sea-ice conditions around Svalbard, in particular sea-ice extent, ice-edge configuration and ice concentration, are controlled or influenced by the regional conditions, such as the geographical setting of Svalbard, the sea-floor topography and the patterns and properties of the regional ocean currents (Walczowski et al. 2012, 2017). Svalbard is situated adjacent to both Arctic and Atlantic water masses, and the sea ice is influenced by warm, saline water on its way from the Atlantic to the Arctic Ocean along the western coast of Svalbard (West Spitsbergen Current, a branch of the North Atlantic Current), and cold, less saline water from the Arctic to the Atlantic along the eastern coast of Svalbard (Svendsen et al. 2002). The latter current continues around the cape Sørkapp and prevails as a coastal current on the shelf along West Spitsbergen. Thus, Atlantic water mixes with Arctic water on the shelf and is advected into the open fjords as Transformed Atlantic Water (Cottier et al. 2005, 2010; Hop et al. 2006; Nilsen et al. 2016). The archipelago, located at the relatively high latitude of 77–80°N, features an Arctic climate. However, these two currents have strong control on the local climate and the winter sea-ice distribution. In particular, the West Spitsbergen Current creates a warmer climate on the west coast of Spitsbergen than in other regions at similar latitudes (i.e., Canadian and Russian Arctic) (Orvik and Niiler 2002; Loeng and Drinkwater 2007; Nilsen et al. 2008; Skagseth et al. 2008, 2011; Cottier et al. 2010; Smedsrud et al. 2011, 2013).

The West Spitsbergen Current reaches the western coast and northern shelf of Spitsbergen, keeping water open and navigable most of the year along the southern part of the west coast. The sea ice around Svalbard is commonly composed of first-year ice and various young ice classes. Multiyear sea ice can appear, transported from the Arctic Basin, especially north and east of Svalbard (e.g., Kwok et al. 2005; Kwok 2009; Onarheim et al. 2014). Fast ice in fjords of western Spitsbergen (e.g. Kongsfjorden and van Mijenfjorden) grows less thick than ice in fjords that are less or not at all influenced by Atlantic water (e.g. Rijpfjorden and Storfjorden), see e.g. Gerland et al. (2008, their Fig. 4.3). Maximum fast-ice thicknesses observed in five Svalbard fjords during winter 2006/07 showed variable thickness from 20 cm in Grønfjorden (part of the Isfjorden system, near Barentsburg) to 66 cm in van Mijenfjorden. The two fjords further east, Storfjorden (Inglefieldbukta, 90 cm) and Rijpfjorden in the northeast (114 cm) had much thicker ice.

Surface snow (snow on ice) and ice growth/melt are important elements of evolution of the ice cover, and weather conditions (air temperature, precipitation and wind) play a main role in this process. Additionally, the ice surface topography is also important for ice and snow growth (see e.g. Nicolaus et al. 2003; Cheng et al. 2008, 2014; Wang et al. 2015).

Formation and evolution of sea ice in Kongsfjorden integrate many atmospheric, oceanic and terrestrial factors, such as air and water temperature, advection of the warm Atlantic water, reorganisation of atmospheric pressure fields and water circulation, winter convection, precipitation (amount, timing) and snow cover, and freshwater runoff from glaciers and rivers (Gerland et al. 1999; Cottier et al. 2005, 2007, 2010; Gerland and Renner 2007).

About 80% of the drainage area in Kongsfjorden is glacier-covered (J. Kohler, Norwegian Polar Institute, unpubl. data). Kongsfjorden is strongly influenced by the tidewater glaciers Kronebreen and Kongsvegen at the head of Kongsfjorden, and Conwaybreen and Blomstrandbreen on its northeastern and northern coasts (Lefauconnier et al. 1994; Trusel et al. 2010; Köhler et al. 2012; Nuth et al. 2012, 2013; Luckman et al. 2015; Schellenberger et al. 2015). During summer (with peak run-off in late July and August), they contribute sediments and freshwater in liquid form and calving of icebergs (Svendsen et al. 2002; Sundfjord et al. 2017; Tverberg et al., Chap. 3). Grounded and drifting icebergs and smaller pieces of ice influence the formation of fast ice by forming fixed points that keep the fast ice in place leading to locally increased or reduced accumulation of snow (Lydersen et al. 2014).

Monitoring of the sea-ice conditions in Kongsfjorden can be used to demonstrate and investigate phenomena related to climate change in the Arctic. Consistent studies of the sea-ice conditions in Kongsfjorden, including monitoring of fast-ice evolution and sea-ice thickness started in the late 1990s. Some sporadic information on fast-ice extent before the mid-1990s exists from biological studies (Lydersen and Gjertz 1986; Mehlum 1991; Parker and Mehlum 1991; Smith and Lydersen 1991). However, these references deal mainly with the ice-associated biota at higher trophic levels and only secondarily with sea-ice extent, and not with its thickness. Snow and ice thickness, physical ice properties and the development of superimposed ice in Kongsfjorden have been investigated more intensively since 1997 (Gerland et al. 1999, 2004, 2008; Svendsen et al. 2002; Nicolaus et al. 2003; Gerland and Hall 2006; Gerland and Renner 2007; Willmes et al. 2009). In particular, physical parameters and surface processes of fast ice in Kongsfjorden for the years 1997, 1998, 2002 and 2003 have been reviewed by Gerland et al. (2004) based on the results of Gerland et al. (1999), Nicolaus et al. (2003), Hamre et al. (2004) and Winther et al. (2004). Different aspects of sea ice were addressed by Gerland et al. (2004), including the development of sea-ice concentration, snow and ice thickness, texture of snow and ice, salinity and temperature, and spectral surface reflectance and albedo during the period from late winter to summer, and they also investigated fast-ice formation, development and decay.

Systematic fast-ice monitoring for Kongsfjorden, as a part of a long-term project at the Norwegian Polar Institute (NPI), was started in 2003. It includes mapping of sea-ice extent and *in situ* measurements of ice and snow thickness, and freeboard at several sites in the fjord. Data collected within this standardized monitoring programme have contributed to a number of studies. A comprehensive analysis of fast-ice evolution in Kongsfjorden (2003–2005) was given by Gerland and Renner (2007), which included quantitative estimates of the fast-ice mass balance in the fjord. Due to increased activities in the framework of the International Polar Year (IPY), more intensive fjord ice studies were performed in several of the Svalbard fjords. This gave a good opportunity to compare the fast-ice evolution in Kongsfjorden with that of other Svalbard fjords (e.g. Gerland et al. 2008; Hendricks et al. 2011; Zhuravskiy et al. 2012; Renner et al. 2013a, b; Wang et al. 2013; Ivanov et al. 2014). For example, Zhuravskiy et al. (2012) analysed the long-term variability of ice characteristics (based on visual and instrumental observations), as well as main oceanographic and meteorological characteristics, in Grønfjorden from 1974 to 2008. The authors reported that, due to the geographical and climatic features of the region, the beginning of stable ice formation varied significantly from year to year, but generally occurred from mid-December to early January. The maximum thickness of fast ice also showed strong variability, with the maximum ice thickness (0.93 m) measured in 1986. Their results also indicate a tendency toward a response of fast ice to a milder climate during the last decades of the 20th and the beginning of 21st century in Grønfjorden.

In this review, we summarize published results, and we present new observational data of ice extent, and ice and snow thickness in Kongsfjorden. This includes a time-series of sea-ice measurements from 2003 to 2016. Changes in sea-ice conditions have implications for the marine ecosystem in Kongsfjorden, from the primary producers of ice algae and phytoplankton to upper trophic levels including seabirds and marine mammals (e.g. Hanssen et al. 2013; Lydersen et al. 2014; Vihtakari et al. 2018). Ecological changes in different compartments of the Kongsfjorden system, partly because of changes in sea ice, have been addressed in other chapters in this book (e.g. Fredriksen et al., Chap. 9; Hegseth et al., Chap. 6; Molis et al., Chap. 11). Because this paper focuses on long-term changes in sea ice, we are limiting the discussion to some of the main ecological implications of reduced sea ice in Kongsfjorden.

4.2 Research Area

Kongsfjorden is located at about 79°N, 12°E on the west coast of Spitsbergen (Fig. 4.1a, b). The fjord is about 25 km long and 5–10 km wide. Characteristic landmarks for Kongsfjorden are: Brandalpynten, a cape just west of Ny-Ålesund; Blomstrandhalvøya, the largest island in Kongsfjorden, north of Ny-Ålesund near the northern shore of the fjord; the archipelago Lovénøyane in the inner fjord, with Storholmen as the largest and westernmost island; Dyrevika, the bay in the northern inner fjord; and several glaciers terminating in the fjord, among them Kongsvegen and Kronebreen (glaciers with one of the highest flux rates on Svalbard) and Kongsbreen (the most active calving glacier on Svalbard) in the innermost part of fjord.

The physical environment, including the hydrography of Kongsfjorden, has been described in several publications (see e.g. Haugan 1999; Svendsen et al. 2002; Cottier et al. 2005, 2010; Prominska et al. 2017) and also more briefly by Gerland and Hall (2006) and Gerland and Renner (2007). Kongsfjorden and Krossfjorden (fjord arm to the north) are hydrographically connected by the Kongsfjordenrenna to the North Atlantic, and receive warm Atlantic water masses from the West Spitsbergen Current, which is the main cause of the late onset of ice formation each winter. Atlantic water enters Kongsfjorden along the southern coast and mixes with

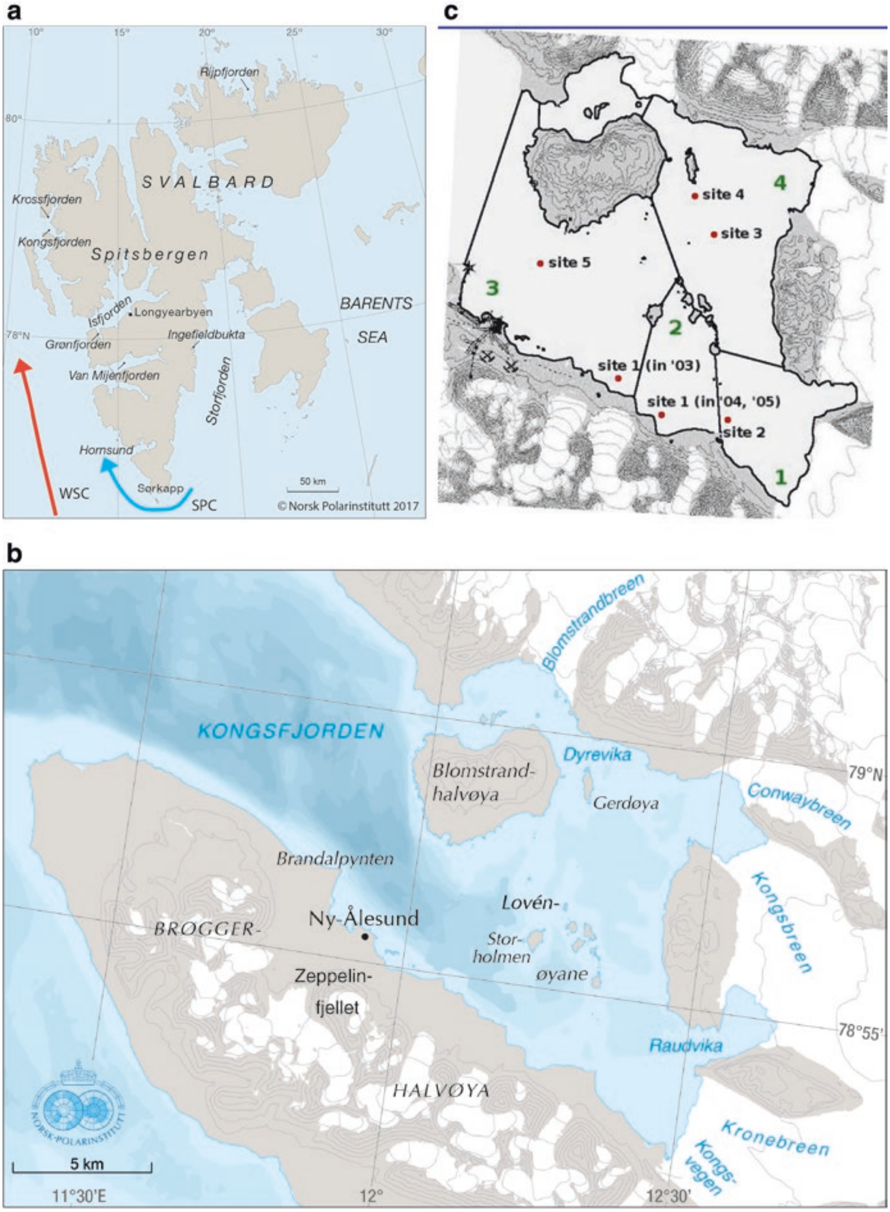


Fig. 4.1 Map of (**a**) Svalbard area. WSC – West Spitsbergen Current, SPC – Spitsbergen Polar Current (coastal current); (**b**) Kongsfjorden; (**c**) Inner part of Kongsfjorden with sectors 1–4 (labelled with green numbers) and monitoring sites. (From Gerland and Renner 2007)

meltwater and runoff water in the inner part, before it exits the fjord on the northern edge, partly via Krossfjorden. The wide mouth of the fjord, with Krossfjorden to the north, enables ocean swells from storms to reach the central part of the fjord, and this can break up the fast ice (Tverberg et al., Chap. 3).

4.3 Methodology

Conception and methodology of the systematic fast-ice monitoring in Kongsfjorden are described in Gerland and Hall (2006) and Gerland and Renner (2007) and include observations and quantification of sea-ice extent and *in situ* measurements of ice and snow thickness, and freeboard. Both types of observation results are needed for quantitative sea-ice mass-balance estimates and for characterization of the ice situation, for example in terms of stability against destruction by waves or after being affected by mild spells during winter (Gerland and Renner 2007). The monitoring was designed to be relatively inexpensive, robust, and consistent over time. However, consistency can be a challenge given the changing conditions of the matter that is being monitored. The permanent presence of staff at the research base of Sverdrup Station (Norwegian Polar Institute) and daily visits to the observatory on the mountain Zeppelinfjellet (just south of Ny-Ålesund) enable regular *in situ* thickness measurements and ice observations. The altitude of Zeppelinfjellet (474 m a.s.l.) gives a reasonable overview on the fjord ice situation, but the part north of Blomstrandhalvøya is not visible from there, and details of the ice situation on the innermost parts of the fjords are difficult or impossible to observe.

4.3.1 Sea-Ice Extent

Sea-ice extent data are derived from ice maps and photography. Observations of fast-ice and drift-ice extent are based on visual observations, and, accordingly, no data are available for days when there is limited visibility (low clouds, fog and darkness). An observation area for ice extent in inner Kongsfjorden was defined to be 120 km^2 (Gerland and Renner 2007). In order to account for locally different conditions during ice formation, the observation area was divided into four sectors (Fig. 4.1c).

The maps of observational areas were drawn by hand visually assessing the ice edge, and photographs were taken from Zeppelinfjellet. In maps and from photographs, we classify the ice as “fast ice” and “drift ice”, usually either pack ice broken off the fast ice, or ice advected from other areas (Krossfjorden and areas outside Kongsfjorden/Krossfjorden). To calculate the area of sea-ice cover, a polygon covering Kongsfjorden was created using ArcMap (Esri.com). Hand-drawn ice maps for selected dates were digitally superimposed on the polygon. The ice cover was divided into the regions of “fast ice”, “drift ice” and “open water”, and the area of

Fig. 4.2 Drillhole measurements in Kongsfjorden. (Photo: S. Gerland, Norwegian Polar Institute)

each region was calculated using ArcMap. As the area north of Blomstrandhalvøya is not visible from Zeppelinfjellet, it was excluded from fast-ice extent and mass balance calculations.

4.3.2 Ice and Snow Thickness Measurements

Monitoring sites in inner Kongsfjorden are accessed by snowmobiles or a small boat (Fig. 4.2). Then, measurements are made at some distance from the ice edge to avoid the effects of melting close to the edge. Ice thickness, snow thickness and freeboard are measured conventionally from drill holes, drilled with an auger, using a measurement stick with a notch or a tape-measure thickness gauge (Kovacs Enterprises, USA). Snow thickness is measured with a metal stake with markings. The monitoring usually consists of observations at four to five sites in inner Kongsfjorden. Drillings are made approximately every 2 weeks as long as it is possible to access the sites. At each site on each occasion, three holes are drilled in the corners of a triangle with 10 m side length to account for variability at the site (see also Gerland and Hall 2006). Measurement data from the three holes are later averaged. Locations of sites are measured with GPS. Additionally, a detailed 1-week field campaign has been carried out every year in April or early May close to the maximum sea ice and snow thickness.

4.4 Observations of Ice Extent and Thickness

Observations of ice extent and thickness have been published for Kongsfjorden, but no long-term series with more than a decade of measurements. We here present updated ice-extent results for the period 2003–2016, before detailing updated ice and snow thickness results for the period 1997–2016.

4.4.1 Fast-Ice Extent for the Period 2003–2016

The evolution of fast ice in Kongsfjorden for the period 2003–2005 (the first 3 years of the systematic monitoring) is presented in detail in Gerland and Renner (2007). The fast-ice coverage reached its maximum (120 km^2) within the defined observation area in all 3 years of observations (Fig. 4.3). The entire observation area was ice-covered in March 2003, mid-January 2004 and late February 2005 (Fig. 4.3). The ice cover persisted to late June in 2003–2005. The decay of fjord ice in 2003 stopped up at a level of about 70 km^2 (late May-early June) before it continued further on in June. Similar decay developments can be seen for 2004 and 2005, but with intermediate stagnation levels at about 80 km^2. The ice decay progressed significantly faster in 2005 than in 2004. The second part of the ice-extent decay appeared similar for 2003 and 2004, but 2005 was different, with an earlier ice-free fjord.

The period of 2006–2016 was characterised by relatively little sea-ice cover, except for 2006 and 2011 when the fast-ice coverage reached its maximum (120 km^2) within the defined observation area (Figs. 4.3 and 4.4). The fast-ice formation in Kongsfjorden during this period started in March for most years, except for 2006, 2011 and 2015 when the ice formation started in February, and melting or break-up generally started in April–May (Fig. 4.3). The behaviour of sea-ice evolution in these 3 years was different. Thus, despite the fact that in 2006 and 2011 the entire observation area was ice-covered with fast ice at the end of February, 2006 was characterised by relatively short fast-ice season (mid-February-end of April) and earlier fast-ice decay. On the contrary, the ice-coverage season was long in 2011 (February–June). The year 2015 was characterized by relatively long fast-ice season (mid-February-beginning of June), but little fast-ice cover.

In most years, the ice cover was both less extensive and of shorter duration, except for 2003–2006 and 2011. In 2007, 2012, 2014 and 2016, the southern shore of Kongsfjorden was never properly connected with fast ice in the inner fjord (Fig. 4.3). The edge of fast-ice cover did not reach Lovénøyane in the inner fjord during winters of 2012 and 2014 (Fig. 4.3). The years 2012, 2014 and 2016 were characterized by the lowest sea-ice extent with a very short period of fast ice, from March to April–May. During all years, the fast ice stayed longest in Dyrevika, the bay in the northern part of the inner fjord. However, not all parts of inner Kongsfjorden can be observed from Zeppelinfjellet, so fast ice in Raudvika and the new bay off the northern glacier front of Kongsbreen are also likely to contain fast ice longer than less protected areas.

Maximum fast-ice coverage for each of 5 months (February–June) in the period 2003–2016 shows alternating periods of extensive and little ice cover (Fig. 4.4). Maximum fast-ice cover values (100%) in February were reached in 2005 and 2011. For 2003, we do not have ice-cover information before March, and in 2004 the entire observation area was ice-covered with fast ice in mid-January (not shown). In March, only the years 2003–2005 had 100% fast-ice coverage, while in April, the two largest maximal fast-ice cover values (93% and 80.5%) were observed in 2004 and 2011, respectively. In the other 2 months (May–June), the maximum fast-ice

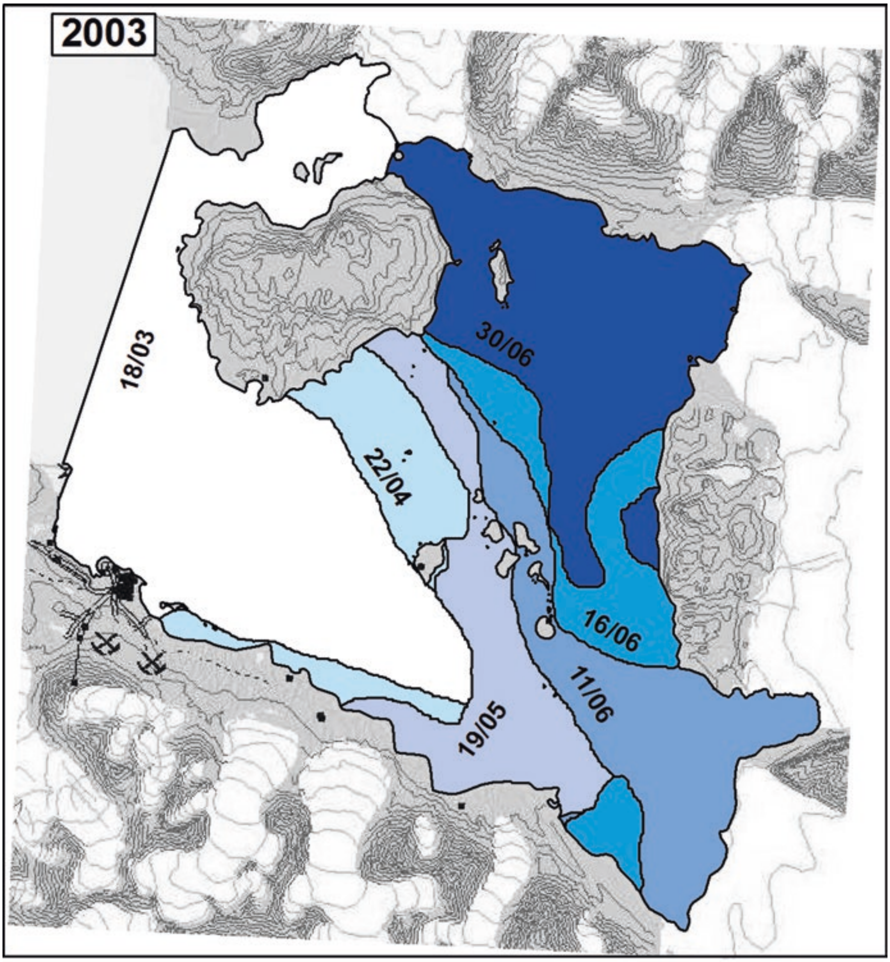
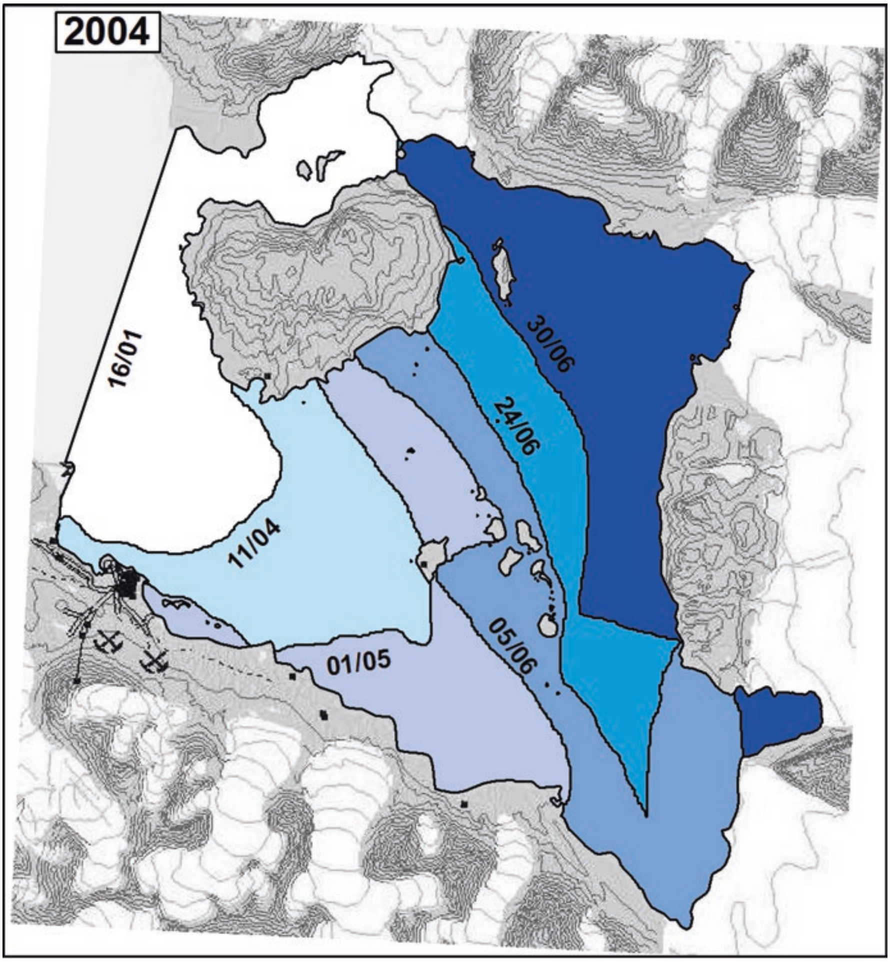


Fig. 4.3 Sea-ice extent for 2003–2005 (from Gerland and Renner 2007) and 2006–2016. Different colours correspond to ice extent on respective dates, and open water (dark blue) is also indicated



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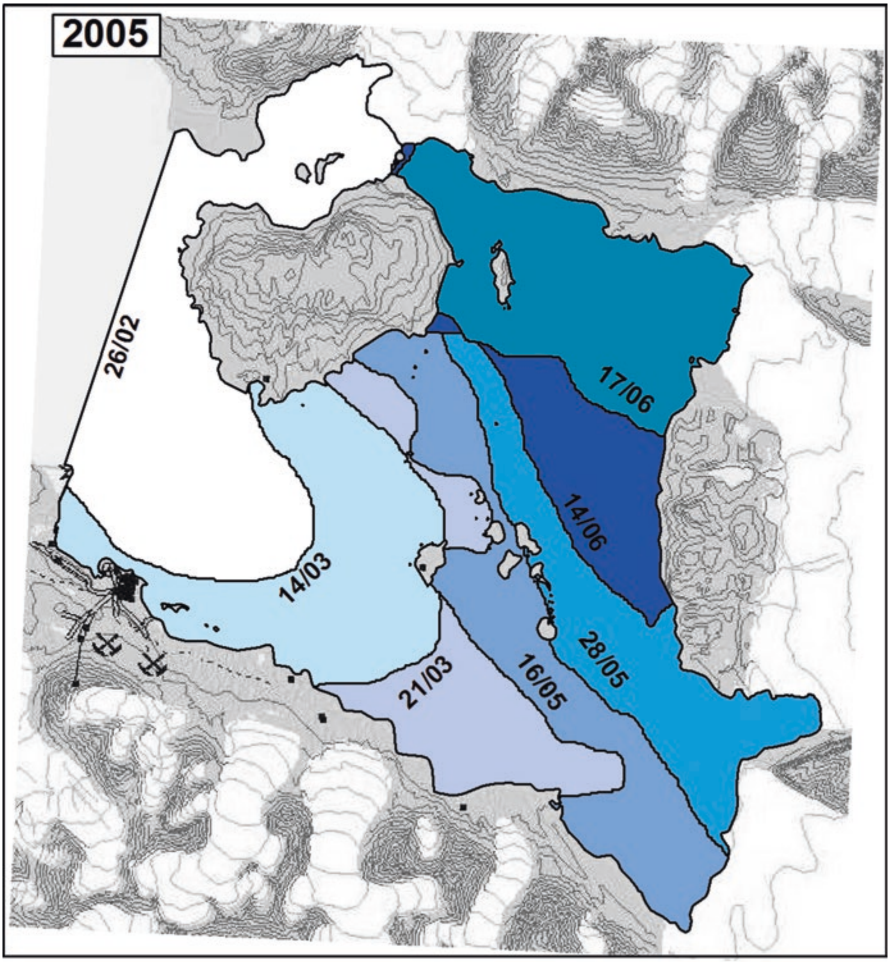
coverage was not higher than 50%, except for the period 2003–2005. Maximum fast-ice coverage of 50% and higher was reached in the years 2003–2006 and 2009–2011 in February–April. During the periods 2007–2008 and 2012–2016, the fast-ice area was <50%, except for February 2008 and 2015 (Fig. 4.4). Both figures (Figs. 4.3 and 4.4) reflect the late ice growth, low coverage and short season of fast ice in the years 2012, 2014 and 2016. Based on conditions from 2003–2016, the fast-ice evolution in Kongsfjorden during this period showed that (i) fast-ice formation scenarios varied annually, but with intervals (2–3 years or more) of relatively high and low sea-ice cover; (ii) most years after 2006 had low ice extent and short season of fast ice.



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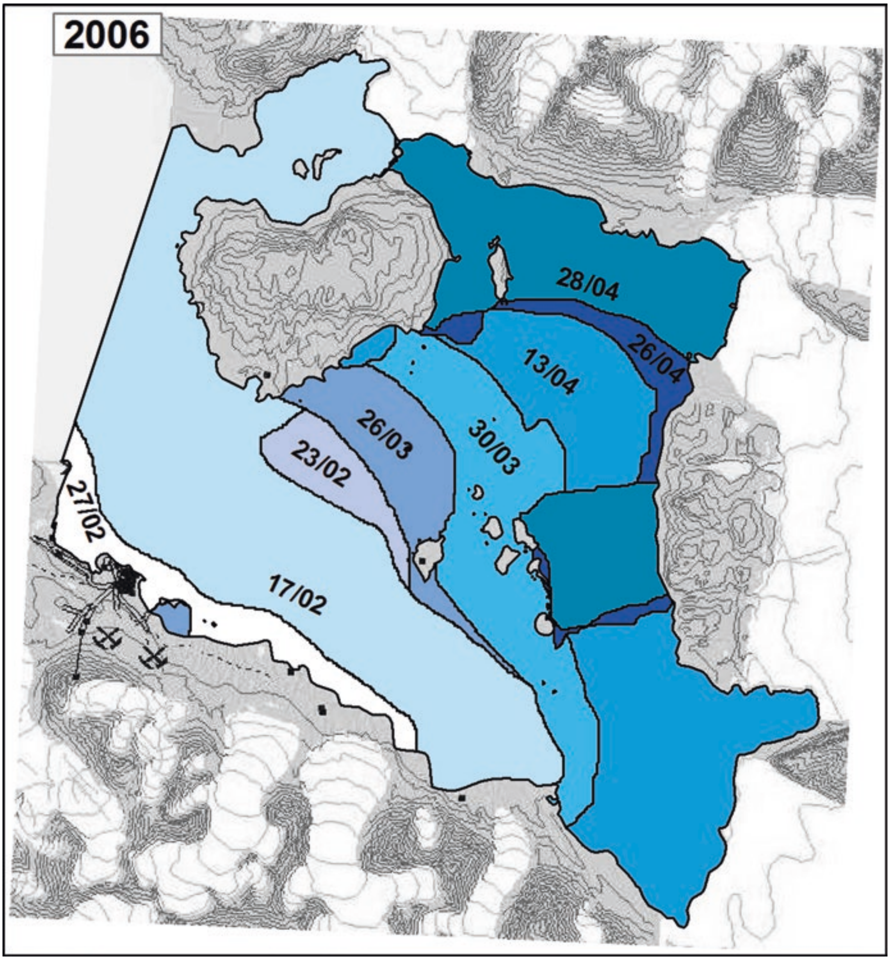
4.4.2 Ice and Snow Thickness

Both fast-ice and snow thickness have experienced negative trends over the observation period (1997–2016), towards thinner ice and snow cover. The thickness of fast ice reached seasonal maxima in the range of 0.7 m during the first years of the monitoring period (Fig. 4.5). In recent years, except for 2011, values decreased to around 0.2 m. The linear trend of that change is −24.7% per decade. However, the inter-annual variation in ice thickness appears to be substantial. In parallel to this development, snow thickness decreased from around 0.2 m to <0.05 m, exhibiting an even larger negative trend in relative values with −41.7% per decade. The last 4 years (2013–2016) were all years with very little snow on the sea ice. The analysis further demonstrates that the two variables are related on the inter-annual time



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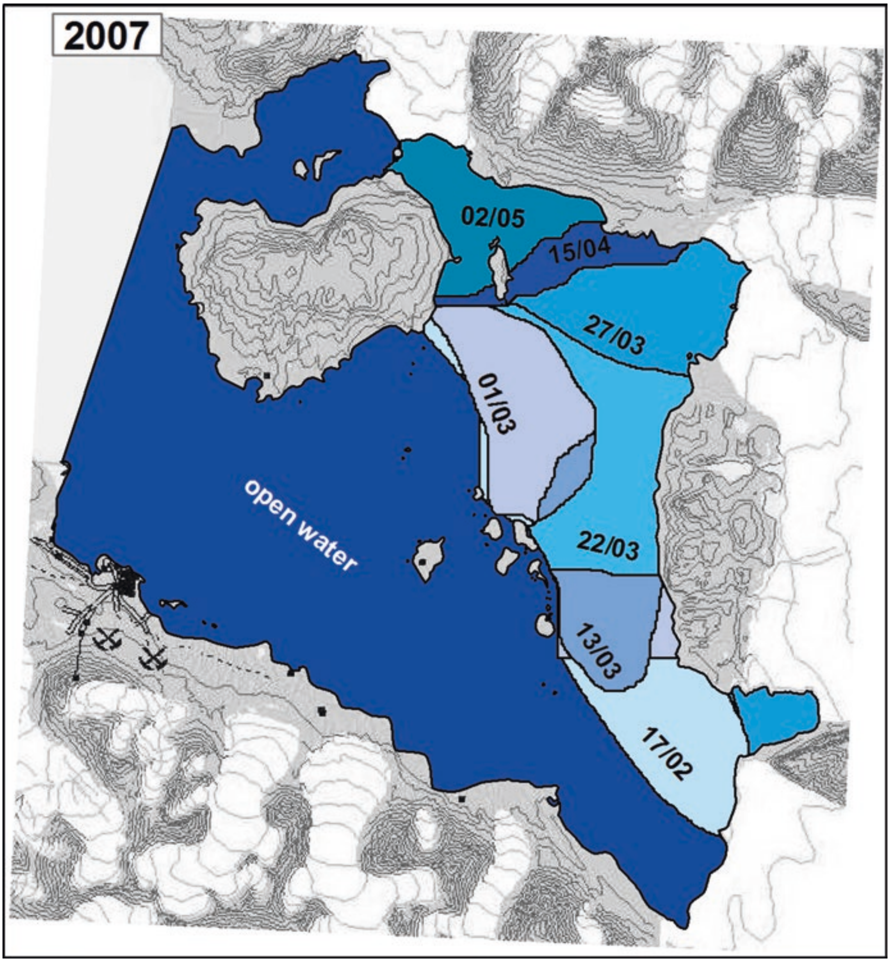
scale. In particular, based on observations for all years our results suggest that the seasonal maximum snow and ice thickness in Kongsfjorden were positively related with $r^2 = 0.42$ (Fig. 4.6). Note that in order to account for the longer-term changes in the two variables they were detrended prior to analysis.

4.4.3 Atmospheric Influence

Among the environmental and physical parameters that strongly influence the fast ice are air and seawater temperature, solar radiation, wind speed and direction, and waves (swell). Cold air and water are an absolute necessity to produce sea ice.



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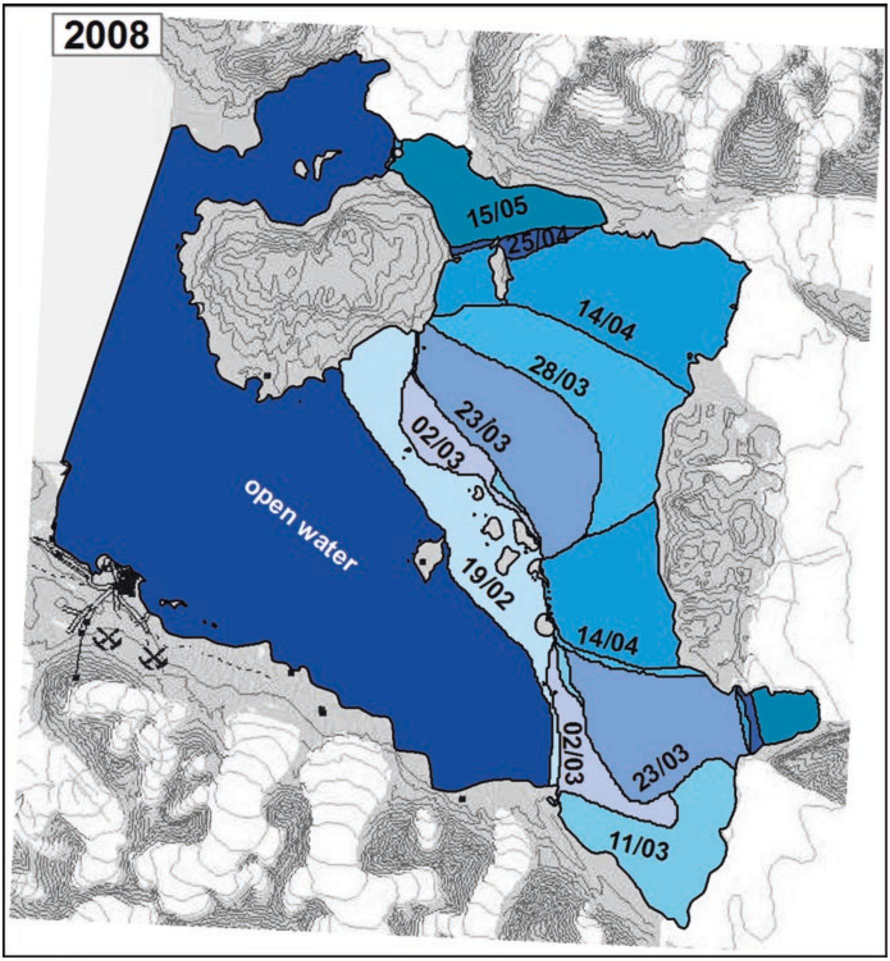
However, often a combination of parameters results in ice formation or decay. The ice-covered area was significantly negatively related to air temperature during winter in Ny-Ålesund, (Table 4.1) with less ice in warmer winters ($r^2 = 0.51$; Fig. 4.7). These two variables were detrended prior to analysis.

Gerland and Renner (2007) showed that daily mean air temperature for Ny-Ålesund in 2005 season was higher than in both 2003 and 2004. During the winter of 2005/2006, the air temperatures showed dramatic changes, and temperature in December 2005 and January 2006 were the highest for 2003–2016 (Table 4.1). In February and March 2006, the temperature was comparatively low but reached high values in April and May. This corresponded with the ice-extent evolution in 2006, which showed relatively short duration and earlier decay compared with the years 2003–2005. The years 2007–2008 had relatively low tempera-



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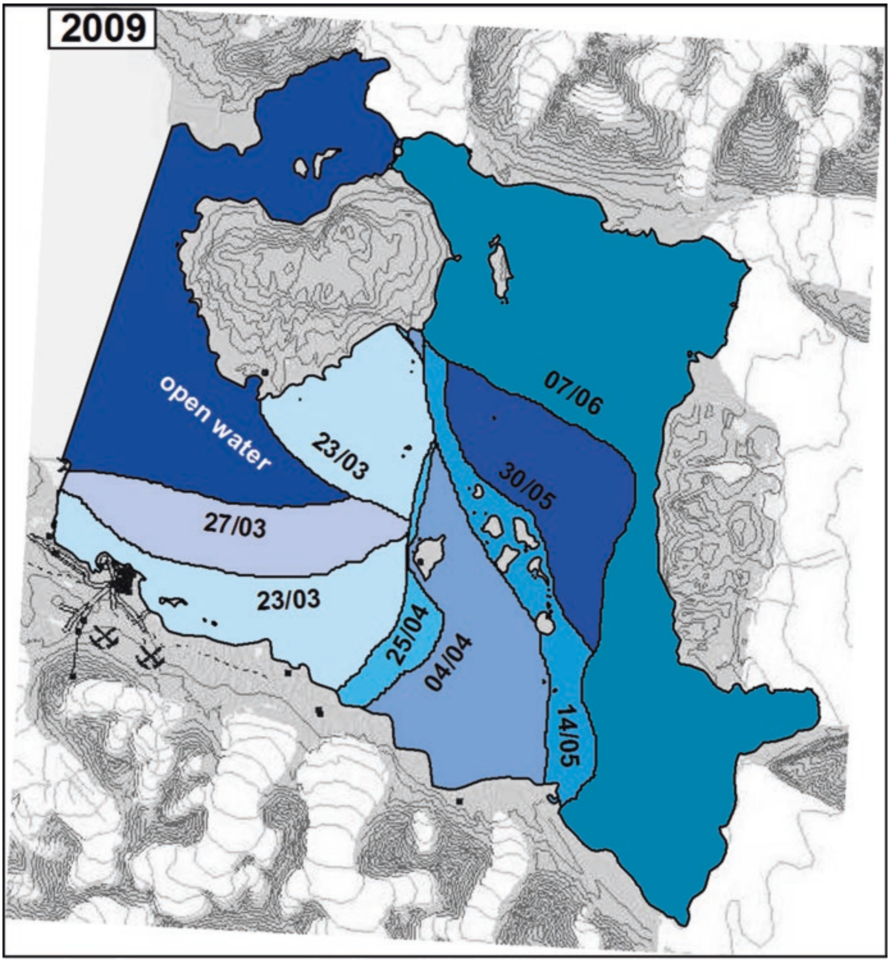
ture in December 2006 and 2007, and in January–April 2007 and 2008. In the years 2009–2011, when the ice extent was relatively high (including the second maximum in 2011), the air temperature was low during all winter-spring months. After 2011, the air temperature became higher during winter (December–March), except for February 2015. Thus, the Kongsfjorden area had two periods of low and high air temperature with corresponding periods of much (2009–2011) and little (2012–2016) fast-ice cover.



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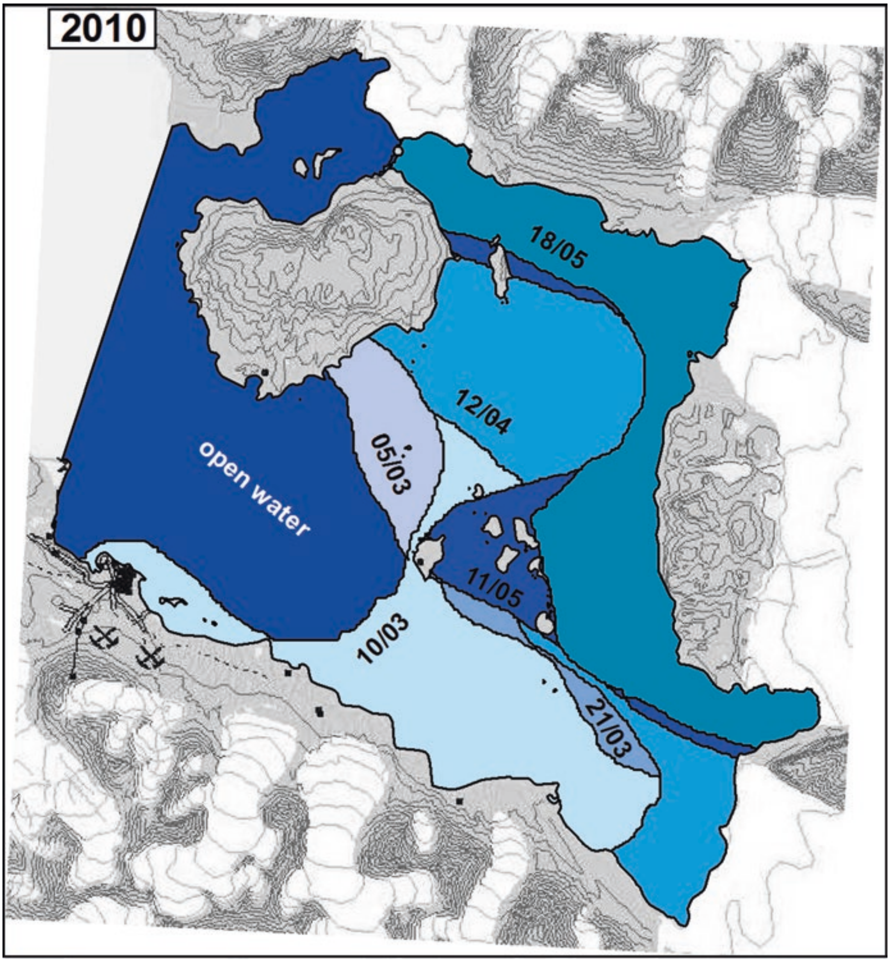
4.5 Discussion and Ecological Implications

Inter-annual variation in fast-ice thickness showed consistent patterns in two studies from Kongsfjorden, conducted during 1997–2005 (Gerland and Hall 2006) and 2003–2005 (Gerland and Renner 2007). The last study included detailed mass-balance observations of fast ice. The fixed geographical setting (coastline, islands) led to a similar ice extent in spring (early May) for all years investigated. The temporal evolution of fast ice in the seasons 2003–2005 showed that, besides physical parameters, the coastline and islands in Kongsfjorden are crucial for the fast-ice extent. The protection by Lovénøyane preserves the fast ice and, thus, makes it suitable for monitoring studies into spring. The ice decay is strongly influenced by the



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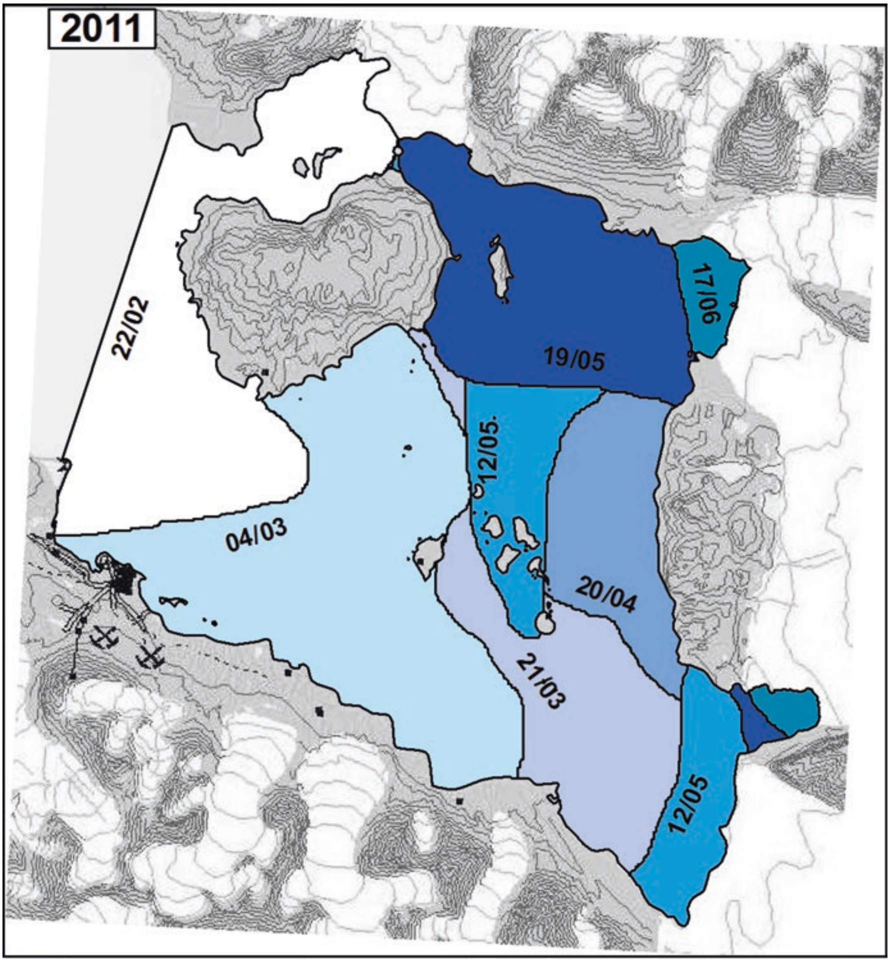
islands, and the plateau in the ice-extent vs time data series reflects this (Gerland and Renner 2007; their Fig. 4.4). These time series also show that ice once disconnected from shore, can stay as pack ice in the fjord for several weeks (e.g. in April 2005).

The duration and extent of fast ice in Kongfjorden are important for heat loss to the atmosphere and, thus for oceanographic processes with regard to formation of local fjord water, and, particularly winter cooled water with temperatures <−0.5 °C (Svendsen et al. 2002; Hop et al. 2006). With more Transformed Atlantic water being advected into Kongsfjorden, particularly during winter (Cottier et al. 2007, 2010), the entire fjord system has become warmer with less sea ice. The overriding effects seem to be oceanographic, with links to processes in Fram Strait (Hop et al. 2006; Walczowski et al. 2017; Tverberg et al., Chap. 3). Climate warming with



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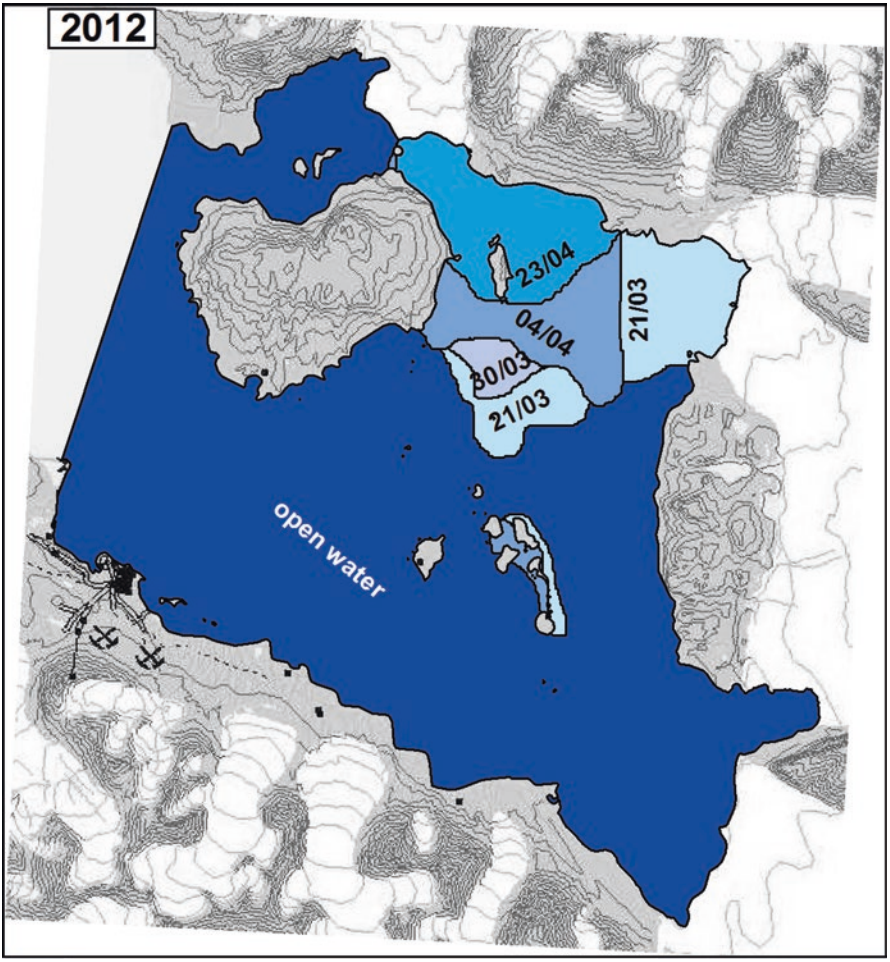
increased atmospheric temperatures, as evident from the temperature record for Ny-Ålesund, is the ultimate driver for changes in the marine environment.

Satellite observations have become a widely used tool for sea-ice studies, and researchers are increasingly able to utilize satellite-generated data, also in coastal areas. Muckenhuber et al. (2016) investigated sea-ice conditions for the period 2000–2014 in two fjords along the west coast of Spitsbergen (Isfjorden and Hornsund). Inter-annual variability of sea-ice cover in these two fjords corresponds well with our observations. For example, their estimates for Isfjorden (their Fig. 4.3) show two periods (2000–2005 and 2009–2011) with relatively high fast-ice coverage (40% and higher) and two periods (2006–2008 and 2012–2014) with relatively low fast-ice coverage (<30%). The authors also marked the years 2012 and 2014 as the years when the fast-ice season was significantly shorter and with maximum



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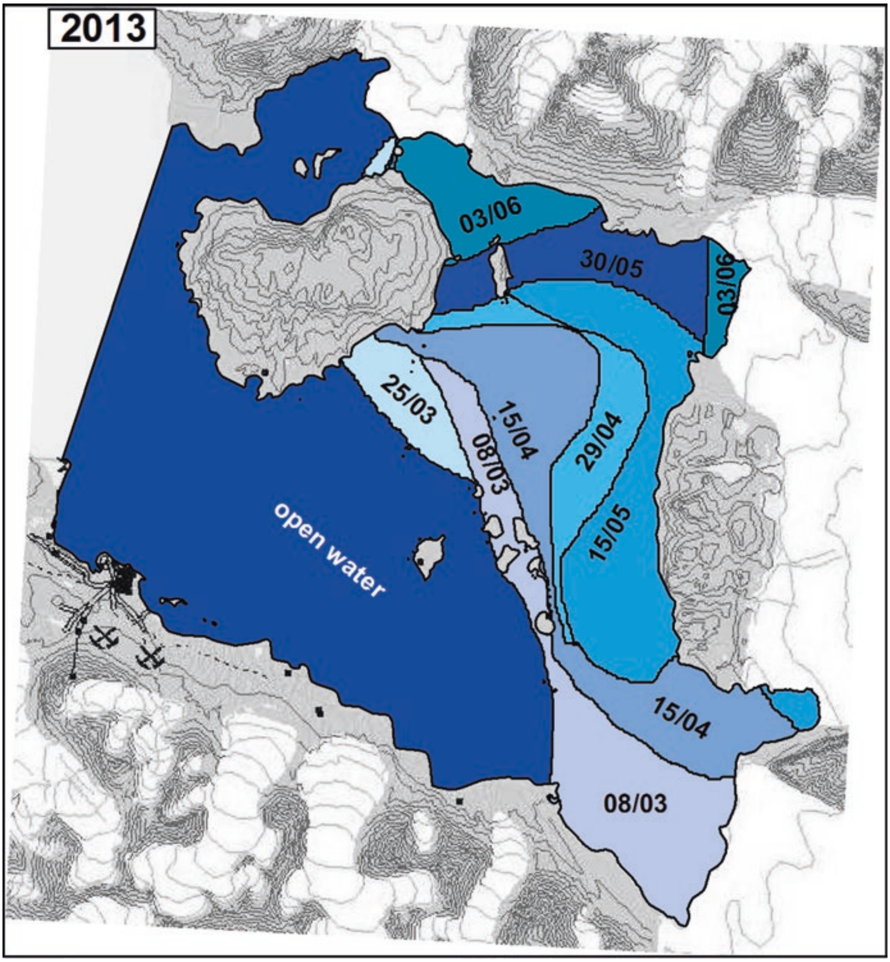
<20%. They concluded that fjord systems along west Spitsbergen changed from an Arctic state to a more Atlantic-water state after the winter 2005/2006. With regard to fast-ice coverage, we found the same periods (in terms of large and little ice coverage) as in Muckenhuber et al. (2016), except for the year 2006.

The winter 2005/2006 has been noted as a turning point toward a warming Arctic as a whole, and particularly in the fjords along West Spitsbergen (e.g. Comiso 2006; Cottier et al. 2007; Tverberg et al. 2007, Chap. 3; Muckenhuber et al. 2016). Based on satellite observations, Comiso (2006) reported on relatively high surface temperature and record-low ice extent during the winters of 2005/2006 in the peripheral seas, mostly in the eastern Arctic Basin. With regard to Kongsfjorden, Cottier et al. (2007) indicated that periods of sustained along-shelf winds during the winter 2005/2006 generated upwelling and cross-shelf exchange that caused extensive



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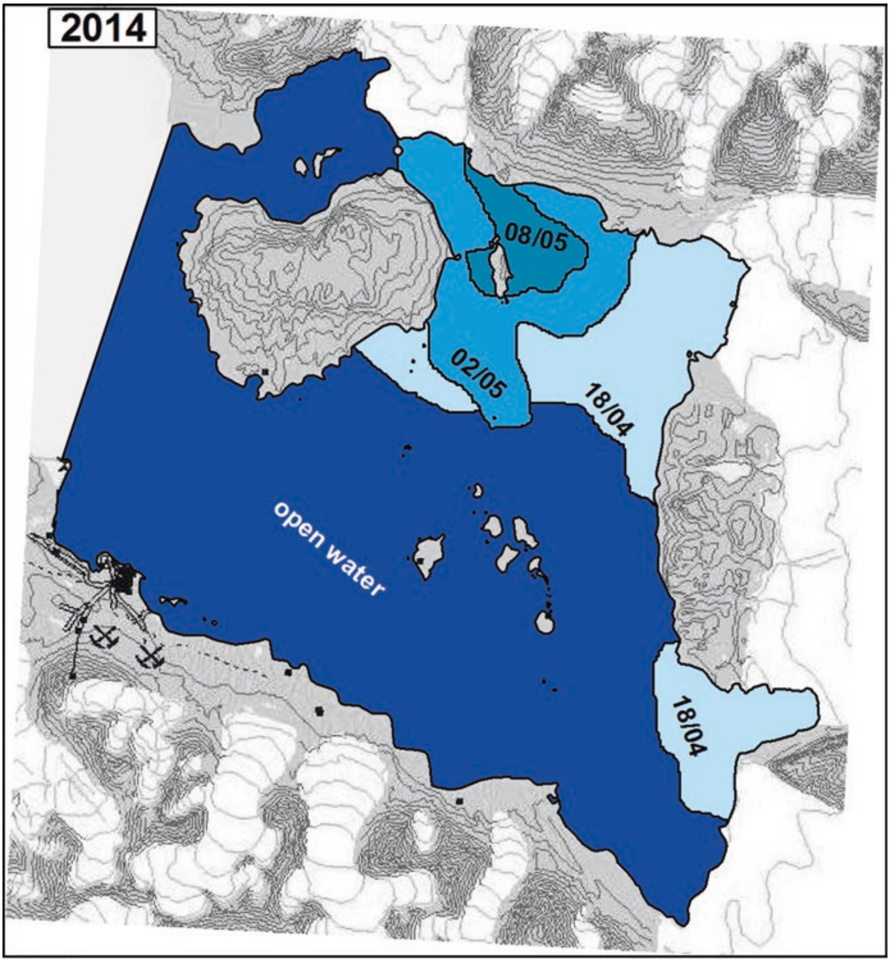
flooding of the coastal waters with warm Atlantic water from the West Spitsbergen Current. Based on analyses of oceanographic data from the period 1997–2007, Tverberg et al. (Chap. 3) suggested that the February 2006 event, with massive intrusion of Atlantic water to the fjord, was a tipping point for the Kongsfjorden environment. Then, the winter temperature of the West Spitsbergen Shelf remained elevated, interrupting the normal cycle of sea ice formation in the region.

Newer hydrographic observations (Cottier et al. 2007, 2010; Pavlov et al. 2013; Nilsen et al. 2016; Tverberg et al., Chap. 3) revealed the important role of wind-driven water masses that bring more Atlantic water to Kongsfjorden (and other West Spitsbergen fjords) than usual, contributing to less fast-ice formation. This, in combination with relatively mild winters, can be seen as main factors for changing fast-ice conditions in Kongsfjorden during the last 10 years.



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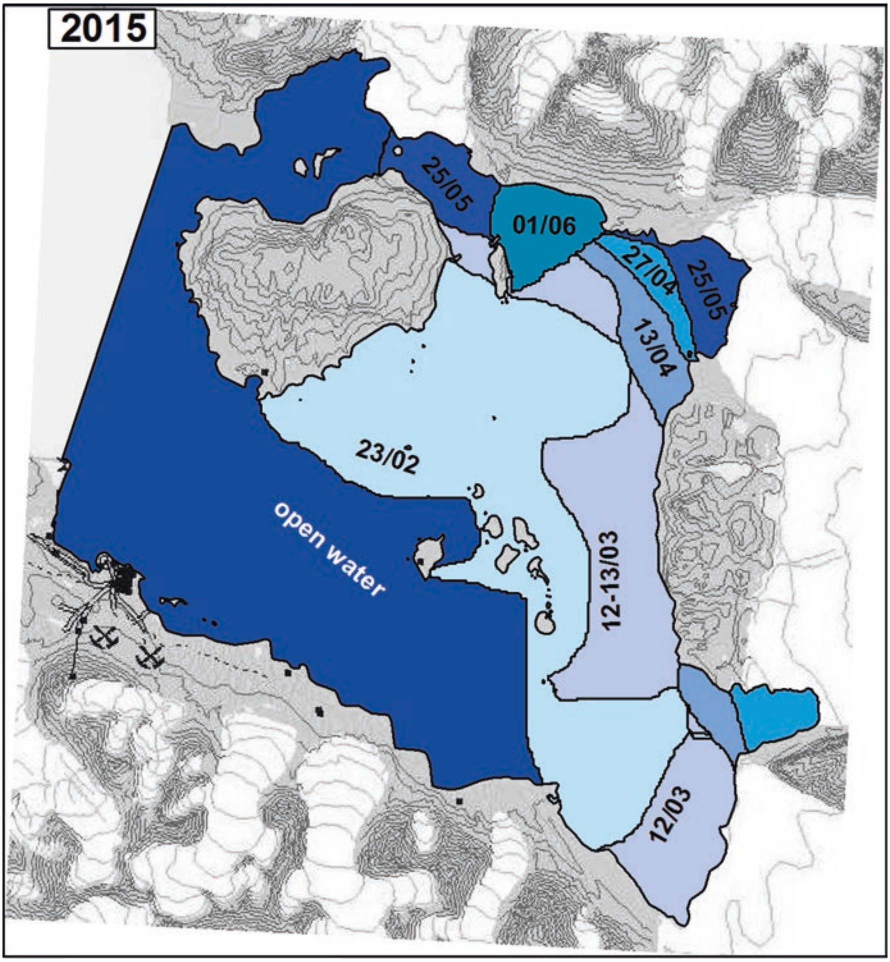
As detailed, ice conditions in the fjord are strongly linked to the atmospheric and hydrographic forcings, with periods of cold air and water necessary for ice formation. However, in addition to that, other factors play important roles: The timing of ice formation along with the given wind scenario influences how much snow accumulates on the fast ice. The snow cover again influences the growth of ice by (i) reducing ice growth speed, (ii) giving the potential of snow-to-ice formation (snow ice, superimposed ice), and (iii) being the base for melt ponds later in the season. Ice that starts to form later in the season might grow faster than ice that already has started to form, and less snow cover also enhances ice growth (Notz 2009). However the forcings appear too weak in recent years to create substantial fast-ice thickness, even with little snow cover.



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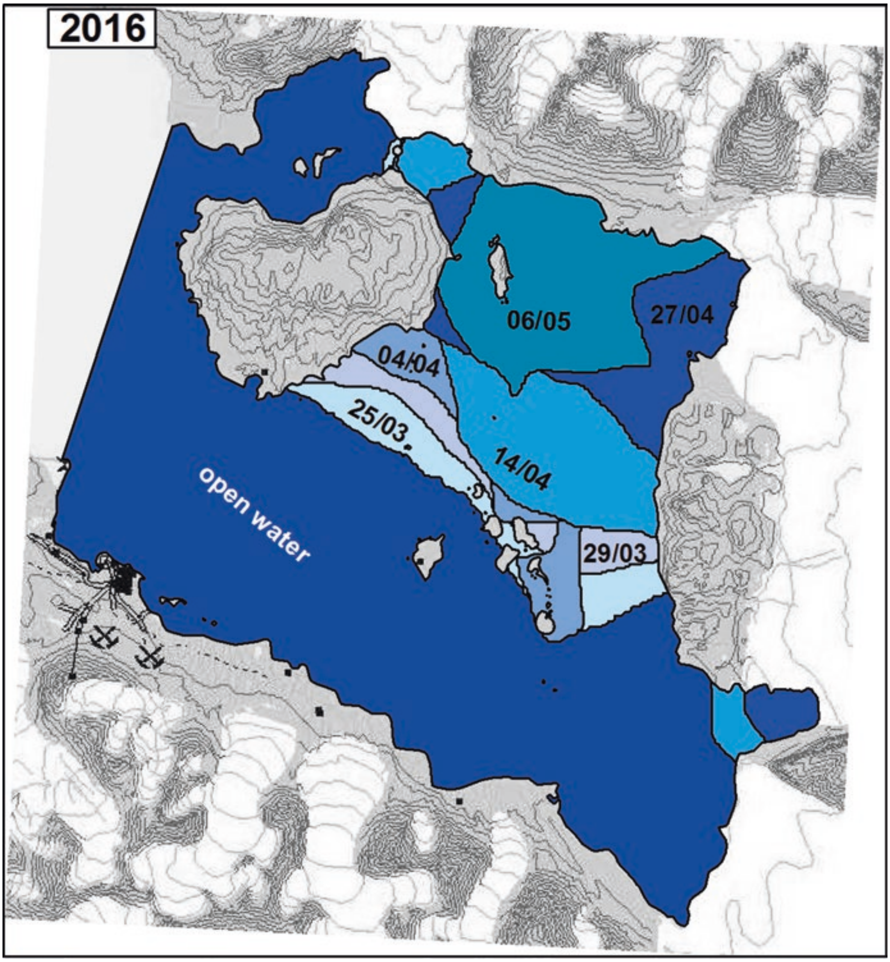
The relationship between snow and ice thickness shows that thick ice typically has more snow on it (Fig. 4.6). Thicker ice typically forms earlier in the season and persists longer, allowing more snow to accumulate. From observations (Gerland et al. 1999, 2004; Nicolaus et al. 2003) and modelling (Nicolaus et al. 2006; Wang et al. 2015), we know that snow ice and superimposed ice do contribute to ice and snow thickness evolution in Kongsfjorden. Based on these studies, we also know that air temperature and precipitation are critical factors for snow ice and superimposed ice formation, and that the total ice formation at the ice surface is more sensitive to precipitation than to air temperature. The precipitation on land in Ny-Ålesund has increased since during the period 1969–2013, particularly during the early snow season (October–February; López-Moreno et al. 2016). However, the number of days with rain also increased during this period, with 43% for the early snow season



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and 13% for the late snow season. This has caused a general decrease in snow pack thickness, water equivalent and duration as the climate warms.

Consistent monitoring of sea ice is challenging because of changing sea-ice conditions. Changes in glacier fronts present a challenge for ice monitoring in Kongsfjorden. For long-term monitoring, changing (retreating) glacier fronts lead to (i) change (increases) in the total surface area of the fjord, and (ii) new coastline and hydrographic conditions, which might be more or less suitable for fast-ice formation. Two examples for such changes are the opening of the area north of Blomstrandhalvøya in the early 1990s, when the glacier Blomstrandbreen retreated so that the former peninsula Blomstrandhalvøya became an island, opening also for water currents in the shallow passage (Svendsen et al. 2002; Burton et al. 2016). However, that change happened prior to the beginning of the monitoring presented

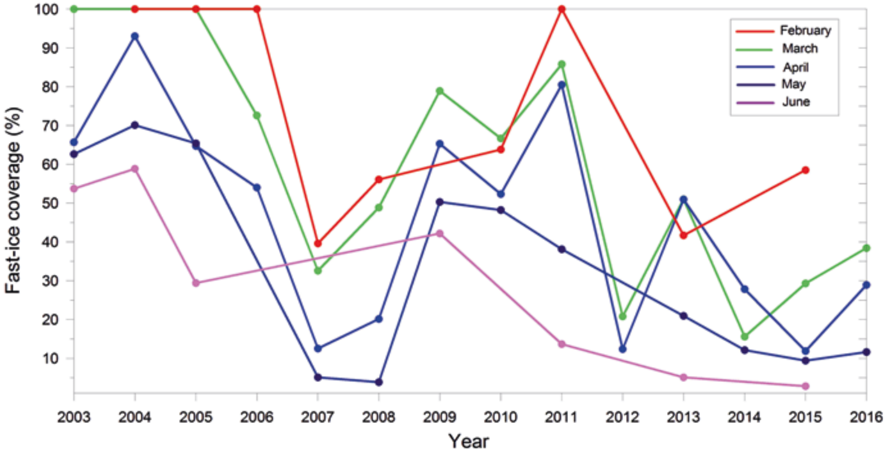

Fig. 4.4 Maximum fast-ice coverage (%) for each month from February to June in the period of 2003–2016

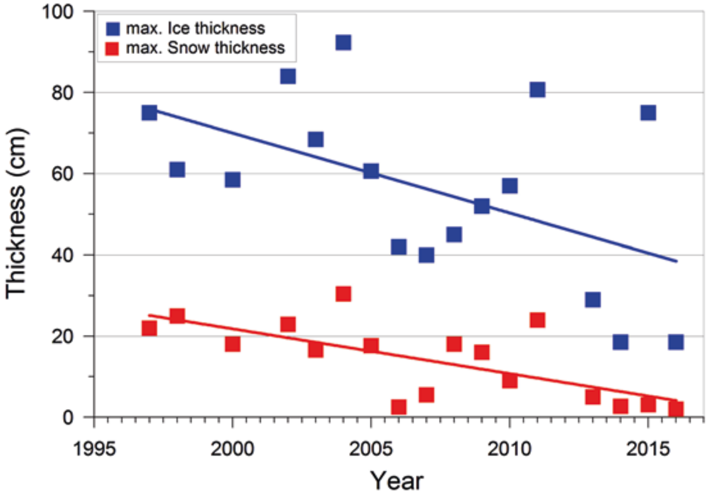

Fig. 4.5 Maximum seasonal sea-ice and snow thickness (cm) in inner Kongsfjorden 1997–2016. Lines show the linear trends: blue – ice-thickness changes (−24.7% per decade) and red – snow-thickness changes (−41.7% per decade). There were no *in situ* measurements in the years 1999 and 2001 because regular monitoring started first in 2003, and none in 2012 because of little ice. Observations from 1997, 1998, 2000 and 2002 were made in connection with research projects

here (Sund and Eiken 2010). A second example is the opening of the bay Raudvika north of Kronebreen in the 1970s (Liestøl 1988), with the main retreat after the 1990s (Urbanski et al. 2017). Well protected from swell and only with a limited opening to the rest of Kongsfjorden, the setting of this bay is suitable for fast-ice formation.

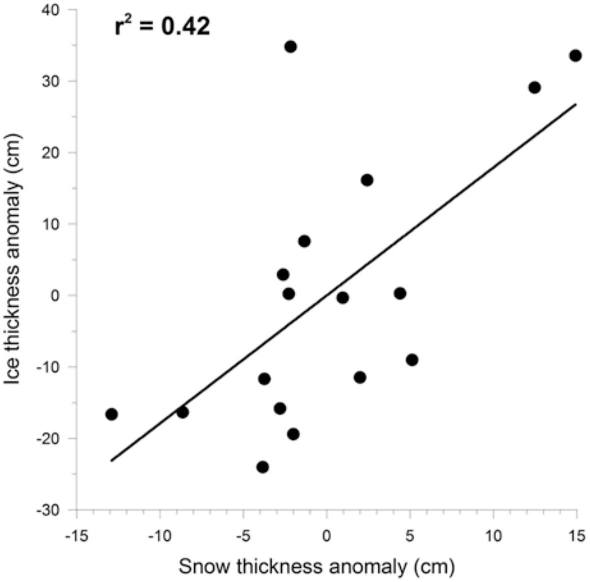

Fig. 4.6 Relationship between detrended maximum snow thickness (cm) and maximum ice thickness (cm) in Kongsfjorden, 1997–2016

Table 4.1 Monthly mean air temperature in Ny-Ålesund, Svalbard, for 2002–2016

Year	January	February	March	April	May	December
2002	-11.7	-12.4	-14.5	-7.1	**-3.9**	-6.9
2003	**-16.4**	-11.4	**-16.3**	-9.7	-3.1	**-17.0**
2004	-15.9	**-16.1**	-7.1	-3.2	-1.8	-7.7
2005	-7.4	-7.5	-14.4	-8.5	-1.8	**-3.9**
2006	**-3.3**	-10.8	-13.2	**-1.0**	0.2	-7.2
2007	-9.1	-8.8	-8.2	-11.4	-3.2	-8.8
2008	-7.7	-8.8	-14.3	-9.5	-2.4	-8.1
2009	-11.8	-10.5	-11.9	**-15.6**	-1.8	-5.2
2010	-8.0	-10.6	-13.9	-7.7	-0.3	-10.9
2011	-13.9	-10.7	-12.8	-5.3	-2.0	-6.9
2012	-3.6	-6.8	**-5.7**	-9.8	-2.1	-8.0
2013	-7.9	-10.8	-13.2	-9.2	-1.8	-8.7
2014	-4.7	**-2.7**	-9.2	-10.4	-3.4	-9.1
2015	-6.1	-13.8	-6.6	-5.8	-2.1	-7.0
2016	-4.8	-6.9	-7.5	-6.9	**1.0**	-6.7

The highest and lowest temperatures for each month are marked in red and blue, respectively

The long-term thickness observations presented here are to some extent biased by the fact that it was impossible to gather observations on identical locations throughout the entire observation period. This is due to that (i) several of the sites where monitoring fjord ice started have been ice free in recent years, and (ii) the inner fjord is often only accessible by small boat, not by snowmobile. When accessing the fast ice from a small boat, the distance from the ice edge that can be reached

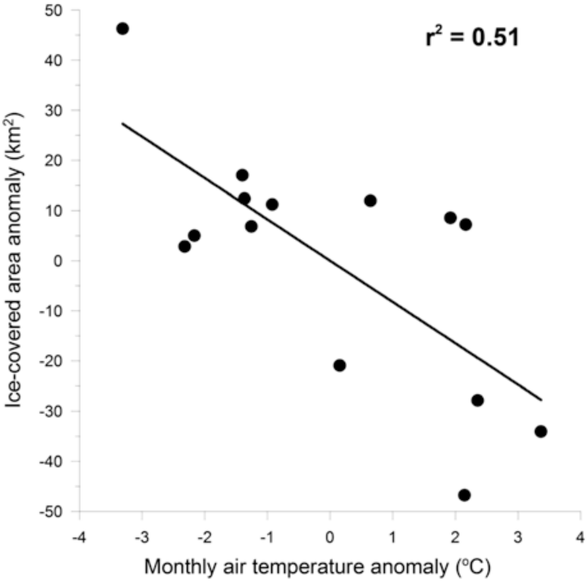

Fig. 4.7 Relationship between detrended monthly air temperature in Ny-Ålesund and sea-ice extent in Kongsfjorden during winter (January–March), 2003–2016

is rather limited. On the other hand, some locations where sea ice is present in recent years such as inner Raudvika and current glacier fronts did not exist as locations with sea ice in the early phase of the monitoring, since they were covered by glaciers.

Presence and properties of sea ice in polar waters are important for production and development of ice algal communities, but also for the later production by phytoplankton in the water column (Leu et al. 2015; Hegseth et al., Chap. 6). The presence of snow on top of sea ice affects both biomass and primary production rates of ice algae by blocking >90% of the light transmission through the ice (Grossi et al. 1987; Welch and Bergmann 1989; Ehn et al. 2011). Reduction of ice and snow thickness on fast ice in Kongsfjorden would likely increase production of ice algae during early spring, and may also shift the production season earlier in the year, as has been observed for other areas in the Arctic (Leu et al. 2015). However, the currently regularly observed thin snow cover will likely result in too much light and photoinhibition (Juhl and Krembs 2010; Campbell et al. 2015), and the concurrent reduction in sea ice in Kongsfjorden further limits the contribution of ice algae to the production in the fjord.

The pelagic spring bloom in Kongsfjorden typically starts in late April and lasts until mid-May, with total production in the range of 27–35 g C m^{-2}, as determined in 2002 by Hodal et al. (2012). At that time, the peak in production likely occurred in late April, in connection with ice break up. In later years (2002–2014), the bloom most often occurs in April, but may also occur later in May or early June (Hegseth et al., Chap. 6). The presence of sea ice, particularly with snow on it, affects the light climate experienced by phytoplankton during spring (Pavlov et al., Chap. 5). However, as pointed out by Hegseth and Tverberg (2013), the timing and magnitude of the spring bloom in Kongsfjorden seem to have little connection to sea ice or temperature during spring, but rather to winter convection, which brings up resting spores from the sediments needed for initiating the diatom bloom. Such blooms may also be intensified with the increased glacial run off in Kongsfjorden (Calleja et al. 2017). In warm years with late blooms (2007, 2008, 2014), the fjord had little sea ice and typically a pronounced thermocline. The late blooms were often dominated by *Phaeocystis pouchetii* (Hegseth and Tverberg 2013), with subsequent blooms of smaller phytoflagellates (Piwosz et al. 2009, 2015).

Sea ice also has influence on the benthos, because of reduction in radiation during early spring and also because of ice scouring in shallow regions. Hansneset, near Blomstrandhalvøya, experienced periods of sea ice before 2007, but generally not in 2007–2016, except for a short time in February 2011. Less ice scouring have caused an increase in abundance and biomass of macroalgae in shallow waters at this location, and the peak in biomass has moved upwards from a maximum at 5 m depth in 1996/98 to maximum at 2.5 m depth 15 years later (Hop et al. 2012; Bartsch et al. 2016). The depth extent of the macroalgal belt decreased by 2–5 m, which may be related to higher turbidity because of increased glacial run-off (Bartsch et al. 2016). Concurrently, the biomass and production of macrozoobenthos have increased in the upper sublittoral zone (Paar et al. 2016). However, the lack of ice and ice algae may have had a negative effect on soft-bottom benthos, which utilize ice algae in the vertical flux as seasonally concentrated food supply (McMahon et al. 2006; Kulinski et al. 2014). Changes in phytoplankton communities towards *Phaeocystis* and smaller flagellates, as seen in Kongsfjorden (Piwosz et al. 2009, 2015) typically leads to hither retention in the pelagic ecosystem and less export flux.

Some species at the upper trophic level have also been particularly influenced by changes in sea ice conditions in Kongsfjorden. Ringed seals (*Pusa hispida*) use snow that has accumulated on the lee side of glacial pieces in sea ice to make birth lairs (Lydersen et al. 2014). With less suitable ice habitat in Kongfjorden, the seal pups have become more vulnerable to predation by polar bears (*Ursus maritimus*), Arctic foxes (*Alopex lagopus*) and glaucous gulls (*Larus hyperboreus*), with resulting decline in reproductive success (Lydersen et al. 2014). During the years of little ice on fjords on the coast of West Spitsbergen, their reproduction was low to non-existent (Kovacs and Lydersen 2008).

Some of the seabird species in the Kongsfjorden area may have benefitted from less sea ice. For surface feeding seabirds, such as the black-legged kittiwake (*Rissa tridactyla*), less sea ice during spring results in larger foraging areas along the coast. With increased Atlantic influence, more prey species have become available for feeding and the population has increased in the years after 2003 (Vihtakari et al. 2018). Common eiders (*Somateria mollisima*) breed on the islands in inner Kongsfjorden, such as Lovénøyane. Less sea ice during spring has caused less access to these islands by one of their main predators, the Arctic fox, which has resulted in higher number of breeding birds (Hanssen et al. 2013).

4.6 Conclusions

Fast ice, and ice and snow thickness in Kongsfjorden have been monitored regularly for 14 years. This study is ongoing, and a major aim is to identify and quantify connections between the fast-ice evolution in Kongsfjorden and climate variability during the last decade. In particular, atmosphere and ocean-related drivers need to be reviewed. The oceanography is typically monitored during regular surveys in Kongsfjorden conducted by NPI and Institute of Oceanology (IOPAN) during summer and by UiT/UNIS during winter, but more detailed CTD-measurements in connection with fast ice in Kongsfjorden are clearly needed.

Further sea-ice monitoring should:

- Quantify the fast-ice mass balance in Kongsfjorden
- Generate a baseline for typical fast-ice evolution scenarios in Kongsfjorden
- Make comparisons of fast-ice coverage in Kongsfjorden and other Svalbard fjords
- Identify possible links between fast-ice mass-balance data and climate index parameters
- Provide background data for interdisciplinary studies

Observations of changes in fast-ice properties, especially when combined with similar observations from other locations, may provide a relatively inexpensive way to monitor changes in the oceans and the atmosphere. Sea-ice monitoring in Kongsfjorden is not only used for climate change research, it also contributes to past, ongoing and future process studies in many disciplines conducted by the international research bases at Ny-Ålesund. In the future, *in situ* measurements will be better complemented by satellite observations. New technology, such as remote sensing with higher resolution and more frequent data recording (e.g. with the new ESA Sentinel satellites), gives possibilities to develop more precise methods and tools to describe the sea-ice regime in Kongsfjorden.

Changes in sea−ice and hydrographic conditions observed in Kongsfjorden from 2003–2016 have altered the production regime from ice algae and early diatom blooms, towards later blooms of flagellates. The reduction in sea ice extent, ice thickness and duration of ice cover have reduced the suitable habitat for ice algae, and therefore their contribution to the total primary production in Kongsfjorden. The production regime for phytoplankton has also changed, as pointed out in Hegseth et al. (Chap. 6), although this is probably more related to changes in advection of water masses and increased run-off from glaciers. The benthic production on hard-bottom have increased in the shallow regions because of less ice scouring, but may have decreased for soft-bottom communities because of less vertical flux of ice algae and large diatoms. For upper trophic levels, reductions in fast ice have been negative for species that rely on sea ice for reproduction, particularly for ringed seals. On the other hand, less sea ice during spring has been beneficial for species that forage in open water, such as the black-legged kittiwake, and eiders breeding on islands in the inner part of Kongsfjorden. Thus, changes in the lower part of the food web have involved a combination of factors (ocean warming, advection of water masses, sea ice reduction, glacial run-off, changes in light regime), whereas effects of declining sea ice on the upper part of the food web have targeted particular species, negatively or positively.

Acknowledgements We are grateful to the station personnel of the Sverdrup station in Ny-Ålesund for conducting ice observation and fast-ice thickness measurements in Kongsfjorden. Fast-ice monitoring in Kongsfjorden is a part of Norwegian Polar Institute long-term monitoring programme.

In addition, the following recent projects contributed to sea-ice studies in Kongsfjorden:

Research Council of Norway no. 112853/720 (SpecRef), no. 151447 (AIO), no. 165112 (MariClim), no. 165064 and no. 178912 (Black Carbon), no. 195143 (Arctic-EO), no. 237906 (Centre for Integrated Remote Sensing and Forecasting for Arctic Operations (CIRFA)), and no. 184724, Variability of Albedo Using Unmanned Aerial Vehicles (VAUUAV), and Mapping sea ice (Fram Centre Flagship Fjord and Coast). We thank Oddveig Øien Ørvoll (Norwegian Polar Institute) for preparation of Svalbard and Kongsfjorden maps. The authors also wish to thank three anonymous reviewers for revisions and useful remarks that improved our manuscript, and Guest Editor Christian Wiencke for his constructive and helpful comments.

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Chapter 5
The Underwater Light Climate in Kongsfjorden and Its Ecological Implications

Alexey K. Pavlov, Eva Leu, Dieter Hanelt, Inka Bartsch, Ulf Karsten, Stephen R. Hudson, Jean-Charles Gallet, Finlo Cottier, Jonathan H. Cohen, Jørgen Berge, Geir Johnsen, Marion Maturilli, Piotr Kowalczuk, Sławomir Sagan, Justyna Meler, and Mats A. Granskog

Abstract Due to its Arctic location at 79°N, Kongsfjorden in Svalbard experiences strong seasonality in light climate, changing from polar night to midnight sun. Sea ice conditions and the optical properties of seawater further modify the amount and the spectral composition of solar radiation penetrating into the water column, thus defining the underwater light climate in Kongsfjorden. Light represents one of the major shaping factors for the entire marine ecosystem. A number of studies focusing on implications of the underwater light for marine organisms have been

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_5

conducted in Kongsfjorden, generating diverse datasets on seawater optical properties, scattered over time and space. This review synthesizes the fragmentary information available from the literature as well as presenting some unpublished data, and discusses the underwater light climate and its main controlling factors in Kongsfjorden. Furthermore, we provide a short synopsis about the relevance of light for different components of an Arctic marine ecosystem, exemplified by studies carried out in Kongsfjorden. Due to its year-round accessibility and its high-Arctic location, Kongsfjorden has become a prime fjord for studying how the strong seasonal changes in light availability, ranging from polar night to midnight sun, affect marine life with respect to primary production, behavioural aspects and synchronization of growth and reproduction.

Keywords Arctic · Svalbard · PAR · UVR · Optical properties · Marine ecosystem

5.1 Introduction

Located in the Arctic at 79°N on the west coast of Svalbard Archipelago, Kongsfjorden is influenced by marine- and land-terminating glaciers (Fig. 5.1). Due to the proximity of the West Spitsbergen Current (WSC), warm and saline Atlantic Water is regularly advected into the fjord throughout the year (Cottier et al. 2007). Furthermore, little landfast sea–ice has been observed in Kongsfjorden during the past decade (Pavlova et al., Chap. 4), which is largely associated with an increase of northward heat flux in the WSC and a consequent warming of West Spitsbergen fjords (Cottier et al. 2007; Spielhagen et al. 2011; Pavlov et al. 2013). This change has affected the underwater light climate and has many biological and ecological implications, such as, increasing exposure of pelagic microalgae to high irradiances

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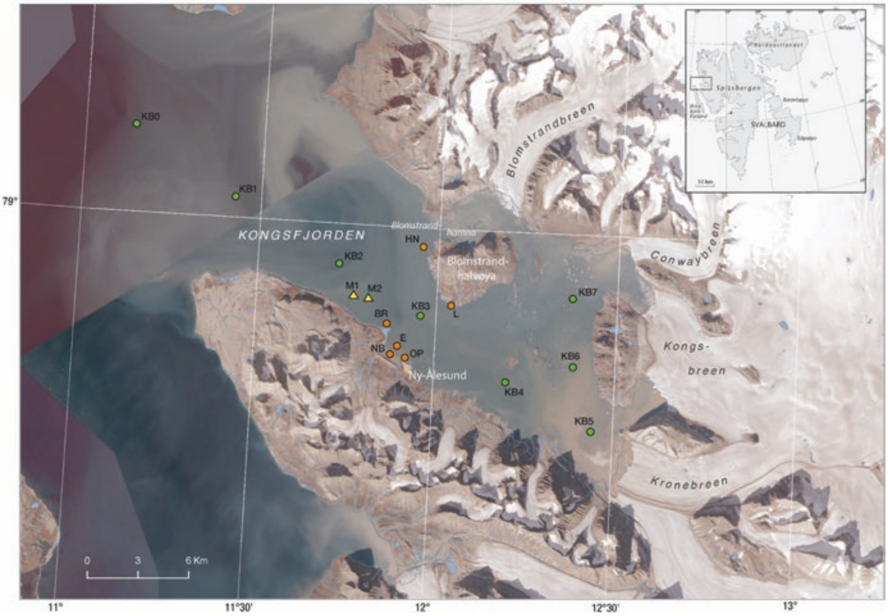

Fig. 5.1 Kongsfjorden, Svalbard. Location of common observation sites: Hansneset (HN), Nansen Bay (NB), Old pier (OP, which is the closest location to the Kings Bay Marine Laboratory), Brandal (BR), London (L), EPOCA mesocosm experiment (E), mooring stations M1 and M2 (2010–present) as well as oceanographic stations KB0 to KB7. Satellite image is a composite of two Landsat 8 satellite scenes taken on 19 and 30 August 2013. (Credits: Norwegian Polar Institute and USGS)

(Leu et al. 2016; Wiencke and Hop 2016) and shifts of kelps to shallower depths (Bartsch et al. 2016).

The strong seasonality of the light climate in Kongsfjorden, alternating from polar night to midnight sun, is characteristic of Arctic marine environments. In addition, the variability of cloud cover (Maturilli et al., Chap. 2) and sea ice cover with snow (Pavlova et al., Chap. 4) at different time scales are important factors defining the amount and spectral composition of light reaching the upper water column. As a water body, Kongsfjorden is also a dynamic system, characterized by an estuarine circulation, water mass exchange with the adjacent West Spitsbergen shelf, processes of sea ice formation and melting, input of local run-off and glacial meltwater introducing inorganic and organic matter into the system (Svendsen et al. 2002), and phytoplankton blooms at diverse times and locations. Together, these factors result in a complex underwater light climate with high variability in time and space (e.g. Hanelt et al. 2001, 2004; Hegseth et al., Chap. 6).

While Kongsfjorden is the site of considerable research efforts (e.g. Wiencke and Hop 2016), one challenge of particular relevance for studies of the underwater light climate is a lack of coordination and standardization of methods. Despite the wealth of multidisciplinary data from this Arctic fjord system, there is a need for both targeted and comprehensive studies addressing the optical properties and the underwater light climate in Kongsfjorden in a systematic way. So far, most of the available optical data are by-products from biologically motivated studies (e.g. Hanelt et al. 2001, 2004; Wiencke et al. 2004, 2006; Leu 2006; Leu et al. 2006a, b, 2016; Volent et al. 2007; Sakshaug et al. 2009; Pavlov et al. 2014; Cohen et al. 2015; Berge et al. 2015a; Taskjelle et al. 2016) at various sites in this fjord (Fig. 5.1).

This review compiles the fragmentary information available (both published and unpublished) on underwater irradiance, absorption, scattering and diffuse attenuation coefficients, and identifies the most important steering factors for seasonal and long-term variability. Moreover, it provides a brief overview as to the relevance of Arctic underwater light conditions for marine organisms and the marine ecosystem in Kongsfjorden. It can serve as a source of useful background information for future studies of processes that influence or are influenced by the underwater light climate in Kongsfjorden and other similar high-latitude marine environments.

5.2 The Underwater Light Climate in Kongsfjorden

5.2.1 Incoming Irradiance

Incoming irradiance (i.e. that reaching the bottom of the atmosphere) represents the boundary condition for the underwater light climate. In addition to strong seasonality, there is a large day-to-day variability in incoming light throughout the season as seen from daily averages of incoming downwelling irradiance in the photosynthetically active radiation (PAR) range. Mean daily irradiance in the PAR range (E_d(PAR)) values during the course of 2012 (Fig. 5.2) is based on measurements of the broadband downwelling planar irradiance (measured with CM11 and CMP21 pyranometers, Kipp & Zonen) over the wavelength range 370–695 nm, which is close to conventional PAR range of 400–700 nm (Maturilli et al., Chap. 2). Monthly means of E_d(PAR) for the period 1993–2013 are presented in Maturilli et al. (Chap. 2), providing insights on inter-annual variability of incoming PAR.

Daily averaged E_d(PAR) values range from <5–10 μmol m^{-2} s^{-1} in October–February, to 720–740 μmol m^{-2} s^{-1} in June (Fig. 5.2). Based on episodic measurements taken between May and July (Table 5.1), maximum E_d(PAR) measured above the water surface is usually below 1300 μmol m^{-2} s^{-1}. During the period of midnight sun, E_d(PAR) values in air during night range from 100 to 300 μmol m^{-2} s^{-1} in May (Leu et al. 2016; Table 5.1).

Daily cycles of E_d(PAR) observed at Baseline Surface Radiation Network (BSRN) at the AWIPEV station in Ny-Ålesund (for details, see Maturilli et al., Chap. 2) under clear sky and overcast conditions demonstrate a strong influ-

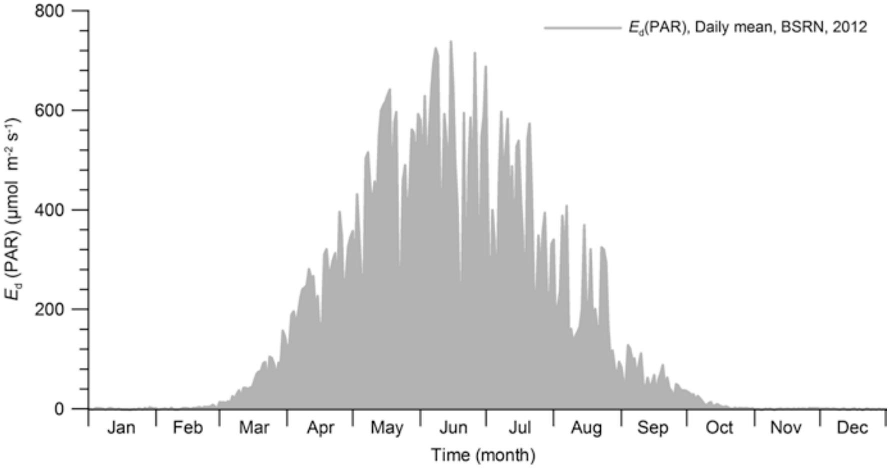

Fig. 5.2 Mean daily irradiance in the PAR range (E_d(PAR)) values during the course of 2012 (data from Maturilli et al., Chap. 2). E_d(PAR) values in the range 370–695 nm were observed by a Baseline Surface Radiation Network (BSRN) pyranometer at the AWIPEV station, and converted to µmol m^{-2} s^{-1} with a conversion factor 4.6. (Morel and Smith 1974; McCree 1981)

ence of clouds (Fig. 5.3a). On a cloudy day, E_d(PAR) values at noon are only about half of those on a day with clear skies. The corresponding incoming downwelling spectral irradiance ($E_d(\lambda)$) was measured with TriOS Ramses ACC-VIS radiometers (TriOS Mess- and Datentechnik GmbH, Rastede, Germany) at the Sverdrup station on the same days (Fig. 5.3b; for methodological details, see Pedersen et al. 2015). In this case, the cloud cover acts as a neutral density filter over the PAR wavelength range, not significantly changing the spectral composition of light (Fig. 5.3b). However, cloud cover does significantly reduce the fraction of incoming solar energy that is outside the PAR wavelengths.

A detailed overview over longer time series of incoming downwelling ultraviolet radiation, E_d(UV) can be found in Maturilli et al. (chap. 2). Data from episodic measurements of incoming E_d(PAR) and E_d(UV) available in the literature are presented in Tables 5.1, 5.2 and 5.3.

5.2.2 *Underwater Irradiance in the PAR Range*

Numerous light measurements have been carried out in Kongsfjorden over the past decades, employing a wide variety of methods and instruments. The following sections summarize the available information, and present also hitherto unpublished material.

Table 5.1 Irradiances of photosynthetic active radiation (E_d(PAR,Z)) measured in Kongsfjorden

Period (month/ year)	Location	Sensor type	K_d(PAR) (m^{-1})	10% depth (m)	1% depth (m)	Daily maximum (µmol m^{-2} s^{-1} if not otherwise specified)	During night (µmol m^{-2} s^{-1} if not otherwise specified)	References
			E_d(PAR,Z) in water			**E_d(PAR) in air**		
Aug–Sep 1995	Nansen Bay	LI-COR LI-192			20–25	1100		Hanelt (1998) and Hanelt et al. (1997)
May–Jul 1997	Old pier	LI-COR LI-190, 192	0.62		7			Wiencke et al. (2000)
				4	*7*			
Jun–Jul 1997	Old pier	LI-COR LI-190, 192	0.19–0.74		6.2–24.2	<1300		Bischof et al. (1998)
				3–12	*6–24*			
Mar–Oct 1996–1998	Old pier	LI-COR LI-190, 192	0.10–0.80	*3–19*	*6–38*			Hanelt et al. (2001)
May–Jul 1998	Kongsfjorden	LI-COR LI-190, 192	0.23	*10*	*20*	1130–1250		Bischof et al. (1999)
May–Jun 2004	Kongsfjorden	LI-COR LI-190, 193 spherical	0.10–0.20	≈20	30–50	1200	100–300	Leu (2006)
				12–23	*23–46*			
May–Jun 2004	Kongsfjorden	LI-COR LI-190, 193 spherical				700–1200		Leu et al. (2006a)
Jun 2004	Between old and new pier	LI-COR LI-190				1200–1400	100–200	Wiencke et al. (2006)
May–Jul 2006	Old pier 500 m east	LI-COR LI-190				1249		Fricke et al. (2001)
May 2008	Station KB3	LI-COR 190, 193	0.09–0.12	*18–24*	*37–48*	894 at noon, cloudless	157 at midnight	Leu, unpubl.

Jun 2008	Brandal	LI-COR LI-190, 192	0.09–0.19	*12–26*	*24–51*			Woelfel et al. (2014)
	Nansen Bay	LI-COR LI-190, 192	0.20–0.21	*11.5*	*22–23*			Woelfel et al. (2014)
	London	LI-COR LI-190, 192	0.19–0.27	*9–26*	*17–24*			Woelfel et al. (2014)
Jun–Jul 2010	EPOCA experiment	LI-COR LI-192	0.30–0.40	*6–8*	*12–15*	700–1500	>150	Schulz et al. (2013)
Jan 2014	Nansen Bay	IMO-PAR				0.000015		Cohen et al. (2015)
Jan 2015	Nansen Bay	QE Pro				0.000013		Cohen et al. (2015)
			E_d(PAR) in sea ice					
Mar 2002	Kongsfjorden	FieldSpec spectrophotometer	*6.14*					60 cm ice with 15 cm snow; Winther et al. (2004)
Apr 2010	Old pier	Ramses spectrophotometer	*1.01–1.74*					15 cm without snow; Taskjelle et al. (2016)

Data are taken from the cited references; new data were calculated from K_d(PAR) values provided in the original references or from raw data (shown in italics). Used instruments: LI-COR 190 cosine corrected flat head air or LI-COR 192 underwater sensors, LI-COR 193 spherical underwater sensor (LI-COR Biosciences, Lincoln, Nebraska, USA), the meteorological sensors of the BSRN station (Baseline Surface Radiation Network), TriOS Ramses ACC-VIS radiometers (TriOS Mess- and Datentechnik GmbH, Rastede, Germany), FieldSpec spectroradiometer (Analytical Spectral Devices Inc., USA), QE Pro spectrometer (Ocean Optics, Dunedin, Florida, USA), IMO-PAR (In-situ Marine Optics, Perth, Western Australia). If no specific location was given in the reference, the site is listed as “Kongsfjorden”. If Nansen Bay has been mentioned in the references, it is considered to be the closer region around Ny-Ålesund, including the northwest and southeast parts of the fjord close to Ny-Ålesund. For other locations, see Fig. 5.1. In addition to water column information, K_d(PAR) values for sea ice are also included where available. Keep in mind potential differences in K_d(PAR) values estimated based on PAR measurements from cosine (LI-COR LI-192) and spherical (LI-COR LI-193) sensors

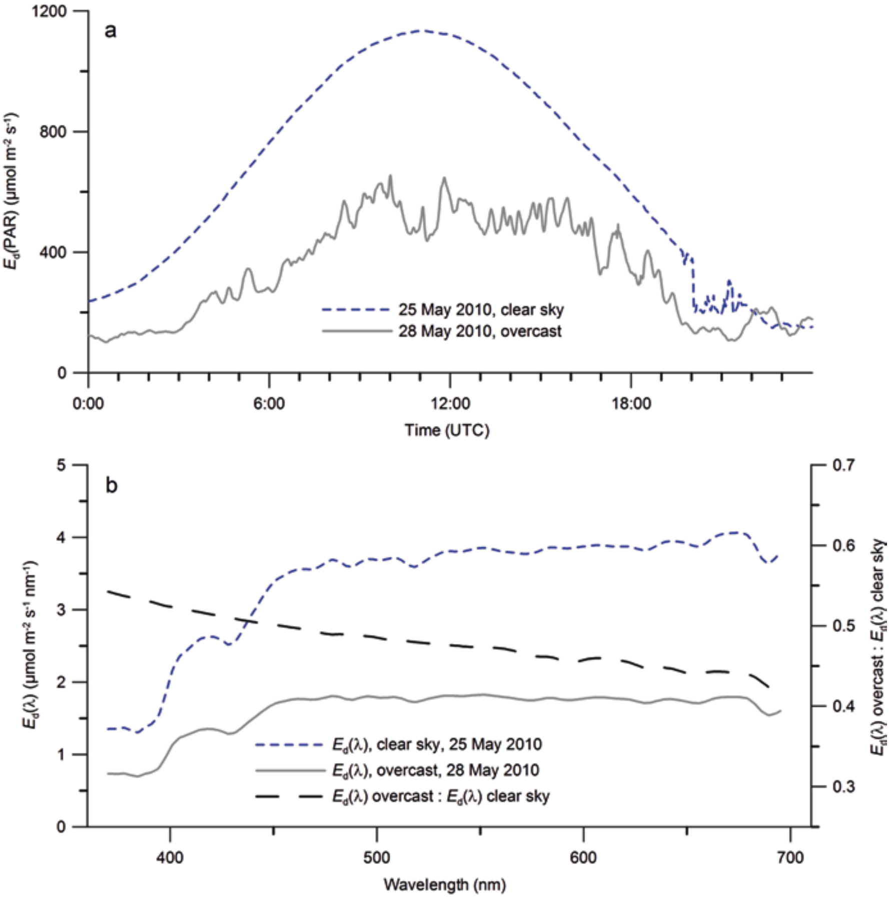

Fig. 5.3 (**a**) Examples of incident irradiance in the PAR range (E_d (PAR)) daily cycles in Ny-Ålesund on a clear day (25 May 2010) and an overcast day (28 May 2010). Data were obtained from Baseline Surface Radiation Network (BSRN) pyranometer measurements at the AWIPEV station and converted from W m^{-2} to µmol m^{-2} s^{-1} by using a conversion factor of 4.6 (Morel and Smith 1974; McCree 1981); (**b**) Examples of incident downwelling spectral irradiance, $E_d(\lambda)$ in the range 370–695 nm at noon on the same dates, as well as their ratio. Data were obtained with TriOS Ramses ACC-VIS radiometers (TriOS Mess- and Datentechnik GmbH, Rastede, Germany) at Sverdrup station

5.2.2.1 Point and Episodic Measurements of Underwater Irradiance in the PAR Range

During summer, attenuation coefficients in water tend to be higher than during clear water conditions in spring (Hanelt et al. 2001) due to the high concentration of optically active substances (OAS), such as inorganic particles and phytoplankton. The diffuse attenuation coefficient of downwelling irradiance in the PAR range (K_d(PAR)), estimated from irradiance measurements with cosine (flat) sensors, ranged between

Table 5.2 Irradiances of UVA radiation (E_d(UVA,Z)) measured in Kongsfjorden

Period (month/year)	Location	Sensor type	K_d(UVA) (m^{-1})	10% depth (m)	1% depth (m)	UV (280–400 nm) ($W m^{-2}$ if not otherwise specified)	UVA ($W m^{-2}$ if not otherwise specified)	References
			E_d(UVA,Z) in water			**E_d(UVA) in air**		
Aug–Sep 1995	Nansen Bay	BSRN-station				14		Hanelt (1998) and Hanelt et al. (1997)
		Gröbel UV RM21			4.0		9–13	
May–Jul 1997	Old pier	32 channel UV spectrometer	0.73	*3.0*	5.1 (320 nm) *6.0*			Wiencke et al. (2000)
Jun–Jul 1997	Old pier	Gröbel UV RM21/BSRN					19	Bischof et al. (1998)
Mar–Oct 1996–1998	NDSC-building	BSRN-station				300–370 nm: 16.8 Daily averages: 5.5–6.2		Hanelt et al. (2001)
27 May 1998	Nansen Bay	Kruse UW spectrophotometer	1.1–1.5	*1.5–2.1*	*3–4*			Hanelt et al. (2001)
7 July 1998	Hansneset	Kruse UW spectrophotometer	0.4–0.8	*2.9–5.8*	*6–12*			Hanelt et al. (2001)
May–Jul 1998	Kongsfjorden	Gröbel UV RM21					16.8–19.0	Bischof et al. (1999)
May–Jun 2004	Kongsfjorden	Ramses spectrophotometer		<15	<28		15–30.3	Leu (2006)
				5–15	20–29			
May–Jun 2004	Kongsfjorden						Daily E_d(UVA): 900–1500 kJ m^{-2}	Leu et al. (2006b)

(continued)

Table 5.2 (continued)

Period (month/ year)	Location	Sensor type	K_d(UVA) (m^{-1})	10% depth (m)	1% depth (m)	UV (280–400 nm) (W m^{-2} if not otherwise specified)	UVA (W m^{-2} if not otherwise specified)	References
1 Jul 2001	Brandal	Kruse UW spectrophotometer 320–400 nm	0–1.5 m: 0.95–1.98 1.5–5.4 m: 0.44–0.71	*1–2* *3–5*	*2–5* *6–10*		5.7	Hanelt, unpubl.
			E_d(UVA) in sea ice					
Mar 2002	Kongsfjorden	FieldSpec spectroradiometer (>350 nm); NILU-UV irradiance meter (<350 nm)	*7.36*					60 cm ice with 15 cm snow; Winther et al. (2004)

Data are taken from the cited references; new data were calculated from K_d(UVA) values provided in the original references or from raw data (shown in *italics*). Used instruments are: the meteorological sensors of the BSRN station (Baseline Surface Radiation Network), the RM 21-UVA sensor of Gröbel (Germany), the AWI 32 channel UV underwater-spectrometer of ISITEC (Bremerhaven, Germany), the handheld Kruse underwater spectrophotometer (Kruse, Bremerhaven, Germany), TriOS Ramses ACC-VIS radiometers (TriOS Mess- and Datentechnik GmbH, Rastede, Germany), and FieldSpec spectroradiometer (Analytical Spectral Devices Inc., Boulder, USA). If no specific location was given in the reference, the site is listed as “Kongsfjorden”. If Nansen Bay has been mentioned in the references, it is considered to be the closer region around Ny-Ålesund, including the northwest and southeast parts of the fjord close to Ny-Ålesund. For other locations, see Fig. 5.1. In addition to water column information, K_d(UVA) values for sea ice are also included where available

Table 5.3 As in Table 5.2 but for UVB radiation

Period (month/ year)	Location	Sensor type	K_d(UVB) (m^{-1})	10% depth (m)	1% depth (m)	UVB ($W\ m^{-2}$)	References
			E_d(UVB,Z) in water			**E_d(UVB) in air**	
Aug–Sep 1995	Nansen Bay	Gröbel UV RM21		From 0.5 m no UVB measureable		0.14	Hanelt et al. (1997)
May–Jul 1997	Old pier	32 channel UV spectroradiometer	0.9		4.5 (305 nm)		Wiencke et al. (2000)
				3	*5*		
Jun–Jul 1997	Old pier	32 channel UV spectroradiometer	0.51–1.34	Max. transmittance <10 m			Bischof et al. (1998)
				2–5	*3–9*		
Mar–Oct 1996–98		32 channel UV spectroradiometer	0.35–0.75	*3–7*	*6–13*	Max. daily E_d(UVB) 24 $kJ\ m^{-2}$	Hanelt et al. (2001)
May–Aug 1998	Nansen Bay	32 channel UV spectroradiometer				Max. daily E_d(UVB) 50 $kJ\ m^{-2}$	Bischof et al. (2002)
Jun–Jul 1997	Nansen Bay	32 channel UV spectroradiometer			2.5–8.5	0.8–1.2	Karsten et al. (1999)
May–Jul 1998	Kongsfjorden	32 channel UV spectroradiometer				1.0–1.2	Bischof et al. (1999)
May–Jun 2004	Kongsfjorden	Ramses spectrophotometer		<7	<14	0.9–0.98	Leu (2006)
			For 310 nm: 0.33–0.49	5–7	12–14.5		
				5–7	*9–14*		

(continued)

Table 5.3 (continued)

Period (month/ year)	Location	Sensor type	K_d(UVB) (m^{-1})	10% depth (m)	1% depth (m)	UVB ($W\ m^{-2}$)	References
May–Jun 2004	Kongsfjorden	Ramsesspectrophotometer				Daily dose 25–48 kJ m^{-2}	Leu et al. (2006b)
Jun 2004	Between old and new pier	ELUV dosimeter	0.67–1.28		3.6–6.9	0.018–0.045 (erythemal)	Wiencke et al. (2006)
May–Jul 2006	Old pier 500 m east mooring	Ramses spectrophotometer	At 0.5 m: 0.18			0.45	Fricke et al. (2001)
12 Jun–4 Jul 2001	Nansen Bay	UV-DNA dosimeter(cyclobutane-pyrimidine dimers, CPD)		CPD 4–8 m detectable			van de Poll et al. (2002)
			E_d(UVB) in sea ice				
Mar 2002	Kongsfjorden	NILU-UV irradiance meter	*9.21*				60 cm ice with 15 cm snow; Winther et al. (2004)

Used instruments are: the meteorological sensors of the BSRN station (Baseline Surface Radiation Network), the RM 21-UV sensor of Gröbel (RM-21, Gröbel UV-Elektronik, Germany), the ELUV electric light dosimeter (AWI, Germany), the home-made dosimeters using calf thymus DNA, 32-channel single-photon counting UV spectroradiometer (Isitec, Bremerhaven, Germany), and NILU-UV Irradiance Meter (Norwegian Institute for Air Research, Kjeller, Norway). In addition to water column information, K_d(UVB) values for sea ice are also included where available

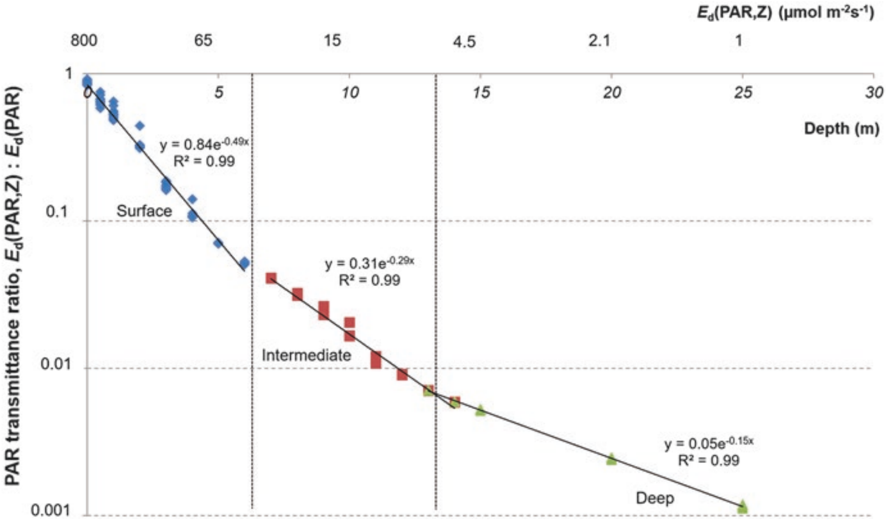

Fig. 5.4 Example of differential water column stratification in August 2012 at a coastal site off Hansneset influenced by freshwater run-off causing an apparent 3-layer structure (named here as Surface, Intermediate, Deep) with regards to attenuation of E_d(PAR,Z) with depth. (Source: D. Hanelt, unpubl.)

0.09 m^{-1} for clear water conditions and 0.80 m^{-1} in turbid waters (Table 5.1). Inflow of turbid glacier water or sediment-loaded meltwater streams can cause a stratification in water turbidity (Hanelt et al. 2001), which may result in several layers with different light attenuation, as observed in August 2012 at Hansneset (K_d(PAR) = 0.49 m^{-1} for 0–6 m depth, K_d(PAR) = 0.29 m^{-1} for 6–13.5 m depth, and K_d(PAR) = 0.15 m^{-1} for 13.5–25 m depth (Fig. 5.4; D. Hanelt, unpubl.). Based on literature data, the 10% depth transmittance of E_d(PAR) ranged between 3 and 26 m and the 1% depth ranged between 6 and 51 m (Table 5.1), with highest values at >50 m depth in waters not significantly influenced by meltwater from glaciers (Woelfel et al. 2014).

5.2.2.2 Temporal Variability of Underwater Irradiance in the PAR Range

Point measurements, such as those presented in Table 5.1 and Fig. 5.4, do not include information on diurnal changes, and reflect poorly seasonal and inter-annual variability and change of the light climate. In recent years, light loggers have been deployed in Kongsfjorden as part of various coastal benthic studies. Additionally, cosine corrected PAR sensors have been mounted on moorings deployed in the pelagic zone of Kongsfjorden since autumn 2009 (M1 and M2 locations, Fig. 5.1), providing a near continuous record of underwater irradiance in the PAR range E_d(PAR,Z). There, the sensor has been deployed at various depths (Z), from a minimum depth of 27 m in 2010–2011 to a maximum of 43 m in 2012–13 (Fig. 5.5b, c; F. Cottier, unpubl.). The E_d(PAR,Z) data were part of a multi-parameter suite of measurements collected from the moorings that have been used to support

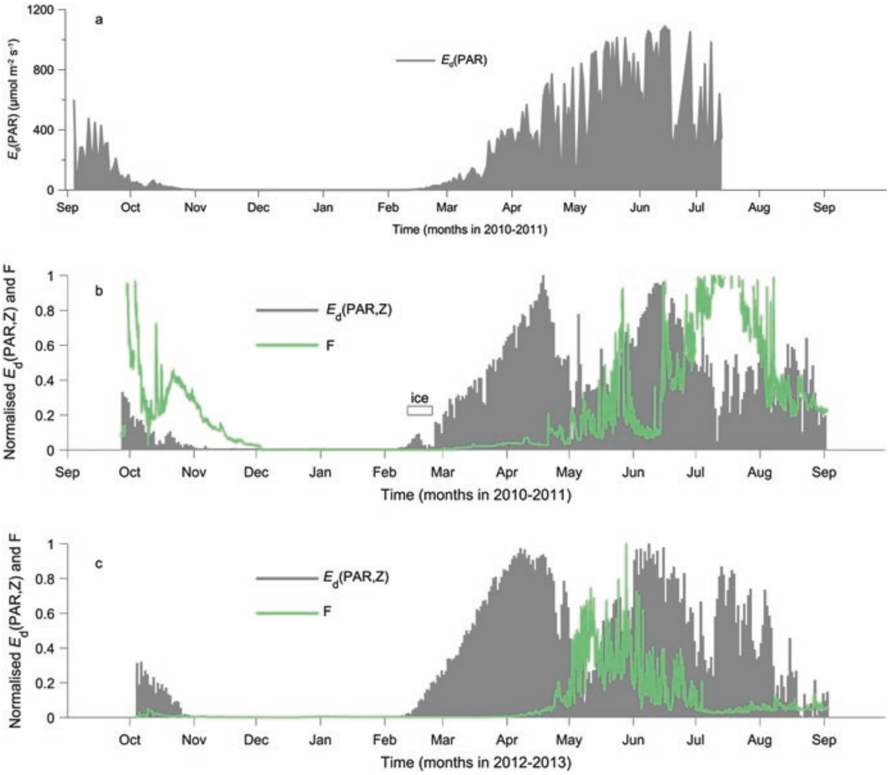

Fig. 5.5 (**a**) Seasonal time series of incident downwelling irradiance, E_d(PAR) at noon in 2010–2011; Data was obtained with TriOS Ramses ACC-VIS radiometers (TriOS Mess- and Datentechnik GmbH, Rastede, Germany) at Sverdrup station. (**b**, **c**) Seasonal measurements of normalized mean daily irradiance, E_d(PAR,Z) (grey) and fluorescence, F (green) at two pelagic mooring sites in 2010–11 (b) and 2012–13 (**c**), respectively (M1 and M2; see Fig. 5.1). Moorings were equipped with Satlantic PAR sensors and Seapoint Chlorophyll fluorometers in addition to standard temperature and salinity sensors and current meter. Due to the extended period of deployment of both sensors and the problems associated with fouling of sensors and their calibration, the data were normalized to each year's maximum value. The occurrence of sea ice (shown as white rectangle) above the mooring was detected using acoustic Doppler current profiler (ADCP) data with the method of Hyatt et al. (2008)

oceanographic and ecological studies in Kongsfjorden since 2002. In addition, an underwater E_d(PAR,Z) time series has been initiated close to Ny-Ålesund, to characterize the light climate of the coastal zone, within the COSYNA measuring network with online information available since autumn 2016 (https://www.awi.de/en/expedition/observatories/water-cosyna.html).

Although in the atmosphere the highest E_d(PAR) at the terrestrial BSRN station is reached in mid-summer (Sect. 5.2.1; Kupfer et al. 2006; Maturilli et al. 2015, Chap. 2), the situation appears more complex underwater. The recent near-shore (Bartsch et al. 2016) and pelagic long-term measurements (Fig. 5.5b, c), show that the highest underwater E_d(PAR,Z) in the years 2011 and 2013 occurred in mid-March to mid-April (neither site was ice-covered), followed by a temporary reduction of E_d(PAR,Z) by >50% in May, and then another maximum in June, slightly lower than in March–April. The pattern is consistent between the 2 years and the different locations (coastal and pelagic), although the second peak in June was more pronounced at the pelagic site, compared to the coastal site (Bartsch et al. 2016). Based on measurements at Sverdrup station, the reduction in underwater E_d(PAR,Z) in May in 2011 is not coincident with a decrease in incoming E_d(PAR) (Fig. 5.5a; J.-C. Gallet, unpubl.). The transient decrease of underwater E_d(PAR,Z) in May is linked to phytoplankton blooms indicated by elevated fluorescence values (Fig. 5.5b, c), which is a typical timing for spring phytoplankton blooms in Kongsfjorden (Hegseth et al., Chap. 6). Lower values and an increasing variability during the summer months (from July onwards) may be caused by two factors: biofouling and meltwater inflow from the marine-terminating tidewater glaciers, leading to strongly variable and rather turbid water conditions from July through September (Zajaczkowski and Legezynska 2001). Biofouling build-up on the sensors during long-term deployment obviously leads to increasingly greater underestimates of the available light. Thus, such time series provide valuable information on seasonal dynamics, whereas absolute values have to be treated with caution.

Besides the pronounced seasonal variability of underwater E_d(PAR,Z), considerable short-term (day-to-day) variation is also apparent throughout the year (Fig. 5.5), owing to changes in both cloud cover and the optical properties of seawater. Underwater diurnal cycles of E_d(PAR,Z) at shallow sites in Kongsfjorden were recently described in details by Sevilgen et al. (2014) and Leu et al. (2016). The spectral composition of irradiance also changes, depending on both solar angle and cloud cover. During night, however, at the lowest solar elevations, the differences between clear sky and cloudy conditions become subtle (Leu et al. 2016). In stands of macroalgae along rocky coasts, an additional variation of irradiance is caused by the algae, as shown by diurnal E_d(PAR,Z) along a depth profile, measured both above and below the kelp canopy (I. Bartsch, unpubl.). Dense kelp beds at 2.5 and 5 m depth (Bartsch et al. 2016) only allowed a low transmission of light, varying between 3% and 29% depending on time of the day, turbidity, and wave exposure and currents, mechanically moving kelp forests.

While the incoming surface radiation at noon in May was approximately 5 times higher than at midnight, irrespective of clear or overcast conditions (Fig. 5.3a), the underwater day–night variation also depends on the content and properties of OAS, mainly non-algal matter delivered along with the glacial run-off, which often experiences diurnal variations in Svalbard during summer (e.g. Hodgkins 2001). At coastal sites (Hansneset) in the beginning of July 2012, the mean underwater E_d(PAR,Z) values at noon were 10–13 times higher than at midnight, but only 5–8 times higher at the end of July. This non-linear response pattern was likely caused by an increase of turbidity due to elevated concentration of non-algal matter during times of glacial melt, as irradiances steadily declined in July 2012 (Bartsch et al. 2016). The two contrasting situations are represented in Fig. 5.6a, b. Because turbidity normally increases even more during August and September (e.g. Paar et al. 2016), the day–night variation presumably drops even further. As to absolute

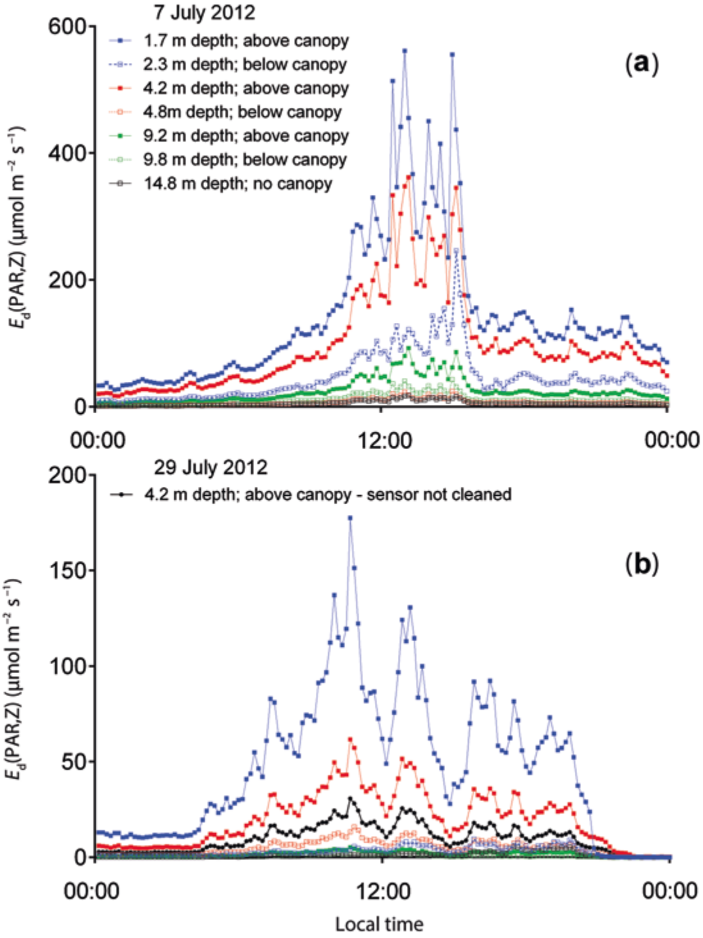

Fig. 5.6 Diurnal variation of irradiance in the PAR range (E_d(PAR,Z)) (10 min intervals) measured at several depths above and below the kelp forest off Hansneset during a day (7 July) with relatively clear waters (**a**) and a day (29 July) with more turbid waters (**b**) in 2012. Two irradiance loggers (Odyssey Dataflow Systems, Christchurch, New Zealand) calibrated against a cosine corrected underwater quantum sensor (LI-192, LI-COR Biosciences, Lincoln, Nebraska, USA) were mounted on each of four vertical racks which were fixed at the seafloor at 2.5, 5, 10 and 15 m depth (Bartsch et al. 2016). One logger was installed below the kelp canopy, approx. 20 cm (±10 cm) above the seafloor representing the "below canopy" situation, and another logger was mounted 90 cm (±10 cm) above the first logger, representing the "above canopy" situation. The diurnal variations in irradiance were possibly related to variable cloud cover but also influenced by tides; correlation to these factors was not achievable. Cleaning of the sensors surface took place approximately every 10 days except for the logger "4.2 m above canopy – sensor not cleaned" (black line, lower graph), which shows the considerable reduction in irradiance through sedimentation or fouling taking place within 3 weeks. Note the scale difference of the Y-axis between (a) and (b). (I. Bartsch, unpubl.)

values, E_d(PAR,Z) values at midnight in July at coastal sites (Hansneset) do not exceed 2.5 µmol m^{-2} s^{-1} at 15 m depth (Fig. 5.6).

Time series data presented in this section reflect the strong variability of E_d(PAR,Z) in a natural system, and underline the importance of these types of measurements as providers of realistic *in situ* data for estimates of primary production, ecological interpretation and for monitoring the potential "darkening" of Kongsfjorden, an increase in light attenuation observed in other Sub-Arctic and Arctic coastal waters as a consequence of increased land run-off due to melting of glaciers (Aksnes et al. 2009).

5.2.3 Underwater Irradiance in the UV Range

Measurements of UVA (320–400 nm) and UVB (280–320 nm) radiation are summarized in Tables 5.2 and 5.3. Some of the references in tables only mention the available K_d(UVA) and K_d(UVB) values, whereas others provide corresponding UV penetration depths.

UV radiation is readily attenuated by snow and ice or absorbed in the upper water layer, especially during summer when relatively high concentrations of coloured or chromophoric dissolved organic matter (CDOM) and particulate matter are present. During the main productive period in spring, however, the 1% depth for E_d(UVA,Z) was between 2 and 29 m, and for E_d(UVB,Z) between 10 and 15 m on sunny days (Leu 2006). Diurnal measurements of E_d(UVB,Z) and E_d(UVA,Z) at 0.5 and 8 m depth, obtained between 29 April and 1 May 2008 close to Ny-Ålesund, showed maximum values for E_d(UVA,Z) at these two depths of 9 and 3.5 W m^{-2}, respectively, and 0.27 and 0.03 W m^{-2} for E_d(UVB,Z) (Fig. 5.4 in Leu et al. 2016). The E_d(UVA) in air was generally in the range of 9–19 W m^{-2}, with values up to 30 W m^{-2} reported by Leu (2006) during late spring 2004. These higher values might partly be attributed to a wider wavelength range of the sensor used (290–400 nm), as opposed to the instruments at the meteorological BSRN station (300–370 nm). Values of K_d(UVA) are higher than K_d(PAR), and range from 0.73 up to 1.5 m^{-1} in the Nansen Bay, resulting in a 10% depth of E_d(UVA,Z) at coastal locations between 2 and 6 m depth, and a 1% depth between 3 and 12 m. Diurnal measurements in May 2008 confirmed that UVB absorption was stronger than UVA absorption between 0.5 and 8 m depth (Fig. 5.4 in Leu et al. 2016).

5.2.4 Light Climate During Polar Night

Knowledge about Arctic marine biological activities during polar night is very limited (Berge et al. 2015b) and only few studies have focused on underwater light climate (Berge et al. 2015a; Cohen et al. 2015). Although light levels during the polar night are not extreme *per se* in that they do resemble night light levels at lower latitudes, they remain constant for prolonged periods during winter. Thus, it is not the low light levels in itself that affect organisms during the polar night, but the fact that the low light levels do not change (Berge et al. 2015b). Despite almost constant low atmospheric illumination for extended periods, light during polar night might still play a role as environmental cue for zooplankton species, as demonstrated from *in situ* observations and behavioural experimental studies in Kongsfjorden (Båtnes et al. 2015; Last et al. 2016). For the end of January, Cohen et al. (2015) reported incoming E_d(PAR) levels of 1.0–$1.5{\cdot}10^{-5}$ µmol m^{-2} s^{-1} over the day–night cycle, with a spectral maximum around 455 nm at solar noon. Further, modelling of the underwater light field in Kongsfjorden demonstrated a shift in wavelength maximum of transmitted light towards longer wavelengths, e.g. 465 nm at 10 m and 485 nm at 30 m (Cohen et al. 2015).

5.2.5 Attenuation of Light by Snow and Sea Ice in Kongsfjorden

When present, snow and sea ice strongly attenuate solar radiation, limiting its transmission into Kongsfjorden waters (Hamre et al. 2004; Winther et al. 2004; Taskjelle et al. 2016). Snow is an effective scattering medium, with low absorption in the visible spectrum, giving it its bright white appearance. While the absorption properties of sea ice and water are similar, sea ice causes much more scattering of light than liquid seawater (e.g. Hamre et al. 2004; Johnsen et al. 2009) due to air and brine inclusions. Data from Kongsfjorden show that 60 cm of bare sea–ice attenuates E_d(PAR) by about 80% (Winther et al. 2004). Snow-covered sea–ice typically transmits less than 1% of E_d(PAR), and even less E_d(UV) (Winther et al. 2004). The effective attenuation coefficients for E_d(PAR) and E_d(UV) of 60 cm of sea ice with 15 cm of snow are nearly an order of magnitude higher than those of the water column (Tables 5.1, 5.2 and 5.3). Thus, the extent and evolution of the sea–ice cover in Kongsfjorden strongly affects the availability of light for photosynthesis, especially during early spring, and protect algae in or under the ice from harmful UV and excessive PAR values (e.g. Vincent and Roy 1993). The coverage by landfast sea–ice in the inner part of the fjord, restricted by a virtual line between Brandal and Tønsneset, has been monitored since 2003 (see Gerland and Renner 2007 for details). Less ice has been recorded in recent years, especially since 2007 (Pavlova et al., Chap. 4), and most importantly this has left most of the optical observation sites (Fig. 5.1) virtually free of landfast sea–ice in spring during the last decade.

5.2.6 Optically Active Substances

Light absorption and scattering is affected not only by seawater and sea ice, but also by optically active substances (OAS). The main subgroups of OAS are CDOM and particulate matter (defined operationally as the material that retains on a filter of nominal pore size of 0.7 µm) including algal pigments, and non-algal particles (matter). Below we summarize the limited knowledge of OAS in fjord waters and sea ice.

5.2.6.1 Optically Active Substances in Seawater

Several studies have been published that contain data on OAS in the water of Kongsfjorden (e.g. Carlsen et al. 2007; Volent et al. 2007; Pettersen et al. 2011; Pavlov et al. 2014). Average spectral absorption coefficient for CDOM ($a_{\mathrm{CDOM}}(\lambda)$) from the fjord in June 2010 (Location E; Pavlov et al. 2014) is shown (Fig. 5.7), along with previously unpublished data on total particulate absorption ($a_{\mathrm{p}}(\lambda)$) from several stations in Kongsfjorden in April 2014 (J. Meler, unpubl.). Absorption by CDOM was measured following Stedmon and Markager (2001), and particulate absorption was measured using a filter-pad technique according to Tassan and Ferrari (2002).

CDOM absorption in Kongsfjorden follows a characteristic exponential increase towards shorter UV wavelengths (e.g. Bricaud et al. 1981). Pavlov et al. (2014) reported $a_{\mathrm{CDOM}}(375)$ values between 0.10 and 0.18 m^{-1} in surface waters of Kongsfjorden, which is similar or slightly higher compared to $a_{\mathrm{CDOM}}(375)$ of

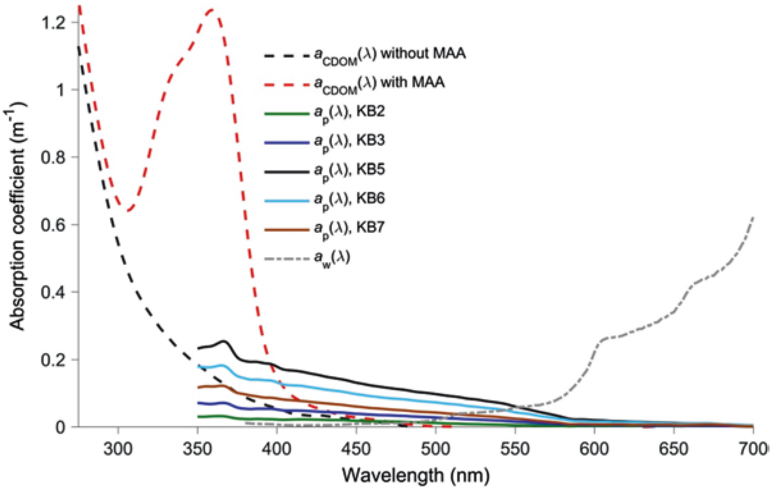

Fig. 5.7 Absorption by chromophoric dissolved organic matter (CDOM), $a_{\mathrm{CDOM}}(\lambda)$ and total absorption by particulate matter, $a_{\mathrm{p}}(\lambda)$ in Kongsfjorden for the wavelength range 380–700 nm. CDOM data are from Pavlov et al. (2014) for marine waters in the fjord (location E, Fig. 5.1) and those influenced by presence of mycosporine-like amino acids (MAA). Data on $a_{\mathrm{p}}(\lambda)$ are the average of 4 samples at surface, 5, 10 and 15 m depth collected at stations KB2, KB3, KB5, KB6, KB7 in April 2014. Spectra of $a_{\mathrm{p}}(\lambda)$ are obtained using the method of Tassan and Ferrari (2002). For station locations, see Fig. 5.1. For reference, the absorption by pure water $a_{\mathrm{W}}(\lambda)$ is also shown (Pope and Fry 1997)

0.10 m^{-1} on average in the core of the WSC outside Kongsfjorden (cf. Granskog et al. 2012; Pavlov et al. 2015). Given that Atlantic Water and its mixing products have been dominant water masses in Kongsfjorden over the past decade, this indicates that Atlantic Water from WSC is an important source of CDOM in the fjord. At the same time, local production of marine CDOM in Kongsfjorden has also been documented and associated with bacterial activity (Pavlov et al. 2014) and with degradation of kelp tissue, which contains CDOM substances (Hulatt et al. 2009). Additionally, phytoplankton in Kongsfjorden may produce mycosporine-like amino acids (MAA), known as photoprotective compounds that are effective absorbers in some UV bands (Karsten 2008; Ha et al. 2012; Pavlov et al. 2014). In some cases, MAA-like absorption peaks appear in CDOM spectra and can increase absorption of UV and PAR in near-surface waters substantially (Fig. 5.7). The contribution of terrestrial CDOM, which is significant in many coastal environments (e.g. Babin et al. 2003), is believed to be low in Kongsfjorden. Pavlov et al. (2014) described the dominance of marine CDOM in surface waters of Kongsfjorden (in June–July 2010), as well as reported relatively low concentrations of dissolved organic carbon (DOC) below 90 μmol L^{-1}, which is low compared to other Arctic coastal waters with prominent terrestrial input of dissolved organic matter (Stedmon et al. 2011; Pavlov et al. 2016). This is most likely caused by sparse terrestrial vegetation and dominance of glacial melt with low fraction of dissolved organic matter.

The contribution of particulate matter to total attenuation is typically significant in glacial environments (Volent et al. 2007; Johnsen et al. 2009; Lund-Hansen et al. 2010; Murray et al. 2015; Holinde and Zielinski 2016). Particulate absorption is then dominated by non-algal particles (Fig. 5.7), while the main algal (phytoplankton) absorption peaks (at 440 and 675 nm) are not pronounced, as these measurements were made early in the season before phytoplankton biomass had developed. For the reference, the timing and magnitude of phytoplankton blooms in Kongsfjorden have been rather variable (for a summary, see Hegseth et al., Chap. 6). These observations are similar to other fjords influenced by glaciers (e.g. Lund-Hansen et al. 2010). Overall, particulate absorption coefficients are quite low in the outer parts of the fjord (stations KB2 and KB3 in Fig. 5.7), and increase towards the inner fjord (stations KB5 and KB6), where the contribution of non-algal matter (most likely coming from glacial meltwater) is significant (Fig. 5.1). Later in the season, large amounts of glacial run-off likely cause the absorption by non-algal material to be even higher (by order of magnitude), with effects on underwater light conditions.

Particulate matter in the water column is known to cause more scattering than absorption (Mobley 1994). Here we present vertical profiles of scattering coefficient at 555 nm, $b(555)$, from a synoptic survey along the main fjord axis (Fig. 5.8; S. Sagan, unpubl.), measured with an ac-9 absorption and attenuation meter (WET Labs, Philomath, OR, USA; for details on methods and data processing, see Granskog et al. 2015). The gradient in $b(555)$ along the fjord is pronounced with

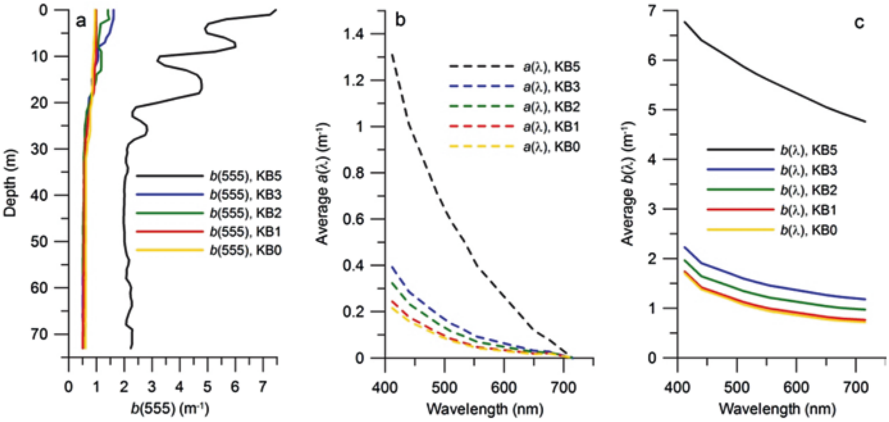

Fig. 5.8 (**a**) Vertical profiles of total scattering coefficient at 555 nm, *b*(555) at 5 stations in Kongsfjorden, measured in July 2010; (**b**) Spectra of total absorption coefficient, *a*(λ) averaged over top 10 m at the same stations; (**c**) Spectra of total scattering coefficient, *b*(λ) averaged over top 10 m at the same stations. (S. Sagan, unpubl.)

highest scattering observed in the inner part of the fjord at station Kb5 (Fig. 5.8a). Corresponding spectra of both absorption and scattering coefficients, averaged over the top 10 m, show that scattering coefficients are 5–6 times higher than absorption coefficients across visible wavebands (Fig. 5.8b, c). For comparison, a higher ratio of scattering to absorption (ca. 12) across PAR wavelengths was reported for Kangerlussuaq fjord in Greenland (Lund-Hansen et al. 2010).

5.2.6.2 Optically Active Substances in Sea Ice

In sea ice, algae that can be found throughout the ice layer are particularly important. These algae quickly colonize new ice (thinner than 15 cm) in spring (Taskjelle et al. 2016) and continue to accumulate, increasing particulate absorption. In snow-free new ice in Kongsfjorden (Taskjelle et al. 2016), the presence of MAA compounds is apparent from absorption spectra with peaks at typical MAA absorption bands around 330–360 nm (cf. Pavlov et al. 2014), and MAA also make a significant contribution to the attenuation of UV radiation in sea ice. In the new ice described in Taskjelle et al. (2016), the absorption by particulate matter is slightly higher than that by CDOM, except at UV wavelengths when MAAs are produced. In thicker ice with snow cover, no indications of MAA absorption peaks have been found (M.A. Granskog and B. Hamre, unpubl.), which is most likely an effect of less E_d(UV) exposure due to high attenuation of UV radiation by snow and ice (Winther et al. 2004).

5.3 Underwater Light: Implications for Organisms and the Marine Ecosystem of Kongsfjorden

Underwater light is critical in many different ecological contexts, from phototrophic primary production of algae to visual orientation in predators. These topics have been a research topic in many studies performed in Kongsfjorden – and the major results are summarized in the following sections.

5.3.1 Light as Energy Source for Arctic Primary Producers: Challenges of Strong Seasonality and Consequences of Ongoing Changes

The pronounced seasonal changes in irradiance in Arctic waters and the generally low incoming radiation have strong implications for primary production and seasonal growth of marine phototrophs, consisting of phytoplankton, microphytobenthos and macroalgae (very sparse data only available on sea ice algae and phototrophic bacteria in Kongsfjorden).

In the pelagic realm, the bulk of annual new primary production takes place during a short time window in spring, with a strong peak in algal biomass concentrations providing the basis for the pelagic food web. Grazers that depend on phytoplankton as food supply for successful reproduction have adjusted their annual cycles to match this timing (Søreide et al. 2010; Varpe 2012). Light availability is the single most important factor controlling the timing of phytoplankton blooms, although other factors might play important roles as well (for details about the situation in Kongsfjorden, see Hegseth et al., Chap. 6). In Kongsfjorden, the phytoplankton bloom usually declines in late spring because of nutrient depletion (Hodal et al. 2012; Piquet et al. 2014; Hegseth et al., Chap. 6), in combination with grazing. The bloom as such may already cause some shading (see Fig. 5.5), but most importantly, light availability drops sharply in late spring/early summer caused by the onset of runoff from land and glacier melt, bringing large amount of particulate matter into the fjord. In the innermost part of the fjord, reduced light availability due to glacier meltwater run-off (Figs. 5.1 and 5.8) and sea ice affects the phytoplankton development already in early spring, resulting in lower biomass development and smaller size composition of the phytoplankton community (Piquet et al. 2014). During summer, pelagic primary production can continue, but is generally lower than in the spring, due to reduced availability of nutrients and light. The few published studies presenting data on phytoplankton in Kongsfjorden indicate primary production rates ranging between 27 and 180 g C m^{-2} yr^{-1} (e.g. Hop et al. 2002; Hodal et al. 2012). These values are within the range of those reported from the Barents Sea and Fram Strait region (see Hodal et al. 2012, and references therein), but higher than annual primary production reported from Young Sound, Greenland (6–10 g C y^{-1}; Rysgaard and Nielsen 2006).

Even during wintertime, living vegetative phytoplankton cells have been found in Svalbard surface waters (Berge et al. 2015a; Vader et al. 2015; Kvernvik et al. 2018), although ambient radiation in Kongsfjorden during the polar night is too low to allow primary production (Kvernvik et al. 2018). Whereas details of their overwintering strategies are still to be resolved, it has been documented that Arctic benthic diatoms and perennial kelps utilize storage compounds (lipids, polysaccharides) to cope with polar winter conditions (Dunton 1990; Karsten et al. this volume).

Microphytobenthic communities in shallow waters are physiologically well adapted to fluctuating light conditions as well as to hydrological gradients and sediment characteristics (Karsten et al. 2009). Benthic diatoms dominate the shallow water sediments in Kongsfjorden, as reflected in high chlorophyll *a* (chl *a*) values of up to 317 mg m^{-2}, but the spatial heterogeneity is large (Woelfel et al. 2010). Daily microphytobenthic gross primary production in Kongsfjorden was estimated to range between 2 and 48 mmol O_2 m^{-2} d^{-1} depending on site and applied model (Woelfel et al. 2010; Sevilgen et al. 2014), resulting in a gross production of 17–554 mg C m^{-2} d^{-1} (Woelfel et al. 2010).

For seaweeds in Kongsfjorden, the majority of annual biomass is probably also formed prior to mid-summer, and the bulk of it is composed of large brown algae of the order Laminariales (kelps), while bushy red algae (Rhodophyta) constitute the understory seaweeds (Bartsch et al. 2016, Hop et al. 2012, 2016; Karsten et al., Chap. 8). There are four biomass dominant species, which occur between 0 and ca. 20 m depths: *Laminara digitata*, *Saccharina latissima*, *Alaria esculenta* and *Saccorhiza dermatodea* (Hop et al. 2016). These kelps form new blades every spring and constituted a maximum of 9.5 m^2 of blade area per m^2 seabed at a depth of 2.5 m at the onset of summer in 2012. The maximum standing stock of seaweeds was 14.1 kg m^{-2} fresh weight at 2.5 m, decreasing to 0.6 kg m^{-2} fresh weight at 15 m depth in 2012–13 (Bartsch et al. 2016). This is the highest seaweed biomass recorded at an Arctic site and normally more characteristic for sub-Arctic to cold–temperate communities (e.g. Sharp et al. 2008).

Physiological studies of algae in Kongsfjorden have furthermore revealed low light compensation points (= irradiance at which gross photosynthesis equals respiration) of about 2–7 μmol m^{-2} s^{-1}. Photosynthesis in kelps was saturated at low light levels of 20–40 μmol m^{-2} s^{-1}, and microphytobenthic photosynthesis was half-saturated at 33 μmol m^{-2} s^{-1} (Latala 1990; Karsten et al. 2006; Roleda et al. 2006; Sevilgen et al. 2014; Krüger 2016). These features constitute adaptations to the highly variable and often low light environment, which are a general characteristic of polar phototrophs (Glud et al. 2002; Gómez et al. 2009).

Climate warming causes changes in the light conditions in Arctic aquatic ecosystems (see Sect. 5.2): decrease in sea ice cover results in increased E_d(PAR,Z) in the water column; glacial melting processes and riverine run-off increase turbidity and reduce the light available for photosynthetic primary production later in the year. The strong decrease in sea–ice cover in Kongsfjorden is probably also one of the major factors behind the increase of seaweed biomass off Hansneset between 1996–98 and 2012–13 (Bartsch et al. 2016). At the outer part of Kongsfjorden, where the community was dominated by crustose coralline algae in 1980, filamentous brown algae had become dominant by 1995, pointing to increased benthic primary productivity as a consequence of an overall more favourable light climate (Kortsch et al. 2012).

5.3.2 Light as Stress Factor: Adverse Effects of High Irradiance in the PAR (E_d(PAR,Z)) and UV Range (E_d(UV,Z)) on Arctic Primary Producers

Although light is necessary as an energy source for primary production, excessive levels of irradiance can also become detrimental to organisms. Primary producers, with their ability to efficiently collect PAR by means of their pigments, are particularly threatened. Of the incoming radiation, UV radiation has the greatest potential to affect organisms negatively due to both its high energy content, and the fact that these wavelengths are absorbed specifically by several important biomolecules, such as proteins and deoxyribonucleic acid (DNA). Due to the relatively high transparency of the water column in Kongsfjorden (except for the inner basin close to glaciers) during the peak production period in spring, irradiances might even become detrimental for organisms residing close to the sea surface. The considerable body of research on the impact of E_d(UV,Z) especially on seaweeds of Kongsfjorden has been reviewed (see Bischof et al. 2006, and references therein), and will not be described in detail here. For over a decade, the effects of UV radiation on macroalgal ecology, physiology, biochemistry, cell biology and molecular biology have been studied in Kongsfjorden. Major insights include a reduced reproductive success because of the pronounced UV-susceptibility of early life history stages such as spores, gametes, gametophytes and juvenile seaweed stages (e.g. Wiencke et al. 2004, and references therein). The UV-susceptibility of kelp spores often determines the upper depth distribution of kelp species (e.g. Wiencke et al. 2006).

Ambient levels of E_d(PAR,Z) in the uppermost part of the water column in Kongsfjorden have been shown to decrease growth rates and affect the biochemical composition of phytoplankton communities (Leu et al. 2006a), decreasing their content of polyunsaturated fatty acids (PUFAs), and inducing the production of photoprotective pigments. Similar results were found in a controlled exposure of diatom cultures at two different depths *in situ* (Leu et al. 2016), however, no negative effects that could be attributed to UV radiation alone were reported. Similarly, a mesocosm study with a natural phytoplankton community, performed in summer 2001, showed no distinct negative effects of UVB (Wängberg et al. 2008). Benthic diatoms in Kongsfjorden are generally not affected by UV radiation, because most taxa avoid this waveband by physiological, biochemical and behavioural mechanisms, which include, for example, the synthesis and accumulation of MAAs or the capability of vertical migration into the upper sediments (Karsten et al. 2012).

5.3.3 Photoperiod as Environmental Signal for Seasonal Growth Patterns in Arctic Kelp Species

Besides the significance of daylength for providing light energy for growth and carbon allocation, photoperiod (daylength) is also a primary trigger for the regulation of seasonal growth and reproduction (Lüning 1989). For the Arctic, little information is available on the impact of photoperiod for the regulation of phytoplankton, microphytobenthos or seaweed growth and reproduction. One exception is the endemic Arctic kelp *Laminaria solidungula,* also present in Kongsfjorden (Hop et al. 2012; Fredriksen et al. 2014), which grows predominantly in winter (Chapman and Lindley 1980). The onset of growth is presumably regulated by an endogenous circannual growth rhythm and short photoperiods. This has been verified for temperate kelp species with a similar growth strategy (Lüning 1991; tom Dieck 1991). The onset of reproduction of *L. solidungula* and another Arctic brown algae, *Saccorhiza dermatodea*, is induced by short daylengths (Hooper 1984; Keats and South 1985; Henry 1987; tom Dieck 1989; Roleda 2016). Two other Arctic kelp species from Kongsfjorden (*Saccharina latissima* and *Saccharina nigripes*) are fully fertile only in autumn (I. Bartsch, pers. comm.), potentially indicating that their fertility is induced by short daylengths.

5.3.4 Visual Predation During Polar Night: Foraging at the Light Limit

For many animals, light is vital for visual predation (Kaartvedt et al. 1996; Torgersen 2001; Abrahamsen et al. 2010; Varpe et al. 2015). In Kongsfjorden, many organisms, including fish, seabirds, euphausiids (krill), amphipods, and copepods that are active and feeding throughout the year adapt their behavioural pattern according to the annual course of fluctuating light levels (Kraft et al. 2013; Båtnes et al. 2015; Berge et al. 2015a). Recent work from Kongsfjorden suggests that even low levels of atmospheric light (diffuse sunlight, moon, Aurora Borealis), during periods when a photoperiod of about 5 h is present (Cohen et al. 2015), may indeed play a role in predator–prey dynamics (Cronin et al. 2016; Last et al. 2016). For example, approximately half of the fish (Polar cod [*Boreogadus saida*], Atlantic cod [*Gadus morhua*], and haddock [*Melanogrammus aeglefinus*]) collected in trawls from Kongsfjorden in winter had stomachs at least half full, with mainly pelagic euphausiids prey, and for polar cod both euphausiids and calanoid copepods (Berge et al. 2015a). Likewise, the gut content of seabirds collected from Kongsfjorden in winter (Little auk [*Alle alle*], Brünnich's guillemot [*Uria lomvia*], and Black guillemot [*Cepphus grylle*]) showed evidence that the birds fed on euphausiids and amphipods (Berge et al. 2015a). Interestingly, lenses in the eyes of polar cod show adaptations for maintaining a focused visual image at low light levels, which is not the case for lenses of boreal Atlantic cod (Jönsson et al. 2014). Collectively, this suggests that ambient light may play a variable role in winter feeding among fish (and perhaps seabird) species in Kongsfjorden, with Arctic species being better adapted to winter light levels and more recently established boreal species relying on other sensory modalities (Varpe et al. 2015).

The pelagic zooplankton in Kongsfjorden, preyed upon by fishes and seabirds, can likewise use available light even at the darkest times of the year. While conventional light meters are not sensitive enough to measure underwater light in the polar night (e.g. Table 5.1), Cohen et al. (2015) used measurements of diffuse skylight irradiances near Ny-Ålesund and measurements of inherent optical properties of seawater (such as spectral absorption and attenuation) from Kongsfjorden to model the underwater light field during the polar night. After weighting the spectrally-resolved light field by the spectral sensitivity of zooplankton visual systems, they determined that Arctic zooplankton (*Thysanoessa inermis* euphausiids and *Calanus* spp. copepods) could detect and utilize ambient light down to 20–30 m depth at midday.

5.3.5 Diel Vertical Migration of Zooplankton During Midnight Sun and Polar Night

Diurnal changes of incoming irradiance are known to cause synchronized diel vertical migration (DVM) in zooplankton. Zooplankton DVM occurs in all oceans of the world and in lakes, and involves a trade-off between increased foraging opportunities in surface layers and a reduced risk of predation at depth (Hays 2003). The phenomenon is generally found to be light-mediated (for reviews, see Hays 2003; Cohen and Forward 2009; Ringelberg 2009). The extreme variability in diurnal light-dark cycles in Polar Regions also has been shown to cause seasonal patterns in DVM (Wallace et al. 2010; Berge et al. 2014). Diel changes in irradiance are most pronounced during the intervening autumn and spring seasons. One would therefore anticipate little or no DVM during the summer and winter, whereas DVM in spring and autumn is likely to offer the greatest benefits (see e.g. Fischer and Visbeck 1993; Berge et al. 2014). One study from Kongsfjorden reported complete absence of synchronized migrations of zooplankton during midnight sun (Blachowiak-Samolyk et al. 2006). In contrast, Cottier et al. (2006) described – also based on data collected in Kongsfjorden – a conceptual model of asynchronous DVM during the Arctic summer, where each individual migrates according to its own needs rather than as part of a population, with the more typical synchronized mode of DVM re-established as soon as the diel cycle of irradiation returns to a more distinct day-night cycle. Findings about DVM during the polar night are similarly diverse: whereas several studies have reported a complete lack of synchronized migrations of zooplankton during the polar night (e.g. Kosobokova 1978; Fischer and Visbeck 1993from the Arctic; Cisewski et al. 2010 from Antarctica), Berge et al. (2009) presented the first evidence of synchronized migration pattern during the polar night in two Svalbard fjords, Kongsfjorden and Rijpfjorden (northern Svalbard). Wallace et al. (2010) provided further evidence of this by examining migration patterns from a continuous acoustic data series covering two annual cycles in Kongsfjorden and Rijpfjorden, addressing as well the impact of sea ice cover on this behaviour. Last et al. (2016) determined that the lunar cycle serves as a proximate cue for zooplankton DVM during polar night.

5.4 Future Directions for Studies of the Underwater Light Climate

The review work has pinpointed some essential knowledge gaps that can be of interest to study in the future. Geographically, waters near marine-terminating glaciers in Kongsfjorden have recently been described as biological hotspots (Lydersen et al. 2014; Urbanski et al. 2017); however, optical observations from these areas are rare and might be an important focus of future studies. Temporally, evidence for high levels of biological activity during polar night has recently been presented (Berge et al. 2015a, b); additional and more thorough optical observations during this time of year would be important to better understand how low light conditions influence the marine ecosystem in Kongsfjorden during winter.

Another knowledge gap relates to a lack of longer time series of optical observations, covering different areas of Kongsfjorden and different ranges of depths, and that are also coordinated with land-based observations of incoming solar radiation (broadband and spectral). Additionally, there is clearly a need for direct observations of inherent optical properties, such as spectral absorption and attenuation coefficients in the water column, which can be further assimilated into radiative transfer and coupled physical-biological models to get a better understanding of the underwater light climate during different seasons and locations in the fjord (cf., Cohen et al. 2015).

To overcome many observational challenges, new technological advances in both instrumentation (e.g. new hyperspectral sensors, setups to prevent biofouling of instruments) and observation platforms (e.g. underwater observatories in the coastal domain, gliders and remotely operated vehicles) will be helpful to better comprehend the variability of underwater light climate, and thus, its ecological implications. In turn, this might create even more challenges when it comes to comparison of different optical datasets. Thus, standardization and intercalibration of optical measurements and subsequent processing and sharing of the data should be prioritized.

Acknowledgement We thank organizers of the Kongsfjorden Ecosystem Workshop (Hamn i Senja, March 2014) for the initiation of this review study. For AP, PK, JM, SH, SS and MAG, this work was partly supported by the Polish–Norwegian Research Programme operated by the National Centre for Research and Development under the Norwegian Financial Mechanism 2009–2014 in the framework of Project Contract Pol-Nor/197511/40/2013, CDOM-HEAT; and for AP, SH and MAG by the Research Council of Norway through the STASIS project (221961/F20). UK gratefully acknowledges financial support through the project KA 899/15-1/2/3 in the framework of the DFG (Deutsche Forschungsgemeinschaft) Priority Programme 1158 "Antarctic Research". SS was supported by the Norwegian Financial Mechanism, project ALKEKONGE, PNRF-234-AI-1/07. We thank Oddveig Øien Ørvoll and Anders Skoglund at the Mapping section of the Norwegian Polar Institute for preparing the map of Kongsfjorden (Fig. 5.1). We thank Colin Griffiths for Kongsfjorden mooring work, funded by UK Natural Environment Research Council and the Research Council of Norway Projects Circa (214271) and Cleopatra (178766). We also thank three anonymous reviewers for constructive feedback that helped to improve this work.

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Part III
Pelagic Production, Phytoplankton and Zooplankton

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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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_6

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

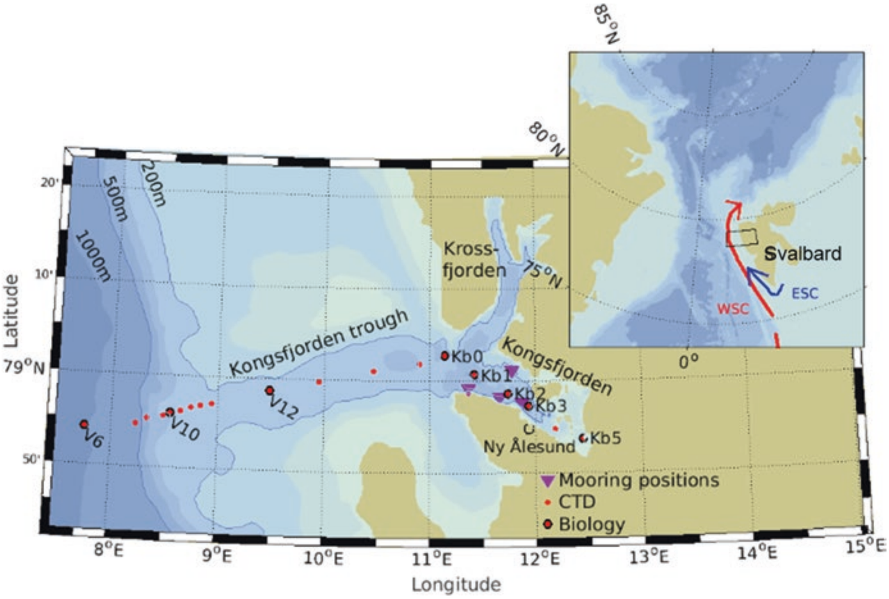

Fig. 6.1 Svalbard with the East Spitsbergen Current (ESC, blue) and West Spitsbergen Current (WSC, red). Enlarged insert with Kongsfjorden mooring locations, CTD and biology stations

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

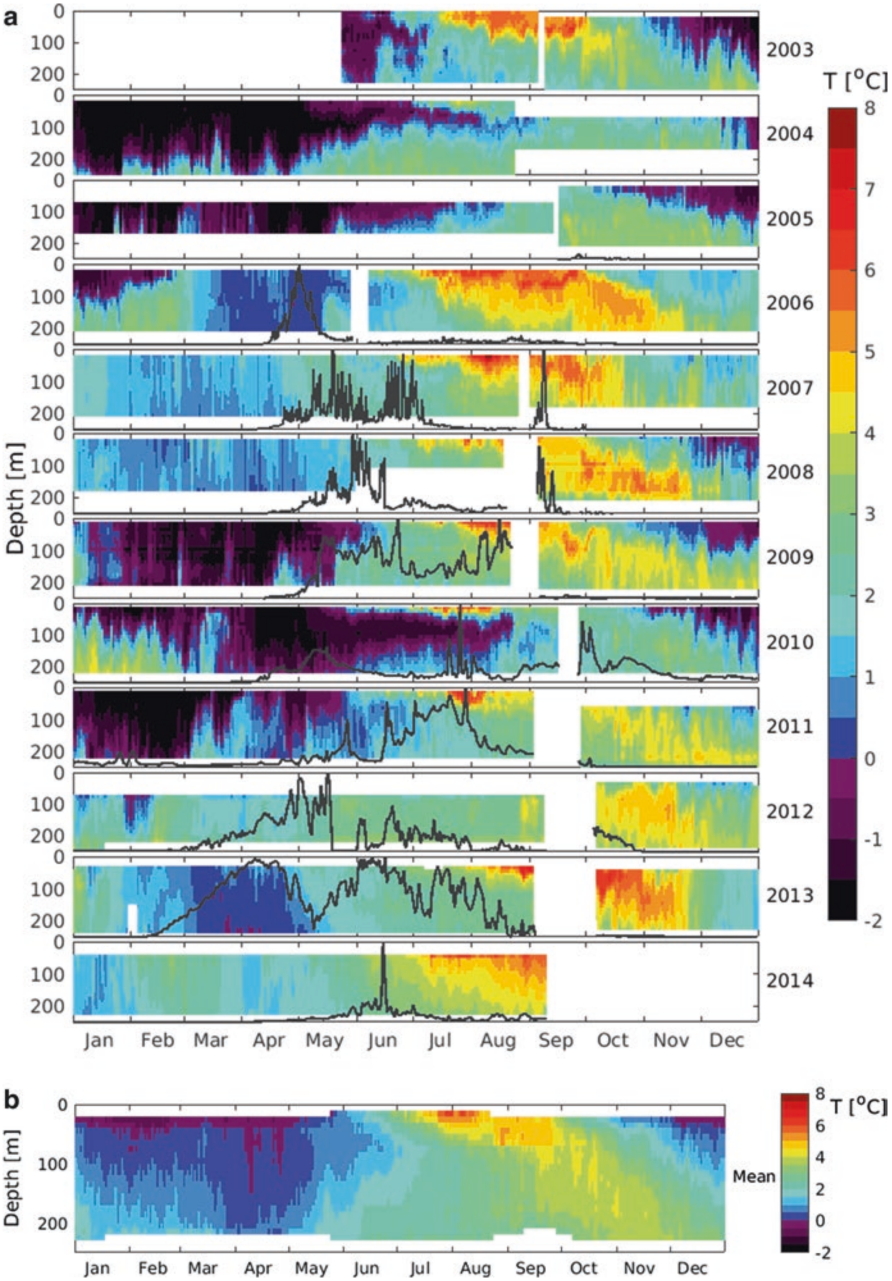

Fig. 6.2 (**a**) Temperature measurements (°C) from the Kongsfjorden Marine Observatory, May 2003 to September 2014. The superimposed black line depicts the normalized fluorescence units (measurements were normalized for each year). Note that the mooring location has been shifted over the years (see 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)

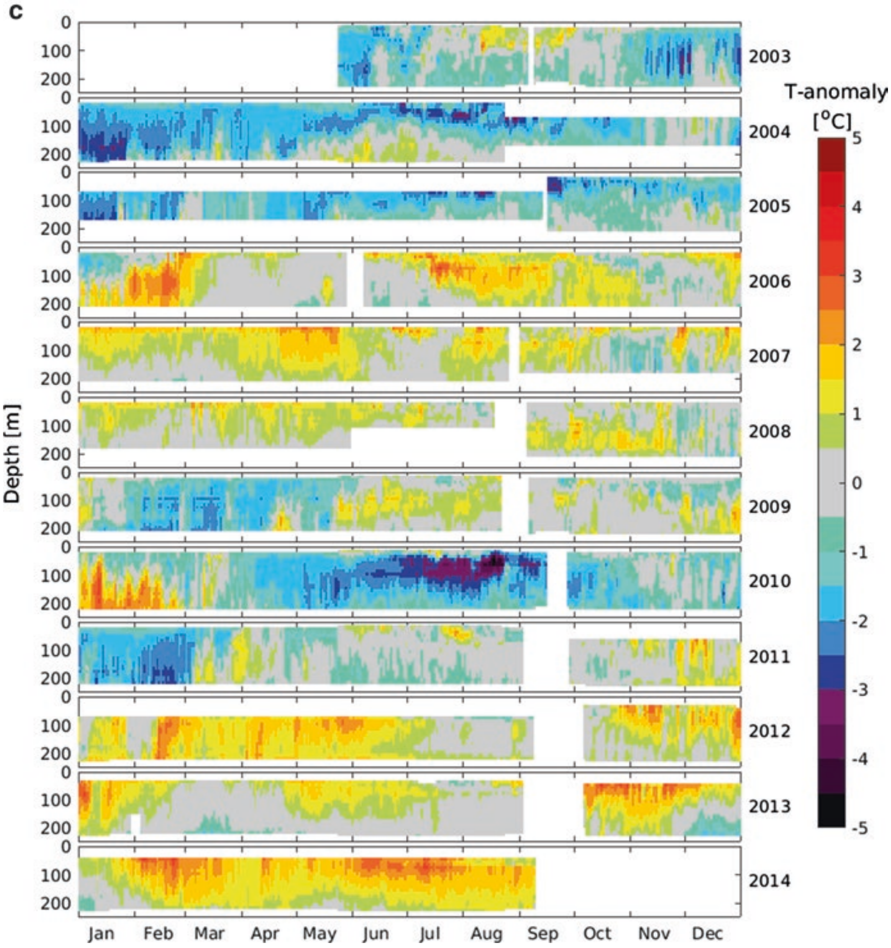

Fig. 6.2 (continued)

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.

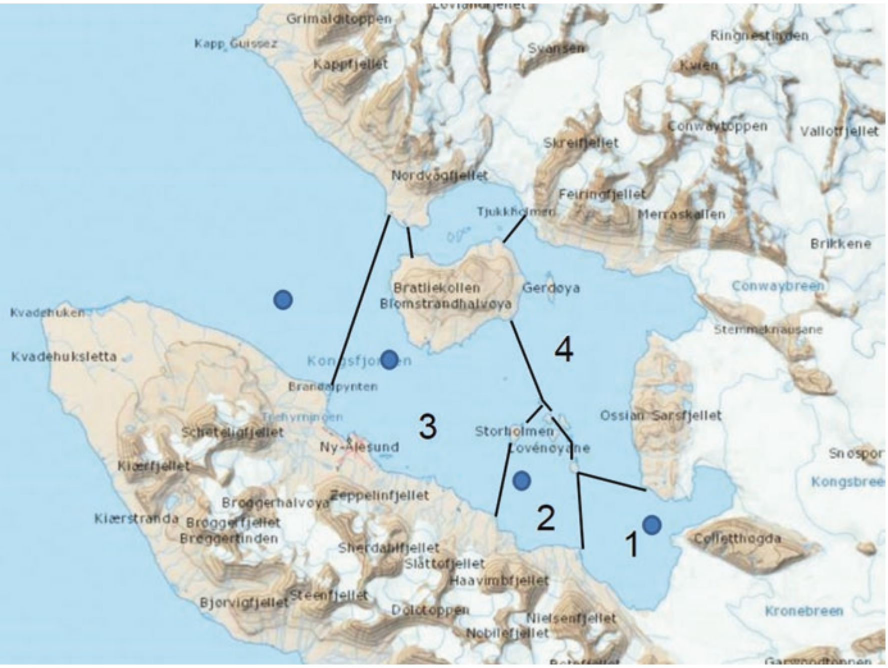

Fig. 6.3 Kongsfjorden showing sectors in the inner fjord related to fast–ice cover (see Table 6.2). Sectors based on Gerland and Renner (2007). Blue dots showing sampling stations in the fjord (Kb5-Kb2)

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

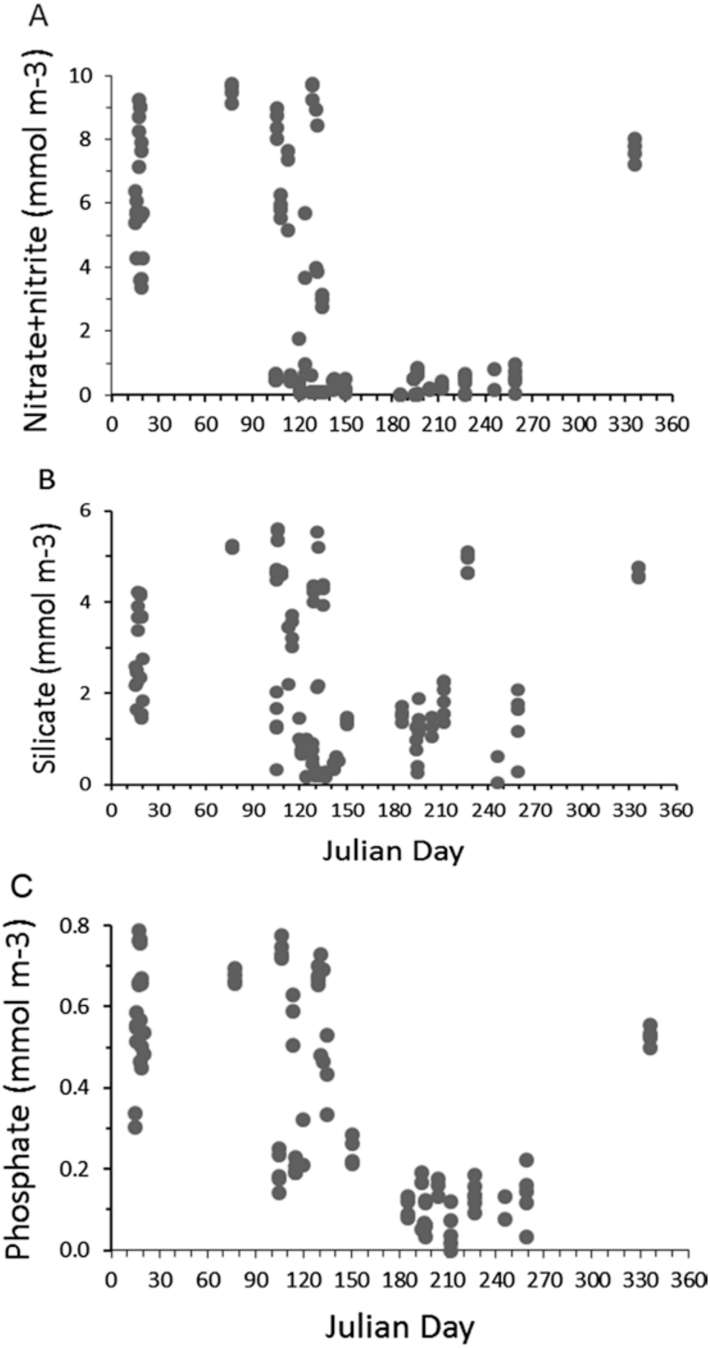

Fig. 6.4 Average concentrations of (**a**) nitrate+nitrite, (**b**) silicate and (**c**) phosphate in mmol m^{-3} in the upper 20 m at station Kb3 versus day of the year. N = 133, 136 and 97 respectively. (S. Kristiansen, unpublished data)

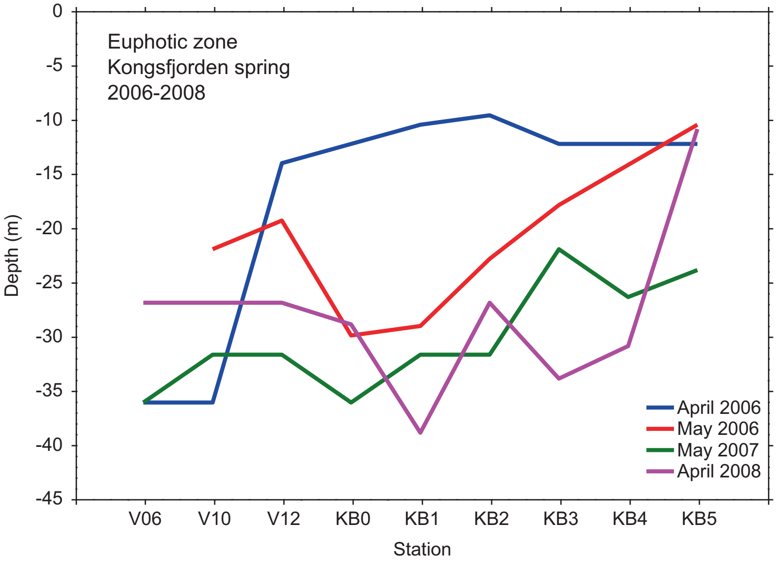

Fig. 6.5 Euphotic depth in Kongsfjorden measured during the spring bloom in 2006 and 2007, after the bloom in 2006 and at the beginning of the bloom in 2008. (Data from Hegseth and Tverberg 2013)

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

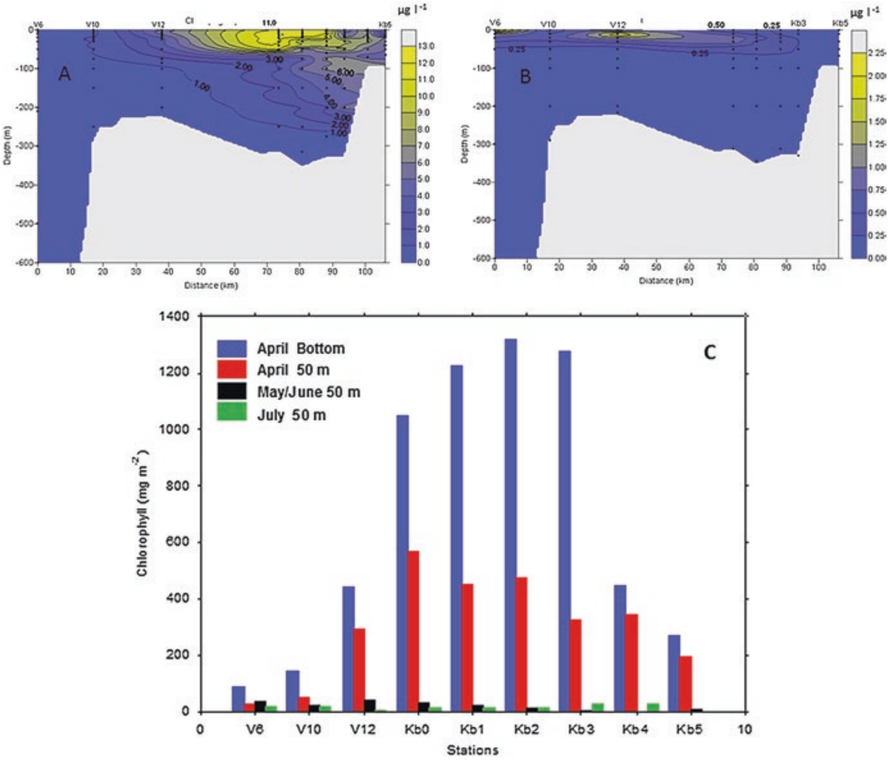

Fig. 6.6 Chlorophyll sections across Kongsfjorden and the adjacent shelf in 2006 during (**a**) the spring bloom in April and (**b**) in late May/early June, when high phytoplankton biomass was restricted to the outermost areas of the shelf and Fram Strait, while the bloom inside Kongsfjorden had terminated. (**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

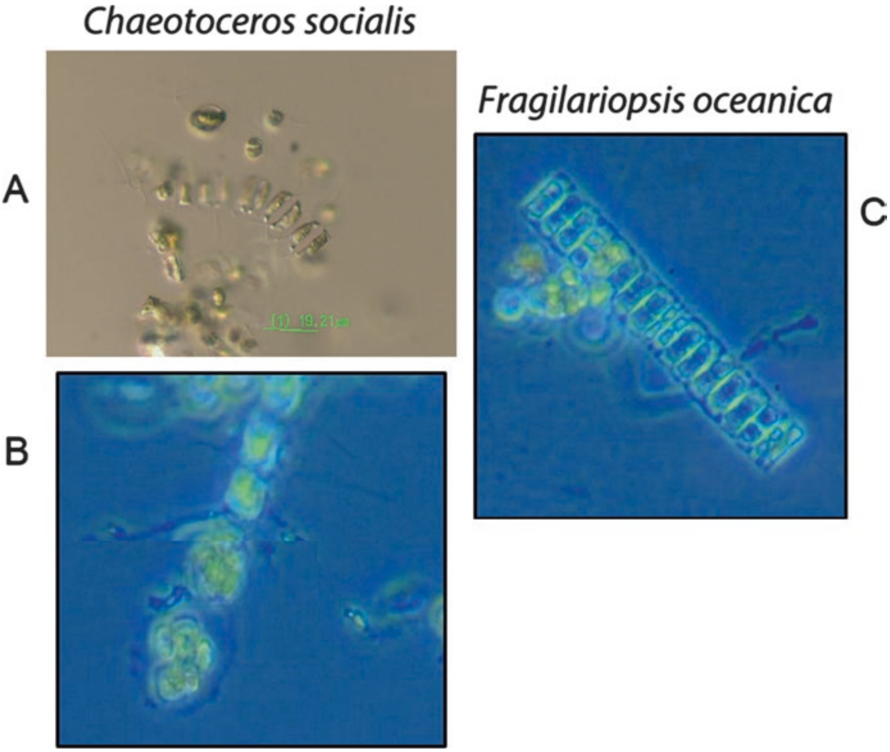

Fig. 6.7 Cells of *Phaeocystis pouchetii* attached to (**a**) and (**b**) chains of *Chaetoceros gelidus*, and (**c**) to a chain of *Fragilariopsis oceanica* at the start of the spring bloom in Balsfjorden, northern Norway. (J.M. Wiktor, unpublished data [A], E.N. Hegseth, unpublished data [B, C])

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.

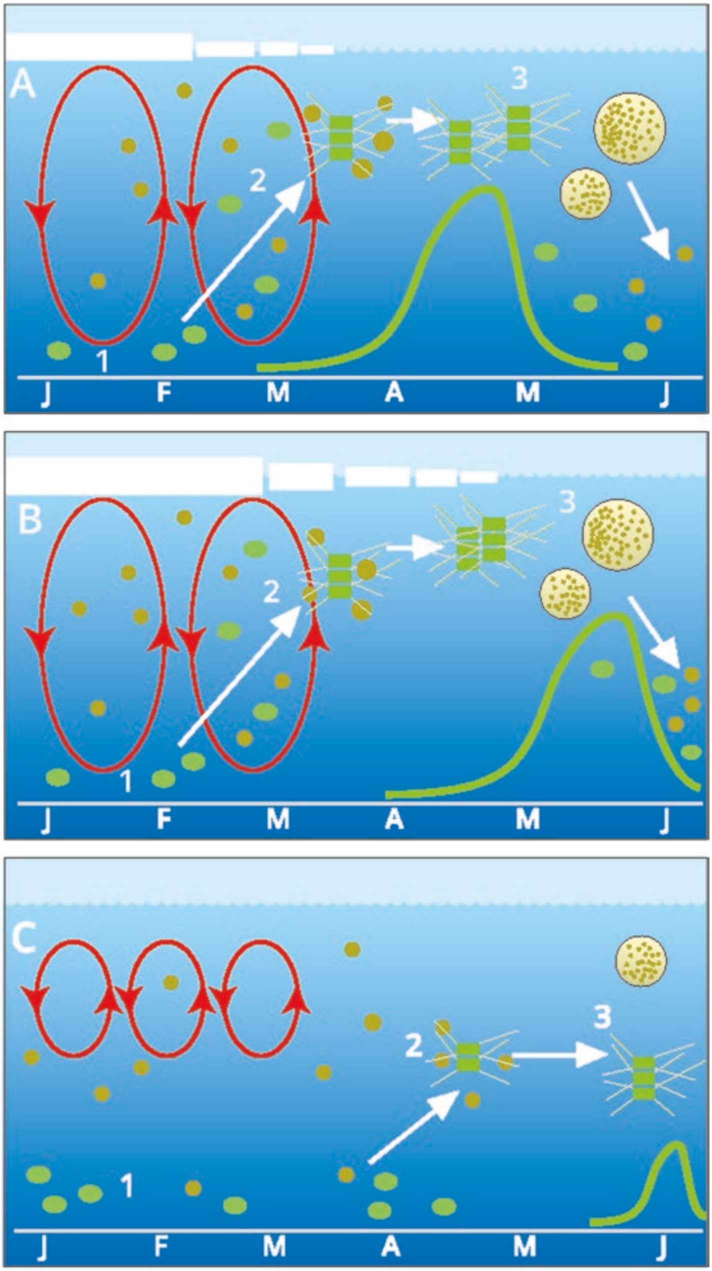

Fig. 6.8 Schemes of the spring bloom types in Kongsfjorden. (**a**) Group A spring bloom (deep convection, early ice melt, early bloom), (**b**) Group B spring bloom (deep convection, late ice melt, late bloom, (**c**) Group C spring bloom (shallow convection, no ice, very late bloom). Green dots = diatom 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},

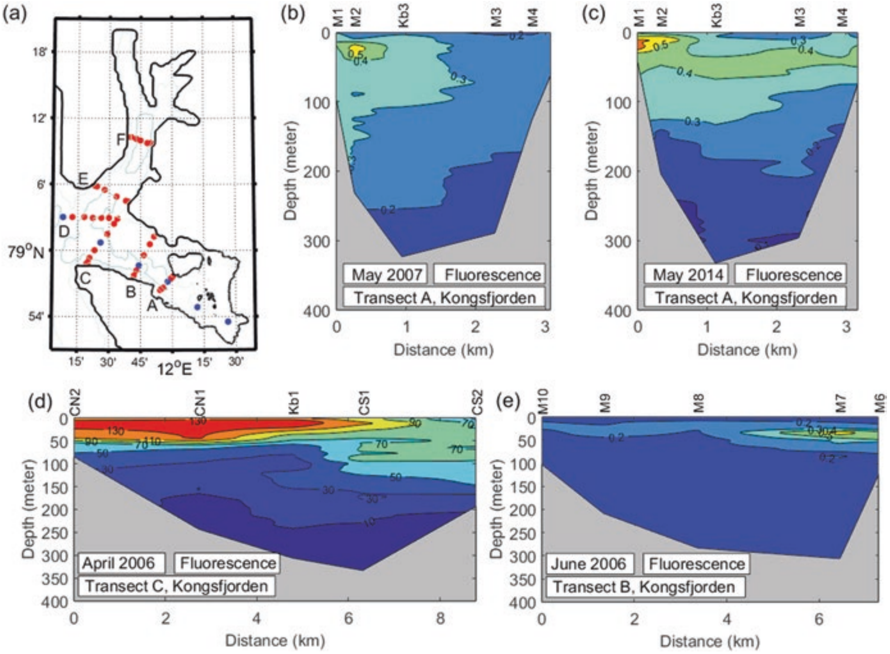

Fig. 6.9 Positions of cross-fjord transects in Kongsfjorden marked A, B, C on the map (**a**). Examples of cross-fjord transects in Kongsfjorden showing earlier bloom development on the northern side (to the left) of the fjord in (**b**) May 2007, (**c**) May 2014, and (**d**) April 2006. In June 2006 (**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)

Species	Cells × 10^3 L^{-1}			
	Whole fjord		Station Kb3	
	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)

	Cells × 10^3 L^{-1}			
	Whole fjord		Station Kb3	
Species	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 × 10³ 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)

	Cells × 10^3 L^{-1}			
	Whole fjord		Station Kb3	
Species	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

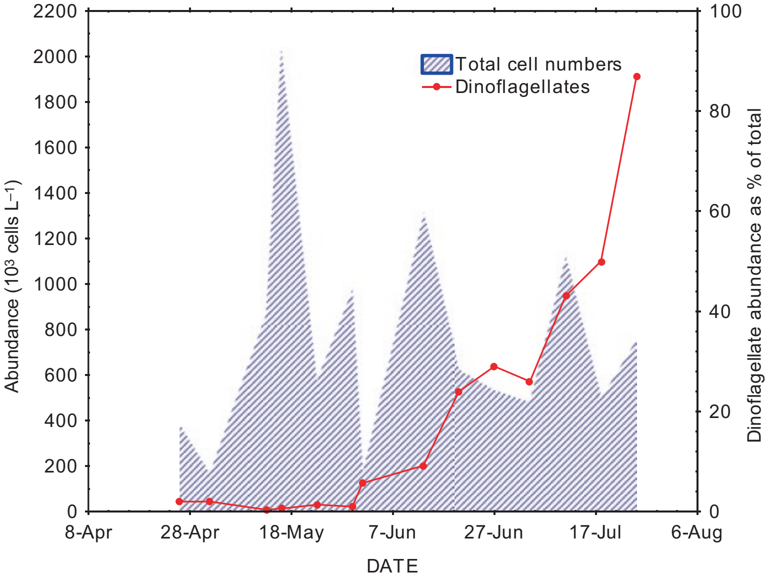

Fig. 6.10 Phytoplankton abundance at station Kb3 in spring and summer 2007. Hatched areas are total cell numbers L^{-1}, while red line represents the % contribution of dinoflagellates. (E.N. Hegseth, unpublished data)

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).

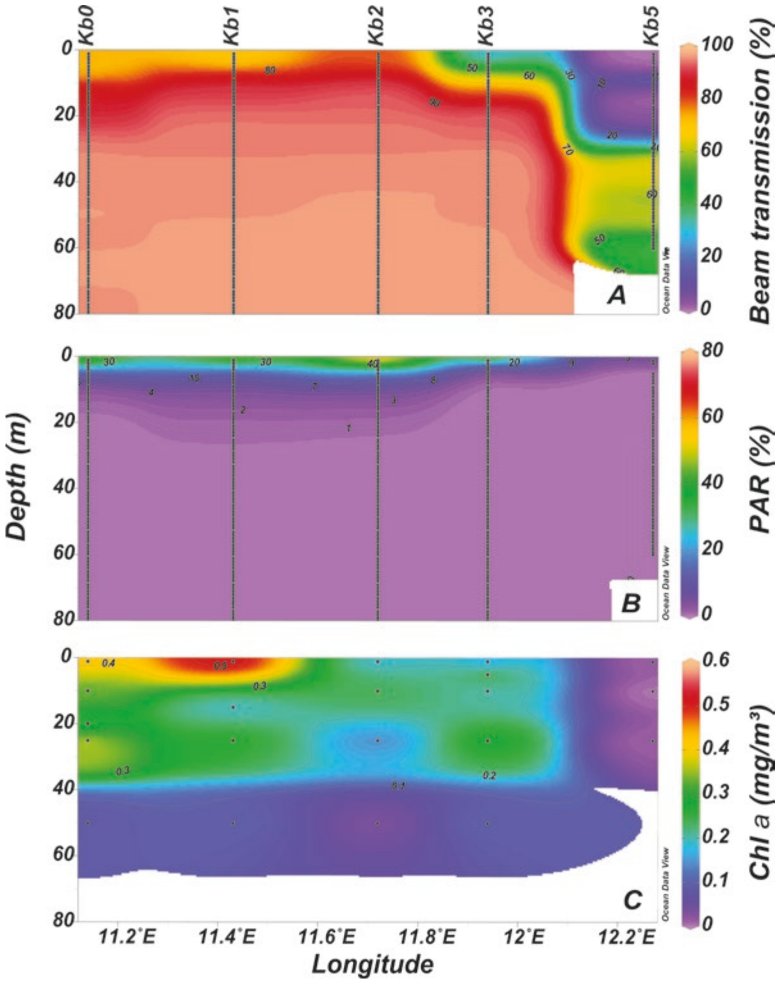

Fig. 6.11 Cross section of the upper 80 m of the water column. Measured from the inner basin (station Kb5, right hand side of plot), to the fjord mouth (station Kb0, left hand side of plot) on 15 July 2011: (**a**) Percentage beam transmission measured with the profiling transmissiometer (measure of 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

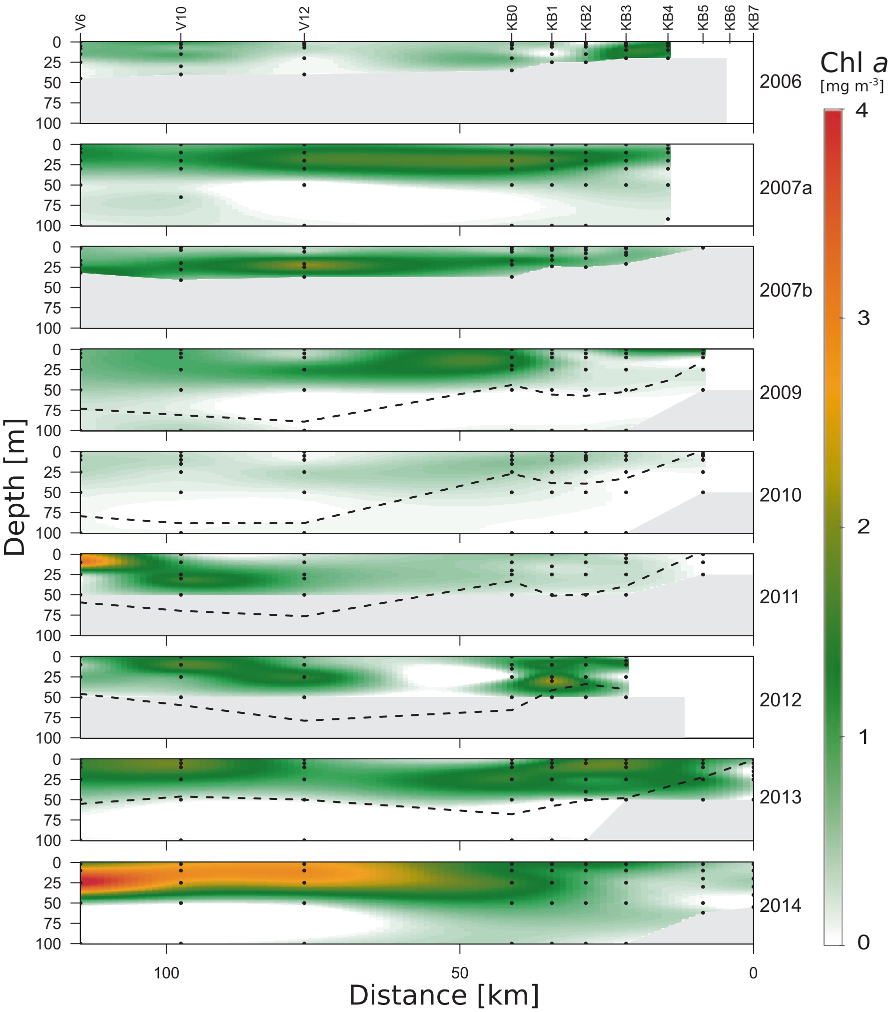

Fig. 6.12 Chlorophyll (in μg L^{-1}) sections from the inner bay (station Kb5) to the shelf break (station V6) during July for the years 2006, 2007 and 2009–2014. In 2007, a second chlorophyll section was obtained in early August during a cruise with RV *Oceania*. Note that the innermost station Kb5 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-

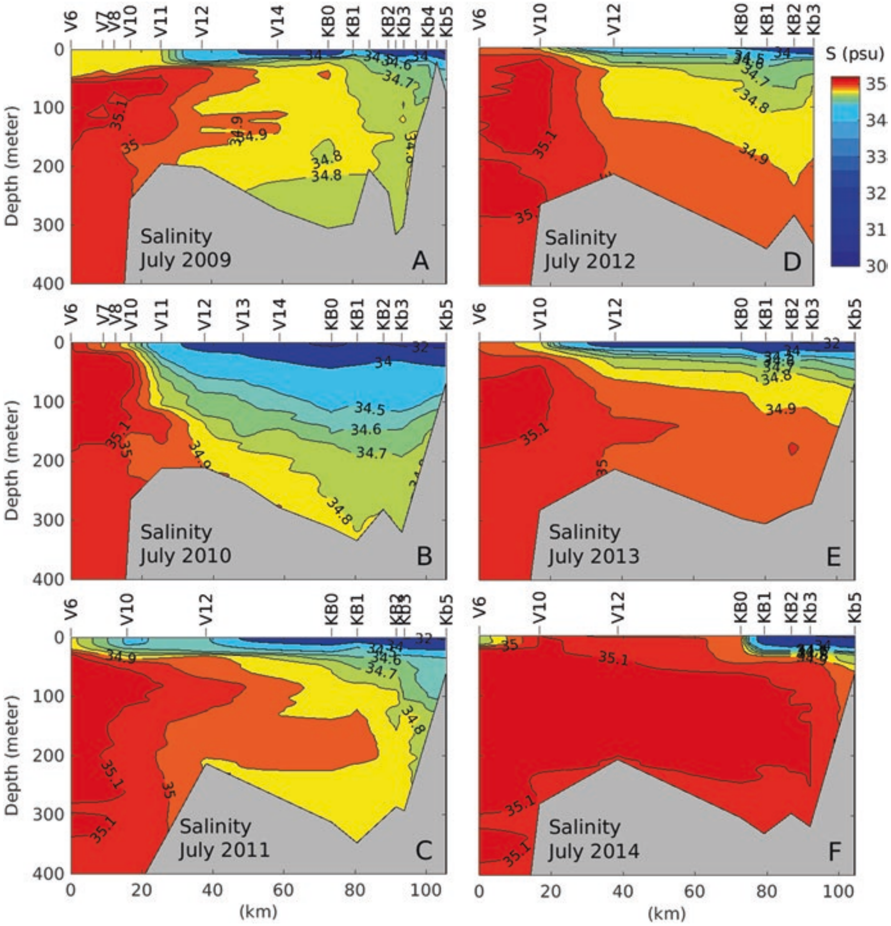

Fig. 6.13 Salinity sections (psu) across Kongsfjorden and the adjacent shelf from July for the years 2009–2014. (NPI, unpublished data)

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

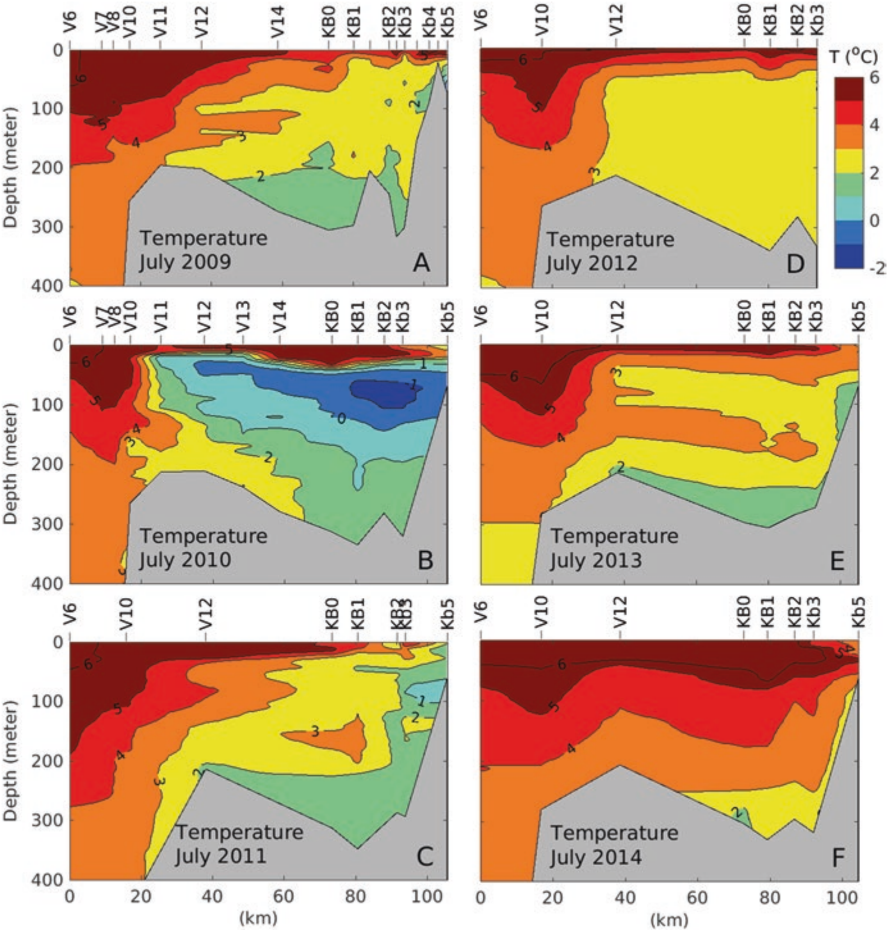

Fig. 6.14 Temperature sections (°C) across Kongsfjorden and the adjacent shelf from July for the years 2009–2014. (NPI, unpublished data)

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

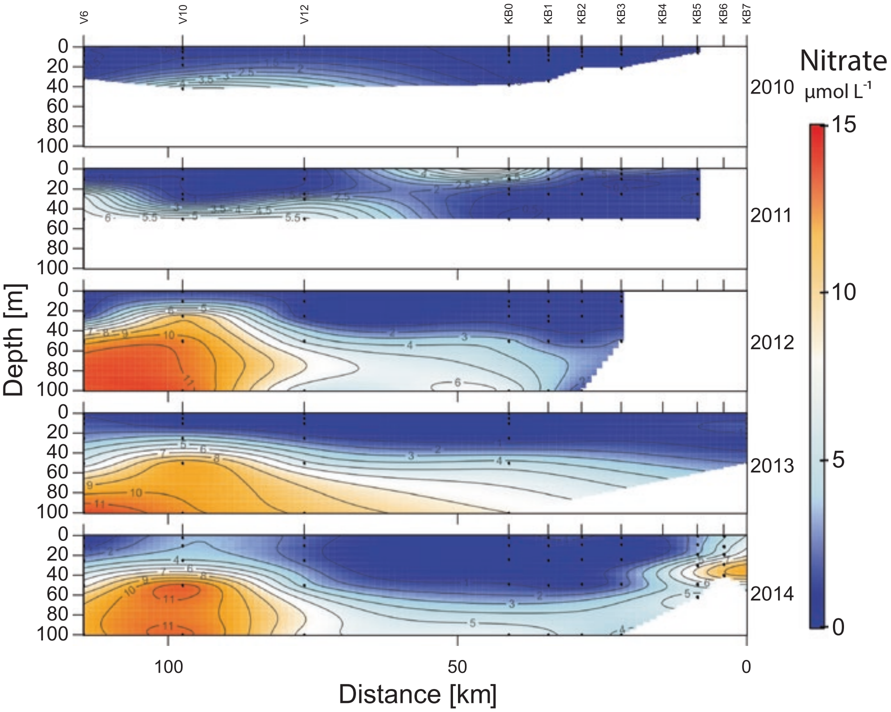

Fig. 6.15 Nitrate concentrations (in µM) in the upper 100 m of the water column across Kongsfjorden and the adjacent shelf in July 2010–2014. (NPI, unpublished data)

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

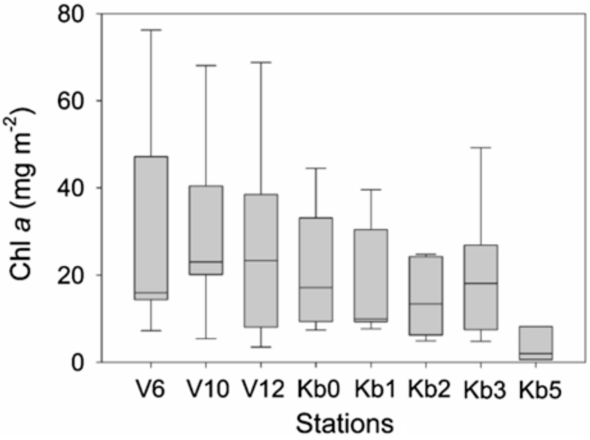

Fig. 6.16 Box-Whisker plot of depth-integrated (upper 25 m) summer chlorophyll *a* standing stocks (mg m^{-2}) for all years depicted in Fig. 6.12 (2006, 2007, 2009–2014)

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

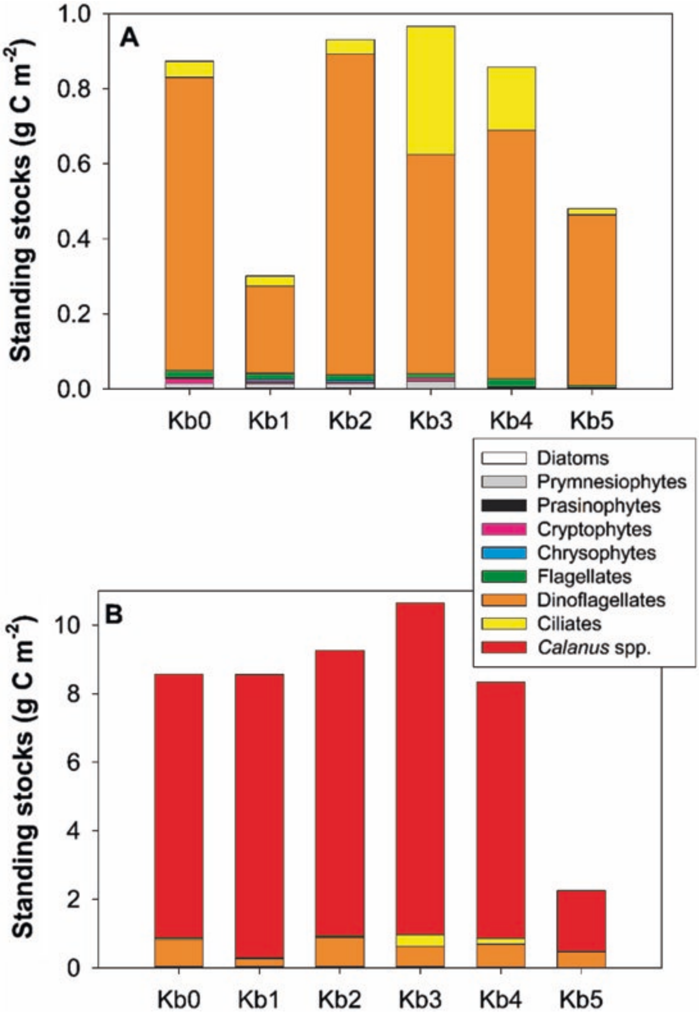

Fig. 6.17 Depth-integrated (upper 50 m) standing stocks (g C m^{-2}) of (**a**) protist plankton and (**b**) protist plankton and *Calanus* copepods in July 2009. Protist plankton was collected in water samples and copepods with Multinet. (NPI, unpublished data)

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-

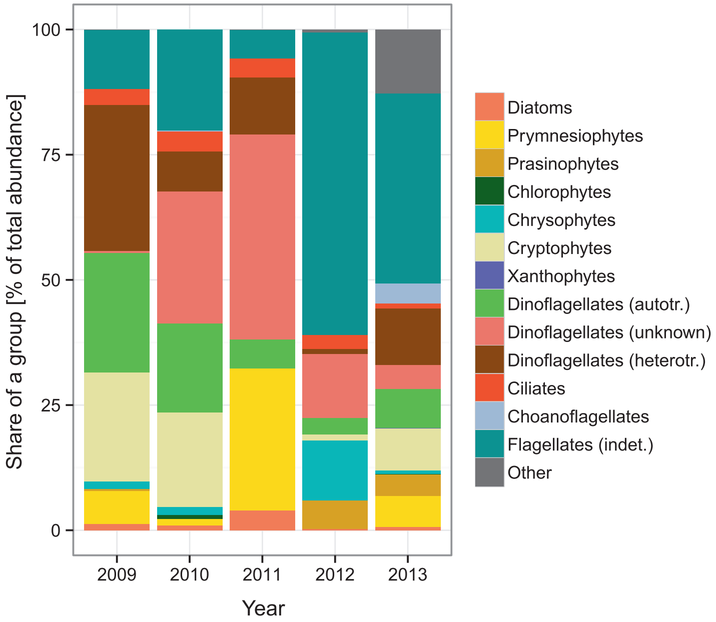

Fig. 6.18 Relative contribution (in terms of abundance) of the major taxonomic groups to total protist plankton at station Kb3 in July 2009–2013. Identification of taxonomic groups is based on microscopy. (NPI, unpublished data)

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.

Acknowledgements We thank the captain and crew of RV *Lance* and RV *Helmer Hanssen* for their assistance at sea. The Norwegian Polar Institute provided the summer CTD, Chl a, nutrient and phytoplankton data from 2009–2014 through the Environmental Monitoring of Svalbard and Jan Mayen (MOSJ) program. The summer Chl a, nutrient and phytoplankton data can be found at the Norwegian Data Centre (doi: https://data.npolar.no/dataset/2bff82dc-22b9-41c0-8348-220e7d6ca4f4).

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Chapter 7
Zooplankton in Kongsfjorden (1996–2016) in Relation to Climate Change

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Abstract Zooplankton in Kongsfjorden, Svalbard, is shaped by irregular advection of seawater from the West Spitsbergen Current as well as input of freshwater of glacial and riverine origin. The zooplankton community reflects contributions of Arctic vs. Atlantic water masses in the fjord, and is changing with increasing temperature and declining sea ice. Here, we review zooplankton studies from Kongsfjorden, and present new data from a 20-year time series (1996–2016) of zooplankton abundance/biomass in the fjord based on annual surveys during summer. During the last decade, the marine environment of the West Spitsbergen Shelf and adjacent fjords has undergone changes with increasing temperatures and volume of inflowing Atlantic Water and declining sea ice. Annual monitoring of mesozooplankton since 1996 has shown high seasonal, spatial, and inter-annual variation

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_7

in species abundance and biomass, and in the proportion of Atlantic and Arctic species. Inter-annual variations in species composition and abundance demonstrate fluctuating patterns related to changes in hydrography. “Warm years” in Kongsfjorden were characterized by higher abundances of Atlantic species, such as *Calanus finmarchicus*, *Oithona atlantica, Thysanoessa longicaudata* and *Themisto abyssorum*. Other krill species, particularly *Thysanoessa inermis* and to a lesser extent *T. longicaudata*, increased in abundance during the warming period in 2006–2007, mainly in the inner basin. “Cold years”, on the other hand, were characterized by higher abundance of *Themisto libellula*. There was no clear impact, however, of changes in environmental factors on the abundance or biomass of the Arctic species *Calanus glacialis* suggesting that the changes in environmental conditions have not reached critical levels for this species. The long-term zooplankton data demonstrate that some Atlantic species have become more abundant in the Kongsfjorden’s pelagic realm, suggesting that they may benefit from increasing temperature, and also that the total biomass of zooplankton has increased in the fjord implying potentially higher secondary production.

Keywords Zooplankton · Time-series · Arctic water · Sea ice · Atlantification · Advection · Fjord · Svalbard · Arctic

7.1 Introduction

The Arctic Archipelago Svalbard is located in a border area between Atlantic and Arctic regimes. Kongsfjorden (78° 59 N, 11–12° E) is an open fjord on the west coast of Spitsbergen, the largest of Svalbard islands (Fig. 7.1a). Connection of the fjord to the adjacent shelf and Fram Strait is allowed through Kongsfjordrenna, a deep channel without sill. Kongsfjorden is therefore largely influenced by advection of both Arctic Water from the coastal current and Atlantic Water from the West Spitsbergen Current (WSC) (Svendsen et al. 2002). The inter-annual variation in the strength of the WSC influences the range of advection of water masses into the Arctic including Kongsfjorden (Saloranta and Svendsen 2001). During winter and spring, the advection between the fjord and the shelf may be limited due to a density front forming in the fjord entrance. This density front usually breaks down during

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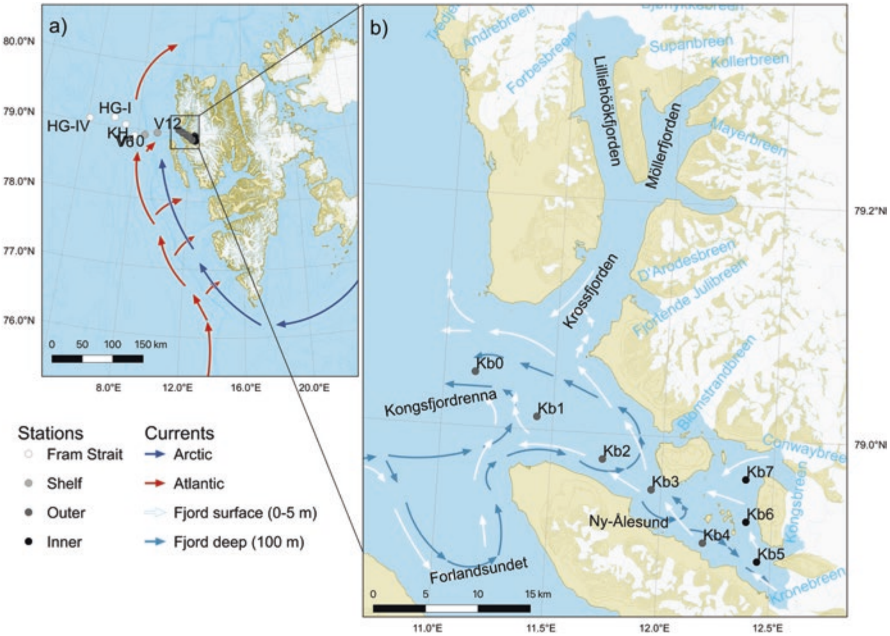

Fig. 7.1 Sampling stations in (**a**) Fram Strait with deep Hausgarten Stations (HG, KH) and stations on the shelf and continental slope (V6, V10, V12) with Atlantic and Arctic currents, (**b**) Kongsfjorden, with main circulation patterns indicated outside and inside the fjord

spring and summer (Cottier et al. 2005) allowing warm Atlantic and transformed Atlantic water masses to enter the fjord at intermediate depths on the south side and circulate in the outer-middle part of the fjord (Fig. 7.1b). The density gradient has become less pronounced after 2006, leading to larger advection of Transformed Atlantic Water (TAW) into the fjord also during winter (Tverberg et al., Chap. 3). Some of the Atlantic-origin waters may continue above the shallow (20 m deep) sill into the inner basin of the fjord (Fig. 7.1b), which is largely influenced by glacial run off and calving of icebergs (Lydersen et al. 2014). The discharge of fresh water and sediments from glaciers peak during the summer melting (Sundfjord et al. 2017). Surface currents, which are influenced by winds and tides, generally flow out of the fjord due to katabatic winds coming down from the glaciers in the inner bay. These surface currents flow along the north side of the fjord and travel via Krossfjorden before exiting (Ingvaldsen et al. 2001).

Kongsfjorden is relatively easily accessible despite its high-Arctic location. A zooplankton monitoring program has been established there in 1996. During the last decade, remarkable changes have occurred in the ocean climate around Svalbard and in Kongsfjorden. The WSC has warmed since 2004, and the core of the Atlantic Water reached the highest temperatures in 2006 and 2011 (Walczowski et al. 2012; Gluchowska et al. 2017). Ocean warming and increased air temperatures have also influenced Kongsfjorden, particularly during the last 20 years, with a positive slope

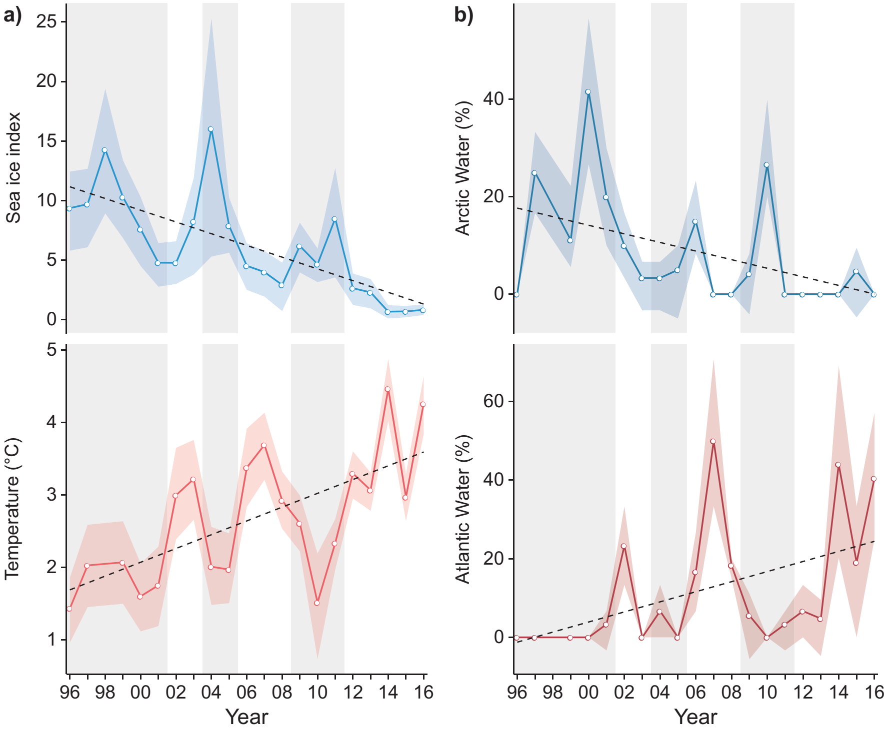

Fig. 7.2 (**a**) Sea ice index (blue) at Northwest Spitsbergen and temperature in Kongsfjorden (red), and (**b**) Arctic Water (%) and Atlantic water (%) in Kongsfjorden, from 1996 to 2016. Grey shading indicates cold years, and dashed lines are the best fitting linear models

for the long-term trend (Fig. 7.2). Mooring records (2002–2017) have shown that the warming trend has been strongest during the coldest months of the year (Geoffroy et al. 2018; Hop et al., Chap. 13). During summer, the percentage of Arctic Water has decreased in the fjord, whereas Atlantic Water has increased (Fig. 7.2b). A comparison of oceanographic transects in Kongsfjorden for warm vs. cold years shows that the Atlantic Water (> 3.0 °C, S > 34.65) and Transformed Atlantic Water (1.0–3.0 °C, S > 34.65) intrude further into the fjord during warm summers, and that the cold water masses are confined to the deep part of the fjord (Fig. 7.3).

Kongsfjorden used to have extensive fast-ice cover during winter, but a large inflow of Atlantic Water during the winter 2005–2006 (Cottier et al. 2007) forced the system into a warmer state with little fast-ice cover in the subsequent years, except for the winters of 2009 and 2011 when fast-ice was more extensive (Pavlova et al., Chap. 4). In the years after 2011, ice-coverage was limited to the inner part of the fjord for only short periods each year, and the ice has become progressively thinner with less snow on it during the monitored period 2003–2016 (Fig. 7.2a; Pavlova et al., Chap. 4).

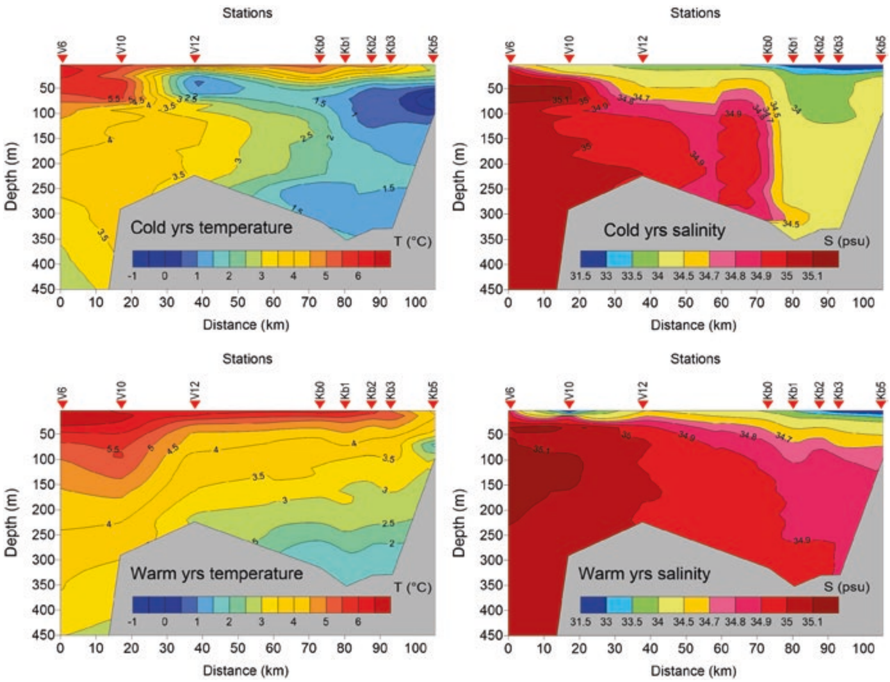

Fig. 7.3 Salinity and temperature profiles from cold years (1996–2001, 2004–2005, and 2009–2011) combined and warm years (2002–2003, 2006–2008, and 2012–2016) combined

Due to the geographic and oceanographic setting, with influence from advection and local processes as well as sea-ice, the pelagic community of Kongsfjorden is composed of both Atlantic and Arctic species (Hop et al. 2006; Walkusz et al. 2009; Ormanczyk et al. 2017). The proportions of zooplankton species with different biogeographic origins vary with the dynamics of water masses outside the fjord and their changing intrusions (Kwasniewski et al. 2003; Basedow et al. 2004; Willis et al. 2006, 2008). Changes observed in zooplankton community composition from sediment traps at the central HAUSGARTEN site of Fram Strait are also reflected in Kongsfjorden, but variations may not be synchronous for the areas (Soltwedel et al. 2016). The circulation pattern within the fjord affects the advection of zooplankton and their residence time in the fjord (Kwasniewski et al. 2003; Basedow et al. 2004). Within the inner part of the fjord, zooplankton can potentially become exposed to glacial run off leading to increased mortality (Weslawski et al. 2000; Zajaczkowski and Legezynska 2001; Urbanski et al. 2017).

Kongsfjorden is one of the most studied fjords of the Svalbard archipelago and numerous studies have focused on different aspects of the zooplankton community, such as life history strategies and population dynamics of copepod species (Kwasniewski et al. 2003; Lischka and Hagen 2005, 2007; Willis et al. 2006, 2008; Narcy et al. 2009; Daase et al. 2013), krill (Buchholz et al. 2010, 2012; Dalpadado et al. 2016), ctenophores (Falk-Petersen et al. 2002; Lundberg et al. 2006; Graeve et al. 2008), pteropods (Böer et al. 2005; Gannefors et al. 2005), seasonality (Walkusz et al. 2009; Lischka and Hagen 2016) and the effect of ocean climate variability on zooplankton communities (Hop et al. 2006). Recent studies (Dalpadado et al. 2016; Ormanczyk et al. 2017) indicate that the zooplankton community inside the fjord, containing a mix of resident and advected species, has changed substantially during the last decade. Other examples, such as studies from 1982 to 2016 on diet of black-legged kittiwakes (*Rissa tridactyla*) nesting in Kongsfjorden, have suggested changes in the pelagic food web towards "Atlantification" (Vihtakari et al. 2018).

This review consists of two parts. In Part I: Zooplankton community composition in Kongsfjorden, we review studies of different aspects of zooplankton ecology in Kongsfjorden, with emphasis on recent literature since Hop et al. (2006). In Part II: Trends in the zooplankton time-series, we: (1) Present unpublished time-series data obtained during the last 20 years (1996–2016) covering hydrography as well as zooplankton abundance and biomass. This dataset represents the longest record of its kind for an Arctic fjord. (2) Increase insight on possible climate and ocean change processes. In particular, we assess whether inter-annual differences in zooplankton abundance and biomass can be related to "cold-" and "warm-year" conditions in the fjord and whether observed long-term changes may be attributed to an increased "Atlantification" after a warming event in 2006 (Fig. 7.2; Cottier et al. 2007).

7.2 Materials and Methods

7.2.1 Sampling During 20-Year Time Series

Zooplankton has been sampled annually at standard stations in Kongsfjorden between 1996 and 2016 during July–August (dates include 13 July–28 August), except for 1998 (when no summer samples were taken). Sampling has been conducted along a transect including three stations in the inner basin (Kb7, Kb6, Kb5), five stations in the outer basin (Kb4, Kb3, Kb2, Kb1, Kb0), two stations at the shelf (V12, V10), and four stations off the shelf (V6, KH, HG-I, HG-IV; Table 7.1 and Fig. 7.1b). Depth-specific measurements of temperature and conductivity have been conducted prior to net sampling at each station using a ship-boarded CTD (Sea-Bird Electronics SBE911 plus). The vertical distribution of mesozooplankton was determined using a multiple plankton sampler (MultiNet type Midi, Hydro-Bios Kiel), consisting of five closing nets with 200 μm mesh size and 0.25 m^2 mouth opening.

Samples for taxonomical analyses were preserved in 4% hexamethylenetetramine-buffered seawater formaldehyde solution immediately after collection. The organisms were identified and counted under a stereomicroscope equipped with an ocular micrometre, according to standard procedures (Postel et al. 2000; Kwasniewski et al.

Table 7.1 Stations sampled (−) in Kongsfjorden, Svalbard 1996–2016

Area	Station	Latitude [N]	Longitude [E]	B. depth [m]	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Inner basin	Kb7	78° 57.99	12° 22.79	62																		–	–	–	–
	Kb6	78° 55.80	12° 23.11	71																		–	–	–	–
	Kb5	78° 53.79	12° 26.45	96					–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–
	Kb4	78° 54.63	12° 11.79	93														–							
Outer basin	Kb3	78° 57.24	11° 57.38	329	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Kb2	78° 58.68	11° 43.91	330	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Kb1	79° 00.67	11° 25.66	352	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Kb0	79° 02.78	11° 08.36	315					–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Shelf	V12	78° 58.79	09° 29.77	224									–		–		–	–	–	–	–	–	–	–	–
	V10	78° 55.96	08° 32.82	291							–		–		–	–	–	–	–	–	–	–	–	–	–
Shelf break	V6	78° 54.39	07° 46.24	1125						–	–		–		–	–		–	–		–	–	–		–
Fram Strait	KH	79° 03.00	07° 00.00	1150																	–	–			
	HG-I	79° 08.00	06° 05.54	1246																			–		
	HG-IV	79° 06.48	04° 36.00	1850																	–	–	–		

2003). In the laboratory, each zooplankton sample was first scanned for macro-zooplankton (organisms with total length > 5 mm), which were picked out, identified and counted in the entirety. The remaining mesozooplankton size fraction was examined for taxonomic composition and abundance by a subsampling method (Postel et al. 2000). Subsamples of 2-ml volume were taken using a macropipette (an equivalent of the Stempel pipette) and all organisms in each subsample were identified and enumerated. Subsampling was continued until at least 500 individuals per sample were identified (Postel et al. 2000). *Calanus* spp. were identified to species for each developmental stage based on the description by Kwasniewski et al. (2003). Other zooplankters were identified to the lowest possible taxonomic level based on available literature.

Zooplankton species found in Kongsfjorden were grouped into main taxonomic groups or size-groups for copepods. *Calanus finmarchicus* and *C. glacialis* were kept as separate species due to their significant contribution to the mesozooplankton biomass. Small copepods were defined as copepods <2.5 mm total length as adults, which mainly included *Oithona similis, Pseudocalanus* spp. and *Microcalanus* spp. Other copepods encompassed copepod species >2.5 mm, excluding *Calanus* spp. Meroplankton comprised Cirripedia nauplii and cypris, and larval stages of Bivalvia, Bryozoa, Echinodermata, Gastropoda and Polychaeta. Other crustaceans included amphipods, euphausiids, cumaceans, mysids, decapods, isopods, ostracods, cladocerans and tanaidaceans. Other zooplankton were non-crustacean zooplankters such as hydrozoans, ctenophores, appendicularians, chaetognaths, pteropods, polychaetes, nemerteans, and larval fishes.

Original data represent abundance values of zooplankters (ind. m^{-3}) for different depth strata (bottom-200-100-50-20-0 m or bottom-600-200-50-20-0 m). Abundance values were converted to biomass estimates (mg dry mass m^{-3}) for statistical comparisons, to reduce potential bias caused by small copepodid stages, which can outnumber older stages seasonally, and for which occurrence can vary from year to year. The dry mass conversion factors were gathered from published sources or measured by the authors (Appendix Table 7.8). The biomasses/abundances for each species or a group of species were summed up by stage, size group and/or species and averaged over depth strata for each station:

$$\sum_{i=1}^{n} \frac{a_i d_i}{d_i}$$

Where a_i is the biomass or abundance of species a at depth stratum i, d_i is the sampled distance for depth stratum i in meters, and n is the number of depth strata per net haul at a station. Resulting averaged estimates for species or a group of species for separate net hauls at each station were used as statistical replicates by grouping the stations according to the Inner basin, the Outer basin, the Shelf, and Fram Strait, named as regions from here on.

7.2.2 Macrozooplankton Sampling

The MultiNet used in our time series has been used during many other studies performed in Kongsfjorden making our observation comparable (Appendix Table 7.9). Amphipods and euphausiids were regularly present in our MultiNet time-series (see Fig. 7.7), but are generally undersampled by this type of net (Pearcy et al. 1983; Søreide et al. 2003; Blachowiak-Samolyk et al. 2017). We therefore combined the abundance and biomass estimates of amphipods and euphausiids from the Multinet with data retrieved from MIK and Tucker Trawl hauls in Kongsfjorden, when considering seasonal variability (Fig. 7.8). The MIK net (2-m diameter opening, 14 m long with main net bag of 1.2 mm mesh size, and the terminal 1.5-m part of 0.5 mm mesh size) has been deployed at the same stations and times as the MultiNet since 2006. Vertical hauls with MIK were taken from ~20 m above the bottom to the surface at a speed of 0.5 ms^{-1} (see Dalpadado et al. [2016] for details). For population dynamics of krill, we included data collected in Kongsfjorden since 2006 with an opening/closing Tucker Trawl with 1 mm mesh size, towed obliquely from near bottom (95–200 m) to the surface (see Buchholz et al. [2010] for details).

7.2.3 Statistical Analyses

Spatial and temporal differences were examined using mean values, bootstrapped confidence intervals (Davison and Hinkley 1997; Canty and Ripley 2017), and nonparametric statistical tests (Kruskal-Wallis [R Core Team 2018], and Dunn's Kruskal-Wallis multiple comparisons (Dunn 1964; Ogle 2018). The difference in biomass between cold and warm years was visualized using logarithmic response ratios (LnR) and 95% confidence intervals for LnR estimates using a *t*-distribution instead of normal distribution as described in Hedges et al. (1999). The significance (alpha level 0.05) of LnR estimates was confirmed using nonparametric two-sample Wilcoxon tests (R Core Team 2018). Patterns in zooplankton community structure were related to explanatory variables (sampling depth, average temperature and salinity, year, location of station along the transect, region, type of year [warm vs. cold]) using a principal component analysis (PCA) and redundancy analyses (RDA; Oksanen et al. 2018) on natural logarithm +1 transformed zooplankton abundance estimates. For this type of analysis, abundance gives a more detailed pattern than biomass, which is dominated by a few bulky species. The best fitting explanatory variables, assessed using the envfit function from Oksanen et al. (2018), were further used to constrain the ordinations, which were split to Inner and Outer basin stations and to Shelf and Fram Strait stations to avoid interactions that were present in the dataset.

7.2.4 *Contribution of Arctic and Atlantic Water Masses in the Fjord*

Percentage contribution of Arctic and Atlantic Water at each station in the Inner and Outer basin was estimated from CTD data accompanying each depth-stratified MultiNet catch, as statistical replicates. The water type definition followed Cottier et al. (2005) and was determined from averaged temperature and salinity values from CTD casts for each depth stratum sampled by MultiNet. Consequently, a single water type was allocated to each depth stratum representing average conditions for the MultiNet sample. Percentage contribution of Arctic and Atlantic water-type zooplankton species was calculated for each sampling event by dividing the corresponding zooplankton counts by the total number of depth strata (typically 5 or 6). These percentages were then used to calculate average water-type contributions in the fjord, with bootstrapped 95% confidence intervals for each year. The water-type definition algorithm is included in the PlotSvalbard package (define_water_type; Vihtakari 2018). All statistics were run using R (R Core Team 2018).

7.3 Part I: Zooplankton Community Composition in Kongsfjorden

7.3.1 *Zooplankton Taxa in Kongsfjorden*

In total 92 species and five genera have been identified in zooplankton samples from Kongsfjorden, and some organisms were identified to higher taxonomic levels, particularly for phyla including meroplankton (Table 7.2). Most of these species were included in our long-term series (1996–2016), as specific groups or lumped as others (Figs. 7.4 and 7.5). Our data show that the mesozooplankton community in Kongsfjorden was dominated by copepods (43 species or 47 taxa, with some identifications to higher level than species; Fig. 7.4). In terms of numbers, small-sized (< 2.5 mm) copepods such as *Oithona similis*, *Pseudocalanus* spp. and *Microcalanus* spp. generally dominated. *Calanus finmarchicus* and *C. glacialis* were the most common larger calanoid copepods. Other important groups were amphipods (10 species), typically consisting of the pelagic hyperiid *Themisto abyssorum* and *Themisto libellula* and other, less frequently found mesopelagic (e.g. *Scina borealis*) or ice-associated species (*Apherusa glacialis* and *Gammarus wilkitzkii*), euphausiids (4 species, mainly *Thysanoessa raschii*, *T. inermis*, and *T. longicaudata*) and Other Crustacea. Meroplankton (12 taxa) was among the abundant groups and included mainly larval forms of bivalves, echinoderms, polychaetes, and cirripedes, as well as decapod zoea larvae of shrimps (*Pandalus borealis* and *Sabinea septemcarinata*). Cnidarians (10 taxa) included different species of Hydrozoa with numerical dominance of *Aglantha digitale*, and not identified

Table 7.2 List of species and taxa found in zooplankton samples from Kongsfjorden in different studies (see Appendix Table 7.8). Taxa collected in the annual surveys (1996–2016) are indicated (*), and these are summarized in Fig. 7.4. Some species are present in the plankton as larval forms (L)

Copepoda (Arthropoda)			
Calanoida			
*Acartia longiremis**	*Microcalanus* spp.*	*Spinocalanus horridus**	**Harpacticoida**
*Aetideopsis minor**	*Neoscolecithrix farrani**	*Spinocalanus longicornis**	Harpacticoida indet.*
*Aetideopsis rostrata**	*Paraeuchaeta barbata**	*Temora longicornis*	*Microsetella norvegica**
*Aetideus armatus**	*Paraeuchaeta glacialis**	*Temorites brevis**	**Monstrilloida**
*Augaptilus glacialis**	*Paraeuchaeta norvegica**	*Tharybis groenlandicus**	Monstrilloida indet.*
*Bradyidius similis**	*Paraheterorhabdus compactus**	*Undinella oblonga**	**Mormonilloida**
*Calanus finmarchicus**	*Pertsovius fjordicus*	*Xantharus siedleckii**	*Neomormonilla minor**
*Calanus glacialis**	*Pleuromamma robusta**	**Cyclopoida**	**Siphonostomatoida**
*Calanus hyperboreus**	*Pseudocalanus acuspes**	Cyclopoida indet.*	*Hyalopontius* sp.
*Chiridius obtusifrons**	*Pseudocalanus minutus**	*Homeognathia brevis**	
*Gaetanus brevispinus**	*Pseudochirella spectabilis**	*Oithona atlantica**	
*Gaetanus tenuispinus**	*Rhincalanus nasutus**	*Oithona similis**	
*Heterorhabdus norvegicus**	*Scaphocalanus brevicornis**	*Oncaea parila**	
*Mesaiokeras spitsbergensis**	*Scaphocalanus magnus**	*Oncaea pumilis*	
*Metridia longa**	*Scolecithricella minor**	*Triconia borealis**	
*Metridia lucens**	*Spinocalanus antarcticus**	*Triconia conifera**	
Other Crustacea (Arthropoda)			
Amphipoda	**Euphausiacea**	**Decapoda**	**Ostracoda***
*Apherusa glacialis**	*Meganyctiphanes norvegica**	*Eusergestes arcticus**	*Boroecia borealis*
*Cyclocaris guilelmi**	*Nematoscelis megalops*	*Hyas araneus* (L)*	*Boroecia maxima*
*Eusirus holmii**	*Thysanoessa inermis**	*Hymenodora glacialis**	*Discoconchoecia elegans*
*Hyperia galba**	*Thysanoessa longicaudata**	*Pagurus pubescens* (L)*	*Obtusoecia obtusata*
*Hyperoche medusarum**	*Thysanoessa raschii**	*Pandalus borealis* (L)*	**Cladocera**
*Onisimus glacialis**	**Cumacea**	*Sabinea septemcarinata* (L)*	*Evadne nordmanni**

(continued)

Table 7.2 (continued)

*Scina borealis**	*Leucon* sp.*	**Isopoda**	**Tanaidacea**
*Themisto abyssorum**	**Mysida**	Bopyridae indet. (L)*	**Cirripedia***
*Themisto libellula**	*Boreomysis arctica**	Isopoda indet. (L)*	
*Gammarus wilkitzkii**	*Pseudomma truncatum**		
Other phyla			
Cnidaria	**Anthozoa (L)**	**Annelida**	**Echinodermata (L)***
Hydrozoa	**Ctenophora**	Polychaeta (L)*	**Chaetognatha**
*Aeginopsis laurentii**	*Mertensia ovum**	*Pelagobia* sp.*	*Eukrohnia hamata**
*Aglantha digitale**	*Beroë cucumis**	*Tomopteris* spp.*	*Parasagitta elegans**
*Botrynema ellinorae**	**Mollusca**	Typhloscolecidae (L)*	*Pseudosagitta maxima**
Bougainvillia spp.*	**Bivalvia (L)***	**Nematoda**	**Chordata**
*Dimophyes arctica**	**Pteropoda**	**Nemertea (L)***	**Appendicularia**
*Halitholus cirratus**	*Clione limacina**	**Platyhelminthes**	*Fritillaria borealis**
*Nanomia cara**	*Limacina helicina**	**Turbellaria**	*Oikopleura vanhoeffeni**
Sarsia spp.*	*Limacina retroversa**	**Bryozoa (L)***	*Oikopleura labradoriensis**
Siphonophora*	**Gastropoda (L)***	**Rotifera**	**Ascidiacea (L)***
Scyphozoa*	**Cephalopoda***	**Enteropneusta (L)**	**Pisces (L)***

species of Siphonophora and Scyphozoa. The ctenophores *Beroë cucumis* and *Mertensia ovum* were typically present, as were pteropods (*Limacina helicina*, *L. retroversa* and *Clione limacina*) and chaetognaths (*Parasagitta elegans*, *Eukrohnia hamata* and *Pseudosagitta maxima*). Chordates were larval fishes and appendicularians (*Fritillaria borealis*, *Oikopleura venhoffeni* and *O. labradorensis*).

Species of Arctic origin included the copepods *C. glacialis*, *Triconia borealis*, *C. hyperboreus* and *Pseudocalanus acuspes*, the amphipod *T. libellula*, and the cnidarian *Aglantha digitale*. Species representative of Atlantic water masses typically included the copepods *C. finmarchicus* and *Oithona atlantica*, the amphipod *T. abyssorum*, the pteropod *L. retroversa*, and the euphausiids *T. longicaudata* and *Meganyctiphanes norvegica*.

7.3.2 Small- to Medium-Sized Copepods

Small-to medium-sized copepods (<2.5 mm in length at their adult stage) are mainly represented by the genera *Microcalanus*, *Pseudocalanus*, *Oithona* and *Triconia*. These are species that generally occur in high numbers during most of the year, have herbivorous or omnivorous feeding patterns, high weight-specific ingestion rates and may produce offspring throughout the year (Svensen et al. 2011). They generally contribute little to biomass because of their small body sizes, but can be important grazers on the small phytoplankton fraction (<10 μm). However, these species - and in particular their young copepodid stages - are typically undersampled in zooplankton surveys, unless finer mesh sizes (60–90 μm) are used for collecting samples.

Among small copepods, the cyclopoid *O. similis* is the most dominant species in Kongsfjorden throughout the year contributing with 30–80% to the abundance of holoplankton and peaking in abundance towards the winter season (November) (Hop et al. 2002; Lischka and Hagen 2005; Piwosz et al. 2009; Walkusz et al. 2009; Kwasniewski et al. 2013; Gluchowska et al. 2016; Ormanczyk et al. 2017). Although small in size, the standing stock biomass of *O. similis* in Kongsfjorden can amount to 0.6–17% of the zooplankton biomass of the size fraction from 0.2 to 10 mm during summer-early autumn (Hop et al. 2002; Ormanczyk et al. 2017); our long-term dataset indicates 2% on average within 0.1–9.0% range. *Oithona similis* is a cosmopolitan species adapted to a wide range of environmental conditions (Fransz and Gonzalez 1995; Gallienne and Robins 2001; Ward and Hirst 2007). Because of this ability, *O. similis* may benefit from the on-going temperature increase in the Arctic (Narcy et al. 2009) possibly due to shorter life span with increasing temperature (Huntley and Lopez 1992; Møller et al. 2012). A large increase in abundance of *O. similis* in Kongsfjorden during the earlier warming period (2001–2003) in Kongsfjorden supports this notion (Hop et al. 2006; Willis et al. 2006).

Oithona similis is an opportunistic omnivorous feeder that also uses detritus, faecal pellets and particle-associated bacteria as food source (Kattner et al. 2003; Castellani et al. 2005; Lischka and Hagen 2007). This allows the species to reproduce continuously throughout the year with two main reproductive periods in May/June and August/September. Accordingly, all copepodid stages occur throughout the year in Kongsfjorden, although in varying proportions (Lischka and Hagen 2005). The species stays active in the upper water column also during winter (Conover and Huntley 1991; Lischka et al. 2007).

The role of lipid storages in *O. similis* has been thoroughly studied in Kongsfjorden. *Oithona similis* stores lipids in form of wax esters and to some extent also triacylgylcerols (Narcy et al. 2009). Winter survival, development, gonad maturation, egg production and the first main reproductive period in May/June are at least partially fuelled by internal lipid reserves that are continuously depleted during the dark season while replenishment of storage lipids occurs in late summer (August/September), along with still on-going reproductive processes (Lischka and Hagen 2007; Lischka et al. 2007). According to Narcy et al. (2009), the realization of *O. similis*' life cycle strategy may vary inter-annually and the lipid stores might be more of an adaptation to short-term food variability than to seasonal variation. In contrast to Lischka and Hagen (2005), Narcy et al. (2009) showed an increase in wax ester content in *O. similis* females and CV copepodids even before the maximum accumulation of phytoplankton biomass in spring and subsequent usage of these lipids during the main reproductive period in June. This indicates that *O. similis* can utilize other food sources, including particulate organic matter of high

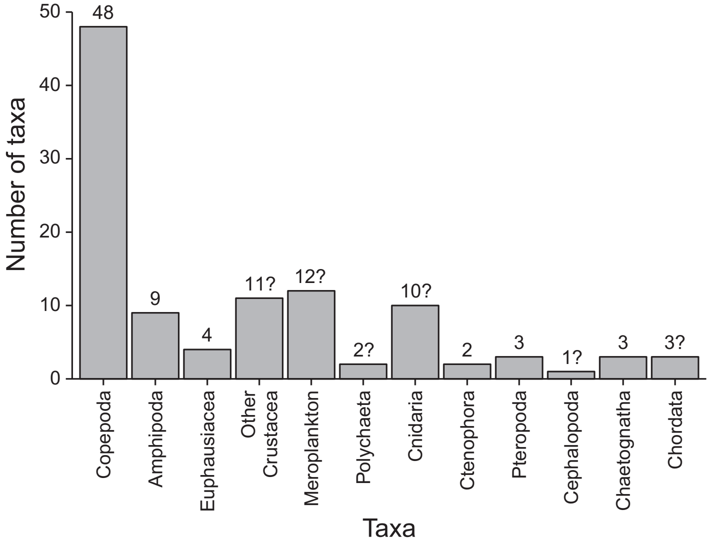

Fig. 7.4 Numbers of taxa (species and higher taxonomic groups) in the mesozooplankton samples collected in Kongsfjorden during 1997–2016 by MultiNet (200 μm mesh size). Numbers marked with question mark include higher level unidentified taxa and actual species numbers are uncertain

nutritional value (i.e. with high proportion of polyunsaturated fatty acids), to accumulate storage lipids in spring.

Oithona atlantica occurs regularly in Kongsfjorden, but is much less abundant than its congener *O. similis*. Throughout the year, the share of *O. atlantica* to the mesozooplankton abundance is generally <1% (e.g. Hop et al. 2006; Piwosz et al. 2009; Walkusz et al. 2009; Lischka and Hagen 2016). In our time series, we detected a trend of increasing abundance of *O. atlantica* between the years 2000 and 2002 (Hop et al. 2006), while the mean contribution of the species to the mesozooplankton community abundance was approximately 1% (range 0–5.2%).

Two *Microcalanus* species, *M. pygmaeus* and *M. pusillus*, and one *Triconia* species, *T. borealis* occur in Kongsfjorden (Walkusz et al. 2009). Compared to *O. similis* and *Pseudocalanus* sp. (see below) they constitute a much lower share of the total mesozooplankton abundance. *Microcalanus* spp. and *T. borealis* are relatively abundant year-round with clear peak in abundance in November (Lischka and Hagen 2016). Their seasonal contributions to mesozooplankton abundance range from 0–9% to 0–6%, respectively (e.g. Walkusz et al. 2003, 2009; Hop et al. 2002, 2006; Kwasniewski et al. 2013; Gluchowska et al. 2016; Ormanczyk et al. 2017). Our long-term data indicate that *Microcalanus* spp. was on average more abundant (3.0%) than *T. borealis* (1.5%). However, Lischka and Hagen (2016) found that abundance proportions of these species varied seasonally, for *Microcalanus* spp. from 0.1% (September 1998) to 29% (May 1999), and for *T. borealis* from 2% (May 1999) to 12% (August 1998). The distinctly higher proportions in their study were likely related to the use of a finer mesh size of 100 μm. In studies using 180–200 μm

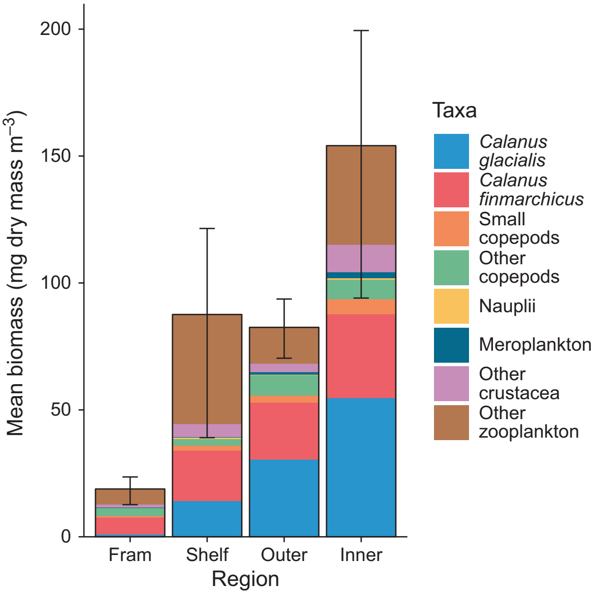

Fig. 7.5 Spatial distribution of zooplankton biomass along the Kongsfjorden transect from Fram Stait to the Inner fjord basin, combined for the years 1996–2016 based on MultiNet (200 μm mesh size) samples. Height of bars indicate the average zooplankton biomass using biomass values from stations sampled during different years as statistical replicates. Stacked coloured parts indicate the contribution of each zooplankton group to this total biomass. Error bars indicate bootstrapped 95% confidence intervals for the total mean biomass estimate. Cnidaria and Ctenophora have been excluded from the estimates due to non-representative sampling of these phyla

mesh size, *Microcalanus* spp. and *T. borealis* typically make up about 1% of the biomass in the small and medium zooplankton size-fraction (Ormanczyk et al. 2017), or less (0.45%) as observed in our long-term data. These species predominantly dwell below 50 m depth in Kongsfjorden (Walkusz et al. 2009; Lischka and Hagen 2016). *Microcalanus* spp. has two major reproductive periods, in February/ March and in June/July. For *T. borealis*, year-round reproductive activities have been suggested with a peak in May/June (Lischka and Hagen 2016).

Pseudocalanus is among the most dominant herbivorous copepod genera and the second-most abundant small copepod in Kongsfjorden, but it is clearly less abundant than *O. similis* (Table 7.3; Piwosz et al. 2009; Walkusz et al. 2009; Gluchowska et al. 2016; Ormanczyk et al. 2017). As for *O. similis*, *Pseudocalanus* spp. has increased in abundance in Kongsfjorden since 1996 (Hop et al. 2006). Lischka and Hagen (2016) observed high variability in the percent contribution of *Pseudocalanus* spp. to the mesozooplankton community from 1% (June 1999) to 31% (September 1998). Walkusz et al. (2009) similarly reported 0.8% in spring (April) and 21% in autumn (September). Abundance peaks of *Pseudocalanus* spp. have been observed late in autumn (November) prior to their overwintering (Lischka and Hagen 2005), and the relative abundance of the species may occasionally be high in late winter-early spring (e.g. 28% in March 1999; Lischka and Hagen 2016). The abundance of

Table 7.3 Abundance (ind. m^{-3}) of copepods in Kongsfjorden during the periods 1996–2006 and 2007–2016, averaged over all sampled stations. The copepodid developmental stages (from stage 1 to stage 6 female or male, C1–C6F/M, which contributed to the summary presented, are listed next to the species names. No specified stage indicates all copepodids C1–C6 are included

	1996–2006		2007–2016	
	All stations		All stations	
Copepoda	Mean ± StDev	Max	Mean ± StDev	Max
Acartia longiremis	4.8 ± 10.9	49.9	4.2 ± 6.9	29.0
Aetideidae indet. C1–C3	0.6 ± 1.7	7.6	1.6 ± 2.4	15.9
Aetideopsis minor C4–C6	0.0 ± 0.0	0.1	0.1 ± 0.6	5.9
Aetideopsis rostrata C4–C6	0.0 ± 0.0	0.0	0.0 ± 0.1	0.4
Aetideus armatus C4–C6	0.0 ± 0.0	0.0	0.0 ± 0.0	0.1
Augaptilus glacialis			0.0 ± 0.0	0.0
Bradyidius similis C4–C6	3.6 ± 8.6	50.6	0.6 ± 3.0	26.4
Calanus finmarchicus	155.2 ± 89.3	415.9	456.7 ± 578.9	3331.8
Calanus glacialis	103.1 ± 94.9	408.8	91.6 ± 92.3	437.8
Calanus hyperboreus	12.8 ± 16.5	111.5	8.4 ± 10.8	69.5
Chiridius obtusifrons C4–C6	0.0 ± 0.0	0.0	0.0 ± 0.1	0.8
Copepoda nauplii	107.3 ± 126.3	583.9	68.9 ± 77.7	496.4
Disco sp. C4–C6			0.0 ± 0.0	0.1
Gaetanus brevispinus C4–C6			0.0 ± 0.0	0.4
Gaetanus tenuispinus C4–C6	0.0 ± 0.1	0.4	0.0 ± 0.1	1.0
Harpacticoida	1.0 ± 3.0	20.3	0.3 ± 0.6	2.5
Heterorhabdus norvegicus	0.1 ± 0.3	2.0	0.1 ± 0.2	1.0
Mesaiokeras spitsbergensis	0.1 ± 0.2	1.2		
Metridia longa	21.5 ± 23.0	101.7	14.3 ± 13.9	73.2
Microcalanus spp.	31.4 ± 23.0	90.6	39.3 ± 31.5	242.2
Microsetella norvegica	0.0 ± 0.0	0.1	0.1 ± 0.2	1.1
Monstrilloida indet. C6F	0.0 ± 0.1	0.7	0.0 ± 0.1	0.4
Neomormonilla minor C5–C6			0.0 ± 0.0	0.3
Neoscolecithrix farrani C4–C6	0.2 ± 1.3	8.8	0.0 ± 0.1	1.0
Oithona atlantica C5–C6	7.9 ± 10.0	38.5	16.8 ± 24.0	194.1
Oithona similis	666.5 ± 786.1	3927.5	560.6 ± 593.7	3419.9
Oncaea parila C6F			0.0 ± 0.0	0.4
Oncaea spp. C6F			0.5 ± 3.7	35.6
Paraeuchaeta barbata C6	0.0 ± 0.0	0.0	0.0 ± 0.0	0.4
Paraeuchaeta glacialis C6	0.0 ± 0.0	0.0	0.0 ± 0.1	0.8
Paraeuchaeta norvegica C6	0.0 ± 0.0	0.1	0.0 ± 0.1	0.6
Paraeuchaeta spp. C1–C5	0.1 ± 0.2	0.9	0.5 ± 0.8	3.8
Paraheterorhabdus compactus C4–C6			0.0 ± 0.0	0.0
Pleuromamma robusta C6F	0.0 ± 0.0	0.1	0.0 ± 0.1	0.4
Pseudocalanus acuspes C6F	15.5 ± 26.6	135.7	3.8 ± 6.8	47.8
Pseudocalanus minutus C6F	3.5 ± 5.0	29.8	3.7 ± 5.2	33.3

(continued)

Table 7.3 (continued)

	1996–2006		2007–2016	
	All stations		All stations	
Copepoda	Mean ± StDev	Max	Mean ± StDev	Max
Pseudocalanus spp. C1–C5, C6M	268.3 ± 462.5	2314.4	158.5 ± 161.0	855.1
Pseudochirella spectabilis C4–C6			0.0 ± 0.0	0.0
Rhincalanus nasutus C4–C6			0.0 ± 0.0	0.4
Scaphocalanus brevicornis			0.0 ± 0.0	0.4
Scaphocalanus magnus			0.0 ± 0.0	0.1
Scolecithricella minor	0.1 ± 0.2	0.6	0.3 ± 0.4	1.9
Spinocalanus antarcticus			0.0 ± 0.0	0.2
Spinocalanus horridus C4–C6			0.0 ± 0.0	0.4
Spinocalanus longicornis C6			0.0 ± 0.0	0.2
Spinocalanus spp. C1–C6	0.0 ± 0.0	0.0	0.0 ± 0.1	0.4
Temorites brevis			0.0 ± 0.0	0.0
Tharybidae indet. C4–C6			0.0 ± 0.1	0.4
Tharybis groenlandicus C6			0.0 ± 0.0	0.0
Triconia borealis C6	5.0 ± 11.4	62.6	20.4 ± 27.7	216.4
Triconia conifera C6F	0.0 ± 0.0	0.0	0.0 ± 0.1	0.8
Triconia/Oncaea spp. C1–C5	0.1 ± 0.3	1.6	0.1 ± 0.3	1.6
Undinella oblonga C4–C6			0.0 ± 0.0	0.0
Xantharus siedleckii	0.0 ± 0.1	0.4	0.0 ± 0.0	0.2

Missing values indicate zero occurrences, while values marked 0.0 mean <0.04 ind. m^{-3}

Pseudocalanus spp. is generally higher in the centre of the fjord than at stations further out (Table 7.5; Walkusz et al. 2009). The biomass contribution of *Pseudocalanus* spp. to the zooplankton size fraction, ranging from 0.2 to 10 mm, was estimated to 2% during summer-early autumn (Ormanczyk et al. 2017).

A mixture of three *Pseudocalanus* species (*P. minutus, P. acuspes* and *P. moultoni*) co-occurs in Kongsfjorden, and their proportion depends on environmental conditions (Aarbakke et al. 2017). *Pseudocalanus minutus* dominated during 2005–2009, although not in 2004 when about 50% of the specimen found were *P. acuspes* (Aarbakke et al. 2017). The share of *P. moultoni* varied between about 5% and 25%, although this species was not present in 2007. *Pseudocalanus minutus* and *P. moultoni* are more oceanic species associated with Atlantic Water, while *P. acuspes* is a coastal/shelf species associated with cold Arctic Water that is subject to mixing processes on the shelf (Cottier et al. 2005). The species composition may vary seasonally with dominance of *P. minutus* during spring and *P. acuspes* during summer and autumn in 2002 (Walkusz et al. 2009). *Pseudocalanus moultoni* was for the first time recorded in Kongsfjorden in summer 2004, based on molecular techniques (Aarbakke et al. 2017). However, the majority of studies present abundance or biomass data for *Pseudocalanus* at the genus level because of difficulties in identification of individuals for the entire size- and age spectrum based on morphology.

Pseudocalanus minutus has a 1-year life cycle in Kongsfjorden with reproduction taking place in May/June. During this time, adult females and males represent a significant share on the total population. The dominant overwintering stages are copepodids C3, C4, and C5 (Lischka and Hagen 2005). According to the lipid signature, *P. minutus* is an opportunistic feeder with predominance for herbivore nutrition exploiting the diatom bloom in spring and changing to a flagellate-based diet during summer-autumn, and omnivorous/carnivorous low-level feeding during winter (Lischka and Hagen 2007; Lischka et al. 2007). This species uses lipid deposits (wax esters) to develop into copepodid stages C3 and C4 in summer/autumn and for gonad maturation in C5 and females during the dark season. Final gonad maturation and reproduction seem to depend on the spring phytoplankton bloom (Lischka and Hagen 2007; Lischka et al. 2007). Whether or not *P. acuspes* successfully reproduces in Kongsfjorden is unclear (Lischka and Hagen 2005), and little is known about *P. moultoni* in the fjord, except that it is present (Aarbakke et al. 2017).

7.3.3 Calanus

Calanoid copepods of the genus *Calanus* dominate the mesozooplankton community in Kongsfjorden in terms of biomass (Fig. 7.5; Kwasniewski et al. 2003; Walkusz et al. 2009). The populations of the Atlantic *Calanus finmarchicus* and the Arctic *C. glacialis* in Kongsfjorden consist of local and advected individuals, with the proportions of each varying annually (Table 7.5). The relative abundances of *C. finmarchicus* and *C. glacialis* in Kongsfjorden likely depend on the timing and volume of Atlantic and Arctic water intrusions and, thus, on the inflow of Atlantic Water (Tverberg et al., Chap. 3). The larger *C. hyperboreus*, which is a deep-water species (Hirche 1997), was only present in low numbers in Kongsfjorden and does not contribute much to the total abundance of *Calanus* (Table 7.5).

Calanus spp. have been extensively studied in Kongsfjorden (Kwasniewski et al. 2003; Walkusz et al. 2009; Daase et al. 2013; Kwasniewski et al. 2013). A 1-year life cycle has been suggested for *C. finmarchicus* (Kwasniewski et al. 2003), while *C. glacialis* may need 1–2 years to fulfil its life cycle (Daase et al. 2013). Seasonal accumulation of lipid stores is linked to the different life strategies of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* (Scott et al. 2000; Falk-Petersen et al. 2009). *Calanus* spp. conduct seasonal vertical migrations with descent to overwintering depth taking place at the end of the summer. In Kongsfjorden, the majority of the population is usually found at depth by the end of July and in August, although the timing may vary among years (Kwasniewski et al. 2003; Walkusz et al. 2009; Daase et al. 2013). The overwintering populations remain at depth during autumn and early winter. Recent studies during the polar night have shown that the ascent from overwintering depth occurs much earlier than previously assumed, and both *C. finmarchicus* and *C. glacialis* are distributed all over the water column as early as late

January or early February (Daase et al. 2014; Berge et al. 2015a, b; Grenvald et al. 2016). The early spring population is dominated by females and overwintering stages (C4 and C5), and the new generation appears before or during the spring bloom and develops rapidly over the summer (June and July) to overwintering stages (Walkusz et al. 2009; Daase et al. 2013). Reproductive strategies vary between *C. finmarchcius* and *C. glacialis*, with the latter being able to mature and reproduce eggs prior to the spring bloom based on its large lipid stores (capital breeding; Varpe 2012). Thus, females of *C. glacialis* are abundant prior to the spring bloom and young copepodids are already present at the onset of the bloom (Daase et al. 2013). Energy reserves accumulated for overwintering become depleted in *C. finmarchicus* and, therefore, this species relies on the spring bloom for reproduction (income breeding; Varpe et al. 2009). As a result, the new generation appears later than that of *C. glacialis*. These differences in reproductive strategies may explain the high variability in *C. finmarchicus* abundance in Kongsfjorden (Table 7.3; Kwasniewski et al. 2003). *Calanus glacialis* shows high flexibility in reproductive strategies as an adaptation to the environmental constraints of Arctic shelf seas (Daase et al. 2013) and may be more successful to reproduce under high-Arctic conditions than *C. finmarchicus*. The relatively stable abundance of *C. glacialis* in Kongsfjorden indicates the presence of a local population, while the high variability in *C. finmarchicus* indicates that the population is likely maintained by both local and advected individuals (Kwasniewski et al. 2003).

7.3.4 Amphipods

Amphipods show large spatial and temporal variability, with higher abundances in the innermost part of the fjord (Fig. 7.6; Dalpadado et al. 2016). The inner part is dominated by the Arctic *Themisto libellula* and the outer parts by the boreal-Atlantic *T. abyssorum* (Dalpadado et al. 2016; Legeżyńska et al. 2017). The Arctic species typically has higher abundance and biomass during cold year, whereas *T. abyssorum* is more abundant during warm periods (Hop et al. 2006). Three cohorts of *T. libellula* have been recorded in Kongsfjorden, and this species likely has two spawning seasons (March–April) in the fjord within their 3-year life span (Dale et al. 2006). As a carnivore species, its growth pattern is similar to carnivorous krill, *M. norvegica*, which feed throughout the winter (Falk-Petersen 1985). The life span of *T. abyssorum* was found to be 1 year in the Norwegian Sea, and 2 years in European Arctic seas (Koszteyn et al. 1995). Ice-associated amphipods, such as *Apherusa glacialis* and *Gammarus wilkitzkii* are occasionally found in Kongsfjorden (Table 7.2). Their occurrence is most probably associated with presence of drifting sea ice in the fjord or on the adjacent shelf, and, thus, their low abundance during summer (Table 7.4) reflects the recent decline in sea ice.

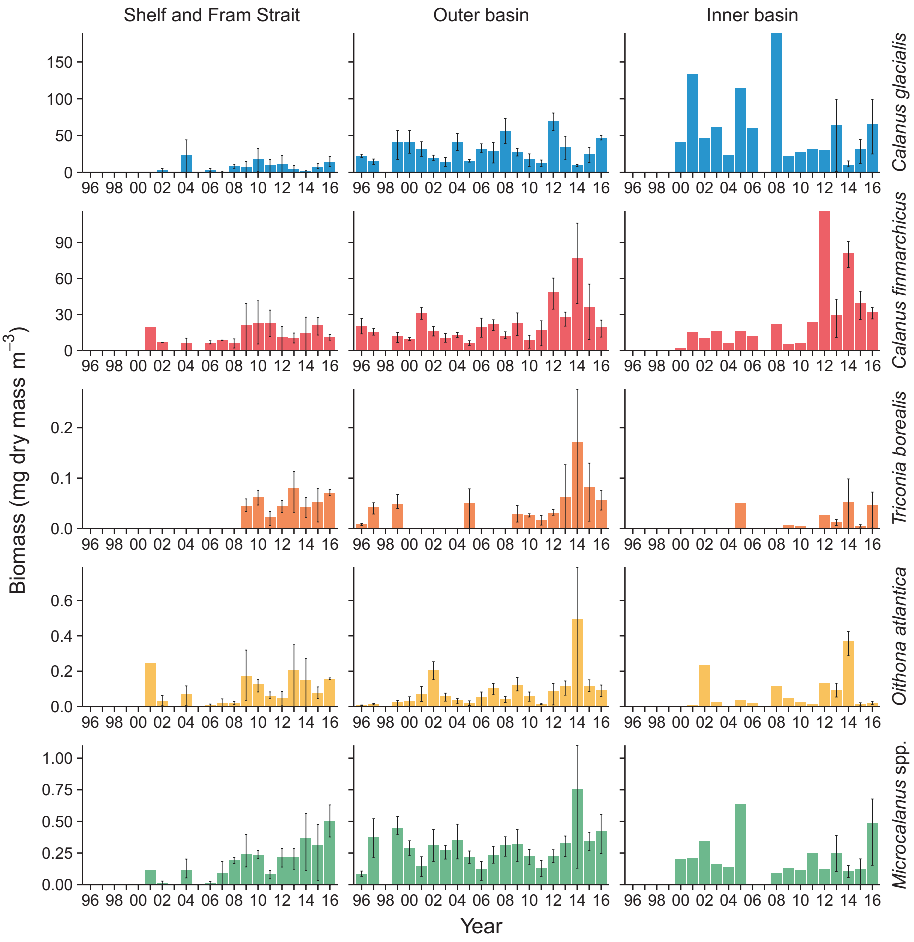

Fig. 7.6 Changes in biomass of copepod species over time, based on MultiNet samples (200 μm mesh size) from 1996–2016. Coloured bars indicate average biomass for each year using stations as statistical replicates. Error bars represent bootstrapped 95% confidence intervals (CIs) for the means. Missing error bars indicate values with only one replicate (e.g. one station). Error bars that reach all the way down to zero represent negative minimum CIs indicating low confidence for the mean estimate. Species that indicated changes over time in the RDA (Fig. 7.10) were selected for the figure

7.3.5 Euphausiids

Recent population studies on Kongsfjorden krill have focused on growth and reproduction and are accompanied by eco-physiological investigations, i.e. energy storage and turnover measurements including experimentation on thermal and trophic requirements (Huenerlage and Buchholz 2015; Huenerlage et al. 2016). During the last decades, the species composition of krill has changed due to recent increased advection of Atlantic water masses carrying characteristic boreal as well as

Table 7.4 Abundance (ind. m^{-3}) of other taxa than copepods in Kongsfjorden during the periods 1994–2006 and 2007–2016, averaged over all sampled stations and based on MultiNet samples

	1996–2006		2007–2016	
	All stations		All stations	
Taxa	Mean ± StDev	Max	Mean ± StDev	Max
Amphipoda				
Amphipoda indet.	0.0 ± 0.0	0.1	0.0 ± 0.1	0.4
Apherusa glacialis			0.0 ± 0.0	0.4
Cyclocaris guilelmi			0.0 ± 0.0	0.0
Eusirus holmii			0.0 ± 0.0	0.4
Hyperia galba	0.0 ± 0.0	0.0		
Hyperiidae indet.	0.0 ± 0.0	0.0		
Hyperoche medusarum	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Onisimus spp.	0.0 ± 0.0	0.0		
Scina borealis			0.0 ± 0.0	0.4
Themisto abyssorum	0.7 ± 0.7	4.0	1.1 ± 1.2	7.7
Themisto libellula	0.7 ± 1.8	9.4	0.3 ± 0.4	1.6
Euphausiacea				
Euphausiacea indet. (larvae)	0.1 ± 0.1	0.6	0.6 ± 0.8	4.7
Meganyctiphanes norvegica	0.0 ± 0.0	0.1	0.0 ± 0.0	0.0
Thysanoessa inermis	0.0 ± 0.1	0.4	0.3 ± 0.6	4.0
Thysanoessa longicaudata	0.1 ± 0.2	0.9	0.0 ± 0.1	0.8
Thysanoessa raschii	0.1 ± 0.8	5.7	0.3 ± 2.4	23.2
Other Crustacea				
Bopyridae indet.	0.0 ± 0.3	1.9	0.6 ± 0.8	4.6
Boreomysis arctica	0.0 ± 0.0	0.0	0.0 ± 0.0	0.1
Cumacea indet.	0.0 ± 0.0	0.2	0.0 ± 0.0	0.4
Eusergestes arcticus			0.0 ± 0.0	0.0
Evadne nordmanni	0.5 ± 3.3	24.2	1.2 ± 11.0	104.7
Facetotecta indet.	0.1 ± 0.4	1.9	0.4 ± 0.7	3.7
Hymenodora glacialis	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Isopoda indet.	0.2 ± 0.2	1.1	0.1 ± 0.2	1.5
Mysidae indet.	0.0 ± 0.0	0.0		
Ostracoda indet.	0.6 ± 2.6	19.1	0.5 ± 0.8	4.5
Pseudomma truncatum	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Tanaidacea indet.	0.0 ± 0.0	0.0		
Meroplankton				
Bivalvia larvae and juveniles	166.7 ± 595.6	4188.9	130.8 ± 310.8	1887.6
Bryozoa larvae	0.1 ± 0.3	1.6	0.1 ± 0.3	2.3
Cirripedia nauplii and cyprid	1.5 ± 4.2	22.9	2.4 ± 9.8	81.5
Decapoda larvae	0.1 ± 0.4	2.7	0.0 ± 0.0	0.5
Echinodermata larvae	114.5 ± 274.5	1244.8	39.7 ± 55.3	248.6

(continued)

Table 7.6 (continued)

	1996–2006		2007–2016	
	All stations		All stations	
Taxa	Mean ± StDev	Max	Mean ± StDev	Max
Gastropoda larvae	0.1 ± 0.2	0.9	2.7 ± 20.9	199.4
Hyas araneus	0.0 ± 0.1	0.4	0.0 ± 0.1	1.0
Nemertea pilidium	0.0 ± 0.1	0.5	0.0 ± 0.1	0.3
Pagurus pubescens	0.0 ± 0.1	0.9	0.1 ± 0.2	1.5
Pandalus borealis	0.0 ± 0.0	0.1	0.0 ± 0.1	0.7
Polychaeta larvae	4.3 ± 8.2	42.1	1.9 ± 2.3	15.3
Sabinea septemcarinata	0.0 ± 0.1	0.6	0.0 ± 0.1	0.5
Typhloscolecidae larvae			0.0 ± 0.1	0.8
Cnidaria				
Aeginopsis laurentii	0.0 ± 0.0	0.0	0.0 ± 0.0	0.2
Aglantha digitale	0.4 ± 0.9	6.1	0.5 ± 1.3	10.7
Botrynema ellinorae			0.0 ± 0.1	0.8
Bougainvillia spp.			0.0 ± 0.0	0.1
Dimophyes arctica	0.0 ± 0.0	0.2	0.0 ± 0.1	0.8
Halitholus cirratus	0.0 ± 0.0	0.0	0.0 ± 0.0	0.1
Hydrozoa indet.	0.0 ± 0.0	0.1	0.0 ± 0.2	0.8
Nanomia cara			0.0 ± 0.0	0.0
Sarsia sp.	0.0 ± 0.0	0.2		
Scyphozoa indet.			0.0 ± 0.0	0.2
Siphonophora indet.	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Ctenophora				
Beroë cucumis	0.3 ± 0.8	6.1	0.1 ± 0.1	1.0
Ctenophora			0.0 ± 0.1	0.6
Mertensia ovum	0.1 ± 0.4	2.8	0.1 ± 0.5	4.3
Pteropoda				
Clione limacina	4.5 ± 25.9	187.8	0.5 ± 3.6	34.6
Limacina helicina	3.3 ± 6.5	27.3	73.8 ± 282.8	2277.5
Limacina retroversa	0.1 ± 0.1	0.6	0.1 ± 0.3	2.6
Annelida				
Pelagobia sp.	0.0 ± 0.0	0.3	0.0 ± 0.1	0.8
Tomopteris helgolandica			0.0 ± 0.0	0.1
Tomopteris spp.	0.0 ± 0.0	0.2		
Chaetognatha				
Eukrohnia hamata	2.0 ± 1.9	9.1	2.5 ± 2.8	15.5
Parasagitta elegans	3.5 ± 6.1	41.4	2.1 ± 2.4	11.8
Pseudosagitta maxima			0.0 ± 0.0	0.0
Appendicularia				
Appendicularia			0.0 ± 0.0	0.1
Fritillaria borealis	26.5 ± 47.4	250.3	10.5 ± 19.0	90.9
Oikopleura spp.	2.8 ± 4.1	21.5	6.3 ± 16.2	131.4
Pisces	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1

Missing values indicate zero occurrences, while values marked 0.0 mean <0.04 ind. m^{-3}

subtropical-boreal euphausiids into the ecosystem (Buchholz et al. 2010; Dalpadado et al. 2016). Concurrently, the temperate-boreal (*Meganyctiphanes norvegica*) and subtropical-temperate krill species (*Nematoscelis megalops*) are regularly found, at low abundances, in Kongsfjorden – in addition to the previously prevailing Arcto-boreal coastal species *T. inermis* and *T. raschii* and oceanic species *T. longicaudata* (Buchholz et al. 2010). A comparison of nutrition and energy storage strategies, stable isotopes, lipid profiles and fatty acid compositions have shown remarkable differences between the krill species. *Thysanoessa inermis* and *T. longicaudata* typically consist of 30–50% lipids of dry mass, mainly stored as triacylglycerols and wax esters, with fatty acids indicating herbivorous feeding (Sargent and Falk-Petersen 1981). This large lipid store may have multiple functions, including winter survival when food sources are low. On the other hand, *M. norvegica* and *N. megalops* appear more carnivorous, with significantly lower mean lipid contents (29 and 10%, respectively) and different energy storage patterns (triacylglycerols and polar lipids, respectively; Huenerlage et al. 2016). Top predators relying on krill as a food source (e.g. Vihtakari et al. 2018) may therefore be exposed to krill species of less quality in their diet.

Thysanoessa raschii was observed spawning for the first time in Kongsfjorden in 2011 (Buchholz et al. 2012; Huenerlage and Buchholz 2015; Huenerlage et al. 2015). Respiration measurements revealed *Thysanoessa* spp. to appear more cold-stenotherm than the other krill species: the upper level of respiratory capacity is reached at 12 °C (K. Huenerlage and F. Buchholz, unpubl.). Thus, thermal stress may have caused the decline after 2011. In contrast, the other temperate-boreal and the subtropical-temperate krill species show higher tolerance to temperature changes, which may explain their recent success with northward expansion.

Krill is probably highly underestimated by all nets used for sampling in Kongsfjorden (Pearcy et al. 1983). A distinct acoustic back scattering layer of krill was recorded with an Acoustic Zooplankton and Fish Profiler with consistent dial vertical migration from surface to 150 m from January to March 2014. High biomass was recorded in June 2014 with 3.2 g m^{-2} and in January with > 0.6 g m^{-2} (Grenvald et al. 2016; Darnis et al. 2017). During a cruise to Kongsfjorden in January 2014, Larsen (2017) recorded very high abundance of krill (mainly *T. inermis*) with 60,000–120,000 krill per 15-min trawl haul with "Harstad" pelagic trawl (20 × 20 m mouth opening, 8 mm cod-end mesh size). *Thysanoessa inermis* was also by far the dominating food for Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and polar cod (*Boreogadus saida*) in January 2014–2016 with a frequency of occurrence in the stomach of 25–50%, while only medium-sized polar cod had copepods as the main food, accounting for 40% (Larsen 2017).

Krill are typically associated with underwater slopes or deep troughs (e.g. 100–200 m slope in front of Ny-Ålesund; 95 m depression in inner fjord), where they feed on the rich nepheloid layer (Buchholz et al. 2010). Bottom topography plays a role for krill aggregations: a minimum water depth of ca. 60 m is typically required to allow for vertical migration or positioning (Falk-Petersen and Hopkins 1981; Falk-Petersen and Kristensen 1985). In April 2013, the highest concentration of krill was 270 ind. m^{-3} near the bottom at 250–300 m depth in mid-fjord (near Kb3; F. Buchholz unpubl. data).

7.3.6 Ctenophores and Other Gelatinous Zooplankton

Gelatinous predators such as ctenophores, hydromedusae, siphonophores and scyphomedusae, can be quite abundant in the Arctic, but relatively little is known about their biology since they are difficult to collect and preserve (e.g. Raskoff et al. 2005, 2010; Purcell et al. 2010). They feed partly on the lower pelagic food web and can be important regulators of zooplankton in the Arctic (Purcell 1991; Swanberg and Båmstedt 1991; Majaneva et al. 2013).

Two ctenophore species are commonly observed in Kongsfjorden: *Mertensia ovum* and *Beroë cucumis* (Table 7.4; Lundberg et al. 2006; Majaneva et al. 2013). *Mertensia ovum* can dominate the gelatinous zooplankton community in Kongsfjorden accounting for up to 70% of the abundance (Hop et al. 2002). *Mertensia ovum* is an opportunistic feeder preying mainly on the large *Calanus* copepods (Falk-Petersen et al. 2002; Majaneva et al. 2013) but also on smaller copepods, pteropods and fish larvae (Swanberg and Båmstedt 1991; Siferd and Conover 1992; Purcell et al. 2010). Peak abundance of *M. ovum* has been found during summer in Kongsfjorden and was likely related to increased zooplankton abundance at the same time (Lundberg et al. 2006). *Mertensia ovum* has special storage structures for lipids originating from their *Calanus* diet (Larson and Harbison 1989; Falk-Petersen et al. 2002), with highest lipid content during autumn (Lundberg et al. 2006; Graeve et al. 2008). Lipids are likely used to fuel prolonged periods of reproduction enabling their 2-years life cycle in Kongsfjorden (Lundberg et al. 2006). The population of *M. ovum* is mainly controlled by another Arctic ctenophore species, *Beroë cucumis* (Swanberg 1974; Tamm and Tamm 1991). Ctenophores are preyed upon by higher trophic levels, such as polar cod, Atlantic cod and sea birds, although the gelatinous masses are difficult to identify in stomach contents of a mixed diet.

7.3.7 Chaetognaths

While most zooplankton studies from Kongsfjorden have focused on copepods, euphausiids or ctenophores, little is known about the chaetognath population in Kongsfjorden despite them being one of the most abundant and consistently present carnivorous zooplankton species (Table 7.4). Chaetognaths form a phylum of pelagic predators that can comprise 7–18% of zooplankton biomass in the Arctic (Kosobokova et al. 1998; Kosobokova and Hirche 2000; Hopcroft et al. 2005). The two chaetognath species found in Kongsfjorden are commonly found in Svalbard waters and across the Arctic (Søreide et al. 2003; Hopcroft et al. 2005). *Eukrohnia hamata* is usually associated with open water, while *Parasagitta elegans* dominates in the fjords (Dunbar 1962; Welch et al. 1996; Kosobokova et al. 2011). *Parasagitta elegans* was the only chaetognath species observed in seasonal studies in Kongsfjorden (Walkusz et al. 2009; Lischka and Hagen 2016). This species dominated in numbers over *E. hamata* during winter (January–February) in Kongsfjorden

(Grenvald et al. 2016). Chaetognaths prey on copepods and other zooplankton species (Solov'ev and Kosobokova 2003; Terazaki 2004; Grigor et al. 2015). They may contain high amounts of lipids (Kruse et al. 2010) and are prey items for larger zooplankton, fish and seabirds (Feigenbaum and Maris 1984), although little is known on their importance as prey in Kongsfjorden. Highest chaetognath abundance is usually observed in summer and autumn (Grigor et al. 2014). Lischka and Hagen (2016) found peak abundance of chaetognaths in Kongsfjorden in November, while Grenvald et al. (2016) observed considerable higher abundance of *P. elegans* in January 2013 and 2014 (342–701,000 ind. m^{-3}) than in February 2013 (16,000–26,000 ind. m^{-3}). The life cycle of *P. elegans* is estimated to be 3 years in Svalbard fjords (Grigor et al. 2014), although both species had longevities of about 2 years in the Canadian Arctic Ocean (Grigor et al. 2017). *Parasagitta elegans* displays signs of ontogenetical vertical migration, with younger individuals distributed shallower and larger/older ones deeper (Grigor et al. 2014). This species has also shown signs of diel vertical migration (DVM) behaviour in February in Kongsfjorden (Grenvald et al. 2016).

7.3.8 Pteropods

The pteropod *Limacina helicina* is an important member of the zooplankton community in the Arctic, and high densities have been found in the Greenland Sea, the area around Svalbard and in the northern Barents Sea (Gilmer and Harbison 1991; Falk-Petersen et al. 1999). It is abundant in Kongsfjorden year-round (Weslawski et al. 2000; Lischka and Hagen 2016), but appeared only in pulses of low density during a study by Gannefors et al. (2005), which might be due to their patchy distribution (Kerswill 1940) and inter-annual variability in population dynamics. Aggregations of adult *L. helicina* can frequently be observed in Kongsfjorden during the period of reproduction in summer when they appear close to the surface drifting with the currents across the fjord while feeding, but they are difficult to sample quantitatively (Gannefors et al. 2005). In our time series data, we observed high variability in abundance of veligers, which are more efficiently caught with the MultiNet compared to adults (Table 7.6). The winter abundance is variable, and may be orders of magnitude higher some years, such as the winter 1998/99 (Lischka and Riebesell 2012; Lischka and Hagen 2016).

Limacina spp. have delicate shells made of aragonite that easily dissolves when the aragonite saturation state (Ω_{Ar}) approaches 1 (Lischka et al. 2011; Bednaršek et al. 2014). Studies performed in Kongsfjorden have reported occurrences of critical Ω_{Ar} levels <1 in winter (February 2010) (Lischka and Riebesell 2012) and of declining Ω_{Ar} gradients towards the inner fjord, where the freshwater input is the largest, with low values of 1.5 (Fransson et al. 2016). Thus, *L. helicina* may be affected by combined effects of ocean acidification (OA) and increased temperature in Kongsfjorden, which has also been indicated by experimental work (e.g. Comeau et al. 2009; Lischka et al. 2011).

The subarctic boreal species *Limacina retroversa* is probably introduced to Kongsfjorden with advected AW (e.g. Hop et al. 2006). The importance of *L. retroversa* in the eastern Fram Strait and also in Kongsfjorden has increased since 2005/06 due to an increased influence of warmer Atlantic water masses (Lischka and Riebesell 2012; Bauerfeind et al. 2014), although we do not see a similar signal in our time-series data comparing 1996–2006 to 2006–2016 (Table 7.4). The occurrence and abundance of this species could be used as an indicator of increasing influence of warm AW in Kongsfjorden and adjacent seas (Lischka and Riebesell 2012; Lischka and Hagen 2016).

Pteropod studies in Kongsfjorden have included both the thecosmes (shell-bearing) *L. helicina* and *L. retroversa* and also the gymnosome *Clione limacina.* Studies have covered aspects of the species life cycles and their lipid dynamics (Falk-Petersen et al. 2001; Böer et al. 2005; Gannefors et al. 2005) as well as of the potential vulnerability of *L. helicina* and *L. retroversa* to OA and warming (Comeau et al. 2009; Lischka et al. 2011; Lischka and Riebesell 2012, 2017).

Limacina helicina has a 1-year life cycle in Kongsfjorden, and reproduction takes place during the summer months (June–August) with a peak usually in August (Gannefors et al. 2005). The veliger larvae make use of the summer phyto-/protozooplankton bloom and develop to juveniles prior to overwintering at reduced metabolic rates. Further development ceases until the next spring when overwintering juveniles continue development into adults using the spring phytoplankton bloom (Gannefors et al. 2005; Lischka and Riebesell 2012, 2017; Lischka and Hagen 2016). The other pteropod *Clione limacina* has a life-cycle of at least 2 years in Svalbard waters. Polytrochous larvae occur in April/May and develop to adults until summer. From September through winter, almost only mature adults with large lipid stores can be found and they feed predominately on *L. helicina* (Böer et al. 2005).

The role and impact of *L. helicina* on the pelagic food web of Kongsfjorden is currently not defined, but can be assumed substantial during spring and summer when *Limacina* develops rapidly from overwintering juveniles to reproducing adults. This species can become extremely abundant, as observed in Rijpfjorden, northern Svalbard, where up to 8000 m^{-3} juveniles were recorded to perform diel vertical migrations in the upper 50 m (Falk-Petersen et al. 2008). In the Southern Ocean, the grazing impact of *L. retroversa* can account for up to 60% of the total plankton production (Hunt et al. 2008).

7.3.9 Appendicularians

Appendicularians (Larvacea) can appear in high abundances in Kongsfjorden (Walkusz et al. 2009; Lischka and Hagen 2016). However, like chaetognaths, appendicularians have not specifically been studied in Kongsfjorden and little is known about this group, species life cycles and their role in the ecosystem. Appendicularians ingest nano- and picoplankton with high efficiency (Acuna et al. 1999, 2002) and mediate the export of these cells from the euphotic layer to the sea floor through the sinking of faecal pellets and discarded mucous houses, which enhance forming of aggregates and the downward vertical fluxes of particles. Representatives of two genera of larvaceans occur in Kongsfjorden, *Fritillaria* represented by *F. borealis*, and *Oikopleura*, with possibly two species *O. vanhoeffeni* and *O. labradoriensis*. *Fritillaria borealis* typically was more abundant than *Oikopleura* spp. in July. High numbers of *F. borealis* in Fram Strait and the Barents Sea have been associated with Atlantic waters (Arashkevich et al. 2002; Blachowiak-Samolyk et al. 2017). Appendicularians can appear in high abundance for short periods. Such outbursts have been related to high fecundity and growth rates resulting in short generation time (days rather than weeks), as well as rapid population growth in response to bacterio- and nanophytoplankton blooms (Hopcroft and Roff 1995). During outbursts, appendicularians can dominate the mesozooplankton community (Arashkevich et al. 2002). In Kongsfjorden, peak abundances of *F. borealis* have been observed in July (Lischka and Hagen 2016), when they can contribute 2.7% of the total zooplankton abundance, although their abundance in July vary substantially among years (0–6.9%; Hop et al. 2006). Peak abundance of *Oikopleura* spp. has been observed in June in Kongsfjorden (Lischka and Hagen 2016). A similar decoupling of abundance peaks between the two appedicularian species has been observed in Rijpfjorden (Weydmann et al. 2013) as well as in the northeastern Chukchi Sea (Questel et al. 2013).

7.3.10 Meroplankton

The occurrence of meroplankton is highly seasonal and outbursts are often restricted to a few weeks during and after the spring bloom. They often occur at the same time as copepod nauplii (Kwasniewski et al. 2013). Studies from Kongsfjorden (Lischka and Hagen 2016) and Adventfjorden (Kuklinski et al. 2013; Stübner et al. 2016) have shown that different meroplankton taxa appear in repeatable sequences, with cirripedia nauplii and polychaete larvae being the first to appear, usually in May–June and occasionally as early as April (Walkusz et al. 2009), then followed by bivalves and echinoderms later in the summer. Mass appearance of cirripede nauplii have been reported during spring (Kwasniewski et al. 2013), whereas Echinodermata larvae might play an important role during summer as they swarm in surface waters (Walkusz et al. 2009). Juvenile bivalves and echinoderms were the dominating meroplanktonic taxa in our time-series data from mid-end July (Table 7.6). Meroplankton were particularly abundant in 2006 in inner fjord, and also partly in 2007 in mid-fjord.

7.3.11 General Seasonality Patterns in the Zooplankton Community

The extreme seasonality in incoming solar radiation and primary production lead to pronounced seasonal variations in zooplankton abundance at high latitudes. Zooplankton abundance peaks are usually observed in late summer and autumn, while abundance minima occur in early spring. This has been commonly observed in Kongsfjorden (e.g. Willis et al. 2006; Walkusz et al. 2009; Lischka and Hagen 2016) and other fjords in Svalbard (e.g. Weslawski et al. 1988; Arnkværn et al. 2005; Weydmann et al. 2013). The zooplankton abundance can be an order of magnitude higher during summer and autumn than in spring in Kongsfjorden, when *C. finmarchicus*, *O. similis* and *Calanus* nauplii dominate the zooplankton community (Walkusz et al. 2009). Recent zooplankton studies performed during the polar night have shown that small copepods (*Microcalanus, O. similis, Pseudocalanus*) dominated in January in Kongsfjorden (Berge et al. 2015a; Grenvald et al. 2016), when they were present in similar abundance (400–1200 ind. m^{-3}) as observed in our time series data from July, while larger zooplankton were generally much less abundant than during the other seasons (Berge et al. 2015a). The reasons and range of zooplankton activity observed during the dark season in Kongsfjorden have been discussed by Berge et al. (2015b).

Advection of Atlantic Water during summer can cause increased abundances of *C. finmarchicus* relative to Arctic species (Willis et al. 2006; Walkusz et al. 2009). *Calanus glacialis* abundances are usually also highest in summer and autumn, at the end of the productive period, especially inside the fjord, where the Arctic species can find refugia in the deepest parts of the fjord basin in cold bottom water (Walkusz et al. 2009).

Many of the zooplankton species in Kongsfjorden perform diurnal vertical migrations, but the pattern varies between seasons from very pronounced DVM during spring and autumn, which continues to some extent during winter (Berge et al. 2009), although being absent or asynchronous DVM during summer with 24 h daylight (Cottier et al. 2006; Wallace et al. 2010). These changes will then also influence where in the water column most of the biomass is located during the day over seasons, typically shallow in connection with the plankton blooms during spring and summer and deeper during late autumn and winter (Walkusz et al. 2009).

7.3.12 Pelagic Food Web and Vertical Flux

Zooplankton have important functions in the pelagic ecosystem of Kongsfjorden, where they occupy the second and third trophic levels in the marine food web (Hop et al. 2002). The secondary production by zooplankton at the second and third trophic level has been quantified as 0.13–5.69 g C m^{-2} $year^{-1}$ (Duarte et al., Chap. 12). They represent important grazers in the system and with 10× greater standing stock than the phytoplankton during summer, they can exert top-down control on the primary production (Hegseth et al., Chap. 6). Faecal pellet from zooplankton constitute a major contribution to the vertical flux (Wassmann et al. 1991, 1996), with higher sedimentation during summer because of the high grazing activity due to higher zooplankton abundance and biomass. Darnis et al. (2017) recently estimated, based on sediment traps, that DVM-mediated carbon transport by krill and copepods represent >25% of the POC flux during the first weeks of autumn and > 40% of during winter.

7.4 Part II: Trends in the Zooplankton Time-Series

7.4.1 Zooplankton in General and Calanus in Particular

Annual monitoring of mesozooplankton over the last 20 years since 1996 has shown that Kongsfjorden hosts a larger zooplankton biomass within the fjord compared to the stations outside Kongsfjorden (Fig. 7.5). The average biomass (mg dry mass m^{-3}) differed significantly among the four areas; inner basin, outer basin, shelf and Fram Strait (Kruskal-Wallis df = 3, $\chi^2 = 36.5$, $p < 0.001$). The average biomass in Fram Strait stations was significantly lower compared to other stations (Kruskal-Wallis multiple comparison). Biomass was highest in the inner basin with an average of 150 mg dry mass m^{-3}. The copepods *C. glacialis* and *C. finmarchicus* contributed approximately 63.3% to the total biomass of inner and outer fjord (Fig. 7.5). *Calanus glacialis* contributed more to the total biomass in the inner and outer basin than *C. finmarchicus*, while the pattern was the opposite at the shelf and Fram Strait stations. The highest integrated biomasses in the water column (mg dry mass m^{-2}) were encountered in outer basin and shelf stations, which are 2–3 times deeper than the inner basin stations (224–352 m at V12-Kb1 vs. 64–96 m at Kb7-Kb5).

The changes in the zooplankton community from 1996 to 2016 were generally nonlinear and differed between stations inside and outside Kongsfjorden. Large variability in the values and the small number of replicate stations complicate the interpretation of the patterns. Nevertheless, an increase in abundance and biomass of *C. finmarchicus* in both the inner and outer basin is evident (Table 7.5 and Fig. 7.6). However, the trend is not continuous, as a decrease was observed in 2015–2016. Thus, it is unclear whether the increase represents a trend or merely fluctuations in the population size. A simultaneous decrease in *C. glacialis* was not observed.

High inter-annual variation in the contribution of different species both in terms of abundance (Tables 7.5 and 7.6) and biomass (Figs. 7.6 and 7.7) in different parts of Kongsfjorden likely relates to the variable inflow of Atlantic Water. The fluctuations in biomass of *Calanus* species appeared to loosely follow the estimated proportions of Arctic and Atlantic Water in the fjord (Fig. 7.2), whereas temporal changes in biomass

Table 7.5 Total abundance (ind. m^{-3}) of copepods in different areas of Kongsfjorden during the periods 1994–2006 and 2007–2016. The copepodid developmental stages (from stage 1 to stage 6 female or male, C1–C6F/M, which contributed to the summary presented, are listed next to the species names. No stage indicates all copepodids C1–C6 are included

	1999–2006								2007–2016							
	Fram Strait		Shelf		Outer basin		Inner basin		Fram Strait		Shelf		Outer basin		Inner basin	
Copepoda	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max
Acartia longiremis	0.0 ± 0.0	0			3.0 ± 6.3	38	20.7 ± 21.2	49.9	0.0 ± 0.2	0.6	1.9 ± 5.7	24.9	5.3 ± 6.5	27.1	7.4 ± 9.4	29
Aetideidae indet. C1–C3	0.0 ± 0.1	0.2	0.1 ± 0.1	0.2	0.8 ± 1.9	7.6	0.7 ± 1.9	5	0.2 ± 0.2	0.8	0.1 ± 0.3	0.9	1.7 ± 1.4	4.9	3.9 ± 4.1	15.9
Aetideopsis minor C4–C6	0.0 ± 0.1	0.1							0.0 ± 0.0	0.1			0.1 ± 0.9	5.9		
Aetideopsis rostrata C4–C6	0.0 ± 0.0	0							0.1 ± 0.1	0.4	0.0 ± 0.1	0.2	0.0 ± 0.0	0.3		
Aetideus armatus C4–C6					0.0 ± 0.0	0			0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1		
Augaptilus glacialis									0.0 ± 0.0	0						
Bradyidius similis C4–C6	0.1 ± 0.1	0.2	0.0 ± 0.0	0.1	4.9 ± 9.9	50.6	1.6 ± 2.2	5.9					0.9 ± 4.2	26.4	1.1 ± 1.9	6.6
Calanus finmarchicus	115.8 ± 134.2	313.3	142.7 ± 80.9	267.7	151.1 ± 77.5	353	209.1 ± 123.8	415.9	67.1 ±53.0	185.6	381.2 ± 303.5	1191.8	444.6 ± 470.8	2115.2	866.2 ± 925.5	3331.8
Calanus glacialis	2.8 ± 2.7	6.6	101.9 ± 172.7	408.8	102.5 ± 80.0	332.3	164.4 ± 95.3	320.3	2.7 ± 2.6	9.3	57.5 ± 67.6	256.4	120.1 ± 87.0	400.3	133.4 ± 106.1	437.8
Calanus hyperboreus	0.5 ± 0.3	0.8	1.6 ± 2.0	5.1	11.2 ± 7.2	31.9	36.1 ± 35.0	111.5	1.7 ± 1.0	3.5	2.8 ± 3.5	15.7	12.5 ± 13.2	69.5	10.5 ± 9.6	34.2
Chiridius obtusifrons C4–C6	0.0 ± 0.0	0							0.1 ± 0.2	0.8	0.1 ± 0.2	0.7	0.0 ± 0.0	0.2		
Copepoda nauplii	47.2 ± 37.6	99.1	65.3 ± 86.1	209.5	76.3 ± 67.3	331.9	339.9 ± 184.8	583.9	23.5 ±28.2	107.8	119.5 ± 118.3	496.4	65.7 ± 60.5	282.2	57.9 ± 58.3	261.3

Disco sp. C4–C6									0.0 ± 0.0	0.1						
Gaetanus brevispinus C4–C6									0.0 ± 0.1	0.4						
Gaetanus tenuispinus C4–C6	0.2 ± 0.1	0.3	0.1 ± 0.2	0.4	0.0 ± 0.0	0	0.0 ± 0.1	0.3	0.2 ± 0.2	1	0.0 ± 0.1	0.4	0.0 ± 0.1	0.3		
Harpacticoida	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1	0.3 ± 0.5	2.2	5.8 ± 6.9	20.3	0.0 ± 0.0	0	0.0 ± 0.1	0.3	0.3 ± 0.5	2.5	0.7 ± 0.9	2.5
Heterorhabdus norvegicus	0.8 ± 0.9	2	0.1 ± 0.1	0.2	0.0 ± 0.0	0.3			0.4 ± 0.2	1	0.1 ± 0.1	0.5	0.0 ± 0.1	0.3		
Mesaiokeras spitsbergensis					0.1 ± 0.2	1.2										
Metridia longa	3.7 ± 2.8	6.5	6.8 ± 5.8	16.7	28.8 ±23.8	101.7	2.7 ± 2.1	6.1	9.8 ± 4.0	17.3	10.2 ± 9.1	43	22.8 ±15.6	73.2	3.5 ± 6.1	26.5
Microcalanus spp.	6.4 ± 7.2	16.7	9.8 ±11.7	24.2	36.3 ±21.1	82.5	34.5 ±28.7	90.6	23.2 ±6.3	29.9	43.4 ± 30.0	114	47.1 ±36.6	242.2	30.3 ± 27.2	116.3
Microsetella norvegica					0.0 ± 0.0	0.1			0.0 ± 0.0	0	0.1 ± 0.2	0.6	0.1 ± 0.2	1.1	0.2 ± 0.3	1.1
Monstrilloida indet. C6F					0.0 ± 0.1	0.7							0.0 ± 0.1	0.4		
Neomormonilla minor C5–C6									0.0 ± 0.1	0.2			0.0 ± 0.0	0.3		
Neoscolecithrix farrani C4–C6					0.0 ± 0.0	0.2	1.8 ± 3.3	8.8							0.1 ± 0.3	1
Oithona atlantica C5–C6	10.9 ± 16.5	35.6	7.4 ± 8.3	20.3	7.9 ± 9.5	38.5	6.7 ± 12.1	33.9	6.1 ± 4.0	14.1	22.8 ± 21.3	84.8	18.2 ± 29.9	194.1	15.7 ± 19.1	66.3
Oithona similis	151.5 ± 61.8	228.1	474.6 ± 209.6	715.2	492.3 ± 406.5	1702.8	2043.5 ± 1340.5	3927.5	87.7 ± 59.4	192.1	439.3 ± 258.8	1267.1	595.4 ± 607.9	3397.3	979.3 ± 745.4	3419.9
Oncaea parila C6F									0.0 ± 0.1	0.4						

Table 7.5 (continued)

	1999–2006								2007–2016							
	Fram Strait		Shelf		Outer basin		Inner basin		Fram Strait		Shelf		Outer basin		Inner basin	
Copepoda	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max
Oncaea spp. C6F									0.2 ± 0.3	1.1	0.1 ± 0.2	0.6	1.0 ± 5.6	35.6	0.2 ± 0.5	2.2
Paraeuchaeta barbata C6			0.0 ± 0.0	0					0.0 ± 0.1	0.4	0.0 ± 0.0	0				
Paraeuchaeta glacialis C6	0.0 ± 0.0	0			0.0 ± 0.0	0			0.1 ± 0.2	0.8			0.0 ± 0.0	0		
Paraeuchaeta norvegica C6	0.0 ± 0.0	0.1	0.0 ± 0.0	0	0.0 ± 0.0	0.1			0.1 ± 0.1	0.6	0.0 ± 0.0	0	0.0 ± 0.1	0.5		
Paraeuchaeta spp. C1–C5	0.4 ± 0.2	0.7	0.4 ± 0.3	0.9	0.1 ± 0.1	0.3	0.0 ± 0.0	0	0.6 ± 0.8	3.2	0.6 ± 0.5	1.8	0.6 ± 0.9	3.8	0.2 ± 0.5	1.7
Paraheterorhabdus compactus C4–C6									0.0 ± 0.0	0						
Pleuromamma robusta C6F	0.0 ± 0.0	0.1	0.0 ± 0.0	0					0.0 ± 0.1	0.4	0.0 ± 0.0	0	0.0 ± 0.1	0.4		
Pseudocalanus acuspes C6F	2.1 ± 2.5	4.8	1.4 ± 2.0	5	11.4 ± 13.1	48.6	55.7 ± 54.0	135.7	0.1 ± 0.1	0.3	1.5 ± 1.6	5.7	3.4 ± 2.7	10.5	10.0 ± 12.8	47.8
Pseudocalanus minutus C6F	0.5 ± 0.7	1.6	0.8 ± 1.2	2.7	3.0 ± 2.7	12.1	10.1 ± 10.6	29.8	0.8 ± 0.6	2.4	3.3 ± 3.8	16.7	3.4 ± 2.8	10.4	7.1 ± 9.3	33.3
Pseudocalanus spp. C1–C5, C6M	6.7 ± 4.3	12.1	64.9 ± 109.2	259.2	165.9 ± 91.8	396	1119.1 ± 915.6	2314.4	7.3 ± 5.7	18.6	94.1 ± 92.4	342.7	177.3 ± 120.6	683.8	302.4 ± 220.5	855.1
Pseudochirella spectabilis C4–C6									0.0 ± 0.0	0						
Rhincalanus nasutus C4–C6									0.0 ± 0.0	0.1	0.0 ± 0.1	0.4				
Scaphocalanus brevicornis									0.1 ± 0.1	0.4						

Scaphocalanus magnus									0.0 ± 0.0	0.1						
Scolecithricella minor	0.3 ± 0.2	0.6	0.2 ± 0.2	0.4	0.1 ± 0.1	0.6			0.4 ± 0.4	1.4	0.4 ± 0.3	1.1	0.3 ± 0.4	1.9	0.2 ± 0.5	1.7
Spinocalanus antarcticus									0.0 ± 0.1	0.2						
Spinocalanus horridus C4–C6									0.1 ± 0.1	0.4						
Spinocalanus longicornis C6									0.0 ± 0.1	0.2						
Spinocalanus spp. C1–C6					0.0 ± 0.0	0			0.1 ± 0.1	0.4						
Temorites brevis									0.0 ± 0.0	0						
Tharybidae indet. C4-C6									0.1 ± 0.1	0.4						
Tharybis groenlandicus C6									0.0 ± 0.0	0						
Triconia borealis C6					6.5 ± 12.8	62.6	3.6 ± 9.5	25.2	20.4 ± 12.0	44.3	23.4 ± 18.4	76.7	23.2 ± 37.4	216.4	11.1 ± 15.7	59.1
Triconia conifera C6F	0.0 ± 0.0	0							0.0 ± 0.0	0.1			0.0 ± 0.1	0.8		
Triconia/Oncaea spp. C1-C5	0.0 ± 0.0	0	0.1 ± 0.2	0.5	0.1 ± 0.2	1	0.2 ± 0.6	1.6	0.1 ± 0.4	1.5	0.2 ± 0.4	1.1	0.1 ± 0.3	1.6	0.1 ± 0.3	1.1
Undinella oblonga C4–C6									0.0 ± 0.0	0						
Xantharus siedleckii					0.0 ± 0.1	0.4							0.0 ± 0.0	0.2		

Missing values indicate zero occurrences, while values marked 0.0 mean <0.04 ind. m^{-3}

Table 7.6 Total abundance (ind. m^{-3}) of other taxa than copepods in different areas of Kongsfjorden during the periods 1994–2006 and 2007–2016, based on Multinet samples

	1999–2006								2007–2016							
	Fram Strait		Shelf		Outer basin		Inner basin		Fram Strait		Shelf		Outer basin		Inner basin	
Taxa	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max
Amphipoda																
Amphipoda indet.			0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.0 ± 0.1	0.3			0.0 ± 0.1	0.4	0.0 ± 0.0	0.1
Apherusa glacialis									0.0 ± 0.0	0			0.0 ± 0.1	0.4		
Cyclocaris guilelmi									0.0 ± 0.0	0						
Eusirus holmii									0.0 ± 0.1	0.4						
Hyperia galba			0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0								
Hyperiidae indet.	0.0 ± 0.0	0														
Hyperoche medusarum					0.0 ± 0.0	0							0.0 ± 0.0	0		
Onisimus spp.					0.0 ± 0.0	0										
Scina borealis									0.0 ± 0.1	0.4						
Themisto abyssorum	0.5 ± 0.2	0.7	0.4 ± 0.2	0.7	0.7 ± 0.7	4	1.0 ± 1.1	2.7	0.4 ± 0.5	2.1	0.9 ± 0.6	2.3	1.2 ± 0.7	2.6	1.7 ± 2.3	7.7
Themisto libellula	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1	0.5 ± 0.8	3.9	3.0 ± 4.2	9.4	0.0 ± 0.0	0.1	0.2 ± 0.3	1.1	0.3 ± 0.4	1.6	0.5 ± 0.6	1.6
Euphausiacea																
Euphausiacea indet. (larvae)	0.1 ± 0.1	0.2	0.2 ± 0.1	0.3	0.0 ± 0.1	0.4	0.2 ± 0.3	0.6	0.9 ± 1.2	4.7	0.8 ± 0.8	2.3	0.4 ± 0.6	2.5	0.4 ± 0.4	1.2
Meganycti-phanes norvegica	0.0 ± 0.0	0			0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.0 ± 0.0	0	0.0 ± 0.0	0				
Thysanoessa inermis	0.1 ± 0.1	0.3	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1	0.2 ± 0.2	0.4	0.0 ± 0.0	0	0.0 ± 0.0	0	0.1 ± 0.2	0.8	1.1 ± 1.0	4

Thysanoessa longicaudata	0.3 ± 0.3	0.6	0.2 ± 0.3	0.6	0.0 ± 0.0	0.1	0.2 ± 0.3	0.9	0.1 ± 0.2	0.8	0.0 ± 0.1	0.2	0.0 ± 0.0	0.1	0.1 ± 0.2	0.5
Thysanoessa raschii	0.0 ± 0.0	0	1.1 ± 2.5	5.7	0.0 ± 0.0	0.2	0.1 ± 0.2	0.4			1.2 ± 5.3	23.2	0.0 ± 0.1	0.5	0.3 ± 0.6	2.4
Other Crustacea																
Bopyridae indet.					0.0 ± 0.1	0.2	0.3 ± 0.7	1.9	0.1 ± 0.3	1	0.3 ± 0.3	0.8	0.6 ± 0.6	2.3	1.1 ± 1.2	4.6
Boreomysis arctica					0.0 ± 0.0	0							0.0 ± 0.0	0.1		
Cumacea indet.					0.0 ± 0.0	0.2							0.0 ± 0.1	0.4		
Eusergestes arcticus											0.0 ± 0.0	0	0.0 ± 0.0	0		
Evadne nordmanni	1.2 ± 2.3	4.7	4.9 ± 10.8	24.2							5.5 ± 24.0	104.7				
Facetotecta indet.	0.0 ± 0.0	0			0.2 ± 0.4	1.9			0.0 ± 0.0	0	0.2 ± 0.4	1.2	0.7 ± 1.0	3.7	0.2 ± 0.4	1.2
Hymenodora glacialis	0.0 ± 0.0	0							0.0 ± 0.0	0						
Isopoda indet.	0.0 ± 0.0	0.1	0.1 ± 0.0	0.1	0.2 ± 0.2	1.1	0.1 ± 0.1	0.4	0.0 ± 0.1	0.4	0.0 ± 0.1	0.2	0.1 ± 0.2	1.3	0.1 ± 0.4	1.5
Mysidae indet.					0.0 ± 0.0	0										
Ostracoda indet.	1.0 ± 0.3	1.3	0.6 ± 0.4	1.1	0.2 ± 0.2	0.9	2.8 ± 7.2	19.1	1.8 ± 1.0	4.5	0.4 ± 0.5	1.8	0.2 ± 0.4	1.5	0.2 ± 0.4	1.4
Pseudomma truncatum					0.0 ± 0.0	0							0.0 ± 0.0	0		
Tanaidacea indet.					0.0 ± 0.0	0										
Meroplankton																
Bivalvia larvae and juveniles	3.7 ± 4.2	9.2	5.4 ± 5.6	12.5	57.6 ± 127.7	564.9	966.9 ± 1473.6	4188.9	2.6 ± 5.2	15.6	28.1 ± 30.7	89.6	195.5 ± 360.3	1887.6	194.9 ± 416.1	1659.5

(continued)

Table 7.6 (continued)

Taxa	1999–2006								2007–2016							
	Fram Strait		Shelf		Outer basin		Inner basin		Fram Strait		Shelf		Outer basin		Inner basin	
	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max
Bryozoa larvae	0.0 ± 0.0	0	0.0 ± 0.0	0	0.1 ± 0.2	0.8	0.4 ± 0.6	1.6	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1	0.1 ± 0.3	1.2	0.1 ± 0.5	2.3
Cirripedia nauplii and cyprid	0.0 ± 0.0	0.1	0.1 ± 0.1	0.2	0.7 ± 0.9	3.3	7.7 ± 10.0	22.9	0.0 ± 0.1	0.3	0.5 ± 0.9	4.1	4.3 ± 14.4	81.5	2.2 ± 3.3	13.1
Decapoda larvae	0.0 ± 0.0	0.1	0.0 ± 0.1	0.2	0.0 ± 0.0	0.1	0.7 ± 1.1	2.7					0.0 ± 0.0	0.1	0.0 ± 0.1	0.5
Echinodermata larvae	2.6 ± 0.7	3.3	21.5 ± 14.4	39.7	111.5 ± 261.9	1211.3	261.7 ± 449.1	1244.8	0.4 ± 0.5	1.5	36.4 ± 54.0	189.4	59.5 ± 58.2	248.6	30.0 ± 55.0	165.6
Gastropoda larvae			0.0 ± 0.0	0.1	0.1 ± 0.2	0.9			0.0 ± 0.1	0.2	0.3 ± 0.5	1.3	5.6 ± 31.4	199.4	0.8 ± 1.9	7.6
Hyas araneus			0.0 ± 0.0	0	0.0 ± 0.1	0.4			0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.1 ± 0.2	1		
Nemertea pilidium					0.0 ± 0.1	0.4	0.1 ± 0.2	0.5			0.0 ± 0.0	0.1	0.0 ± 0.1	0.3	0.0 ± 0.0	0.2
Pagurus pubescens	0.0 ± 0.0	0			0.0 ± 0.0	0	0.2 ± 0.4	0.9			0.0 ± 0.2	0.8	0.0 ± 0.1	0.7	0.2 ± 0.4	1.5
Pandalus borealis					0.0 ± 0.0	0	0.0 ± 0.0	0.1			0.0 ± 0.0	0.1	0.0 ± 0.1	0.7	0.1 ± 0.2	0.5
Polychaeta larvae	0.1 ± 0.1	0.3	0.4 ± 0.4	1	3.5 ± 5.8	27.3	13.5 ± 16.4	42.1	0.3 ± 0.3	1	1.2 ± 0.9	3.5	2.9 ± 1.7	7.1	1.9 ± 3.7	15.3
Sabinea septemcarinata					0.0 ± 0.1	0.6									0.0 ± 0.1	0.5
Typhloscolecidae larvae									0.1 ± 0.2	0.8	0.0 ± 0.0	0	0.0 ± 0.0	0.1		

Cnidaria																
Aeginopsis laurentii					0.0 ± 0.0	0					0.0 ± 0.1	0.2				
Aglantha digitale	2.2 ± 2.8	6.1	0.5 ± 0.8	1.9	0.2 ± 0.3	1	0.1 ± 0.2	0.5	0.4 ± 0.7	2.4	1.1 ± 2.5	10.7	0.3 ± 0.6	2.4	0.1 ± 0.3	1
Botrynema ellinorae									0.1 ± 0.2	0.8	0.0 ± 0.1	0.2				
Bougainvillia spp.													0.0 ± 0.0	0.1		
Dimophyes arctica	0.1 ± 0.1	0.2	0.0 ± 0.0	0.1	0.0 ± 0.0	0.1			0.1 ± 0.2	0.8	0.0 ± 0.0	0.2	0.0 ± 0.0	0		
Halitholus cirratus	0.0 ± 0.0	0			0.0 ± 0.0	0			0.0 ± 0.0	0			0.0 ± 0.0	0.1		
Hydrozoa indet.			0.0 ± 0.0	0.1	0.0 ± 0.0	0.1			0.0 ± 0.0	0	0.0 ± 0.2	0.8	0.1 ± 0.2	0.8	0.0 ± 0.2	0.7
Nanomia cara									0.0 ± 0.0	0						
Sarsia sp.			0.1 ± 0.1	0.2	0.0 ± 0.0	0										
Scyphozoa indet.													0.0 ± 0.0	0.2		
Siphonophora indet.					0.0 ± 0.0	0			0.0 ± 0.0	0			0.0 ± 0.0	0		
Ctenophora																
Beroë cucumis	0.0 ± 0.0	0	0.1 ± 0.1	0.1	0.2 ± 0.3	1.5	0.9 ± 2.3	6.1	0.0 ± 0.0	0.1	0.1 ± 0.1	0.5	0.1 ± 0.2	1	0.0 ± 0.1	0.2
Ctenophora									0.0 ± 0.0	0.1	0.0 ± 0.1	0.6	0.0 ± 0.0	0.1		
Mertensia ovum			0.7 ± 1.2	2.8	0.1 ± 0.2	0.7	0.1 ± 0.2	0.7	0.0 ± 0.1	0.4	0.3 ± 1.0	4.3	0.1 ± 0.2	0.6	0.2 ± 0.4	1.5
Pteropoda																
Clione limacina	0.0 ± 0.0	0	44.7 ± 81.5	187.8	0.4 ± 1.7	10.6	0.3 ± 0.5	1.5	0.1 ± 0.2	0.8	1.9 ± 7.9	34.6	0.1 ± 0.2	0.7	0.1 ± 0.2	0.7

(continued)

Table 7.6 (continued)

	1999–2006								2007–2016							
	Fram Strait		Shelf		Outer basin		Inner basin		Fram Strait		Shelf		Outer basin		Inner basin	
Taxa	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max	Mean ± StDev	Max
Limacina helicina	0.3 ± 0.6	1.1	8.2 ± 12.2	27.3	2.8 ± 5.6	23.1	4.2 ± 7.3	16.9	0.3 ± 0.4	1.2	45.6 ± 148.7	647.2	65.7 ± 195.5	968.5	178.6 ± 543.2	2277.5
Limacina retroversa	0.1 ± 0.2	0.4	0.2 ± 0.3	0.6	0.0 ± 0.1	0.4	0.1 ± 0.2	0.5	0.0 ± 0.1	0.2	0.1 ± 0.3	1	0.1 ± 0.5	2.6		
Annelida																
Pelagobia sp.	0.1 ± 0.1	0.3							0.1 ± 0.2	0.8	0.0 ± 0.1	0.5	0.0 ± 0.0	0.1		
Tomopteris helgolandica									0.0 ± 0.0	0.1						
Tomopteris spp.	0.0 ± 0.0	0.1			0.0 ± 0.0	0.2										
Chaetognatha																
Eukrohnia hamata	3.2 ± 1.5	5.3	5.6 ± 2.2	9.1	1.7 ± 1.3	5	0.1 ± 0.2	0.5	3.6 ± 2.3	9.2	3.7 ± 2.7	11.3	2.4 ± 3.0	15.5	0.7 ± 1.6	6.5
Parasagitta elegans	0.2 ± 0.1	0.4	0.9 ± 1.2	2.9	2.4 ± 1.5	6.6	13.2 ± 13.4	41.4	0.1 ± 0.1	0.3	0.8 ± 0.8	2.4	2.2 ± 1.5	7	4.8 ± 3.5	11.8
Pseudosagitta maxima									0.0 ± 0.0	0						
Cephalopoda																
Cephalopoda											0.0 ± 0.0	0	0.0 ± 0.0	0		
Appendicularia																
Appendicularia													0.0 ± 0.0	0.1		
Fritillaria borealis	0.7 ± 1.0	2.1	13.9 ± 19.7	44.1	31.7 ± 51.4	250.3	22.4 ± 50.4	136.1	4.3 ± 10.0	37.8	21.8 ± 32.1	90.9	10.3 ± 14.0	53	3.8 ± 8.7	36.2
Oikopleura spp.	1.7 ± 2.6	5.5	7.8 ± 9.6	21.5	2.8 ± 2.9	10.7	0.0 ± 0.0	0.1	0.6 ± 0.7	2.2	17.5 ± 31.9	131.4	5.0 ± 5.5	23.4	2.1 ± 7.0	29.8
Pisces					0.0 ± 0.0	0	0.0 ± 0.0	0.1	0.0 ± 0.0	0			0.0 ± 0.0	0.1		

Missing values indicate zero occurrences, while values marked 0.0 mean <0.04 ind. m^{-3}

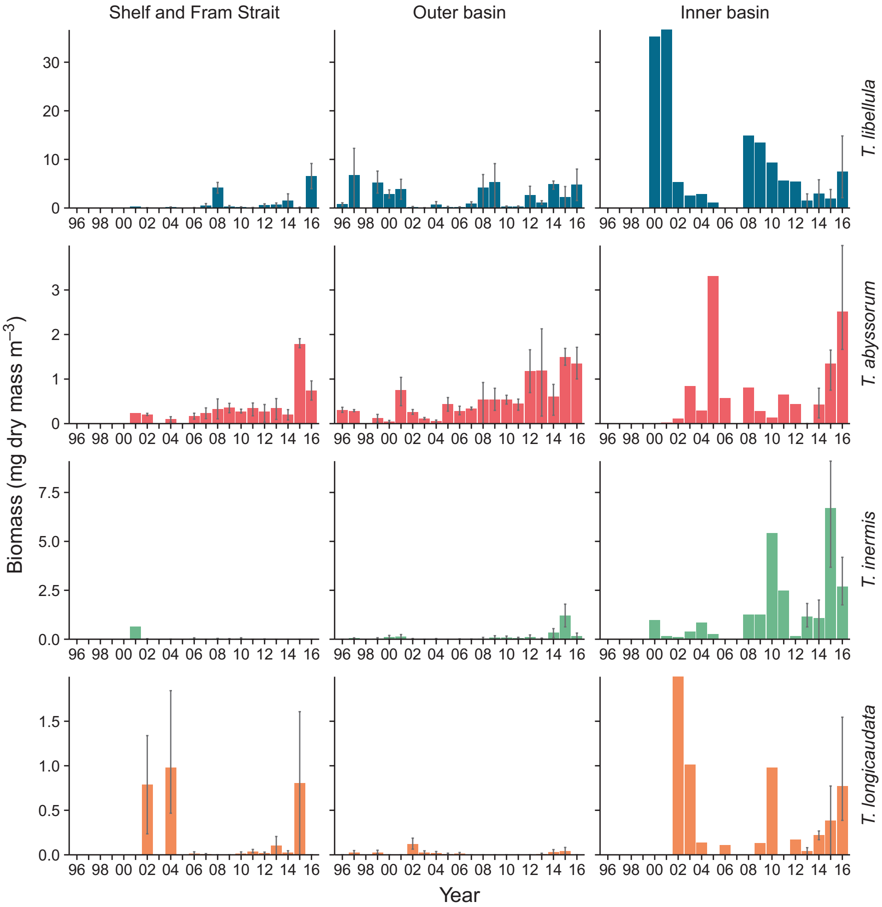

Fig. 7.7 Changes in biomass of most commonly encountered krill and amphipod species in the zooplankton time series sampled from 1996–2016 by MultiNet (200 µm mesh size). See Fig. 7.6 for explanation

of other copepod species were less clear (Fig. 7.6). As an example, the biomass of the Arctic *T. borealis* appears to have increased: the species appeared irregularly in the samples until 2009 and occurred in low biomass thereafter.

7.4.2 Amphipods and Euphausiids

The biomass of larger crustaceans, such as *T. libelulla*, *T. abyssorum* and euphausiids, also followed similar temporal patterns as found for *Calanus* spp. and small copepods inside the fjord (Fig. 7.7). However, the increase in biomass started already in 2006 and was most pronounced after 2010 for the Atlantic *T. abyssorum* in the outer basin. The Arctic *T. libellula* showed a peak in biomass around 2000–2001, particularly in the inner basin. After a decline in mid-2000, it increased in biomass from 2008, but then decreased in the inner basin after 2009. On the shelf and in Fram Strait, there was no distinct temporal trend for these larger crustaceans. Krill, particularly *T. inermis* and to a lesser extent *T. longicaudata*, increased in abundance during the warming period in 2006–2007, mainly in the inner basin (Fig. 7.7). While abundance estimates from MultiNet may underestimate their true abundance, the data should nevertheless be comparable within the time series since the method remained the same throughout the time series. Thus, changes in their occurrence in the samples should reflect changes in the environment between years, i.e. years/locations with high abundance should result in higher numbers caught in the MultiNet compared to years/locations with low abundance.

Seasonal abundance (ind. m^{-3}) for euphausiids and pelagic amphipods, based on composite data from the outer basin from April to October (Fig. 7.8), also include abundance estimate from larger nets that catch these groups more efficiently (see Methods). Highest abundances of the *T. inermis*, *T. longicaudata* and *T. raschii* have been recorded during spring, while they declined through the summer. *Meganyctiphanes norvegica* was mainly caught in October, but was also present during spring-summer, with juveniles in April. The pelagic amphipods *T. libellula* and *T. abyssorum* had highest abundances during July, and the abundance of *T. abyssorum* remained elevated though the autumn.

7.4.3 Changes in Zooplankton Abundance 1996–2006 Versus 2007–2016

The time-series patters were best visualized by patterns in biomass (Figs. 7.6 and 7.7), whereas the seasonal data for krill and amphipods were based on abundance (Fig. 7.8). The abundance of copepods (Table 7.3) and other taxa (Table 7.4), including their spatial distribution in Kongsfjorden (Tables 7.5 and 7.6) have shown changes in abundance from the early (1996–2006) to the later sampling period (2007–2016). The abundance of *C. finmarchicus* more than doubled in Kongsfjorden from a mean of 176 to 431 ind. m^{-3}, and maximum values increased by a factor of six between the two periods (Table 7.3). At the same time, the abundance of *C. glacialis* remained about the same, 90–100 ind. m^{-3}. The abundance of *Pseudocalanus* sp. decreased to about half after 2006. Small copepods, such as *O. similis* were also reduced by about 25% during the later period. Changes related to abundance of other taxa included an increase in the pteropod *L. helicina* from 5 to 72 ind. m^{-3}. Particularly the maximum increased substantially, from 86 to 2278 ind. m^{-3} between periods, reflecting the ephemeral mass occurrence of this species during summer. Changes in larger zooplankton generally reflected changes in biomass, as described above.

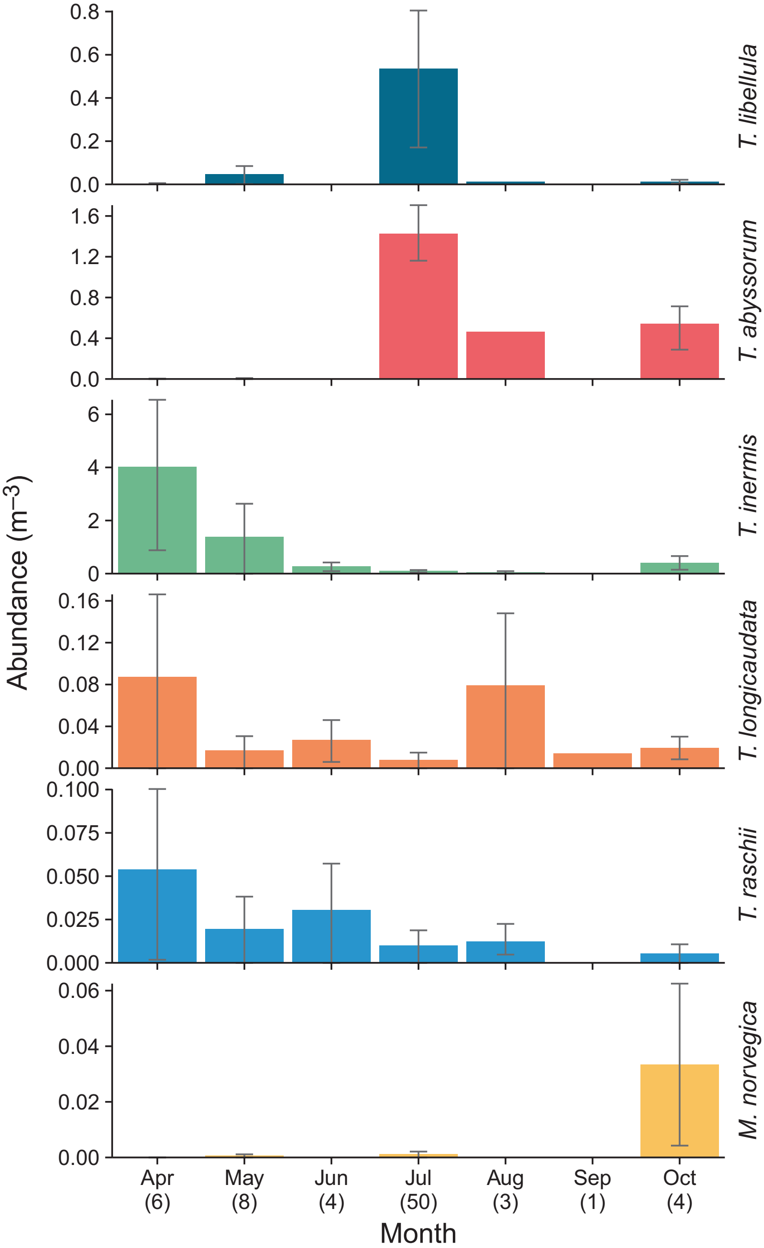

Fig. 7.8 Seasonal variability in mean abundance (ind. m^{-3}) of euphausiids (*Thysanoessa inermis*, *T. longicaudata*, *Meganyctiphanes norvegica*, and *T. raschii*) and pelagic amphipods (*Themisto libellula* and *T. abyssorum*) for the outer basin of Kongsfjorden. Data are combined for stations and sources, with samples from MultiNet as well as MIK and Tucker trawl (Dalpadado et al. 2016; Long-term series, F. Buchholz unpubl.). Number of replicates (stations and samplings) for each month is given in parenthesis under x-axis labels. Error bars that reach all the way down to zero represent negative minimum CIs indicating low confidence for the mean estimate. The figure contains data from 2006–2013

7.4.4 Effect of Temperature on the Zooplankton Community

The zooplankton community within Kongsfjorden appears to have responded differently to environmental changes compared to the communities outside Kongsfjorden (Fig. 7.9). While Atlantic species (*C. finmarchicus, O. atlantica, T. abyssorum, T. longicaudata*) have generally increased in abundance and biomass in inner Kongsfjorden (Fig. 7.9), the opposite pattern appears to have happened outside Kongsfjorden with an increase in some Arctic species (*T. libellula* and *C. hyperboreus*).

Water depth, type and temperature as well as year and station location fitted best to the unconstrained PCA ordination using the zooplankton abundance community matrix (Table 7.7). Due to interactions caused by station location along the time-series transect, the dataset was split into two community matrices: samples from the inner and outer basin, and samples from the shelf and Fram Strait stations. The resulting ordinations were further constrained to the best fitting linear gradients: depth, year and temperature. The fit of station location and region to the resulting RDA ordinations were rather low indicating that these factors explained the split datasets poorly (Table 7.7). Temperature and contribution of Atlantic Water increased throughout the study period (Fig. 7.2), but temperature and sampling depth were negatively correlated making it difficult to separate the effects of these variables on the zooplankton community composition. Nevertheless, temperature and depth “explained” well the community ordination with R^2 values between 0.41 and 0.55 (Table 7.7). *Metridia longa* and *Microcalanus* spp. were generally more abundant in deep or cold habitats than *O. similis*, Echinodermata, Bivalvia, copepod nauplii and *C. finmarchicus* (Fig. 7.10). Also *O. atlantica* was identified by the RDA to have increased in recent years, but the increase may have been caused by exceptional high biomass in 2014, while there was no clear increasing trend in the biomass of this species over the entire time period. *Microcalanus* spp., on the other hand, showed a trend towards an increase outside Kongsfjorden. Salinity explained poorly the average community composition (Table 7.7).

Fig. 7.9 (continued) 95% confidence intervals. If the error bars do not cross the zero-line, the difference in biomass between warm and cold years is statistically significant. Significant LnR values have been indicated with red for higher values during warm years and with blue for higher values during cold years. Values on the y-axis are natural logarithms of mean biomass ratio for a given region and the range for y-axes vary among taxa. Colours for taxa names indicate the origin relative to the study location: red implies Atlantic, blue Arctic origin, and black indicates species that originates from both regions. Averaged biomasses over all depth-strata within a MultiNet multiple plankton sampler (MPS) cast were used as replicates and the ranges of number of replicates are given under a taxa name for warm years/cold years. Size of mean LnR point is scaled with the minimum number of replicates available for each Region

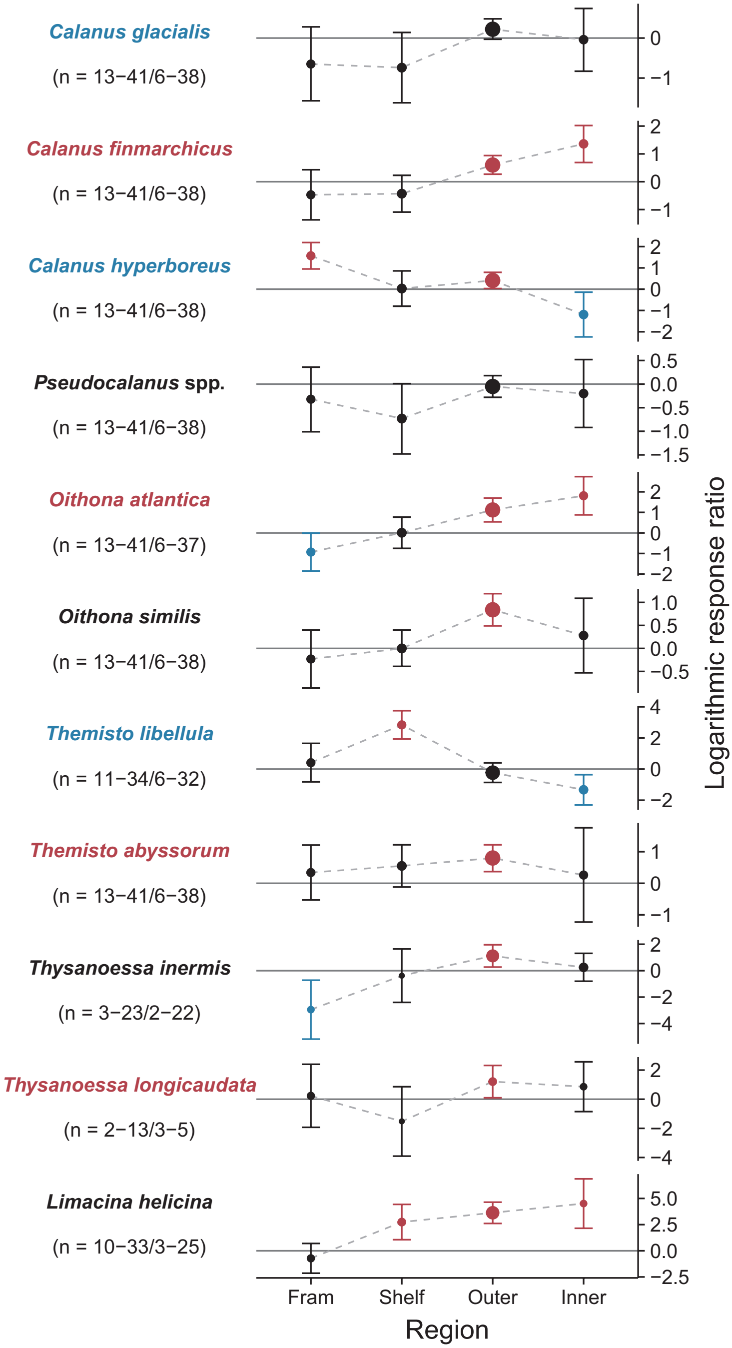

Fig. 7.9 Logarithmic response ratio (LnR) analysis of zooplankton taxa biomass allocation between warm and cold years. Values >0 indicate that biomass of given taxa was higher during the warm years compared to the cold years, and values <0 indicate the opposite. Error bars indicate

7.5 Discussion of Data from the 20-Year Time Series in Context with Other Data

The mesozooplankton community in Kongsfjorden resembles, in many aspects, communities found in pelagic ecosystem in other Svalbard fjords and the northern Barents Sea, with a dominance of copepods in terms of species numbers, a numerical dominance of small-sized copepods and biomass dominance of larger copepods of the genus *Calanus*.

7.5.1 Interannual and Long-Term Changes

Recent decades have revealed large changes in the West Spitsbergen Current and a general warming of the Arctic (Beszczynska-Möller et al. 2012: Walczowski et al. 2012). The long observation record (2000–2017) from Fram Strait showed the warming peak around 2006, but has not revealed a general warming for the water column (Walczowski et al. 2017). However, the salinity has increased during this period as did the temperature in the Atlantic water layer in Fram Strait, which likely has affected the heat transport to West Spitsbergen and the Arctic Ocean. Given the seascape of Kongsfjorden and its neighbourhood, oceanographic conditions outside the fjord do affect the advection of water masses into it and, thus, the hydrological conditions inside the fjord. Particularly, two warming anomalies of Atlantic Water passing through Fram Strait in 1999–2000 and 2005–2007 have been responsible for two major warming periods in Kongsfjorden in 2001 and 2006 (Fig. 7.2; Tverberg et al., Chap. 3). In addition, climate warming affects ice conditions, glacier run-off and water temperatures directly in the fjord (Sundfjord et al. 2017). Atlantic or Transformed Atlantic Water occupy Kongsfjorden to a variable degree, and can modify the zooplankton community accordingly (Ormanczyk et al. 2017; Prominska et al. 2017; Weslawski et al. 2017). Previous studies from Kongsfjorden have related the proportions of zooplankton species with different biogeographic origins to the distribution of Arctic and Atlantic water masses and their mixing and exchange on the shelf (Kwasniewski et al. 2003; Basedow et al. 2004; Cottier et al. 2005; Willis

Fig. 7.10 (continued) the Shelf and Fram Strait stations. Individual samples from a MPS (MultiNet multiple plankton sampler) cast were used as “sites” and are illustrated using grey dots. Species scores are illustrated using red crosses and species abbreviations for scores with absolute value >0.4 are presented as labels where the line points to the corresponding cross. Species names are abbreviated from Table 7.2. Twelve most contributing species to RDA axes 1 and 2 have been shown in “lollipop charts” on the right side of RDA plots. The y-axis value responds to the axis score, and values inside the heads indicate the contribution of a given species to total axis eigenvalue with all species in the dataset adding up to 100%. Heads are color-coded with red indicating shallower sampling depths, warmer temperatures or/and later years during the time series than the blue heads, which are the opposite. Total PCA inertia explained by each RDA axis is given in parenthesis in axis labels

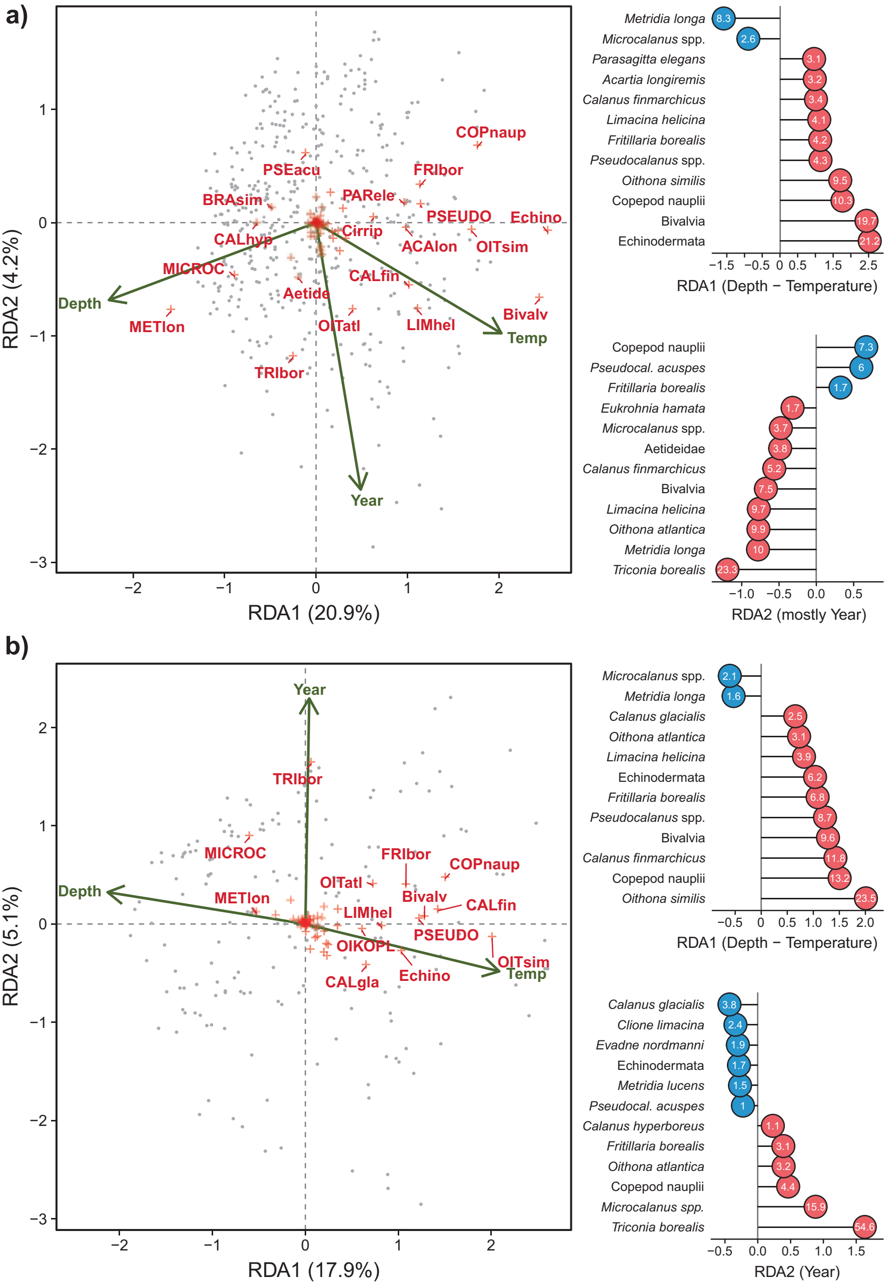

Fig. 7.10 Redundancy analysis (RDA) of the zooplankton abundance time series (1996–2016) with temperature, maximum depth of sampling strata and year as linear environmental gradients (green arrows). (**a**) The analysis for Inner and Outer basins of Kongsfjorden, and (**b**) analysis for

Table 7.7 Explanatory variable fit to the unconstrained PCA ordination (Region = All) and to the constrained RDA ordinations (Region = Inner and Outer basins, and Shelf and Fram Strait) using the zooplankton abundance community matrix

	All		Inner and outer basins		Shelf and Fram strait	
Variable	R^2_{factor}	R^2_{vector}	R^2_{factor}	R^2_{vector}	R^2_{factor}	R^2_{vector}
Depth	0.41	0.34	0.46	0.55	0.45	0.40
Temperature		0.43		0.48		0.40
Year	0.17	0.02	0.43	0.47	0.34	0.52
Water mass	0.27		0.27		0.18	
Station	0.25		0.03		0.14	
Region	0.23		0.01		0.10	
Salinity		0.11		0.12		0.05
Warm vs. cold year	0.06		0.11		0.01	

R^2_{Factor} gives the coefficient of determination for variables that were treated as categorical leading to centroid fits and allowing nonlinearity, while R^2_{Vector} gives similar value for continuous variables treated as linear gradients

et al. 2006, 2008; Buchholz et al. 2010; Dalpadado et al. 2016; Gluchowska et al. 2016). Thus, variable and increased inflow of Atlantic Water, with warming trend inside the fjord during our observation period (Fig. 7.2) and resulting changes in the pelagic fauna phenology, may be responsible for the observed changes in the zooplankton community of the fjord between 1996 and 2002 (Hop et al. 2006) and 2006–2016.

However, only few species showed clear trends of either increase or decrease in the time series. Large interannual variations in *C. finmarchicus* abundance and biomass seem to be correlated to changes in hydrography, particularly the influx of Atlantic Water, i.e. warm years led to an increased abundance of *C. finmarchicus* compared to cold years. *Calanus finmarchicus* is an Atlantic boreal deep-water species and considered an expatriate species in the Arctic. The ability of *C. finmarchicus* to survive and colonize the Arctic Ocean is hampered by short algal blooms and low temperatures (Jaschnov 1970; Tande and Båmstedt 1985; Ji et al. 2012), and it fails to reproduce in the Arctic Ocean and partly also in the surrounding shelf seas (Hirche et al. 2006). The high interannual variability in *C. finmarchicus* abundance in Kongsfjorden may indicate that the species in Kongsfjorden is composed of a resident population reproducing locally and an advected one reproducing outside the fjord, most likely in the WSC. Thus, the abundance in the fjord is dependent on the strength of the inflow from the outside, with strong inflow of Atlantic Water and consequently an increased abundance of that species in what is referred to as “warm years” (Espinasse et al. 2017). In such years, the size of the population in the WSC also increases (Gluchowska et al. 2017; Weydmann et al. 2018). Furthermore, the variability in *C. finmarchicus* abundance in Kongsfjorden may not only be explained by variability in advection, but also by variability in local reproduction, which is more successful during “warm years” leading to increased population size (Kwasniewski et al. 2013).

Calanus glacialis, on the other hand, is an Arctic shelf species, spawning in waters all around the Arctic shelf and in the White Sea (Kosobokova 1999; Daase et al. 2013). This species displays high flexibility in its reproductive strategies as an adaptation to living in seasonal ice covered seas with high inter-annual variability in the timing of ice break up and bloom phenology. Relatively little variability in *C. glacialis* abundance in Kongsfjorden indicates that Kongsfjorden harbours a resident *C. glacialis* population that is successfully reproducing there (Kwasniewski et al. 2003), but can also include a supplementary population from outside the fjord, advected with the coastal current. The results of our observations showed no clear impact of changes in environmental factors on the number or biomass of *C. glacialis*. The inter-annual variability observed in its biomass is likely related to the stage composition at the time of sampling, as biomass increases with developmental stage; adult specimens might have six times as much biomass as a young copepodids (copepodid stages C1–C3). Thus, low biomass may indicate higher abundance of small stages and not a general decrease in abundance. For example, the *C. glacialis* population in 2010 consisted to >70% of copepodid stages C1–C3 leading to low biomass in the inner basin, while in 2013 (high biomass) the population consisted >80% of C4 and C5. These differences in stage composition between years reflect differences in phenology (for this species as well as others), including timing of reproduction, which is tightly coupled to the onset, duration and magnitude of the spring bloom, which can vary considerable between years (Daase et al. 2013; Hegseth et al., Chap. 6). The spring bloom occurred earlier (mid-May) in 2013 than in some of the previous years (mid-June in 2010 and 2011), which may explain the high percentage of older copepodids in 2013. The persistence of Arctic *C. glacialis* in the zooplankton community demonstrates that this species can tolerate a wide range of environmental conditions and suggests that ongoing changes in the environmental conditions in Kongsfjorden have not reached critical levels for this species.

Temporal trends were apparent in larger crustaceans, with increased biomasses of the Atlantic amphipod *T. abyssorum* and euphausiids (*T. inermis, T. longicaudata*) in the most recent years and decreased abundance of the Arctic *Themisto libellula*. Increase in *T. abyssorum* has also been recorded in the HAUSGARTEN area of Fram Strait and related to the prevailing influence of North Atlantic water masses in the upper part of the water column (Kraft et al. 2012). We recognize that larger individuals of these species may be undersampled by MultiNet, and high predatory mortality by e.g. capelin (*Mallotus villosus*) may impact krill densities in Kongsfjorden (Dalpadado et al. 2016). Population increases in the currently present five species of krill were noted with the exception of *T. raschii*, and the seasonal data (with samples from larger nets) indicate that they are most abundant in the fjord during spring. Overall, the Arcto-boreal expatriate *T. inermis* appears to be well suited to withstand the challenges of an Arctic environment with vital rates similar to temperate species and congeners (Huenerlage and Buchholz 2015). The vital rates typically remain high during the spring bloom, but then drop during the summer. Changes in krill occurrence may indicate changes in food-webs; if krill numbers increase around Svalbard – i.e. on the basis of the successful completion of a full reproductive cycle for *Thysanoessa* spp., higher trophic levels will likely follow them. In the Barents Sea, increasing krill numbers during the last decades may have supported substantial increases in fish stocks (Eriksen and Dalpadado 2011). The rapid increase in population density in Kongsfjorden may be interpreted as consequence of increasing Atlantic input, which carried the krill along having been spawned in the warming Barents Sea. However, a proportional change in the repertoire of krill species in the Arctic and sub-Arctic waters would possibly lead to a decrease in the availability of the lipid-rich, high-quality food represented by *T. inermis* that would likely be replaced by the currently strongest expanding krill species *M. norvegica*, which carries far less lipids, (Huenerlage et al. 2016). This Atlantic species was present in the outer basin of Kongsfjorden mainly during the late autumn, but is more abundant outside Kongsfjorden (Dalpadado et al. 2016).

7.5.2 Potential Effects of Changes in Winter Temperatures

Temperature time series from ocean observatories have shown that the largest temperature increase in the fjord over the last decade occurred during winter (Geoffroy et al. 2018; Hop et al., Chap. 13). This is in agreement with results of studies on water-mass transport in the West Spitsbergen Current, which show that that in winter the WSC tends to be wider and stronger with two-fold higher transport (Beszczynska-Möller et al. 2012). Zooplankton abundance and species composition recorded during surveys may to some degree reflect the occurrence of water masses just prior to or during sampling, particular in open water and highly advective regions. However, hydrographic events and progress occurring in previous seasons may also have an effect on how zooplankton communities are structured during summer, particular in more secluded locations such as fjords. Increased winter temperatures may affect the survival of zooplankton populations either negatively (due to increased metabolic cost at increased water temperature) or positively (more favourable conditions for boreal species advected during summer and autumn that may otherwise not survive under cold Arctic winter conditions). Furthermore, zooplankton advected with inflowing Atlantic Water during winter (e.g. Cottier et al. 2007) may persist throughout the year. Thus, some of the long-term changes discussed above may be related to the increase in winter temperatures in Kongsfjorden. For example, the higher biomass of *C. finmarchicus* in recent years may be due to increased winter survival related to more favourable (i.e. higher) winter temperatures, which may also have caused favourable bloom phenology (see below) increasing recruitment in the local population during spring. However, we generally lack long-term seasonal data on zooplankton from Kongsfjorden, except for a few studies (Walkusz et al. 2009; Lischka and Hagen 2016), and therefore cannot determine seasonally-delayed effects on the zooplankton composition during summer. Furthermore, more factors than just winter temperature need to be considered, such as the effect of increased winter temperatures on duration of sea ice cover and timing of spring plankton blooms, in addition to the timing of advection. Future monitoring efforts may benefit from increased seasonal sampling resolution to untangle these effects.

7.5.3 Sea Ice, Plankton Blooms and Increased Bio-production in Ice-Free Waters

Arctic zooplankton communities are also affected by sea ice. Sea ice limits the penetration of light into the water column and the freeze/melt cycle of sea ice affects water mass stratification and mixing processes. These physical processes control the replenishment of essential nutrients to the euphotic zone, and thereby the onset and duration of ice algae and pelagic blooms (Søreide et al. 2010; Leu et al. 2015). The timing, quality and quantity of these blooms influence recruitment, growth and development of primarily herbivorous zooplankton species (Leu et al. 2011). One of the major changes between the 1996–2006 and the 2007–2016 period is the loss of sea ice in Kongsfjorden. The fjord had little ice cover of only short duration after 2006, except for 2009 and 2011 when the ice coverage was more extensive but thinner than in earlier years (Pavlova et al., Chap. 4). Several controlling factors, such as winter/early spring convections and mixing, in addition to duration of sea ice cover, are involved in the timing of the spring bloom in Kongsfjorden, which varies from mid-late April to late May or early June (Hegseth et al., Chap. 6).

The general increase in zooplankton abundance between these two periods likely reflects these changes: the loss of sea ice was accompanied with increased (winter) temperatures promoting growth and development, and the peak of the bloom typically happens 2–3 weeks after the ice break-up (Hegseth et al., Chap. 6). However, the magnitude of the bloom is also dependent on stratification of water masses, which is weaker in cold years than in warm years in Kongsfjorden. The algae species composition also changes with dominance of diatoms in cold years and more flagellates and prolonged blooms throughout the summer months during warm years (Hegseth et al., Chap. 6). Thus, for *C. glacialis* the conditions become more favourable during the cold years with early spring blooms of diatoms, whereas for *C. finmarchicus*, Atlantic amphipods and krill the conditions get better during warm years. Espinasse et al. (2017) related years with higher *C. finmarchicus* abundance in Kongsfjorden to years with a delayed spring bloom, which they explained with improved feeding conditions for the younger developmental stages accelerating growth and development of the boreal calanoid. The decrease in sea ice during the last decades in the European Arctic, including Svalbard waters, has opened up large areas for new bio-production (Smedsrud et al. 2013; Falk-Petersen et al. 2015). This has led to higher production of herbivorous zooplankton as well as higher trophic-level animals (Eriksen et al. 2017). A similar pattern can be seen for Kongsfjorden with regard to total biomass of zooplankton (Fig. 7.11). The biomass has generally increased in Kongsfjorden during the last decade, which infers a probable increase in bio-production, although this pattern was less apparent and more variable for

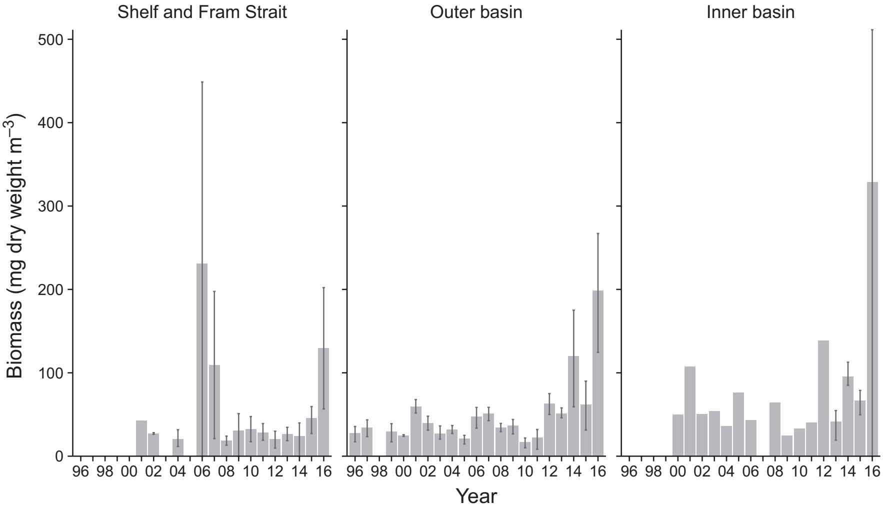

Fig. 7.11 Changes in total zooplankton biomass over time. See Fig. 7.6 for explanation

Fram Strait. On the other hand, the negative trend in sea–ice extent and increased temperature in the marine environment have caused declines in higher trophic levels of Arctic organisms, such as polar cod and ringed seals (*Pusa hispida*), partly because of changes in the food web and competitor populations, but also because of habitat loss with regard to Arctic seals (Renaud et al. 2012; Lydersen et al. 2014; Vihtakari et al. 2018).

7.5.4 Food-Web Effects of Changes in Zooplankton Community

Arctic zooplankton species tend to be larger and more lipid rich than their boreal congener species (Falk-Petersen et al. 2009). As planktivorous seabirds and fish species tend to be size-selective in search of prey, changes in abundance and biomass of Arctic and Atlantic species may have repercussions for the pelagic food web. For example, little auks (*Alle alle*) have a strong preference for larger *Calanus* (e.g. *C. glacialis*) and years with a dominance of the smaller *C. finmarchicus* inside the fjord may force the birds to fly longer distances to find suitable food, thereby increasing their energetic demands that in turn reduce their survival and recruitment success (Karnovsky et al. 2003; Kwasniewski et al. 2010; Hovinen et al. 2014a, b). The prey base of *C. glacialis* seems to be maintained in the Outer and Inner basins of Kongsfjorden, with highest biomass in the Inner basin. However, for visual predators it may be more difficult to selectively prey on them in the Inner basin because of turbid glacial water at the surface (Pavlov et al., Chap. 5). Other seabirds, such as the surface feeding black-legged kittiwake, are able to change prey based on their abundance in the fjord (Vihtakari et al. 2018). The frequency of occurrence of Arctic species in seabird stomach was positively related to the sea ice index, whereas the frequency of Atlantic species increased with temperature. Thus, the negative trend in sea–ice extent and positive trend in temperature have caused increased "Atlantification" of the ecosystem in Kongsfjorden, with consequences for upper trophic levels (Vihtakari et al. 2018). In this study, we noticed such correlations for *C. finmarchicus*, *T. abyssorum* and krill.

However, the size structure of the zooplankton population may not only change due to changes in the species composition from larger Arctic species to smaller Atlantic species. Increased water temperature, changes in light climate and an extended productive season, due to less sea ice, can push populations towards faster development, shorter life cycles and smaller body size (Leinaas et al. 2016; Renaud et al. 2018). *Calanus finmarchicus* and *C. glacialis* are traditionally distinguished based on size classes (prosome length). Recent advances in molecular techniques have revealed larger overlap in size between the two species than previously assumed (Gabrielsen et al. 2012; Choquet et al. 2017, 2018). In particular *C. glacialis* may be smaller than assumed, and using size classes may therefore lead to an underestimation of *C. glacialis* in samples that contain both species. The extent of this bias varies with geographical location (Gabrielsen et al. 2012; Choquet et al. 2017). Along the Norwegian coast, there is a 100% overlap in size between the two species in some locations (Choquet et al. 2018), making species determination based on size highly problematic and also indicating that under increased water temperature and a prolonged primary productive season the *C. glacialis* population is driven to smaller body size. In Svalbard waters, the overlap is less severe (Gabrielsen et al. 2012; Choquet et al. 2017), thus using size classes will provide a realistic picture of the species composition. However, one should be aware of the potential to underestimate *C. glacialis* abundance and that this problem will increase with increased warming leading to a decrease in mean body size. A proper documentation of length-frequency distributions of *Calanus* spp. in future time-series studies may shed more light on changing size structure of the *Calanus* population in Kongsfjorden.

Recent years have also involved changes in the fish community in Kongsfjorden with an increased abundances of Atlantic fishes that contribute to the predation pressure on zooplankton (Szczucka et al. 2017; Vihtakari et al. 2018). This may be a response to the general increase in abundance of zooplankton, and particularly krill (Dalpadado et al. 2016). Furthermore, changes in the zooplankton species composition may affect diets of both polar cod and capelin (Hop and Gjøsæter 2013; Dalpadado et al. 2016). Nahrgang et al. (2014) found that the prey composition of polar cod differed between polar cod feeding in Arctic domains compared to those feeding in Atlantic domains such as Kongsfjorden, with the diet in the Atlantic domain being much more variable. Further warming with expansion of Atlantic water masses are also expected to extend to the northern distribution ranges for boreal fish species, which will result in increased competition with Arctic species and also increased top-down effects on the zooplankton prey (Eriksen and Dalpadado 2011; Eriksen et al. 2017).

7.6 Methodical Considerations

7.6.1 Sampling Resolution

Zooplankton, particularly in highly seasonal environments as the high Arctic, show high seasonal variability in abundance. This raises the question how representative annual sampling is. While high seasonal resolution would be preferable to address questions on phenology and life cycles, such endeavours would be logistically and financially challenging to maintain. Annual sampling in July/August has the advantage of the fjord being accessible with regard to sea-ice conditions. The pelagic ecosystem in Kongsfjorden is in a post-bloom situation mid-end July/beginning of August, with most zooplankton populations still being active in the water column. This time is also important for feeding by seabird populations around the fjord and for recruitment in fish species. Thus, monitoring the zooplankton population in July/August provides an estimate of the available energy in the system for higher trophic levels. Part of the pelagic community inventory is missed by sampling with the MultiNet and MIK net. Tucker trawl can be used to sample zooplankton near the bottom (Hirche et al. 2016), and use of echosounders and Acoustic Doppler Profiler (ADCP) can provide additional information about temporal and spatial distribution of larger zooplankton and their diurnal vertical migrations (e.g. Darnis et al. 2017). For long-term monitoring of a system like Kongsfjorden, it is important that standardized sampling is continued annually at the same time of year, which is currently conducted as part of MOSJ (www.mosj.npolar.no). In order to determine changes over time, and for comparisons between fjords or regions, it will be important to coordinate and standardize the zooplankton sampling in different institutions and sampling campaigns. Such initiatives were discussed during a Plankton Research in Svalbard (PRiS) workshop at UNIS in 2014, but need to be implemented in future studies.

7.7 Conclusions

Zooplankton in both Kongsfjorden and the Shelf/Fram Strait area have responded to changes in fluctuating patterns in temperature related to warm-water anomalies (Beszczynska-Möller et al. 2012) as well as to decline in sea ice (Barber et al. 2015; Pavlova et al., Chap. 4), although the changes in abundance are not synchronous between Kongsfjorden and Fram Strait. Fluctuating patterns of the zooplankton composition during summer in Kongsfjorden are related to advection of Atlantic Water, particularly during winter, with an increase of some Atlantic species during warm years, but no concurrent decline in Arctic species except for the Arctic amphipod *T. libellula*. Zooplankton abundance and biomass in the fjord appear to have increased, while a similar pattern is not evident for the Shelf/Fram Strait. However, increases in Atlantic zooplankton species have been recorded after the warm 2006 in Fram Strait (Walczowski et al. 2012), and at the central HAUSGARTEN station (Kraft et al. 2012; Soltwedel et al. 2016). Within Kongsfjorden, the Atlantic *C. finmarchicus* is mainly responsible for the increasing trend in biomass and abundance, whereas *C. glacialis* has been relatively stable, possibly indicating its plasticity with regard to “Atlantification”.

Data availability Zooplankton data and updated list of conversion factors are available in the MarineDatabase (Norwegian Polar Institute 2018) package for R (R Core Team 2018). The zooplankton data set in this paper is available at: https://doi.org/10.21334/npolar.2019.94b29b16.

Acknowledgements We thank the different researchers and technicians that have been involved in zooplankton collections at our sampling stations in Kongsfjorden during the 20-year time series. Olga Pavlova, Norwegian Polar Institute, is thanked for making CTD files from stations in Kongsfjorden available, and making transect plots of temperature and salinity. Padmini Dalpadado, Institute of Marine Research, is thanked for data on krill and amphipods sampled by MIK (Method Isaacs Kidd) in Kongsfjorden. MG participation was funded by the Polish Scientific Council projects: KongHau4 (W84/KongHau4/2016) and KongHau5 (W88/KongHau5/2017).

Monitoring of water masses and zooplankton in Kongsfjorden is conducted as part of Environmental monitoring of Svalbard and Jan Mayen (www.mosj.npolar.no), which currently funds the annual survey by the Norwegian Polar Institute, and as a part of Long-term studies on the Arctic marine ecosystems funded by the Institute of Oceanology Polish Academy of Sciences (IOPAN). Our sampling along the Kongsfjorden transect extends to HAUSGARTEN stations in Fram Strait when time and weather permit.

Appendix

Table 7.8 Abundance to dry mass conversion factors used in the study

Taxa	Origin	DM conversion	References
Copepoda			
Acartia longiremis	Arctic	0.0099	1, 2, 3
Aetideidae C1–C3	Unknown	0.0696	1, 2, 3
Aetideopsis minor C4–C6	Both	0.1325	1, 2, 3
Aetideopsis rostrata C4–C6	Arctic	0.2346	1, 2, 3
Aetideus armatus C4–C6	Atlantic	0.121	
Augaptilus glacialis	Both	0.6922	1, 2, 3
Bradyidius similis C4–C6	Arctic	0.111	1, 2, 3
Calanus finmarchicus AF	Atlantic	0.2822	4, 5, 6, 7
Calanus finmarchicus AM	Atlantic	0.2139	4, 5, 6, 7
Calanus finmarchicus C5	Atlantic	0.2139	4, 5, 6, 7
Calanus finmarchicus C4	Atlantic	0.0745	4, 5, 6, 7
Calanus finmarchicus C3	Atlantic	0.0295	4, 5, 6, 7
Calanus finmarchicus C2	Atlantic	0.011	4, 5, 6, 7
Calanus finmarchicus C1	Atlantic	0.0051	4, 5, 6, 7
Calanus glacialis AF	Arctic	1.303	4, 5, 6, 7
Calanus glacialis AM	Arctic	0.6201	4, 5, 6, 7
Calanus glacialis C5	Arctic	0.6201	4, 5, 6, 7
Calanus glacialis C4	Arctic	0.1979	4, 5, 6, 7
Calanus glacialis C3	Arctic	0.0618	4, 5, 6, 7
Calanus glacialis C2	Arctic	0.0216	4, 5, 6, 7

(continued)

Table 7.8 (continued)

Taxa	Origin	DM conversion	References
Calanus glacialis C1	Arctic	0.009	4, 5, 6, 7
Calanus hyperboreus AF	Arctic	3.2932	4, 5, 6, 7
Calanus hyperboreus AM	Arctic	1.2093	4, 5, 6, 7
Calanus hyperboreus C5	Arctic	1.2093	4, 5, 6, 7
Calanus hyperboreus C4	Arctic	0.3784	4, 5, 6, 7
Calanus hyperboreus C3	Arctic	0.1121	4, 5, 6, 7
Calanus hyperboreus C2	Arctic	0.0293	4, 5, 6, 8, 7
Calanus hyperboreus C1	Arctic	0.0108	4, 5, 6, 8, 7
Chiridius obtusifrons C4–C6	Both	0.2821	1, 2, 3
Copepoda nauplii	Unknown	0.0045	1, 2, 3
Disco sp. C4–C6	Unknown	0.001	
Gaetanus brevispinus C4–C6	Both	0.3392	1, 2, 3
Gaetanus tenuispinus C4–C6	Both	0.1082	1, 2, 3
Harpacticoida	Unknown	0.007	1, 2, 3
Heterorhabdus norvegicus	Arctic	0.1595	1, 2, 3
Homeognathia brevis	Atlantic	0.0069	1, 2, 3
Mesaiokeras spitsbergensis	Arctic	0.0164	1, 2, 3
Metridia longa AF	Both	0.287	9
Metridia longa AM	Both	0.137	9
Metridia longa C5	Both	0.12	9
Metridia longa C4	Both	0.034	9
Metridia longa C3	Both	0.016	9
Metridia longa C2	Both	0.007	9
Metridia longa C1	Both	0.003	9
Metridia lucens	Atlantic	0.0295	1, 2, 3
Microcalanus spp.	Both	0.007	9
Microsetella norvegica	Atlantic	0.0011	1, 2, 3
Monstrilloida C6F	Unknown	0.0595	1, 2, 3
Neomormonilla minor C5–C6	Atlantic	0.0167	1, 2, 3
Neoscolecithrix farrani C4–C6	Atlantic	0.0285	1, 2, 3
Oithona atlantica C6	Atlantic	0.0069	1, 2, 3
Oithona similis	Both	0.0025	10
Oncaea parila C6F	Arctic	0.0025	10
Oncaea spp. C6F	Unknown	0.002	10
Paraeuchaeta barbata C6F	Atlantic	9.056	1, 2, 3
Paraeuchaeta glacialis C6F	Arctic	5.907	1, 2, 3
Paraeuchaeta norvegica C6F	Atlantic	4.6717	9
Paraeuchaeta spp. AM	Both	1.7892	9
Paraeuchaeta spp. C5	Both	1.6813	9
Paraeuchaeta spp. C4	Both	0.3775	9
Paraeuchaeta spp. C3	Both	0.1215	9
Paraeuchaeta spp. C2	Both	0.0485	9

(continued)

Table 7.8 (continued)

Taxa	Origin	DM conversion	References
Paraeuchaeta spp. C1	Both	0.0384	9
Paraheterorhabdus compactus C4–C6	Both	0.0951	1, 2, 3
Pleuromamma robusta C6F	Atlantic	0.17	1, 2, 3
Pseudocalanus acuspes C6F	Arctic	0.0131	9
Pseudocalanus minutus C6F	Arctic	0.0146	9
Pseudocalanus spp. C6M	Both	0.012	9
Pseudocalanus spp. C5	Both	0.0086	9
Pseudocalanus spp. C4	Both	0.0051	9
Pseudocalanus spp. C3	Both	0.0032	9
Pseudocalanus spp. C2	Both	0.0015	9
Pseudocalanus spp. C1	Both	0.0006	9
Pseudochirella spectabilis C4–C6	Both	1.156	
Rhincalanus nasutus C4–C6	Atlantic	0.4116	1, 2, 3
Scaphocalanus brevicornis	Both	0.0333	1, 2, 3
Scaphocalanus magnus	Both	0.1593	1, 2, 3
Scolecithricella minor	Both	0.0243	1, 2, 3
Spinocalanus antarcticus	Arctic	0.0439	1, 2, 3
Spinocalanus horridus C4–C6	Arctic	0.089	1, 2, 3
Spinocalanus longicornis C6	Both	0.017	
Spinocalanus spp. C1–C6	Unknown	0.0167	1, 2, 3
Temorites brevis	Both	0.0378	1, 2, 3
Tharybidae C4-C6	Unknown	0.0186	1, 2, 3
Tharybis groenlandicus C6	Arctic	0.02	1, 2, 3
Triconia borealis C6	Arctic	0.002	10
Triconia conifera C6F	Atlantic	0.015	10
Triconia/Oncaea spp. C1–C5	Unknown	0.002	10
Undinella oblonga C4–C6	Both	0.044	
Xantharus siedleckii	Arctic	0.0239	1, 2, 3
Amphipoda			
Amphipoda	Unknown	4.1089	1, 2, 3
Apherusa glacialis	Arctic	3.8947	1, 2, 3
Cyclocaris guilelmi	Arctic	1.4412	1, 2, 3
Eusirus holmii	Arctic	4.3022	1, 2, 3
Hyperia galba	Atlantic	0.9042	1, 2, 3
Hyperia medusarum	Atlantic	0.9042	1, 2, 3
Hyperiidae	Unknown	0.5715	1, 2, 3
Hyperoche medusarum	Atlantic	0.9042	1, 2, 3
Onisimus glacialis	Arctic	6.7962	1, 2, 3
Onisimus spp.	Arctic	0.227	
Scina borealis	Atlantic	0.5715	1, 2, 3
Themisto abyssorum 0–5 mm	Atlantic	0.3111	11, 12

(continued)

Table 7.8 (continued)

Taxa	Origin	DM conversion	References
Themisto abyssorum 5–10 mm	Atlantic	1.4511	11, 12
Themisto libellula 0–5 mm	Arctic	3.8988	13, 12
Themisto libellula 5–10 mm	Arctic	9.5337	13, 12
Euphausiacea			
Euphausiacea calyptopis	Unknown	0.0948	1, 2, 3
Euphausiacea furcilia 0–5 mm	Unknown	0.3413	1, 2, 3
Euphausiacea furcilia 5–10 mm	Unknown	0.6614	1, 2, 3
Euphausiacea nauplii	Unknown	0.004	1, 2, 3
Meganyctiphanes norvegica	Atlantic	2.4315	
Thysanoessa inermis	Both	2.4315	14
Thysanoessa longicaudata	Atlantic	2.3183	1, 2, 3
Thysanoessa raschii	Both	2.633	
Ostracoda			
Ostracoda 0–1 mm	Unknown	0.0136	6
Ostracoda 1–2 mm	Unknown	0.0438	6
Ostracoda 2–3 mm	Unknown	0.2666	6
Ostracoda 3–5 mm	Unknown	0.429	6
Cladocera			
Evadne nordmanni	Atlantic	0.0025	18
Decapoda			
Decapoda larvae	Unknown	1.1897	1, 2, 3
Eusergestes arcticus zoea	Both	0.0713	1, 2, 3
Hyas araneus megalopa	Arctic	0.45	1, 2, 3
Hyas araneus zoea	Arctic	0.25	1, 2, 3
Hymenodora glacialis	Arctic	7.9846	1, 2, 3
Pagurus pubescens megalopa	Arctic	0.69	1, 2, 3
Pagurus pubescens zoea	Arctic	0.63	1, 2, 3
Pandalus borealis zoea	Both	4.3669	1, 2, 3
Sabinea septemcarinata zoea	Both	0.9571	1, 2, 3
Isopoda			
Bopyridae	Unknown	0.019	1, 2, 3
Isopoda	Unknown	0.019	1, 2, 3
Mysida			
Boreomysis arctica	Arctic	1.2253	15
Mysidae	Unknown	1.2253	1, 2, 3
Pseudomma truncatum	Both	1.2253	1, 2, 3
Cumacea			
Cumacea	Unknown	0.9571	1, 2, 3
Cirripedia			
Cirripedia cypris	Unknown	0.012	4
Cirripedia nauplii	Unknown	0.012	4

(continued)

Table 7.8 (continued)

Taxa	Origin	DM conversion	References
Facetotecta			
Facetotecta nauplii	Unknown	0.012	4
Polychaeta			
Pelagobia sp.	Atlantic	0.1131	1, 2, 3
Polychaeta adult	Unknown	0.4492	1, 2, 3
Polychaeta metatrochophore	Unknown	0.0016	1, 2, 3
Polychaeta mitraria	Unknown	0.0052	1, 2, 3
Polychaeta secondary	Unknown	0.0019	1, 2, 3
Polychaeta trochophore	Unknown	0.0009	1, 2, 3
Tomopteris spp.	Atlantic	0.5382	1, 2, 3
Typhloscolecidae	Unknown	0.113	1, 2, 3
Nemertea			
Nemertea pilidium	Unknown	0.001	1, 2, 3
Bryozoa			
Bryozoa larvae	Unknown	0.001	1, 2, 3
Gastropoda			
Clione limacina veliger	Both	2.6146	16
Clione limacina 0–5 mm	Both	2.8607	16
Clione limacina 5–10 mm	Both	3.5494	16
Margarites and *Velutina* veliger	Unknown	0.074	1, 2, 3
Limacina helicina veliger	Both	0.257	17
Limacina helicina 0–5 mm	Both	0.8013	17
Limacina helicina 5–10 mm	Both	3.1325	17
Limacina retroversa 0–5 mm	Atlantic	0.8013	17
Limacina retroversa 5–10 mm	Atlantic	3.1325	17
Bivalvia			
Bivalvia veliger	Unknown	0.004	1, 2, 3
Echinodermata			
Echinodermata larvae	Unknown	0.001	18
Hydrozoa			
Aeginopsis laurentii 0–5 mm	Both	0.2628	1, 2, 3
Aglantha digitale 0–5 mm	Arctic	0.045	1, 2, 3
Aglantha digitale 5–15 mm	Arctic	1.4898	1, 2, 3
Botrynema ellinorae	Arctic	2.1767	1, 2, 3
Bougainvillia spp.	Arctic	2.0551	1, 2, 3
Ce-ass *Dimophyes arctica*	Arctic	10.3325	1, 2, 3
Halitholus cirratus	Arctic	0.305	1, 2, 3
Hydrozoa larvae	Unknown	0.0019	1, 2, 3
Hydrozoa medusae indet.	Unknown	2.1767	1, 2, 3
Nanomia cara	Arctic	3.7958	1, 2, 3
Sarsia sp.	Both	2.1767	1, 2, 3
Siphonophora	Unknown	3.7958	1, 2, 3

(continued)

Table 7.8 (continued)

Taxa	Origin	DM conversion	References
Ctenophora			
Beroë cucumis	Both	0.56	1, 2, 3
Ctenophora larvae	Unknown	0.0019	1, 2, 3
Mertensia ovum	Both	1.6063	1, 2, 3
Scyphozoa			
Scyphozoa larvae	Unknown	0.56	1, 2, 3
Chaetognatha			
Eukrohnia hamata 0–5 mm	Both	0.0057	1, 2, 3
Eukrohnia hamata 5–10 mm	Both	0.1377	1, 2, 3
Eukrohnia hamata 10–20 mm	Both	0.9266	1, 2, 3
Eukrohnia hamata 20–30 mm	Both	6.3154	1, 2, 3
Eukrohnia hamata	Both	1.8463	1, 2, 3
Parasagitta elegans 0–5 mm	Both	0.0039	14
Parasagitta elegans 5–10 mm	Both	0.0575	14
Parasagitta elegans 10–20 mm	Unknown	0.2332	14
Parasagitta elegans 20–25 mm	Unknown	1.0556	14
Parasagitta elegans	Both	1.3572	14
Pseudosagitta maxima	Unknown	25.869	
Appendicularia			
Fritillaria borealis	Both	0.0014	1, 2, 3
Oikopleura spp. 0–5 mm	Unknown	0.001	1, 2, 3
Oikopleura spp. 5–10 mm	Unknown	0.035	1, 2, 3
Oikopleura spp. 10–20 mm	Unknown	0.4288	1, 2, 3
Oikopleura spp. 20–30 mm	Unknown	2.1989	1, 2, 3
Oikopleura spp.	Unknown	0.6659	1, 2, 3
Tunicata larvae	Unknown	0.001	
Pisces			
Pisces larvae	Unknown	6.378	19

Columns from the left: taxon, either species or a higher taxonomic rank; stage (C): adult female (AF); adult male (AM); length group (mm); biogeographic origin related to Kongsfjorden, used in classification to Arctic and Atlantic taxa; dry mass conversion factor in mg^{-1}; and source for the conversion factor. Missing reference means that an educated guess, based on a value for a similar sized species, was used as conversion factor. Entries are alphabetic within each taxonomic group

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Table 7.9 Total abundance (ind. m^{-3} or ind. m^{-2}) and biomass in different studies sampling zooplankton in Kongsfjorden, Svalbard

References	Year (month)	Area	Gear	Zooplankton group	Abundance	Other data
Scott et al. (2000)	1997 (Aug–Sep)	Outer (Kb3)	WP2 180 µm	*Calanus* spp.	*Calanus finmarchicus* 80–207 ind m^{-3} *Calanus glacialis* 13–33 ind m^{-3} *Calanus hyberboreus* 15–12 ind m^{-3}	Lipid class; fatty acid
Weslawski et al. (2000)	1996 (Jul)	Inner-outer	Tucker trawl 2 mm	Macrozooplankton	*Limacina helicina* > 1000 ind *100 m^{-3} *Themisto libelulla* > 300 ind *100 m^{-3} *Thysanoessa inermis* 100 ind *100 m^{-3}	Wet weight; Energy content; Length
Hop et al. (2002)	1996 (Jul) & 1997 (Jul, Sep)	Inner-shelf	MultiNet 200 µm	Mesozooplankton	Jul 96, total 30–310 *1000 ind m^{-2} Jul 97, total 70–270 *1000 ind m^{-2} Sep 97, total 100–350 *1000 ind m^{-2}	Dry weight (8.8–5.1 g m^{-2})
Kwasniewski et al. (2003)	1996 (Jul) & 1997 (Sep)	Inner	MultiNet 180 µm & WP2 180 µm	*Calanus* spp.	Jul 1996 *Calanus finmarchicus* 35–200 ind m^{-3} *Calanus glacialis* 46–272 ind m^{-3} *Calanus hyberboreus* 5.6 ind m^{-3} Sep 1997 *Calanus finmarchicus* 103–446 ind m^{-3} *Calanus glacialis* 15–192 ind m^{-3} *Calanus hyberboreus* 13.4 ind m^{-3}	

Walkusz et al. (2003)	2002 (Sep)	Outer	WP2 180 μm & WP3 1000 μm	Mesozooplankton	Mesozooplankton 2700 ind m^{-3}	
Basedow et al. (2004)	2001 (May)	Inner-shelf	MultiNet 200 μm	Mesozooplankton	*Calanus finmarchicus* 3–421 ind m^{-3} *Calanus glacialis* 2–428 ind m^{-3}	ADCP
Lischka and Hagen (2005)	1998–1999 (Sep–Jul)	Outer	Modified Apstein 100 μm	Small copepods	*Pseudocalanus minutus* 1088–111,297 ind m^{-2} *Oithona similis* 4483–704,633 ind m^{-2} Nauplii 31,617 ind m^{-2}	Relative stage distribution
Hop et al. (2006)	1996–2002	Inner-outer	MultiNet 180 μm & WP3 1000 μm	Mesozooplankton	*Calanus finmarchicus* 50–600 ind m^{-3} *Calanus glacialis* 20–330 ind m^{-3} *Calanus hyberboreus* 2–110 ind m^{-3} *Metridia longa* 1–100 ind m^{-3} *Pseudocalanus* sp. 35–1370 ind m^{-3} *Oithona similis* 75–3930 ind m^{-3} *Triconia borealis* 3–180 ind m^{-3}	
Walkusz et al. (2009)	2002 (Apr, Jul, Sep)	Inner-shelf	MultiNet 180 μm	Mesozooplankton	Apr, total 40–2010 ind m^{-3} Jul & Sep, total 410–10,560 ind m^{-3} Data on single species also included	
Buchholz et al. (2010)	1996 & 2006	Inner-shelf	Tucker trawl 2 mm	Euphausiids	*Thysanoessa inermis* 7 ind 100 m^{-3} *Thysanoessa longicaudata* 3 ind 100 m^{-3}	Total lipid

(continued)

Table 7.9 (continued)

References	Year (month)	Area	Gear	Zooplankton group	Abundance	Other data
Willis et al. (2006)	2002 (Apr–Jun & Jul–Sep)	Outer	SAMS mooring sediment trap (65 m)	Mesozooplankton		ind/trap
Wallace et al. (2010)	2006–07 (Jun–Aug) & 2007–08 (Aug–Aug)		SAMS mooring 300-kHz ADCP & sediment trap (100 m)	Mesozooplankton	ind/trap	Absolute volume backscatter (Sv)
Daase et al. (2013)	2006 (Apr–Sep) & 2007 (May–Oct)		MultiNet 200 μm;	*Calanus glacialis*	2006: 233,100 ind m^{-2} (peak May) 2007: 20,000–30,000 ind m^{-2} (May–Oct)	Dry weight: 7000–11,000 mg m^{-2} 700–12,000 mg m^{-2}
Kwasniewski et al. (2013)	2003 (Apr–Jul) & 2004 (May–Jun)	Outer (Kb3)	WP2 180 μm & MultiNet 180 μm	Mesozooplankton	Total mesozooplankton: Early spring 788–1030 ind m^{-3} Spring bloom 410–7065 ind m^{-3} Summer 795–6016 ind m^{-3}	Dry weight: 23–188 mg m^{-3}
Berge et al. (2015a, b)	2013–2015 (Jan)	Outer (Kb3)	MultiNet 200 μm & MultiNet 64 μm	Mesozooplankton	Small copepods 650–2100 ind m^{-3} *Calanus* spp. 6–15 ind m^{-3}	Respiration; ADCP
Grenvald et al. (2016)	2013 (Jan) & 2014 (Feb)	Kb3	MultiNet 200 μm & MultiNet 64 μm MIK	Micro, Meso & Macrozooplankton	Total zooplankton 64 μm 1477–3002 ind dm^{-3} Small copepods 300–1250 ind m^{-3} *Calanus* 20–50 ind m^{-3} *T. inermis* 51–1096 (Feb 2013), 1848–2536 (Jan 2014) ind m^{-3}	

Dalpadado et al. (2016)	2006–2011	Inner-outer	MIK 1.5 mm	Euphausiids & Amphipods	Euphausiids 0–3140 ind m^{-2} (inner) Euphausiids 4–267 ind m^{-2} (outer) Amphipods 0–3078 ind m^{-2} (inner) Amphipods 1–907 ind m^{-2} (outer)	
Ormanczyk et al. (2017)	2013 (Jul)	Outer	WP2 56 µm & MultiNet 180 µm & Tucker trawl 1 mm	Small zooplankton; Medium zooplankton; Large zooplankton	Small zooplankton 5688 ind m^{-3} Medium zooplankton 4131 ind m^{-3} Large zooplankton 13 ind m^{-3}	Dry weight: Small 3.6 mg m^{-3} Medium 42.7 mg m^{-3} Large 39.2 mg m^{-3}

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Part IV
Benthic Microbes, Macroalgae and Fauna

Chapter 8

Living on Cold Substrata: New Insights and Approaches in the Study of Microphytobenthos Ecophysiology and Ecology in Kongsfjorden

Ulf Karsten, Iris Schaub, Jana Woelfel, Duygu S. Sevilgen, Carolin Schlie, Burkhard Becker, Angela Wulff, Martin Graeve, and Heiko Wagner

Abstract Organisms in shallow waters at high latitudes are under pressure due to climate change. These areas are typically inhabited by microphytobenthos (MPB) communities, composed mainly of diatoms. Only sparse information is available on the ecophysiology and acclimation processes within MPBs from Arctic regions. The physico-chemical environment and the ecology and ecophysiology of benthic diatoms in Kongsfjorden (Svalbard, Norway) are addressed in this review. MPB biofilms cover extensive areas of sediment. They show high rates of primary production, stabilise sediment surfaces against erosion under hydrodynamic forces,

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_8

and affect the exchange of oxygen and nutrients across the sediment-water interface. Additionally, this phototrophic community represents a key component in the functioning of the Kongsfjorden trophic web, particularly as a major food source for benthic suspension- or deposit-feeders.

MPB in Kongsfjorden is confronted with pronounced seasonal variations in solar radiation, low temperatures, and hyposaline (meltwater) conditions in summer, as well as long periods of ice and snow cover in winter. From the few data available, it seems that these organisms can easily cope with these environmental extremes. The underlying physiological mechanisms that allow growth and photosynthesis to continue under widely varying abiotic parameters, along with vertical migration and heterotrophy, and biochemical features such as a pronounced fatty-acid metabolism and silicate incorporation are discussed. Existing gaps in our knowledge of benthic diatoms in Kongsfjorden, such as the chemical ecology of biotic interactions, need to be filled. In addition, since many of the underlying molecular acclimation mechanisms are poorly understood, modern approaches based on transcriptomics, proteomics, and/or metabolomics, in conjunction with cell biological and biochemical techniques, are urgently needed.

Climate change models for the Arctic predict other multifactorial stressors, such as an increase in precipitation and permafrost thawing, with consequences for the shallow-water regions. Both precipitation and permafrost thawing are likely to increase nutrient-enriched, turbid freshwater runoff and may locally counteract the expected increase in coastal radiation availability. So far, complex interactions among factors, as well as the full genetic diversity and physiological plasticity of Arctic benthic diatoms, have only rarely been considered. The limited existing information is described and discussed in this review.

Keywords Microphytobenthos · Benthic diatoms · Polar regions · Climate change

8.1 Introduction

The Arctic Ocean is characterised by a large shelf area (depths of <200 m) that comprises approximately one-fifth of the global shelf (Menard and Smith 1966), resulting in extensive coastal regions with a mean water depth of less than 80 m (Gattuso et al. 2006; Jakobsson et al. 2008). The biomass of infaunal and epifaunal organisms in this extensive area is generally high compared to other, similar communities in temperate shallow-water regions, and thus responsible for high biological activity (Piepenburg et al. 1995; Sejr et al. 2000), in conjunction with high levels of benthic mineralisation (Rysgaard et al. 1998). All these organisms are strongly dependent on primary producers. Although pelagic and ice-related primary production in the Arctic can be high (Arrigo et al. 2008; Hodal et al. 2012), it typically has a narrow seasonal and local significance (Hsiao 1988). In addition, efficient microbial turnover rates for carbon and nutrients have been documented in the Arctic water column (Rysgaard et al. 1999), resulting in reduced sedimentation of particulate organic material. Consequently, at many locations in the Arctic, heterotrophic benthic organisms benefit little from the primary production of phytoplankton and ice-algae, and hence are dependent on benthic primary producers as their main food source (Glud et al. 2002). Benthic primary production in Arctic shallow-water regions is mainly mediated by seaweeds (Wiencke 2004; Fredriksen et al., Chap. 9), which form high standing-stock biomasses on hard substrata such as rocks; and by microphytobenthos (MPB) communities that grow mainly on soft sediments and as epiphytes on macroalgae (Karsten et al. 2006; Glud et al. 2009).

MPB communities are generally dominated by diatoms, which play an important role in the ecology of many Arctic coastal habitats (Glud et al. 2009). Glud et al. (2002) reported that at shallow depths, benthic microalgal productivity far exceeds that of pelagic microalgae, and can account for more than 90% of the total production. Similar studies on MPB productivity in subtidal Arctic regions remain scarce (Woelfel et al. 2010, 2014; Sevilgen et al. 2014), mainly due to the logistical constraints of high-latitude fieldwork. Nevertheless, the few data available from Arctic locations clearly indicate relatively high MPB primary production rates that are comparable to those from temperate regions (Glud et al. 2002, 2009; Woelfel et al. 2010, 2014; Sevilgen et al. 2014). In addition, MPB communities stabilise and modify sediment surfaces by the excretion of sticky extracellular polymeric substances (EPS) (De Brouwer et al. 2005), thereby reducing hydrodynamic erosion and acting as a biological filter (biofilm) for fluxes of oxygen and other elements at the sediment-water interface (Risgaard-Petersen et al. 1994). Consequently, MPB communities seem to be a key component in the functioning of trophic webs on soft substrates in Arctic coastal regions.

Many components of the pelagic and benthic food webs of higher trophic levels in the Arctic Kongsfjorden, a model ecosystem for high latitudes, are well described (Hop et al. 2002; Wiencke 2004). However, little information is available on the different primary producers, particularly benthic diatoms. The Arctic is currently facing a strong temperature increase due to global climate change (IPCC 2007; Bischof et al., Chap. 14). In addition to changes in hydrodynamics and local water temperatures, warming will entail enhanced freshwater input from melting snow, ice, glaciers and permafrost. This has consequences for coastal water salinity, sediment and nutrient runoff, as well as for the underwater light regime due to rising turbidity. In addition, drastic changes in the extent of sea-ice cover influences the light regime and consequently the potential time of onset of Arctic primary production throughout the year (Serreze et al. 2007; Zhang et al. 2012; Laxon et al. 2013), which might be beneficial for benthic primary producers. Furthermore, rising levels of $p\mathrm{CO}_2$ will lead to increased ocean acidification. Thus, the possible effects on MPB communities are indeed complex, and they must cope with altering conditions in the Arctic. The present review discusses ecological, physiological, bio(geo)chemical, cell-biological and molecular-biological aspects of benthic microalgae, in order to highlight their performance, interactions and acclimation potential under Arctic environmental conditions and global-change scenarios. Most of the data presented were obtained for benthic diatoms collected at different stations in Kongsfjorden and nearby Adventfjorden (Fig. 8.1).

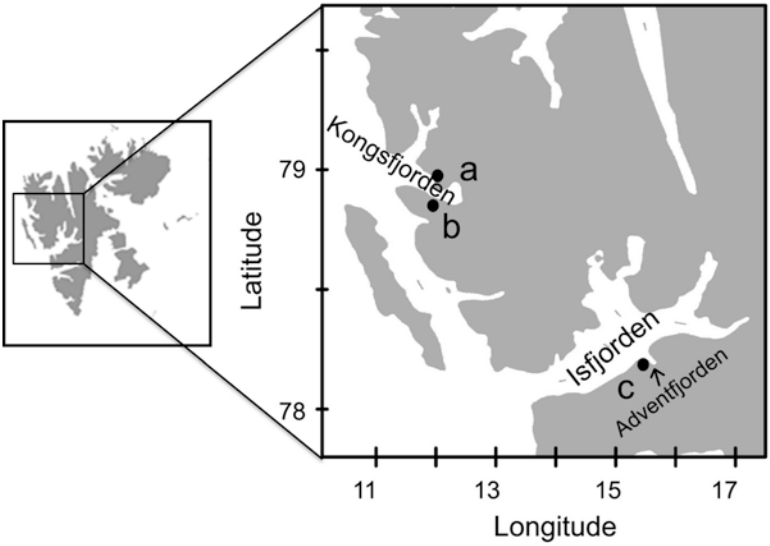


Fig. 8.1 Map of Svalbard showing Kongsfjorden and Adventfjorden, where all benthic diatoms were sampled. The black dots (a) and (b) indicate the London and Brandal stations in Kongsfjorden; dot (c) is the sampling location in Adventfjorden. For station details, see Woelfel et al. (2010)

8.2 Physico-Chemical Environment of Kongsfjorden and MPB Acclimation and Adaptation

Seasonally fluctuating solar radiation, low temperatures, and long periods of ice and snow cover are the key environmental factors controlling primary production in the Arctic (Hop et al. 2002).

8.2.1 The Polar Night

Benthic diatoms experience only short periods of sufficient light over the course of the year, with the polar day extending from mid-April until the end of August, and twilight conditions prevailing in spring and autumn (Svendsen et al. 2002). The polar night lasts for about 4 months, from the end of October to mid-February, and the annual surface incident solar radiation at 80°N is about 43% less than at the equator (Thomas et al. 2008). In the inner part of Kongsfjorden, the long period of winter darkness is further extended by the formation of sea ice, which breaks up sometime between April and July (Svendsen et al. 2002), although there has been much less ice in Kongsfjorden after 2006 (Cottier et al. 2007; Pavlova et al., Chap. 4). If the ice is also covered by snow, solar radiation can decrease to less than 2% of the surface level. Consequently, MPB communities may undergo as much as about

10 months of darkness or very low light conditions (Chapman and Lindley 1980; Dunton 1990). In addition, MPB experience shifts to dark and partly anoxic conditions due to vertical migration into the sediment and because of burial by bioturbating animals (Petrowski et al. 2016).

8.2.2 Dark Survival of Polar Benthic Diatoms

Polar benthic diatoms from Kongsfjorden show a high potential for dark survival, as they can live up to 5 months in complete darkness (Schlie et al. 2011), which may be beneficial in the polar night. Other studies have shown that polar pelagic and benthic diatoms survive these long periods of darkness, although the maximum survival time seems to be species-specific (Bunt and Lee 1972; Palmisano and Sullivan 1983; Peters and Thomas 1996; Zhang et al. 1998). The underlying physiological, biochemical and molecular mechanisms are still poorly understood, such as, for example, the physiological state in which polar diatoms survive darkness.

Different potential adaptive mechanisms for long-term dark survival have been described (McMinn and Martin 2013). These mechanisms include the utilisation of stored energy products (Palmisano and Sullivan 1982), adjustment of metabolic rates (Peters and Thomas 1996), formation of resting stages (reviewed by McQuoid and Hobson 1996), or a facultative heterotrophic lifestyle (Hellebust and Lewin 1977; Armbrust et al. 2004). These adaptive mechanisms are not considered to be mutually exclusive, and probably vary in relative importance among polar species (Palmisano and Sullivan 1985).

8.2.3 The Physiological State of Overwintering Diatoms in Kongsfjorden

From an ecological perspective, growth is the most relevant indicator to describe the ecophysiological performance of algal species in a specific habitat, because it integrates all intracellular acclimation processes, both positive and negative (Schlie et al. 2011). Positive growth rates indicate that algae have intact cell structures and hence an intact metabolism. In order to assess biological changes in the cells during dark incubation, two fluorescent stains were applied to benthic diatoms from Kongsfjorden (C. Schlie unpubl.). The stains were SYTOX® Green Nucleic Acid Stain and PDMPO [2-(4-pyridyl)-5{[4-dimethylaminoethyl-aminocarbamyl-methoxy] phenyl}oxazole]. SYTOX® attaches to the DNA of the target organism (Veldhuis et al. 1997), which is only possible in non-vital cells with damaged cell membranes. The fluorophore PDMPO is co-deposited with silica into the newly synthesised cell wall of diatoms, so in addition to cell vitality, active growth can be observed and followed as bright-green fluorescence (Shimizu et al. 2001) (Fig. 8.2).

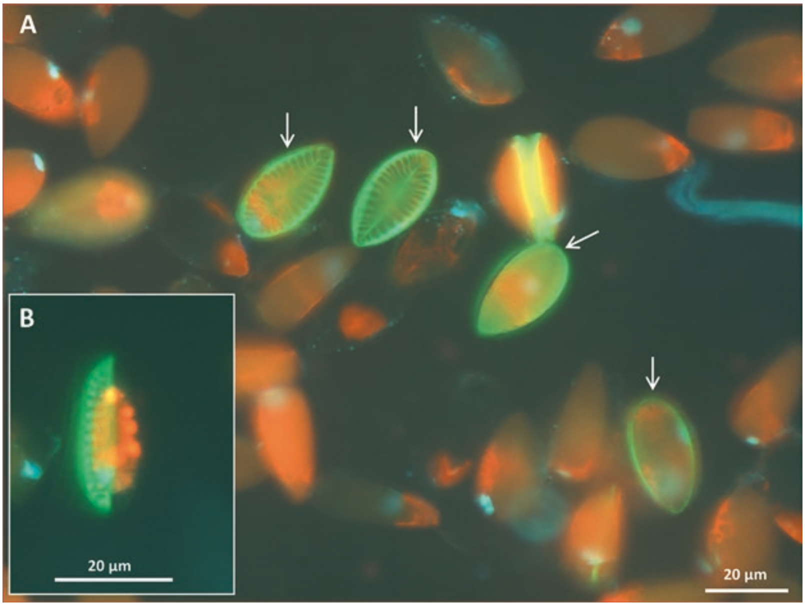


Fig. 8.2 Epifluorescence images of the benthic diatom *Surirella* cf. *minuta* from Kongsfjorden. (**a**) New silica deposition in the diatom valves as observed by using PDMPO [2-(4-pyridyl)-5{[4-dimethylaminoethyl-aminocarbamyl-methoxy] phenyl}oxazole] fluorescence probe (green colour), while the red colour originates from Chl. *a* autofluorescence. Red colour is typical for older cells not involved in the latest cell growth, together with younger cells. The bright green-coloured structures (white arrows) indicate newly synthesised valves (silica incorporation), viewed from above. (**b**) Newly synthesised valves seen from lateral position. (C. Schlie et al. unpubl.)

Applying SYTOX and PDMPO to the benthic diatom *Surirella* cf. *minuta* during 5 months of darkness indicated that an increasing number of cells exhibited damage over time, although after 1 month about 80% were still viable (C. Schlie et al. unpubl.). In addition, active silica incorporation in the dark was measured, i.e. 5% of all diatom cells showed staining after 2 months of darkness, indicating that growth processes were continuing (Schlie et al. unpubl.) (Fig. 8.2).

Experiments on the dark-survival potential were performed with a Kongsfjorden isolate of the benthic diatom *Cylindrotheca closterium* (Schlie et al. 2011). This species was kept for more than 5 months in darkness, and sub-samples were re-irradiated each month with continuous low irradiances (2.2–3.3 W m^{-2}). After 1, 2, 3 and 5 months of dark incubation, *C. closterium* showed high growth rates in the light within a few days, indicating a high capability of withstanding the polar night (Schlie et al. 2011). However, chloroplast size was reduced with increasing incubation time.

Originally ovoid chloroplasts of *S.* cf. *minuta* from Kongsfjorden shrunk after 2 weeks in darkness (C. Schlie unpubl.). Photosynthetic pigments begin to degrade after a few days without light. In particular, chlorophyll degradation provides nitrogen for maintenance metabolism. Karsten et al. (2012) mentioned that the benthic *Fragilaria striatula* from Kongsfjorden showed a 30–40% reduction in chloroplast length after 3 months of darkness, indicating a reallocation of energy towards maintenance metabolism through the decomposition of organelle components. After re-irradiation, this diatom had a long lag-phase before growth resumed. Other benthic diatoms from Kongsfjorden showed increasingly long lag-phases as a function of a longer dark incubation period, before optimum growth could be re-established (Karsten et al. 2012). This lag-phase includes a recovery period, in which the diatoms acclimate to sudden light conditions after dark treatment, rebuilding their cell structures and metabolism. The length of the lag-phase seems to be species-specific in benthic diatoms from Kongsfjorden (Karsten et al. 2012).

8.2.4 The Biochemical State of Overwintering Diatoms in Kongsfjorden

From a biochemical viewpoint, the utilisation of storage products, such as carbohydrates and lipids, can provide energy for the cellular maintenance metabolism during long-term darkness. The principal storage products in diatoms consist of the carbohydrate chrysolaminarin and the neutral lipid triacylglycerol, which are stored in cell vacuoles and in cytoplasmic lipid droplets, respectively (Beattie et al. 1961; Darley 1977).

High proportions of lipid droplets have previously been detected in species of polar phytoplankton and ice diatoms in late autumn (Fryxell 1989; Zhang et al. 1998). In the benthic diatom *Nitzschia* cf. *dubiiformis*, from Adventfjorden, Svalbard, large amounts of cytoplasmic lipid droplets were observed (Schaub et al. 2017; Fig. 8.3). During 12 weeks of dark incubation, this species exhibited a continuous decrease in the volume of the lipid droplets, indicating intracellular

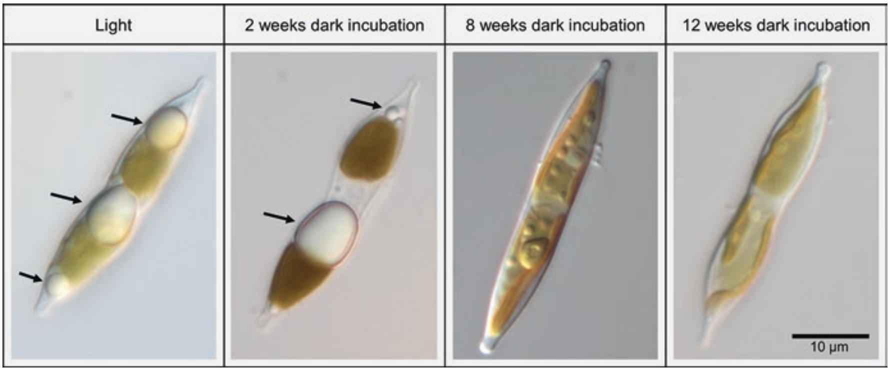


Fig. 8.3 Cells of the benthic diatom *Nitzschia* cf. *dubiiformis* from Adventfjorden, Svalbard, grown under light conditions (late log phase) and after 2, 8 and 12 weeks of darkness. Black arrows indicate lipid droplets in the cell. Cells were kept in a batch culture under 25 µmol photon m^{-2} s^{-1} in a 16:8 h light:dark rhythm, at 8 °C in F/2 medium with metasilicate (0.6 ml l^{-1}) and a salinity of 33. Photomicrographs were made with an Olympus BX51 microscope and ColorView12

degradation and, most probably, utilisation for maintenance metabolism (Schaub et al. 2017). Smith and Morris (1980) observed that diatoms from the Southern Ocean showed enhanced incorporation of 80% of the assimilated carbon into the lipid fraction under conditions of low irradiance (12.5 W m^{-2} PAR – photosynthetically active radiation, 400–700 nm) and low temperature (−1.0 °C), compared to carbohydrate synthesis under higher temperature (+0.2 °C) and irradiance (305.4 W m^{-2} PAR).

The two major lipid classes in diatoms are (i) polar lipids (glycolipids, sulfolipids and phospholipids), and (ii) neutral lipids such as triacylglycerols (TAG) and free fatty acids (Dunstan et al. 1993). Polar lipids are common membrane components, consisting of high proportions of polyunsaturated fatty acids (PUFA). TAG generally have more saturated (SFA) and monounsaturated fatty acids (MUFA) (Sukenik and Wahnon 1991), and serve primarily as a form of carbon and energy storage (Dunstan et al. 1993). Since lipids are important for energy storage in polar benthic diatoms, qualitative and quantitative analytical methods are crucial to understand the catabolic pathways that contribute to dark-survival mechanisms. Examining different lipid classes or fatty-acid composition of diatoms requires the use of high-performance liquid chromatography (HPLC) or gas–liquid chromatography (GC), often in combination with mass spectrometry (MS) (Christie 1996; Kattner and Fricke 1986; Nordbäck et al. 1998; Graeve and Janssen 2009). Total lipid content can be determined in intact diatom cells using Fourier transform infrared (FTIR) spectroscopy (Wagner et al. 2014; Schaub et al. 2017).

In order to understand the utilization of lipophilic storage products during the polar night, *Nitzschia* cf. *dubiiformis* from Adventfjorden was exposed to up to 8 weeks of darkness, with weekly analyses of fatty acid and total lipid content using GC-MS (Fig. 8.4) and FTIR in parallel (Fig. 8.5). Total fatty acid content per cell decreased sharply (by about 50%) in the first 2 weeks, with much slower degradation rate thereafter (Fig. 8.4). The ratio of SFA + MUFA/PUFA decreased continuously from 1.70 after the first week of darkness to 1.47 after 8 weeks without light, indicating greater reduction of MUFA and SFA than of PUFA. Since TAG consists mainly of MUFA and SFA, it can be assumed that Arctic benthic diatoms preferentially use this storage product during long-term darkness. In contrast, FTIR measurements showed a decrease in the overall lipid content (Fig. 8.5a, b; lipid ester, wavenumber 1700–1800 cm^{-1}) after the first week, and a sharp second decrease after the fourth week of dark incubation, which was also reflected in a strong increase in the amide/lipid ratio (Fig. 8.5c). This confirms that lipids are the principal storage products during prolonged darkness. Furthermore, the chrysolaminarin peak (Fig. 8.5a, wavenumber 1300–1400 cm^{-1}) decreases strongly during the first week of darkness, indicating a rather short-term degradation of this carbohydrate storage compound (Schaub et al. 2017).

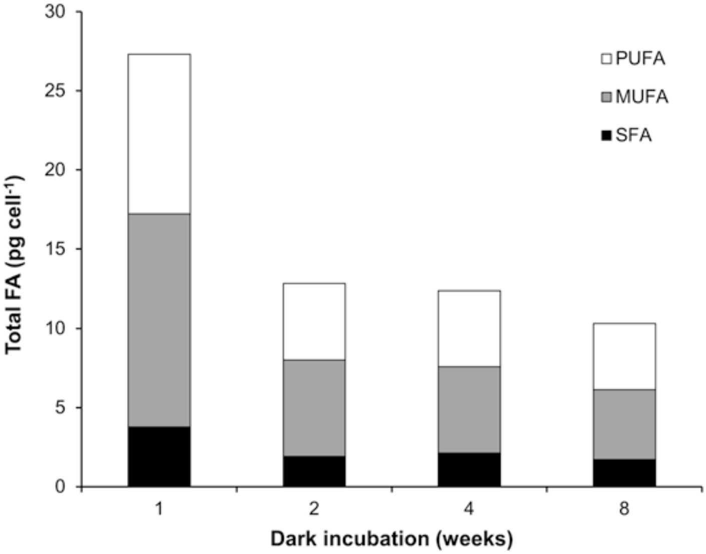


Fig. 8.4 Total fatty-acid content (pg cell^{-1}) in the benthic *Nitzschia* cf. *dubiiformis* from Adventfjorden, Svalbard, under 1, 2, 4, and 8 weeks of dark incubation at a temperature of 8 °C. Total fatty-acid content, determined with GC/MS, is separated into polyunsaturated (PUFA), monounsaturated (MUFA) and saturated (SFA) fatty acids. Incubation in F/2 medium with metasilicate (0.6 ml l^{-1}) at a salinity of 33

8.2.5 The Underwater Light Climate in Kongsfjorden

With the onset of the polar day in spring, the ice cover in Kongsfjorden produces dim light conditions, even in shallow waters. After the sea ice break-up in spring, solar radiation penetrates deeply into the water column, except in the inner bay. UV-radiation (UVR) and blue light are strongly attenuated in coastal waters because of the prevailing optical properties, which are influenced by particles (from e.g. glaciers) and yellow substances originating from meltwater and terrestrial runoff (Hanelt et al. 2001; Pavlov et al., Chap. 5). In the Arctic summer, even at noon the angle of the sun is always low, resulting in maximum surface irradiances of 283 W m^{-2} PAR (400–700 nm), 19 W m^{-2} UV-A (320–400 nm) and 1.1 W m^{-2} UV-B (280–320 nm) (Bischof et al. 1998). The 1% depth for UV-B radiation, which represents the approximate threshold irradiance of UVB with potential to negatively affect primary plant productivity, is between 4 and 8 m in Kongsfjorden (Hanelt et al. 2001). Peak irradiances during clear-water periods may reach a maximum of 40 W m^{-2} PAR at 5 m water depth, however for a few weeks only, followed by much lower values between 5 and 10 W m^{-2} PAR due to increasing turbidity (Bischof et al. 2002). During late spring and early summer, water transparency in Kongsfjorden decreases sharply, due to the development of phytoplankton blooms and the inflow of meltwater (Pavlov et al., Chap. 5). With increasing turbidity, the irradiance decreases and spectrum shifts from blue to green wavebands in deeper waters

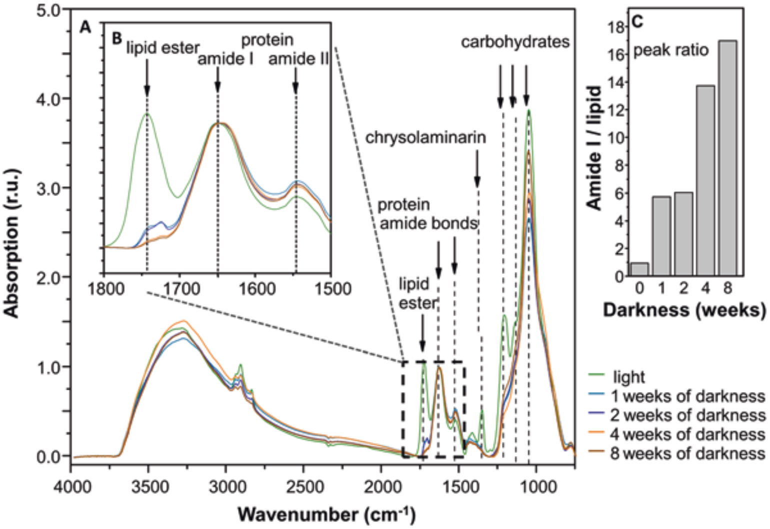


Fig. 8.5 Fourier transform infrared (FTIR) spectra of *Nitzschia* cf. *dubiiformis* from Adventfjorden, to determine changes in the cellular macromolecular composition according to Wagner et al. (2010). Cell spectra were measured after prolonged darkness of 8 weeks at 0 °C to follow the changes in lipid content (**a**). Inset (**b**) shows a magnification of the waveband range between 1500 and 1800 cm^{-1}. Peak ratios (**c**) for the protein:lipid content have been quantified from the amide I absorption band (showing the amide bond of proteins at 1649 cm^{-1}) and the lipid ester bond (1740 cm^{-1}) (**b**). Spectra were plotted as relative units (r.u.)

(Jerlov 1976). Consequently, benthic diatoms in Kongsfjorden experience widely fluctuating radiation conditions both seasonally and diurnally, and most of the time they live under a low light environment of <5–10 W m^{-2} PAR, without biologically harmful UVR (Woelfel et al. 2014).

8.2.6 The Acclimation of Polar Benthic Diatoms to Low Light

The few data available on benthic diatoms from Kongsfjorden indicate a very high capability to acclimate to the prevailing irradiances and continue photosynthesis (Karsten et al. 2006, 2012; Woelfel et al. 2010, 2014; Sevilgen et al. 2014).This high adaptive capacity is well supported by similar studies from Greenland (Kühl et al. 2001) and Antarctica (Wulff et al. 2008, 2009). Even under extremely low irradiances of 0.1, 1.1 and 2.2 W m^{-2} PAR, high growth rates were reported for *Nitzschia* cf. *aurariae* (Karsten et al. 2012) and two *Fragilaria* species (Karsten et al. 2006). Support for the shade acclimation of benthic diatoms in polar areas derives also from their low light requirements for photosynthesis. The Antarctic benthic diatom *Trachyneis aspera* was able to grow at ambient radiation of <0.6 μmol photons m^{-2} s^{-1} (= 0.13 W m^{-2} PAR), with saturated photosynthetic rates (E_k values) between 7 and 16 μmol photons m^{-2} s^{-1} (=1.5 and 3.5 W m^{-2} PAR) (Palmisano et al. 1985).

Adaptation to low light is also apparent in the reported low half-saturation and compensation irradiances for the entire MPB community from Brandal, Kongsfjorden (Sevilgen et al. 2014). By virtue of their low light requirements for photosynthesis, benthic diatoms are capable of successfully colonising deep bottoms. McGee et al. (2008) found living benthic diatoms even at a water depth of 191 m, where the midday insolation averaged 0.1 μmol photons m^{-2} s^{-1} (= 0.02 W m^{-2} PAR), i.e. <0.03% of surface incident radiation. The ability of benthic diatoms to acclimate not only to such extreme low-light conditions but also to high-light conditions in Antarctica (up to 350 W m^{-2} PAR) has been reported, emphasising that polar benthic diatoms are very well adapted to fluctuating radiation conditions (Wulff et al. 2008; Salleh and McMinn 2011).

8.2.7 Vertical Migration as a Response to Fluctuating Light Conditions

Vertical migration of benthic diatoms has been recognised as a main factor controlling the short-term variability of MPB productivity. The migratory patterns in subtidal benthic diatoms are closely linked to the diel cycle, and vertical migration is more affected by the photoperiod than by a combination of light and physical/hydrodynamic regimes (Longphuirt et al. 2006; Du et al. 2010).

Published studies on vertical migration of benthic diatoms in high-latitude regions with polar day and night conditions are lacking. Sevilgen et al. (unpubl.) recorded *ex situ* surface chlorophyll *a* concentrations in MPB communities in intact sediment cores from Kongsfjorden using back-reflectance spectra of the surface as a proxy for migration patterns. Two scenarios reflecting the Arctic summer and a temperate day/night light cycle were applied (Fig. 8.6). Chl. *a* showed a decline in concentration with decreasing photon fluence rates, and *vice versa,* indicating vertical migration of MPB (Fig. 8.6). In addition, the appearance and disappearance of the typical brownish benthic diatom layer (fucoxanthin) on the sediment surface could be followed visually.

In a similar study, the heterogeneity of benthic diatom occurrence, caused by vertical migration as well as patchiness, was studied by IMAGING-PAM (Pulse Amplitude Modulation) analysis (IMAG-MIN, Walz, Efferich, Germany) in sediment cores from Kongsfjorden (Fig. 8.7) (J. Woelfel unpubl.; stations according to Woelfel et al. [2014]).

The top 5 mm sections of sediment cores were measured at 2 °C, following a specific protocol: (1) 2-D images of the fluorescence parameters F_0 (minimum fluorescence of dark-acclimated cells) and F_m (maximum fluorescence under saturating light) were taken after 10 min dark adaptation. (2) The cores were then exposed to three increasing photon fluence rates, each provided for 15 min: low light (LL, 15 μmol photons m^{-2} s^{-1}), medium light (ML, 100 μmol photons m^{-2} s^{-1}) and high light (HL, 1000 μmol photons m^{-2} s^{-1}). After 5, 10 and 15 min, F_0 and F_t (fluorescence in the light) were determined with low measuring light, followed by

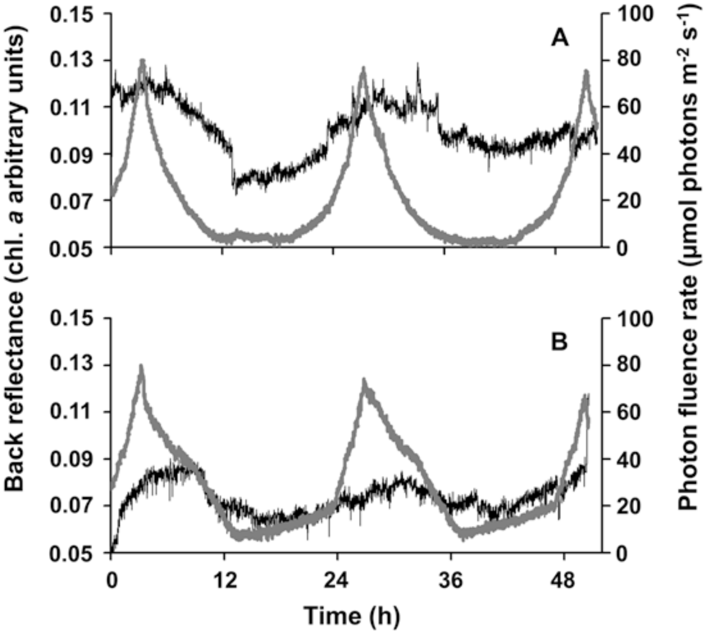
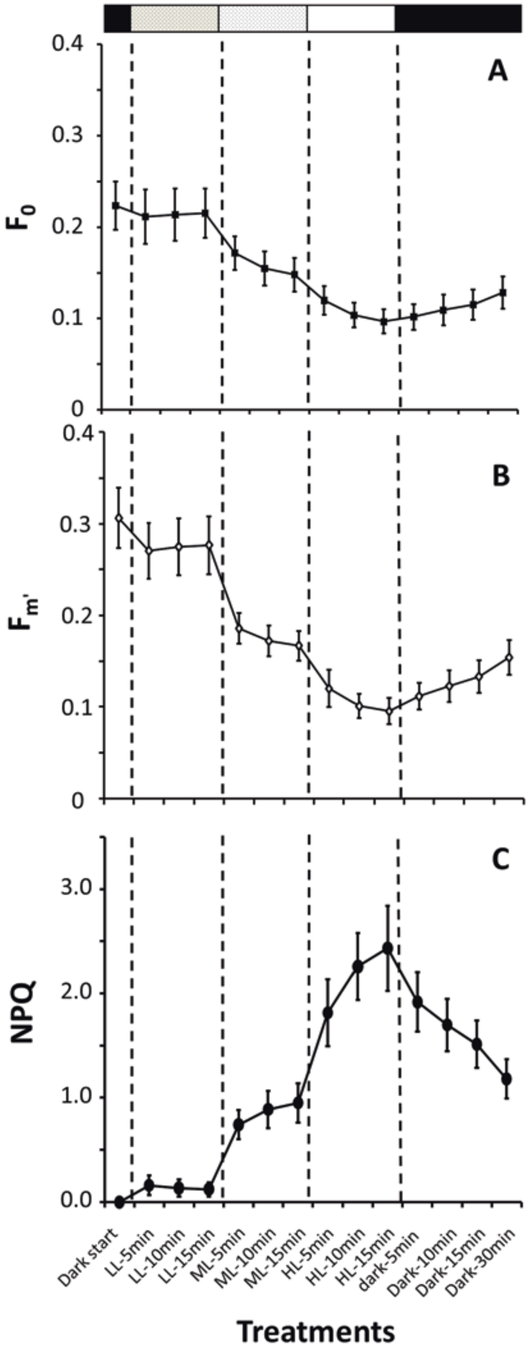


Fig. 8.6 Relative surface chlorophyll *a* (Chl. *a*) changes as derived from back-reflectance measurements in sandy sediment cores from Brandal station (5 m), Kongsfjorden, in July 2012. (**a**) Relative Chl. *a* changes with mimicked *in situ* light dynamics (polar summer); and (**b**) changes with mimicked light conditions of a temperate region (6 h of darkness). Vertical lines in photon fluence rates reflect temporal shading of the setup due to experimental reasons. Grey line: photon fluence rate; black line: relative Chl. *a* units. (D.S. Sevilgen et al. unpubl.)

maximal fluorescence F_m and $F_{m'}$ (maximum fluorescence under actinic light) after applying a 800 ms saturating light pulse. (3) Exposure to 30 min darkness followed by measurements of all parameters during dark recovery.

All fluorescence parameters decreased with increasing photon fluence rates, followed by a subsequent increase during the 30-min dark period (Fig. 8.7). These changes in F_0/F_t and $F_m/F_{m'}$ could, in principle, reflect either vertical migration of benthic diatoms or a down-regulation of Chl. *a* fluorescence excitation. The strong decrease of both F_0/F_t and $F_m/F_{m'}$ is interpreted as a migratory response to increasing light levels due to the short time intervals used in the experiments. Non-photochemical quenching (NPQ) is a photoprotective mechanism against excessive irradiance. NPQ increased continuously under more-intense light, and decreased during the dark treatment. This pattern led, partly, to decreases in $F_{m'}$. The incomplete recovery within 30 min in darkness can be explained by the possible "resting" of motile diatoms in the sediment, since these algae need a radiation impulse for upward migration (L. Polerecky, MPI for Marine Microbiology, Bremen, pers. comm.).

Fig. 8.7 Changes in the fluorescence parameter F_0 (**a**), after irradiation parameter $F_{m'}$ (**b**) and non-photochemical quenching (NPQ) (**c**) in surface sediment cores. Data, shown as mean ± SD, were plotted over time (min) and as a function of irradiance: Low light (LL) = 15, medium light (ML) = 100 and high light (HL) = 1000 µmol photons m^{-2} s^{-1}. Data represent samples from three stations in Kongsfjorden (BRL, NAT, LON). Grey bars indicate periods of dark adaptation as well as increasing levels of irradiance. (J. Woelfel et al. unpubl)



8.2.8 The Prevailing Water Temperature in Kongsfjorden

While solar radiation exhibits extreme seasonal qualitative and quantitative variability, temperatures in Kongsfjorden change only slightly, between −1.8 °C in winter and about 5.0 °C in summer (Hanelt et al. 2001), although local temperature fluctuations can reach 8.8 °C (D.S. Sevilgen unpubl.). However, there are strong indications that this rather typical temperature regime changed after a massive intrusion of warmer Atlantic-derived water masses into the fjord in February 2006 (Cottier et al. 2007). The resulting warmer period of Kongsfjorden over the last 7–8 years overlapped with a period of very small amounts of drift ice on the shelf west of Svalbard (Kwasniewski et al. 2012). Arctic water masses have generally warmed by 0.7–1.2 °C per decade since 1981 (Serreze and Francis 2006), with unknown consequences for the MPB and other marine organisms (Hegseth and Tverberg 2013). Independently of the underlying mechanisms, the signs of continuing warming of the Arctic Ocean are numerous (Polyakov et al. 2005; Overland et al. 2014). The annual mean temperature from June 2011 until June 2012 was 2.4 +/− 2.1 °C at the shallow (5 m water depth) coastal sandy sediment site of Brandal in Kongsfjorden (Sevilgen et al. 2014). However, during summer, water temperatures can temporarily increase to over 8 °C at this station, and exhibit a wide dynamic range, with daily temperature fluctuations of up to 5 °C (Sevilgen et al. unpubl.). In contrast, the temperatures in deeper waters >5 m were relatively constant, ranging from 1 to 5 °C from June through August in 2006, 2007, 2008 and 2011 (Woelfel et al. 2009, 2010, 2014; D.S. Sevilgen unpubl.).

8.2.9 The Influence of Water Temperature on Growth

Temperature has a major influence on MPB growth rates (Karsten et al. 2006; Schlie et al. 2011). Arctic benthic diatoms seem to require higher temperatures than do endemic Antarctic species. Two *Fragilaria* species from Kongsfjorden showed optimum growth rates at 12–14 °C, grew more slowly at 0 °C, and did not survive at 20 °C (Karsten et al. 2006). Similarly, *Nitzschia* cf. *aurariae* from the same location grew at temperatures between 5 and 15 °C, did not grow at 0 °C, and died at 23 °C (Karsten et al. 2012). The optimum growth temperature for *N.* cf. *aurariae* was 15 °C, which clearly indicates moderate temperature requirements. Schlie and Karsten (2017) studied eight benthic diatom species isolated from Adventfjorden (Svalbard, Norway), and confirmed as a general response patterns a preference for 6–15 °C. Thus, Arctic benthic diatoms can be characterised as eurythermal and psychrotolerant microalgae (organisms tolerant of low growth temperatures), and hence they will be able to cope well with the predicted increasing water temperatures. This is in sharp contrast to a related endemic Antarctic benthic diatom, *Odontella litigiosa*, which typically exhibits maximum growth at 0 °C and complete inhibition of cell division at 7–9 °C (Longhi et al. 2003). It is reasonable to assume that other

Antarctic benthic diatoms might also be rather polar stenothermal and psychrophilic (i.e., require low temperatures for growth), as has been reported for many Antarctic seaweeds (Wiencke and tom Dieck 1990).

8.2.10 Salinity Fluctuations in Kongsfjorden and Their Effects on Benthic Diatoms

While salinity is a relatively constant factor in the offshore region of all oceans, it may vary both locally and seasonally in the near-shore water of Kongsfjorden due to the high volume of meltwater runoff, particularly during summer (Hanelt et al. 2001). Horizontal and vertical gradients between freshwater and fully marine conditions are apparent in the fjord (Svendsen et al. 2002). In addition, hydrological conditions, wind, precipitation and evaporation can influence salinity. During periods of calm weather, water bodies often develop a freshwater layer above the denser seawater. However, due to wave- and wind-induced vertical mixing, deeper water layers in Kongsfjorden can also be affected by freshwater runoff, with reductions in salinity from 33 to 20, down to about 20-m depth (Hanelt et al. 2001).

The effect of salinity on benthic diatoms in Arctic waters is generally little studied. *Nitzschia* cf. *aurariae* from the Kongsfjorden MPB grows in salinities between 15 and 45 (Karsten et al. 2012). The highest growth rates occur between salinities of 20 and 40, and growth is inhibited at 10 and 50 (Karsten et al. 2012). Therefore, *Nitzschia* cf. *aurariae* exhibits a growth-response pattern that can be characterised as moderately euryhaline. The underlying mechanisms, such as osmotic acclimation, have not yet been studied in Arctic benthic diatoms.

8.2.11 Nutrient Availability in Kongsfjorden for Benthic Diatoms

The European Arctic is one of the most productive marine regions in the world (Arrigo and van Dijken 2011), since nutrient-rich water enters from the south during part of the year via the West Spitsbergen Current. While nitrogen and phosphorus concentrations in the water column are relatively high during the winter months, both macronutrients are almost fully depleted in summer after the phytoplankton blooms. In contrast, benthic diatoms benefit from the high nutrient levels in the sediment pore water, where dissolved inorganic nitrogen (DIN) levels, ranging from 1.9 to 36.7 mM and soluble reactive phosphorous (SRP) from 0.9 to 5 mM, are generally much higher (approximately 5–20-fold) than in the overlying water column (Woelfel et al. 2009), and probably available year-round. This suggests that benthic diatoms in Kongsfjorden are not nutrient-limited.

Table 8.1 Annual primary production (g C m^{-2} $year^{-1}$) estimates in Kongsfjorden, Svalbard

	Study period	g C m^{-2} $year^{-1}$	Reference
Pelagic	July 1996	4–180	Hop et al. (2002)
	July 1979/1980	150	Eilertsen et al. (1989)
	April/May 2002	27–35	Hodal et al. (2012)[a]
Benthic	July 2008	71	Woelfel et al. (2010) (Kongsfjorden)[b]
	July 2008	165	Woelfel et al. (2010) (Brandal)[b]
	June–July 2010	49.2	Sevilgen et al. (2014)[b]

[a]Spring only (18 April–13 May); [b]Estimates calculated for 90 light days

8.2.12 Hydrodynamic Conditions

In polar coastal areas with high wave energy, benthic communities are often strongly impacted by icebergs and rafted sea ice, which can reach depths of about 40 m and thereby scrape the sea floor, resulting in disturbance or even mechanical damage (Gutt 2001). In Kongsfjorden, area Chl. *a* values as a proxy for MPB biomass varied from 49 to 165 mg m^{-2} (Table 8.1), and were related to water depth, current or wave exposure, as well as geographical location (Woelfel et al. 2009, 2010). In contrast, MPB biomass was independent of other abiotic parameters such as sediment properties, salinity or temperature (Woelfel et al. 2009), and Chl. *a* levels did not correlate with primary production rates (Woelfel et al. 2010). However, hydrodynamic conditions seem to be a driving force for differences in sediment colonisation by benthic diatoms. One study from a temperate region indicates that increasing the current velocity from 15 cm s^{-1} to 40 cm s^{-1} stimulates photosynthesis and other physiological and biochemical processes in benthic diatoms (Lamb and Lowe 1987).

8.3 Biodiversity of Benthic Diatoms in Kongsfjorden

Biodiversity is important for the function of benthic diatoms. Recent investigations of benthic diatoms from Kongsfjorden and Adventfjorden have provided the first floristic list for these ecosystems (Stachura-Suchoples et al. 2016; Fredriksen et al., Chap. 9). The list of 47 identified diatom species forms a baseline for a high-latitude fjord system (Fredriksen et al., Chap. 9). The data from these studies reveal a highly variable community with a patchy, heterogeneous distribution of most taxa. The MPB communities likely change over time because of prevailing dynamic, seasonally changing environmental parameters, which act as strong structuring forces (Fredriksen et al., Chap. 9).

8.4 Primary Production of Benthic Diatoms in Kongsfjorden

In contrast to temperate coastal ecosystems, only a few studies have examined MPB primary production in Arctic regions. The latest review of benthic microalgal production in Arctic waters (Glud et al. 2009) comprised 10 peer-reviewed and three unpublished studies of shelf areas off Siberia, Svalbard, Greenland and North America. As indicated in this review, the productivity of benthic polar microalgae exceeds the pelagic productivity by a factor of 1.5 for water depths down to 30 m, and hence benthic diatom assemblages may represent an important organic food source for zoobenthos. Since the review of Glud et al. (2009), few additional studies have addressed Arctic MPB primary production (Woelfel et al. 2010, 2014; Attard et al. 2014; Sevilgen et al. 2014). All these studies pointed out that Arctic MPB communities contribute significantly to coastal ecosystem production, and therefore need to be taken into account for carbon budget calculations.

Although Kongsfjorden is considered a model high-latitude ecosystem with abundant available data, basic information on benthic primary production of the different phototrophic organisms was lacking for a long time (Hop et al. 2002). To fill this gap, primary production of MPB was determined during various summer expeditions between 2006 and 2012 at several soft-sediment stations along the coastline of Kongsfjorden (Woelfel et al. 2010, 2014; Sevilgen et al. 2014). The production data were obtained from experiments with benthic chambers (*ex* and *in situ*), using samples from water depths of ≤5 to 30 m (Woelfel et al. 2010, 2014), and oxygen microsensor measurements (*ex* and *in situ*) with samples at water depths of ≤5 m (Sevilgen et al. 2014).

Gross primary production rates (*ex situ* approach) ranged between 0.2 and 46 mmol O_2 m^{-2} d^{-1} at 18 sites in Kongsfjorden from ≤5 m to 30 m water depth (Woelfel et al. 2009). Three sites showed low but variable rates of net primary production (NPP) (*in situ* approach), ranging from −7.2 to +14.4 mmol O_2 m^{-2} d^{-1} (Woelfel et al. 2014). Based on these data, the numerical model of Walsby (1997) was applied to estimate seasonal and regional rates of near-shore NPP, using *in situ* photosynthesis-light curve parameters (derived during the same measuring campaign), total solar radiation, wind data and satellite-derived sea surface temperatures (SSTs). The highest daily NPP rates, calculated for the entire Arctic spring-summer season at depths <15 m, ranged from 15 to 18 mmol O_2 m^{-2} d^{-1}, slightly higher than but well in accordance with values determined from benthic-chamber measurements. Primary production rates under stratified and fully mixed water-column conditions were also calculated by the model, which showed small differences (<10%) between the two conditions (Woelfel et al. 2014).

Sevilgen et al. (2014) combined laboratory measurements of photosynthesis and respiration with *in situ* measurements of oxygen profiles and photon fluence rates, to derive daily oxygen budgets of 10.1–23.0 mmol O_2 m^{-2} d^{-1} for one of the sites

(Brandal) previously studied by Woelfel et al. (2010). While the latter authors based their calculations on fixed photon fluence rates that generally were higher than those measured under *in situ* light conditions, Sevilgen et al. (2014) integrated *in situ* photon fluence rates for their calculations. The two approaches resulted in only slightly different production rates, and confirmed the range of values derived from the benthic chambers.

The results of these studies highlight one of the most common problems in studying MPB primary production, namely the high degree of spatial and temporal heterogeneity (Glud et al. 2009; Sevilgen et al. 2014). This is explained by the typical heterogeneous micro- and mesoscale distribution (patchiness) of MPB abundance and community composition on sediments, which can change dynamically over both short and long time periods; as well as by methodological constraints such as the application of technological approaches (e.g. microsensors, benthic chambers), which can provide low numbers of replicates. All MPB production estimates for Kongsfjorden are within the same range as the data for pelagic primary production (Table 8.1).

8.5 Grazing

Grazing pressure is difficult to assess, and represents an obstacle to the comparison of MPB primary production from different habitats, as well as extrapolations to secondary production. Both the organic matter that is produced by benthic diatoms and the organic matter that originates from the overlying water column are consumed by herbi- or omnivorous grazers, mainly zoobenthos. Dense populations of macrozoobenthic organisms have been described for Arctic waters (Glud et al. 2009), as well as for soft sediments from different depths in Kongsfjorden (e.g. Brandal station) (Laudien et al. 2007). A dense infauna population at the same site (Brandal station, 5 m) and correspondingly high respiration rates were documented by Sevilgen et al. (2014), with subsurface respiration rates 6 times higher (-31.8 mmol O_2 m^{-2} d^{-1}) than rates within the euphotic zone (-5.4 mmol O_2 m^{-2} d^{-1}).

High infaunal abundances can be linked to increased organic matter input from phytoplankton blooms. Spring blooms in Kongsfjorden produce a large amount of bio-available organic matter, which, if not grazed in the water column, sinks to the sea floor where it either is used directly or buried (Hodal et al. 2012). As discussed by Sevilgen et al. (2014), this spring bloom production can support a high abundance of infauna, which in turn affects the sediment biogeochemistry and the biomass of MPB, and consequently also their production rates. Thus, in addition to bottom-up factors that control MPB primary production, locally top-down mechanisms may also play an important role.

8.6 Benthic Diatoms as an Important Food Source

Although the role of MPB communities as a food source has not yet been determined in Kongsfjorden, benthic diatoms are vitally important for ecological functioning in many other marine shallow-water habitats, where they can directly sustain grazers, deposit-feeders and suspension-feeders (Cahoon 1999). The MPB communities in Kongsfjorden, as in other regions, likely constitute an important trophic link, directly and indirectly, between bacteria and organisms at higher trophic levels, from micro- to meio- and macrofauna. Furthermore, benthic diatoms produce extracellular polymeric substances (EPS), an important source of carbohydrates for bacteria and deposit-feeders (Goto et al. 2001). Analysis of the gut contents and scanning electron microscopy examination of the benthic hydroid *Silicularia rosea* from intertidal communities of Potter Cove (King George Island, Antarctica) indicated that benthic diatoms comprised more than 95% of the food source (Gili et al. 1996). The same was true for Antarctic sponges and ascidians (Klöser 1994). The gastropod *Nacella concinna* is abundant along the Antarctic Peninsula (Brêthes et al. 1994) and feeds on benthic microalgae (Zacher et al. 2007). Furthermore, the abundance of benthic diatoms was correlated with the soma and gonad mass of *N. concinna* (Brêthes et al. 1994), which emphasises the trophic link between benthic microalgae and this gastropod. In a stable-isotope analysis (^{13}C), Corbisier et al. (2004) demonstrated the existence of a tight coupling between Antarctic benthic diatoms and benthic grazers, deposit-feeders and nematodes. Surprisingly, benthic diatoms proved to be an important food element for krill in both summer and winter, particularly when phytoplankton biomass was low (Ligowski 2000). In the Arctic, a detailed study of carbon cycling in a fjord system showed that the primary production of pelagic and ice algae could not meet the carbon requirements of the benthos, and hence benthic diatoms supplied a substantial part of their carbon intake (Glud et al. 2000; Rysgaard et al. 2001).

8.7 Modern Approaches to Study Polar Benthic Diatoms

Modern molecular approaches provide important information on gene expression and regulation in relation to stress and adaptation. In addition, these data help to distinguish whether the host diatom cell itself or the associated bacteria contribute to the mechanisms of interest. Over the last decade, various modern molecular genomic, transcriptomic, proteomic and metabolomic tools have been successfully applied to polar microalgae (reviewed by Lyon and Mock 2014), contributing to a new fundamental understanding of adaptation and acclimation mechanisms. Metagenomics and metatranscriptomics provide molecular tools to evaluate the biodiversity and ecology of all algae present at the same time, directly from an environmental sample (Tyson et al. 2004). Metagenomics is, in principle, even capable of sequencing nearly complete microbial genomes. The impact of the different stressors on algae under natural conditions can be assessed based on such results combined with transcriptomes of algae cultured under controlled stress conditions. In parallel with new developments in sequencing technologies, bioinformatic tools to process the enormous amounts of data generated have also improved.

A (meta)transcriptomic approach was undertaken for the first time on Kongsfjorden benthic diatoms in connection with a recent research project (B. Becker, University of Cologne, Germany). Cultures of *Surirella* cf. *minuta* were exposed to constant light or darkness for 1 week, followed by mRNA isolation and sequencing (Holzinger et al. 2014). About 80% of the analysed sequences yielded significant BLAST-Hits (BLAST: Basic Local Alignment Search Tool; Fig. 8.8), and nearly half could be functionally annotated. The BLAST results allowed easy assignment of the sequences to *Surirella* cf. *minuta* from Kongsfjorden, as well as to two bacteria species present in the culture. The top-hit species distribution of the BLAST analysis indicated that 55% of the sequences were represented by other diatoms (*Phaeodactylum tricornutum*, *Thalassiosira oceanica*, *Thalassiosira*

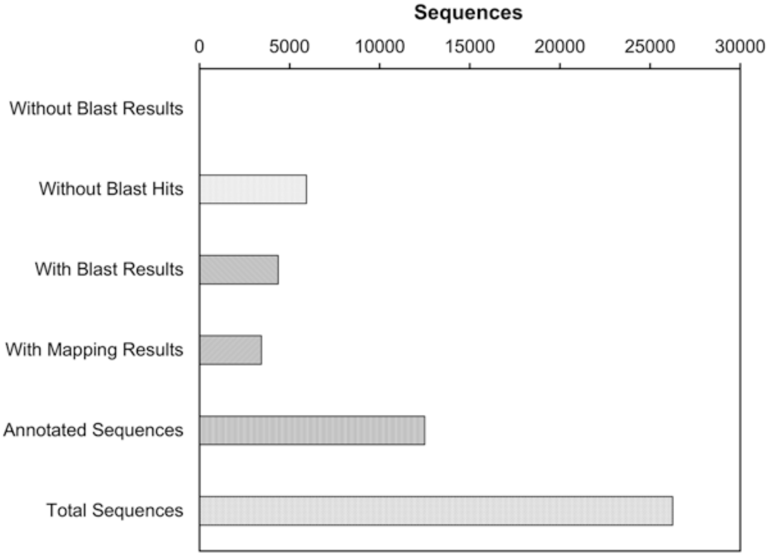


Fig. 8.8 Data distribution of the BLAST2GO (BLAST: Basic Local Alignment Search Tool) automatic annotation. About 23% of the Arctic benthic *Surirella* sequences yielded no BLAST hits. For 15% of the sequences, we retrieved similar proteins by BLAST, although the similarity was too low to map the sequences on KEGG pathways, and no Gene Ontology terms could be retrieved from the BLAST results. For roughly 50% of the sequences, the GO and/or KEGG mapping was specific enough that the putative function of the protein could be inferred, and the sequence was annotated. For 12% of the sequences, GO terms were retrieved, but the results were not specific enough to infer function

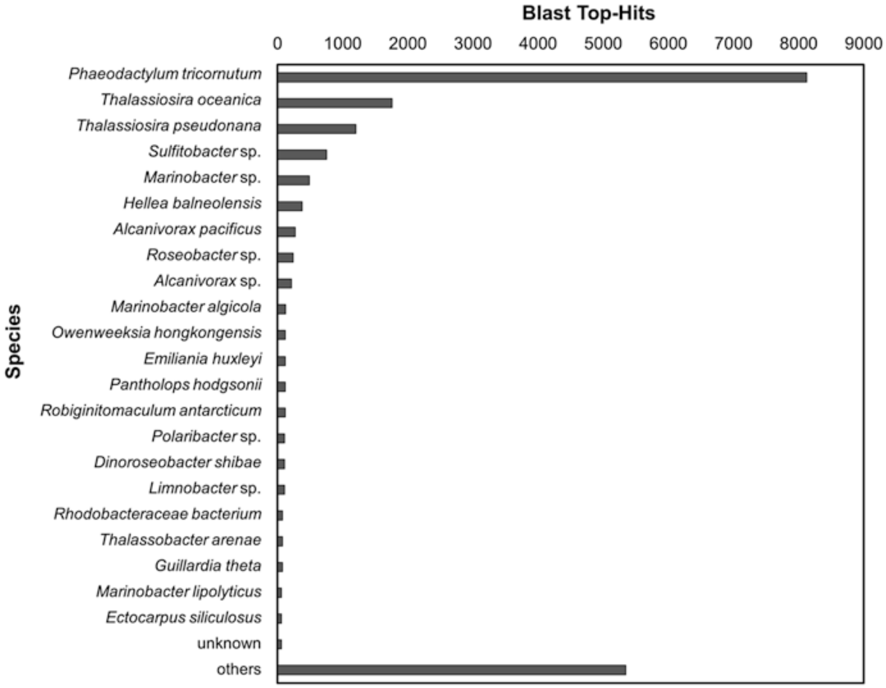


Fig. 8.9 Top-hit species distribution using about 26,000 contigs (a set of overlapping DNA segments that together represent a consensus region of DNA) with a length of at least 600 bases and the BLAST program as implemented in the BLAST2GO software (www.blast.ncbi.nlm.nih.gov/). BLAST (Basic Local Alignment Search Tool) is a bioinformatic tool for comparing primary biological sequence information, such as the nucleotides of DNA sequences, which can be used to help to identify members of gene families

pseundonana) (Fig. 8.9). Sequences related to *Emiliania huxleyi*, *Ectocarpus siliculosus* and *Guillardia theta* most likely also represent specific sequences from *Surirella* cf. *minuta*, since the genomes of diatoms are characterized by a complex combination of genes acquired from a variety of different source organisms (Armbrust 2009).

According to the BLAST analysis (Fig. 8.9), the two most frequent bacteria were a *Marinobacter* species (γ-Proteobacteria) and a *Sulfitobacter* species (α-Proteobacteria). Using known 16S rRNA sequences from both species, it was possible to find the corresponding rRNA sequences in the (meta)transcriptomic data. Blasting of the putative 16S rRNA sequences similar to *Marinobacter* 16S rRNA confirmed the presence of a *Marinobacter* species in the *Surirella* culture. However, the second bacterium proved to be an *Algimonas* species (an α-proteobacterium related to *Sulfitobacter*). *Algomonas* has previously been isolated from a culture of *Porphyra yezoenis* (Fukui et al. 2013). It seems that both bacteria strongly interact with *Surirella* cf. *minuta*.

8.8 MPB Ecology in the Context of Global Warming and Outlook

It has been estimated that the annual pelagic production of the Arctic Ocean has already increased by 5–6% because of enhanced light availability (Arrigo et al. 2008). Based on field data from Kongsfjorden in combination with ecological modelling, Woelfel et al. (2014) concluded that rising temperatures in the Arctic will have only a marginally stimulating effect (<3%) on MPB primary production.

Besides increasing light availability, the number of "newly" available shallow-water areas with different types of substrate is expected to expand. In recent decades, most of the fjordic tidal glaciers of Spitsbergen have been continuously regressing (e.g. Kongsbreen and Kongsvegen glaciers, inner Kongsfjorden; Lefauconnier et al. 1994; Kramer et al. 2013), thus providing new areas of seabed for settlement of benthic organisms (Włodarska-Kowalczuk et al. 1998). While bedrocks represent only 35% of the Arctic coastline, unlithified, ice-bonded sediments characterise 65% of the remaining coast (Lantuit et al. 2011). Ice-released sediments of the four Kongsfjorden glaciers will likely affect the fjord water regime (e.g. DOC load, turbidity). On the other hand, increasing meltwater runoff and precipitation may lead to a rise in the sea level, unless the isostatic rebound is higher (e.g. most of Svalbard). The effects of these changes (both individually and combined) on MPB ecology and primary production in the Arctic environment remain unstudied. Hence, more fieldwork, holistic/multi-factorial experiments and modelling approaches are needed to fill this gap in knowledge as well as to make realistic predictions for the future.

Higher temperatures generally stimulate metabolic activity, influencing both autotrophic and heterotrophic microbenthic organisms. In a subarctic spring community, the presence of benthic diatoms appeared to moderate the temperature response (4 °C elevation) of particularly heterotrophic but also autotrophic variables (Alsterberg et al. 2011). It was concluded that the photosynthetic activity of benthic diatoms could dampen the ecological consequences of global warming in shallow-water sediment systems, thus maintaining the system in a net-autotrophic state. Initial estimates have shown that a suggested increase of summer sea surface temperatures by 2 °C, according to the IPCC scenario (A1B in 2007) and MacDonald (2010), would only marginally stimulate MPB NPP in Kongsfjorden (Woelfel et al. 2014). A sensitivity analysis of the model used clearly showed the crucial dependence of NPP on the Q_{10} values. Therefore, additional studies on Q_{10} values are needed for input into existing eco(physio)logical models, in order to improve their power. Interestingly, at least one study showed that increased $p\mathrm{CO}_2$ levels might have negative effects: the growth rate of the polar benthic diatom *Navicula directa* was reduced by 5% (Torstensson et al. 2012) when $p\mathrm{CO}_2$ rose from 380 ppm to 960 ppm. In the same study, the combination of elevated temperature and increased $p\mathrm{CO}_2$ had no synergistic effects, but the growth rate at 4.5 °C was 43% higher than at 0.5 °C.

In summary, stressors act synergistically, and although species-specific treatment responses of polar benthic diatoms are apparent, at the community level the effects on associated bacteria, grazers etc. could both reduce and enhance these effects. In the coming years, more long-term studies should be undertaken and permanent *in situ* observatories installed, which will aid our understanding of the annual performance and dynamics of MPB communities and their responses to changing environmental parameters in the course of global climate change. Deeper knowledge of the molecular mechanisms involved in bioenergetics, resource allocation, metabolic fluxes and community composition are expected to improve our ability to understand the influence of polar benthic diatoms on biogeochemical processes and the responses to global-change scenarios.

Acknowledgements Part of this study was performed at the Ny-Ålesund International Arctic Environmental Research and Monitoring Facility, under the agreement on scientific cooperation between the Alfred Wegener Institute and the University of Rostock. The authors thank the crew at the AWIPEV-base in Ny-Ålesund, the German dive team (P. Leopold, M. Schwanitz, I. Vieweg), and P. Kumm (workshop of the Institute of Chemistry, University of Rostock) for assistance in the field and technical equipment. Financing and logistical support of the research in Ny-Ålesund was kindly provided by the European Centre for Arctic Environmental Research (ARCFAC V; project no. 026129-02). Furthermore, we gratefully acknowledge financial support by the German Research Council in the framework of the Priority Programme 1158 (DFG, KA899/12-1/2/3, KA899/15-1/2/3).

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Chapter 9
Biodiversity of Benthic Macro- and Microalgae from Svalbard with Special Focus on Kongsfjorden

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

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_9

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

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

9.1 The Abiotic Environment of the Arctic

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

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

Above the Arctic Circle (66°34′N) the sun does not set after the summer solstice and does not rise after the winter solstice. At the North Pole, the sun even rises and sets only once each year; as a consequence there are 6 months of continuous daylight and 6 months of continuous darkness. This extreme seasonal light situation has severe consequences for organisms that are dependent on light to photosynthesise and is perhaps the most striking factor for the benthic algae in the Arctic. The changing light climate during the year is the main factor influencing the development of benthic macro- and microalgae (Pavlov et al., Chap. 5). Polar algae are usually low light adapted, but must also tolerate high light after the ice break up (Gómez et al. 2011; Zacher et al. 2011) and many adaptations exist to overcome the pronounced seasonality in light climate (Dunton 1985; Dunton and Schell 1986; Lüning 1990; Wiencke et al. 2007, 2011; Pavlov et al., Chap. 5). In Kongsfjorden (Svalbard), which is situated at 79° N, the incident light is continuous from April to September. Besides its obliquity, the available light for submerged algae is diminished by the temporal ice cover that may last until spring and the turbidity during summer due to glacier melting and river run-off (Hanelt et al. 2001; Pavlov et al. 2013; Pavlova et al., Chap. 4).

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

9.1.1 Macroalgae

9.1.1.1 Ecological Importance

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

9.1.1.2 Historical Background

Investigations of benthic algae from Svalbard have a long but scattered history. The first study on macroalgae was done by Sommerfelt (1832), who received herbarium material from M. Keilhau. Sommerfelt described 5 different algal species from Svalbard, in addition to 1 species from Bear Island, the southernmost island of the Svalbard archipelago. Lindblom (1840) compiled literature from 5 earlier papers and counted a total of 16 marine and 3 freshwater macroalgae. Agardh (1862, 1868) expanded previous species lists to 51 species. Agardh's findings were based on material received from different Swedish expeditions. He noted that the material arrived in good condition, both with respect to freshness and colour, owing to the preservation method of putting the algae in barrels with salt.

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

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

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

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

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

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

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

9.1.1.3 Time Series

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

9.1.1.4 Macroalgae in Kongsfjorden

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

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

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

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

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

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

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

(continued)

Table 9.1 (continued)

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

(continued)

Table 9.1 (continued)

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

(continued)

Table 9.1 (continued)

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

(continued)

Table 9.1 (continued)

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

(continued)

Table 9.1 (continued)

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

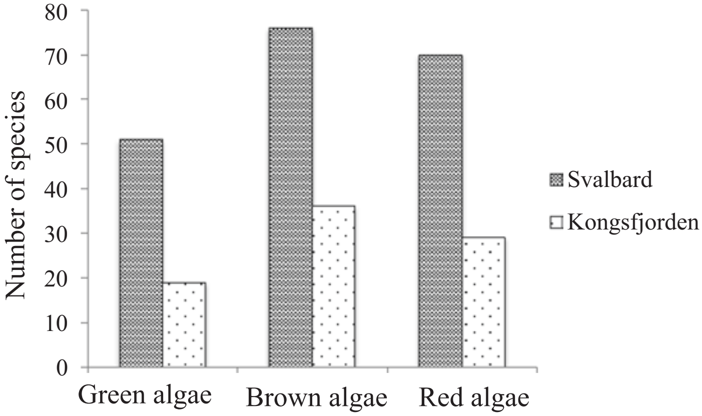

Fig. 9.1 Total number of species of the three different algal groups of benthic macroalgae from Svalbard and in Kongsfjorden

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

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

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

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

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

9.1.1.5 Taxonomic Problems

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

Small Green Algae

Genera like *Acrosiphonia, Cladophora, Ulothrix* and *Urospora* all contain species in need of a taxonomic revision. For example, there are 4 species of *Acrosiphonia* listed in Table 9.1. The two species described by Kjellman, *A. flagellata* and *A. incurva*, are currently considered valid species (Guiry and Guiry 2018). The diagnostic characteristics used to separate these from *A. arcta* and *A. sonderi* are doubtful. Both *Acrosiphonia flagellata* and *A. incurva* may reach a cell diameter of 150 μm (Kjellman 1893), which may overlap with *A. sonderi*, a species with cell diameter > 120 µm (Pedersen 2011). *Acrosiphonia incurva* has the same type of hooked branches close to the base as *A. arcta*, but with some differences in chloroplast structure (Kjellman 1893). *Acrosiphonia flagellata* produces small mats with interwoven rhizoids, a description that also fits *A. arcta* (Brodie et al. 2007). According to Kjellman (1893) both *A. flagellata* and *A. incurva* are known from Northern Norway only, but they are included in the Svalbard checklists by Vinogradova (1995b) and Hansen and Jenneborg (1996) as well as for Kongsfjorden (Hop et al. 2012). *Acrosiphonia duriuscula* (Ruprecht) Yendo was recorded in Hornsund by Florczyk and Latala (1989) and in Isfjorden by Weslawski et al. (1993). This species is taxonomically valid but it is a Pacific species (Guiry and Guiry 2018). Florczyk and Latala (1989) noted that the species had a cell size of 90 to 150 µm, which could overlap with *A. sonderi*, so we consider *A. duriuscula* to be a misidentification, a conclusion also supported by Vinogradova (1995b). Similar taxonomic problems exist for the other genera mentioned, with overlapping cell diameters described for species of *Ulothrix* and *Urospora*. A variety of species described in the genus *Cladophora* only possess weak morphological characters for clear distinction (Pedersen 2011). New insight using both morphological and molecular markers is needed to resolve these taxonomic issues.

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

A similar problem is ascertained for *Monostroma lubricum* Kjellman 1877 (Table 9.1) and *M. grevillei* var. *lubricum* (Kjellman) Collins 1909 (Table 9.4), however, they are the same taxon since they are based on the same type specimen (*Monostroma bullosum* (Roth) Thuret 1854). Guiry and Guiry (2018) recognize all these three taxa as valid species, so there clearly must be some taxonomic confusion. By nomenclature rules priority should be given to *Monostroma bullosum* (Roth) Thuret as a valid name. Following Vinogradova (1995a), *M. lubricum* is probably related to *M. grevillei* (Thuret) Wittrock. According to Brodie et al. (2007) the type species, *M. bullosum*, may lack a *Codiolum* – phase and as presently circumscribed *Monostroma* may not be monophyletic (O'Kelly et al. 2004). In a paper by Gordillo et al. (2016) they used *Monostroma arcticum* from Kongsfjorden as a test species to study effects of temperature and acidification on biochemical composition and photosynthetic performance. According to Guiry and Guiry (2018) *M. arcticum* is a variety of *M. grevillei*. Before any further studies are done on this genus *M. lubricum* is the only *Monostroma* species included in Table 9.1. Some previously described *Monostroma* species have been transferred to other genera like *Ulvaria*, *Gayralia* and *Protomonostroma* (Brodie et al. 2007).

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

Fucales

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

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

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

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

Laminariales

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

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

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

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

Acrochaetiales

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

Crustose Corallines

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

9.1.1.6 Changes in Flora and Possible Causes

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

It has been recently proposed that the changing light conditions may lead to light driven tipping points in future polar systems (Clark et al. 2013). In the sublittoral, Kortsch et al. (2012) showed an increase in algal cover and explained their results by an increased temperature in the surface waters. This caused a rise in the number of ice-free days, which presumably ameliorated light availability to algae, but continuous measurements of underwater light to support this assumption are missing. According to Cottier et al. (2007) and Pavlov et al. (2013) the West Spitsbergen current has advected more warm Atlantic water to Kongsfjorden after 2005/2006 than previously, particularly during winter. This has led to an increased temperature both in the surface and in deeper water masses which influences the biota. For example, increased temperature has also led to a spawning krill population in Kongsfjorden (Buchholz et al. 2012). If temperatures continue to increase, one would expect that a number of more temperate species will become established. The rise in temperature also leads to an enhanced inflow of turbid melt water into the fjord resulting in higher water turbidity, especially from July onwards (Pavlov et al. 2013). In addition, this melt water decreases salinity, especially in surface waters, and changes nutritional conditions (Rysgaard and Glud 2007). Low salinities in combination with exposure to ultraviolet radiation (UVR) inhibit germination of spores of e.g. *A. esculenta* and have the potential to limit the settlement of species in shallow waters (Fredersdorf et al. 2009), but all kelp species are still present at the upper sublittoral (Fredriksen et al. 2014; Bartsch et al. 2016). Various macroalgae inhabiting shallow water regions of Kongsfjorden, such as *Palmaria palmata* and *Saccharina latissima* amongst others, exhibit pronounced stenohaline features. Hence, under hyposaline conditions (15‰, melt water inflow) a strong loss of pigments (bleaching) or even high mortality can be observed (Karsten et al. 2003; Karsten 2007). On the other hand, increased water turbidity may have differential effects on kelps: while sediments may negatively influence the germination of spores and recruitment of juvenile sporophytes (Zacher et al. 2016), sediments may also protect seaweeds from the damaging effects of UVR (Roleda et al. 2008).

9.1.1.7 Comparison to Other Arctic Sites

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

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

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

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

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

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

9.1.2 Marine Benthic Microalgae

9.1.2.1 Ecological Importance

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

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

9.1.2.2 Historical Background

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

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

9.1.2.3 Production Aspects

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

9.1.2.4 Diversity of Benthic Diatoms

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

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

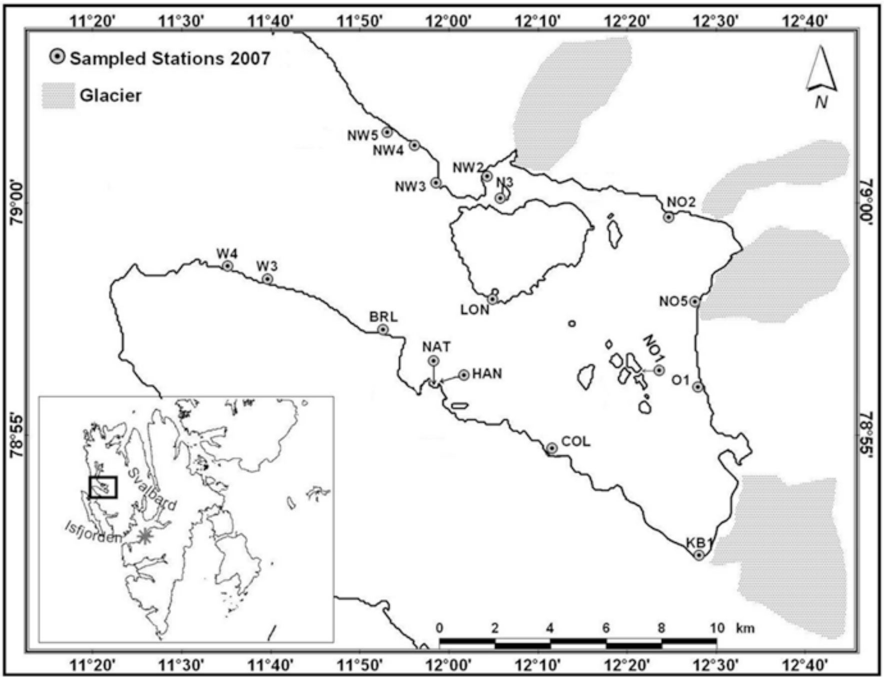

Fig. 9.3 Sampling stations for benthic microalgae in Kongsfjorden in 2007 (see Table 9.2; for details see Woelfel et al. 2009). Kongsfjorden on Svalbard is depicted on the insert

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

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

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

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

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

(continued)

Table 9.2 (continued)

Station	W4	W3	BRL	NAT	HAH	COL	KB1	O1	NO5	NO2	LON	N3	NW2	NW3	NW4	NW5
Gyrosigma sp.			+											+		
Licmophora gracilis (Ehrenberg) Grunow				+												
Licmophora sp.		+++	++													+++
Navicula bipustulata Van der Werff & Huls			+++				++				+++				+++	
Navicula directa (W.Smith) Ralfs			++		++					+++		+++				
Navicula gregaria Donkin				++		++	++				++					
Navicula kariana Grunow in Cleve & Grunow														+		+
Navicula sp.		+++	++	++	++	+++	+++			+++	+++	+++		++		+++
Navicula transitans Cleve		+++			++	++			+++							++
Navicula trigonocephala Cleve		+++														
Nitzschia arctica Cleve			++				+++		+++							
Nitzschia distans W. Gregory											+					
Nitzschia frigida Grunow			+	++												
Nitzschia promare Medlin & Hasle			+													
Pauliella taeniata (Grunow) F.E.Round & P.W.Basson				+												
Pinnularia quadratarea Pankow			++			+										

Pinnularia sp.															+++	
Plagiotropis sp.				+												
Pleurosigma siberica (Grunow) A.Cardinal, M.Poulin & L.Bérard-Therriault										+++						
Porosira sp.															+	
Pseudo-nitzschia delicatissima (P.T. Cleve) Heiden					++				+++		++					++
Pseudo-nitzschia granii (G.R.Hasle) G.R.Hasle				+++									+++			
Stauroneis sp.									+++							
Stenoneis sp.					+											
Surirella striatula P.J. Turpin										+++						
Synedropsis sp.		+++	++		++						++					
Thalassiosira sp.						++				+++				+++		

Abundances according to Sevilgen et al. (2014) were determined. These authors quantified abundances as frequent (+ + +), rare (+ +), very rare (+) (unpubl. data). The stations are given in Fig. 9.3

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

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

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

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

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

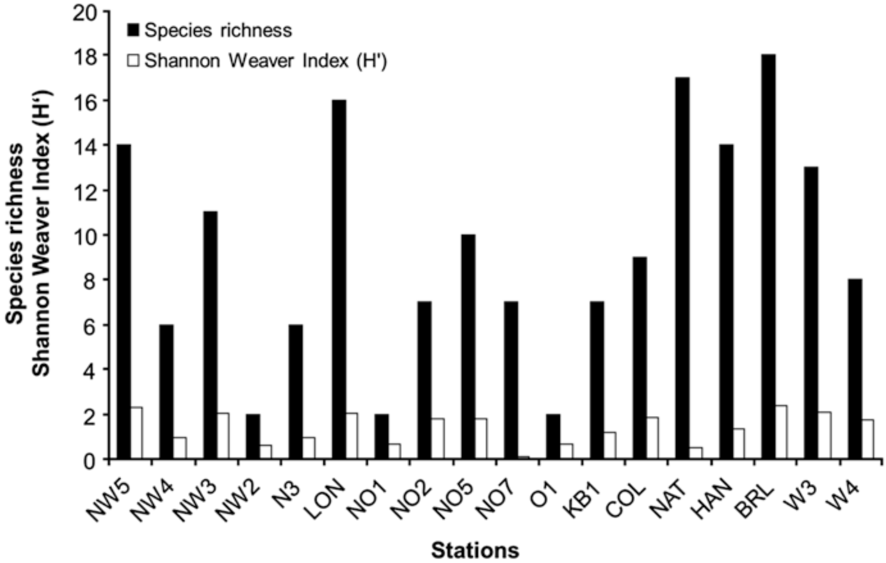

Fig. 9.4 Number of benthic diatom species at 5 m water depth across Kongsfjorden in 2007 and Shannon Weaver Index (H′) for benthic diatoms at 5 m water depth at different stations across Kongsfjorden. (For station details see Woelfel et al. 2009) (Koblowsky et al., unpublished data)

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

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

In their paleoecological study on Arctic microphytobenthos off the south-eastern Arctic Beaufort Sea, Campeau et al. (1999) characterised four of the ten most abundant species as polar species or as typical of cold waters, whereas six species were described as cosmopolitan taxa. Similarly, the ten most abundant species found at Svalbard in 2007 can be classified into four polar to cold temperate, five cosmopolitan species and one unidentified species of *Navicula*. It is difficult to distinguish between "polar water" and "sea-ice" species, since numerous benthic pennate diatoms contribute at least temporarily to sea–ice communities (von Quillfeldt 2004; Ratkova and Wassmann 2005). *Fossula arctica*, for example, was described by Hasle et al. (1996) and von Quillfeldt (2000) as a dominant species in Arctic waters. In addition, this species was associated with sea ice in the White Sea and Barents Sea (Ratkova and Wassmann 2005). The tychoplanktonic *Fragilariopsis cylindrus* was found in early phytoplankton spring blooms all over the Arctic Ocean (von Quillfeldt 2000) and is often associated with sea-ice (Gersonde and Zielinski 2000; Lizotte 2001; Mock and Thomas 2005). *Gyrosigma concilians* is characterised by Poulin (1991) as a sea-ice diatom from the Canadian Arctic, whereas *Navicula vanhoeffenii* has been documented as a cryopelagic species by Wiktor and Wojciechowska (2005). In the past, sea-ice diatoms received much more research attention as compared to their benthic counterparts in polar waters. Hence it is difficult to evaluate the available information about species-specific habitat preferences.

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

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

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

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

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

9.1.2.5 Diversity of Epiphytic Diatoms

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

9.2 Conclusion

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

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

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

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

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

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

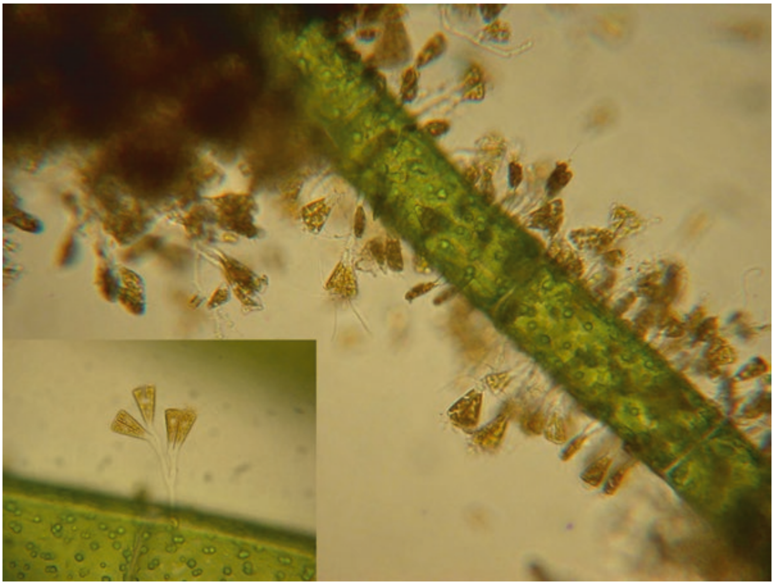

Fig. 9.6 Shallow water *Acrosiphonia arcta* collected at Hansneset (78°39'N, 17°57′E) with high numbers of epiphytic diatoms of the stalked genus *Licmophora*

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

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Chapter 10

Kelps and Environmental Changes in Kongsfjorden: *Stress Perception and Responses*

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Abstract On rocky substrata along shallow water cold-temperate and Arctic coastlines, large brown seaweeds ("kelps") form structure- and organism-rich habitats of vast ecological significance. The distribution of these ecosystem engineers is largely controlled by the prevailing temperature, light regime and substrate availability, but can also be influenced by biotic interactions within the kelp communities. In Kongsfjorden, right in the transition of an Arctic to an Atlantic fjord system, the

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_10

aforementioned factors are likely to be altered as a consequence of regional and global environmental change. The drivers of change entail increasing surface irradiances of harmful ultraviolet B radiation due to stratospheric ozone depletion, and variations related to increased atmospheric carbon dioxide concentrations, such as increase in atmospheric and sea surface temperatures with their marked influence on sea ice formation and ocean acidification. Other factors potentially driving the Kongsfjorden system into change might be alterations of current and wind patterns resulting in the increased inflow of Atlantic waters into the bay (Atlantification), and increased precipitation, and terrestrial and glacial runoff, yielding an altered salinity regime and sediment discharge into the fjord with the potential impact of reducing light availability to marine photosynthesizers. Hence, this article is aiming to provide an overview on ecologically relevant abiotic and biotic factors influencing kelp distribution, and with the potential to eventually act as environmental stressors. We assess responses on different organisational levels of kelp by following the effects cascading from the initial sensing of the environment, signal transduction to gene expression, physiological reactions, changes in cellular ultrastructure and subsequent consequences for growth, reproduction and population biology for the different species of kelps present in Kongsfjorden.

Results synthesized from more than 20 years of seaweed research in Kongsfjorden point to the overall large adaptability of most of the kelp species being present in the system. Such species are to be expected to cope with the levels of increased ultraviolet radiation and temperature predicted in climate scenarios. However, susceptibility largely differs among the various life history stages of kelps, with the microscopic reproductive stages responding sensitively. Manipulation experiments conducted at ecologically relevant amplitudes, however, do not point to an inhibition of kelp viability and reproduction under proceeding change. Still, there is the important exception of an Arctic endemic kelp species, *Laminaria solidungula,* which will largely suffer from temperature increase. Thus, changes in kelp community composition, but also system productivity are to be expected. Subsequent to the synthesis of seaweed responses, this review concludes by identifying the major research gaps and priority topics for future kelp studies in Kongsfjorden.

Keywords Kelps · Seaweed · Physiology · Ecology

10.1 General Introduction & Objectives

The rocky coastline of Kongsfjorden harbours a rich seaweed-dominated community. While the term "kelp" in a strict sense refers to seaweed species belonging to the phaeophyceaen order of Laminariales, we will here rather regard "kelps" as a functional entity by also including another large brown seaweed with a leaf-like phylloid present in Kongsfjorden: *Saccorhiza dermatodea* (de la Pylaie) J. Agardh, order Tilopteridales.

Kelp species have a broad geographical distribution and are a major source of primary production and serve as an important biogenic habitat in coastal waters (Dayton 1985; Steneck et al. 2002). The three-dimensional underwater habitat formed by kelp harbours numerous associated species of both algae and animals and contributes significantly to the secondary production in shallow areas (Carlsen et al. 2007; Christie et al. 2009; Norderhaug and Christie 2011). Kelps are generally cold-water species and are limited by a maximum summer temperature of approximately 20 °C, except for some occurrence in deep-water refugia in more tropical areas where the upper warm mixing layer is shallower than the light compensation depth thereby allowing kelp to grow in the cooler deeper water (Graham et al. 2007).

Kelps have a heteromorphic alternation of generations whereby two free-living phases are morphologically and ecologically distinct. The macroscopic and morphologically-complex sporophyte is diploid and undergoes sporogenesis. Meiospores are released, which settle and germinate into microscopic filamentous haploid male and female gametophytes. Further development of the microstages leads to spermatogenesis and oogenesis, respectively; fertilization and embryogenesis then give rise to the next generation of diploid sporophytes. Enormous numbers of these microscopic propagules are produced by kelps but only a small fraction directly forms sporophytes. These microstages serve as 'seed bank' for the next generation of the ecosystem-engineering macroscopic population. Changes in the viability of microscopic stages could be expected to have effects on recruitment and development of the macroscopic community (see Sect. 10.4.5). Physical stressors such as light, both quantity and quality, ultraviolet radiation (UVR) and temperature account for much of the mortality among spores, embryos and juveniles.

Basically, the seaweed flora of the European Arctic represents a depleted cold-temperate North Atlantic flora with a low degree of endemism. This is easily explained by the comparatively recent colonization history of Arctic coastlines, repopulated by seaweeds from the North Atlantic and also the North Pacific (Wulff et al. 2009) after the last glacial maximum approx. 18,000 years ago. During the glaciation period, all seaweed life became extinct from the Arctic due to ice coverage and exclusion of sunlight. Not before the onset of retreating ice masses, shorelines became accessible again to benthic colonizers and coastlines were repopulated by seaweeds following the northward migration of the ice edges (Wiencke and Bischof 2012). Thus, the recent establishment of an Arctic seaweed flora was fuelled from southern, cold-temperate populations, which gradually also adapted to thrive under the distinct high Arctic environmental conditions. As their conspecifics from lower latitudes, individuals of most Arctic species still display a comparatively broad tolerance range to changing environmental conditions. In contrast to Antarctica, the Arctic region is hardly geographically isolated, allowing for continuous connectivity between populations. Hence, and in addition to the recent event of repopulation, speciation processes have been limited. However, a re-evaluation of species connectivity and taxonomic identity for high Arctic kelp populations will be an important objective of future research.

Nowadays, researchers working at Kongsfjorden and other Svalbard fjords witness considerable changes in the physical, and commencing changes in the biotic environment. Most likely, these changes result from global climatic changes, shifting abiotic conditions within the fjord to a more boreal/Atlantic regime. These changes will impact the various biota to a different extent, and in order to predict the likely consequences of change to Kongsfjorden, the responses of kelps as ecosystem engineers need to be addressed urgently. Thus, the state of knowledge with respect to the Kongsfjorden kelp flora is presented and prominent gaps in knowledge are identified as a focus for future research.

10.2 The Kelp Flora of Svalbard and Kongsfjorden

In the cold-temperate areas along the coast of Norway, species like *Laminaria hyperborea* (Gunnerus) Foslie and *Saccharina latissima* (L.) C.E. Lane, C. Mayes, Druehl et G.W. Saunders (Fig. 10.1b) are the two dominating kelps in depths down to 25–30 m, while *Laminaria digitata* (Hudson) J.V. Lamouroux and *Alaria esculenta* (L.) Greville (Fig. 10.1a) are mostly limited to a narrow band in the transition zone between the littoral and the sublittoral (Rueness 1977). In the northernmost part of Norway, *Saccorhiza dermatodea* occurs frequently (Rueness 1977).

Laminaria gunneri Foslie is another species described from north Norway by Foslie (1884), but the current status of this species is questionable. On the western side of the Atlantic, *Saccharina latissima* is replaced by *Saccharina longicruris* (Bachelot de la Pylaie) Kuntze, a species with a hollow stipe. However, according to McDevit and Saunders (2010) *S. longicruris* is now reduced to synonymy with *S. latissima.* In addition *Agarum clathratum* Dumortier may be found in deeper waters (Adey and Hayek 2011). On Greenland, Rosenvinge (1893) described a new kelp species as *Laminaria groenlandica*, meanwhile recognized as *Saccharina groenlandica* (Rosenvinge) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, but now eventually reduced to synonymy with *S. latissima* (Longtin and Saunders 2015).

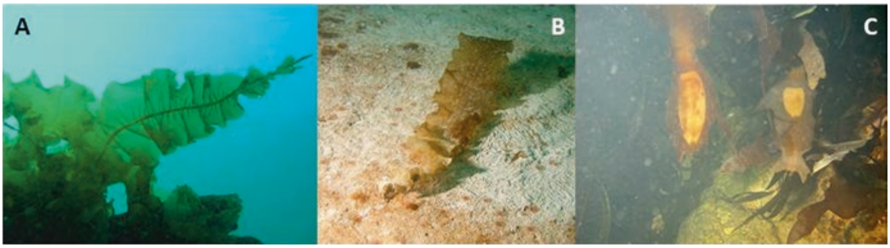

Fig. 10.1 Examples of kelps from Kongsfjorden: (**a**) *Alaria esculenta* is a kelp of Arctic to temperate distribution; due to its marked adaptive capacity it has been used in a multitude of ecophysiological studies on kelp responses to environmental changes. (**b**) *Saccharina latissima* on a small drop-stone drifting on soft bottom sediments; detached kelps are important vectors of organic matter transfer between hard and soft bottom habitats in Kongsfjorden. (**c**) *Laminaria solidungula* with characteristic hoof-shaped sori: As the only kelp endemic to the Arctic this species is believed to be particularly challenged by environmental change in Kongsfjorden. (All photos by Max Schwanitz, Alfred Wegener Institute)

According to Pedersen (2011), all digitate *Laminaria* species on Greenland belong to *Laminaria nigripes* J. Agardh, a species originally described from Svalbard by Agardh in 1868 (Agardh 1868). According to Longtin and Saunders (2016), *L. nigripes* should be included in the genus *Saccharina* as *Saccharina nigripes* (J. Agardh) C. Longtin & G.W. Saunders.

Kelp species in Svalbard are mostly the same as found along the Norwegian mainland. However, one additional species, *Laminaria solidungula* J. Agardh (Fig. 10.1c), occurs scattered around the entire island group (Hansen and Jenneborg 1996). Recent investigations from Isfjorden on Svalbard have reported the presence of *Laminaria digitata, Saccharina latissima, Alaria esculenta, Saccorhiza dermatodea*, and some small individuals of *Laminaria solidungula* (Fredriksen and Kile 2012). In Kongsfjorden, Hop et al. (2012) reported the same species to be present in an investigation from Hansneset in 1996/98. Fredriksen et al. (2014) revisited the same site as Hop et al. (2012) and found the same kelp species to be present in 2012/2013. The investigation by Hop et al. (2012) and Fredriksen et al. (2014) also pointed out the importance of kelp species for an overall rich benthic algal flora and fauna in Kongsfjorden. Recent investigations have shown the presence of *Saccharina groenlandica* at several sites in Svalbard, including Kongsfjorden (Lund 2014; Moy 2015; Fredriksen et al., Chap. 9). However, latest investigations suggest that this species should rather be regarded as a synonym to *S. latissima* (Longtin and Saunders 2015). The most important growth sites for kelps in Kongsfjorden are shown in Fig. 10.2.

Seaweed zonation patterns in Kongsfjorden have been studied intensively by diving down to 30 m depth at Hansneset, Blomstrand (78°39′N, 11°57′E) from 1996 to 1998 (Hop et al. 2012) and from 2012 to 2014 (Fredriksen et al. 2014; Bartsch et al. 2016). Between time periods, considerable differences in the zonation pattern and especially in the floral biomass distribution along the shore became evident. In their investigation Fredriksen et al. (2014) surprisingly recorded the highest number of species in the littoral zone, a zone often considered to be a harsh environment due to the fluctuations in environmental factors. Compared to Hop et al. (2012), Fredriksen et al. (2014) found twice as many species growing in the littoral zone, 20 and 45 species, respectively.

The kelps *Laminaria digitata* and *Alaria esculenta* were found down to 15 and 18 m respectively, while *Saccharina latissima* was found between 1.5 and 16 m depth. *Laminaria digitata* and *A. esculenta* were dominant between 1.5 and 9.5 m while *S. latissima* reached its maximum dominance between 7.5 and 11.5 m as identified by a combination of biomass data and cover. The endemic Arctic kelp *Laminaria solidungula* was present there as an understorey species as well but never reached dominance. The kelp-like species *Saccorhiza dermatodea* grew between 1.5 and 13 m with maximum abundance between 1.5 and 5.5 m. *Laminaria digitata*, *A. esculenta* and *S. dermatodea* reached highest biomasses at 5 m depth, whereas maximum biomass in *S. latissima* was recorded at 10 m (Table 10.1).

Below the kelp forest, a variety of brown and red algae were common to dominant. The brown algae *Desmarestia aculeata* (L.) J.V. Lamouroux and *D. viridis* (O.F. Müller) J.V. Lamouroux as well as the red alga *Polysiphonia arctica* J. Agardh occurred down to 20.5 m depth. The red algae *Phycodrys rubens* (L.) Batters and *Ptilota gunneri*

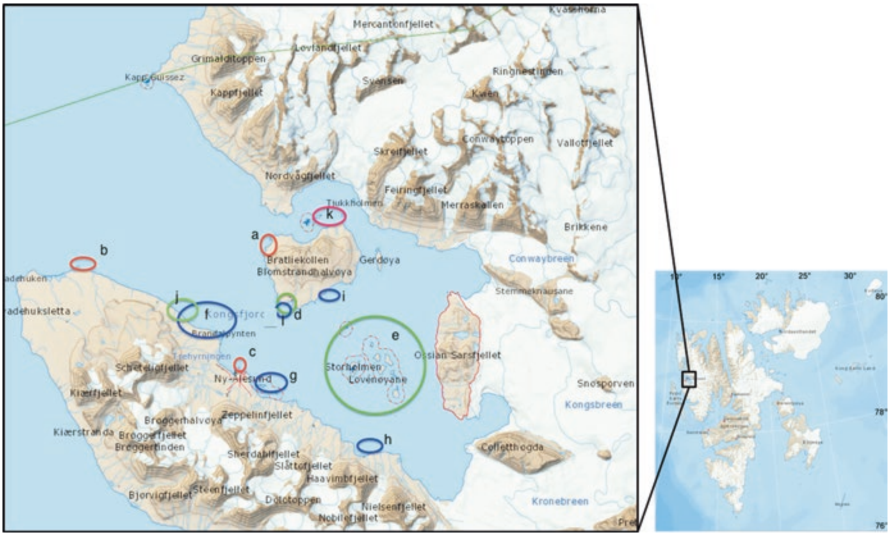

Fig. 10.2 Location of Kongsfjorden within the Svalbard Archipelago; main growth sites of kelps in Kongsfjorden as observed by scientific diving (maps compiled from toposvalbard.npolar.no):

Location	Site characteristics	Dominant species
a	Kelp forest on rocky substrate	*Alaria esculenta, Saccharina latissima, Laminaria digitata, Laminaria solidungula*
b	Kelp forest on rocky substrate	*A. esculenta*
c	Kelp forest on rocky substratum (mainly artificial structures)	*A. esculenta, S. latissima*
d	Minor kelp assemblages in the upper subtidal zone	*S. latissima, A. esculenta, L. digitata*
e	Minor kelp assemblages in the upper subtidal zone	*S. latissima, A. esculenta, L. digitata*
f	Seaweed on dropstones on sandy bottom	*A. esculenta, L. digitata*
g	Seaweed on dropstones on sandy to muddy bottom	*A. esculenta, L. digitata*; below 17 m also *L. solidungula*
h	Seaweed on dropstones on muddy bottom	*A. esculenta, L. digitata*
i	Seaweed on dropstones on sandy sediment, coarse gravel and rocky structures	*A. esculenta*, *L. digitata*
j	Small kelp assemblages in the upper subtidal zone (narrow rocky band along the coast)	*S. latissima, A. esculenta, L. digitata*
k	Kelp assemblages on dropstones or rocky structures covered with muddy sediment	*S. latissima*
l	Seaweed on dropstones on sandy to muddy sediment or on large boulders	Mainly *A. esculenta* and *S. latissima,* some *L. digitata* on shallow rocks close to the coastline

Table 10.1 Comparison of depth distribution of kelps at Hansneset (site "a" in Fig. 10.2), Kongsfjorden between 1996–1998 and 2012/2013 and occurrence of maximum biomass value (dark grey: high biomass, light grey: species recorded). The lower depth distribution limits (LDL) were recorded in 1996–1998 and in 2014

	Depth (m)								
	0.0	1.5	2.5	5.0	7.0	10	15	LDL (m)	Year
Saccorhiza dermatodea		░	░	▓	░	░		13	1996–1998
	░		▓	░	░	░		12	2012–2014
Alaria esculenta		░	░	▓		░	░	15	1996–1998
	░		▓	░		░	░	18	2012–2014
Laminaria digitata		░	░	▓	░	░	░	15	1996–1998
	░		▓	░	░	░		10	2012–2014
Laminaria solidungula			░	░				5	1996–1998
			░			░		10	2012–2014
Saccharina latissima		░	░	░	░	▓	░	16	1996–1998
	░		▓	░	░	░		14	2012–2014

Compiled from Hop et al. (2012) and Bartsch et al. (2016)

P.C. Silva, Maggs et J.N. Heine grew at least down to 30 m depth. During a study using a remotely operated vehicle (ROV) in 2005, *P. rubens* was observed growing attached at 60 m depth (C. Wiencke, unpubl.). In contrast, the red alga *Odonthalia dentata* (L.) Lyngbye grew down to 15.5 m depth. Many of the species of this belt below the kelp forest occur also within the understorey of the kelp forest. Further subcanopy species with varying dominances as identified by a combination of biomass data and cover were the red algae *Devaleraea ramentacea* (L.) Guiry, *Palmaria palmata* (L.) Kuntze and *Coccotylus truncatus* (Pallas) M.J. Wynne et J.N. Heine.

When re-examining species composition at Hansneset in 2012/2014, several mostly small and inconspicuous species were recorded for the first time (Fredriksen et al. 2014). One species, *Sphacelorbus nanus* (Nageli ex Kützing) Draisma, Prud'homme & H. Kawai, represents a new record for Svalbard, 14 species are new records for Kongsfjorden. A considerable increase from 20 to 45 species was recorded in the littoral zone between both sampling periods. Overall, the total macroalgal species diversity of Kongsfjorden increased to 78 (Fredriksen et al., Chap.9). While 62 species were found in 1996/98 and 58 in 2012/2013, only 42 were common to both investigations. Strikingly, some conspicuous red algae that had been recorded in 1996/98, such as *Hildenbrandia rubra* (Sommerfelt) Meneghini, *Palmaria palmata* (L.) Weber & Mohr, *Polysiphonia* spp., or *Scagelia pylaisaei* (Montagne) M.J. Wynne were not found again. Based on these results, Fredriksen et al. (2014) came to the conclusion that indirect signs of global warming are apparent. Although the number of species in the two investigations was similar, there was a striking increase in species number in the littoral zone, possibly a result of reduced ice-scouring over the last years. In a follow-up-study performed in 2012–2014 at the same site, Bartsch et al. (2016) showed changes in biomass and depth distribution of most dominant brown algae. In particular, they demonstrated a 1.7 fold increase in overall seaweed biomass and a 4.7 fold increase of seaweed biomass at 2.5 m depth compared to 1996–98. The species with the highest biomasses were in this sequence: *L. digitata*, *A. esculenta* and *S. latissima*. It is important to note that biomass of these perennial species increased considerably in 2012–14, while the biomass of the annual *Saccorhiza dermatodea* decreased strongly compared to 1996/1998. Moreover, the biomass maximum recorded in 1996/1998 at 5 m was shifted to more shallow waters in 2012–2014. Additionally, the lower depth limit of most dominant brown algae was elevated by approx. 2–3 m. This complex pattern was regarded by Bartsch et al. (2016) as a consequence, firstly, of the reduction of fast ice since the winter 2005/2006 (Cottier et al. 2007) and, secondly, of the insufficient light conditions for kelp growth in greater depths because of an increased water turbidity as a result of increased sedimentation. One exception, however, was *A. esculenta*, which was found 3 m deeper in 2012–2014 compared to 1996/1998 (Table 10.1). This species presumably takes advantage of the relatively thin structure of the phylloid allowing a better potential for acclimation to low light conditions.

Overall, these findings support similar observations obtained between 1980 and 2010 at Kongsfjordneset (78°58.60′N, 11°30.10′E) and Smeerenburgfjorden (79°41.33′N, 11°04.00′E; Kortsch et al. 2012). In both Arctic fjords, abrupt and substantial changes in the structure of benthic communities were documented concurring with a gradual increase in annual average sea-surface temperature (SST) and increasing duration of the ice-free period. The structure of the two benthic communities remained relatively uniform between 1980 and 1992/1994 but changed rapidly thereafter. In Kongsfjorden, brown algal cover was sparse until 1995 but increased rapidly to 80% in 1996. After this period, macroalgal cover fluctuated around 40%. Similar findings were obtained in Hornsund, in the south of Svalbard, where a threefold increase in biomass was recorded between 1988 and 2008 (Weslawski et al. 2010). Kortsch et al. (2012) concluded that the changes at Kongsfjordneset and Smeerenburgfjord were related to changes in sea surface temperatures, increasing length of the ice-free season and concomitant enhanced light conditions together with changes in competition and grazing.

The described species composition and zonation pattern at Hansneset changes considerably along the fjord axis (Hop et al. 2016), and are certainly depending on the temperature, sedimentation and light regime and the degree of exposure in the different parts of the fjord.

10.3 Environmental Settings for Kelps Populating Kongsfjorden

10.3.1 Light Availability & Radiation Climate

The overall atmospheric radiation conditions over Kongsfjorden are governed by pronounced seasonal differences resulting from the location's high latitude. The fundamentals of the light regime in Kongsfjorden have been characterized by Hanelt et al. (2001).

The most obvious peculiarity of radiation conditions at such high latitude is the change in atmospheric radiation conditions during the polar day and night. At Kongsfjorden (78°55′N, 11°56′E), the polar day lasts from 21 April to 22 August and the polar night from 26 October to 14 February. Even during the summer season with 24 h of daylight, maximum irradiances of photosynthetically active radiation (PAR) are comparatively low as a consequence of the low solar angle over the Arctic (Svendsen et al. 2002). Hence, maximal irradiance is considerably lower than at the equator and in temperate regions and hardly exceeds 1200 μmol photons PAR m^{-2} s^{-1} (Bischof et al. 1998a). Average annual PAR flux in Ny-Ålesund has been estimated at approximately 1000 MJ m^{-2}, as determined by the local station of the Baseline Surface Radiation Network (BSRN; Hanelt et al. 2001). For comparison, at Helgoland, German Bight, North Sea at 54°N the annual PAR flux is approximately twice as high (Lüning 1990).

Obviously, apart from the seasonal changes, prevailing weather conditions largely govern the atmospheric radiation regime, while aerosols and other airborne particles currently play a minor role at this high latitude, apart from emissions of combusted fuel during the cruise ship peak season in summer (Eckhardt et al. 2013). Next to the photosynthetically active radiation range, the spectral component of ultraviolet radiation (UVR) has been shown to have considerable impact on kelp biology and this influence has been intensively studied at Kongsfjorden (Bischof et al. 2006). Maximum values of ultraviolet B (280–320 nm, UVB) radiation have been measured to be about 0.27 W m^{-2} (Hanelt et al. 2001), and in addition to season and weather conditions are furthermore influenced by stratospheric ozone concentration (Harris et al. 2008).

While we observe high variability in atmospheric radiation conditions, the underwater light climate is shaped by a multitude of further parameters, including water turbidity as influenced by any kind of particle load (phytoplankton cells, suspended sediments etc.), height of water column resultant from vertical depth distribution and additionally governed by tidal changes, and the presence/absence of sea ice cover. The optical characteristics of the water column can be characterised in a straightforward manner by determining the vertical attenuation coefficient Kd, as described for Kongsfjorden by Hanelt et al. (2001). Irrespective of atmospheric and hydrographic conditions on the larger scale, the only meaningful radiation conditions to kelps are those shaping the *in situ* microenvironment. Hence, regardless of atmospheric light availability, only photons captured by the photosynthetic antennae or by light-sensing pigments matter to the respective individual of kelp. Also, the amount of quanta in the ultraviolet range of the spectrum, which may hit the actual kelp surface and eventually damage any kind of biomolecule is still difficult to assess from surface radiation measurements. The *in situ* (micro)light climate is modulated by the orientation to solar exposure, the slope of the substrate, the presence or absence of a canopy (either from the same or different species), to name just a few of the influencing factors. Moreover, identical radiation conditions may exert differential effects on kelp cells, depending of the different tissues, age, life-history stage etc. (see Sect. 10.4.5).

With respect to environmental changes to be expected in the Kongsfjorden ecosystem, one of the most burning questions concerns the future radiation climate in Kongsfjorden. It needs to be carefully evaluated whether light availability to benthic kelp communities will be increasing or decreasing as the outcome of environmental change in Kongsfjorden. Obviously, sea ice cover persisting into spring and, thus, shielding benthic communities from radiation during a period usually characterized by very transparent water conditions (Hanelt et al. 2001) will become an extremely rare event. Conclusively, more light will become available in early spring, which may facilitate an earlier onset of the productive season. It may thus be argued that the flourishing season for kelps might become extended by an earlier and higher light availability in the absence of sea ice. On the other hand, the extremely clear waters right at that time, connected to the higher UVB irradiance reaching the earth surface in early spring season may confer inhibitory processes to kelp photosynthesis and production (Bischof et al. 2006), counterbalancing the promoting effect described above. Moreover, new records of stratospheric ozone loss over the Arctic have been registered recently (Manney et al. 2011), as a direct outcome of the interaction with climate warming. Increase in CO_2 will lead to temperature increases in the troposphere and will prevent the efflux of heat energy to the stratosphere. Thus, a considerable cooling of the stratosphere is expected, which will promote the formation of polar stratospheric clouds and ultimately facilitating ozone breakdown (Harris et al. 2008). Consequently, for atmospheric radiation conditions, a higher UVB burden in the Arctic is likely. It is, however, questionable to what extent the higher UVB load will propagate into subtidal communities: The higher UVB load might be most critical in early spring, but might also be diminished if not completely prevented by increased water turbidity later in season. This is because of another likely scenario Kongsfjorden might face: higher atmospheric temperatures will promote glacier melting and, in combination with a likely increase in precipitation, result in increasing terrestrial run-off and particle discharge into the fjord system, which will result in increased attenuation, with higher absorbance in the shorter wavelength range (Hanelt et al. 2001, Sect. 10.3.2). The modulation of the underwater light climate by an increased sediment load is documented by attenuation measurements along the fjord axis. High loads of glacier-derived sediment reduce light availability in the inner part of the fjord, while overall the effect of sediment diminishes westward along the fjord axis (Svendsen et al. 2002, Wlodarska-Kowalczuk et al. 2005).

10.3.2 Terrestrial Run-Off: Sedimentation & Salinity Change

In Kongsfjorden, sediment accumulation rates range from 200–20,000 g m^{-2} yr^{-1} from the outer to inner fjord, respectively (Svendsen et al. 2002). The sediments being released to the fjord may affect kelp communities in two ways: On a larger scale (and as outlined above), sedimentation will result in a reduction of PAR, which may result in a reduction of maximum photosynthetic rates and ultimately affect system productivity. At the same time, kelps might be shielded from harmful UV radiation (Roleda et al. 2008). However, whether this represents an effect of ecological significance remains to be resolved. On a smaller scale, sinking sediments may eventually settle on kelp blades, where they may become adhesive, being glued by the polysaccharide mucilage covering the phylloid surface (Roleda et al. 2008). This may interfere with (i) light availability, but also with (ii) nutrient exchange and (iii) hydrodynamics of kelp blades, as sediment-laden phylloids will be considerable heavier. In this way, massive discharge events may ultimately result in a smothering of entire benthic communities, turning an originally rocky habitat into a regime dominated by sediments with little substratum suitable for kelp settlement.

Another environmental variable in coastal waters altered by increased particle discharge from land and consequently potentially affecting kelp physiology is salinity. A gradient of decreasing salinity from the fjord mouth to the inner part of the fjord is established each summer, as a result of riverine freshwater run-off and glacier melting (Svendsen et al. 2002, Wlodarska-Kowalczuk et al. 2005). During summer, salinity drops from 34 to 28 in surface waters are frequently observed under the influence of glacial melting. Such low salinities may be reduced even further in riverine discharge plumes. Reduced salinity has been described as a stress factor to kelp zoospores and in particular in combination with other physico-chemical stressors. Fredersdorf et al. (2009) showed that photosynthetic quantum yield of spores of *Alaria esculenta* has been inhibited by salinities of approximately 20 and that spore germination is markedly impaired by the interaction of reduced salinity, elevated temperature and UV-exposure. As we will see below, the particular susceptibility of kelp spores towards environmental perturbation is of utmost significance to kelp population biology.

10.3.3 Temperature Increase and Ocean Acidification

The rising anthropogenic CO_2 emissions trigger the atmospheric greenhouse effect and also influence ocean warming. Subsequent CO_2 dissolution that buffers climate change in the terrestrial system further makes the world's ocean less basic (i.e. lower pH). The decadal 0.15 °C increase in global surface temperature (IPCC 2013) is most likely responsible for the 0.7 °C increase in global average sea surface temperature (SST) during the last century (Hulme et al. 2002). The recently projected increase in average surface temperature by 1.0–4.0 °C in the year 2100 (IPCC 2013) may further increase the average global SST.

On Spitsbergen, continuous monitoring of atmospheric CO_2 was commenced in October 1988 and has continued ever since (Engardt et al. 1996). From the atmospheric CO_2 record, the oceanic CO_2 uptake and terrestrial net CO_2 uptake was estimated using a high resolution regional atmospheric transport model and supported by complimentary $\delta^{13}C$ data (Engardt and Holmén 1996). Moreover, long-term time-series of air temperature measurements in Spitsbergen (1898–2012) showed a significant temperature increase from the 1960s. The trend showed an annual mean increase of 2.6 °C century^{-1} and a high seasonal increase during spring at 3.9 °C century^{-1}. Svalbard has experienced the greatest temperature increase during the last three decades compared to other regions in Europe (Nordli et al. 2014).

Approximately one third of the global anthropogenic CO_2 emissions is absorbed by the world's oceans. The reaction of CO_2 with H_2O perturbs the seawater carbonate system and the increase in hydrogen ion concentration lowers pH because $pH = -\log_{10}[H^+]$, a process known as ocean acidification (OA). For example, in present surface seawater with pH of ~8.07, approximately 91% of the inorganic carbon (Ci) is HCO_3^-, 8% CO_3^{2-}, and only 1% $CO_{2(aq)}$. Under a more acidified ocean scenario in the year 2100, concentrations of $CO_2(aq)$ and HCO_3^- are predicted to increase by 200% and 9%, respectively, and CO_3^{2-} decrease by 56%, with a concomitant decline in pH to 7.65 (Royal Society 2005). The Polar Seas and the cold temperate regions, e.g. the northern Atlantic, are projected to be more vulnerable to OA because cold water absorbs more CO_2 (McNeil and Matear 2008; Roleda and Hurd 2012).

CO_2 is the substrate for photosynthesis, but only 1% of Ci present in today's oceans exists as CO_2, while 91% exists as HCO_3^-. Therefore, it is not surprising that most seaweeds are able to utilize HCO_3^- from the bulk seawater to compensate for the low availability of $CO_{2(aq)}$. The diverse mechanisms involved in the use of HCO_3^- are termed CO_2 concentrating mechanisms (CCMs) which in most cases comprise at least three functional elements: (1) influx of CO_2 and/or HCO_3^-, (2) uptake of Ci inside the cell (usually as HCO_3^-) and (3) production of CO_2 from the Ci pool around the CO_2-fixing enzyme Ribulose 1,5, bisphosphate Carboxylase/Oxygenase (RuBisCO). The role of different isozymes of carbonic anhydrase (CA) in the reversible enzymatic conversion of HCO_3^- to CO_2 in different cellular compartments suggests that photosynthesis is saturated under the current seawater Ci concentration (cf Fernández et al. 2015). Studies on the carbon physiology of various Atlantic kelp species, e.g. *Laminaria digitata*, *Laminaria hyperborea*, *Saccharina latissima*, *Alaria esculenta* and *Phyllariopsis purpurascens* (Surif and Raven 1989; Flores-Moya and Fernández 1998; Axelsson et al. 2000; Klenell et al. 2004; Mercado et al. 2006), suggest diverse species-specific inorganic carbon uptake mechanisms (details reviewed in Fernández et al. 2014).

The effects of OA in isolation and in interaction with other stressors on kelp physiology have been studied extensively on the Pacific giant kelp *Macrocystis pyrifera* (L.) Agardh (e.g. Roleda et al. 2012a; Brown et al. 2014; Fernández et al. 2014, 2015; Gaitan-Espitia et al. 2014;), i.e. more than in any other Atlantic kelp species (e.g. Olischläger et al. 2012; Gordillo et al. 2015). Only Gordillo and co-workers (2015) investigated OA and UVR on the Arctic population of *Saccharina latissima* and *Alaria esculenta* from Kongsfjorden. It has been suggested that fleshy seaweeds, such as kelps, will likely benefit under high CO_2 concentrations as they will increase their CO_2 use and down-regulate 'energetically-expensive' active HCO_3^--use mechanisms, thereby saving energy to allocate more resources into growth. This hypothesis, however, requires further physiological experiments such as those by Fernández and co-workers (2014, 2015), who showed that HCO_3^- remains the main source of inorganic carbon (Ci) assimilated by the geographically widely distributed, i.e. from warm-temperate to sub-polar regions, giant kelp *Macrocystis pyrifera* to support photosynthesis under both high (= pH 7.65) and low (= pH 9.00) $p\mathrm{CO}_2$. Consequently, photosynthetic (O_2 evolution) and growth rates of *M. pyrifera* were not significantly enhanced under ocean acidification (Fernández et al. 2015). On the contrary, under high CO_2 and UVR exposure, higher growth rates in *Saccharina latissima* and *Alaria esculenta* from Kongsfjorden were reported (Gordillo et al. 2015). The use of pulse-amplitude modulated (PAM) chlorophyll fluorescence for photopysiological measurements of e.g. the maximum quantum yield of PSII (Fv/Fm) as a proxy to measure effects of ocean acidification should be interpreted with care as the mechanism of how quantum yield may be affected by the bulkwater pH still needs to be elucidated (Rautenberger et al. 2015).

A fundamental understanding of organismal physiology, especially for the structural canopy-forming kelps, is very important as scientists assess how foundation species and ecosystem engineers might respond to the changes in seawater carbonate chemistry predicted under OA. However, it should be noted that despite the 200% increase in CO_2, HCO_3^- concentration remains 97% higher compared to CO_2 (Raven et al. 2005). Whether the overall effect of OA is negative, positive or neutral will depend on its direct and indirect effects: is the effect due to increase in CO_2 alone or due to the increase in total dissolved inorganic carbon (DIC: $CO_2 + HCO_3^-$) and/or due to the concomitant decrease in pH and increase in H^+? For example, a 0.1 unit decrease in pH corresponds to a 30% increase in H^+; how this substantial increase in H^+ affects organismal metabolism requires in-depth studies (cf Roleda et al. 2012b). Among the several functions of H^+, it modulates membrane channel functioning, intracellular signalling and ion availability (Busa 1986; Taylor et al. 2012). Therefore, OA studies should be conducted under rigorously controlled experimental conditions in which only specific carbonate chemistry parameters are manipulated and all other conditions (e.g. light, temperature, water flow, nutrients) are kept at optimum levels.

The effects of OA have been studied on early life history stages of different cold-temperate kelp species, e.g. *Macrocystis pyrifera* and *Laminaria hyperborea*. In *M. pyrifera*, meiospore germination was reduced by 9% only under extreme OA ($p\mathrm{CO}_2$ = 1200 ppm; pH = 7.59–7.61). Moderate OA ($p\mathrm{CO}_2$ = 830 ppm; pH = 7.76) had no effect on meiospore germination rate, and cells even grew bigger compared to those grown under pre-industrial CO_2 levels ($p\mathrm{CO}_2$ = 270 ppm; pH = 8.19) (Roleda et al. 2012a). In concurrence, Gaitan-Espitia et al. (2014) showed that meiospore mortality was enhanced only under interactive effects of extreme OA ($p\mathrm{CO}_2$ = 1800 ppm) and increase in temperature (+5 °C of the ambient); at ambient temperature and high CO_2, meiospores were observed to undergo dormancy (Gaitan-Espitia et al. 2014). On the other hand, a study on various life history stages of another cold-temperate kelp species, *Laminaria hyperborea,* showed that female gametogenesis and sporophyte growth can be significantly enhanced under high CO_2 (Olischläger et al. 2012).

Aside from the effect of OA on species physiology, growth, reproduction, and survival, it is also important to consider the effect of OA on species competition, top-down control by herbivores, and ecosystem diversity and resilience (Harley et al. 2012; Connell et al. 2013; Falkenberg et al. 2014). Whether kelps and other fleshy seaweed will benefit from OA and competitively exclude OA-sensitive species such as coralline algae requires detailed investigation with robust experimental design (Roleda et al. 2015). A diverse benthic algal assemblage may be able to buffer the negative effects of OA on pH-sensitive species, e.g. calcifying organisms (Jury et al. 2013, Jokiel et al. 2014, Roleda et al. 2015). For example, high CO_2/low pH has a neutral rather than negative effect on net primary productivity of coralline-kelp assemblages (Tait 2014). Overall, research on the impacts of OA on fleshy seaweeds and benthic algal communities from Polar Regions is limited; however, kelp species from cold-temperate regions appear to be resilient to OA. To clarify whether the seaweed community of Kongsfjorden (as described in Sect. 10.2) will experience long-term changes under the impact of OA will require intense research efforts including benthic *in situ* manipulation experiments.

The upper survival temperatures (USTs) of 16 non-canopy forming seaweed species from Greenland were observed to be much higher than the ambient temperatures (Bischoff and Wiencke 1993). A group of stenothermic species grows within 0–20 °C range, with a growth optima between 0 and 10 °C and a UST of 17–23 °C. Another group of eurythermic species grows in the same temperature range but with optimum growth at 10 or 15 °C and a UST of 24–31 °C (Bischoff and Wiencke 1993). Among the large canopy-forming kelp species, the large-scale disappearance of *Saccharina latissima* in 2002 in southern Norway was partly attributed to increasing summer water temperatures; and recovery of the species has been limited at low abundances (Moy and Christie 2012). Seawater temperature does not only control survivorship but also growth and reproduction. For example, temperatures higher than 15.5 °C reduced the productivity of farmed *Saccharina japonica* (Areschoug) C.E. Lane, C. Mayes, Druehl & G.W. Saunders by 10% compared to cooler years (Suzuki et al. 2008); while high summer seawater temperature (18 °C) inhibited sporogenesis in another species, *Laminaria digitata,* where sorus formation is optimal between 5–10 °C (Bartsch et al. 2013). Moreover, seawater temperatures above 17.5 °C induce a higher tissue erosion rate, exceeding that of growth rate (Suzuki et al. 2008). The projected increase in surface ocean temperature is predicted to have major impacts on coastal ecosystems, including the decimation of kelp forests at their southern range limit, and their poleward range extension (Müller et al. 2009a; Raybaud et al. 2013; Brodie et al. 2014). However, early life history stages of Arctic endemic kelp and Arctic ecotypes of North Atlantic Laminariales can survive temperatures higher than ambient (Roleda 2009, 2016). Whether species have distinct strategies to respond to climate change by adaptation or migration, or will succumb to local extinction remains to be investigated.

10.3.4 Nutrient Regime

There is only scant information about the nutrient regime governing pelagic and benthic primary productivity in Kongsfjorden, but this has been the focus of some of the most recent on-site research activities. Nitrogen compounds have long been recognised to limit macroalgal productivity. In the Arctic, the maintenance of metabolism at near-freezing temperatures requires a high concentration of enzymatic proteins (Machalek et al. 1996), which constitute a major nitrogen-containing cell component. Thus, polar algae in general are expected to have a considerable demand for nutrients. However, unlike in Antarctica, Arctic waters show strong seasonality in nutrient availability. The general pattern of nutrient availability in Kongsfjorden is as follows: a relatively high concentration of nitrate, phosphate and silicate during winter allowing phytoplankton blooms to develop in spring once the sun has returned and waters are free of ice (Rokkan Iversen and Seuthe 2011; Hegseth and Tverberg 2013; Piquet et al. 2015). Annual variations of nitrate for the year 2006 are shown in Fig. 10.3. During the phytoplankton bloom, nutrients are assimilated by microalgae and seawater gradually becomes nutrient depleted from late spring to autumn. This means that the period of maximum light availability is concomitant with a scarcity of nutrients and vice-versa. Although it is generally assumed that inorganic nitrogen is the main limiting factor for primary production in coastal systems, some tropical waters have been reported to be P-limited (e.g. Lapointe 2004). Following low N:P ratios during summer, this seems not to be the case in Kongsfjorden (Fig. 10.3).

Nutrient uptake and assimilation characteristics of macroalgae from temperate waters have been shown to vary among populations and species under local nutrient regimes (e.g. Hernández et al. 1993; Gordillo et al. 2001a). Arctic species are also

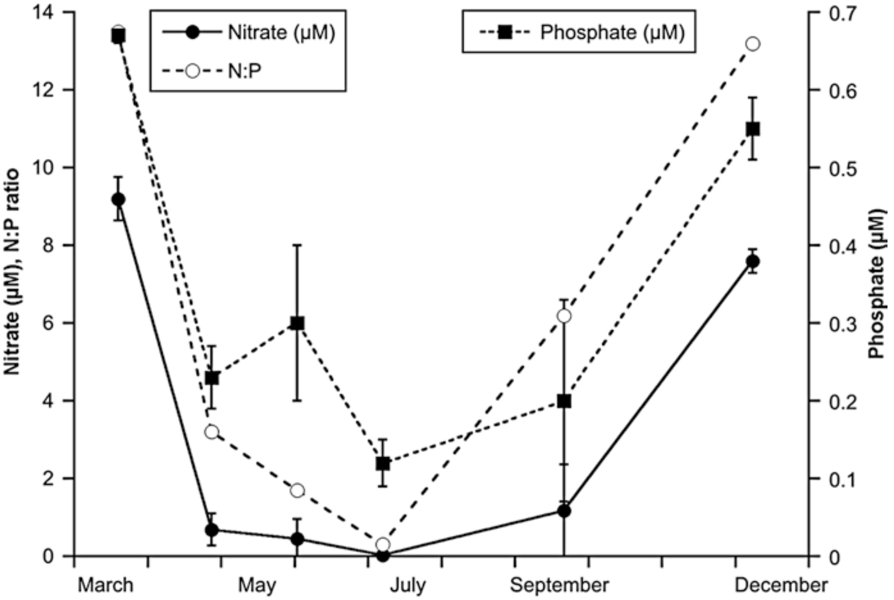

Fig. 10.3 Nitrate (+ nitrite) as well as phosphate concentrations, and N:P ratios in the upper 50 m of the water column near the village of Ny-Ålesund in 2006. Bars for ±SD (n = 6). (Re-drawn from Rokkan Iversen and Seuthe 2011)

reported to show nutritional traits that allow them to cope with the long periods of darkness in winter and nutrient depletion in summer (Korb and Gerard 2000a, b). Kelps living in the Arctic rely on stored photosynthates accumulated during the ice-free N-depleted summer period, supporting new growth during winter, during which, however, nutrient supply is sufficient. According to Korb and Gerard (2000a), the endemic *Laminaria solidungula* can be considered a “storage specialist” for nitrogen assimilation. Its high maximum nitrate uptake rate (Vmax), along with low growth rates, allows it to take advantage of seasonally elevated nutrient concentrations and to accumulate large internal pools of nitrate and organic N-reserves. Traditionally, it was thought that this seasonal growth pattern was a direct consequence of N availability (Chapman and Lindley 1980) as well as light availability (Henley and Dunton 1997). However, it has been proposed that, at least in some species, this pattern might be under the control of an endogenous free-running circannual rhythm entrained by a critical minimum daylength in autumn (Lüning 1991, Schaffelke and Lüning 1994). This genetic clock would imply that the addition of nitrate to N-limited kelps during summer would have only a marginal effect on growth and biochemical composition, presumably due to the prevailing internal clock (Henley and Dunton 1997). Gordillo et al. (2006) confirmed that the effects of nutrient enrichment in midsummer on kelp biomass composition play only a marginal role in a number of species from Kongsfjorden. When thalli of 21 seaweed species collected in July were incubated for two days in nitrate- and phosphate-enriched seawater, the C:N ratio was only affected by 7% on average, and it did not decrease significantly in any of the three kelps included in the study (*Alaria esculenta*, *Saccharina latissima*, and *Laminaria solidungula*). This lack of N-accumulation would be in agreement with the internal clock prevailing over external nutrient conditions, which in summer would promote active photosynthesis over nutrient uptake.

However, N-availability is not to be considered alone, as other factors might influence N use. Henley and Dunton (1997) reported changes in the biochemical composition of *L. solidungula* as an effect of light availability and the interaction of light and N rather than the addition of N alone. More recently, Iñiguez et al. (2016) found that increased levels of CO_2 promoted N assimilation in *Alaria esculenta* collected in July, and incubated under N sufficiency. Similar stimulation of N assimilation by increased CO_2 has been observed in the temperate *Ulva rigida* (Gordillo et al. 2001b). From the report by Gordillo et al. (2006) it could be concluded that N storage via NO_3^- internalisation during winter to early spring might be sufficient to overcome at least part of the summer with sufficient nitrogen availability. Kelps showed an accumulation factor (internal relative to external concentration) of up to 7000 (Table 10.2). However, in a later campaign in July 2009, the same authors failed to detect internal levels of inorganic N (unpublished), evidencing an interannual variation in N storage. Strong interannual changes in macroalgal cover have been reported for Kongsfjorden (Hop et al. 2012; Kortsch et al. 2012; Fredriksen et al. 2014; Bartsch et al. 2016), and further details are described in Sect. 10.2 of this review; but it is unknown to what extent nutrients contributed to this variability. It can be hypothesised that maximum biomass yield

Table 10.2 Total C:N ratio, internal nitrate+nitrite concentrations (mM) and concentration factor (internal:external) of three kelp species (*Alaria esculenta, Laminaria solidungula, Saccharina latissima*) from Kongsfjorden sampled in July 2002. Standard deviations in brackets (n = 5)

	C:N	Internal nitrate + nitrite	Concentration factor
Alaria esculenta	23 (0.6)	1.9 (0.4)	4750
Laminaria solidungula	20.5 (0.9)	2.7 (1.3)	6750
Saccharina latissima	24.5 (0.1)	2.8 (1.4)	7000

Taken from Gordillo et al. (2006)

and later survival during the long nutrient-limited season could be influenced by the timing of the phytoplankton bloom; but this pelago-benthic connection remains to be investigated.

Only for a few weeks in early spring, seaweeds encounter optimal conditions, i.e. an increasing availability of light, an increase in water temperature and ample nutrient availability before phytoplankton blooms initiate depletion. This period coincides with the maximum growth rate for some seaweeds, especially the season responders such as *Saccharina latissima*, which grow when irradiance and temperature are optimal for the species (Wiencke et al. 2009), and, in contrast, the so-called season anticipators grow under short-day or even dark conditions in winter and spring. An extreme example is *Laminaria solidungula*, where phylloid expansion begins in early winter and continues through the spring (Chapman and Lindley 1980). Nitrate availability is claimed to regulate growth (Chapman and Craigie 1977) in both cases. However, the timing of the phytoplankton bloom and the connected nutrient depletion can be quite variable. The presence/absence of sea ice and the depth of vertical mixing are important factors for the onset of the spring phytoplankton bloom (Hodal et al. 2011; Hegseth and Tverberg 2013). According to Hegseth and Tverberg (2013), the influx of Atlantic water to Kongsfjorden directly determines these two factors, and blooms can be anticipated as early as April or may be delayed to the end of May.

On the other hand, a warmer Arctic implies an increased volume of meltwater from glaciers. This increased influence of meltwater is expected to reduce the spring phytoplankton bloom, leading to low biomass and small cell-size communities (Piquet et al. 2014), which may in turn have consequences in nutrient availability for seaweeds during spring and summer. The nutrient distribution between phytoplankton and seaweeds might determine further changes in the main routes of the Kongsfjorden food web as depicted by Hop et al. (2002) and quantified by Duarte et al. (Chap. 12).

In addition to a possible nutrient-derived inter-annual variability, it has to be taken into account that globally increasing temperatures will be a main driver in seaweed distribution also in Svalbard (Kortsch et al. 2012, Jueterbock et al. 2013) as already reported for kelp beds in West Greenland (Krause-Jensen et al. 2012) and Norwegian mainland fjords (Husa et al. 2014), but the interaction of temperature and nutritional regimes have been rarely investigated in polar seaweeds (Korb and Gerard 2000b).

10.4 From Stress Perception to Community Responses

10.4.1 Stress Sensing & Signal Transduction

Evidently, under field conditions a multitude of factors is shaping the physico-chemical environment of any species, and various abiotic drivers may or may not interact in a synergistic or antagonistic way. Thus, ecophysiological research on the consequences of environmental change needs to foster research on interactive effects, although these are complicated to assess. In order to reveal the molecular physiological bases of adaptive responses it is of particular interest to (1) discriminate between stress-specific vs. general stress responses and (2) characterise how environmental signals are perceived by kelps and transduced in order to trigger the respective physiological responses.

Algal growth, development, and reproduction are drastically affected by changes in temperature, humidity, salinity, irradiance (both PAR and UVR) and nutrient availability (Dring 1982; Davison and Pearson 1996; Gévaert et al. 2003; Gao and Xu 2010; Karleskint et al. 2010; Hurd et al. 2014). The expected increase in UVR as well as in atmospheric CO_2 (with concomitant ocean acidification) may increase (or repress) the effect of those stressors, and the response and strategies of adaptation and acclimation to the stressors must be studied. In order to survive, macroalgae must adequately respond to changes in the environment. In general, survival in constantly changing environments requires metabolic networks capable of detecting stress signals and transducing them to the nucleus of the cell. These stress response mechanisms must be rapid as well as strongly regulated.

Susceptibility or tolerance to abiotic stresses is coordinated by various genes (Sect. 10.4.2), which are switched on and off and may cross-talk with other components of stress signal transduction pathways. Overall, in the case of seaweeds, stress tolerance is a complex phenomenon because as sessile organisms, seaweeds may go through multiple stresses at the same time. Mitogen-activated protein kinases (MAPK) are a group of cytoplasmic phosphoproteins that constitute the central core of the signalling network to respond to stress in most organisms. These kinases are highly conserved serine/threonine kinases found in all eukaryotic cells in combination with their upstream activators (MAPK kinases and MAPKK kinases), forming a "signalling cascade". The kinases are phosphorylated and activated in a sequential way to the associated downstream protein kinase. In animals, the p38 and stress-activated protein kinase/c-Jun N-terminal kinase (SAPK/JNK) cascades are responsible for stress adaptation, whereas the extracellular signal-regulated kinase (ERK) cascade is involved in mitogenic stimuli and differentiation (Widmann et al. 1999).

Despite the fact that the study of signal transduction in algae is very recent, different studies with both macro- and microalgae (Jiménez et al. 2004, 2007; García-Gómez et al. 2012; Parages et al. 2012, 2013, 2014a, b) have clearly shown the presence of p38-, JNK- and ERK-like components in algae, as well as their crucial role in acclimation to stress and in cell division (Parages et al. 2014a, b), revealing that phosphorylation of p38- and JNK-like MAPKs occurs in Arctic kelps in response to increasing UVR exposure and temperature (Parages et al. 2013) as well as in intertidal seaweeds at the onset of emersion and during periods of the highest irradiation (Parages et al. 2014a, b).

In a recent study, Parages et al. (2013) demonstrated a differential behaviour of MAPK response to changes in the environment (temperature and UVR) in two Arctic kelps from Kongsfjorden. The endemic *Laminaria solidungula* presented phosphorylated JNK- and p38-like proteins at steady-state conditions (PAR at 2 °C), increasing after exposure to UVR and increased temperature (from 2 to 7 °C). In contrast, *Saccharina latissima*, a non-endemic species, showed a decrease in both JNK and p38 phosphorylation after temperature increase at any radiation condition, while UVR, as expected, also induced an increase in phosphorylation. In this species, p38 was more activated than JNK. The reason for this different response may be found in the fact that for *L. solidungula* an increased temperature to 7 °C was close to its upper tolerance limit due to its endemic character, while in the case of *S. latissima*, 2 °C was close to its lower tolerance limit (Fig. 10.4). The differential behaviour of p38 and JNK phosphorylation in response to environmental stress also occurs in intertidal macroalgae (Parages et al. 2014a) and in microalgae (Jiménez et al. 2004, García-Gómez et al. 2012). These authors have concluded after analysis of six species of intertidal Chlorophytes, Phaeophytes and Rhodophytes and two species of the microalga *Dunaliella* that phosphorylation of p38-like MAPK always preceded that of JNK-like MAPK during acclimation to stress.

Evidence of the physiological role of p38-like and JNK-like pathways in algae is provided by the use of highly specific inhibitors of the signalling pathways. Jiménez et al. (2004) and Parages (2012) have shown that inhibition of p38 or JNK phosphorylation in both micro- and macroalgae highly impaired acclimation under stressing conditions, eventually leading to cell death.

10.4.2 Gene Expression & Transcriptomics

In a second step, cells perceiving environmental signals respond with an up- or down-regulation of the expression of the appropriate genes, and regulation of gene expression plays a critical role in cellular differentiation, growth, development, as well as acclimation and adaptation to a variable environment in any organism (Rayko et al. 2010; Hurd et al. 2014).

Transcriptome profiling provides insights into an organism's response to changes in abiotic and biotic conditions, which helps to understand the physiological state of an organism across its range (Hofmann and Place 2007; Jamers et al. 2009). The availability of the first brown algal genome sequence (Cock et al. 2010) as well as the improvement and decreasing costs of high throughput sequencing gave rise to several *de novo* transcriptome-sequencing studies in kelps. Hence, transcriptomes of *Saccharina japonica*, *Saccharina latissima*, and *Macrocystis pyrifera* are now available among others (Heinrich et al. 2012a; Konotchick et al. 2013; Sun et al. 2014; Wu et al. 2014). Nevertheless, studies on comparative genome-wide gene

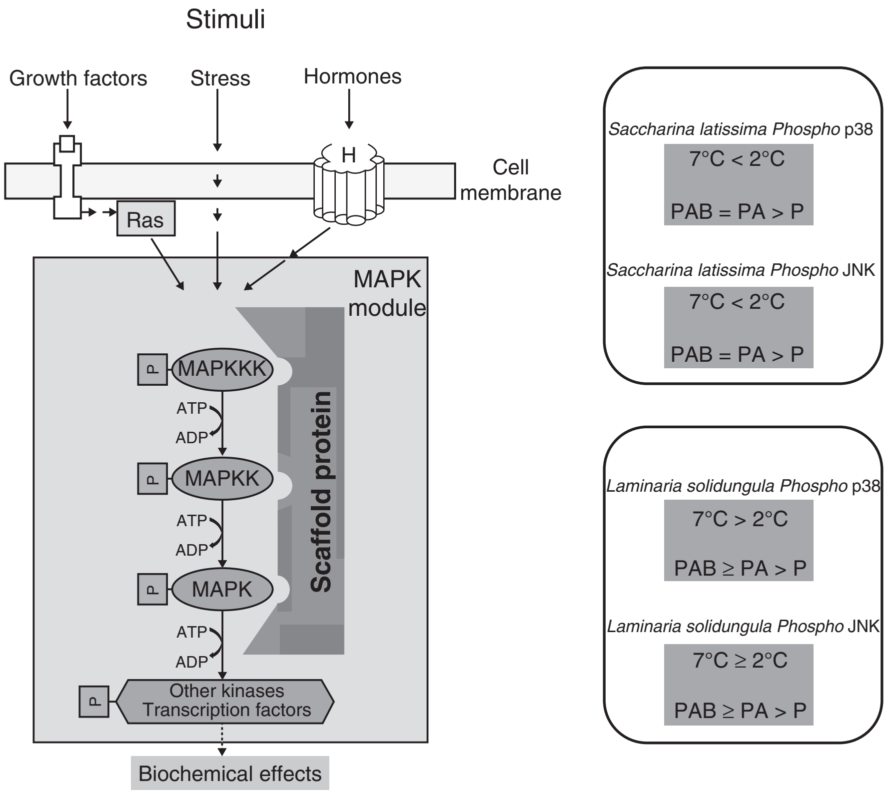

Fig. 10.4 General description of a MAPK module, with indication of its activation from the external stimuli to the biochemical effects (left panel). Ras refers to a family of GTPase proteins, which when activated by an external signal subsequently activate other proteins downstream in the signal cascade by phosphorylation. Right panel: Summary of a case study of the activation of p38 and JNK in *Saccharina latissima* (top) and *Laminaria solidungula* (bottom) in response to increased temperature (from 2 to 7 °C) and UVR (5.01 W m^{-2} UVA and 0.48 W m^{-2} UVB). (Re-drawn and modified from Krauss (2008) and Parages et al. (2013))

expression profiling in kelps, e.g. examining expression profiles under changing abiotic factors or across geographical gradients, are still scarce. Heinrich et al. (2012b, 2015) investigated gene expression under multiple abiotic stressors in *Saccharina latissima*; Konotchick et al. (2013) analysed four *Macrocystis pyrifera* transcriptomes across the water column and seasons. Another two studies compared transcriptomes of *Saccharina japonica* under specific light quality in order to examine light regulated gene expression (Deng et al. 2012; Wang et al. 2013).

In genome-wide gene expression studies of *Saccharina latissima* from Kongsfjorden, Heinrich et al. (2012b, 2015) analysed gene expression profiles in response to different combinations of PAR, UVR and temperatures. Furthermore, a study on comparative gene expression analysis in field vs. laboratory-grown sporophytes was carried out. These studies showed that *S. latissima* responds to abiotic stress with a multitude of transcriptional changes, and high temperature and high PAR had stronger effects on gene expression than low temperature and low light. These results are in agreement with physiological studies showing that *S. latissima* is well adapted to low temperature and low light conditions (Bolton and Lüning 1982; Dunton 1985; Davison and Davison 1987; Hanelt 1998). Main temperature effects on the molecular level were induction of genes associated with the glycine, serine and threonine metabolism in response to low temperature, and repression of transcripts encoding carbohydrate biosynthetic and catabolic processes at high temperature. A crucial acclimation process to high PAR in *S. latissima* constitutes regulation of photosynthesis, e.g. induction of components of photosystem I/II, thylakoid proteins, as well as regulation of light-harvesting complex proteins (LHCs). The molecular data support former studies, showing that changes in light availability and temperature, as well as the age of the thalli, influence the pigment content and composition in *S. latissima* (Davison et al. 1991; Machalek et al. 1996; Hanelt et al. 1997). In addition, high PAR caused induction of catabolic processes for energy supply, heat shock proteins and ROS (reactive oxygen species) scavenging enzymes. The regulation of various ROS scavenging enzymes in response to multiple stressors demonstrates the crucial role of ROS metabolism in acclimation to abiotic stress in *S. latissima.* Here, the molecular data indicates a compartment-specific regulation of ROS defence. Another critical component of the molecular acclimation mechanisms to excessive light in *S. latissima* seems to be the induction of the vitamin B_6 metabolism. Vitamin B_6 exhibits antioxidant activity comparable to that of vitamins C and E. For this reason, Vitamin B_6 is suggested to play an important role in protecting cells from oxidative stress (Ehrenshaft et al. 1999). Gene expression profiling in *S. latissima* showed that acclimation to UVR includes enhanced regulation of genes encoding photosynthetic components and ROS scavenging enzymes, short acclimation to UVR furthermore comprises enhanced regulation of DNA replication and DNA repair. The combination of the stressors through high PAR, and UVR caused interactive effects on photosynthesis and gene expression (Fig. 10.5). The combination of high temperatures with high light intensities caused the strongest response and proved most harmful for the alga, leading to strong repression of crucial metabolic processes, e.g. photosynthesis and amino acid metabolism. Comparisons of gene expression profiles in field and cultivated sporophytes of *S. latissima* showed that principal effects of UVR were similar in culture and field sporophytes, indicating that laboratory experiments are well suited for investigating basic molecular mechanisms of acclimation to abiotic stresses. However, field material of *S. latissima* reacted less strongly than laboratory cultures, i.e. by a lower number of regulated genes, indicating that the severity of transcriptomic responses in the field may be over-estimated from laboratory experiments (Heinrich et al. 2016).

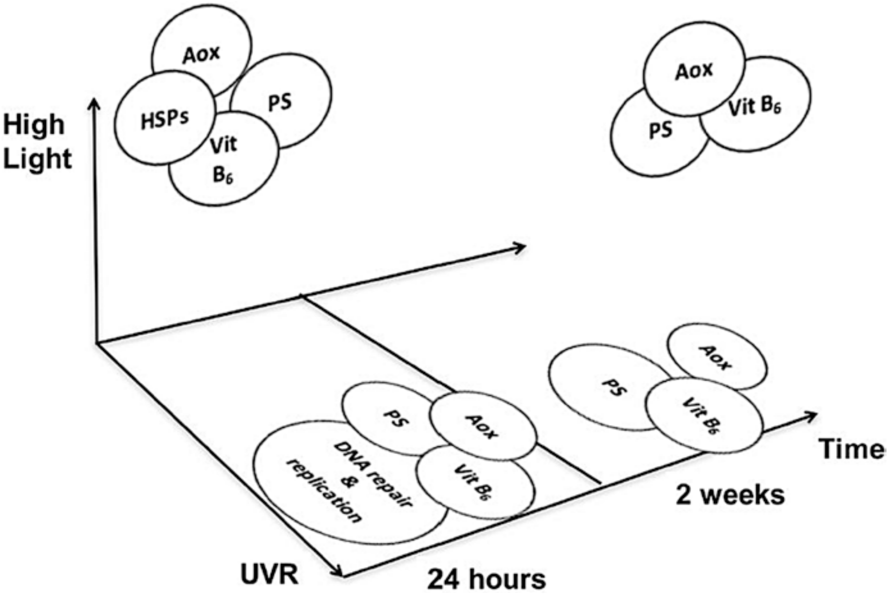

Fig. 10.5 Main molecular acclimation processes in *Saccharina latissima* induced by high PAR and UVR (*Aox* Antioxidative enzymes, *HSPs* heat shock proteins, *PS* photosynthesis, *Vit* B_6 vitamin B_6 metabolism. (Compiled from Heinrich et al. 2012b, 2015))

10.4.3 Eco- and Stress Physiology

Genetic control provides the frame for physiological responses in an altered environment. Depending on their response time and the extent of metabolic and genetic change required, those adaptive reactions are distinguished as regulation (as an immediate response), acclimation (as an adjustment in physiology being active over days or weeks) or adaptation (over multiple generations and requiring changes in the genome; Hurd et al. (2014)). Beyond the limitations of such acclimatory reactions, virtually any physico-chemical variable may provoke (transient or chronic) physiological stress, which may ultimately result in cellular damage or death of the individual. In order to use physiological responses as a proxy for kelp susceptibility under climate change scenarios, a multitude of combined field and laboratory experiments has been conducted at Kongsfjorden. Field-collected samples reveal the current adaptive state of an organism at its specific growth site, while lab experiments are suitable to unravel the limits of acclimation and the interaction of multiple stress factors (Fredersdorf et al. 2009). The priority of ecophysiological research on kelps of Kongsfjorden has been placed on photophysiology, i.e. light utilisation, photoinhibition and susceptibility to ultraviolet radiation. Photosynthetic performance is widely used as an indicator for plant fitness, as virtually all kinds of physico-chemical stressors will ultimately affect proper photosynthetic functions. This is frequently connected to the generation of reactive oxygen species (Bischof and

Rautenberger 2012), which may result in the photooxidation of cellular components but is also considered as part of signal transduction pathways (Mackerness et al. 1999). Thus, the investigation of the reactive oxygen metabolism and its significance for the sensing of and release from abiotic stress remains a relevant research task also in Arctic kelp species.

With respect to kelp photophysiology, the responses to different irradiances of PAR and the effect of ultraviolet radiation should be carefully distinguished. As both spectral ranges may induce quite different genetic responses (see Sect. 10.4.2), also the physiological effects in response to high irradiances of both differ largely. However the phenological outcome, i.e. the inhibition of photosynthetic primary reactions, may be quite similar (Bischof et al. 2002a). In this respect, rapid and sometimes superficial assessments of photosynthetic performance of kelps should be carefully evaluated. The widely used non-invasive and fast measurement of maximal quantum yield of photosystem II by monitoring pulse-amplitude modulated chlorophyll fluorescence provides a good indicator of the efficiency of energy transfer from photosynthetic antenna systems to the reaction centres and may thus be used as an easy-to-measure fitness indicator (Schreiber et al. 1994). However, sole measurements of maximal quantum yield (the ratio of variable to maximum fluorescence; Fv/Fm) do not allow for any interpretation on the physiological bases of observed changes. In general, observing the *dynamics* of change in Fv/Fm is much more insightful, particularly as restored Fv/Fm values after a stress event indicate recovery (Hanelt 1998). Observing the dynamics of recovery allows for discrimination of damaging versus regulatory processes in kelp physiology, which are both associated with more or less transient reductions in Fv/Fm.

From the multitude of investigations conducted on photosynthetic responses of kelp sporophytes from Kongsfjorden, the most striking findings are highlighted below:

With respect to the impact of PAR (without UV), most of the kelps show a remarkable regulatory ability to respond to transient high light stress by dynamic photoinhibition (Hanelt 1998). This phenomenon is related to the depth distribution of the respective species and, thus, represents an adaptive feature to the *in situ* light climate. Overall, the depth gradient as a determinator of underwater light availability (Hanelt et al. 2001) is an effective modulator of kelp photosynthetic efficiency, capacity and UV-susceptibility (Bischof et al. 1998a, b). It has also been shown that photosynthesis in the winged kelp *Alaria esculenta* can be “hardened” against the harmful impact of UVR within 3–5 days by repeated exposure to moderate irradiances of UV (Bischof et al. 1999). Such increase in UV-tolerance can also be observed in *Saccharina latissima* as part of its acclimation towards a seasonally changing radiation climate, as specimens displayed high UV-susceptibility when collected early in spring under the sea ice, and progressively increased tolerance towards the summer (Bischof et al. 2002b). Thus, overall UVR sensitivity among different Arctic kelp species is related to their depth distribution (see Sect. 10.2) and corresponding light history at the respective depth (Wiencke et al. 2000, 2006; Roleda et al. 2006d, 2010).

Evidently, other environmental factors, such as temperature, do modulate stress responses and may either act synergistically, but also in an antagonistic way. For example, it has been shown that temperatures up to 13 °C (well above the ambient SST in Kongsfjorden) may compensate for inhibitory UV-effects of maximal quantum yield in *Alaria esculenta* (Fredersdorf et al. 2009). This becomes understandable when taking into account the geographic spread of *A. esculenta* with a Southern distribution limit in Brittany, which implies that the population at Svalbard currently still thrives under permanent suboptimum temperatures. Overall, by linking our knowledge on stress perception (Sect. 10.4.1), gene expression (Sect. 10.4.2) and individual ecophysiology (this section) we already receive a quite complete picture on the wide range of mechanisms and capacity of acclimatory features applied by kelps in order to respond to and endure in a changing environment. Conclusively, it is likely that those kelps, which populate Kongsfjorden and have their main distribution in somewhat lower latitudes, will rather perform better under scenarios of temperature increase in the Arctic (Krause-Jensen and Duarte 2014). This is also suggested in the modelling study by Müller et al. (2009a), which, based on a combination of temperature tolerance data and predictions of changes in sea surface temperature, implies future northern range expansion and increased productivity of those kelp species inhabiting Kongsfjorden. In contrast, for the endemic, and strictly cold-adapted kelp *Laminaria solidungula* a retreating distributional range is very likely.

The above-mentioned studies have been mostly conducted on the adult, sporophyte phase of kelps. As we will see below, other developmental stages of kelp, and in particular the microscopic spores, may reveal specific and pronounced differences in stress susceptibility (Sect. 10.4.5). Although the multitude of ecophysiological studies have considerably advanced our understanding of the mechanisms of functional responses of kelps towards most abiotic stressors, still such studies do not allow for evaluating the capacity for adaptation. Studying adaptation in macroorganisms is tricky business, as genetic adjustments need to be studied over a series of generations. Thus, the central question of whether adaptive adjustments in kelp physiology keep up with the pace of environmental change remains to be addressed.

10.4.4 Cellular Ultrastructure

Investigation of the cellular structure of different life history stages of kelps is vital to understand development and survival of the species. Already 50 years ago electron microscopy was used to describe cellular features of brown algae, firstly from temperate regions (Bouck 1965). However, to our knowledge, detailed analyses of cellular structures of kelp thalli from Kongsfjorden have been made only for *S. latissima* (Hanelt et al. 1997; Holzinger et al. 2011) and *A. esculenta* (Lütz et al. 2016). In case of *Laminaria hyperborea* from Helgoland (Steinhoff et al. 2008) and *S. latissima* from Kongsfjorden (Steinhoff et al. 2011a), the ultrastructural features of zoospores and developing gametophytes have been characterized. Despite the species-specific growth habits of the adult sporophytes, the ultrastructure of the spores shares several general features: one chloroplast per cell, a large and dominating nucleus, large lipid globules, dictyosomes and several small mitochondria. The fate of the lipid storage was followed in spores from *S. latissima* from Kongsfjorden during development into gametophytes (Steinhoff et al. 2011a). The lipid globules changed electron density during spore germination, which could be explained by changes in fatty acid composition. The turnover of lipid material continued until the chloroplasts took over most of the energy formation. The few small physodes, vesicles containing the phenolic compound phlorotannin, did not change under applied UV-stress, but major changes were described for the nucleus. Whether physodes in this stage of development are able to protect from UV-stress remains unclear as *A. esculenta* spores from Kongsfjorden may exudate phlorotannins to the surrounding medium as a photo-protective feature. Additionally, the cellular physodes are unevenly distributed in the cells and may thus only marginally protect against UV radiation (Wiencke et al. 2007).

Most physiological studies were performed with the fully developed phylloid, preferentially to follow different photosynthetic activities and to perform analyses of e.g. proteins and other constituents. A light microscopic overview for *A. esculenta* is given in Lütz et al. (2016) showing the typical anatomical structure of leathery thalli of brown algae. A similar tissue organization can be found in *S. latissima* from Kongsfjorden (Holzinger et al. 2011), but also in *Ecklonia radiata* from Australia (Lüder and Clayton 2004) or *Sargassum cymosum* from Brazil (Polo et al. 2014). Figure 10.6a shows for *A. esculenta* the meristodermal layer with smaller cells containing most of the plastids, and thick outer walls. Frequently dictyosomes appear, often close to the nuclear envelope (Fig. 10.6c), which was already marked by Bouck (1965). Less often lipid droplets (Fig. 10.6d) can be seen. An effective compound transport can be assumed by the regularly visible plasmodesmata (Fig. 10.6e,f) as suggested also for *S. latissima* and *L. hyperborea* (Schmitz and Kühn 1982).

The ultrastructure does not change in samples taken from a depth range of 3–10 m (own observations), but further studies of possible depth influence are required because, especially, the light regime changes drastically. Neither in *S. latissima* nor in *A. esculenta* could we observe any aggregated material for protein- or carbohydrate-storage (comparable to starch grains or protein crystals). When carbohydrate storage occurs, an amorphous accumulation of laminaran e.g. in the vacuoles of medulla or cortex cells may be assumed. The cortex cells contain only few plastids and the inner medulla is free of most organelles. Based on the number of organelles in the cells visible by transmission electron microscopy (TEM), one can estimate that roughly 90% of the metabolic, especially photosynthetic, activity takes place in the meristodermal layer and the adjacent outer layer of the cortex.

Under exposure to elevated UVA plus UVB radiation only chloroplasts show a response in ultrastructure, while all other cell organelles remain unchanged at least in membrane appearance (Holzinger and Lütz 2006; Holzinger et al. 2011; Lütz et al. 2016). An example of disturbed thylakoid structure under PAR+UVA/B is given in Fig. 10.6b. Such membrane dilations are a typical, but not a specific sign of UV-damage. Other stresses like copper on *S. latissima* (Brinkhuis and Chung 1986),

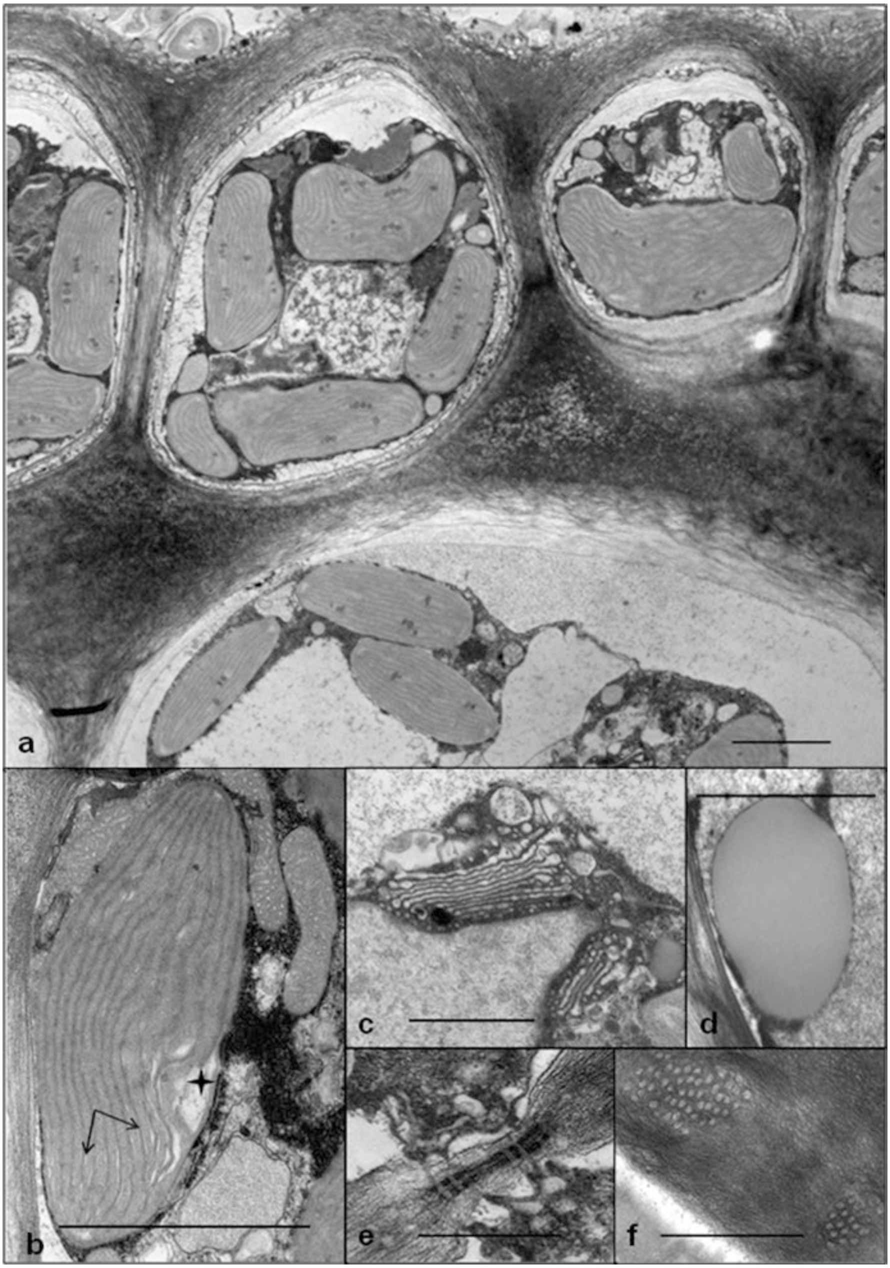

Fig. 10.6 Ultrastructure and cellular details of *Alaria esculenta* from Kongsfjorden. (**a**) Part of the meristodermal layer and a large cortex cell of the phylloid. (**b**) Thylakoid dilations after PAR+UV--A/B treatment (arrows). Star: DNA region of the plastid. The large mitochondria remain unaffected. (**c**) Two dictyosomes flanking a part of the nucleus, a constellation frequently observed. (**d**) Lipid droplet, probably containing neutral lipids because of the greyish staining. (**e, f**) Plasmodesmata between meristodermal cells shown in two different section planes. For details on sample preparation and transmission electron microscopy (TEM) methods see Lütz et al. (2016). Scale bars: a, b, d: 2 µm; c: 1 µm; e, f: 500 nm

or SO_2 on higher plant leaves (Schiffgens-Gruber and Lütz 1992), generate comparable membrane damage as well. The interpretation of UV-effects is difficult on the ultrastructural level, because the phylloid is mostly exposed to a solar input of diffuse and scattered radiation at the growth site and not in a more or less perpendicular angle like in simulation experiments.

Nevertheless, UV-effects in simulation studies on ultrastructure and photosynthetic parameters as well as recovery experiments have shown that algae from shallow waters can be affected, but not in a lethal way, i.e. for *A. esculenta* and *Saccorhiza dermatodea* (Bischof et al. 1998a, Wiencke et al. 2004, Roleda et al. 2006a). In contrast kelp species from deeper sites like *L. solidungula* or *S. latissima* may be seriously affected not only by higher short-wave, but also by higher PAR exposure (Karsten et al. 2001; Wiencke et al. 2004, 2006; Roleda et al. 2010; Bischof and Steinhoff 2012).

The interpretation of the role of physodes and similar phlorotannin containing, often globular structures, is connected with the question whether UVR results in a stress or a strain. Larger physodes can easily be detected by light microscopy after staining, like in Holzinger et al. (2011) for *S. latissima* from Kongsfjorden. Their cellular distribution can only be viewed in TEM and is well described for a number of brown algae (Schoenwaelder 2002; Lüder and Clayton 2004). Often the role of physodes is interpreted as an effective UV-shield, because their molecular properties support this idea. However, their uneven and in general not surface-oriented distribution in the thallus cells does not underpin a primary shielding function. Recently, Halm et al. (2011) showed for *L. hyperborea* that phlorotannins are inducible by PAR alone, and by PAR + UVA/UVB radiation, which points towards their function as photoprotective compounds. In addition, phlorotannins are induced by mechanical wounding to simulate herbivory (see also Amsler and Fairhead 2006).

In the cytological studies with *S. latissima* and *A. esculenta* (Holzinger et al. 2011; Lütz et al. 2016) no UV-dependent changes in amount or localization of physodes or putative phlorotannin containing vesicles could be found. Even in the sensitive stage of zoospore formation, UV does not induce phlorotannin accumulation in Arctic Laminariales (Steinhoff et al. 2008; Müller et al. 2009b), but induction phenomena and a possible multiple role of physodes deserve more detailed investigations.

When studying the meristodermal layer e.g. in case of *A. esculenta* it was surprising that larger areas of the outer cell wall show many, and structurally very different, biota (Fig. 10.7). From size and structure of these attached organisms it may be assumed that they are bacteria or small fungi. The occurrence of such biota on brown algae, but also other marine algae worldwide, is summarized by Friedrich (2012) and by Potin (2012). In Fig. 10.7 (c, d), the arrows point to many small physode like globules which accumulate in the cell wall opposite to the "epiphytes". Other globules can be found outside the cell wall close to these organisms, and the meristodermal cells contain large amounts of phlorotannins. Similarly, Schoenwaelder and Clayton (1998) describe for zygotes from Australian brown algae, that physodes "are secreted into the primary zygote wall", and Schoenwaelder (2002) mentioned reports about physodes in the cell wall of brown algae. As is dis-

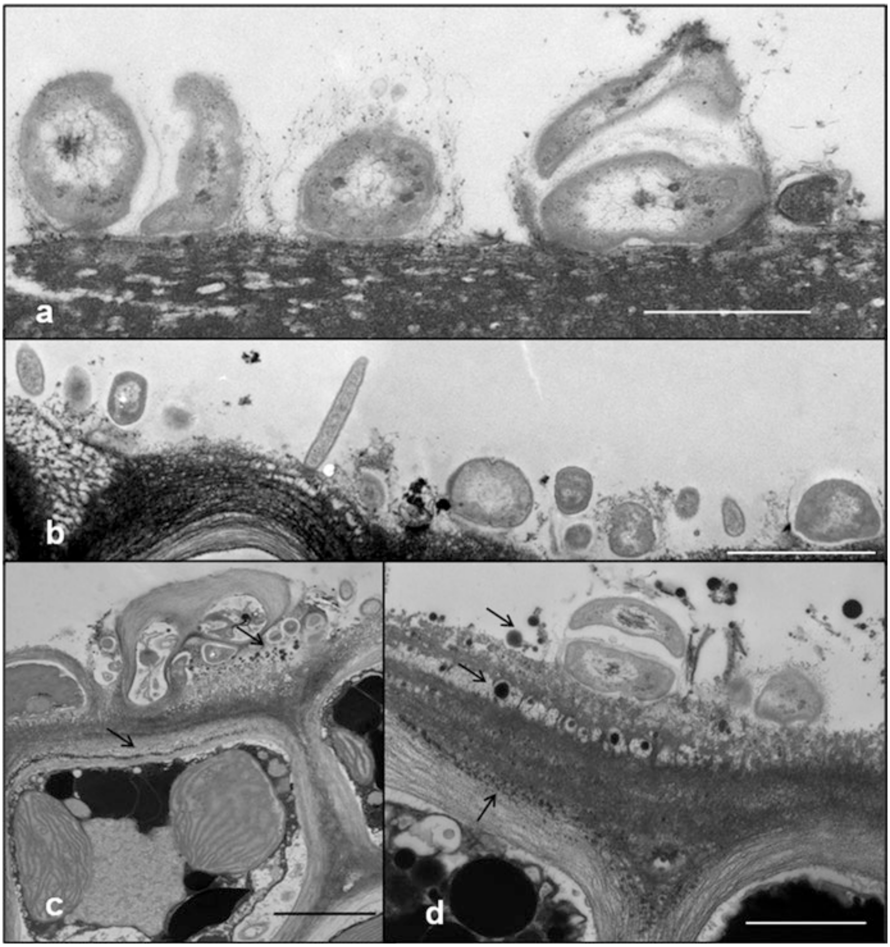

Fig. 10.7 Different appearances of microbial organisms growing on or adhering to the thallus surface of *Alaria esculenta*. Species identification was not possible. Arrows (**c**, **d**): accumulation of phlorotannin like material in the outer cell wall and in the matrix outside. Scale bars: **a** 0,5 µm; **b, d** 1 µm; **c** 2 µm

cussed in Lütz et al. (2016), one important role of phlorotannins may be reduction of such probably pathogenic microbial activities. This supports the findings of Amsler and Fairhead (2006) discussing phlorotannins as defence compounds. A related aspect is presented by Lüder and Clayton (2004), Halm et al. (2011) and Falkenberg et al. (2014), who defined the role of phlorotannins as protectors against herbivory.

Figure 10.7 indicates another interesting structural aspect: several of the small bacterial-like structures or the phlorotannin globules do not have any visible connection to the cell wall. Normally, they would have been removed completely by the numerous washing and incubation steps during fixation for TEM, if they were only slightly attached. We, thus, assume the presence of a non-stainable thin matrix outside the cell wall, which is probably stabilized by glutaraldehyde crosslinking (proteins) fixation. Here further studies are required.

Other open questions regarding the structural features of kelp species are, whether strong changes in salinity induced by glacier melting, enhanced oxidative stress loads or the winter situation change tissue and cellular internal structures, either as adaptation or in a possible deleterious way.

10.4.5 Impacts of Stress on Various Developmental Stages, Tissue Types, and Implications for Growth & Reproduction

The reaction of kelps to the abiotic variables, which finally determine their performance (fitness) in the ecosystem, depends on the balance between the stimulating and inhibiting effects of the diverse environmental variables. In this respect, growth and reproduction are key parameters integrating responses of the various molecular and physiological mechanisms described above to changes in the abiotic environment.

The heteromorphic life-cycle of kelps has been introduced in Sect. 10.1 and basically entails the macroscopic and diploid sporophyte producing haploid spores to give rise to the microscopic and haploid gametophytes, which produce gametes. Once released, these fuse to form a zygote, from which the sporophyte develops. It is evident, that all these different generations and developmental steps are under control of the physical environment and may all have individual optimum conditions.

Arctic and cold-temperate seaweeds experience pronounced seasonal changes in water temperature, light quantity and quality. A species' physiological optimum and upper survival temperature are known to be higher than in its natural environment. For example, the optimum quantum yield of meiospores' photosynthesis of various Arctic kelp species was maximal between 7–13 °C and lowest at 2 °C (Roleda 2009). Gametophytes of Arctic to cold-temperate species survive temperatures of 19–20 °C (tom Dieck 1993). For the diploid life stage, growth rates of endemic Arctic *Laminaria solidungula* sporophytes were comparable at 0 °C, 5 °C and 10 °C (Wiencke and Fischer 1990); the main difference is that growth under 0 °C is saturated already at lower light intensity (20 μmol photons m^{-2} s^{-1}) compared to 5–10 °C (55–60 μmol photons m^{-2} s^{-1}). Growth of the sporophyte of this species is possible up to 15 °C, the upper survival temperature (UST) is 16 °C (tom Dieck 1992). Sporophytes of *S. latissima* and *L. digitata* grow between 0 and 20 °C and exhibit UST's of 20 or 21 °C (Wiencke et al. 1994).

At the other end of the spectrum, most species of the Arctic and cold-temperate gametophytes tested were able to survive the lowest tested survival temperature of 0–1 °C for more than a year of total darkness (tom Dieck 1993). The sporophytes of endemic Arctic *L. solidungula* are also able to survive 7 months of continuous darkness with positive but minimal growth (Henley and Dunton 1997). High PAR in excess to their photosynthetic requirement can also be damaging. Gametophytes of the Arctic - cold-temperate *L. digitata* are less sensitive to high PAR (500 µmol photons m^{-2} s^{-1}) compared to corresponding sporophytes (Hanelt et al. 1997). Relative to the age and size class of the sporophytes, the capacity to cope with high PAR increases with increasing age of the thalli (Hanelt et al. 1997).

The effects of UVA and UVB radiation on growth have been studied in various kelps from Kongsfjorden. Growth rates in *Laminaria digitata*, *Saccharina latissima* and *Saccorhiza dermatodea* collected in the field and exposed in July at the water surface are significantly inhibited by UVR. There was, however, no significant difference between individuals exposed to PAR (P), PAR + UVA (PA) and PAR + UVA + UVB (PAB) and full solar radiation (Aguilera et al. 1999). In contrast, this effect was demonstrated by Michler et al. (2002) in *Alaria esculenta* in the laboratory. The effect of PA was relatively small, however, additional UVB resulted in a considerable reduction of the growth rate. The effect of PA was much stronger in the undergrowth- and deep-water species *L. solidungula,* compared to the more sunlight-adapted *A. esculenta.* Additional UVB led to tissue necrosis after only a few days of exposure indicating for the first time that the effect of UVR on growth may be correlated to depth distribution.

Similar results were obtained by Roleda et al. (2005a, 2006b): Growth rates of very small sporophytes (initial size 30 mm^2) exposed to PAB in the laboratory decreased successively from *A. esculenta*, over *L. digitata* and *S. latissima* to *L. solidungula* (Fig. 10.8). Interestingly, a considerable acclimation potential was found in *A. esculenta* and *L. digitata*. This pattern closely corresponds to the depth

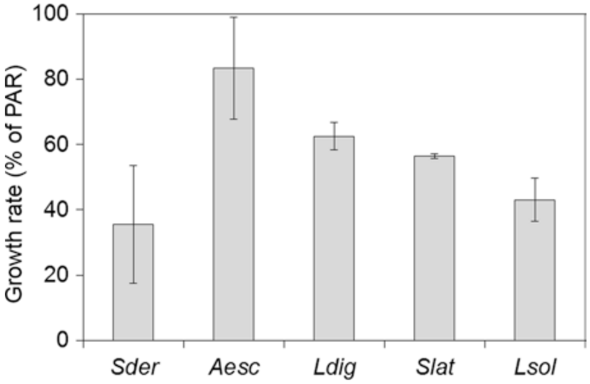

Fig. 10.8 Growth rates of juvenile Arctic kelp species under the full radiation spectrum (PAR+UVA+UVB) expressed as percent of their respective PAR controls. Species are *Saccorhiza dermatodea* (*Sder*), *Alaria esculenta* (*Aesc*), *Laminaria digitata* (*Ldig*), *Saccharina latissima* (*Slat*) and *Laminaria solidungula* (*Lsol*) grown under 8 °C and 16:8 light-dark photoperiod of 3.6 W m^{-2} PAR, and 6 hours UVR in the middle of the light phase consisting of 4.92 W m^{-2} UVA and 0.41 W m^{-2} UVB. Bars are means (n = 3; ±SD). (Compiled and modified from Roleda et al. 2005a, 2006b))

distribution described for this time period by Hop et al. (2012; see Sect. 10.2) and corresponds to results obtained on three kelp species from Helgoland (North Sea; Roleda et al. 2006c). The only species not fitting into this pattern is *S. dermatodea* (Fig. 10.8). This species exhibits the lowest growth rate of all species under the full radiation spectrum although it occurs together with *A. esculenta* and *L. digitata* in shallow waters. So this species obviously takes a loss when exposed to excessive PAB in shallow waters. On the other hand germinating spores of this species are extremely tolerant to PAB as we will see below.

Spores are the life-history stage of kelps most susceptible to environmental perturbations. Relative to light quality, the early life-history phases of kelps are also more susceptible to UVR compared to their respective adult life stages (Roleda et al. 2007; Fredersdorf et al. 2009). When exposed in the laboratory to PA, spore germination of kelps from southern Spain, Helgoland and Kongsfjorden was inhibited considerably, and after exposure to additional UVB even more so (Wiencke et al. 2000, 2004; Roleda et al. 2005b). The degree of inhibition was highest in deep-water and undergrowth species. The species from Kongsfjorden strongly affected by PAB were *L. solidungula*, *S. latissima* and *L. digitata* (Wiencke et al. 2004; Roleda et al. 2010). In contrast, *A. esculenta* and *S. dermatodea* were much less affected by exposure to the full spectrum (Wiencke et al. 2004, 2007, Roleda et al. 2006a) and there was a potential for recovery from PAB-induced damage during post culture without UVR in *A. esculenta*. In *S. dermatodea,* Wiencke et al. (2004) demonstrated even a full recovery. Again, this pattern mirrors quite nicely the depth distribution described by Hop et al. (2012; Sect. 10.2).

Direct comparison between mature and young field-collected Arctic *Saccharina latissima* and meiospores released from fertile samples, showed highest sensitivity to PAR and PAR+UVR in meiospores and lowest in mature sporophytes compared to control (dim white light; Fig. 10.9). However, positive carry-over effects from reproductive adults inhabiting high-UV environments onto the next generation of meiospores have been reported among kelps. Meiospores of kelps released from adults growing under low-UV environments are more susceptible to UV-stress experiments in the laboratory compared to progeny of adult kelps from high-UV environments (Swanson and Druehl 2000). This indicates ecotypic acclimation and adaptation under high-UV environments (Hanelt and Roleda 2009).

In field experiments, the tolerance of spores to the full solar spectrum was highest in the shallow water species *S. dermatodea*, intermediate in the upper to mid sublittoral *A. esculenta* and lowest in the upper to mid sublittoral *L. digitata* (Wiencke et al. 2006). Unexpectedly, there was no difference in the susceptibility of spores exposed to ambient solar radiation compared to solar radiation depleted of UVB, as known from laboratory experiments. Nevertheless, UVR tolerance is a major, probably even one of the most important factors determining the upper distribution limit of kelps on the shore (Bischof et al. 2006). This becomes particularly obvious when comparing the relationship between effective UVB dose and germination rate (Fig. 10.10).

However, the UVR susceptibility of spores changes seasonally. Steinhoff et al. (2011b) demonstrated a strong inhibition of spore germination in *S. dermatodea*

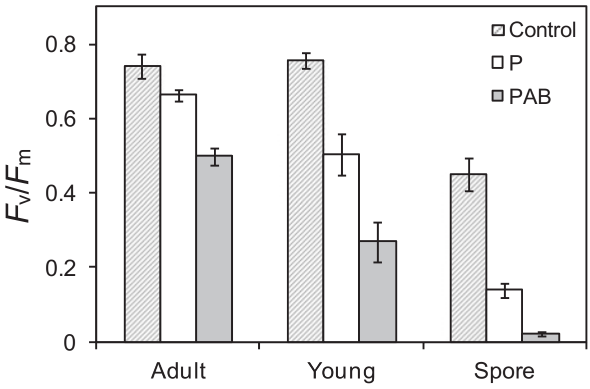

Fig. 10.9 Optimum quantum yield of photosynthesis (Fv/Fm) of *Saccharina latissima* vegetative sporophytes (adult and young) and meiospores released from fertile samples after 2 hours exposure under PAR (P) and PAR+UVA+UVB (PAB) at 2 °C. PAR = 22 μmol photons m^{-2} s^{-1}, UVA = 6 W m^{-2}, UVB = 0.45 W m^{-2}. Control = 4 μmol photons m^{-2} s^{-1}. Bars are mean ± SD (n = 6). (Roleda, Gómez and Huovinen, unpublished data)

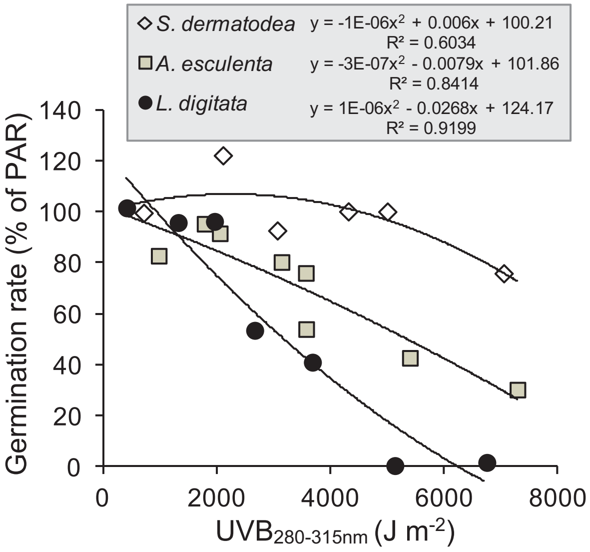

Fig. 10.10 Dose-response curves for *Saccorhiza dermatodea*, *Alaria esculenta* and *Laminaria digitata*. Germination rate under PAR+UVR expressed as percent of PAR after exposure of spores to *in-situ* radiation at different depths in Kongsfjorden. Figure modified from Wiencke et al. (2006); $UVB_{280–315nm}$ dose calculated after McKenzie et al. (2004). $UVB_{280–315\ nm}$ doses needed to achieve 50% inhibition of germination are >7550 J m^{-2}, 5285 J m^{-2} and 3156 J m^{-2} for *S. dermatodea*, *A. esculenta* and *L. digitata*, respectively

exposed to ambient solar radiation in August. This contrasts sharply to the results obtained in the above mentioned field study by Wiencke et al. (2006), who found no differences between the germination under solar radiation depleted of UVR and the full solar spectrum even at the low water depth of 0.5 m. Similar seasonal changes in the UVR susceptibility of kelp spores were found also in laboratory experiments with kelps, especially in studies investigating the interactive effects of environmental variables (see below).

Besides UVR, also temperature has strong effects on germination. Spores of *S. dermatodea*, *A. esculenta*, *L. digitata* and *S. latissima* germinate optimally at temperatures between 2 and 12 °C. Exposure to 17 °C inhibits spore germination slightly in *S. dermatodea* and 18 °C is lethal for the latter three species (Müller et al. 2008; Steinhoff et al. 2011b).

The interactive effects of elevated temperatures and UVR have been examined in several studies. Germination of spores from *S. dermatodea* was not inhibited by PAB at 2, 7 and 12 °C, but it was quite strongly inhibited at 17 °C (Steinhoff et al. 2011b). Similarly, spore germination of *A. esculenta* was not inhibited by PAB at 2 and 7 °C in May (Müller et al. 2008). In July, however, spores of this species exhibited a higher PAB susceptibility at 2 °C compared to 7 °C (Olischläger and Wiencke 2013). At 12 °C, and especially at 16 °C, germination was inhibited in this species after PAB exposure (Müller et al. 2008; Fredersdorf et al. 2009). Germination of *L. digitata* spores was very strongly inhibited under PAB exposure at 2 °C both in May and in July to September (Müller et al. 2008; Olischläger and Wiencke 2013). At 7 °C, no inhibition of germination was recorded in May (Müller et al. 2008), whereas in July to September germination was inhibited by about 50–80% in this species (Olischläger and Wiencke 2013). A comparable degree of inhibition was also demonstrated at 12 °C in May (Müller et al. 2008).

Salinity, as another important environmental variable influencing spore germination, has been tested in *A. esculenta* (Fredersdorf et al. 2009). At 16 °C, i.e. at a temperature close to the upper survival limit, germination of spores exposed to P was considerably, although insignificantly, inhibited at a salinity of 20. Exposure to 16 °C, salinity of 20 and PA or PAB resulted, however, in strong and significant inhibitions of germination. In summary, the responses of spores to environmental perturbations depend on the type of perturbation (radiation regime, temperature, salinity and probably other factors) as well as on the season.

When early developmental phases of kelps i.e. meiospores and microscopic sporophytes are subjected to environmental stressors, e.g. low light, low nutrients, high temperature, and UVR (e.g. Gerard 1997; Roleda et al. 2006d; Roleda 2009), the stressed samples are photoinhibited and have reduced growth rates. However, when they were allowed to recover and cultivated under control or optimal conditions, cells and sporophytes are able to recover their photosynthetic functions and growth rates are comparable to the control group (Gerard 1997; Roleda et al. 2006d; Roleda 2009). Despite the higher susceptibility of early life-history stages to environmental stressors, they are also capable of rapid recovery without negative effects persisting into the later developmental stages when the stress factors are eliminated (Gerard 1997). However, chronic and long-term exposure of juvenile kelp sporophytes to

UVR caused morphological damage such as tissue lesions, blistering and deformation, and necrosis (Michler et al. 2002; Roleda et al. 2004), despite photosynthesis of sporophytes being able to acclimate to UVR (Roleda et al. 2004).

Sporogenic and vegetative tissue of Laminariales exhibit distinctive sensitivity to UVR (Gruber et al. 2011; Holzinger et al. 2011). Less DNA damage was observed in soral compared to non-soral tissue (Gruber et al. 2011). This could be explained by the presence of phlorotannin-containing paraphysis cells in soral tissue (see Sect. 10.4.4). These cells are found towering over the sporangia and shielding the meristoderm from UVR, thus offering protection to the UV-sensitive meiospores and different organelles e.g. mitochondria, golgi bodies, and nucleus, respectively (Holzinger et al. 2011). Moreover, soral tissues have 3× higher antiradical power (ARP) capacity compared to non-soral tissue (Holzinger et al. 2011). Among juvenile sporophytes, the susceptibility of vegetative tissue to UVR depends on thallus thickness and optical density (Roleda et al. 2005a, 2006b); whereby thinner and translucent thalli incur more DNA damage compared to thicker and highly pigmented tissue (Roleda et al. 2007).

10.4.6 Biotic Interactions Affecting Kelp Performance

The presence of an adult canopy of Arctic kelp species has the potential to modify stress regimes for early life stages of con- and heterospecific recruits, which may have a higher susceptibility to environmental stress than adult kelps (references in Franklin and Forster 1997, see Sects. 10.4.3 and 10.4.5). In particular the modification of understory irradiance regimes through moderate shading of an adult kelp canopy could possibly enhance germination success of zoospores of Arctic kelp species, which is suppressed under high light intensity and ultraviolet radiation as revealed by a field experiment in Kongsfjorden (Wiencke et al. 2006; see Sect. 10.4.5).

In the cold-temperate zone, Sjøtun et al. (2006) reported on reduced survival of *L. hyperborea* recruits under a dense adult canopy, which the authors explained by photon fluence rates that were insufficiently low for growth, ultimately killing recruits. Likewise, in the warm-temperate zone microscopic stages of *L. ochroleuca* did not grow under an adult canopy, but quickly replenished the canopy in areas where the canopy had been completely removed (Barradas et al. 2011), suggesting shading as a proximate cause for recruitment failure. Maternal facilitation of kelp recruitment (*L. hyperborea*) was also reported from moderately wave-exposed sites and where partial canopy removal from trawling or experimental manipulation had been done along the west coast of mainland Norway (Christie et al. 1998; Pedersen et al. 2012). Probably, a reduced adult canopy generates an optimal light regime for the growth of conspecific microscopic stages and juvenile sporophytes. Besides the modification of environmental conditions by conspecifics, interspecific interactions may also affect kelp recruitment. For instance, a study by Gagnon et al. (2003) indicates that kelp recruitment (*Agarum cribrosum*) may benefit from canopies of a non-kelp species (*Desmarestia viridis*). Wave-induced sweeping movements of the canopy keep green sea urchins (*Strongylocentrotus droebachiensis*) away from *D. viridis*, generating a refuge for *A. cribrosum* recruits. Furthermore, light regimes under kelp canopies may generate an insufficient light regime for epiphytes and algal turfs (Christie et al. 1998). The latter were shown to suppress the growth of at least macroscopic life stages of kelp (Graham 1997).

As ecosystem engineers, kelps provide habitat and/or food for numerous associated species ranging from mobile invertebrates and fish to sessile epibionts, which use kelp as substratum (Christie et al. 2009). This facilitative effect, by which diversity and presumably productivity are locally enhanced, is also true for Arctic coastal systems although their associated species assemblage is impoverished in comparison with similar habitats at lower latitudes (Rózycki and Gruszczynski 1986; Carlsen et al. 2007; Ronowicz et al. 2013). Lippert et al. (2001), for example, identified a total number of 104 faunal species associated with different kelp species in Kongsfjorden, with bryozoans and amphipods yielding the highest species number. Wlodarska-Kowalczuk et al. (2009) even detected a total of 208 species associated with a kelp forest in Hornsund, where bryozoans, polychaetes and hydrozoans represented the dominant taxonomic groups. Such close association with many organisms also implies multiple direct and indirect interactions, which may also affect the habitat-forming kelps by causing biotic stress. From temperate regions, for example, it is well known that mobile kelp-associated grazers (e.g. urchins and snails) are important drivers of kelp population dynamics (e.g. Sivertsen 1997; Sjøtun et al. 2006; Feehan et al. 2012; Iken 2012). However, grazer effects on population dynamics in Arctic kelps seem to be of minor importance due to a comparatively low number of herbivorous species at higher latitudes, which is also reflected in rather low levels of defence mechanisms against herbivores in Arctic seaweed species (Wessels et al. 2006).

Considering sessile kelp-associated species, most of them are concentrated on the holdfast of the macroalgae. In Kongsfjorden and Hornsund, kelp bed bryozoans and hydrozoans represent the most diverse taxonomic groups of epibionts attached to algal holdfasts (Carlsen et al. 2007; Ronowicz et al. 2008; Wlodarska-Kowalczuk et al. 2009). However, many colony-forming species such as bryozoans may also occur in high densities attached to stipes and blades (Rózycki and Gruszczynski 1986) and, therefore, may alter biologically relevant processes at the kelp-seawater interface (e.g. nutrient uptake). Additionally, when calcified, these encrusting epibionts may change mechanical thallus properties (e.g. flexibility), which can lead to increased susceptibility to breakage. This may negatively affect kelp population dynamics, especially when many blades break below the intercalary meristems of the algae. In this context, it has been suggested that crusts of bryozoans may also reduce kelp growth and promote premature senescence and fragmentation during storms (Lampert et al. 1992). Additionally, it is reported that encrusting colonial epibionts reduce spore release of overgrown kelps (Saier and Chapman 2004), and all of these effects can place stress on kelp populations.

Knowledge about intraspecific kelp interactions such as competition is missing for Arctic habitats. Moreover, most of the interspecific interactions between kelps and their associated organisms have been examined at lower latitudes and knowledge on Arctic kelps is extremely scarce. Currently, it seems that neither grazing by herbivores nor overgrowth by epibionts strongly affects the kelp population dynamics but experimental evidence from field studies is missing. Yet, it has been postulated that Arctic ecosystems will experience profound changes by the direct and indirect effects of global warming (IPCC 2013; Pavlov et al. 2013). A warmer Arctic is expected to lead to a spatial enlargement of Arctic kelp beds and a northward extension of many species including North Atlantic seaweed species (Krause-Jensen and Duarte 2014; Müller et al. 2009a) and also kelp-associated organisms (Bartsch et al. 2012; Wiencke and Amsler 2012; Raybaud et al. 2013). This may result in an increased number of biotic interactions within seaweed beds at higher latitudes (Weslawski et al. 2011), which is likely to alter the effects of epibionts, grazers, and competitors on Arctic kelp population dynamics in the future. In addition, the observed warming-induced reduction in the extent and thickness of sea ice in Svalbard (Pavlov et al. 2013) in combination with more intense and/or frequent storm events (Young et al. 2011) may increase internal bed dynamics through an increase in kelp detachment rates and ultimately strongly alter intra- and interspecific interactions in Arctic kelps. Besides wave-exposure, changes in temperature and nutrient concentration have the potential to interact with canopy effects on kelp recruitment (Kortsch et al. 2012; see Sect. 10.3.4 "Nutrient regime").

Present knowledge on the effects of kelp canopies and associated species on kelp performance and fitness comes predominantly from non-polar habitats. Most of these effects are kelp species-specific and/or site-specific and conclusions cannot be transferred directly to kelps from Arctic regions. As adult canopies are able to alter abiotic conditions for understory organisms, upcoming studies on intra- and interspecific interactions need to be conducted as manipulative field experiments with Arctic kelp species. Such studies will increase our understanding of how, and by how much, adult canopies and associated species alter kelp population dynamics in a present and future Arctic ocean.

10.5 Future Scenarios & Outlook

The data collected from studies on the kelps of Kongsfjorden have increased substantially during the last two decades and this has greatly improved our understanding of kelp responses towards environmental variation in general, albeit mostly on the species level, while studies on the community level and on biotic stressors are still scarce. On the basis of the current knowledge, we can at least speculate with a higher degree of certainty on what the future kelp community of Kongsfjorden may look like. Proceeding Atlantification will most likely result in the Kongsfjorden seaweed flora and associated organisms to further resemble a more cold-temperate community, similar to those along the Norwegian west coast. An immigration of seaweed species is to be expected from Norwegian mainland coasts and taking advantage of Bear Island as a stepping-stone. For the kelp flora, this most likely entails the establishment of *Laminaria hyperborea* as another large macroalgal species. The modelling study by Müller et al. (2009a) allows some prospective view into the future biogeographical distribution patterns of North Atlantic kelps, based on current temperature tolerance ranges associated with biological traits such as growth, reproduction and recruitment, and predicted sea surface temperature distribution patterns. Based on that, the northward extension of current northern temperature limits can be taken for granted and may facilitate the spread of more and more temperate species migrating to the west coast of Svalbard. It is more difficult to predict to what extent increase in sea surface temperature in the North Atlantic will also set new southern distribution boundaries, as adaptive processes facilitating the adjustment of biological performance towards a changing temperature regime are difficult to implement in the models. However, recent large-scale kelp declines have already been reported from the North of Spain; the Southern distributional limit of a variety of cold temperate Atlantic kelps (Voerman et al. 2013). Thus, we can expect new seaweed arrivals to the Kongsfjorden area (Krause-Jensen and Duarte 2014); whether some species will have to depart from Kongsfjorden to more northern and eastern locations of Svalbard still needs to be evaluated.

While our predictions on changes in species community and distribution shifts are becoming more precise, present studies are still far from being conclusive as it comes to future trends in kelp productivity. Light availability as a driver of kelp productivity will undergo substantial alterations resultant from environmental change, but whether or not it will ultimately result in an overall change in underwater light availability has still to be resolved (see Pavlov et al., Chap. 5). Undoubtedly, ongoing Atlantification will reduce the extent and duration of sea ice cover, which potentially may result in an increase in light penetration into the water column (Krause-Jensen et al. 2012). On the other hand, increased atmospheric temperature and precipitation may increase snow melting, terrestrial run off and glacier calving, which both may result in an increase in the sediment load of Kongsfjorden waters, thus, reducing water transparency. Overall, these two scenarios may imply, that benthic organisms will experience an earlier start of the spring season, as light transmits earlier, deeper, and with higher irradiance into the water under the absence of ice and before the onset of the melting and run-off season (Krause-Jensen et al. 2012). Under run-off conditions light availability might be largely reduced, but the overall implications to kelp productivity remain to be evaluated.

Furthermore, the contribution of detached and degrading kelps to the flux of organic matter in Kongsfjorden is still understudied. Increased temperature may fuel overall microbial activity, but potentially also increase kelp detachment under intensified storms and wave action (Young et al. 2011). These two factors along with higher rates of primary productivity may result in an increased turnover of kelp debris. In this way carbon release to the system might be enhanced. Petrowski et al. (2016) show that even single kelp thalli may strongly affect diversity and structure of benthic soft bottom communities in Kongsfjorden when detached macroalgae are drifting on, or are being trapped in the sediment.

After almost 25 years of intense kelp research at Kongsfjorden, our understanding of physiological responses of kelps to a changing environment has advanced considerably. New analytical tools in molecular biology are becoming available for work on kelps as well, and a lot of new insights into stress perception and molecular control of acclimation processes are to be expected within the near future. These studies are of utmost importance in order to understand mechanisms and limitations of acclimation and adaptation for single species. Nevertheless, we need to accept and to be aware that the ecological significance of monospecific and/or monofactorial experiments is limited, given the enormous complexity of responses on the ecosystem level.

Still, the physiological studies on kelps of Kongsfjorden so far allow for some founded conclusions: In line with their generally wider distributional range, most kelp species found in the Arctic have broad tolerance ranges to most environmental variables. Regarding each of the kelp species in itself, and with the exception of the Arctic endemic *Laminaria solidungula*, most species will likely tolerate an increase in UV radiation, temperature and/or ocean acidification at the predicted ranges (see Sect. 10.3.3, 10.4.1, 10.4.2, 10.4.3, and 10.4.4). Still, as the early life-history stages are particularly susceptible, this has to be evaluated for the respective most sensitive stage (Sect. 10.4.5). In contrast, it is much more likely that a multitude of new ecological interactions will be formed (Sect. 10.4.6). Changing abiotic conditions will facilitate the arrival of organisms from lower latitudes and maybe also the introduction and establishment of non-indigenous species, all of which may alter the strength and direction of biotic interactions, including competition, epibiosis and grazing.

Conclusively, with respect to Kongsfjorden as a “hot spot” for environmental change, the following research priorities are proposed: More experiments addressing the interactive effects of abiotic and/or biotic stressors have to be conducted both on the physiological and ecological level. With the ecophysiological responses being extensively characterised already, molecular mechanisms and ecosystem consequences come into focus: we have to deepen our insights into regulatory mechanisms by large-scale gene expression and transcriptomic analyses on the one hand. On the other hand, we need to implement our findings in the context of species biology and ecology. Furthermore, population ecology and population genetics of kelps from the North Atlantic need to be revisited, checking for speciation processes or new connectivities facilitated by climate change. In this context, a timely examination and, if necessary, taxonomic revision of kelps populating the Arctic is also required.

The current, and certainly essential, debate on likely consequences of climate change, however, has led us to neglect another vital aspect in polar ecological science: Still our knowledge on the basic physiological adaptations allowing organisms to thrive in high polar environments is remarkably scarce. We need to make use of the latest analytical tools in order to improve our understanding of environmental signalling and the whole cellular machinery in order to reveal what makes kelps work under all constraints in high latitude environments. Further, there is an urgent need to implement the factor of seasonality in such studies. Knowledge of seaweed ecosystem functioning under Arctic winter conditions is near to non-existent, but essential to understanding adaptive life strategies under polar conditions and adaptability in an era of climate change. Still, with its rich kelp flora on the doorstep and a superb infrastructure, Kongsfjorden and Ny-Ålesund represent the prime locations for addressing these scientific challenges.

Acknowledgements This review is largely based on the research conducted in the frame of the long-term project KOL 06 - Biology of Arctic benthic algae, performed at AWIPEV station, Ny-Ålesund. Authors are most grateful for the continuous support by the entire AWIPEV base team. Most of the studies presented would not have been possible without the AWI diving team.

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Chapter 11
Ecological Drivers of and Responses by Arctic Benthic Communities, with an Emphasis on Kongsfjorden, Svalbard

Markus Molis, Frank Beuchel, Jürgen Laudien, Maria Włodarska-Kowalczuk, and Christian Buschbaum

Abstract Knowledge on the causes and consequences that structure benthic communities is essential to understand and conserve Arctic ecosystems. This review aims to summarize the current knowledge on the effects of abiotic and biotic factors on species interactions and community traits, i.e. diversity, structure, and functioning of Arctic coastal hard- and soft-bottom habitats, with emphasis on Kongsfjorden (Svalbard). Current evidence indicates that descriptive and mensurative studies on the distribution of species prevail and few studies allow inferences on the underlying processes generating observed patterns. Furthermore, Arctic hard- and soft-bottom communities show some fundamental differences in their ecology. The recovery in hard-bottom communities from disturbance, for instance, takes exceptionally long (i.e. > decadal) due to slow growth and/or sporadic recruitment, while it is considerably shorter in soft-bottom communities. Also, Arctic hard-bottom communities display strong competitive hierarchies that appear negligible in communities populating sedimentary shores. This review concludes with a suggestion to shift the focus in Arctic benthos research from pattern to processes and the identification of major research gaps. These include (i) the apparent demarcation of studies

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_11

being devoted to either rocky or to sedimentary shores, which hamper studies on habitat connectivity, (ii) the lack of studies addressing the effects of pathogens and diseases on community ecology, and (iii) the incomplete assessment of potentially significant drivers of community ecology, such as trophic interactions, recruitment success, and competition.

Keywords Arctic ecosystems · Biotic interactions · Climate change · Disturbance · Polar biota · Rocky habitats · Sedimentary habitats · Succession

11.1 Introduction

One goal of ecology is to identify the factors and underlying processes by which the distribution of species and ultimately the structure of ecological communities are controlled in space and time. Such knowledge is particularly sought for polar ecosystems because global change is expected to be strongest at high latitudes (IPCC 2013). Predictions about, for instance, the future heat budget of the Arctic ocean indicate that its warming will be significantly above that of the global average (Serreze et al. 2009). The predicted ecological consequences of global change may be dramatic for Arctic ecosystems (IPCC 2014), which are connected by ocean currents, e.g. the West Spitsbergen Current, to the temperate zone. This connection will likely spur a warming-induced introduction of non-indigenous, cold-temperate biota to the Arctic (Krause-Jensen and Duarte 2014). As a consequence, the type and frequency of species interactions might increase and change food web structure in marine Arctic ecosystems (Kortsch et al. 2015). This will include benthic habitats because the dispersal ability of many benthic species, including sessile forms, by pelagic propagules may be sufficiently high to reach Arctic shorelines under favourable oceanographic conditions (e.g. Sirenko and Gagaev 2007; Alvsvåg et al. 2009; Matishov et al. 2012; reviewed in Renaud et al. 2015a).

While the northward extension of species ranges may affect frequency and type of species interactions in coastal, benthic communities, a warmer Arctic may also affect the interactions among species that are currently present. At higher seawater temperature, the physiological responses and demands of species will generally change, with variations among species (Doney et al. 2012). As a consequence, it can be assumed that the direction and/or intensity of interactions between resident competitors, consumers and their prey, or the effectiveness of pathogens will change. Furthermore, global warming will reduce the extent and thickness of sea ice, enhance glacial retreat, and increase riverine discharge (Polyakov et al. 2010; Sahade et al. 2015). All of these indirect effects of warming will affect the abiotic environment and disturbance regimes in which Arctic benthic communities thrive and will ultimately alter community organisation (see Grebmeier 2012 for the Arctic; Sahade et al. 2015 as an example for Antarctica).

As a prerequisite for the conservation of coastal Arctic ecosystems and the development of management strategies, it will be necessary to understand the underlying processes that modify coastal Arctic ecosystems. Their protection should be a prime interest of human society because near-shore benthic organisms provide significant services to (a) sustain coastal ecosystems, (b) protect coastlines, and (c) attenuate the effects of global climate through (i) retention of senescent matter and fixation of external energy, fueling higher trophic levels, including humans, (ii) the reduction in coastal erosion by sea-floor consolidation (Fig. 2 in Wang et al. 2012), and (iii) as a carbon sink, respectively. The major goal of this review is to provide an overview on benthic research conducted in Kongsfjorden since the synopsis by Hop et al. (2002), who collated the achievements of the initial research period preceding the year 2000. Until the review by Hop et al. (2002), the state-of-the-art for benthos research in Kongsfjorden comprised qualitative rather than quantitative information about the vertical and horizontal distribution of species. Furthermore, descriptive studies with a trophic perspective prevailed, providing fundamental information sought for the construction of quantitative ecosystem and carbon flow models for Kongsfjorden. Hop et al. (2002) also identified major research gaps. However, basic information on primary production, the role of biological factors in shaping ecological communities, and the effects of seasonal variation in abiotic and biotic conditions, especially during winter, had not been gathered by then.

The scope of this review is on the ecology of species assemblages that populate coastal rocky and sedimentary substrata in the Arctic with an emphasis on Kongsfjorden (Fig. 11.1), a flagship site of marine ecological research in the Arctic. Unless stated otherwise, we use the term coastal to refer to hard-bottom habitats from intertidal down to a depth of 30 m, i.e. within the operating range of SCUBA divers and to soft-bottom habitats down to 400 m, as this is within the typical depth range of Arctic fjords, including Kongsfjorden. Subjects with very limited or lacking information on the ecology of Kongsfjorden benthos will be supplemented by knowledge obtained in studies conducted in other Svalbard regions or, if applicable, other regions of the Arctic. Differences in research foci of rocky and sedimentary habitats entail an unbalanced presentation of research topics between both habitats in this review. Facilitation, for instance, had been studied in Arctic hard-bottom, but not in soft-bottom communities. Regarding the taxonomic scope of this review, we considered algae and invertebrates >0.5 mm in size (for micro-phytobenthos see review by Karsten et al., Chap. 8). Besides the temporal dynamics in the assemblage of benthic species, we summarize the results of studies assessing the processes that structure benthic communities rather than the spatial patterns in community structure and diversity. We present the available knowledge about the role of abiotic factors separately for rocky and sedimentary habitats, followed by studies addressing the influence of biotic factors on (i) species interactions, (ii) diversity, (iii) structure, and (iv) function of benthic communities. As a final consideration, we propose perspectives for future research on Arctic marine ecosystems.

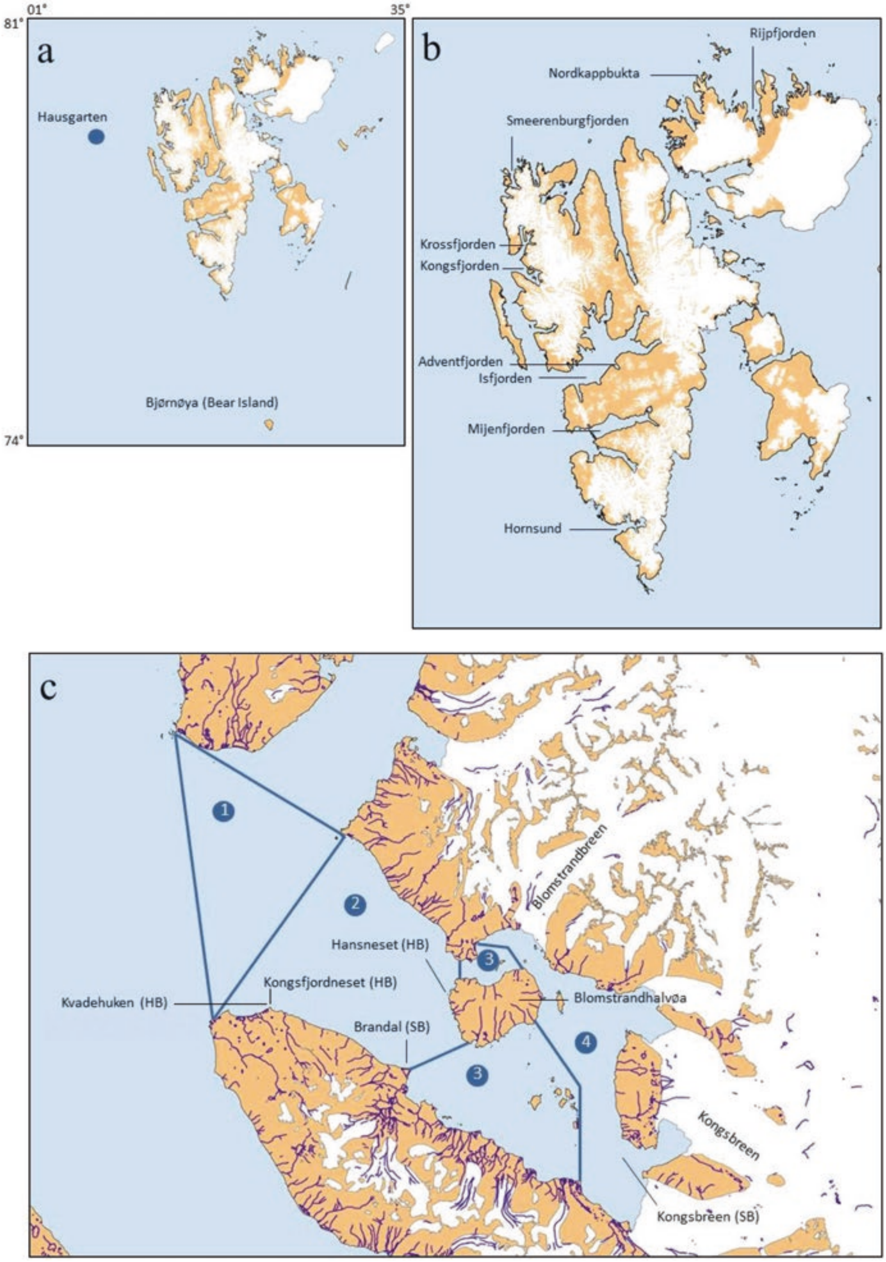

Fig. 11.1 Map indicating sampling sites referred to in this review from outside (**a**) and within (**b**) the Svalbard archipelago and different zones in Kongsfjorden (**c**, adopted from Hop et al. 2002): 1 = outer, 2 = middle, 3 = transitional, and 4 = inner. *HB* hard-bottom, *SB* soft-bottom

11.2 Rocky Habitats

The proportion of hard-bottom habitats in Kongsfjorden is much lower than that of sedimentary habitats. Nevertheless, rocky shores are algae-dominated ecosystems with significant functions such as sites of high primary production and a sink for carbon. As bioengineers (Krause-Jensen and Duarte 2014), algae provide habitat and nursery grounds and function as a food source that sustains a diverse suite of associated fauna (e.g. Christie et al. 2003; reviewed in Bartsch et al. 2008). Much sampled study sites of hard-bottom communities in Kongsfjorden include Kvadehuken (78°58.6'N; 11°30.1'E), Kongsfjordneset (78°58.37'N; 11°29.35'E), and Hansneset (78°59.1'N; 11°57.8'E) (Fig. 11.1c). At these locations, observational and experimental long-term studies on the succession of species and temporal shifts in biodiversity have been conducted (Table 11.1).

11.2.1 Species Succession

The non-seasonal, continuous, and directional sequence of species replacement in newly exposed areas is referred to as primary succession while secondary succession comprises the recolonization of previously populated areas that were cleared by a disturbance (Ricklefs 1990). Overall, information on the succession of species in polar marine hard-bottom communities is extremely scarce (Dunton et al. 1982; Newell et al. 1998; Barnes and Conlan 2007) and lacking for the underlying processes. Information about research on the succession of benthic species in the Arctic is summarized in Table 11.1, but presently misses, to the best of our knowledge, intertidal rocky shores and hard-bottom areas >20 m water depth. Polar hard-bottom benthos is considered to have relatively slow rates of growth, reproduction, and, hence, low rates of colonization and recolonization (Bowden et al. 2006; Konar 2007; Zacher et al. 2007; Fricke et al. 2008). Methods for studying species succession of hard-bottom communities include placement of settlement panels (i.e. primary succession) and experimental clearing of natural substrata (i.e. secondary succession) followed by non-destructive monitoring of species abundances through (i) *in-situ* observation or (ii) underwater photography (e.g. Barnes and Kukliński 2005b; Beuchel and Gulliksen 2008; Fig. 11.2).

11.2.1.1 Primary Succession

The primary succession of species has been studied in subtidal hard-bottom habitats of Kongsfjorden through manipulative field experiments in conjunction with potential drivers of community structure and diversity (Fricke et al. 2008). They followed the initial 8 weeks of primary species succession on newly deployed (i.e. empty) ceramic settlement panels at 0.5 m water depth close to Ny-Ålesund harbour. During

Table 11.1 Summarizing information about environmental conditions and set-up of studies on succession of species of hard-bottom assemblages

Studied factor	Authors	Year	Study site	Sampling method	Depth [m]	Start of experiment	Duration [y]	Seasonal timing	Temperature [°C]	Primary colonisers	Response variables
Primary succession	Schmiing	2005	Kongsfjordneset (KF)	Polyethylene tiles (ø 40 cm)	20	2002	3	June–August	~ 3.6	Bryozoa, algae, polycheats	Species abundance, biomass, cover
Secondary succession	Beuchel and Gulliksen	2008	Kvadehuken (KF)	Photo quadrats (50 × 50 cm)	15	1980	23	August–September	3–5	Sea anemones, tunicates, algae	Species abundance, cover
Primary and secondary succession	Fricke et al.	2008	Near Ny Ålesund harbour (KF)	Ceramic tiles (9.6 × 9.6 cm)	0.5–8	2004, 2005	1.75	August, May	0.6–6.2	Algae (Bacillariophyta), polycheats	Species abundance, cover
Primary succession	Streicher	2014	Kongsfjordneset (KF)	Polyethylene tiles (ø 40 cm)	20	2002	10	June–August	~ 3.6	Bryozoa, algae, polycheats	Species abundance, biomass, cover
Primary succession	Barnes and Kukliński	2005a, b	Southern Isfjord (IF)	Acrylic panels (15 × 15 cm)	12	2002	1	August	−1.8 to 4	Bryozoans, polychaets	Species abundance, cover
Primary succession	Kukliński et al.	2013	Adventfjorden, 3 locations (IF)	Acrylic panels (15 × 15 cm)	6	2007	1	January	−1.5 to 8.3	Bryozoans	Species abundance, cover

KF = Kongsfjorden, IF = Isfjorden

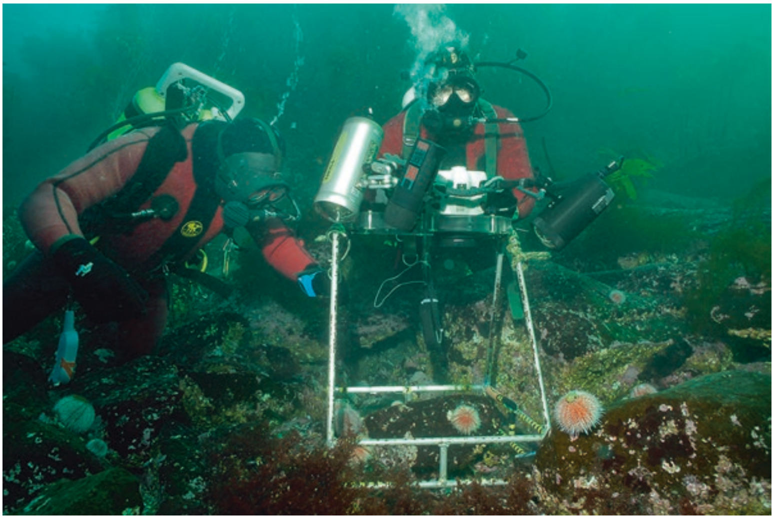

Fig. 11.2 SCUBA divers taking photo samples at a monitoring site. (Courtesy of Erling Svensen)

the first 4 weeks, opportunistic groups such as Bacillariophyta and filamentous green algae, including *Urospora* sp. and *Ulothrix implexa*, monopolized the substratum. In the course of the next 4 weeks, an additional green alga of the family Acrosiphoniaceae appeared. These pioneering species have inhibitory and/or facilitating effects on the succession of species (Fricke et al. 2008; Zacher and Campana 2008). From temperate regions it is known that, for instance, mat-forming Bacillariophyta precondition the substrate by providing UV-free space (Vinebrooke and Leavitt 1999) or by the production of extracellular polymers (Lam et al. 2005), thereby facilitating the colonization by propagules of certain algal species. In contrast, Bacillariophyta may preempt the substrate, inhibiting the settlement of e.g. red algal propagules (Huang and Boney 1985; Zacher and Campana 2008). In Kongsfjorden, primary succession of species was also followed beyond the initial phase for communities developing on ceramic settlement panels at 8 m depth. After 12 months, communities were dominated by members of the Ectocarpales (Phaeophyceae), such as *Pylaiella littoralis*, *P. varia*, and *Ectocarpus siliculosus* and the green alga *U. implexa*. Furthermore, the first sessile invertebrates were encountered at that time. After 21 months of panel deployment, communities showed a higher cover in members of the green algal class Ulvophyceae, the brown alga *Dermatocelis laminariae*, and invertebrates, particularly the polychaete *Cireis spirillum*, than 12 month old communities (Fricke et al. 2008). Despite differences in species composition, there was no significant difference in species richness between the 12 and 21 months old communities, suggesting slow assemblage of species.

To the south of Kongsfjorden, in Isfjorden (Fig. 11.1b), Barnes and Kukliński (2005b) followed the initial colonization by animals on settlement panels (225 cm^2) immersed at 12 m depth. Colonists were absent during the first 3 days, but one bryozoan and several specimens of polychaetes had settled by the end of the first week. After a year of immersion, panels were 3–11% covered with, on average, 250 individual colonists. This is at least an order of magnitude lower than the coverage on most non-polar rocky shores (Barnes and Kukliński 2005b), but higher than what has been recorded for an Antarctic locality (Pearse and Pearse 1991). Most individual colonists (80–93%) were sessile tube-dwelling polychaetes (*Spirorbis tridentatus*), but bryozoans constituted the most speciose group of colonizers. According to Barnes and Kukliński (2005b), species richness (i.e. 20 taxa) was as high as or higher than in many similar colonization studies along the north Pacific or north Atlantic coasts. Using a similar set-up, Kukliński et al. (2013) followed species succession in Adventfjorden on settlement panels deployed in January (i.e. during the polar night) for 1 year. A total of 22 taxa of primary colonizers were recorded. The first settlers were mainly polychaetes, while the last settlers comprised hydroids, cheilostome bryozoans, and spirorbid polychaetes, appearing in February and November, respectively. The settlement and rapid increase in the density of some groups of organisms (e.g. polychaetes and cirripeds) were positively correlated to the timing of blooming phytoplankton.

Later stages of primary succession of hard-bottom communities were studied near Kongsfjordneset in the middle zone of Kongsfjorden (Fig. 11.1c) at 20 m depth from 2002 to 2004, using polyethylene panels (Schmiing 2005). Highest densities of recruits were recorded after 1 year (up to 20,600 ind. m^{-2}) with strongly declining density during the second year (2–4,000 ind. m^{-2}) and an increase to an average of about 7,700 ind. m^{-2} after the third year of panel incubation. A different pattern was observed in biomass, which was lowest after the first year (4.2 g dry mass m^{-2}) and increased to 8.3 and 8.7 g dry mass m^{-2} after the second and third year, respectively. The differences in recruit density between years could be explained by the gradual decline in the abundance of juvenile barnacles and mobile species over time during which the density of bryozoans and algae increased. Bryozoans (24 species) dominated the community in abundance and biomass towards the end of the monitoring. Schmiing (2005) concluded that, at least initially, communities developed comparatively slowly. Using the same set-up, Streicher (2014) analyzed annual photos taken between 2002 and 2012 (Fig. 11.3a-f). He found 32 taxa on the panels, indicating relatively species-poor communities compared to the 75 taxa encountered by Schmiing (2005). This difference in taxon richness may be partly due to different sampling methods (*in-situ* observation vs. photography) (Jørgensen and Gulliksen 2001). Streicher (2014) reported on a significant change in species composition of the coralline algae-dominated community in the course of the 10-year study (Fig. 11.3a-f). Some taxa showed a monotonical increase in abundance (i.e. algae, anthozoans, polychaetes, and chitons), while the abundance of other taxa (bryozoans, echinoderms, gastropods, and crustaceans) was without trend and highly variable between years. Colonization by sponges and hydrozoans did not occur until several years after panel deployment. The findings by Streicher (2014) principally corroborate results of studies indicating a slow succession of Arctic hard-bottom communities (Fig. 11.3g–l; Beuchel and Gulliksen 2008; Konar 2013). The extremely low abundance of presumably competitive superior species such as the sea anemones *Urticina eques* and *Hormathia nodosa* on 10-year-old settlement panels indicates that succession had most likely not reached a climax stage by then.

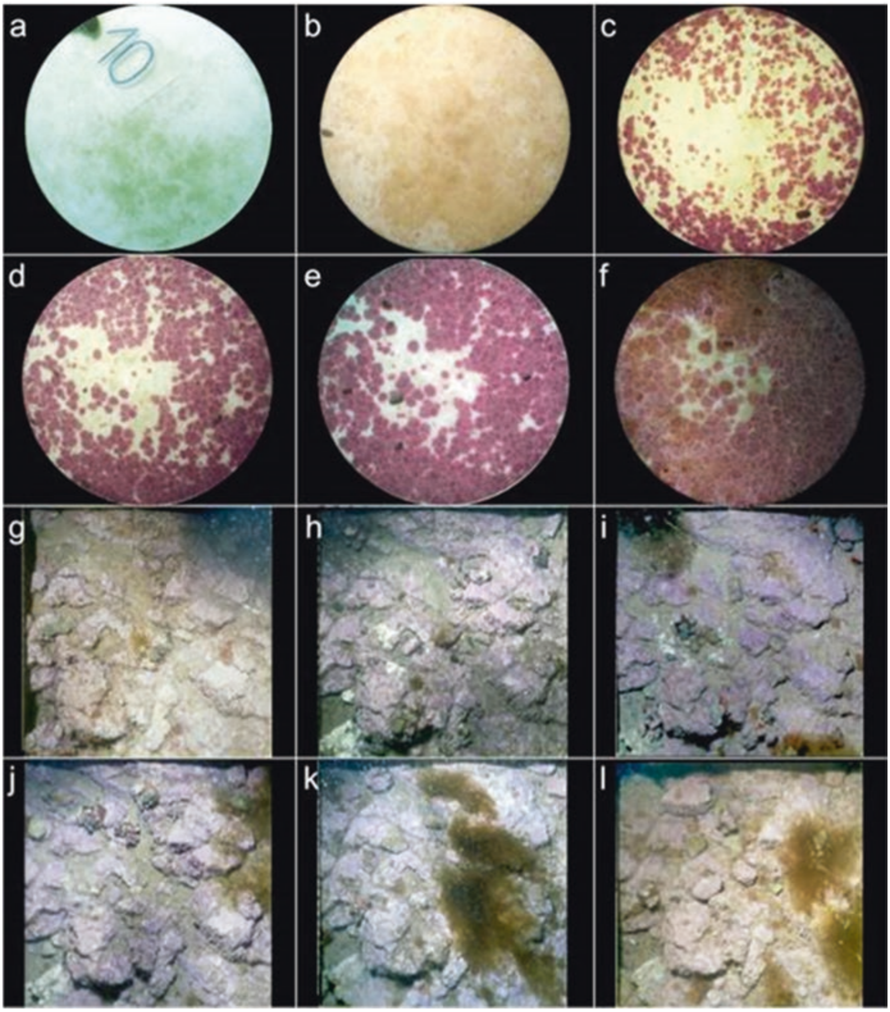

Fig. 11.3 Species succession on hard-substrates. Primary species succession on white polyethylene panels (40 cm Ø = 1256 cm^2 surface area) deployed at Kongsfjordneset for 2 (**a**), 4 (**b**), 7 (**c**), 9 (**d**), 10 (**e**), and 12 years (**f**) of exposure (Streicher 2014). Secondary succession on 2500 cm^2 submerged rock face at Kvadehuken after 1 (**g**), 3 (**h**), 4 (**i**), 5 (**j**), 7 (**k**), and 10 years (**l**) of initial clearing (Beuchel and Gulliksen 2008)

11.2.1.2 Secondary Succession

We are aware of only two studies addressing the secondary succession of species on hard substrata in Kongsfjorden. Fricke et al. (2008) recorded the initial period of secondary succession (i.e. 8 weeks) of benthic communities developing for 12 or 21 months at 8 m water depth on ceramic settlement panels after their transplantation to 0.5 m water depth. Panel transplantation simulated an environmental disturbance related to the break-up of sea ice cover. The species composition of transplanted communities changed significantly, but some effects were dependent on community age. Four weeks after transplantation of the 12 months old communities, Bacillariophyta abundance increased, while brown algae had disappeared and the abundance of green algae was strongly reduced. These significant changes in species composition resulted also in a significant reduction in species richness. During the next 4 weeks, macrobenthic biota started to recover. For instance, the abundance of sessile invertebrates, mainly the hydroid *Obelia dichotoma*, increased greatly. At the same time, the abundance of Bacillariophyta declined significantly. While transplantation did not affect species richness of 21 months old communities, their species composition was similarly affected by this treatment as was that of 12 months old communities. A species-specific acclimation potential and capacity to recover from stress were regarded as structuring mechanisms of species composition. Bacillariophyta, for instance, seemed to be more tolerant than algae to the near surface conditions in this experiment (Fricke et al. 2008).

In a long-term study on secondary species succession, most visible organisms were scraped off the subtidal bedrock at Kvadehuken (Fig. 11.1c) at the start of the study in 1980 (Beuchel and Gulliksen 2008). Subsequently, the succession of species was documented through annual photographic surveys on cleared (Fig. 11.3g–l) and untreated plots (Fig. 11.2). At the species level, the conspicuous sea anemones *U. eques* and *H. nodosa* recovered from the disturbance after 8 to 10 years. At the community level, where 23 taxa of epifauna were recorded, significant differences between cleared and untreated areas prevailed for the first 13 post-disturbance years (Beuchel and Gulliksen 2008). Their study suggests that different recolonization patterns for individual species were related to differences in their longevity, rate of maturity, predation pressure, and recruitment success. No climax stage was reached by the benthic community at Kvadehuken, which may be explained by frequent disturbance events (e.g. ice-scour and storm events), which could keep the community at an early to intermediate successional stage (sensu Huston 1979, this review Sect. 11.2.3.4 *Disturbance*). The length of time required to recolonize cleared bedrock at Kvadehuken indicates that recovery from disturbance takes longer in Arctic communities than in those from lower latitudes (e.g. Sousa 1979). This notion is corroborated by Konar (2013) who studied secondary species succession of experimentally turned boulders on the coastal Beaufort Sea of Alaska. She showed in her experiment that <10% of completely cleared boulder surfaces were recolonized after 7 years. Partial clearings, however, recovered substantially within 4 years due to vegetative regrowth of sponges and encrusting coralline algae.

In conclusion, a very limited number of studies on the succession of species have been conducted in Arctic hard-bottom habitats. As an incipient trend, species succession of Arctic benthic communities appeared to be much slower than in temperate areas (Dunton et al. 1982). In addition, coastal Arctic benthos experiences high levels of disturbance (Dayton 1990; Grebmeier and Barry 1991) due to increased physical (e.g. ice-scour), biological (e.g. consumer activities), and anthropogenic disturbances (Jewett et al. 1999). Consequently, Arctic communities are recurrently set back to earlier successional stages. The slow succession in combination with frequent disturbances results in a low recovery potential of Arctic benthos, which should heighten the vulnerability of coastal Arctic ecosystems to anthropogenic disturbances, such as effluent discharge (Krumhansl et al. 2015). Current knowledge on the succession of species on Arctic rocky shores is, however, insufficient to draw strong conclusions. Future research on species succession will benefit from placing clearance studies into a larger context. The performance of clearance studies at different water depths or distances to sites affected by anthropogenic stress (e.g. melting glaciers resulting from industry-related global warming), will improve our ability to predict the consequences of climate change on coastal Arctic ecosystems and unravel the underlying processes of species succession.

11.2.2 Long-Term Change

Comparative and monitoring studies were used to assess historic changes in Kongsfjorden hard-bottom communities. Repeating the 1996–1998 benthos survey at Hansneset (Hop et al. 2012; Voronkov et al. 2013, Fig. 11.1c) in 2012–2014 aimed to unravel changes along a depth gradient (Fredriksen et al. 2014; Bartsch et al. 2016; Paar et al. 2016). For documentation of gradual changes, species abundance has been recorded annually at Kvadehuken since 1980 (Beuchel and Gulliksen 2008) and at Kongsfjordneset since 2002 (Streicher 2014).

11.2.2.1 Comparative Studies

Overall, growth (only algal species), total biomass, and species richness (only fauna) was higher in 2012–2014 and species composition had changed considerably between surveys conducted in the periods 1996–1998 and 2012–2014. Algal biomass peaked in the 1996–1998 survey at greater depth (i.e. 5 m) than in the 2012–2014 survey (i.e. 2.5 m), when it had increased almost fivefold (Bartsch et al. 2016). There was a general upward shift in the lower depth limit of most dominant brown algal species by ca. 2–3 m (Fredriksen et al. 2014; Bartsch et al. 2016). Across the entire depth gradient, algal biomass increased by 70% since 1996–1998, although the biomass of annual species declined during this period (Bartsch et al. 2016). The total number of species of algae was comparable between 1996–1998 (i.e. 62) and 2012–2014 (i.e. 58), but not the composition of species as only 42 species were present in both investigations. Four species of red algae that were commonly found in 1996–1998 were absent at Hansneset in 2012–2014, while two red algal species were newly recorded (Fredriksen et al. 2014). In the upper littoral zone (intertidal down to 1.5 m water depth), the number of algal species increased from 20 to 45 between both surveys, including two and seven new records of green and brown algae, respectively (Fredriksen et al. 2014). Similarly to algae, faunal biomass and secondary production increased tenfold at shallow water depth (2.5–5 m) between 1996–1998 and 2012–2014 (Paar et al. 2016). Moreover, animal biomass and secondary production increased with increasing water depth in 1996–1998, but decreased along the depth gradient in 2012–2014. These trends in temporal change of biomass and diversity of Kongsfjorden hard-bottom benthos were corroborated by Węsławski et al. (2010) for intertidal communities sampled in southern Spitsbergen (i.e. Hornsund Fjord and the adjacent Sørkappland coast, Fig. 11.1b) in 1988 and in 2007–2008. Their study revealed "a two-fold increase in species numbers, a three-fold increase in the biomass of macroalgae, and an upward shift in algal occurrence (mainly *Fucus distichus*) on the coast." However, new species records were not reported by Węsławski et al. (2010). The authors concluded that the relatively higher stability in intertidal community structure in Hornsund Fjord than in Kongsfjorden was a result of the isolation of the former from warm Atlantic waters (Węsławski et al. 2010).

The authors of the above-mentioned comparative studies suggest that the warming of the Arctic is most likely the ultimate cause for the observed changes in biomass maxima, species distribution and composition of hard-bottom communities. The reduction in ice-scour was considered as the proximate reason for an increase in biomass at shallow water depth, as Kongsfjorden has been free of fast ice during most of the last decade (Pavlova et al., Chap. 4). The upward shift in the vertical distribution of many types of algae, including kelp species, was also attributed to warming, as the glacial meltdown is expected to lead to higher loads of terrigenous particles and hence, reduced solar irradiance at depth in coastal waters. The upward shift of kelp may have indirectly caused the increase in secondary production and animal biomass at shallow water depth because kelps are an attractive habitat for a large number of associated fauna in Kongsfjorden and other Svalbard fjords (Lippert et al. 2001; Włodarska-Kowalczuk et al. 2009, this review Sect. 11.2.4.3 *Epibiosis*).

11.2.2.2 Monitoring Studies

The hard-bottom communities at Kvadehuken, Kongsfjorden and further north in Smeerenburgfjorden, Svalbard (Fig. 11.1b,c) have been monitored for more than 30 years. In both fjords, community structure was relatively stable during the 1980s and early 1990s. After this period, however, biodiversity increased and this was accompanied by a decline in the abundance of actinarians and increase in density of the sea urchin *Strongylocentrotus droebachiensis* in combination with the abrupt and substantial formation of dense carpets of brown algae (mainly *Desmarestia* spp. in Kongsfjorden). As a consequence of this regime shift, average algal cover increased from 8% to 40% in Kongsfjorden and from 3% to 26% in Smeerenburgfjorden (Kortsch et al. 2012).

11.2.3 Abiotic Factors in Hard-Bottom Habitats

The effects of solar irradiance on community traits were studied most thoroughly in hard-bottom habitats. This bias in research effort may be due to the strong dependency of algal growth and survival to the available quality and quantity of photosynthetic active radiation (PAR). Algae function as bioengineers by attracting invertebrates through the provision of food, shelter, and settlement substratum and ultimately the predators of these invertebrates (Christie et al. 2003; Watt and Scrosati 2013; Krause-Jensen and Duarte 2014). The exponential attenuation of PAR with water depth may explain why water depth was the most important environmental driver in the species composition of hard-bottom fauna (Voronkov et al. 2013) or sea-ice break-up for the regime shift in marine benthos (Kortsch et al. 2012). Compared with the research effort on Arctic sedimentary habitats (see below), it seems that less experimental evidence has been accumulated on the disturbance effects of icebergs and sedimentation stress on the structure and diversity of Arctic hard-bottom communities.

11.2.3.1 Temperature

Many long-term studies reported on the relation between macrobenthos change and indicators of climate change. In these studies, temperature is considered one of the most important environmental drivers of ecological change. Even though most of the species observed in Arctic waters thrive at a relatively wide temperature range (Węsławski et al. 1993), a change of less than 2 °C in sea surface temperature may trigger a significant reorganization of benthic community structure (Mueter and Litzow 2008; Kortsch et al. 2015; Renaud et al. 2015b). Temperature may be also one of the major factors affecting hard-bottom communities in Kongsfjorden because a missing sill facilitates the inflow of the relatively warm Atlantic water transported by the West Spitsbergen Current into Kongsfjorden. A documented strengthening of the West Spitsbergen Current (Saloranta and Haugan 2001) is considered as one of the main reasons of the above mentioned faunal and floristic changes in Kongsfjorden benthos (Beuchel et al. 2006; Fredriksen et al. 2014; Paar et al. 2016). During the winter of 2005–2006 for instance, substantial inflow of warmer water of the West Spitsbergen Current changed the hydrographic situation to a “warm mode” with year-round water temperatures >0 °C (Cottier et al. 2007). While direct evidence on the effects of altered temperature regimes on Kongsfjorden hard-bottom benthos is missing, Beuchel et al. (2006) showed that species diversity was negatively correlated to shifts in the North Atlantic Oscillation (NAO). An increase in biodiversity of hard-bottom communities, for instance, was observed in Kongsfjorden as well as Smeerenburgfjorden between 1994 and 1996 at a time when the NAO shifted to a negative mode (i.e. an increase in seawater temperature). Besides the possible direct effects of higher seawater temperature on algal and animal physiology, warming results in reduction of sea ice cover, and glacial retreat that indirectly frees up colonization areas and alters salinity, irradiance, disturbance, and sedimentation regimes. In the course of global warming, cold-temperate biota may succeed Arctic species (Węsławski et al. 2010, 2011), as distribution ranges of the former are expected to shift northward (Müller et al. 2009; Krause-Jensen and Duarte 2014; Kortsch et al. 2015).

11.2.3.2 Salinity

During the polar summer, large amounts of freshwater enter Kongsfjorden through glacial and river drainage, generating vertical and horizontal salinity gradients. While studies on species-specific salinity tolerances exist e.g. for kelps (Karsten 2007), studies explicitly assessing the influence of salinity on hard-bottom communities are to our knowledge missing. Kukliński et al. (2013) argued that low salinity reduced survival of polychaete larvae in Adventfjorden (Fig. 11.1b), which is highly influenced by ice and freshwater discharge from rivers. Since the response of this and other studies that advocate salinity effects (e.g. Fricke et al. 2008) were confounded by concomitantly changing environmental factors such as irradiance or sedimentation rate, it is impossible to conclude on the magnitude and direction of salinity effects at the community level.

11.2.3.3 Irradiance

Polar organisms encounter unique, extreme seasonal changes in light conditions. In particular photoautotrophic organisms have to cope with long periods of either complete lack or continuous supply of light as an essential resource, which is why polar algae are low-light adapted, yet tolerant to high light (Zacher et al. 2009). While physiological adaptions of algae to minimum light conditions have been well described (reviewed in Gómez et al. 2009; Bischof et al., Chap. 10), information about seasonal irradiance effects at higher levels of ecological organization is missing. Existing evidence suggests, however, three environmental factors that mainly affect light regimes in the Arctic with consequences on the structure of benthic communities.

Firstly, physical processes alter the quality and quantity of solar radiation with water depth, resulting in an exponential gradient in the available photon density and energy. Algae are confined to live on PAR-exposed hard substrata, including bedrock, scattered stones in sedimentary habitats, and biological or anthropogenic structures. Herein, different groups of algae deploy different photosystems to capture solar radiation with different efficacy at a given depth, which causes vertical bands that are dominated by different algal assemblages and associated fauna. This light-mediated vertical zonation of hard-bottom communities and temporal changes in zonation patterns have been documented for Kongsfjorden (Hop et al. 2002, this review Sect. 11.2.2 *Long-Term Change*).

Secondly, tidal glaciers and river discharge in Arctic fjords have a strong influence on light attenuation due to the release of terrigenous particles (Zacher et al. 2009). This generates strong spatial gradients in water transparency, along which turbidity decreases with increasing distance from tidal glaciers and river mouths. In addition, temporal changes in the concentration of dissolved and particulate matter lead to variation in water transparency through time (Hanelt et al. 2004). In Kongsfjorden, for instance, the depth of the euphotic zone (>1% of surface PAR) decreases at Hansneset from 18–24 m in spring to 6–7 m in summer (Hanelt et al.

2004; Hop et al. 2012). In the Stefansson Sound Boulder Patch site (Beaufort Sea, Alaska), kelp grows slower at shallower sites because these are closer to the mouth of a major river delta, which carries considerable amounts of turbid water to the boulder patch compared to sites at greater depth, which are further away from the river delta and are characterized by clearer water (Aumack et al. 2007). The presence of kelp and other canopy-forming algae may alter the physical environment for the benthic sub-canopy community in terms of irradiance, although empirical evidence for this is missing for polar systems (Bischof et al., Chap. 10). Therefore, changes in the light regime are likely to be reflected at the community level, affecting function (e.g. productivity) or structure of the understory benthos. Observational evidence for light-driven community responses on Arctic rocky shores comes from the study by Kortsch et al. (2012). The authors report on an abrupt five to eight-fold increase in algal abundance in two Arctic fjords (Kongsfjorden and Smeerenburgfjorden) during a 30 y period in which ice-cover (i.e. the third major factor affecting light regimes in polar waters) got gradually reduced. Their study suggested that reduced ice cover will increase PAR, hence supporting algal growth and abundance (this review Sect. 11.2.2 *Long-Term Change*). This interpretation is corroborated by Clark et al. (2013). According to their models, the interaction of relative small changes in a seasonally variable factor (i.e. solar irradiance) with step-change events (i.e. sea-ice break-up) are likely to induce tipping points, by which shallow polar benthic communities may shift from a heterotrophic to an autotrophic state (Clark et al. 2013).

Kelp species were reported to grow mainly during the dark winter period, by mobilization of carbohydrate deposits from summer photosynthesis (Dunton et al. 1982). Some animal species in the Alaskan Arctic showed that during winter there are shifts in the dependency of carbon from phytoplankton to kelp sources (Dunton and Schell 1987). Hence, kelp growth may fuel benthic food webs with carbon during the polar night, though empirical support on this and potentially other ecological consequences of winter-grown kelp tissues are missing (Berge et al. 2015b). Experimental evidence of irradiance effects on Arctic benthic communities from manipulative experiments is scarce. Fricke et al. (2008) showed that algae bleached and died within 4 weeks after transplantation from 8 to 0.5 m water depth in Kongsfjorden. The effects of near-surface conditions were different for 1-year than for 2-year old assemblages, indicating that the timing of altered irradiance levels may be important for the magnitude of light effects. In this transplantation experiment, however, several factors changed besides irradiance levels (e.g. wave exposure), which may also affect the species composition, making conclusions about irradiance effects at the community level difficult. The only experiment manipulating light conditions for field-grown benthic assemblages in the Arctic is the study by Fricke et al. (2011). In contrast to the many reported detrimental UV-effects at the physiological level (reviewed in e.g. Häder et al. 2015), their study revealed few UV-effects on community structure. Younger communities were more sensitive to UV-B radiation than older ones, which may be due to the protective function of some community members, e.g. diatoms, for UV-sensitive taxa. Despite the limited experimental evidence, it becomes apparent that irradiance can affect the structure of benthic communities, but these effects are dependent on other factors (e.g. successional age) and will not affect all community members in the same way.

11.2.3.4 Disturbance

Sea Ice

The near-shore is one of the most disturbed marine habitats worldwide. As a disruptive force, ice-scour is an important structuring factor for Arctic coastal benthic communities (Węsławski et al. 1993; Barnes 1999; Gulliksen and Svensen 2004; Sahade et al. 2004). During winter, only the zone of the coast above the high water line freezes solidly, forming an ice-foot (Ellis 1955). While the latter may physically protect freezing-resistant algae, it also makes colonization of hard substrates by algae and macrofauna extremely difficult (Svendsen 1959; Keats et al. 1989; Barnes 1999; Zacher et al. 2009). Estimates indicate that the total number of macrozoobenthic species in the hard-bottom intertidal of Svalbard (Węsławski et al. 1993; Szymelfenig et al. 1995), Baffin Island (Ellis 1955), Bjørnøya (Węsławski et al. 1997), and Greenland (Sparck 1933; Madsen 1936; Ellis 1955) does not exceed 100 species (Węsławski et al. 2011). On rocky shores (down to depths of a few metres), ice-scour impedes persistent macrobenthos colonization and limits organisms to ice-protected areas, such as crevices and small rock pools (Ellis and Wilce 1961; Zacher et al. 2009; Hop et al. 2012). As a result, biomass is considerably reduced on the exposed coastline (Svendsen 1959; Wilce 1959; Krapp 2002). At ice-disturbed locations (down to 2.5 m water depth), annual and pseudo-perennial algae (in the latter, parts of the thallus are cast off every year) survive the winter as microscopic stages or rhizoidal cushions, which are characterized by high growth rates and short resilience times (Keats et al. 1985; Wiencke et al. 2007; Zacher et al. 2009; Hop et al. 2012). Locations sheltered from drifting ice, such as Hansneset (Fig. 11.1c), are characterised by higher macroalgal species richness in the upper sublittoral zone than ice-exposed sites (Wiencke et al. 2004; Włodarska-Kowalczuk et al. 2009; Hop et al. 2012). The climate-induced reduction of fast ice (e.g. Pavlova et al., Chap. 4) and ice-scouring have also been proposed as the most likely causes for the observed increase in algal biomass and species richness in Kongsfjorden during the last 15 years (Fredriksen et al. 2014; Bartsch et al. 2016).

In Kongsfjorden, icebergs and smaller pieces of ice (i.e. bergy bits, *sensu* Armstrong et al. 1966) calve from five tidewater glaciers (e.g. Dowdeswell and Forsberg 1992), including Kongsbreen (Fig. 11.1c), which is the most active glacier in the Svalbard archipelago (Lefauconnier et al. 1994). Principally, scouring frequency is negatively correlated with water depth, i.e. shallow zones are more frequently disturbed by ice-scour than deeper areas (Dowdeswell and Forsberg 1992; Laudien et al. 2004, 2007).

Studies on the effect of ice on sublittoral hard-bottom communities below 5 m water depth are still lacking from Kongsfjorden. In this fjord, signs of ice-scour on rocky shores are mainly found at Hansneset (J. Laudien pers. obs.), where icebergs scour small, horizontal areas of bedrock. Experimental removal of benthos from rocky shores, simulating the effects of a physical disturbance like ice-scour indicates that complete recovery of these communities may take more than a decade (this review Sect. 11.2.1.2 *Secondary Succession*).

Wave-Exposure

Qualitative and quantitative information about the effects of waves on hard-bottom benthos is missing. Kukliński et al. (2006) recorded more diverse and species-rich bryozoan assemblages on large rather than on small boulders. As a possible explanation for this pattern, they proposed a higher wave-induced turnover rate of small boulders, thereby resetting the colonization process more frequently on small than on large boulders.

Submarine Rock Avalanches

Knowledge on the impact of substrate movements on benthic communities below the low-salinity surface water layer is scarce and mainly covers ecological effects on soft-bottom communities (e.g. Okey 1997). However, substrate sliding is a common event not only in the Arctic (e.g. Hjelstuen et al. 2007), but also in all coastal and continental slopes including a large range of types and scales of seafloor disturbances (e.g. Schuster and Highland 2007). These range from the movement of a few grains to movements of hundreds of square kilometres and disturbances may be very variable in intensity, as well as in their temporal and spatial range (Okey 1997). Submarine rock avalanches destroy biota, but they also open up new space, which may be colonized subsequently by benthic communities. Timing and size of the disturbed area are important factors modulating the colonization process and diversity patterns (e.g. Gutt and Piepenburg 2003).

Near Kvadehuken (Fig. 11.1c), the scour of a submarine rock avalanche was discovered during an investigation using a remotely operated vehicle (ROV) in 2009 (J. Laudien unpubl. data). In a 20 m wide area, the sessile fauna was destroyed from 75 m water depth down to at least 200 m, i.e. at the depth where the ROV transect ended. Only mobile macrofauna was observed in the impacted zone, the green sea urchin *S. droebachiensis* being, by far, the numerically dominant species. No algae were recorded on the disturbed barren ground, in contrast to the surrounding zone (Laudien and Orchard 2012). To the best of our knowledge, no further information on the impacts of rock falls or avalanches in Kongsfjorden exists. Using information on geological characteristics of the sea floor (e.g. lithology, faults, slope, or topography) and coast (e.g. morphology and rivers) may facilitate detection of rock-fall impacted benthos (e.g. Kamp et al. 2008) and spur research about the ecological effects of this type of disturbance.

Sedimentation

Global warming causes glacial retreat and increased river drainage that result in higher sedimentation loads that affect hard-bottom organisms. Sedimentation reduces access of sessile organisms to their resources by, for instance, clogging mouth parts of suspension feeders (Torre et al. 2014), covering photosynthetic active surfaces of algae (Chapman and Fletcher 2002), or increased light attenuation (this review Sect. 11.2.3.3 *Irradiance*). The distance to tidal glaciers should generate a gradient in sedimentation rate, along which sedimentation impact diminishes with increasing distance from a glacier (Holte et al. 1996; Voronkov et al. 2013). We found no studies assessing the effects of sedimentation on entire rocky shore communities. Ronowicz et al. (2008) reported on lower diversity, frequency of occurrence, and sexual output of hydroid assemblages growing epiphytically on kelps near-by than further apart from a tidal glacier in Hornsund Fjord (Fig. 11.1b).

11.2.4 Biotic Factors in Hard-Bottom Habitats

11.2.4.1 Consumers

Grazers and predators strongly alter benthic community structure and functioning in non-polar ecosystems (e.g. Paine 2002; Estes et al. 2011). For Arctic hard-bottom habitats, however, little information exists on consumer feeding preferences and community responses to consumption.

Primary Consumption

The study by Wessels et al. (2006) is to our knowledge the only systematic assessment of feeding preferences for herbivores living in Arctic habitats. This study suggests that only two species of the algae-associated fauna, i.e. the amphipod *Gammarellus homari* and the green sea urchin *S. droebachiensis* significantly feed on algae. While *G. homari* preferred delicate red algae, *S. droebachiensis* preferably consumed leathery kelps (Fig. 11.4). These feeding preferences were, however, not reflected by fatty acid trophic markers, which may be due to low lipid content in grazers or strong fatty-acid modification during algal digestion (Wessels et al. 2012). In contrast to seaweeds in Antarctica (Amsler et al. 2009), Wessels et al. (2006) found few Arctic species of algae (e.g. *Ptilota gunneri* and *Desmarestia viridis*) to be chemically defended against herbivores and that *G. homari*, but not *S. droebachiensis* consumption appeared to be deterred by morphological as well as tissue-specific algal traits. In the middle zone of Kongsfjorden (Fig. 11.1c), lush algal communities dominate the shallow rocky shores (Hop et al. 2016), suggesting that herbivores are unable to control algal biomass throughout the fjord. The notion of negligible grazer effects on Arctic benthos is corroborated by the study of Konar

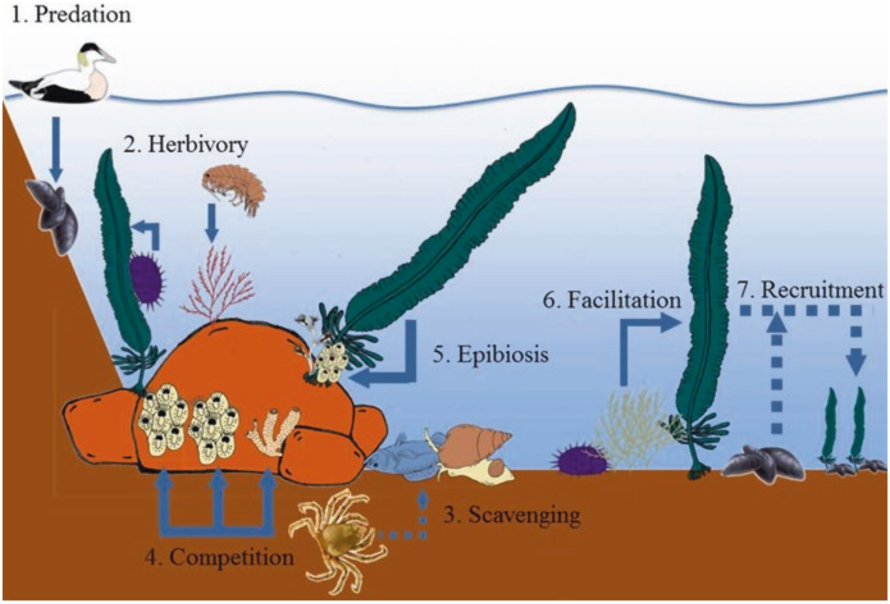

Fig. 11.4 Rocky shores. Main forms of documented (solid line) and hypothesized/scarcely observed (stippled line) biotic drivers of coastal (<30 m) Arctic hard-bottom communities. Consumption by (1) avian predators on benthic invertebrates, (2) benthic grazers on seaweeds, and (3) scavengers such as the crab *Hyas araneus* or the gastropod *Buccinum undatum* on carrion; (4) interference competition among encrusting species (mainly bryozoans); (5) invertebrate and seaweed epibionts on kelp surfaces; (6) associational defence in trophic interactions; (7) recruitment of seaweeds and invertebrates. Line width indicates relative magnitude of effects

(2007) that demonstrated low recolonization on cleared surfaces of caged and uncaged boulders. Nevertheless, persistence of algae-denuded areas in the presence of urchins in Kongsfjorden (Molis et al. 2008) and other sub-Arctic habitats (e.g. Sivertsen 2006) suggest that *S. droebachiensis* consumption will locally maintain barren grounds. The activity of consumers has also been hypothesised by Beuchel and Gulliksen (2008) and Streicher (2014) to be responsible for slow recolonization of rocky areas, although consumer abundance was not manipulated in these studies to draw thorough inferences.

Secondary Consumption

Knowledge on predator-prey interactions of Arctic hard-bottom habitats is extremely scarce. The spider crab (*Hyas araneus*) and the whelk *Buccinum* spec. were observed feeding on fish bait (Fig. 11.4; Markowska et al. 2008) and both species are trophically classified as omnivorous (Legeżyńska 2001; Kaczmarek et al. 2005). The field study by Lippert and Iken (2003) assessed the food value of abundant sessile or sluggish invertebrate species for the natural suite of consumers of Kongsfjorden hard-bottom habitats. Their study showed that the natural assemblage of consumers preferred fish (control food) to invertebrate food. This pattern was principally confirmed in laboratory assays using the non-native sea star *Asterias rubens* as consumer (Lippert and Iken 2003). Lack of preference for the naturally abundant invertebrates may not necessarily result from anti-predator defences, but could also be explained by a relatively high nutritional value of the control food. The study by Lippert et al. (2004) corroborates the notion that anti-predator defences may have been rarely evolved in prey species living on Arctic rocky shores as a result of low predation pressure. Yet, Lippert et al. (2004) only tested the amphipod *Anonyx nugax* as an Arctic predator. Hence, more predatory species need to be tested before generalizations about the frequency of anti-predator defences in and the level of predation pressure on Arctic prey can be inferred.

Food Webs

A large research effort has been undertaken to characterize food webs of the Arctic Ocean (reviewed in e.g. Wassmann et al. 2006; Renaud et al. 2008; Kędra et al. 2015). Studies using, for instance, biochemical markers, such as stable isotopes or fatty acids revealed qualitative descriptions of the structure of numerous local Arctic food webs (e.g. Renaud et al. 2011; McMeans et al. 2013). Although >300 food web studies have been conducted, the general processes governing the structure of Arctic food webs are still not well understood (Kędra et al. 2015). To advance from patterns towards a mechanistic understanding of food webs, several limitations in the research of Arctic food webs have to be overcome. Firstly, spatial limitations exist as studies collating large-scale data sets are missing and there is a strong bias in regional research efforts. For instance, more than 20% of benthic food web studies were conducted in the Canadian Arctic (Kędra et al. 2015). Secondly, taxonomic limitations occur as the number of species considered in food web studies may represent a relatively small fraction of the total species pool. The study by McMeans et al. (2013), for instance, included just four benthic species that dwell on rocky shores. Thirdly, temporal limitations are clearly apparent as few food web studies were conducted during the polar night (but see Berge et al. 2015b; Morata et al. 2015). Fourthly, methodological limitations exist as consistent food web data are yet missing (Kędra et al. 2015). Last but not least, there are conceptual limitations as empirical manipulations in the laboratory and in the field are required to elicit basic (e.g. feeding preferences and consumption rates) and more advanced information (e.g. density-dependent or indirect consumer effects) that drive consumer-prey interactions. The structuring role of the non-consumptive effects of predators (i.e. predation risk) and particle consumption of plants/seaweeds by grazers for benthic food webs, which receive growing attention in non-polar ecological research (Peckarsky et al. 2008), has been thus far neglected in Arctic community ecology research.

11.2.4.2 Facilitation

Facilitation denotes a biological interaction, which is, directly or indirectly, beneficial to at least one participant without being detrimental to the other organism (Bruno et al. 2003). Until recently, facilitative processes have been largely unanticipated and neglected by ecological theory, though necessary for a more integrative understanding of the drivers of community structure and function (Bruno et al. 2003). Positive interactions between Arctic species are known from observational and experimental studies. Seaweeds may serve a species-rich associated fauna as shelter against consumers, substrate, or improve access to food sources, e.g. for filter feeders living attached to kelp blades (this review Sect. 11.2.4.3 *Epibiosis*). A temperature-induced increase in algal biomass in two Svalbard fjords, for instance, was accompanied by higher invertebrate abundance (Kortsch et al. 2012), suggesting that algae facilitated invertebrate subsistence. Teichert et al. (2012) observed that the sheet-like coralline red algae seem to host 55% of the organisms observed in their study sites at Nordkappbukta, Svalbard (see also Chenelot et al. 2008, 2011 for detailed descriptions on corraline algae ecology from the Aleutian Islands). The associated fauna seeks refuge by either living in the gaps between or inside hollow parts of the rhodoliths. By their provision of microhabitats, rhodoliths may enhance diversity in areas of low complexity and, thus, act as ecosystem engineers (Teichert et al. 2014). The rhodoliths themselves profit from giving shelter to grazers such as the chiton *Tonicella rubra* because grazers remove the algal epibionts from the surface of rhodoliths (Teichert et al. 2012). Moreover, associational defences have been documented in Kongsfjorden. There, multi-year persistence of species-rich patches dominated by the kelp *A. esculenta* on an urchin-barren was mediated by the presence of the brown alga *D. viridis* (Molis et al. 2008). Evidence from field experiments suggests that the presence of the chemically defended *D. viridis* reduced the density of *S. droebachiensis*, which has been shown to readily consume *A. esculenta* (Wessels et al. 2006). High concentration of sulphuric acid inside *D. viridis* vacuoles generate pH levels as low as 0.7 (Pelletreau and Muller-Parker 2002) affecting the direction and speed of urchin movements (Molis et al. 2008). Facilitation may also occur across Arctic ecosystems when coastal benthic food chains receive seabird-mediated support from pelagic production. Zmudczyńska-Skarbek et al. (2015) reported that seabirds may fertilize the coastal benthos in the vicinity of a mixed colony of Brünnich's guillemots (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*) in Isfjorden (Fig. 11.1b). However, seabird-derived nutrient enrichment did not affect algal production directly. Rather seabirds indirectly enhanced, at least partly, the supply of food for benthic secondary consumers such as the hermit crab *Pagurus pubescens* via fertilization of phytoplankton, which is consumed by suspension feeders, which are preyed upon by *P. pubescens*.

11.2.4.3 Epibiosis

Epibiosis is the facultative association between two organisms, in which one, i.e. the epibiont, lives attached to the surface of the other organism, i.e. the basibiont (Wahl 1989). Epibiosis is a typical, though not exclusive phenomenon in aquatic environments that incurs a tight interaction between organisms due to spatially close bonds, which may has neutral, positive, or negative effects on the performance of at least one of the associates (Wahl 1989; Karez et al. 2000). There is anecdotal information on epibiosis from the rocky intertidal of Kongsfjorden (Hansen and Haugen 1989; Kukliński et al. 2006). Almost all studies about epibiosis on Arctic rocky shores looked at subtidal algae, mainly kelps (Fig. 11.4), fouled by bryozoans as the most speciose group of epibionts, followed by polychaetes and hydroids (Rozycki and Gruszczyski 1986; Lippert et al. 2001; Carlsen et al. 2007; Włodarska-Kowalczuk et al. 2009). In Hornsund Fjord (Fig. 11.1b), a total of up to 308 animal species may live on kelps, at a mean of 11.5 and a maximum of 47 species on individual kelps (Włodarska-Kowalczuk et al. 2009). Neither species richness nor composition of (i) the total epifauna (Lippert et al. 2001; Włodarska-Kowalczuk et al. 2009), (ii) bryozoans (Carlsen et al. 2007), or (iii) hydroids (Ronowicz et al. 2013) varied significantly between different algal species, suggesting low host-specificity of the algal-attached macrofauna. The richness of epibiotic animal species depended on algal morphology, was variable among kelp parts (Lippert et al. 2001), but independent of algal age (Ronowicz et al. 2008). More animals exist on- and inside the holdfast of kelps than on the lamina or stipe, presumably as a consequence of habitat persistence and superior protection by a holdfast against consumers and wave action (e.g. Włodarska-Kowalczuk et al. 2009).

11.2.4.4 Pathogens and Parasites

The presence of pathogens and parasites are a fundamental and ubiquitous component of ecological systems that helps keeping the abundance of interacting species balanced (Wilson et al. 2013). Despite the occurrence of, for example, parasitic trematodes throughout the Palearctic, comprehensive parasitological research is thus far missing for the coastal habitats around Svalbard (Rokicki 2009). Several intermediate hosts of parasites, including molluscs, crustaceans, and echinoderms live on Arctic rocky shores (Scheibling and Stephenson 1984; Rokicki 2009; Wilson et al. 2013), suggesting that the biotic conditions for the existence of parasites are given. While parasite-induced mass mortalities in the sea urchin *S. droebachiensis* have been reported from sub-Arctic shores (e.g. Skadsheim et al. 1995), this has not been yet recorded for Svalbard coastal waters. The extent of a mass mortality in urchins is correlated with seawater temperature and the transmission of pathogenic agents is effective at ≥8 °C (Scheibling and Stephenson 1984), i.e. above the maximum sea water temperature in west Spitsbergen fjords during the last century (Pavlov et al. 2013), but this may change in a warming Arctic.

11.2.4.5 Competition

The few studies that assessed the role of competition in structuring Arctic hard-bottom communities exclusively considered encrusting species, usually dominated by bryozoans that assembled on boulders (Fig. 11.4). Space is a limiting resource for these species (Konar 2007), which they deplete by spreading over hard substrata and eventually growing over and killing neighbouring species, i.e. interference competition (Barnes and Kukliński 2003). Ecological theory suggests a negligible role of competition under high environmental stress (Menge and Sutherland 1987), which is partly supported empirically by Barnes (2000), who reported of decreasing importance of interspecific competition with increasing latitude in the southern hemisphere. It is also corroborated by the absence of interspecific competition in encrusting Arctic communities growing on boulders in the intertidal (Barnes and Kukliński 2004b), where ice-scour is most intense. However, in subtidal boulder fields (e.g. at Stefansson Sound, Beaufort Sea) and rhodolith beds (e.g. at Nordkappbukta, Fig. 11.1b) interspecific competition was apparent (Dunton et al. 1982; Konar and Iken 2005; Chenelot et al. 2008; Teichert et al. 2012, 2014). Moreover, Barnes and Kukliński (2004a, b) reported on interspecific competition between bryozoans growing on stones in the shallow waters of two Svalbard fjords (Hornsund Fjord and Kongsfjorden, Fig. 11.1b), but also that different aspects of competition (e.g. intensity, transitivity) varied significantly at different spatial scales. The effects of interspecific competition may also explain the temperature-mediated shift from a sea anemone-dominated community to a state, in which filamentous and canopy-forming algae prevail in Kongsfjorden and Smeerenburgfjorden (Kortsch et al. 2012). Presumably, the sea anemone *U. eques* pre-empted the substrate, thereby precluding successful recruitment of inferior competitors such as filamentous algae, which are typical pioneering species in coastal benthic habitats (Connell and Slatyer 1977).

Barnes and Kukliński (2003) found an exceptionally strong, consistent competitive hierarchy among encrusting species (mainly bryozoans) in boulder communities of Hornsund Fjord (Fig. 11.1b). Superior competitors were superior everywhere and inferior competitors were inferior everywhere. Only species with intermediate competitive abilities varied in dominance between sites at the local, but less so at the regional scale (Barnes and Kukliński 2004b). This infers that patterns in species succession can vary between sites, although the end result of this succession will be similar at all locations. Higher taxonomic membership (i.e. phylum affiliation) of encrusting Arctic species was an appropriate predictor for their competitive performance, which decreased from the rare demosponges and ascidians, via the common cheilostome and rare cyclostome bryozoans to the common hydroids, polychaetes, and cirriped crustaceans (Barnes and Kukliński 2004a). Similarly, Konar and Iken (2005) showed that sponges, bryozoans, and tunicates were superior space competitors compared to crustose corallines, while hydroids were the least competitive group in an Alaskan boulder community. As the amount of available space for settlement rather than recruit density determined the level of intensity of competition

(Barnes and Kukliński 2004b), colony size and thus growth rates of the encrusting species are important drivers of competition. Therefore, interspecific competition may be generally low in the Arctic as a result of the relative low growth rates in Arctic encrusting species (Barnes and Kukliński 2005b; Fricke et al. 2008; Konar 2013). In addition, the rare occurrence of competitively superior species (Barnes and Kukliński 2004a) due to, for instance, limited available space for their settlement, favours inferior space competitors such as crustose corallines in an Arctic Alaska boulder community (Konar and Iken 2005). The conclusion that interspecific competition may be generally low in the Arctic is supported by the results of Barnes and Kukliński (2004b) who found that competition intensity varied significantly at the regional scale, i.e. between Arctic and boreal sites. Competitively inferior pioneering species display by and large faster growth rates than superior competitors (Connell and Slatyer 1977), which explains, why intraspecific competition prevails in encrusting Arctic communities (Barnes 2000). In Hornsund Fjord, for instance, nearly 80% of all observed competitive interactions involved intraspecific encounters (Barnes and Kukliński 2003), but varied considerably (at a range of 3–79%) at the local scale, indicating (i) strong patchiness in the conditions that promote competition and (ii) that species succession is repeatedly set back and far from reaching a climax state in these subtidal encrusting communities (Barnes and Kukliński 2005a) as well as in more algae-dominated benthos after even 24 years (Beuchel and Gulliksen 2008, this review Sect. 11.2.1 *Species Succession*). The second notion corroborates the fact that the most inferior space competitor, the bryozoan *Hameria scutulata* was also the most abundant species, showing an exceptionally high proportion (i.e. 97%) of tied encounters with conspecifics.

11.2.4.6 Recruitment

The vast majority of Arctic recruitment research focuses on fish species. The few studies that addressed recruitment onto hard substrata mainly considered encrusting fauna, but rarely algae (Fig. 11.4). Overall, recruit density of Arctic encrusting fauna is about one order of magnitude lower than in most non-polar studies (Barnes and Kukliński 2005b), but clearly higher than in Antarctica (Barnes 2000). According to the model of Menge and Sutherland (1987), low recruitment should increase the importance of physical disturbance over competition and consumer effects in community regulation (this review Sects. 11.2.3.4 *Disturbance* and 11.2.4.5 *Competition*). In terms of taxon richness, recruitment of fauna onto settlement panels deployed in Kongsfjorden, but also in Isfjorden (Figs. 11.1b and 11.3), was comparable (20 taxa) to what has been reported for temperate sites (Barnes and Kukliński 2005b; Schmiing 2005). Yet, apart from the tube dwelling polychaete *Spirorbis tridentatus* as the dominating recruiting species (80–93% of total recruits), the remaining recruits were all bryozoans, indicating exceptionally low recruit diversity at higher taxonomic (i.e. phylum) levels. Studies including benthic photoautotrophs in their sampling indicate relatively high recruitment success of diatoms and green, filamentous macroalgae in Kongsfjorden (Fricke et al. 2008). In striking contrast, algal recruitment was negligible even after 7 years in an experiment conducted in Arctic Alaska in the Beaufort Sea (Konar 2013). Grazer activity does not explain this limited recruitment success (this review Sect. 11.2.1 *Species Succession*). Konar (2013) suspects that, in addition to low recruitment intensity, recruitment of at least some Arctic benthic biota may also be infrequent (at a decadal range) compared to that in non-polar habitats. Barnes and Kukliński (2005b) also inferred rarity of recruitment events as an explanation for the absence of sponge, ascidian, and barnacle recruits in areas that were surrounded by reproductive adults. Hence, vegetative, lateral regrowth (e.g. of sponges and coralline algae), rather than larval supply seems to be a faster, i.e. more important and efficient mechanism for recolonization of, for example, boulders (Konar 2013).

To our knowledge, only MacGinitie (1955) and Kukliński et al. (2013) reported on seasonal patterns in larval presence of Arctic benthos, with the latter also studying recruitment. In Adventfjorden (Fig. 11.1b), the meroplanktonic larvae of most species occurred with pronounced abundance for a few weeks in spring or early summer, while larvae were absent during winter (Kukliński et al. 2013). Surprisingly, settlement intensity of most benthic invertebrates peaked in July, i.e. after the phytoplankton bloom. This mismatch decoupled recruits from a major food supply. Probably, alternative food sources such as detritus (Renaud et al. 2015a) may be available for recruits on rocky shores in late summer and autumn. Settlement greatly vanished until and throughout winter. In the Chukchi Sea, larvae of many species were present throughout the winter (MacGinitie 1955).

11.3 Sedimentary Habitats

In contrast to hard-bottom habitats, soft-bottoms offer extensive three-dimensional substrate, in which many inhabitants (infauna) find shelter. The substrate instability of sedimentary shores strongly limits algal recruitment and survival. Hence, the standing stock of autochthonous, photoautotroph biomass is less in soft- than hard-bottom areas and the fauna of the former depends more on pelagic primary production than the latter. For these and other reasons, the soft-bottom communities respond differently to environmental factors and are, in part, structured by different processes than hard-bottom communities. Furthermore, different methods are used to sample hard- and soft-bottom communities, due to differences in substrate characteristics. This may be one reason why hard- and soft-bottom communities are frequently studied separately (Table 11.2), despite their frequent spatial proximity in coastal environments (Voronkov et al. 2016). Similar to studies on hard-bottoms, mensurative approaches prevail, but manipulative experiments have been very scarcely applied in studying the structure and diversity of soft-bottom benthos in Svalbard (Table 11.2).

Table 11.2 List of publications published since Hop et al. (2002) that report on the effects of abiotic and biotic factors on the ecology of species assemblages in hard- (H) and soft-bottom (S) habitats in Kongsfjorden

Studied factor	Habitat	Location	Study type	Target organisms	References
Succession	H	KF	Mensurative	Epifauna	Schmiing (2005)
	H	KF	Mensurative	Epifauna	Beuchel and Gulliksen (2008)
	H	KF	Mensurative	Epifauna	Fricke et al. (2008)
	H	KF	Mensurative	Epifauna	Streicher (2014)
	H	KF	Mensurative	Epifauna, macroalgae	Schwalfenberg (2011)
Long-term change	H	IF	Observational	*Mytilus edulis*	Berge et al. (2005)
	H	KF	Mensurative	Epifauna, macroalgae	Beuchel et al. (2006)
	H	HSF	Observational	Epifauna, macroalgae	Węsławski et al. (2010)
	H	KF,SBF	Mensurative	Epifauna, macroalgae	Kortsch et al. (2012)
	H	KF	Observational	Seaweeds	Fredriksen et al. (2014)
	H	KF	Mensurative	Epifauna	Paar et al. (2016)
	H	KF	Mensurative	Macroalgae	Bartsch et al. (2016)
	H,S	BF,IF,GF,BB,YB,YH	Mensurative	Decapod fauna	Berge et al. (2009)
	S	MF	Mensurative	Macrofauna	Renaud et al. (2007)
	S	KF	Mensurative	Macrofauna	Kędra et al. (2010a, b)
	S	KF	Mensurative	Macrofauna	Węsławski et al. (2011)
Zonation	H	IF to WF	Mensurative	Epifauna	Hansen and Haugen (1989)
	H	KF	Mensurative	Epifauna	Sahade et al. (2004)
	H	KF	Observational	Macroalgae	Hop et al. (2012)
	H	KF	Mensurative	Epifauna	Laudien and Orchard (2012)
	H	KF	Mensurative	Epifauna	Voronkov et al. (2013)
	S	KF	Mensurative	Macrofauna	Kaczmarek et al. (2005)
	S	KF	Observational	Meio-, macrofauna	Bick and Arlt (2005)
Irradiance	H	KF	Manipulative	Epifauna, macroalgae	Fricke et al. (2011)
Disturbance	H	Alaska	Manipulative	Epifauna, macroalgae	Konar (2007, 2013)

	S	KF	Mensurative	Macrobenthos, infauna	Laudien et al. (2007), Nowak et al. (2016)
	S	KF	Mensurative	Meiofauna	Veit-Köhler et al. (2008)
	S	KF	Manipulative	Macrobenthos	Petrowski et al. (2016b)
Bioturbation	S	KF	Manipulative	Macrofauna	Petrowski et al. (2016a)
Sedimentation consumption	H	HSF	Mensurative	Epiphytic hydroids	Ronowicz et al. (2008)
	S	KF	Mensurative	Macrozoobenthos	Włodarska-Kowalczuk and Pearson (2004)
	S	KF	Mensurative	Infauna	Włodarska-Kowalczuk et al. (2005, 2012), Kędra et al. (2010a), Kendal et al. (2003), and Włodarska-Kowalczuk and Kędra (2007)
	S	HSF	Mensurative	Infauna	Włodarska-Kowalczuk and Węsławski (2008), and Włodarska-Kowalczuk et al. (2013)
	S	IF	Mensurative	Infauna	Włodarska-Kowalczuk et al. (2007)
	H	KF	Manipulative	Natural suite of predators	Lippert and Iken (2003)
	H	KF	Manipulative, lab	*Anonyx nugax*	Lippert et al. (2004)
	H	KF	Manipulative, lab	19 seaweeds, 2 grazer species	Wessels et al. (2006)
	H	Greenland	Observational	Eider prey items	Merkel et al. (2007a, b)
	H	GF	Observational	*Hyas araneas*, *Buccinum* sp.	Markowska et al. (2008)
	H	KF	Manipulative, lab	9 seaweeds, 2 grazer species	Wessels et al. (2012)
	H	Nunavut	Observational	Species of 4 functional groups	McMeans et al. (2013)
	S	KF	Mensurative	Amphipods	Legeżyńska (2001)
	S	KF	Mensurative	Seals	Lydersen et al. (2001)

(continued)

Table 11.2 (continued)

Studied factor	Habitat	Location	Study type	Target organisms	References
	S	KF	Mensurative	Macrofauna	McMahon et al. (2006)
	S	KF	Mensurative	Amphipods	Legeżyńska (2008)
	S	KF	Manipulative	Macrofauna	Petrowski et al. (2016a)
Competition	H	HSF	Observational	Bryozoans	Barnes and Kukliński (2003)
	H	KF & HSF	Observational	Encrusting taxa	Barnes and Kukliński (2004a)
	H	KF & HSF	Observational	Encrusting taxa	Barnes and Kukliński (2004b)
	H	KF & HSF	Observational	Encrusting taxa	Barnes and Kukliński (2005a)
	H	KF	Observational	Bryozoans	Kukliński et al. (2006)
Recruitment	H	IF	Observational	Encrusting taxa	Barnes and Kukliński (2005b)
	H	KF	Manipulative	Kelp	Wiencke et al. (2006)
	H	KF	Manipulative, lab	Kelp	Müller et al. (2008)
	H	AF	Observational	Encrusting species	Kukliński et al. (2013)
Facilitation	H	KF	Manipulative	Epifauna	Molis et al. (2008)
	H	Svalbard	Observational	Epifauna	Teichert et al. (2012)
	H	IF	Mensurative	Selected fauna of trophic levels	Zmudczyńska-Skarbek et al. (2015)
Epibiosis	H	KF	Mensurative	Seaweed epibionts	Lippert et al. (2001)
	H	KF	Mensurative	Seaweed epibionts	Carlsen et al. (2007)
	H	HSF	Mensurative	Seaweed epibionts	Włodarska-Kowalczuk et al. (2009)
	H	14 Svalbard sites	Mensurative	Hydroids	Ronowicz et al. (2013)
	H	Svalbard	Mensurative	Epibiontic hydroids	Ronowicz et al. (2013)
	H	HSF	Mensurative	Epibiontic hydroids	Ronowicz et al. (2013)

Exemplary studies from Svalbard and, if appropriate, elsewhere in the Arctic were only included, if no study from Kongsfjorden was found

Abbreviation of locations: *KF* Kongsfjorden, *HSF* Hornsund Fjord, *SBF* Smeerenburgfjorden, *IF* Isfjorden, *AF* Adventfjorden, *GF* Grønfjorden, *WF* Wijdefjorden, *MF* van Mijenfjord, *MGF* Magdalenefjorden

11.3.1 Species Succession

Generally, very few studies have addressed the succession of species in Arctic soft-bottoms. This is particularly so for research on primary succession, while several studies have investigated the recolonization of disturbed sedimentary habitats. Here, most attention has been given to the recolonization of ice-scours.

11.3.1.1 Primary Succession

In Kongsfjorden, the initial colonization of soft-bottom meiofauna was studied by Veit-Köhler et al. (2008) and that of the macrofauna by Nowak (2012) and Nowak et al. (2016). At a depth of 20 m, Veit-Köhler et al. (2008) deployed containers filled with organism-free sediments to follow the succession of species and to compare the species composition of experimental communities to that of ambient communities. While the total number of meiofauna individuals reached levels of ambient communities within 1 year, the composition of meiofauna species remained different between experimental and ambient communities throughout the period. In the succession of macrofauna a shift was observed from pioneering species (e.g. the cumacean *Lamprops fuscatus*) to more specialised taxa, as well as from surface detritivores towards subsurface detritivores (Alvsvåg et al. 2009). Species composition of experimental and unmanipulated macrofauna communities was comparable after 3 years, but changed in subsequent years, probably due to elevated water temperature, which kept the fjord ice-free. Several species of naturally abundant macrofauna, e.g. the polychaete *Dipolydora quadrilobata*, did not settle in experimental plots. The studies by Veit-Köhler et al. (2008) and Nowak et al. (2016) demonstrate that neither meio- nor macrofauna develop mature communities within 3 years, indicating the possibility of long-lasting disturbance effects on Arctic soft-bottom benthos.

11.3.1.2 Secondary Succession

In Arctic Canada, the recolonization of disturbed, i.e. ice-scoured, soft-bottoms is characterized by a clear disturbance-associated fauna that shows a distinct species composition compared to communities of unscoured areas (Conlan et al. 1998). As a result, soft-bottom communities at a depth of 5 m, which get frequently ice-scoured, feature a more disturbance-associated fauna than communities at greater depth. This pattern has also been observed in Kongsfjorden (Laudien et al. 2007). Recently ice-scoured soft-bottoms host pioneering species, such as cumaceans and polychaetes (e.g. Capitellidae and Spionidae) (Conlan and Kvitek 2005). The abundance and biomass of the scour-associated fauna increased with scour age, but did not exceed that of unscoured areas. Species composition of scour-associated communities was, however, different for many years compared to that of communities inhabiting unscoured areas (Conlan and Kvitek 2005). Recovery of ice-scoured soft-bottom communities had reached about 75% of pre-scour conditions after 8–9 years, indicating slow recolonization.

11.3.2 Long-Term Change

Each summer since 1997, the soft-bottom macrofauna of Kongsfjorden has been sampled by the Institute of Oceanology PAN (IOPAN, Sopot, Poland) with a van Veen grab (sediments sieved on 0.5 mm sieve) at three stations: (i) Kongsbreen glacial bay (N78.89 E12.47) in the inner zone at 90 m, (ii) close to Blomstrandøya (N78.99 E11.98) in the transitional zone at 80 m, and (iii) in the middle zone (N78.99 E11.57) at 270 m (Figs. 11.1c). The three stations represent the gradual change in benthic community composition along the fjord axis (from the taxonomically and functionally impoverished communities of the glacier-impacted inner basin to the more diverse communities inhabiting the stable sediments at the entrance of the fjord) as documented by Włodarska-Kowalczuk and Pearson (2004). Although the stations are located at different depths, this should not affect the comparison of communities between stations. Włodarska-Kowalczuk et al. (2005) showed that density and biomass of macrozoobenthos in Kongsfjorden were not significantly correlated with depth between 40 and 380 m, while there was no or a very weak relationship between diversity and depth. The other two benthic monitoring programs in Svalbard waters comprise (i) the Hausgarten program, in which 15 stations off Kongsfjorden at depths from 1,000 to 5,500 m have been sampled since 1999 by the Alfred Wegener Institute Helmholtz Centre of Polar and Marine Research (described in Soltwedel et al. 2005), and (ii) three stations along the fjord axis of Hornsund at depths from 80 to 230 m (sampled since 2001 by the IOPAN, JM Węsławski unpubl. data) (Fig. 11.1b). The first published results from the Kongsfjorden monitoring show the temporal stability of benthic species richness at the station located in the inner zone, in Kongsbreen glacial bay (Fig. 11.1c). Species richness remained at the level of about 20 species (with very little variation among the replicate samples) throughout the period from 1997 to 2008 (Węsławski et al. 2011). The number of species recorded in the middle zone of Kongsfjorden was much more variable and strongly varied inter-annually with a general trend of increase – from below 60 species per sample in 1997 to almost 80 species per sample in 2008. Węsławski et al. (2011) attributed the temporal stability of the fauna in the inner zone to a much lower interannual variability in hydrological conditions as these parts of Kongsfjorden are isolated by sills or shallows (as Lovénøyane shallows) from the influence of oceanic water masses. The decade-long stability in diversity and species composition within the inner basins, isolated from the open sea, was also shown in van Mijenfjorden (Fig. 11.1b) where stations studied in 1980 were revisited in 2000–2001 (Renaud et al. 2007). A similar study in Kongsfjorden compared fauna sampled at the same stations in 1997–1998 and 2006 (Kędra et al. 2010b). They studied 31 stations located throughout the fjord at depths ranging from 27 to 365 m. The basic separation of the fauna into the communities – the one inhabiting the inner zone and the one in the central basin (including the Hop et al. [2002] transitional, middle and outer zones) was clearly visible in both sampling periods. In the inner zone, the macrobenthic density, biomass, species richness, and diversity did not differ significantly between the two sampling periods and species composition differed little between 1997–1998 and 2006. In the central basin, some changes in the attributes of benthic communities were observed. Firstly, the separation of the fauna into the two associations (transitional and middle zones) documented in 1997–1998 was not visible in samples collected in 2006. Species richness, diversity, and total biomass increased significantly between the two sampling periods. Also, an increase in relative density of annelids and a decrease in the relative density of molluscs were noted. Within the annelid group, an increase in the number of tube-dwelling species such as the polychaetes *Maldane sarsi* and *Laene ebranchiata* was observed. The warming of fjord water in the central basin may have resulted in increased pelagic primary productivity, further reflected in the higher concentrations of organic matter in sediment and the increase in benthic biomass as documented by Kędra et al. (2010b).

For epifauna, the extensive study by Berge et al. (2009) of decapod fauna in Isfjorden compared the communities sampled in 1908, 1958, and 2007. Their study showed that the species composition remained stable, but the relative proportion of dominant taxa changed over the years. They related the observed change from specialized shrimp predators towards more opportunistic, scavenging crabs to increased levels of disturbance from more trawling activities and climate fluctuations.

11.3.3 Abiotic Factors in Soft-Bottom Habitats

Substrate stability in sedimentary habitats is greatly affected by a number of abiotic factors, of which several have been carefully studied, especially scouring by icebergs. Interestingly, the more direct effects of temperature, salinity, and wave-exposure, typically studied with regard to ecology of communities of the temperate zone, and to a certain degree of Arctic hard-bottom habitats, have achieved less attention in the research of Arctic sedimentary habitats.

11.3.3.1 Irradiance

To the northeast of Spitsbergen, i.e. between 79° and 81°, light conditions are insufficient for primary production by late September (Eilertsen et al. 1989) and a seasonal peak in pelagic biomass production has been reported for several Arctic locations (for an overview see Węsławski et al. 1991). Consequently, the supply of fresh food from the water column to the benthos is highly seasonal. This, together with lower water temperature during the following winter months may reduce growth of some (e.g. Iceland cockle *Clinocardium ciliatum*), but not all filter-feeding species (e.g. Greenland smoothcockle *Serripes groenlandicus*), as the study by Ambrose et al. (2012) suggests. An *in vitro* experiment with intact sediment cores sampled during the polar night revealed that infauna activities quickly increased after experimental addition of fresh food (Morata et al. 2015).

11.3.3.2 Disturbance

Icebergs

Scouring by icebergs is among the most significant disturbances that coastal polar ecosystems experience (Gutt and Starmans 2001). For Brandal, a soft-bottom site in the middle zone of Kongsfjorden (Fig. 11.1c), empirical data suggest that 17, 4, and 0.5% of icebergs plough the ground at 5, 10, and 21 m depth, respectively (Dowdeswell and Forsberg 1992; Laudien et al. 2007). Large scratches, where the benthos is disturbed by grounded ice, can commonly be observed at shallow sublittoral areas in the inner zone of Kongsfjorden (Laudien et al. 2007). Besides causing high benthic faunal mortality, ice-scour also changes sediment characteristics, bottom topography, and near-bottom current regimes, resulting in resuspension and transport of sediments (Woodworth-Lynas et al. 1991; Gutt 2001; Barnes and Conlan 2007). In addition, scour depressions may be affected by winter infill of brine, which causes local hypoxia (Kvitek et al. 1998; Barnes and Conlan 2007). Overall, the impact of ice-scour causes changes in the abundance, diversity, biomass, and species composition of soft-bottom communities and presumably shifts in ecosystem processes (e.g. bioturbation intensity, resource use) and function (e.g. in primary productivity or nutrient cycling) (Conlan et al. 1998; Gutt 2001; Conlan and Kvitek 2005; Laudien et al. 2007).

The ‘Intermediate Disturbance Hypothesis’ (IDH) (Connell 1978; Huston 1979) states that biotopes affected by moderate disturbance are characterized by higher diversity. In contrast, frequently disturbed habitats are only colonized by pioneer communities, while mature and less diverse assemblages dominate zones with low disturbance impact. Laudien et al. (2007) provide evidence that the soft-bottom communities of Kongsfjorden at 30 m water depth, which are rarely affected by ice-scour, are characterized by lower species richness (species richness of a number of sampling units from a site of defined area, i.e. SR_S *sensu* Gray 2000). Knowledge on intra- and interspecific competition of soft-bottom fauna from this ecosystem is scarce. The pattern of SR_S observed may, however, be explained by competitive exclusion of species. With moderately increasing rate and intensity of ice-scouring at intermediate water depth, the potential competition for space and food (Wilson 1990) of dominating species would be mitigated by the disturbance, reducing the abundance of competitively superior species. Thus, inferior competitors co-occur, resulting in higher species richness and manifold life strategies (Węsławski et al. 2011). At shallow water depth, ice-scour is frequent and intense, and may locally result in low diversity and biomass. Results from benthic assemblages of a moderately scoured (yearly 1–7 times) habitat at Barrow Strait (Conlan and Kvitek 2005) also support the IDH. They found that macrofaunal recolonization of Arctic ice-scours progressed as a linear increase in resemblance from the scoured relative to the unscoured community. The significant correlation of the community parameters with the scour age also supports the IDH. Species succession upon ice impact results in a variety of simultaneous stages of recolonization, which characterise the impacted grounds and thus beta-diversity increases on a larger scale (Conlan and Kvitek 2005).

Global warming and resulting higher calving activities of glaciers will increase the level of physical disturbance caused by ice scouring for high-latitude, near-shore benthic communities in the coming decades. In the long term, however, physical impact will be reduced as retreating glaciers will become disconnected from the sea (Węsławski et al. 2011). At present, five tidewater glaciers calve into Kongsfjorden and the icebergs drift through the fjord. As a result of their fast diminishment, >75% of the icebergs are likely to melt in less than 2 days (Dowdeswell and Forsberg 1992), with the effects on the benthos varying along the fjord axis.

Whiplash

Besides icebergs, though on a smaller spatial scale, movements of individual kelp thalli feature another source of physical disturbance for soft-bottom communities. A field experiment conducted by Petrowski et al. (2016a) revealed that disturbance by movements of a *Saccharina latissima* thallus reduced the number of individuals and species in a soft-bottom community in Kongsfjorden by as much as 49% and 36%, respectively. Hence, detached algae may promote small-scale patchiness in coastal sedimentary areas.

Sedimentation

Sediment input of terrigenous material through river drainage and glacial inflow is a major structuring force of Arctic soft-bottom communities (e. g. Feder and Jewett 1988; Blanchard et al. 2010). For Kongsfjorden, fluxes of particulate inorganic matter of up to 800 g m^{-2} day^{-1} have been reported in front of Kongsbreen glacier (Svendsen et al. 2002). Sediment load decreased gradually with distance from glaciers (Paar 2012) and was <25 g m^{-2} day^{-1} in the outer zone of Kongsfjorden (Zajączkowski 2008). Sedimentation of inorganic material is particularly stressful and energetically expensive to most filter feeders, which have to remove mineral particles to minimize clogging of feeding and respiration organs (Moore 1977). Additionally, the proportion of organic material decreases with increasing turbidity, which results in more intensive feeding efforts. Likewise, phytoplankton and benthic primary production are depressed in highly turbid surface waters, lowering feeding efficacy of filter feeders (Moore 1977). The deposition of inorganic material also hinders settlement of larvae and stresses benthic species, which need to maintain contact with the sediment surface (Rhoads and Young 1970; Fetzer et al. 2002). Thus, sedimentation strongly modulates the community structure of Arctic fjord communities.

In zones with high sedimentation impact, infaunal organisms are smaller, more mobile, less abundant, and do not penetrate as deeply into the substrate as conspecifics of less impacted zones (Hop et al. 2002; Włodarska-Kowalczuk and Pearson 2004; Blanchard et al. 2010). Consequently, infaunal communities near glaciers tend to be less complex and diverse than those in the outer zone of Kongsfjorden (Fig. 11.1c), where sedimentation impact is less strong (Kaczmarek et al. 2005; Włodarska-Kowalczuk et al. 2005, 2012). The pattern of decreased diversity in the glacial-impacted inner basin of Kongsfjorden is apparent at the species level and higher taxonomic levels of macrobenthos, as well as major taxonomic groups comprising the soft-bottom macrobenthic community (Wlodarska-Kowalczuk et al. 2007). Declining biodiversity was also reported with decreasing distance to glaciers or glacial outflows in other Arctic fjords for soft- and hard-bottom communities (Kendall 1994; Holte et al. 1996; Włodarska-Kowalczuk and Węsławski 1996; Włodarska-Kowalczuk et al. 2007, 2013). The physically-controlled communities in glacial bays were less diverse and more homogenous in terms of spatial variability compared to the benthic communities in outer basins (Kendall et al. 2003; Włodarska-Kowalczuk and Węsławski 2008).

Close to the glacier margin in Kongsfjorden, small mobile bivalves such as *Thyasira dunbarii*, *Yoldiella lenticula*, and *Y. solidula* dominate the assemblage (Włodarska-Kowalczuk and Pearson 2004; Kędra et al. 2010b). The latter are mobile deposit-feeding bivalves, which are able to maintain their vertical position in the uppermost layers of unstable, rapidly depositing sediment (Ockelmann 1958). The small, mobile polychaete *Chone* cf. *paucibranchiata*, which can feed on suspended and deposited organic particles (Cochrane 2003), is numerically dominating in this habitat.

Moderate levels of sedimentation in the middle zone of Kongsfjorden allow coexistence of sessile tube-building (e.g. *Maldane sarsi, L. ebranchiata*) and motile polychaetes (e.g. *Cossura longocirrata*), together with mobile detritus-feeding bivalves (Wlodarska-Kowalczuk and Pearson 2004; Wlodarska-Kowalczuk et al. 2005, 2012; Kędra et al. 2010b). The progressive increase in less mobile, larger organisms that also penetrate deeper into the sediment, as well as the increasing fraction of bioturbators and suspension feeding fauna, and concomitant increase in complexity in physical community structure, taxonomic and functional diversity, characterize the soft-bottom community down fjord (Elverhøi et al. 1993; Włodarska-Kowalczuk and Pearson 2004; Włodarska-Kowalczuk et al. 2005, 2012; Kędra et al. 2010b). This is accompanied by reduced turbidity and sedimentation (Zajaczkowski 2008; Paar 2012).

While surface deposit-feeders and sub-surface detritivores dominate the Kongsfjorden inner zone, their contribution diminishes in the middle zone of the fjord (Fig. 11.1c), where the abundance of suspension feeders increases (Włodarska-Kowalczuk et al. 2005; Laudien et al. 2007). This pattern reflects the general trend that deposit-feeders are of greater importance towards glacier margins and with intensified glacier activity (Syvitski et al. 1989; Włodarska-Kowalczuk and Pearson 2004).

The biomass of soft-bottom communities decreases toward glacial sediment sources, i.e. rivers and glacier margins (Feder and Matheke 1980; Włodarska-Kowalczuk et al. 1998; Włodarska-Kowalczuk et al. 2005, 2007; Laudien et al. 2007; Blanchard et al. 2010). The high concentration of suspended inorganic matter in front of glaciers proximately reduces irradiance and ultimately depresses primary production. This is reflected in a scarcity of food accessible to sub-surface detritivorous fauna (Gorlich et al. 1987). However, a relationship between microphytobenthic biomass and turbidity at 5 m water depth along the longitudinal axis of Kongsfjorden (excluding areas in front of the glaciers) was not detected (Woelfel et al. 2010).

Ongoing warming of the coastal waters around Svalbard is predicted to increase the natural glacial disturbance in the inner zone of Kongsfjorden (Kędra et al. 2010b). This will increase glacial run-off and river discharge into the fjord leading to increased siltation, lower salinity, and a reduction in the depth of the euphotic zone. As a result, Węsławski et al. (2011) assume that coastal habitats will become more homogenous with biodiversity subsequently decreasing. By comparing soft-bottom community data from 1997 to 1998 with the one from 2006, changes in structure, diversity, and species composition are already evident in the central basin of Kongsfjorden (Kędra et al. 2010b). Blomstrandbreen glacier (Fig. 11.1c) significantly retreated within the last two decades. This has increased river run-off (Nowak and Hodson 2013) and changed the input of sediment (Lantuit et al. 2012). Kędra et al. (2010b) suggest that a decreased impact of sedimentation on the benthic fauna may be the reason for the reduced abundance of species typical for glacial bays in the central part of the fjord. In the long-term, glaciers may retreat extensively or disappear, which should improve water transparency. This should restructure Arctic coastal habitats and communities adjacent to fjords and force them into a new state (Węsławski et al. 2011).

11.3.4 Biotic Factors in Soft-Bottom Habitats

Numerous studies assessed species distribution patterns of Kongsfjorden soft-bottom benthos and considered mainly the role of abiotic factors for the generation of these patterns (e.g. Włodarska-Kowalczuk and Pearson 2004; Włodarska-Kowalczuk et al. 2005; Laudien et al. 2007; Kędra et al. 2010b; Węsławski et al. 2011). Little information is available, however, on the role of biotic factors affecting soft-bottom species assemblages at higher latitude (Table 11.2). We found no information on whether and how facilitation, epibionts, pathogens or parasites, and recruitment affect the structure and diversity of soft-bottom species assemblages. Therefore, this part of the review focuses on those biotic factors that are generally assumed to be important for sedimentary marine ecosystems, i.e. consumption, competition, and bioturbation (Woodin 1999), and potentially so for the coastal soft-bottom areas in Kongsfjorden (Fig. 11.5).

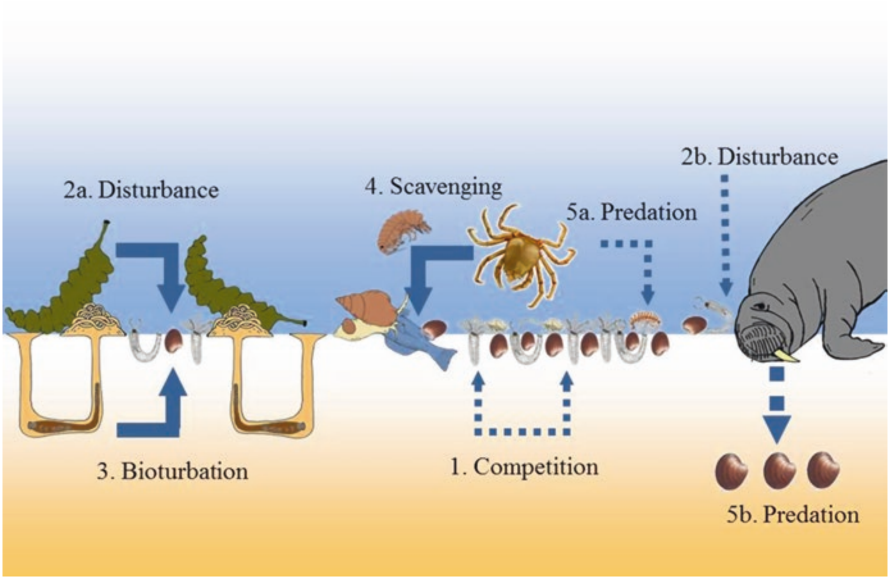

Fig. 11.5 Sedimentary shores. Main forms of documented (solid line) and hypothesized/scarcely observed (stippled line) biotic drivers of Arctic soft-bottom communities (coastal to 400 m water depth). (1) Competition for space among infauna species; Disturbance by (2a) movements of detached kelps, (2b) foraging mammals, and (3) burrowing of bioturbators such as the lugworm *Arenicola marina*; Consumption by (4) scavengers such as amphipods, *Buccinum undatum*, and *Hyas araneus* on carrion, (5a) benthic predators such as *H. araneus* (presumably density-dependent), and (5b) carnivorous mammals. Line width indicates relative magnitude of effects

11.3.4.1 Consumers

Arctic soft-bottom communities depend on the deposition of organic material as food that originates from pelagic (e.g. Grebmeier and Barry 1991), benthic (e.g. Renaud et al. 2015a), or sympagic (e.g. Sun et al. 2009) production.

Primary Consumption

Besides the input of organic matter from the outer shelf, i.e. outside Kongsfjorden, the sedimentation of phytoplankton and ice-algae produced inside Kongsfjorden offers additional large amounts of food for benthic organisms (McMahon et al. 2006; Sun et al. 2007; Kim et al. 2011; Kuliński et al. 2014; Morata et al. 2015). Furthermore, macroalgae may also contribute to the input of organic material into soft-bottom areas down to 900 m after their detachment from rocky shores (Krumhansl and Scheibling 2012). In Kongsfjorden, Petrowski et al. (2016a) documented that detached kelp covered, on average, 11% of the seafloor at a shallow sedimentary site (Fig. 11.6), although spatial dynamics were high (Buschbaum et al. unpubl. data). The accumulation rate of detached macroalgae at deeper parts

Fig. 11.6 Natural accumulation of detached seaweeds (mainly *Saccharina latissima*) at Brandal, Kongsfjorden. (Photo: C. Buschbaum)

of Kongsfjorden is unknown as is the consumption rate of macroalgal detritus by soft-bottom fauna and how this may affect food web structure. Using stable isotopes, however, Renaud et al. (2015a) have shown that in another Svalbard fjord, in Isfjorden (Fig. 11.1c), organic carbon originating from kelp may contribute >50% to the diet of several suspension-feeding bivalves. Future availability of kelp as a food source for benthic fauna will presumably increase as a result of a warming-induced expansion of vegetated coastal habitats (Kortsch et al. 2012; Krause-Jensen and Duarte 2014) and the projected intensification of storms (Young et al. 2011). Arctic subtidal shallow soft-bottom areas down to 30 m water depth can also show high microphytobenthos productivity, which may exceed pelagic primary production (Glud et al. 2009; reviewed in Karsten et al., Chap. 8). Sevilgen et al. (2014), for instance, found that the summer primary production of benthic microalgae in a subtidal nearshore area of Kongsfjorden is similar to that of temperate sedimentary sites and constitutes an additional important food source for the densely populated benthic animal community.

The concentration of particulate organic carbon (POC) in sediments decreases from about 10–12 mg POC g^{-1} sediment in the outer zone to 2 mg g^{-1} in the inner zone of Kongsfjorden (Fig. 11.1c; Kuliński et al. 2014), similar to other Svalbard fjords (Winkelmann and Knies 2005). That trend is at least partly explained by the presence of three retreating tidal glaciers in the inner zone of Kongsfjorden. The glacial meltdown increases water turbidity in the inner zone through the release of terrigenous material, which ultimately lowers pelagic primary production and the concentration of organic matter on the seafloor (Włodarska-Kowalczuk and Pearson

2004). Kim et al. (2011) documented also a significant decrease of marine organic matter contribution from 55% in the outer zone to 9% in the inner zone (based on $\Delta^{14}C$ data and the concentration of retene, i.e. a compound formed upon maturation of higher plant triterpenoids). The lower quantity of organic matter and the glacier-induced disturbance (i.e. high water turbidity, high sedimentation rate of mineral matter, unstable sediment, and ice-scour) result in decreased benthic biomass and diversity in the Kongsfjorden glacial bays (Włodarska-Kowalczuk et al. 2005; Kędra et al. 2010b).

Despite the pronounced seasonality in Arctic primary production, benthic food-web structure appears to be quite stable in Kongsfjorden between winter and summer (Kędra et al. 2012). Additionally, sediment respiration did not vary seasonally at greater depth (Berge et al. 2015b). Likewise, standing stock and diversity of soft-bottom organisms remained similar at shallow (Kędra et al. 2011) and greater depth (Włodarska-Kowalczuk et al. 2016). This evidence indicates that food reserves of labile POC may be stored in Kongsfjorden sediment year-round to support benthic standing stocks and activity (see also the ‘Food Bank Theory’ developed for the Antarctic shelf, Mincks et al. 2005; Glover et al. 2008; McClintic et al. 2008; Smith and DeMaster 2008). The seasonal stability of Kongsfjorden in May–June and September can be ascribed to two phytoplankton blooms occurring near the mouth of the fjord (Hegseth et al., Chap. 6). These blooms cause multiple input of fresh organic material to the area. This can be quickly used by benthic organisms, but may also serve as more continuous food source for polar deposit- and suspension-feeders, which are quite flexible in their food choice and are also able to use older, resuspended organic matter (Gili et al. 2001; Renaud et al. 2011; Kędra et al. 2012). Berge et al. (2015a) and Włodarska-Kowalczuk et al. (2016) suggest that the insensitivity of benthic biota to the strong variability in pelagic productivity in Kongsfjorden may also be related to the large contribution of benthic macroalgae-derived materials. The latter is part of the diet of benthic consumers, as recently reported from Isfjorden by Renaud et al. (2015a). Thus, the lack of seasonal effects in biomass and diversity of benthic communities in Kongsfjorden may strongly differ from other, less productive fjords. For example in Rijpfjorden (Fig. 11.1b), Morata et al. (2015) documented lower benthic biomass in winter than in summer, but a strong, quick increase in activity of benthic organisms (collected during polar night) in response to experimentally added food to the sediment.

Secondary Consumption

Modes of consumption in Arctic soft-bottom fauna comprise suspension- and deposit-feeding, grazing, predation, and scavenging (Feder et al. 2005, 2007; Kaczmarek et al. 2005; Tamelander et al. 2006; Berge et al. 2009; Kędra et al. 2010a, 2012; Pabis et al. 2015). All these feeding modes are well represented in high latitude soft-bottom communities and many species deploy multiple feeding modes depending upon food availability (Fig. 11.5). Several species of amphipods, decapod crabs, and whelks, for example, can switch between predation and scavenging (Legeżyńska et al. 2000; Thompson 2002; Legeżyńska 2008; Markowska et al. 2008) and a high flexibility in feeding modes is also reported for many other soft-bottom organisms in Kongsfjorden (Renaud et al. 2011; Kędra et al. 2012; Legeżyńska et al. 2014). Thus, many organisms show an opportunistic feeding behaviour.

Predation is considered as a key factor affecting species occurrence and population dynamics in marine sedimentary systems from the tropics to temperate regions (e.g. Ambrose 1984; Reise 1985; Wilson 1990; Quijon and Snelgrove 2005). Arctic marine mammals such as walrus (*Odobenus rosmarus*) feed by rooting in the sediment on the bottom with their muzzles up to a depth of 0.2 m (Johnson and Nelson 1987). The diet of walrus consists of various soft-bodied species such as polychaete and echiurid worms (Sheffield and Grebmeier 2009) as well as larger endobenthic invertebrates, including the bivalves *Mya truncata* and *S. groenlandicus* (e.g. Wiig et al. 1993; Born and Acquarone 2007) (Fig. 11.5). This feeding behaviour affects the structure of soft-bottom communities directly through the removal of prey and indirectly through regeneration of nutrients in and bioturbation of the sediment (Ray et al. 2006). Feeding behaviour that scours the sediment is also described for ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) by which especially the latter species intensively forages for soft-bottom invertebrates (Lowry et al. 1980a, b; Lydersen et al. 2001). However, abundances of predatory mammals are comparatively low in Kongsfjorden and, due to their high spatial and temporal variability, the overall consequences of their activity for the entire soft-bottom system are difficult to assess (Hop et al. 2002). Besides information on predatory mammals, knowledge on predator-prey interactions is relatively scarce for Arctic soft-bottom systems and it has been suggested that predation plays a minor role as a structuring factor for soft-bottom communities in high Arctic regions (Gulliksen et al. 1999; Quijon and Snelgrove 2005). Berge et al. (2009) intensively investigated the species composition of the decapod fauna from Isfjorden (Fig. 11.1b) where they found, in addition to eight shrimp species, only two crab species (the brachyuran spider crab *H. araneus* and the anomuran hermit crab *P. pubescens*). These two crab species were also exclusively found in coastal waters of southern Svalbard (Węsławski 1987) and at a shallow soft-bottom site in Kongsfjorden (Legeżyńska 2001; Petrowski et al. 2016b). However, reports on high numbers of predatory crabs (e.g. snow crab *Chionoecetes opilio*), sea stars, and the brittle star *Ophiura sarsii* exist for the Bering, Beaufort, and Chukchi Seas (Feder et al. 2005; Bluhm et al. 2009; Harris et al. 2009) as well as the Barents Sea (Sundet and Bakanev 2014). Although the studies from Svalbard fjords do not provide quantitative data, it can be concluded that the predatory crab fauna there is relatively species-poor compared to the Arctic open shelf systems.

To investigate potential predation effects on a soft-bottom community at a shallow site in Kongsfjorden, Petrowski et al. (2016b) conducted a predator exclusion experiment at Brandal (Fig. 11.1c) using cages (0.5 × 0.5 cm mesh). They found no differences in species number and density of organisms in areas with and without predator access although the spider crab (*H. araneus*) was regularly observed and predatory fish species such as Atlantic cod (*Gadus morhua)* and shorthorn sculpin

(*Myoxocephalus scorpius*) commonly occur at the experimental site (Brand and Fischer 2016). Presumably, natural predator densities were too low to affect the benthic community in this area. This notion is corroborated by Bender (2014), who manipulated in an enclosure study at the same site the abundance of *H. araneus* and detected a significantly reduced species diversity and number of infauna individuals in plots with three-times above ambient crab density. These results indicate that natural predation pressure by epibenthic predators may currently be of minor importance for population dynamics of shallow soft-bottom species assemblages in Kongsfjorden (Fig. 11.5) because predator densities seem to be low and strongly reduced in comparison to many sedimentary environments of temperate regions (e.g. Reise 1985; Beukema 1991). This might change in a warmer Arctic due to the postulated northward expansion of boreal predatory crab species (Woll et al. 2006; Fagerli et al. 2014) and/or an increase in the abundance and activity of resident predators such as *H. araneus* (Berge et al. 2009).

Many marine benthic predators are omnivorous and feed on carrion (Fig. 11.5). This is also true for the predatory benthic invertebrate fauna in the Arctic. The common crab species, *H. araneus* and *P. pubescens,* have been sampled with carrion-baited traps and regularly observed feeding on carcasses of dead invertebrates in Kongsfjorden (Legeżyńska 2001, C. Buschbaum pers. obs.). Further examples of necrophagous organisms include the whelk *B. undatum,* a very abundant gastropod in nearshore soft-bottom areas in Kongsfjorden (Kaczmarek et al. 2005, C Buschbaum pers. obs.) and other Svalbard fjords (Markowska et al. 2008), as well as several scavenging amphipod species such as the lysianassoid amphipods *A. sarsi* and *Onisimus caricus* (Legeżyńska et al. 2000; Legeżyńska 2001, 2008; Nygard et al. 2012). Due to the high abundance of short-lived, small-sized organisms in soft-bottom areas of Kongsfjorden and resulting high availability of dead invertebrates (Legeżyńska et al. 2000), it is very likely that many omnivorous consumers favour this readily accessible food source. This feeding behaviour together with the comparatively low densities of predators may explain current missing predatory effects in soft-bottom communities of Kongsfjorden (Petrowski et al. 2016b).

11.3.4.2 Competition

In Kongsfjorden, mean density of macrobenthic invertebrates (body size >1 mm) in soft-bottom habitats ranges from 4,000 to 14,000 individuals m^{-2}, depending on water depth and proximity to the glacier (Bick and Arlt 2005; Włodarska-Kowalczuk et al. 2005; Laudien et al. 2007). These values are somewhat similar to densities reported from tropical and temperate soft-bottom environments, where mean densities range from 1,000 to 20,000 individuals m^{-2} (Petrowski et al. 2016b and references therein). The high individual numbers in Kongsfjorden may cause competition for space in soft-bottom habitats (Bolam and Fernandes 2003). In comparison to rocky shores, however, the role of competition in soft-bottom community organization can be reduced due to the more three-dimensional nature of the substrate and the resulting opportunity for the organisms to live at different depths within the sediment (Wilson 1990).

Petrowski et al. (2016a, b) reported a density of about 45,000 individuals m^{-2} in a shallow subtidal soft-bottom site in Kongsfjorden (i.e. Brandal, Fig. 11.1c), with 98% of the individuals occurring in the top 5 cm of the sediment. Although most of the organisms of that area belong to small-sized species (<1 cm), it is surprising that despite these extremely high densities, sediment layers below 5 cm were relatively scarcely colonized. As the sediment of the study site appeared well oxygenated (e.g. no black anoxic layer) to a depth of at least 10 cm, oxygen depletion seems an unlikely explanation for the aggregation of species to the upper 5 cm of the sediment. The low level of colonisation between the uppermost sediment layer and very deep-burrowing species (up to 30 cm depth), such as the lugworm *Arenicola marina* and *M. truncata* (Laudien et al. 2007; Petrowski et al. 2016b), can be a hint that competition for space seems to be of minor importance as a structuring factor for soft-bottom assemblages at least for specific sites in Kongsfjorden. Otherwise, the organisms would more intensively use deeper sediment layers, especially in areas or at water depths with low physical disturbance by e.g. icebergs (this review Sect. 11.3.3.2 *Disturbance*). However, experimental evidence for this assumption does not exist and more detailed studies are needed to test whether competition may be generally of minor importance in the regulation of soft-bottom community structure in Kongsfjorden and other Arctic regions.

Like competition for space, competition for food may also be of minor importance for the existing sedimentary assemblages in Kongsfjorden because, otherwise, densities of several 10,000 individuals m^{-2} of the same feeding mode (especially suspension- and deposit-feeding) would not be reachable. Low competition for food among epibenthic predators and scavengers is assumed, too. As mentioned above, their comparatively low abundance and opportunistic feeding behaviour (e.g. in amphipods) as well as the high availability of carcasses of relatively small-sized benthic and pelagic organisms may diminish food shortage (Legeżyńska 2008). Missing food competition is reflected, for example, by widely absent intra- and interspecific aggression behaviour of crabs and whelks (*H. araneus*, *B. undatum*) at experimentally offered carrion baits (Legeżyńska et al. 2000; Legeżyńska 2001; Markowska et al. 2008).

Clear patterns of succession after disturbance with opportunistic species as first recruiting organisms followed by species that are more competitive suggest potential competition effects in soft-bottom communities of Kongsfjorden. However, a disturbance experiment at a near-shore area in Kongsfjorden revealed that the macroinvertebrate species community of physically disturbed areas (digging of sediment) may reach the pre-disturbance condition within 7 days (Petrowski et al. 2016b). Thus, recovery that included direct competition between the species happened very rapidly after the physical disturbance. These results, obtained from a small-scale experiment performed at one site in the shallow subtidal zone of Kongsfjorden, thus indicate that competition between soft-bottom macrobenthic organisms is presently not a strong factor for structuring communities in Kongsfjorden.

In contrast to macrobenthos, the benthic meiofauna community shows succession patterns in soft sediments of Kongsfjorden. Veit-Köhler et al. (2008) determined experimentally that primary succession of meiofauna takes about 3 years, i.e. the period when species composition of previously animal-free plots was similar to that of natural control plots. However, whether this is a consequence of competition or rather of different temporal colonisation by the species remains unclear.

11.3.4.3 Bioturbation and Ecosystem Engineering

The sedimentary habitats of Kongsfjorden are inhabited by a variety of invertebrate species, which use the soft-bottom as habitat, but may also alter its characteristics through their bioturbating and engineering activities. Włodarska-Kowalczuk and Pearson (2004), for example, mention that mobile organisms, e.g. protobranch bivalves, may decrease the stability of the uppermost sediment layers. On the other hand, a high density of sedentary tube-dwelling invertebrates can increase the sediment integrity in the middle and outer zone of Kongsfjorden. Thus, different kinds of sediment reworking by numerically dominant species differently modify the properties of the bottom and may cause indirect sediment-mediated inhibition or facilitation for other organisms (Bouma et al. 2009).

At shallow subtidal sites of Kongsfjorden, Bick and Arlt (2005) and Petrowski et al. (2016b) identified the tube-dwelling polychaetes *Euchone analis* and *Pygospio elegans* as dominating species. Both species use sand particles to construct their tubes and form aggregations of several square meters with densities >4,000 individuals m^{-2}. In the temperate zone, dense polychaete mats may suppress other species by hampering, for example, movements of burrowing species (Wilson 1990), yet, their potential effects on Arctic species assemblages have not been studied. Włodarska-Kowalczuk and Pearson (2004) and Włodarska-Kowalczuk et al. (2005) showed that also deeper areas of Kongsfjorden may be densely populated with ecosystem engineering and bioturbating organisms, but consequences for other organisms are largely unknown. However, the recent study by Petrowski et al. (2016b) provides experimental evidence that bioturbators cause structuring effects on Arctic soft-bottom communities. At a shallow sedimentary site (Brandal, Fig. 11.1c), they found aggregations of large-sized (up to 23 cm in length) and deep-burrowing lugworms *A. marina* with a mean abundance of 12 individuals m^{-2} (Fig. 11.7). Experimental exclusion of lugworms modified the species composition and increased species richness, number of individuals, and dry mass of the benthic community in comparison to control plots where lugworms were present. Thus, the intensive burrowing activity by *A. marina* seems to hamper the establishment of other species, which are sensitive to sediment disturbances. These results reveal that sediment-mediated species interactions may be an important biotic driver of soft-bottom community structure in at least specific areas of Kongsfjorden and possibly elsewhere in the Arctic if bioturbating organisms occur in high abundances or have a large size.

Fig. 11.7 Natural density of mounds formed by the bioturbating activity of the lugworm *Arenicola marina* at Brandal, Kongsfjorden. (Photo: C. Buschbaum)

11.4 Synopsis and Outlook

The structure of our review exemplifies the rather artificial separation into studies addressing either hard- or soft-bottom communities. This research divide is not unique to ecological studies of Arctic benthos, but seems common in benthic ecology. This habitat classification is, however, a mediocre reflection of the natural situation, which is characterized by a plethora of connections between both habitat types. The mobility of larger macrozoobenthos (e.g. crabs, molluscs), and demersal fishes, for instance, allows migrations between sedimentary and rocky shores. In Kongsfjorden, spider crabs crossed several hundreds of metres of soft-bottom area in a few days to get from one rocky area to another (A. Bender unpubl. data). Another example of habitat connectivity involves soft-bottom communities that benefit from storm-induced detachment and subsequent dislocation of large algal species (e.g. kelp) from rocky shores as food subsidies (Renaud et al. 2015a), but soft-bottom communities also suffer from disturbances mediated through thallus movements (Petrowski et al. 2016a). In a warmer Arctic, the frequency of ecological links between rocky and sedimentary areas may increase due to sea ice retreat-accompanied intensification of storm effects, species additions in the course of a borealization of Arctic shores, or temperature-mediated increase in consumer activity levels. Hence, to gain a more comprehensive understanding on the ecology of benthic communities and to stress its role as a flagship site for Arctic marine research, future studies in Kongsfjorden should focus on connectivity among hard- and soft-bottom habitats.

Since the review by Hop et al. (2002), research in Kongsfjorden has changed from mainly qualitative species inventories to quantitative description of patterns of the distribution of species in space and time. These observational studies revealed, for example, changes in community structure and diversity along vertical (Laudien et al. 2007; Laudien and Orchard 2012; Bartsch et al. 2016) or horizontal gradients (e.g. Włodarska-Kowalczuk and Pearson 2004). In addition, monitoring and comparative studies at different times helped to elicit successional and historical changes in the species composition of benthic communities (e.g. Beuchel and Gulliksen 2008; Berge et al. 2009; Kędra et al. 2010b). During the last 15 years, a considerable number of studies related changes in community traits to the effects of environmental factors, for example, ice-scour (e.g. Laudien et al. 2007), sea ice retreat (e.g. Kortsch et al. 2012), climate variability (Beuchel et al. 2006), and melting glaciers (e.g. Ronowicz et al. 2008). These mensurative studies provide valuable hints for the possible drivers of patterns of species distributions and organisation of ecological communities. A mensurative approach, however, is conducted at the risk of missing the influence of unknown, simultaneously acting factors, by which the interpretation of patterns may be confounded. For instance, patterns of species distributions along a depth gradient, which were related to changes in the frequency of iceberg-mediated disturbance, may be confounded by additional environmental factors that also change with water depth such as substrate composition, wave-exposure, or light attenuation. To increase certainty in the causality between environmental factors and community responses, manipulative experiments turn out to be a powerful tool in studying benthic ecology in the temperate zone. In benthic systems, multiple factors commonly act simultaneously, causing additive or multiplicative effects. The simultaneous manipulation of multiple factors offers insight into the relative contribution and interactive effects of the environmental factors under investigation. Manipulative experiments are, however, usually restricted in space and time. Consequently, the combination of mensurative, monitoring, and manipulative field experiments represents a useful approach to (i) identify the factors that drive benthic community traits, (ii) rank factors by their importance, and (iii) unravel the underlying processes that generate community change. Moreover, future investigations could intensify the assessment of functional community responses such as productivity, respiration rates, or filtration rates to estimate the capacity of Arctic benthos in the provision of ecosystem services.

Research on Kongsfjorden benthos, and probably in other parts of the Arctic as well, displays at several instances prioritization, which likely obscure general conclusions. Firstly, there is an apparent taxonomic bias in ecological studies. Studies on epibiosis, for instance, in some regions largely focused on kelp-associated organisms. Likewise, competitive interactions were mainly addressed through studies with encrusting animal species, which seem to be overwhelmingly dominated by cheilostome bryozoans. Secondly, there is a habitat-specific research bias. The succession of species has been mainly investigated for rocky shore communities (but see Veit-Köhler et al. 2008 and Nowak et al. 2016 for exceptions), while facilitation has been exclusively studied in hard-bottom communities. Similarly, competition studies appear restricted to rocky shore communities. Whether competition plays an inferior role in sedimentary areas is unknown, although possible, as soft-bottom communities were shown to be densely populated (e.g. Petrowski et al. 2016b). This situation may be amplified through the postulated arrival of boreal species (e.g. Müller et al. 2009). Presently, the biogeographic range of marine species expands at a rate of 50 to 70 km per decade poleward (Krause-Jensen and Duarte 2014) and first reports of the reappearance of boreal species on Arctic shores exist (e.g. Berge et al. 2005; Sirenko and Gagaev 2007), but see Feder et al. (2003) and Norton and Feder (2006). Thirdly, there is a methodological bias. For the construction of food web models, many studies use stable isotopes to elicit trophic interactions (e.g. Iken et al. 2005; Feder et al. 2011; Kędra et al. 2012; McMeans et al. 2013; Renaud et al. 2015a). While stable isotope studies help to establish trophic links, this method provides limited information on e.g. feeding preferences, feeding rates, diet switch and resulting consumer fitness and performance. Furthermore, the prevalence of omnivory may exacerbate the interpretation of results obtained from stable isotope analyses. An improved knowledge of consumer effects on benthic communities could be achieved by direct observational and experimental investigations.

Last, but not least, there is a topical bias in Arctic benthos research. Very few Arctic studies have considered recruitment. This is surprising because ecological theory predicts that the relative importance of the major drivers of community regulation is modulated through the intensity of recruitment (Menge and Sutherland 1987). For most of the benthic species in Kongsfjorden it is neither clear when, how often, and on which spatial scales settlement happens, nor what kind of post-settlement processes affect recruitment success. For example, Petrowski et al. (2016b) encountered adult lugworms (*A. marina*) in high abundances at a shallow soft-bottom site in Kongsfjorden, but were unable to find juveniles. Laudien et al. (2007) did not detect any. This may be a consequence of, for instance, irregular recruitment events or spatial segregation between juvenile and adult lugworms. Similar uncertainties exist for other, ecologically key species at higher latitudes such as the Greenland smoothcockle, which is the prime food source for Arctic marine mammals. Recruitment success may be also altered as a result of climate change. Arctic kelp, for instance, germinate less successfully in a warmer, more UV-exposed Arctic Ocean (Wiencke et al. 2006; Müller et al. 2008), which may also have effects at the community level (Bischof et al. 2006). Furthermore, successful recruitment to Arctic habitats by cold-temperate species with a relatively long pelagic phase may be supported by warmer surface waters and altered current patterns. As the Arctic Ocean is surrounded by land masses inhabited by cold-temperate biota, the future Arctic may experience the arrival of those biota that are able to cross the sea and recruit onto the rocky shores further north (Müller et al. 2009; Krause-Jensen and Duarte 2014; Kortsch et al. 2015). For this migration process, the island of Bjørnøya (Fig. 11.1a) has been suggested as a potential stepping stone (Węsławski et al. 1997). Without a better understanding of recruitment patterns, their natural dynamics as well as the factors affecting recruitment success of Arctic benthic species, it will be difficult to distinguish between the effects of global change and natural variability in recruitment success.

Another topic which has been thus far unjustifiably neglected in Arctic benthos research is the role of symbionts (but see Hoberg et al. 1980, 1982), pathogens, and diseases. As there is clear evidence that global warming will increase disease risk (Altizer et al. 2013), polar regions are among the particularly sensitive areas of future parasitic impact (Kutz et al. 2009). Besides pole-ward range extensions of parasites and potential hosts (Post et al. 2013), increased temperatures may reduce the immune competence in host species (Rokicki 2009). Thus, the benthos may be more adversely affected by parasites and diseases in a warmer Arctic, with yet unknown implications on community structure and function.

Undoubtedly, coastal Arctic ecosystems are challenged by global warming. Besides the direct, physiological effects of higher temperatures, glacial and sea ice retreat will initially amplify sedimentation and freshwater impact and in the long run storm-induced effects, all of which will indirectly affect the ecology of Arctic benthic communities as it has been already documented for an Antarctic coastal benthic ecosystem (Sahade et al. 2015). Moreover, the expected changes resulting from the arrival of boreal species on Arctic shores will alter species interactions. This may be particularly momentous for consumer-prey interactions because consumers play a fundamental role in shaping benthic communities of the temperate zone, while consumer impact in the Arctic seem to be presently of minor importance.

Acknowledgements We are grateful to Tobias Dolch who kindly supplied maps displayed in Fig. 11.1. We thank one anonymous reviewer, H.M. Feder, and H. Hop for their constructive comments, which greatly improved the quality of this review. MWK was supported by the Polish-Norwegian Research Programme operated by the National Centre for Research and Development under the Norwegian Financial Mechanism 2009–2014 in the frame of Project Contract No Pol-Nor/201992/93/2014 (DWARF) and by the National Science Centre grant based on a decision No DEC-2012/05/B/NZ8/02654 (BIOSIZE).

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Part V

Arctic Fjord Ecosystem Model and Autonomous Marine Observatories

Chapter 12

Outline of an Arctic fjord Ecosystem Model for Kongsfjorden-Krossfjorden, Svalbard

Pedro Duarte, Jan Marcin Weslawski, and Haakon Hop

Abstract The main objective of this work is to present a detailed outline of an Arctic fjord ecosystem model using Kongsfjorden-Krossfjorden as a case study. Marine ecosystem models are compared, with emphasis on fjord models, towards defining best available modelling technologies. This comparison is based on an analysis of the differences in the variables and processes simulated by different models. We argue about the importance of: (i) coupling Arctic fjord models with land and glacier drainage models; (ii) including thermodynamic, hydrodynamic and ice dynamic sub-models; (iii) simulating biogeochemical processes in the water, ice and benthic environments for, at least, the macro-elements carbon, nitrogen and phosphorus. Furthermore, the energetic importance of higher trophic levels is discussed and used as an argument for their inclusion in fjord ecosystem models towards the development of end-to-end models. The complexity of all the processes mentioned above and respective interactions emphasizes the need for using different model tools and efficient couplers allowing the flow of data between them. A community-based approach with open source software seems to be the proper approach to handle the large complexity of the model strategy proposed herein.

Keywords Arctic fjords · Ecosystem models · Model coupling · End-to-end models

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_12

12.1 Introduction

Modeling in Arctic fjords has been limited to physical models for advected water masses, circulation and ocean-atmosphere interactions (e.g. Ingvaldsen et al. 2001; Nilsen et al. 2008). The biological components are rarely modelled.

Norwegian ecological fjord models have been reviewed by Salvanes (2001) with emphasis on their relevance for fisheries management. The author classifies models as bottom-up and subdivides them into: (i) multispecies ecosystem models; (ii) hydrographical drift models for early life stages; (iii) life history models comprising age-structured Leslie matrix population models, and static and dynamic optimization models of behaviour. The "bottom-up" classification is based on oceanographic and meteorological drivers. The term "ecosystem model" is used to aggregate all models that simulate part of an ecosystem such as species interactions, physical transport processes or population dynamics of some species, according to the groups (i), (ii) and (iii) defined by Salvanes (2001). In this work, we choose to define "ecosystem model" as a mathematical representation of an ecosystem that includes interactions between different species and/or functional groups and interactions with the physical and chemical environment. Following this definition, population dynamic or behavioural models are not viewed as ecosystem models but may be part of them. However, models dealing with physical processes representing water circulation, biogeochemical cycles and their links with a different number of trophic levels are considered "ecosystem models" and these will be the focus of the present work, independently of the emphasis given to different processes.

The review presented by Salvanes (2001) suggests that models applied to Norwegian fjords are not all of the types defined here as "ecosystem model". However, the results obtained with those models provide some insight into the functioning of fjord ecosystems by focusing on specific parts of their complex physical, chemical and biological realms. Multispecies ecosystem models show that fish production in fjords is strongly dependent on production imported from the sea, decreasing from the open sea boundaries to the inner fjords. Hydrographical models show how wind direction might induce shifts in vertical circulation of fjords along the west coast of Norway, with alongshore northern and southern winds inducing upwelling and downwelling, respectively, as a result of Ekman pumping. Upwelling seems to reduce fish production by "diluting" zooplankton concentration as fjord deep water mixes with zooplankton-richer, advected seawater, whereas downwelling has the opposite effect since it facilitates the import of zooplankton from coastal areas. It is expectable that upwelling may enhance primary production in fjords, similarly to what happens in other coastal ecosystems (e.g. Figueiras et al. 2002) but, possibly, this effect does not enhance zooplankton abundance as much as the downwelling regime. Interestingly, in the Arctic-located Kongsfjorden, large surface mesozooplankton concentrations at its inner reaches, probably advected from the sea and displaced vertically by upwelled fresh water from the melting of calving glaciers, become prey to the surface feeding predators. This has been suggested to be the cause of large concentrations of birds and mammals in the area (Węsławski et al. 2000a; Lydersen et al. 2014).

A fjord ecosystem box model was developed by Ross et al. (1993) including a simplistic description of the physical processes. The fjord is divided vertically into surface, intermediate and bottom layer. A turbulent mixing parameterization is used to calculate fluxes between the different layers. Tidal exchanges are calculated between the sea boundary and the intermediate and surface layers – water enters the fjord through the intermediate layer, part of it is entrained in the surface layers and the exit to the sea occurs through these two layers. Freshwater runoff enters and leaves the fjord through the surface layer. Horizontal homogeneity of water properties is assumed for all layers. The biogeochemical component of the model comprises dissolved nitrogen, phytoplankton, zooplankton and carnivores, represented by the corresponding carbon and nitrogen stocks.

Ross et al. (1993) obtained a good semi-quantitative fit between predicted and observed data. However, this possibly could have resulted from the strong influence of external forcing on the internal system properties. In fact, tidal exchange corresponded to 80% of the surface layer volume per day. According to Ross et al. (1993), the simulated system (Loch Linnhe) behaves like a chemostat, being critically influenced by the balance between the inward and outward fluxes of nutrients and phytoplankton. In open fjord systems, such as Kongsfjorden-Krossfjorden where the width exceeds the baroclinic (internal) Rossby radius of deformation and circulation is strongly influenced by the Coriolis effect (Svendsen et al. 2002), the formation of eddies is expected to create more heterogeneity across the fjord axes and falsifying the assumption of lateral homogeneity, as used in box models.

A slightly more biologically complex version of the box model of Ross et al. (1993) was applied to other fjords of Scotland and Ireland, and the authors confirmed the physically dominated behaviour of the modelled fjords, with residence times <=1 day (Ross et al. 1994). They also report that phytoplankton is nitrogen limited only during the spring bloom, being limited by irradiance and grazing pressure for most of the year. Based on their results, they suggest that experimental sea loch studies should not focus only on nutrient dynamics and primary production but that equal efforts should be spent on studying secondary production and on accurate sampling of nutrients and phytoplankton along the sea boundaries.

In the eighties and early nineties, the paradigm followed by Ross et al. (1993, 1994), with a simple parameterization of physical processes, neglecting tidal variability, not coupling biogeochemical with hydrodynamic models and the assumption of well-mixed large compartments, was adopted by several authors in various types of coastal ecosystem models (e.g. Baretta and Ruardij 1988; Bacher et al. 1998). The general approach was to calculate residual circulation from freshwater inputs and use mixing coefficients to guarantee the transport of properties against the residual flows. There were no attempts to realistically simulate 1, 2 or 3D circulation from hydrodynamic principles. Later, the usage of fully coupled hydrodynamic-biogeochemical models became more frequent (e.g. Luyten et al. 1999; Byun et al. 2005; Azevedo et al. 2014).

Apart from the trends of increasing physical complexity in coastal ecosystem models, some paradigm shifts appeared from the traditional Nitrogen-Phytoplankton-Zooplankton (NPZ) or the NPZ-Detritus (NPZD) approaches (e.g. Fasham et al. 1990; Franks 2002) to more complex models based on internal nutrient limitation and dynamic stoichiometry (e.g. Baretta-Bekker et al. 1997; Vichi et al. 2007). Most coupled hydrodynamic-biogeochemical models have focussed on lower trophic levels (LTL), but more recent efforts have involved end-to-end models for a complete description of the marine trophic web (Rose et al. 2010).

Physical models for the Arctic fjord Kongsfjorden-Krossfjorden have included upper layer circulation based on the SINMOD model (Slagstad 1987) with tides and wind patterns (Ingvaldsen et al. 2001), ocean-atmosphere interactions with a 1D ocean mixing model (Price et al. 1986) with wind, temperature and cloud cover as drivers (Cottier et al. 2007). Eddy overturning across the shelf edge front outside Kongsfjorden has been described by Tverberg and Nøst (2009) based on the MIT general circulation model (MITgcm), a finite volume incompressible Navier Stokes model (Marshall et al. 1997).

A study from Masfjorden in western Norway (Aksnes et al. 1989) suggests that transport of mesozooplankton may exceed local growth significantly and that advection may be an important factor underlying the carrying capacity for mesozooplankton predators. Most likely, similar conditions exist for Kongsfjorden, which is an open fjord system without a sill at the entrance and therefore well connected to the water masses in the West Spitsbergen Current (Basedow et al. 2004; Willis et al. 2006; Hegseth and Tverberg 2013).

The marine food web in Arctic fjords has mainly been described (rather than modelled), with estimates of production, ingestion rates and growth. Studies on ecosystem energy flows, carbon budgets, food webs (involving stable isotopes and fatty acids) and benthic metabolism have been conducted in Arctic fjords or embayments (Hobson and Welch 1992; Welch et al. 1992; Hobson et al. 1995, 2002; Hop et al. 2002, 2006; Rysgaard and Nielsen 2006; Renaud et al. 2011; Wold et al. 2011; McMeans et al. 2013; Sevilgen et al. 2014). Much of this type of information from marine food webs, with descriptions and estimates, is highly relevant for modelling work that may add quantitative projections of the conceptual models.

The main purpose of this work is to outline the structure of a state-of-the-art Arctic fjord ecosystem model using Kongsfjorden-Krossfjorden as a case study, considering much of what was described above with regard to development of marine ecosystem models and ongoing modeling work in this fjord system. Such a model may be used to answer several questions regarding, for example, possible shifts in ecosystem functions such as primary and secondary production, in a scenario of global warming with increasing effects of Atlantic Water (AW).

12.2 Conceptuals

Ecosystem models may include hydrodynamic, thermodynamic and biogeochemical sub-models and their feedbacks. In the next paragraphs, the structure of an Arctic fjord ecosystem model will be discussed in the light of available models. For the purpose of clarity, this will start with the general model structure in terms of domain, boundary and forcing conditions, with emphasis on the need to integrate various sub-models. Thereafter, separate sections will deal with forcing functions, physical and biogeochemical, lower trophic level (LTL) and higher trophic level (HTL) processes. Biogeochemical processes, such as biogeochemical cycles, are closely simulated with LTL interactions in available models. Therefore, the term "biogeochemical" is used to aggregate both biogeochemistry and LTL thereafter. The Kongsfjorden-Krossfjorden system will be used as a case study to illustrate the concepts discussed herein.

The general transport equation solved by a coupled physical-biogeochemical model takes the form (Eq. 12.1):

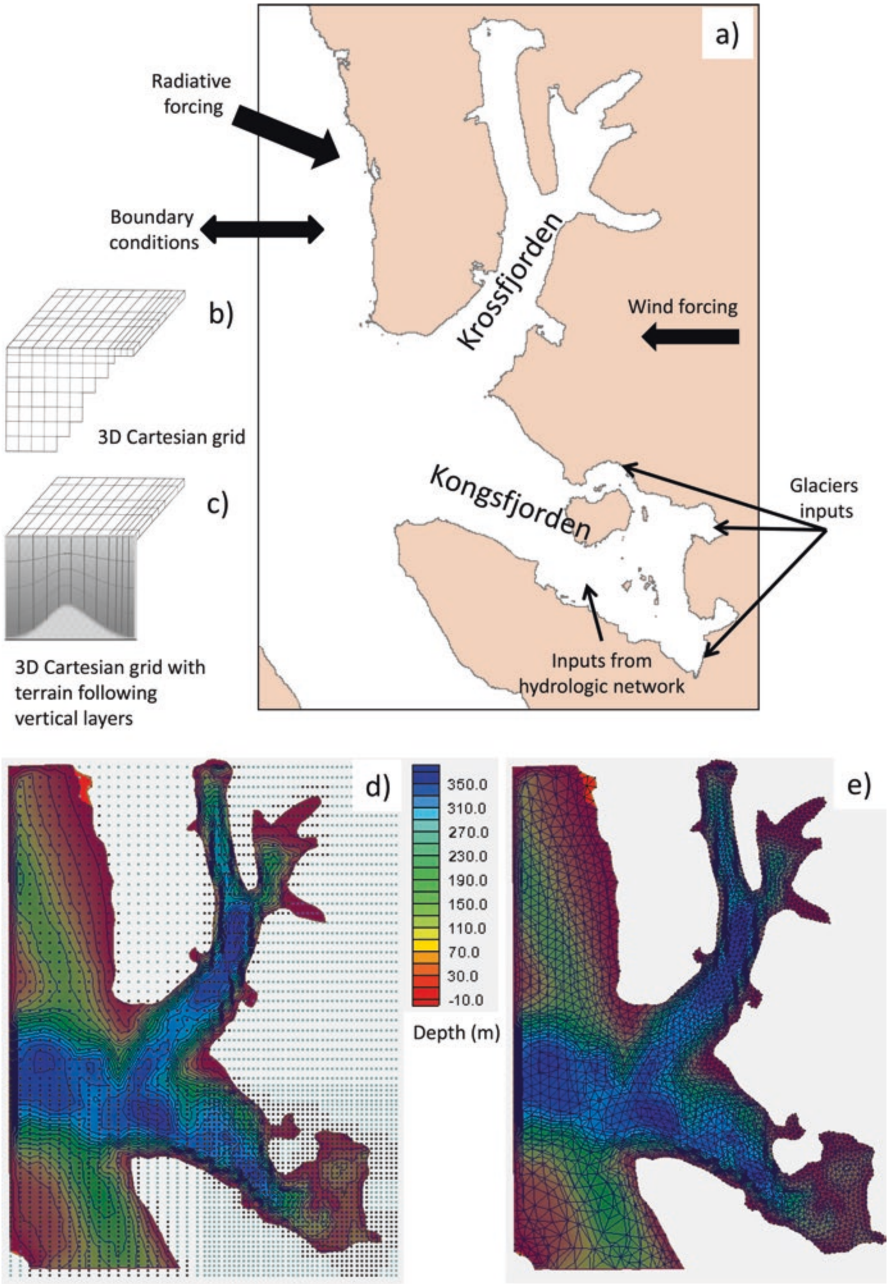
$$\frac{\partial S}{\partial t} + \nabla\left(v \cdot S\right) = \nabla\left(A \cdot \nabla S\right) + \text{Sources} - \text{Sinks} \tag{12.1}$$

Where, v is current velocity (in m s^{-1}); S is the concentration of any dissolved or particulate (living or non-living) property (in kg or other mass unit per m^{-3}); A is the eddy diffusivity of the mentioned property (in m^2 s^{-1}); and ∇, the nabla operator, inCartesian coordinates – it is a first order spatial derivation operator $\frac{\partial}{\partial x}, \frac{\partial}{\partial y}, \frac{\partial}{\partial z}$ .Velocity is calculated by a hydrodynamic sub-model. The derivative on the left side of Eq. 12.1 represents advection, whereas that on the right side represents turbulent mixing. The "*Sources*" and "*Sinks*" terms are null for conservative properties and must be calculated by proper rate equations for the thermodynamic and the biogeochemical variables by different sub-models. Typically, these rate equations are dependent on forcing functions or other variables. For example, photosynthetic rates depend on light intensity, which is an external forcing function of time and space, and it may also be dependent on nitrogen concentration, which is a model state variable. In the case of nekton or other highly mobile organisms, motion must be calculated based on habitat preferences or behavioural patterns, forced by food abundance or environmental conditions even though it may also be influenced by hydrodynamic processes.

12.2.1 General Structure

One of the first steps in the implementation of any ecosystem model is the definition of its domain and boundaries. In defining these, it is important to place the boundaries far enough away from the area of interest to make it possible to assume that they are not influenced by the simulated system. This condition may be relaxed when model nesting is used, in which case feedbacks across the boundaries of nested grids are possible. A map of the Kongsfjorden-Krossfjorden system illustrates some of the forcing and interactions with/from the atmosphere, the land and the ocean boundaries, that may be provided by time series of relevant variables and/or outputs from other models (Fig. 12.1a).

The next step is to define a grid to represent the horizontal and vertical domains. Grids may differ in the way the vertical and the horizontal domains are represented. Three-dimensional (3D) grids are often used in ocean circulation modelling. Such a grid can be Cartesian in all three dimensions (Fig. 12.1b), or include a terrain following vertical coordinates (Fig. 12.1c). The former has a number of vertical layers of constant thickness across the horizontal, whereas the latter has layers of variable thickness and proportional to water depth, which allows for better vertical resolution in shallow than in deep areas. Horizontal grids applied to the Kongsfjorden-Krossfjorden system can be, for instance: a finite-difference Cartesian grid of variable spatial resolution (Fig. 12.1d) or a finite volume triangular unstructured grid (Fig. 12.1e). In both cases, resolution is increased in the more topographically complex areas for a better representation of the bathymetry and land boundaries. The type of grid used depends largely on the hydrodynamic model selected to simulate water circulation. For example, the Regional Ocean Model System (ROMS) (https://www.myroms.org/) uses finite-difference Cartesian horizontal grids and a vertical terrain following sigma coordinate system (Fig. 12.1c), EcoDynamo uses Cartesian grids with variable horizontal and vertical resolutions (Duarte et al. 2014; Fig. 12.1b, d) and the Finite-volume Community Ocean Model (FVCOM) uses horizontal unstructured triangular finite volume grids combined with a terrain following vertical grid (Huang et al. 2008; Fig. 12.1c, e). In Arctic fjords, it is also necessary to define a grid to simulate sea ice. This should also be a 3D grid if sea ice processes are to be resolved vertically as suggested by several authors (e.g. Arrigo et al. 1993; Mock and Gradinger 1999; Duarte et al. 2015). For example, the Los Alamos sea ice model (CICE) uses a 3D orthogonal grid (Hunke et al., 2013). If sediment biogeochemistry is included in the model, then a 3D sediment grid is also necessary to account for horizontal and vertical variability in simulated processes and organism distribution. The model of Chapelle (1995), developed for coastal lagoons, may be used to simulate sediment biogeochemistry in a two-layered system. Using grids for the ice and the sediments with the same horizontal resolution as for the water facilitates the calculation of exchanges between the different environments.



Finite difference Cartesian

Finite volume triangular grid

Fig. 12.1 (**a**) Kongsfjorden-Krossfjorden system illustrating some of the forcing and interactions with/from the atmosphere, the land and the ocean boundaries; (**b**) and (**c**) Examples of three-dimensional grids with different vertical coordinate systems; (**d**) Finite difference Cartesian grid of variable spatial resolution, and (**e**) Volume finite triangular unstructured grid

Whatever grid is used, it is important to decide both on horizontal and vertical resolution ranges and it is difficult to agree on some general criteria for that. Regarding the vertical dimensions and considering the frequent presence of three distinct water layers in Arctic fjords (Cottier et al. 2010) – a fresh surface layer with a thickness of a few tens of metres, an intermediate layer with ~100 m thickness at the sill depth, and a deep layer below – it seems logical to have a higher vertical resolution at the surface layers, using thicknesses of ~10 m to properly resolve the mixed layer. This type of resolution may allow proper simulation of the vertical motions of phytoplankton and of the variability of production rates as a function of several potentially limiting factors such as irradiance, temperature and nutrient concentrations. This resolution may be decreased with depth, where less vertical variability is expected both in physical and in biogeochemical properties. However, for a better description of sediment water interactions, layer thickness should be reduced again at the bottom boundary layer. The horizontal resolution depends on the types of heterogeneity that are to be resolved by the model. Better resolution in the inner parts of the fjords is needed to properly represent and locate river and glacier outputs and respective plumes. The distribution and abundance of benthic organisms may also be important criteria. If their patchiness is not properly described by a coarse grid when biomass density is averaged over an area larger than the area of local patches, then local effects on the water and the sediments and their feedbacks on the benthic organisms will not be properly quantified. For instance, bivalve growth and production may be severely overestimated when local densities are not properly resolved (Duarte et al. 2003, 2005). The problem of soft-bottom fauna patchiness in Kongsfjorden was presented by Kendall et al. (2003), who showed that the size of a uniform patch of benthic fauna on flat deep sublittoral is about 800 m.

The most straightforward manner of coupling biogeochemical processes at LTL with physical processes is to use the same grids for the former as for the latter. Higher trophic levels may deserve a different treatment, as discussed below. The physical components are mostly based on well-established quantitative physical laws, such as the Newton laws of motion and the energy and mass conservation principles (Dike 2001). However, with the exception of this last principle that applies to all ecosystem variables, the biogeochemical counterpart is not based on well-established laws or generally accepted theories; it is much more “parameter dependent”. This may lead to highly variable model results obtained with different models (Scholten and Van der Tol 1998). The degree of detail used to describe different processes may be determined by the importance assumed for each of them or by available knowledge (Pereira et al. 2006). The variables used to describe the physical realm, such as the velocity components, water density, temperature and salinity, are generally simple to select. However, when it comes to the biogeochemical components, there is a lot of ambiguity about which variables should be considered in each model.

12.2.2 Model Forcing

Critical aspects of model forcing include: (i) meteorological data such as wind velocity and direction, air temperature, relative humidity, precipitation, heat and radiation exchanges with the atmosphere and solar radiation; (ii) hydrological data such as glacier and river discharges and associated nutrient and particulate matter loads; (iii) oceanographic data such as water, dissolved and particulate matter exchanges across the sea boundaries and tidal forcing; (iv) species migrations and utilization of the fjord system by species living in neighbouring areas.

In the case of Kongsfjorden-Krossfjorden, meteorological forcing data may be obtained from available databases or from models. Atmospheric fields, including wind stress and radiation forcing may be obtained from simulations of the higher-resolution Weather Research and Forecasting (WRF) model (Skamarock et al. 2008). Local meteorological data, including long-term time series from Ny-Ålesund, can be obtained from the Sverdrup Station (www.npolar.no), Alfred Wegener Institute (www.awi.de) and the Norwegian Meteorological Institute (www.yr.no), and in a recent review by Maturilli et al. (Chap. 2).

Tidal glaciers discharge fresh water directly into the fjords while terrestrial glaciers may feed a seasonal river network. The former discharge may hardly be measured directly, but it may be calculated using a distributed energy balance model (Reijmer and Hock 2008). Energy and mass balances have been determined for several glaciers in the Kongsfjorden area with models (Rasmussen and Kohler 2007; Nuth et al. 2012; Kramer et al. 2013). This discharge may have important implications on fjord hydrography and ecology (Beszczynska-Möller et al. 1997; Zajaczkowski and Legezynska 2001; Svendsen et al. 2002; Lydersen et al. 2014). In front of the terrestrial glaciers of Kongsfjorden-Krossfjorden, there is a seasonally active river network and some rivers have permanent valleys (Svendsen et al. 2002). The SWAT (Soil Water Assessment Tool) model may be used to calculate river flows to force the fjord model. SWAT is a model developed by the USDA Agricultural Research Service to predict the impact of land management practices on water, sediment and agricultural chemical yields in large complex watersheds with varying soils, land use and management conditions over long time periods (Neitsch et al. 2002). It is a continuous time model, not designed to simulate detailed, single-event flood routing. Both the glacier and the river network models may be forced by the meteorological data mentioned above.

Migrations are a sort of model forcing since they constitute inputs/outputs from/to the model domain. However, the abundance and/or biomass of migrating species may be treated as "normal" state variables in the model for the time periods of their permanence within the fjord model boundaries. Species migrations and utilization of the fjord system concern intermediate-to-higher trophic level taxa (Hop et al. 2002; Weslawski et al. 2006; Lydersen et al. 2014). This may include fish, bird and mammal migrations, and removal of food and deposition of excreta by birds (Stempniewicz et al. 2007).

12.2.3 Physical Processes

Different physical models can be used to simulate fjord circulation, e.g., the Princeton Ocean Model (POM) [Blumberg and Mellor 1987], FVCOM [Huang et al. 2008] or ROMS [https://www.myroms.org/]). In the specific case of Kongsfjorden-Krossfjorden there are two issues that may have very important influence on fjord circulation, ice build-up and biogeochemical processes: inputs of AW and freshwater discharges from calving glaciers. Svendsen et al. (2002) present results for Kongsfjorden-Krossfjorden obtained with the POM model to describe upper circulation and analyse the interactive effects of freshwater and local winds. They show up-fjord and down-fjord flows along the southern and northern margins, respectively. This pattern is intensified under down-fjord wind but it is also observable under up-fjord wind, which piles up water at the fjord's head and produces a down-fjord pressure gradient. The Bergen Ocean Model (Berntsen 2000) was used by Cottier et al. (2005) to model shelf-fjord dynamics, concluding that northern winds enhance frontal instabilities near the shelf break leading to pockets of AW being advected onto the shelf. These authors use the model to explain the restrictions to the intrusion of AW in winter by the density gradients at the fjord mouth. In summer, the relaxation of these gradients allows AW to enter into the fjord. In recent years, advection of AW into Kongsfjorden has also happened during winter, as shown by mooring data for the winter of 2005/06 (Cottier et al. 2007). EcoDynamo has been used to implement a 3D model for Kongsfjorden-Krossfjorden. Details on the numerics of EcoDynamo can be found in Duarte et al. (2014). Model runs were carried out to test the effects of tides and glacier discharges on fjord circulation as part of an effort to implement a coupled physical-biogeochemical model. Model resolution was increased in the inner parts of Kongsfjorden with the aim of obtaining a more detailed description of the effects of fresh water flow on hydrodynamics at the fjord's head. The current velocity field for a sub-surface layer (roughly between 10 and 20 m depth) indicates that most of the water flows along the southern margins of both fjords during flood tide (Fig. 12.2a), whilst during the ebb most of the water flows along the northern margins (Fig. 12.2c). An eddy pattern becomes visible at the mouth of Kongsfjorden during slack of both flood and ebb tide (Fig. 12.2b, d). Rotational effects tend to be more important in Arctic fjords due to the higher latitude and corresponding Coriolis parameter. During the ebb, the flow pattern is similar to what was described by Svendsen et al. (2002), with most of the water flowing out along the northern margins. These patterns are mostly apparent at surface layers and become simpler with depth (not shown), with the fluxes exhibiting a more linear behaviour following the direction of the tide with less eddies and cross-fjord velocity gradients as likely results of the increased drag (not shown).

A high-resolution (160 m in the horizontal) hydrodynamic numerical model has been established recently for Kongsfjorden (Sundfjord et al. 2017). This model was nested into a larger scale model with a 4-km grid covering the Nordic and Barents seas and the Arctic Ocean, and an 800-m grid regional model covering the shelf and fjords in Svalbard. This model system is an extension of the NorKyst800 implemen-

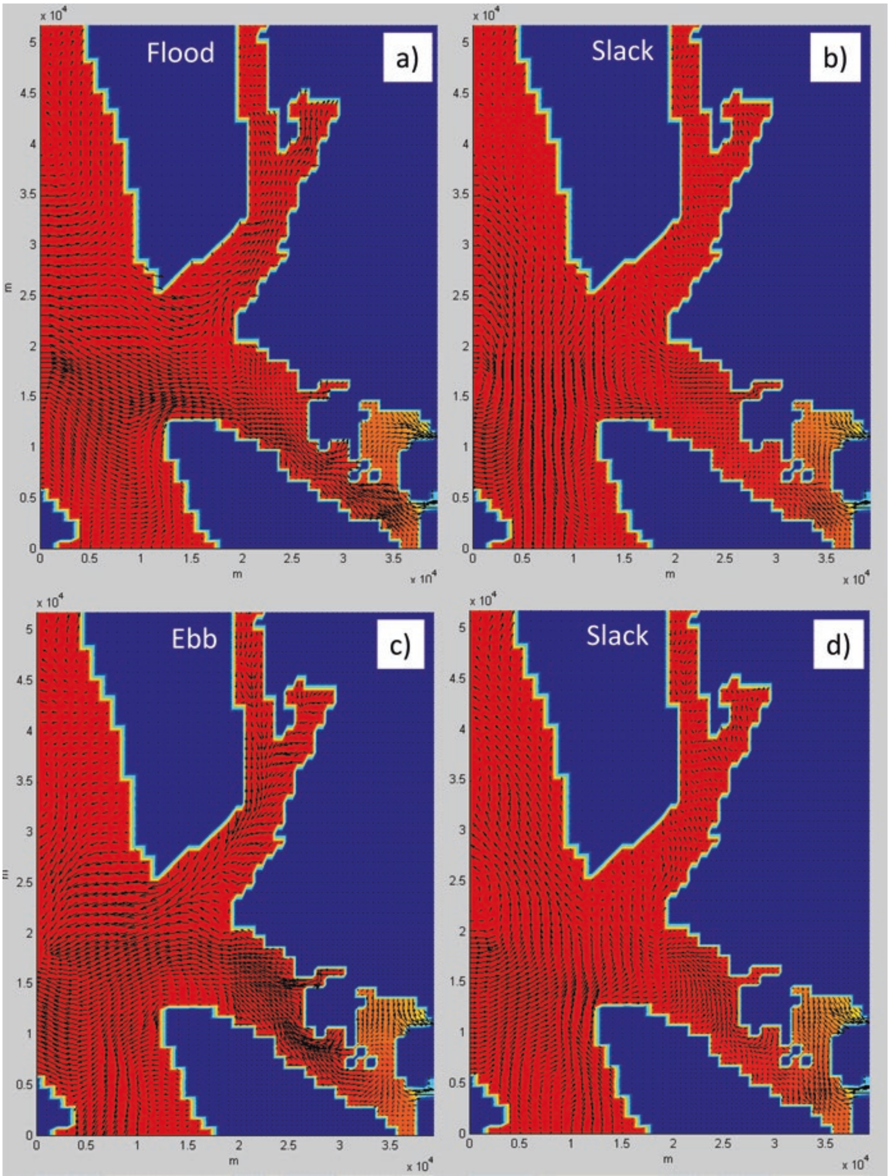


Fig. 12.2 EcoDynamo results regarding current velocity field for a sub-surface layer (roughly between 10 and 20 m depth), based on the grid shown in Fig. 12.1b, d (refer text). Maximum velocities are ~7 cm s^{-1}

tation of the ROMS ocean model (Haidvogel et al. 2008; Albretsen et al. 2011). This nesting solves some of the problems related to the definition of boundary conditions (see Sect. 12.2.1). One of the reasons why high-resolution simulations may be necessary in Kongsfjorden-Krossfjorden is the need to properly represent the plumes of freshwater released from calving glaciers that may have an important impact on zooplankton, through osmotic shock, and on the associated food web (Węsławski and Legezynska 1998; Węsławski et al. 2000a; Zajaczkowski and Legezynska 2001).

Whatever physical model is implemented to simulate water circulation, it is desirable to couple it with a sea ice model. When considering which sea ice model to use, it is important to take into account the need to simulate sea ice biogeochemistry and to resolve corresponding processes vertically within the ice (Duarte et al. 2015). Thus, the community Los Alamos Sea Ice Model (CICE V5) seems to be one of the best available options (Jeffery et al. 2011; Hunke et al. 2013). The CICE model resolves physical processes vertically in a variable number of ice layers and it has been used in pan-Arctic simulations coupled with ocean circulation and biogeochemical models (Jin et al. 2012). The Louvain-la-Neuve Sea Ice Model (LIM) also resolves vertically the ice and has been used in pan-arctic simulations (http://www.elic.ucl.ac.be/repomodx/lim/).

12.2.4 Biogeochemical, LTL and HTL Processes

Arctic fjord models are rather scarce, but biogeochemical (Jin et al. 2008) and coupled hydrodynamic-biogeochemical models have been implemented and used at a pan-Arctic scale (e.g. Popova et al. 2010; Slagstad et al. 2011; Jin et al. 2012). An analysis of these models reveals some important differences with regard to how hydrodynamic and biogeochemical processes were simulated. Regarding the former, less variability is observed since such models are all based on the same physical laws of momentum conservation and continuity. Therefore, differences among models are mostly related to the type of grids used, their spatial resolution and the turbulence closure schemes employed. However, differences between the biogeochemical counterparts are often substantial, as discussed below.

The biological sub-models of Jin et al. (2008), Popova et al. (2010) (the MEDUSA model [Yool et al. 2010]) and Slagstad et al. (2011) (Figs. 12.3, 12.4 and 12.5) have several conceptual similarities, with a strong emphasis on the nitrogen cycle, even though silicate limitation (regarding diatoms) and iron limitation, in the case of the MEDUSA model, are also considered. Nutrient limitation of phytoplankton and ice algae growth is based on a Michaelis-Menten dependence of nitrate and ammonium or silica present in the environment (in the case of the Jin's model, this may be sea ice or water). There are some small differences in the detritus, phytoplankton and zooplankton compartments, but these are still relatively consistent among the three models. The model of Slagstad et al. (2011, Fig. 12.5) is more detailed since it includes dissolved organic carbon (DOC), part of the microbiological food web,

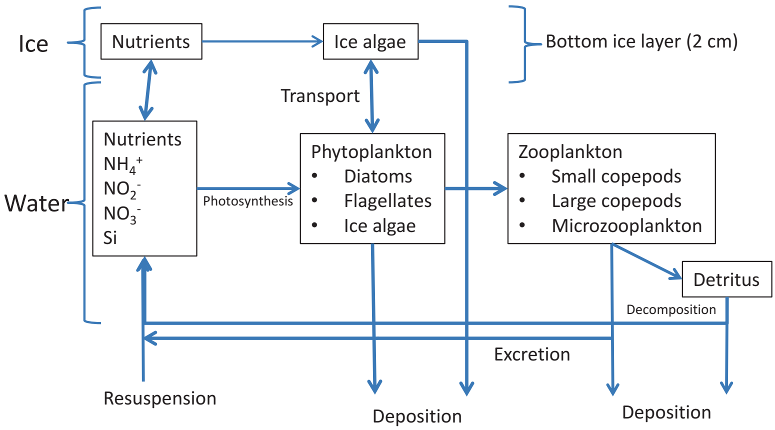


Fig. 12.3 Ice-ocean ecosystem model for 1-D and 3-D applications in the Bering and Chukchi seas. (Jin et al. 2008)

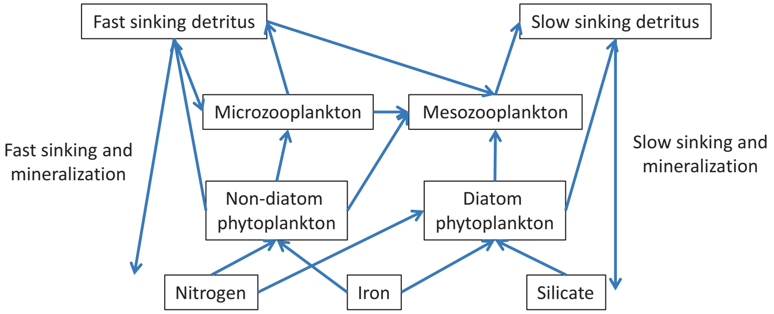


Fig. 12.4 Model for Ecosystem Dynamics, Carbon Utilisation, Sequestration and Acidification (MEDUSA) (Yool et al. 2010)

with the explicit inclusion of bacteria, and marine copepods characteristic of Arctic mesozooplankton (*Calanus finmarchicus* of Atlantic origin and *C. glacialis*, an indicator of Arctic waters). It is important to emphasize the relevance of including DOC, since some fraction of new production is not exported, but it is accumulated in the surface ocean as DOC and particulate organic matter (POM; Sanders et al. 2005).

The model of Moore et al. (2002; Fig. 12.6) has been coupled to CICE to investigate the relationship between Arctic sea ice extent and primary production (Jin et al. 2012). Moore's biogeochemical model is based on a different paradigm than that of all previous models. The Moore model considers several nutrients simultaneously, including phosphate and iron as well, possibly stimulated by the discovery of the High Nitrate – Low Chlorophyll regions of the Southern Ocean and the iron limitation Martin's hypothesis (see Smetacek et al. 2012) and keeps track of their values in the various compartments. This allows the calculation of phytoplankton cell quotas and constrains them to biologically realistic values. This approach

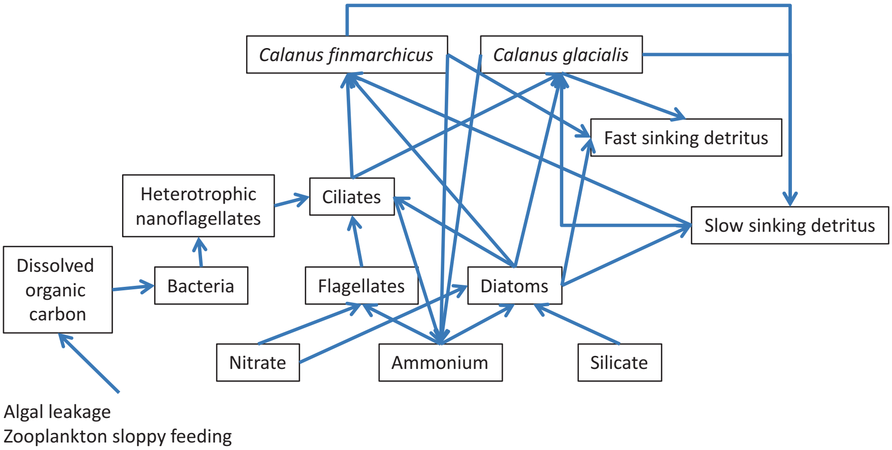


Fig. 12.5 Biogeochemical component of the SINMOD model. (Slagstad et al. 2011)

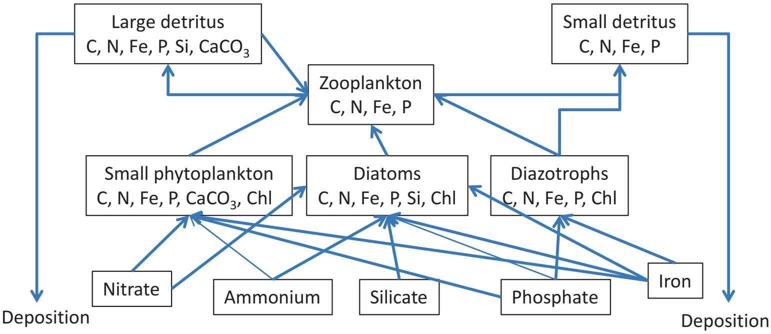


Fig. 12.6 Marine ecosystem model of intermediate complexity for the global domain. (Moore et al. 2002)

implies the acceptance of limitation by other nutrients than nitrogen and silica. Furthermore, it permits calculating nutrient limitation based on phytoplankton cell-quotas instead of the usual environmental concentrations. Therefore, limitation becomes dependent on the capacity of cells to absorb and accumulate nutrients and the models must use more proxies (e.g. carbon, nitrogen, phosphorus,…) to represent organism abundance/concentration for book keeping calculations. This is more realistic from a biological perspective, since it is known that microalgae have some capacity for luxury consumption of nutrients. The approach of decoupling carbon assimilation through photosynthesis from nutrient uptake has been suggested by other authors (e.g. Baretta-Bekker et al. [1997] in the ERSEM model). Another important point in favour of this model is the possibility of "following" the atomic ratios of particulate matter. In fact, some studies have shown that when Redfield ratios are applied in models that use nitrogen as their "currency" to calculate carbon sinking, this may be underestimated due to the higher C:N ratios of sinking matter in the Arctic than those predicted by the traditional Redfield ratio (Daly et al. 1999; Tamelander et al. 2013). Results obtained by Thingstad et al. (2008), using mesocosm experiments with Arctic plankton, emphasize the importance of stoichiometric coupling between carbon and limiting nutrients not only in the autotrophic but also in the heterotrophic food web compartments, with emphasis on the nutrient-competing role of bacteria. These results point to the need for incorporating the microbial loop in models that aspire to capture the details of pelagic interactions in Arctic food webs. Several studies of microbial processes have been carried out in Kongsfjorden (Piquet et al. 2010; de Corte et al. 2011; Rokkan Iversen and Seuthe 2011; Seuthe et al. 2011). The work of Hessen et al. (2008) demonstrated the coupling between the intensity of photosynthetically active radiation (PAR) and the stoichiometric ratios in Arctic photoautotrophs and suggested that increased PAR leads to increased C:N and C:P ratios. In a study conducted in the Sylt-Rømø Bight ecosystem of the German Wadden Sea, Baird et al. (2011) report that nitrogen and, especially, phosphorus are recycled much faster than carbon. All these lines of evidence emphasize the importance of simulating separately the main macronutrients instead of forcing their stoichiometry by using Redfield ratios.

None of the previous models includes dissolved organic pools, except for dissolved carbon in the case of the Slagstad model. Thus, it is not possible to close completely the biogeochemical cycles represented in the various models. The importance of these pools is related to nutrient recycling in the water column and regenerated production. Guildford and Hecky (2000) stress the importance of total nitrogen and phosphorus, i.e., dissolved inorganic plus organic forms and not only the former, as it is usually the case in studies conducted in the marine realm, for a more realistic assessment of nitrogen and phosphorus availability in their various forms.

In sea-ice biogeochemical modelling, most of the models are based on the traditional approaches inherited from NPZ models as, for example, the models of Arrigo et al. (1993), Lavoie et al. (2005) and Jin et al. (2008; Fig. 12.3). However, there are also models based on the more recent paradigms discussed above of internal nutrient limitation and dynamic stoichiometry (e.g. Tedesco et al. 2010). Sea ice biogeochemical models published over approximately the last 20 years have been reviewed by Tedesco and Vichi (2014). These may be roughly classified into three groups, according to the vertical distribution of ice algae and associated biogeochemical processes: a) one-layer models of prescribed thickness; b) one-layer models of variable thickness, and c) multi-layer models (Fig. 12.7). The first type simulates biogeochemical processes only at the ice bottom (e.g. Jin et al. 2008). The second type simulates the same processes only in the bottom permeable layer that has a variable thickness – the Biological Active Layer (BAL) – (Tedesco et al. 2010, 2012; Tedesco and Vichi 2014). The third type resolves vertically the concentration of ice algae and associated biogeochemistry within the ice for a given number of layers (e.g. Arrigo et al. 1993; Vancoppenolle et al. 2010; Pogson et al. 2011; Saenz and Arrigo 2012; Duarte et al. 2015). Therefore, when considering sea-ice algal and biogeochemical modelling, the diversity of

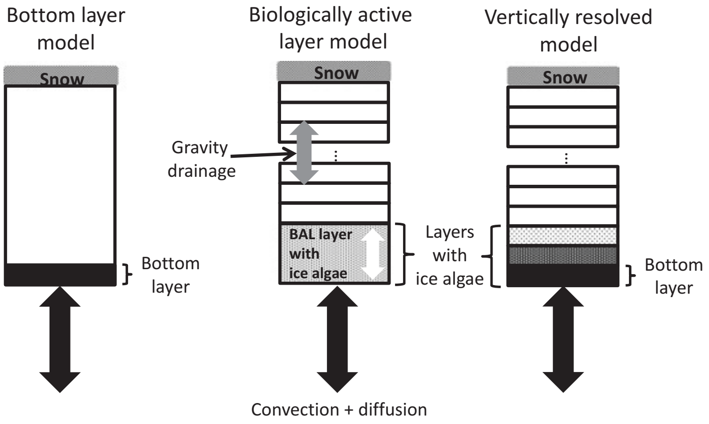


Fig. 12.7 Schematic representations of different sea ice biogeochemical models. Bottom layer models consider biogeochemical processes only at the bottom layer (e.g. Jin et al. 2008). Biologically active layer models assume that biogeochemical processes may occur not only at the ice bottom, defining the thickness of the biological active layer (BAL) as a function of brine channel density but not resolving the biological processes within the BAL, as a function of environmental variability (e.g. Tedesco et al. 2010). Vertically resolved models resolve vertically the sea–ice biogeochemical processes (e.g. Arrigo et al. 1993). (Adapted from Duarte et al. 2015)

approaches results not only from the way the same processes are simulated by different models, but also from the model's vertical extent and corresponding resolution. The rationale to justify using only one ice layer in several models applied to the Arctic Ocean is because ice algae are usually found in highest concentrations near the bottom of sea ice (Tedesco and Vichi 2014). Mock and Gradinger (1999), using a method of measuring ice algal primary production that resolved its vertical variability, concluded that traditional methods restricted to the study of bottom communities may have severely underestimated Arctic as well as Antarctic primary production. Also, empirical and model results presented by Tedesco et al. (2010) provide further evidence that ice algal biomass and production can be vertically highly variable within sea ice. Most recent CICE versions include a new halo-thermodynamic scheme that enables 3D computations of the sea ice microstructure and a vertical bio-grid, which can be used to resolve the vertical transport equations of biogeochemical tracers (Jeffery et al. 2011; Hunke et al. 2013).

It is important to emphasize that increasing model complexity brings the need to use more parameters that may not be easily obtained and, especially, to properly constrain within biologically realistic values due to the lack of knowledge about some of them. Furthermore, several authors suggest that there is a parabolic relationship between model efficiency and model complexity, whereby, efficiency is maximized at intermediate complexity. As science evolves, the parabolic curve shifts towards higher complexity (Hannah et al. 2010 and references therein).

All the previously discussed models focus on biogeochemistry and LTLs. However, there is growing interest in end-to-end models of marine ecosystems, i.e., models combining physicochemical oceanographic descriptors and organisms ranging from microbes to HTL, including humans, in a single modeling framework (Fulton 2010; Rose et al. 2010). According to the last authors, ecosystem-based management requires quantitative tools dealing with bottom-up and top-down controls of the food webs, allowing to test the effects of global climate change, among other possible environmental changes. Another argument in favour of this type of model is the need to properly close the biogeochemical processes in a more realistic manner, embedding the functional role of HTL organisms in the biogeochemical cycles. This argument will be developed below using the Kongsfjorden-Krossfjorden system as a case study.

The integration of processes in end-to-end models poses several challenges such as dealing with different spatial and temporal scales, acclimation and adaptation, behavioural movement, software and technology and model coupling (Rose et al. 2010). Most of these challenges may be dealt with by using available tools and technology (e.g. the Atlantis model; Fulton 2010). One of the crucial aspects here is the way different sub-models are coupled in different modelling environments.

Whereas variables related to biogeochemistry and LTL*s* are generally simulated over the entire model domain, except in the case of benthic organisms that are substrate dependent, the spatial complexity in the distribution of HTLs may be handled by using individual-based models (*IBM*) with organism distribution being influenced by environmental drivers and biological factors (Fulton 2010) provided by the physical and the LTL models. HTL models may be based on mechanistic principles to simulate physiology and population dynamics. For example, physiology may be based on the Dynamic Energy Budget (*DEB*) theory (Kooijman 2000). Molnár et al. (2010a, b) attempted to predict survival, reproduction, abundance and litter size of polar bears under climate warming scenarios using a *DEB* model combined with a population dynamics model. The *DEB* model was used to predict starvation (Molnár et al. 2010a) and litter size (Molnár et al. 2010b). These physiological variables may be integrated in a population dynamics model to predict changes in the abundance of different age or size/weight classes by using, for example, a stage-structured matrix population model. HTL models may be influenced by environmental conditions predicted by physical and biogeochemical models and may also include feedbacks through consumption, excretion and mortality. The end-to-end model by Serpa et al. (2013) integrates all these complex feedbacks. Furthermore, population dynamic models of different species may feedback onto each other by using, for example, predation, as a closure term for part of the mortality losses of prey organisms.

Links between physiologic, population dynamic, consumption, migratory and transport processes for a species or functional group are represented in Eq. 12.2 and may be replicated for any number of age, size or weight classes:

$$\frac{\partial Ni}{\partial t} = G_i - M_i + R_i - E_i + I_i \pm Tr_i \tag{12.2}$$

Where,

i is class number (for the sake of simplicity only the class index is indicated but indices are also needed to identify the geographical position of the organisms in the grid); G_i – growth; M_i– mortality; R_i – recruitment; E_i – emigration; I_i – immigration; Tr_i – transport.

It is noteworthy that this is just another form of representing the dynamics of a biological variable analogous to Eq. 12.1, but emphasizing here the biological processes integrated in Eq. 12.1 in the *Sources* and *Sinks* terms. These are discriminated here in G_i, M_i, R_i, E_i and I_i. The last three terms represent transport processes but, whereas E_i and I_i are active transport resulting from the motility capacity of the organisms, Tr_i is passive transport and it is calculated from the advection and turbulent mixing of Eq. 12.1. Even HTL organisms may be under some influence of physical transport. For example, fish velocity results from swimming speed and background currents. A *DEB* sub-model can be used to calculate G_i and M_i. These values may be used in a population dynamics model solving the above equation for each class, which may be represented by a homogeneous number of individuals or, if an *IBM* is used, by individuals or groups of homogeneous individuals.

Studies in Kongsfjorden suggest a trophic web with up to six trophic levels (TLs). Pelagic and benthic food webs have been adapted from Hop et al. (2002), respectively (Figs. 12.8 and 12.9), including the TLs and their net production (*NP*) estimates, in the case of the pelagic food web. Phytoplankton Net Primary Production (*NPP*) estimates (4 – 180 g C m^{-2} y^{-1}) reported by Eilertsen et al. (1989), Hop et al. (2002) and Piwosz et al. (2009) have been used to calculate the *NP* of consecutive TLs, assuming a 10% energy transfer efficiency (*ETE*) (Pauly and Christensen, 1995; Eq. 12.3):

$$NP = NPP \cdot ETE^{TL-1} \tag{12.3}$$

Each value of the secondary production ranges (Fig. 12.8) was based on the minimum and maximum values of *NPP,* and when a TL range is presented (for example, in the case of 2nd-3rd TLs) instead of a unique value, the median value of the range was used to replace TL in Eq. 12.3. The decreasing magnitude of *NP* along the food web may lead to the wrong impression of a relatively low importance of higher TLs for ecosystem total throughput. However, bearing in mind that TL consumption is larger than *NP*, due to losses associated with the efficiency with which prey are utilized by predators, it is more meaningful to look at consumption values. Using values reported in Hop et al. (2002), after converting mass of food to carbon, assuming carbon contents to be roughly 40% of dry weight, food consumption should be

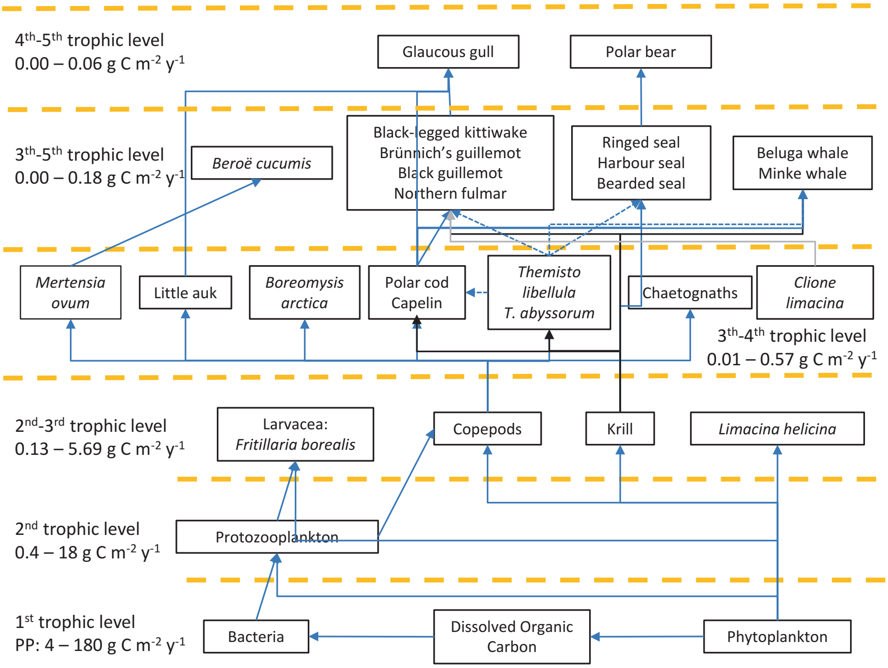


Fig. 12.8 Kongsfjorden pelagic food web. (Adapted from Hop et al. 2002). Trophic levels and corresponding net productions are also shown (refer text)

around 0.2 and 0.3 g C m^{-2} y^{-1} for the birds and the mammals, respectively. These values imply that birds and mammals alone may consume an amount of food that may be up to 13% of *NPP*. Some other estimates of historical food web (Weslawski et al. 2000b) and present day HTL energy demand in Svalbard fjords show similar proportions of energy division (Weslawski et al. 2006). Considering the potential importance of consumption by fish, it is most likely that HTL*s* have an important impact on ecosystem functioning including nutrient recycling. Therefore, model efforts should be towards an end-to-end model for a realistic representation of the fjord ecosystem. There are obviously other non-quantitative arguments in favour of including HTL*s* in an ecosystem model, when species have a special economic, conservation or aesthetic value.

Regarding the benthic food web, primary production values are not available, except for the microphytobenthos (Woelfel et al. 2010). These authors report values in the range 2–14 g C m^{-2} $year^{-1}$. Considering that the microphytobenthos values alone may be of the same order of magnitude as those of phytoplankton (Glud and Rysgaard 2007; Woelfel et al. 2010; Hodal et al. 2011), it seems important to include the benthos in a fjord ecosystem model. To get a full picture of benthic primary production, it is necessary to account for the macroalgal contribution as well. The distribution of kelp in Kongsfjorden is generally limited to a band from 2 to 15 m

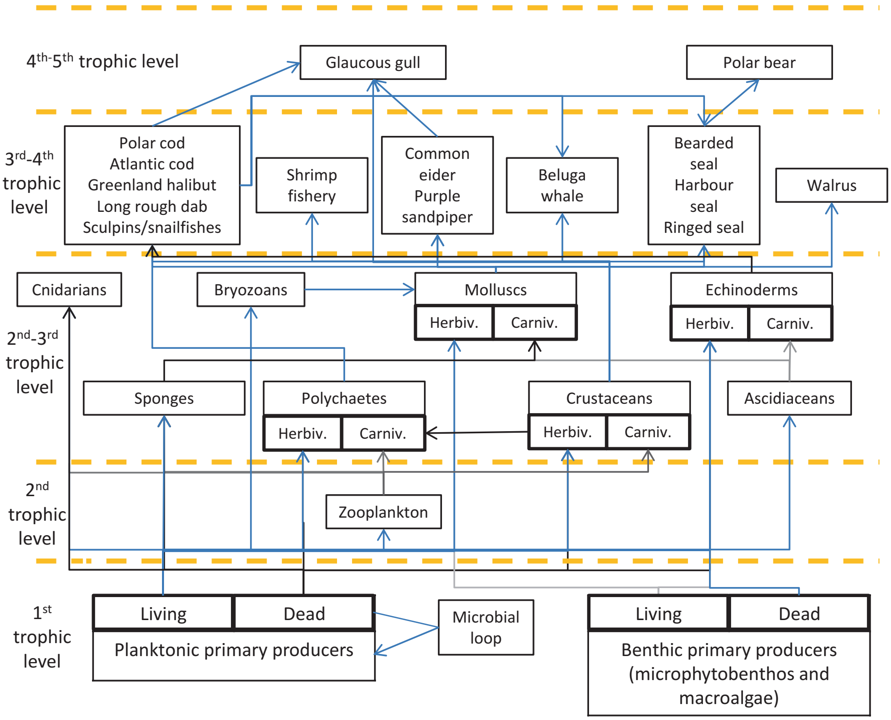


Fig. 12.9 Kongsfjorden benthic food web. (Adapted from Hop et al. 2002). Trophic levels are shown on the left (refer text)

depth on hard substrata, except for the inner bay where there are few macroalgae below 5 m depth (Hop et al. 2012; Kruss et al. 2012; Fredriksen et al., Chap. 9). Since macroalgae are mostly associated with hard substrata, the distribution within the fjord is probably limited to about 20–30% in outer-middle fjord and <10% in inner fjord. The macroalgal belt is wide (100–200 m) at the outer locations of Kongsfjorden, such as Kapp Mitra and Kapp Guissez, but less (<50 m) at Hansneset and Juttaholmen (Hop et al. 2016). The annual production in the shallow coastal waters may be 2–3 kg C m^{-2} y^{-2}, as determined for fjords in Greenland (Borum et al. 2002; Krause-Jensen et al. 2007, 2012).

12.3 Synthesis

A schematic setup of an end-to-end fjord ecosystem model for Kongsfjorden includes exchanges and inputs, biogeochemical cycles, food web components for pelagic and benthic food webs and trophic interactions, as shown in Fig. 12.10. In the upper right corner, a diagram shows the sub-models necessary for the end-to-end coupled model as well as their feedbacks. Sub-models simulate ice physics, water circulation, biogeochemistry and LTLs, and single species dynamics for HTL*s* (possibly including *IBM* models). All sub-models interact with each other. Biogeochemistry and LTLs are simulated in water, ice and benthic compartments using different grids (cf. – General structure) that are shared with the physical counterparts. For simplicity, only the grid used to represent water circulation is shown in Fig. 12.10.

The number of HTL sub-models may increase with time as knowledge is accumulated about more species. The physical and biogeochemical sub-models provide the environmental context for the HTL models. Ideally, biogeochemical models should combine the approaches of the SINMOD model (Fig. 12.5) and those described by Moore et al. (2002, Fig. 12.6), including micro- and mesozooplankton, the microbial loop and variable stoichiometry. Part of the LTL organisms may later be replaced by detailed population dynamics models, depending on accumulated knowledge, questions of interest and available computer power. According to Rose et al. (2010), the extent to which multistage (composed of several weight, size or age classes) LTL models will be required to describe the development of some species groups, for example, the copepods, is yet unknown.

Biogeochemical cycles in the water and benthic compartments and their interactions are also in Fig. 12.10. These include sedimentation, re-suspension, adsorption, desorption and diffusion fluxes across the bottom-water interfaces. Ideally, soft bottom areas should be represented by, at least, two layers to account for aerobic (surface layer) and anaerobic processes. Sediment biogeochemistry should include the same dissolved variables in the pore water that are simulated in the water column for proper closure of pelagic-benthic coupling. Furthermore, macroelements associated with some of those variables, such as nitrogen and phosphorus, should be simulated in the sediment solid phase as well (e.g. Duarte et al. 2007; Serpa et al. 2013).

In parallel with the biogeochemical cycles, the pelagic and benthic schematic trophic webs and their interactions are presented in Fig. 12.10 as closed structures, not to mean that trophic chains are closed to exchanges across the system boundaries but to emphasize the importance of closing the loss terms of some species or functional groups as input terms for other species or other trophic groups. Also, there is a tight link between trophic interactions and the biogeochemical cycles since the former feeds back on the latter through processes such as photosynthesis, respiration, excretion, and faecal production. Dots in the grid represent the hypothetical distribution of a high trophic level species. In this case, it is suggested that the same grid used for hydrodynamics and water biogeochemistry may be used to represent the spatial distribution of a HTL species. However, this may not be appropriate for all species and it may be desirable to overlay different spatial grids applicable to different species, integrating different spatial and temporal scales.

The forcing functions and boundary conditions shown earlier (cf. – Fig. 12.1) are also represented in Fig. 12.10: (i) inputs from glaciers and rivers (water, nutrients, suspended matter, etc.); (ii) exchanges with the atmosphere (in the form of precipitation, evaporation, radiation, wind momentum transfer, carbon dioxide, oxygen, etc.); (iii) exchanges with the open ocean (water, momentum transfer, nutrients, suspended matter, dissolved gases, plankton, nekton). Contaminants may also be added if relevant for the study area. Ice inputs influence directly the ice model,

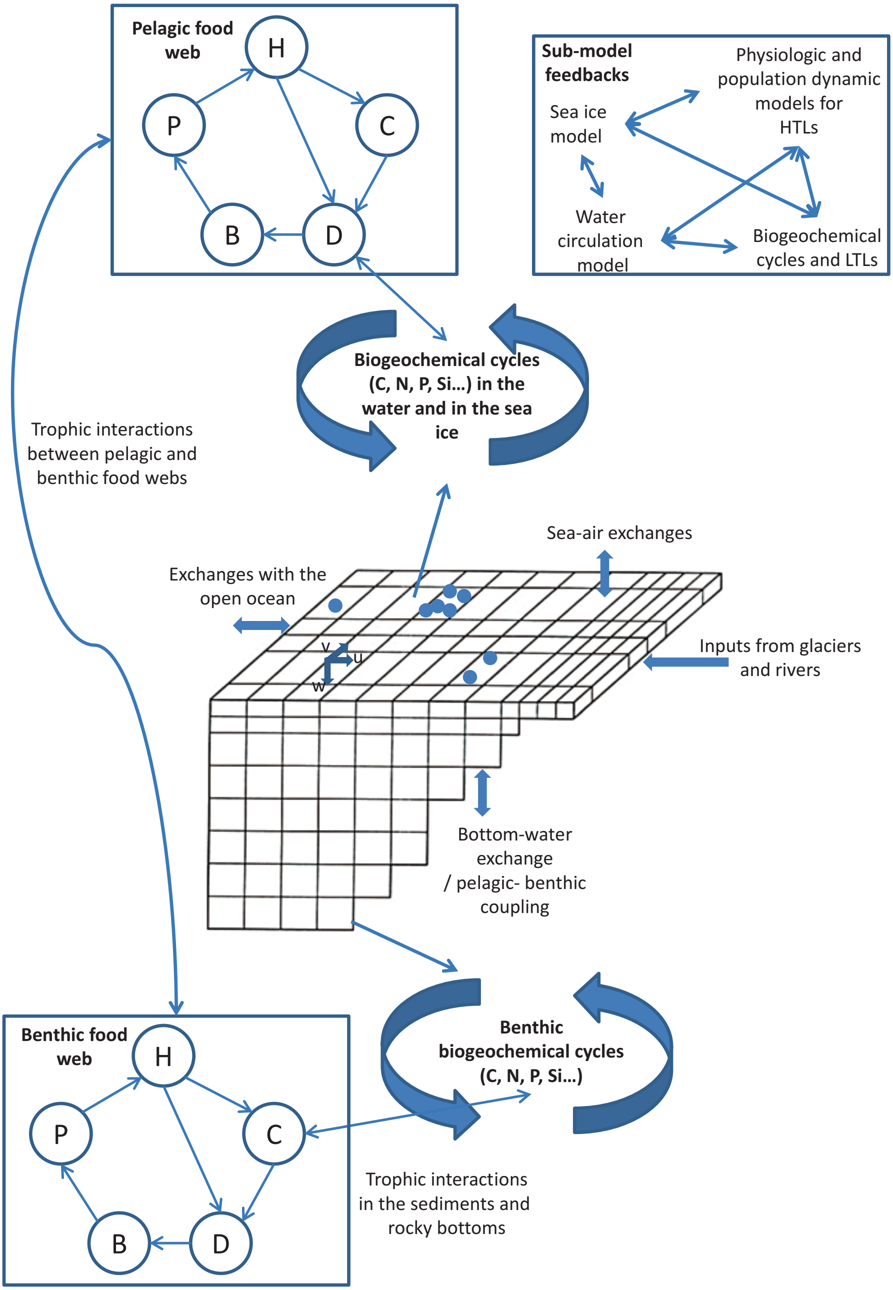


Fig. 12.10 Schematic setup of an end-to-end fjord ecosystem model. In the upper right corner, a simple diagram shows the sub-models necessary for the end-to-end coupled model as well as their feedbacks. More “high trophic level” (HTL) species may be added as long as relevant physiologic and population dynamics data are gathered and made available for model development. Biogeochemical processes in the water, the ice and the sediments (mineralization, nitrification,

whereas water inputs influence directly the hydrodynamic model because of density differences with the fjord water and because of momentum transfer. Ice and water properties (including plankton) are advected by the current velocity field of the hydrodynamic model and changed locally by thermodynamic and biogeochemical processes.

The complexity of a model such as the one represented in Fig. 12.10 poses several technical challenges. Frequently, biogeochemical models, such as those available in ROMS, include all biogeochemistry in one subroutine (https://www.myroms.org/). This makes it very difficult to combine different approaches to simulate the various components of the biogeochemical system. Also, the number of HTL species in the pelagic and benthic webs (Figs. 12.8 and 12.9) potentially implies a large number of sub-models. Therefore, it is important to have a coupling method that makes it easy to link more models as these become available and they should be as modular as possible. Object-oriented programming is one sound approach towards this modularity following Ferreira (1995). Whatever the approach followed, the recommendations of Rose et al. (2010) about adopting a community-based approach with open source software seems to be the right way to handle the large complexity of end-to-end models.

Ecosystem model complexity is a matter of great debate (see for example: Allen and Fulton (2010); Hannah et al. (2010) and references therein). According to Hannah et al. (2010), the optimal model complexity shifts to higher values as knowledge accumulates. Therefore, increasing model complexity is a sort of "natural" process whether it happens by increasing feedbacks, processes, temporal or spatial details. It is important to stress that no matter the sophistication of ecosystem models, the challenge is to build a model capable of dealing with species composition changes. The focus of current models is on quantitative changes in the background of a relatively fixed structure. The large uncertainty in the model outcomes that partly result from the poor knowledge about model parameters and partly from the complexity of the systems being modelled was discussed by Hannah et al. (2010). These authors suggest the need to move towards ensemble simulations to overcome some of these limitations and handle system stochastic-

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Fig. 12.10 (continued) ammonification, denitrification, etc.) and their links are represented in parallel with pelagic and benthic food webs. These have a circular form to emphasize the importance of closing the terms associated with gains and losses of the different functional groups (*P* primary producers, *H* herbivores, *C* carnivores, *D* detritivores, *B* bacteria/decomposers). Dots in the grid represent the hypothetical distribution of a high trophic level species. The 3D grid necessary for water column processes includes: (1) inputs from glaciers and rivers (water, nutrients, suspended matter, etc.); (2) exchanges with the atmosphere (in the form of precipitation, evaporation, radiation, wind momentum transfer, carbon dioxide, oxygen, etc.); (3) exchanges with the open ocean (water, momentum transfer, nutrients, suspended matter, dissolved gases, plankton, nekton); (4) water circulation (represented in the grid by the three velocity components u, v and w) (cf. -Synthesis) ity. However, these types of simulations are a great challenge with very complex models demanding a great deal of computer power.

The conceptual model presented here is a sort of "idealization" rooted in the concept of "ecosystem". It by no means implies that all the mentioned complexity is necessary to obtain meaningful results. It merely seeks to suggest a model environment that, in direct interaction with field and experimental work, can address some of the current concerns related with a changing Arctic Ocean, whilst building on recent advances in ecology and modeling. Such an "ideal" model would make it possible to evaluate the relative importance of HTL on ecosystem biogeochemistry – a question that remains largely unanswered in quantitative terms, up to our best knowledge, although that it has been addressed in recent years (e.g. Lavery and Roudnew 2014; Doughty et al. 2015). Such a model could be used to analyse the impacts of warming on the LTL, HTL and their feedbacks, and it would be useful for addressing management and conservation issues. These aspects may become more relevant in the near future, considering the ongoing development of fisheries in the Arctic under the new ice regime. However, the development of such a model is limited by the availability of calibration and validation data. Here, it is important to stress that data-limiting problems are not just related to the model state variables but also to the simulated rates. These rates depend on parameters that should be better constrained, which could be achieved though experimental studies.

Acknowledgement JMW was supported by the project GAME Polish National Science Center no. DEC-2012/04/A/NZ8/00661.

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Chapter 13
Autonomous Marine Observatories in Kongsfjorden, Svalbard

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Abstract Several moored autonomous marine observatories, with a variety of sensors and scientific instruments have been installed in Kongsfjorden, Svalbard, since 2002. These provide seasonal and inter-annual data on a number of physical, chemical and biological variables, as well as biological variables that serve as important baselines for the measurement of seasonal variability and the interpretation of climate-induced changes in this fjord system. Oceanographic and ecological changes observed in Kongsfjorden are, to some extent, related to larger-scale changes in Fram Strait because of the advection of Atlantic Water into the open fjord. We here provide an account of the location of moored observatories in Kongsfjorden, with a list of parameters measured at the different moorings, and review the scientific advances that have been made through data collection from these marine observatories. Several nations collaborate on moorings in Kongsfjorden (Norway, Sweden, UK, Germany, and France), whereas others have separate moorings in the fjord (India and Italy). Some of the moorings in Kongsfjorden have become part of The Svalbard Integrated Arctic Earth Observing System (SIOS). To maximise the scientific benefits of moorings, two priorities need to involve:

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_13

(i) coordination of the infrastructure and (ii) securing their long-term viability in support of Arctic marine science.

Keywords Moorings · Long-term monitoring · Climate change · Svalbard · Arctic

13.1 Introduction

Svalbard is located in the high-Arctic and many of the processes occurring in the region are strongly influenced by the state of the ocean and ice. The west coast of Spitsbergen is affected by inflow of Atlantic Water in the West Spitsbergen Current (WSC) in an area where important boundary fluxes (between atmosphere, ocean and sea-ice) are occurring. Long-term monitoring of key Arctic Ocean gateways has revealed important changes in the Arctic Ocean and its marginal seas, such as increased influence of Atlantic Water (Polyakov et al. 2017; Lind et al. 2018), reduced winter sea ice cover (Onarheim et al. 2014) and modified fluxes of freshwater (Carmack et al. 2016).

Fram Strait is the main gateway with regard to heat and water mass exchange in the Arctic Ocean, and the large quantities of heat carried northwards by the WSC influence climatic processes throughout the Arctic (Beszczyńska-Möller et al. 2011, 2012; Hunt et al. 2016). Regionally, the oceanographic conditions in Fram Strait directly influence the fjords of West Spitsbergen (Pavlov et al. 2013), particularly open fjords such as Kongsfjorden (Hop et al. 2006; Tverberg et al., Chap. 3) and Isfjorden (Nilsen et al. 2008, 2016). Warm Atlantic Water in the WSC crosses the West Spitsbergen Shelf where it mixes with colder Arctic-origin water before being advected into the fjords as Transformed Atlantic Water (Svendsen et al. 2002; Cottier et al. 2005; Nilsen et al. 2008). In recent years, this process has also become more prevalent during winter (Cottier et al. 2007) leading to reductions in sea ice within the fjords (Muckenhuber et al. 2016; Pavlova et al., Chap. 4). The Atlantic Water influences the entire fjord, although the inner basin is largely influenced by run-off from tidal glaciers (Calleja et al. 2017; D'Angelo et al. 2018).

Traditionally, most of the field observations conducted in Svalbard fjords have been biased towards the spring, summer and autumn. This is particularly the case for the collection of biological data (e.g. Hop et al., Chap. 7), whereas oceanographic surveys have also included the winter and polar night periods (e.g. Berge et al. 2015c; Tverberg et al., Chap. 3). Kongsfjorden is arguably the best-studied Arctic system during winter and polar night, partly due to the year-round observatories that have been in operation there over the last two decades, but also to field expeditions that have specifically targeted the polar night in this fjord (Berge et al. 2015a; Lønne et al. 2015; Grenvald et al. 2016). The application of autonomous technologies in marine science to improve seasonal observations have become more prevalent (Nilssen et al. 2015; Ludvigsen et al. 2018), but in restricted coastal locations the use of ocean gliders, autonomous underwater vehicles (AUVs) or drifting buoys each brings their own challenges. The radio silence area in the vicinity of

Ny-Ålesund limits the use of AUV's in Kongsfjorden, especially within the 2–32 GHz frequency range (kingsbay.no/research/radio_silence/).

Instrumentation deployed on moorings have the capacity for making year-round measurements of key physical, geochemical and biological properties. Such moorings that contain some level of complexity in the arrangement of instrumentation (e.g. incorporating physical, optical and biogeochemical sampling) are commonly referred to as marine observatories (e.g. Smyth et al. 2015). They can capture processes occurring on sub-hourly to decadal time-scales (Nilssen et al. 2015), and when the datasets are integrated with complementary earth system parameters they become a powerful resource for determining the drivers and impacts of environmental change. An example of data integration within Kongsfjorden is the co-analysis of satellite imagery of glacier dynamics, collected throughout the year with 11-day repeat satellite passes, with similarly resolved time series of water temperature from a mooring to establish significant geophysical correlations that allow us to better understand glacier ablation (Luckman et al. 2015).

Moorings, by design, support data collection with rather limited spatial resolution. More powerful analyses of processes of varying spatial scale can be achieved through coordination and integration of data collected from multiple moorings. Since 2006, a pair of marine observatories in Kongsfjorden (Atlantic dominated fjord) and Rijpfjorden (Arctic dominated fjord) have been operated in a coordinated manner to investigate the role of water masses, sea ice cover and species diversity on the timing and rates of ecologically-relevant processes (e.g. Berge et al. 2009, 2014; Wallace et al. 2010) or to contrast the conditions and responses to aid interpretation of paleo-records of the environment (e.g. Howe et al. 2010; Ambrose et al. 2012). Data from paired moorings in Kongsfjorden have been used to describe complex wave propagations that support the exchange of water in the fjord (Inall et al. 2015), and integration of Svalbard moorings with those from around the Arctic Ocean have been used to establish pan-Arctic responses of zooplankton to winter illumination (Last et al. 2016) and sea ice (Hobbs et al. 2018).

Marine observations around Svalbard have been collated to derive long-term records of change (e.g. Renaud and Bekkby 2013). These are principally linked to the physical system (Pavlov et al. 2013), but also aligned with long-term records of pelagic and benthic ecology (e.g. Soltwedel et al. 2005, 2016; Beuchel et al. 2006; Kedra et al. 2010; Kortsch et al. 2012; Bauerfeind et al. 2014; Nöthig et al. 2015; Hop et al. (Chap. 7)), and proxies of environmental change (Ambrose et al. 2006; Vihtakari et al. 2016, 2017). An array of oceanographic moorings have been maintained in Fram Strait at 78° 50′N since 1998 extending from the shelf west of Svalbard through the deep part (2500 m) to the eastern Greenland shelf (Schauer et al. 2008). Thus, it covers the oceanographic variability in temperature, heat transport, sea ice and salinity both in the WSC and the cold East Greenland Current (Beszczyńska-Möller et al. 2011). The Long Term Ecological Research observatory HAUSGARTEN has been maintained in the eastern Fram Strait since 1999 (Soltwedel et al. 2005, 2016). Ecological variability as well anthropogenically-induced variation have been determined based on annual sampling campaigns coupled with autonomous instruments in anchored devices (i.e. moorings and profiling systems). Observatories can also acquire data in support of modelling – either to provide the essential boundary conditions to drive the model, or to provide robust *in situ* data for model calibration and validation (Cottier et al. 2007; Wallace et al. 2013; Drysdale 2017; Sundfjord et al. 2017).

Marine observatories have been an important element for many years in the community data collection within Kongsfjorden, and the number of moorings increased after the fjord became closed for commercial trawling in February 2007. Whilst there have been some actions to document the existence of marine observatories around Svalbard (e.g. www.sios-svalbard.org), there is no systematic review within the scientific literature. Over recent decades, scientific endeavours with respect to the Kongsfjorden system have drawn on data collected during long deployments of automated recording instruments within the fjord. Either these have been designed primarily for the deployment of moorings, or the availability of mooring data has been opportunistic, providing valuable ancillary data to the sampling program. Despite the prevalence of marine databases, awareness of these mooring deployments and the availability of the data are often retained within a rather limited subset of Arctic researchers, and the locations of moorings and operators are not widely known. The aim of this paper is to present a brief overview of the recent moorings in Kongsfjorden and review the scope of publications from these marine observatories. Note that these are fixed, autonomous instruments, rather than sites of monitoring by sampling. However, moorings may change in composition and position over time, and thus, our presentation represents the current situation in Kongsfjorden.

13.2 Moored Instrumentation and their Scientific Advances

Sensors for physical and chemical parameters have been installed on marine observatories in Kongsfjorden for monitoring: currents, temperature and salinity, fluorescence, turbidity, dissolved oxygen, photosynthetically active radiation (PAR), nitrate (NO_3), pCO_2 and pH (Table 13.1). Biological parameters are also collected by sediment traps, active acoustic instruments (e.g. acoustic zooplankton and fish profilers) and water samplers, and passive acoustics are used for monitoring of vocalizing marine mammals (Table 13.1).

Biofouling is a common problem of moored instrumentation, particularly in fjords where sediments from tidal glaciers are an additional source of fouling. Much of the fouling can be mitigated by wipers or covers that are automatically moved before recording, and flushing of sensors with pumped systems can also be effective. Nevertheless, it is essential for the sensors to undergo cleaning during maintenance periods. All scientific sensors will experience drift in recorded values because of sensor degradation, which may not occur linearly over time. Ideally, sensors should have pre- and post-deployment calibrations, but often this is not done routinely due to limited numbers of instruments and the need to replace them in the field annually. Finally, battery endurance, rather than data storage, is the usual limiting factor for moored instrumentation, particularly for acoustic instruments. This requires that the sampling frequency optimises the balance between endurance, temporal resolution of the data and measurement biases. Some instruments allow variable sample frequencies; an example of this is the multi-bottle sediment trap. Sampling interval can be set for each bottle independently with increased frequency during periods of rapid change or high activity (e.g. during spring bloom) and low frequency during the rest of the year.

Currents are measured with either electromagnetic (EM) sensors or acoustic Doppler technology. An acoustic Doppler current profiler (ADCP) is primarily used to measure depth-varying currents in layers of water either for long-term measurement of exchange or for short-term dynamics (Inall et al. 2015; Tverberg et al., Chap. 3). Secondary data streams include vertical velocity and acoustic backscatter from which the vertical movements of organisms in the water column can be quantified (Cottier et al. 2006; Wallace et al. 2010). Presence and absence of sea ice can also be derived from such acoustic profiling instruments (Hyatt et al. 2008) to give additional environmental context to the time series.

Temperature sensors are the most robust and reliable instruments. The accuracy may be better than 0.01 °C, and the drift of such instruments is generally small. There is a range of manufacturers of temperature sensors, but there are no agreed protocols on ensuring data quality. Each operator of an observatory tends to follow their own protocol – either calibrated *in situ* using a ship CTD system or with sensors being brought ashore for calibration at fixed temperatures.

Salinity, derived from measurements of conductivity, is a key parameter for determining water density, but it is more difficult than temperature to attain high quality records in long-term measurements due to issues of fouling and sensor drift. During long deployments in water with high sediment loads, the performance of the conductivity cells can deteriorate. Again, a variety of sensors are used and calibration is not done systematically across all operators of the observatories. In a region of high fouling, it may not be possible to apply calibrations to correct the data to the highest oceanographic standards. However, *in situ* calibration will indicate major drift/offsets and temperature-salinity scatter plots of the data will highlight portions of the data that are significantly affected by fouling. It is important that the salinity sensors receive factory refurbishment and calibration on regular intervals.

Optical instruments are generally placed in the upper water column to monitor phytoplankton biomass (chlorophyll *a*) of the water through their fluorescent properties. Photosynthetically active radiation is often measured in addition to fluorescence (Wallace et al. 2010; Pavlova et al., Chap. 4). Fouling issues associated with the lens can be a problem, but wipers can be used on lenses before recordings. To circumvent the issues of fouling and attaining precise calibrated values, fluorescence and PAR data have been published as normalised values relative to the maximum value (e.g. Wallace et al. 2010; Hegseth and Tverberg 2013; Berge et al. 2014) from which onset, duration and peak can be reliably determined for each parameter. Fluorescence data have also suffered from significant spikes caused by the occupation of the beam path in the sensor by zooplankton (e.g. feeding individuals have green guts). Recent deployments have used simple mesh coverings to maintain a flow of water and limit the impact of zooplankton on the signal.

Chemical sensors have been installed on some recent moorings, including recorders for dissolved oxygen, nitrate, pCO_2 and pH.

Sediment traps are used on some moorings (e.g. in Kongsfjorden and Rijpfjorden) to record the seasonal vertical flux of particulate organic matter (POM) (Howe et al. 2010; Darnis et al. 2017). Both algae and faecal pellets from zooplankton can be recorded, as well as zooplankton (swimmers) that eventually end up in the traps (Willis et al. 2006, 2008). The trap contains a number of bottles with fixative (2% formalin buffered with sodium borate), and its rotational sampling frequency can be set. Typically, the sampling is more frequent in association with the spring plankton bloom, although the main flux of particles generally occur in late autumn.

Water samplers on moorings can sample water periodically. These include pumps that push water through changing filters, and samples can be fixed in preservative. Measurements of nutrients (e.g. nitrate concentration) from these samplers can be used to calibrate continuously recording moored nitrate sensors located at the same depth (E. Leu, Univ. Oslo, pers. comm.).

Biological samples, such as clams or settlement plates, have been suspended from the mooring cable at different depths. Growth or uptake rates (e.g. chemical elements) in shells can then be directly correlated with measurements of the physical parameters from the mooring (Ambrose et al. 2012; Vihtakari et al. 2016, 2017).

Remote controlled stereoscopic camera systems are used to assess species abundance, species compositions and length-frequency distributions in shallow water. In Kongsfjorden, a vertical profiling system is located close to the old pier in Ny-Ålesund at 12 m water depth.

Passive acoustics, or listening devices, are hydrophones moored at different locations to detect vocalizing marine life, such as seals and whales, as well as ship traffic and airgun surveys. These have been used to record vocal complexity of the bearded seal (*Erignathus barbatus*) in Kongsfjorden (Parisi et al. 2017).

13.3 Marine Observatories in Kongsfjorden

Several marine observatories have been installed in Kongsfjorden by different nations responsible for their operation (Table 13.1, Fig. 13.1). Most of these observatories have been of the 'single-point, sub-surface' variety, resolving the vertical structure of the water column for some parameters. Typically, these moorings are deployed with annual schedules for maintenance and data retrieval. The hydrographical setting of the moorings can be related to seasonal and inter-annual variability in hydrography along the Kongsfjorden Transect (Kb1-Kb7; Tverberg et al., Chap. 3), as well as detailed descriptions of the respective moorings (e.g. Aliani et al. 2016; Venkatesan et al. 2016).

UK and Norway have established *The Kongsfjorden Marine Observatory*, which is operated in collaboration by Scottish Association for Marine Sciences (SAMS), UiT The Arctic University of Norway, and The University Centre in Svalbard (UNIS). This mooring contains an array of sensors and a rotating sediment trap

Table 13.1 Recent moorings in Kongsfjorden, Svalbard, with responsible institutions, locations, depth (distance to the surface) and parameters being monitored (i.e. in operation 2017–2018), including currents by current meter (not acoustic) (CM), Acoustic Doppler Current Profiler (AP), temperature (T) and salinity (S), fluorescence (FL), turbidity (TU), dissolved oxygen (DO), photosynthetically active radiation (PAR), nitrate (NO_3), $p CO_2$, total alkalinity (TA), pH, sediment trap (ST), water samplers (WS), passive acoustics (PA) for wildlife monitoring, stereooptic time-lapse camera (SCA). Reference, or contact e-mail, and number for registered projects in Research in Svalbard (RiS) are listed together with start/end time for mooring deployment

Mooring name	Institution	Country	Latitude (N)	Longitude (E)	Depth (surface) (m)	Parameters	Reference (or contact)	RiS #	Start time	End time
CNR-ISMAR	CNR-Dirigible Italia	IT	78°54.863’	12°15.530’	105 (15)	CM, TS, STR	Aliani et al. (2016)	4375	2010	Ongoing
KB-FRAM-AMUST	AWI	GE	78°56.501’	11°57.053’	303 (21)	TS, FL, DO, PAR, NO_3, p CO_2, pH, WS	Daniel.Scholz@awi.de	6790	2017	2018
IndARC-3	NCAOR	IN	78°56.789’	12°00.889’	198	CM, AP, TS, FL, TU, DO, PAR, NO_3, p CO_2	Venkatesan et al. (2016)	10,309	2016	Ongoing
IndARC-3	NCAOR/NPI/IMR	IN/NO	78°56.789’	12°00.889’	30	pCO_2	Agneta.Fransson@npolar.no	10,139	2016	Ongoing
LoTUS-Bottom Lander #8	Uni. Stockholm/UNIS	SE/NO	78°53.046’	12°32.141’	82 (67)	T	nina.kirchner@natgeo.su.se	10,783	2016	2017
Hydrophone-SM2-Open	CNR-Dirigible Italia	IT	79°03.219’	11°32.814’	75	PA	Giuseppa.buscaino@cnr.it	6616	2015	Ongoing
Hydrophone-SM2-Glacier	CNR-Dirigible Italia	IT	78°54.732’	21°24.250’	75	PA	Giuseppa.buscaino@cnr.it	6616	2015	2016
Hydrophone-SM2-Harbour	CNR-Dirigible Italia	IT	78°56.199’	11°54.628’	30	PA	Giuseppa.buscaino@cnr.it	6616	2015	2016
Hydrophone-Cabled-Harbour	CNR-Dirigible Italia	IT	78°55.902’	11°56.403’	30	PA	Giuseppa.buscaino@cnr.it	6616	2015	2017
Kongsfjorden Marine Obs.	SAMS, UIT, UNIS	UK/NO	78°57.4’	11°49.6’	225 (18)	TS, AP, FL, DO, PAR, NO_3, pH, p CO_2, ST, PA	www.mare-incognitum.no	11,107	2002	2027
AWIPEV-COSYNA	AWIPEV	GE/FR	78°55.747’	11°54.99’	11 (0)	TS, AP, FL, TU, DO, PAR, pH, p CO_2, TA, SCA	Fischer et al. (2016)	5742	2012	Ongoing

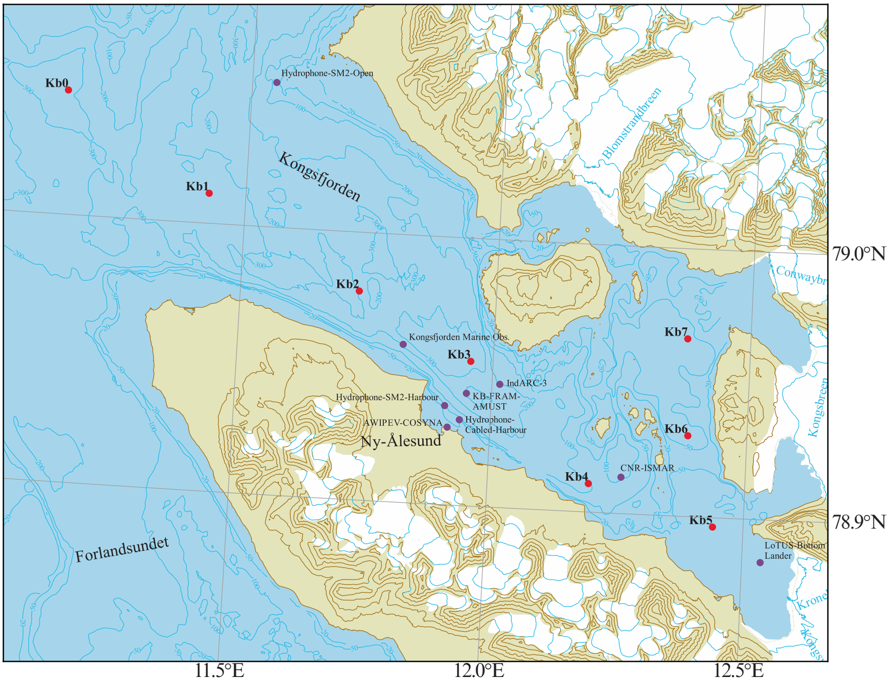

Fig. 13.1 Kongsfjorden, Svalbard, with locations of moorings and standard sampling stations (Kb1-Kb7) for the annual research survey in Kongsfjorden during July-early August (www.mosj.npolar.no; see Hop et al., Chap. 7). These stations, as well as others are also sampled annually in Kongsfjorden by the Institute of Oceanology, Sopot, Poland. Mooring information is in Table 13.1

(Table 13.1, Fig. 13.2), and has produced the longest time series from Kongsfjorden for a fixed mooring. Its record of temperature profiles from 2002–2018 shows the annual cycles in temperature, which can be averaged for the oceanographically warmest (Sept-Nov) and coldest (March–May) months (Fig. 13.2). Temperature variations during the warmest months indicate periods of enhanced warming in 2002, 2007–2009, and years after 2013, on the backdrop of an increasing temperature trend of 0.11 °C y^{-1}. These cycles can also be seen during the coldest months, although with a seasonal shift indicating warming of the coldest months prior to warming of the warmest months and the coldest months having a more pronounced long-term temperature increase of 0.16 °C y^{-1}. Similar long-term increase in fjord temperature has also been found in winter months (Nov-Feb) (Geoffroy et al. 2018).

A more detailed temperature record for the winter 2005–2006 showed the influx of warm water in February 2006 (Fig. 13.3), which has been linked to warming on the shelf in response to large-scale atmospheric circulation (Cottier et al. 2007) and a long-term reduction in fast ice in western fjords (Muckenhuber et al. 2016). These shifts in temperatures became only apparent based on such mooring records and have been used as background information for interpretations of shifts in the marine ecosystem, particularly after the warming events in winter 2006 and 2007, which

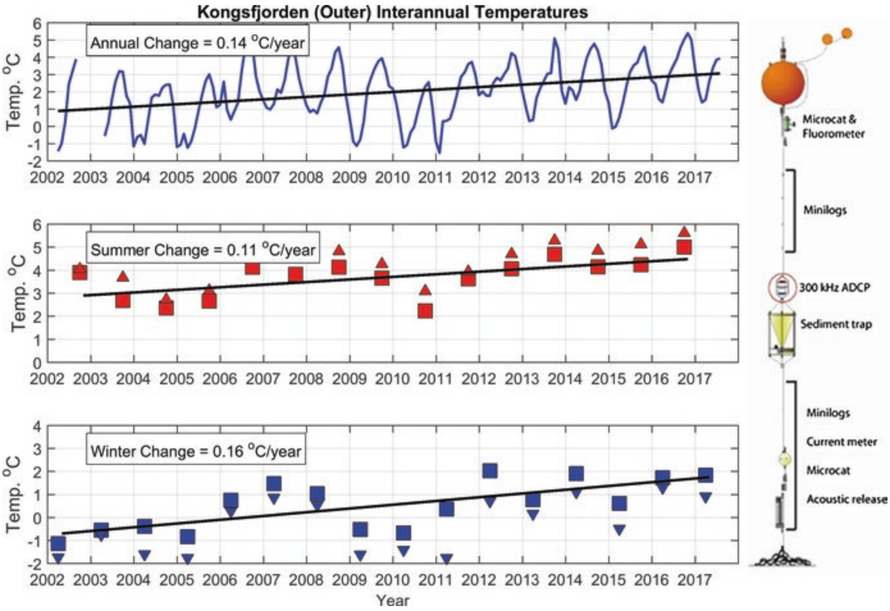

Fig. 13.2 Seasonal cycle of temperature in Kongsfjorden for 2002–2017 (top). Mean temperatures, averaged over depth for September–November – which are climatologically the warmest months (middle). Mean temperature, averaged over depth for March–May – which are climatologically the coldest months (bottom). Triangles show the maximum (warmest) and minimum (coldest) depth-averaged temperatures within the entire record. Simple regression lines indicate the annual change in temperature during the period. Data from Kongsfjorden Marine Observatory (N79°3.250′, E011°18.00′) (SAMS/UiT) are reported to www.sios-svalbard.org. The arrangement of instrumentation for this mooring is included as example. For other mooring arrangements we refer to cited papers

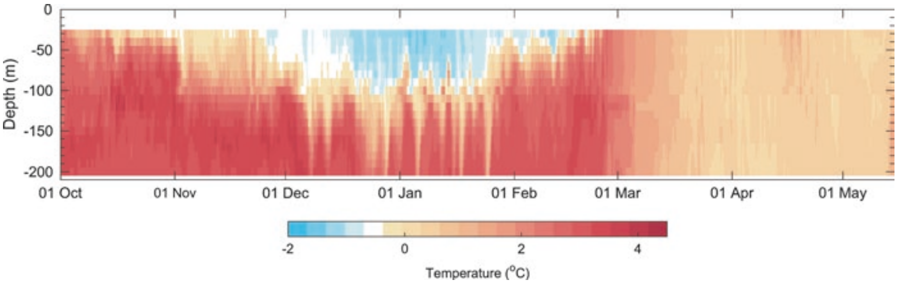

Fig. 13.3 Temperature observations from the Kongsfjorden Marine Observatory between 30 m and 200 m from October 2005 to May 2006. (Modified from Cottier et al. 2007)

resulted in warmer conditions in Kongsfjorden (Tverberg et al., Chap. 3) and less sea ice (Pavlova et al., Chap. 4). These changes in oceanographic conditions caused changes in the pelagic ecosystem, with larger influx of Atlantic species (Willis et al. 2008; Dalpadado et al. 2016; Vihtakari et al. 2018; Hop et al., Chap. 7). Warmer waters in the winter and spring period have also been implicated in the greater prevalence of Atlantic fish species (Berge et al. 2015b) and jellyfish (Geoffroy et al. 2018).

Timing and duration of key primary production events have been interpreted from the complementary data series (Hegseth and Tverberg 2013; Hegseth et al., Chap. 6). Time series of fluorescence (normalised) were recorded in the period 2006–2010 and interpreted against the temperature record from the same mooring. The spring blooms occurred April in 2006, and mainly in May–June during 2007, 2008 and 2010 (Hegseth and Tverberg 2013; Vihtakari et al. 2017), with high biomass of diatoms and *Phaeocystis pouchetii* in the early bloom and low biomass consisting of mainly *Phaeocystis* in the late blooms. The different bloom developments in 2006–2008 were related to the Atlantic Water inflow, which seemed to be the main controlling factor of the spring blooms.

Diurnal vertical migration (DVM), performed by many zooplankton species is a light-mediated behaviour in response to the trade-off between predation risk and the need to feed (Hays 2003). The zooplankton typically form aggregations in the water that can scatter sound and thus the phenomenon can be investigated from the backscatter signal recorded by upward-looking ADCP (300 kHz) mounted on a mooring. Acoustic data have shown the DVM signal is strong in Kongsfjorden during spring and autumn, but absent or unsynchronized during the summer (Fig. 13.4; Cottier et al.

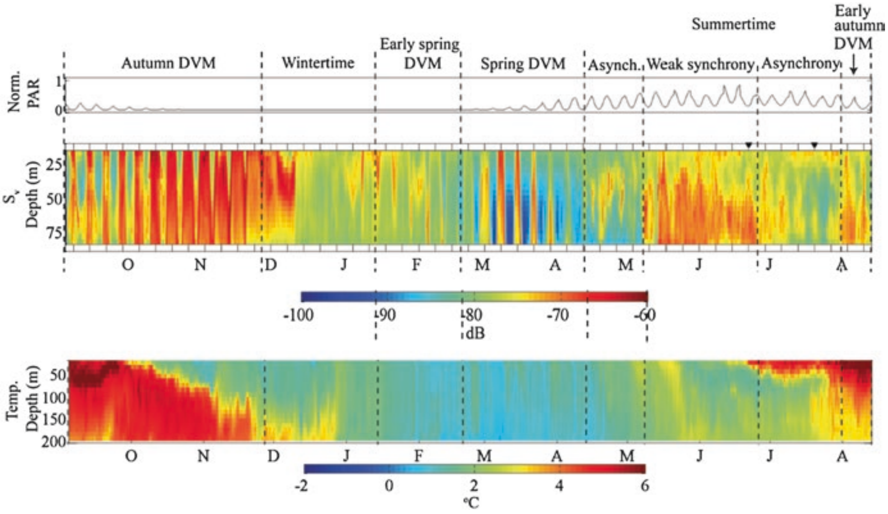

Fig. 13.4 Normalized (relative to maximum) photosynthetically active radiation (PAR), Acoustic Doppler Current Profiler (ADCP) and temperature data from Kongsfjorden, 2006–2007. The patterns in diel vertical migration (DVM) for zooplankton through the annual cycle is indicated above. (Modified from Wallace et al. 2010)

2006; Wallace et al. 2010). However, the DVM signal in autumn continues to some extent through the winter, indicating activity in the pelagic ecosystem even during winter with 24 h of darkness (Berge et al. 2009, 2015a). Further analyses of the ADCP data have shown that the zooplankton can adjust their DVM timing from solar cycle (24 h) to lunar cycle (24.8 h) within days around the full moon (Berge et al. 2009).

A study in Kongsfjorden and Rijpfjorden used marine observatories to understand how changes in the water column properties become imprinted on the growth lines of clams (Ambrose et al. 2012). Greenland cockles (*Serripes groenlandicus*) and hairy cockle (*Clinocardium ciliatum*) were placed in baskets at 25 m depth on the moorings. They had been marked with calcein dye, which becomes imbedded in the shells, and were then retrieved from the moorings a year later. Growth over the year could be studied and related to seasonal temperature and salinity pattern from the thermal loggers and algal biomass determined by Chl *a* fluorescence (Fig. 13.5). The study concluded that growth lines in Greenland and hairy cockle shells are formed inter-annually. Further studies on these clam species determined oxygen isotope signals to model seasonal growth patterns and correlate variation in element ratios (Li/Ca, Mg/Ca, Li/Mg, Li/Sr, Mn/Ca, Sr/Ca, Mo/Ca, and Ba/Ca) with temperature and fluorescence recordings from mooring instruments to determine the clams' potential as environmental proxies (Vihtakari et al. 2016, 2017). These studies found that element ratios in Greenland and hairy cockle shells reflect conditions in the internal body fluids (metabolism) rather than the environment where the bivalves are living.

Italy (CNR) has maintained the oceanographic array named *Mooring Dirigibile Italia* (MDI) since 2010 at 103 m depth in Kongsfjorden, outside the sill severing the inner bay (Fig. 13.1). The array includes current meters and temperature-conductivity recorders and regularly monitors the input of water through the inner morainic sill across Lovénøyane southern passage toward tidewater glaciers. Aliani et al. (2016) used a combination of time series from this mooring and CTD casts in the inner bay to estimate the volume of Atlantic Water in the inner bay and the ocean heat content. The heat content in Atlantic Water advected into the inner bay likely contributes to accelerated melting at the base of tidewater glaciers, which may cause instability of the glacial fronts (Jenkins 2011; Schild et al. 2018). A recent study by D'Angelo et al. (2018) used a data set (2010–2016) from this mooring to determine variability and composition of particle flux in Kongfjorden. The mass fluxes, predominantly from sub-glacial run off, varied by two orders of magnitude over the duration of study and indicate that land-derived input will increase over time in a warming scenario.

India (NCAOR) has run a multi-sensor moored observatory *IndARC* in middle of Kongsfjorden since 2014, with a suite of sensors for physical and chemical data collection (Fig. 13.1). Data include annual records of temperature, salinity, dissolved oxygen, currents based on recordings from current meters and ADCP as well as other parameters (Venkatesan et al. 2016; Table 13.1). Their observations confirm stratification of the water column during summer and mixing during winter. Their mooring data will be used in development of a bio-physical regional model for Kongsfjorden. Norway collaborates with India on this mooring with regard to

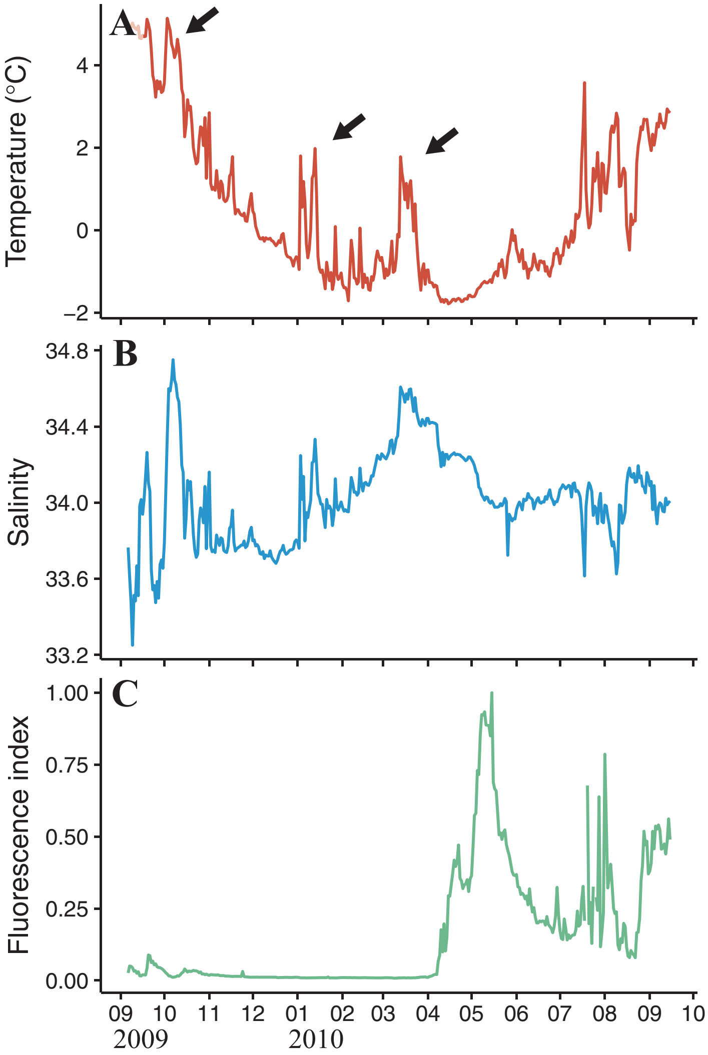

Fig. 13.5 Seasonal data (2009–2010) from the Kongsfjorden Marine Observatory at 36 m depth. A) Seawater temperature, B) salinity, and C) fluorescence index over the deployment period as measured by mooring instruments. Black arrows point to Atlantic inflow events. (Modified from Vihtakari et al. 2016)

annual maintenance (ship-based), and the Norwegian Polar Institute/Institute of Marine Research added a $p\mathrm{CO}_2$ sensor to this mooring in 2016.

Germany in collaboration with France (AWIPEV) have established an underwater observatory for long-term monitoring of the shallow water ecosystem in Kongsfjorden in 2012 (Fischer et al. 2016). The installation was done in the framework of COSYNA (Coastal Observation System for the Northern and Arctic Seas).

The Observatory is located in front of the Old Pier in Ny-Ålesund and is the northernmost-cabled online underwater observatory in the world. The system can be controlled from the home institution via high-speed internet connection for remote controlled sensors and *in situ* experiments. The system includes a fully equipped ferry box, with a water intake at 11 m water depth, for year-round measurements of physical and chemical parameters (temperature, salinity, turbidity, dissolved oxygen, pH, $p\text{CO}_2$, Total Alkalinity [TA] and PAR). In addition, recordings are made of water-mass properties and currents (ADCP, 1200 kHz), tides, and ice coverage. Periodical sampling from the ferry box can complement samples from other locations in the fjord, and one recent study used this to elucidate effects of Atlantic advection on spatial phytoplankton chlorophyll *a* and taxonomic composition (van De Poll et al. 2016). They suggested that glacial melt water governs spring bloom spatial timing and composition in the absence of sea ice driven stratification.

Daily profiles of temperature, salinity, turbidity, dissolved oxygen, pH and PAR, are performed vertically from the bottom (12 m depth) to surface along a fixed system at the Old Pier, and concomitant assessments of the mobile fauna in the water column are made by stereo-optic still camera system (Remos1). From these images, the daily and seasonal abundance of large zooplankton (e.g. pteropods, ctenophores, medusas, chaetognaths and decapods) can be determined as well as presence and development of pelagic fish larvae and juveniles based on length measurements. This system has great potential for providing new information about the shallow-water marine ecosystem on a seasonal basis, particularly during seasons of low sampling activity by field campaigns.

Germany (AWI) established a mooring, *KB-FRAM-AMUST*, 1.4 km south of the monitoring sampling station Kb3 in 2017. The purpose of this mooring was to test the long-term performance of different *in-situ* sensors, and it has served to monitor the bio-chemical processes going on close to Kb3 during a full year.

13.4 Further Considerations with regard to Marine Observatories in Kongsfjorden

Long-term observations have been central to documenting fundamental shifts in the Arctic marine environment (Grebmeier et al. 2006; Polyakov et al. 2017). Marine observatories are elements of the core infrastructure for such long-term monitoring, but also play an important role in supporting shorter-term process studies linked to specific research projects. Through this review we have shown that marine observatories offer the capabilities needed to address critical research areas such as the coupling between physical, biological and chemical processes and systems, and ecosystem change or resilience to climate variability. In Kongsfjorden, the utility of marine observatories has resulted in numerous systems being deployed (Table 13.1), all of them funded through different routes. To maximise the scientific benefits, two priorities need to be addressed: (i) coordination of the infrastructure and (ii) securing their long-term viability through financial support.

In terms of coordination, there exists no mechanism to achieve formal coordination of the observatories. They are often driven by national priorities and projects and there is relatively little exchange of information between the operators. However, there have been a number of efforts to summarize long-term data series around Svalbard (e.g. Renaud and Bekkby 2013) and collating information on marine observing activities through the Svalbard Science Forum Ocean Flagship (e.g. Beszczyńska-Möller and Sagen 2015; Falk et al. 2016) and Kongsfjord Flagship Workshops (Gabrielsen et al. 2009).

Despite these efforts to document activity, there exists a desire from both the science community and national agencies to establish a group of mooring operators to provide a more informed and coordinated approach to marine time series in Kongsfjorden. The Svalbard Integrated Arctic Earth Observing System (SIOS) has started to integrate long-term measurements in and around Svalbard (www.sios-svalbard.org) through a cooperative project. This exercise in collating data, joint analyses and reporting necessitates increased collaboration among the partners and may evolve into a coordinating body for marine observatories. Further coordination activity may include agreements on placement of observatories to maximise coverage, standardisation of instrumentation and calibration protocols, joint preparation of data products for the science community, and increased visibility of the marine observatories in Kongsfjorden and around Svalbard. Ultimately, marine observations should become better coordinated with observations currently performed on land, on glaciers and in the atmosphere.

With respect to long-term support of marine observatories in Kongsfjorden, the ocean module of SIOS-InfraNor encompasses several observatories along the west coast of Svalbard and Fram Strait, including the Kongsfjorden Marine Observatory (www.sios-svalbard.org/InfraNor). This provides financial security for observations until 2027. Additional observatories are likely to be supported by national programs and discrete research projects. Further resilience to the observing effort in Kongsfjorden will come when there is a clear network of marine observatories around Svalbard. SIOS may well have a coordinating role to play here, as might the Arctic Regional Ocean Observing System (Arctic-ROOS) and/or the Sustained Arctic Observing Network (SAON; www.arcticobserving.org). Ultimately, to maximise the scientific return and longevity of the observatories in Kongsfjorden, they need to have relevance beyond the fjord and this is best achieved through pan-Arctic data integration initiatives, e.g. Last et al. (2016) and Hobbs et al. (2018).

Acknowledgements We thank the mooring contacts at respective institutions for supplying updated information for Table 13.1. The moorings have been supported financially by many funding agencies and projects. The acknowledgement of funding for specific projects that have used data from the moorings are found within the cited publications. We thank Colin Griffiths (SAMS) for overseeing the Kongsfjorden Marine Observatory programme, managed from SAMS with support from the UK Natural Environment Research Council, the Research Council of Norway and the EU. Considerable in-kind support has been given over the years from UiT The Arctic University of Norway, UNIS and NPI in its operation. We finally thank Mikko Vihtakari (NPI) for assembling the map.

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Part VI
Kongsfjorden as Harbinger of the Future Arctic

Chapter 14
Kongsfjorden as Harbinger of the Future Arctic: Knowns, Unknowns and Research Priorities

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Abstract Due to its year-round accessibility and excellent on-site infrastructure, Kongsfjorden and the Ny-Ålesund Research and Monitoring Facility have become established as a primary location to study the impact of environmental change on Arctic coastal ecosystems. Due to its location right at the interface of Arctic and Atlantic oceanic regimes, Kongsfjorden already experiences large amplitudes of variability in physico/chemical conditions and might, thus, be considered as an early warning indicator of future changes, which can then be extrapolated in a pan-Arctic perspective. Already now, Kongsfjorden represents one of the best-studied Arctic fjord systems. However, research conducted to date has concentrated largely on small disciplinary projects, prompting the need for a higher level of integration of future research activities. This contribution, thus, aims at identifying gaps in knowledge and research priorities with respect to ecological and adaptive responses

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H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*,
Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1_14

to Arctic ecosystem changes. By doing so we aim to provide a stimulus for the initiation of new international and interdisciplinary research initiatives.

Keywords Flagship program · Monitoring · Land-sea-ocean-interaction · Indicator species · Pan-Arctic

14.1 Introduction

Polar systems, and in particular the High Arctic, are environmentally sensitive regions in which the impacts of global climate change will be manifested faster than elsewhere on our planet (Larsen et al. 2014). Arctic marine communities can therefore be regarded as sensitive indicators signalling the onset of environmental change. Kongsfjorden, a fjord located on the west Spitsbergen coast, is one of the northernmost areas influenced by the inflow of warm Atlantic water from the West Spitsbergen Current, and is positioned right at the interface of High Arctic and Atlantic influences. The marine communities of this ecosystem therefore dynamically respond to the variability and changes in environmental conditions occurring today. The Atlantic-Arctic climate signals vary between years, leading to measurable effects on biological processes, such as alterations in benthic and pelagic primary production (Hegseth and Tverberg 2013; Krause-Jensen and Duarte 2014;

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Bartsch et al. 2016; Hegseth et al., Chap. 6), and changes in composition of zooplankton (Beuchel et al. 2006; Willis et al. 2006, 2008; Dalpadado et al. 2016) as well as fish communities (Brand and Fischer 2016), with potential consequential negative implications for seabirds and mammals (Lydersen et al. 2014; Vihtakari et al. 2018). In the current era of global environmental change, documented and projected alterations in the physico-chemical environment in the Kongsfjorden system include changes in atmospheric and seawater temperature, decreases in winter sea–ice cover, changes in the salinity regime ("Atlantification"; Hegseth and Sundfjord 2008), decrease in seawater pH ("ocean acidification"; Fransson et al. 2016; Lou et al. 2016), increased terrestrial run-off potentially altering nutrient, sediment and soil-associated contaminant loadings (Granberg et al. 2017), changes in light climate, particularly ultraviolet B exposure (due to stratospheric ozone depletion; Hanelt et al. 2001), and glacier retreat (Kohler et al. 2007; Blaszczyk et al. 2009). In addition, air- and waterborne pollutants emitted from low latitudes (Gabrielsen 2007; Jæger et al. 2009) as well as originating from local pollution sources such as dumping sites and remains from mining activities (Skei 1994; Szczybelski et al. 2016; Vázquez Alonso 2016) are detected in the Kongsfjorden region, and can impact marine life.

Any of the above-mentioned environmental alterations may impose stress on organisms, and species-specific responses are expected. Grime (1989) and Vinebrooke et al. (2004) basically defined stress as *the impact of any set of abiotic and biotic factors negatively affecting the performance individually, and eventually deteriorating the growth rate of the population through the reduction of individual survival, growth and reproduction.* Thus, stress can be invoked by abiotic or biotic drivers, and both can interact producing combined (additive, synergistic, antagonistic) impacts. In addition, the effects of stress depend on a) its intensity, duration and periodicity, b) the target organism, and c) any interaction between the stressors themselves. Davison and Pearson (1996) proposed that growth rate of a certain organism can be affected by "limiting factors" as well as by "disruptive factors", and among the latter we can consider high irradiance (both PAR and UV), high or low temperature, desiccation, freezing, low pH, osmotic stress and contaminant exposure.

Such widespread and profound environmental changes will provoke species-specific responses, which may further result in new inter-specific interactions, such as competitive or trophic changes and, thus affect ecosystem functions (e.g. Russell et al. 2012; AMAP 2013; Pörtner et al. 2014). At the organism level, responses to environmental changes are often summarised by the simple phrase: 'Move, adapt or die'. This kind of simplistic view, however, neglects the plasticity of organism responses, which may buffer against the stress impacts of environmental changes. Physiological plasticity has evolved along temporal gradients of environmental stability, with organisms from evolutionarily stable habitats generally being less plastic (Peck et al. 2006). However, due to the Arctic's comparatively short cold-water history (compared to Antarctica) we might expect a higher degree of plasticity in the majority of inhabiting organisms (Wiencke and Amsler 2012). When characterising individual *vs.* species responses towards environmental change we should discriminate between the different timescales for expressing such response: the term "regulation" means an immediate response of an individual to varying environmental factors, for instance by activation/up−/down-regulation of existing enzymes. "Acclimation" is a mid-term response (hours or days) and usually involves changes in gene expression. "Adaptation" represents the genetic framework, which sets the limits for acclimation. Adaptation to new environments requires alterations of the genome, drives speciation processes and is, thus, usually active over longer timescales or at least sequentially develops over a number of generations. Future studies on environmental impacts on Arctic coastal ecosystems will thus need to address responses on different timescales and hierarchical levels (molecular/cellular, individual, population, community, ecosystem). An improved understanding of acclimative, interactive and adaptive responses is urgently needed to reduce the level of uncertainty in our predictions on the consequences of climate change.

How physiological and molecular responses translate into structural and functional ecosystem processes is almost completely unexplored for most species inhabiting the Kongsfjorden system. Without this knowledge, predicting or modelling climate change effects on biota becomes an impossible task. Improved understanding of general mechanistic principles applying to a wide range of organisms and the overall adaptive capacity ("thresholds, tipping points") of the system has yet to be established for any environmental stressor, either in isolation or in combination with other abiotic and biotic drivers (Wassmann and Lenton 2012; AMAP 2013).

The Kongsfjorden area (Fig. 14.1) has a rich history of scientific research and monitoring focused on the research station at Ny-Ålesund, and is ideally suited to play a leading role in establishing such in-depth knowledge on Arctic change. Given the high degree of complementary expertise in the international community conducting science at Kongsfjorden, greater integration of research activities would provide the opportunity to accelerate development of mechanistic understanding of adaptation processes, life-cycle control of key organisms, and ecosystem structure, function and services. A compilation of the current state of knowledge is provided by this book. Starting from an improved topical research focus on the Kongsfjord marine ecosystem, principles found should be addressed and compared across systems and across phyla (e.g. by identifying common principles across marine and terrestrial systems, or connectivity between atmosphere-land-ocean) and within a pan-Arctic perspective.

In the light of this complex changing environmental scenario, a set of key scientific questions have been formulated by the Kongsfjord ecosystem research community. They provide a framework for future integrative research applied to the Kongsfjorden system.

1. Is Kongsfjorden a suitable model system to project the future of marine ecosystems on Svalbard and beyond? Are contemporary changes harbingers of the future in other fjords?
2. What consequences will 'Atlantification' have for ecosystem processes and services such as carbon uptake and storage, sources/sinks of nutrients, or dynamics of contaminants in the food webs?
3. Can effects of climate change be mitigated by acclimation and adaptation, and, if so, what will those responses be? What is the timescale of responses towards

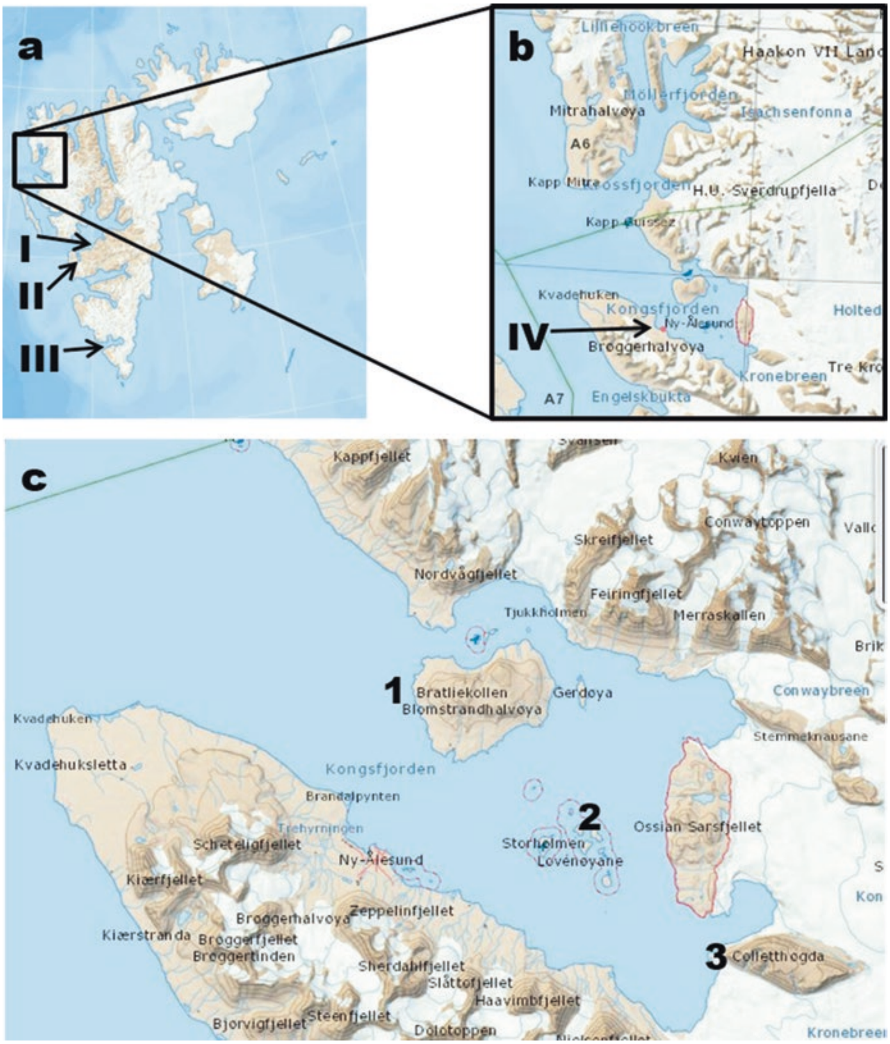

Fig. 14.1 (**a**) Map of the Svalbard archipelago; location of **I**: Longyearbyen, **II**: Barentsburg, **III**: Hornsund. (**b**) Map of the Kongsfjorden and neighboring Krossfjorden system, **IV** location of Ny-Ålesund. **c**: map of Kongsfjorden, indicating important study sites for marine research along the fjord axis; **1**: Hansneset, **2**: Juttaholmen, **3**: Collethøgda. (Map retrieved from Topo Svalbard, Norwegian Polar Institute)

different and interacting environmental drivers and can they help sustain ecosystem services?

These research questions are based on the following hypotheses:

1. Warming and acidification in Arctic coastal waters will continue and develop beyond the range of current natural variability.

2. Tidewater glaciers will disappear, with major consequences for seawater circulation and associated biological systems in Arctic fjord systems.
3. "Atlantification" will continue, leading to local extinction of endemic species and/or the colonization by and establishment of temperate species in Arctic marine ecosystems.

This contribution aims to provide a research framework or catalyst for addressing climate-related changes in Kongsfjorden, and the Arctic generally, with respect to productivity, ecosystem functions and biodiversity, regime shifts, and ecosystem services. Gaps in knowledge and research priorities identified by the community of marine researchers working in Kongsfjorden are summarized and discussed. This summary represents the outcome of discussions held in a workshop funded by the Svalbard Science Forum and the Norwegian Polar Institute and focused on "Adaptation to environmental changes in the Arctic" that took place in Tromsø, Norway, in October 2016. Its results are presented here as a starting point to stimulate further discussion and development of research.

14.2 Assessment of the status of marine research in Kongsfjorden

The 'Ny-Ålesund Science Plan' adopted by the Svalbard Science Forum in 2010 states that Ny-Ålesund shall be developed as a premier international Arctic research and monitoring facility. Research at this globally unique facility is organised in four topical research flagships (Atmosphere Research, Glaciology Research, Terrestrial Ecosystem, Kongsfjorden System; see http://nysmac.npolar.no/research/flagships/). Due to its location right at the interface of Arctic and Atlantic systems, Kongsfjorden is a crucial site for the detection of environmental changes. At the Ny-Ålesund research facility, a large number of individual monitoring and research activities are clustered around the central topic of the changing Arctic environment, its ecosystems and their components. Ongoing research activities on response patterns in organisms related to the marine environment include studies on all taxonomic and functional levels, from bacteria to vertebrates, and from primary producers to top predators (Hop et al. 2002a, Berge et al. 2015a, b). Amongst others, the ecophysiology of phyto- and zooplankton, seaweeds, benthic invertebrates, the local fish fauna, and seabird communities are studied in the context of changes in the degree of Atlantification, UV-radiation, ocean acidification or with respect to their trophic interactions. However, as yet research and data management have failed to achieve a higher level of integration of data, holding back the identification of common (or contrasting) principles in the response patterns across phyla.

The small settlement of Ny-Ålesund hosts 14 permanent research stations operated by 10 different nations. Scientists from all over the world visit Ny-Ålesund to conduct research, with approximately 13,000 research days being registered annually. Logistical support is provided by Kings Bay AS and the Norwegian Polar

Institute, including a marine laboratory and a research vessel. The multitude of technological infrastructure available on site further comprises, amongst others, a wide range of observation platforms with focus on physical and chemical oceanography, including various mooring systems (e.g. Cottier et al. 2007; Venkatesan et al. 2016), an underwater observatory fitted with radiation sensors, a Ferry Box system for the assessment of sea water chemistry and which is now delivering the first Arctic time series for the seawater carbonate system (Fischer et al. 2016), and sediment traps along the fjord axis, in addition to long-standing time series of CTD data.

Oceanographic processes observed in Kongsfjorden can be closely linked to long-term time series of atmospheric data recorded in Ny-Ålesund, comprising records of temperature, precipitation, radiation transfer including UV-radiation (Maturilli et al. 2013). The coupling with physical data from atmospheric and oceanographic records also facilitates research with respect to the movement patterns of the higher vertebrate fauna (birds, seals, whales, polar bears) in the system (Lydersen et al. 2014; Goutte et al. 2014; Hanssen et al. 2016) or the distribution and deposition patterns of anthropogenic and non-anthropogenic contaminants (Gabrielsen 2007). Such monitoring efforts have already allowed for deeper understanding of the functionality of the Kongsfjorden system and its adjacent environments (Svendsen et al. 2002). Amongst others, models on the glacial mass balances and their discharge rates to Kongsfjorden, as well as an oceanographic circulation model for the Kongsfjorden, and adjacent Krossfjorden system have either already been implemented or will soon become available (Ingvaldsen et al. 2001; Cottier et al. 2007; Tverberg and Nøst 2009; Aas et al. 2016; Duarte et al., Chap. 12). The world-class infrastructure hosted in Ny-Ålesund now also supports an increasing number of research projects during the winter season, which is of utmost importance to complete our understanding of marine ecosystem functionality (e.g. Berge et al. 2015a, b). With this foundation, and in order to provide a basis for a more structured and integrative approach to studying the Kongsfjord ecosystem in an interdisciplinary manner, we will now discuss some important gaps in knowledge.

14.3 The Abiotic Environment

In order to gain a better understanding of ecosystem functionality, improved and integrated monitoring of a number of physical drivers is of utmost importance, including ice and glacial regimes, air and water temperatures, oceanographic forcing, light and nutrient regimes (including nearshore areas), as well as the discharge dynamics and chemical characteristics of the freshwater sources (glaciers and streams).

There is a high level of uncertainty with respect to the future radiation environment in Kongsfjorden (Hanelt et al. 2001). Sea ice cover in Kongsfjorden will be reduced, with presumably drastic negative effects to higher ice-associated biota (seals, polar bears), but with a likely promotion of pelagic and benthic primary producers. Reducing impacts of sea-ice may allow for earlier and deeper penetration of solar radiation into the water column, eventually stimulating primary production. However, increased terrestrial run-off will also increase the discharge of sediments to near-shore ecosystems, conversely resulting in increased water turbidity and decreased light availability (Svendsen et al. 2002). The consequences for the phenology and productivity of the phytoplankton and phytobenthos communities need to be evaluated. Intensified monitoring and, eventually, modelling of radiation and nutrient environments may allow prediction of the phenology, primary productivity and species composition of phytoplankton blooms (Hegseth et al., Chap. 6) and changes in the distribution of seaweeds with water depth (Bartsch et al. 2016). Increased spectral resolution of underwater radiation will allow quantifying the role of sediments for sun-screening, i.e. as a UV-protectant. An expanded mooring system with photosynthetically active radiation (PAR) sensors determining turbidity by beam attenuation in different water depths along the fjord gradient (e.g. at Hansneset, Juttaholmen, Colletthøgda; Fig. 14.1) would be a valuable approach.

The inflow of Atlantic and Arctic water masses into the fjord has been identified as a key driver for water column stability and, furthermore, represents an important source of inorganic nutrients, contaminants, and seeding populations of planktonic organisms (van de Poll et al. 2016; Hunt et al. 2016; Hegseth et al., Chap. 6). Thus, characterizing patterns of, and changes in, advection dynamics will become the key for understanding the environmental controls of the Kongsfjorden marine ecosystem. Here, closer connections with monitoring data from the Fram Strait (see: https://www.pangaea.de/?count=10&q= project%3Ahausgarten) may provide valuable insight into community composition of local *vs.* advected organisms.

The extent to which remote sensing might offer improved tools for monitoring the Kongsfjord environment, for instance with respect to sea ice and ocean color at high spatial, temporal and spectral resolutions, should be investigated. Glacial influences, phytoplankton bloom events and sediment discharge rates in time and space should be evaluated further.

14.4 Land-Sea-Atmosphere-Interactions

The coupling of atmosphere, land and sea has been largely overlooked in the research conducted in the Kongsfjorden area to date, although being of primary importance to coastal processes. Changes in glacial discharge, as well as increased terrestrial sediment run off caused by melting snow or increased precipitation, will affect the Kongsfjorden ecosystem along a spatial gradient from glacial fronts and shores to the open water (Fig. 14.2, Svendsen et al. 2002; van de Poll et al. 2016). Apart from changes with respect to radiation transfer from the atmosphere into pelagic and benthic systems, increased sediment load may result in a smothering of benthic substrates and thus impact associated community structure and function (Roleda and Dethleff 2011). However, benefits of increased sediment loads have also been reported, such as a screening function against harmful short-wavelength radiation, which contributes to UV-protection of kelps (Roleda et al. 2008). Glacial

Fig. 14.2 Interface of a sediment-laden river plume and saline fjord water in front of the Bayelva river mouth, Kongsfjorden. (Photo: K. Bischof)

and terrestrial meltwater discharge will alter the in-fjord salinity regime. How the shallow-water communities present in Kongsfjorden may adapt to the changing spatial gradients in light, sediment load and desalination along the fjord axis is as yet poorly understood (Wiencke et al. 2006; Karsten 2007; Fredersdorf et al. 2009). Increasing run-off events also have the potential to alter the input of nutrients from the terrestrial system into Kongsfjorden, in particular with respect to different forms of inorganic N and P along with dissolved organic carbon from the soil. Under elevated temperature, soils from northern latitudes may achieve mineralization rates similar to those found in soils that undergo annual thawing processes (i.e. periglacial or discontinuous permafrost soils). We hypothesise that increased contribution to the N and P content in the fjord in summer may affect growth and metabolic performances of both pelagic and benthic primary producers. Some preliminary data indicate that several species of macrophytes benefit from N and P enrichment in summer (Gordillo et al. 2004, 2006). However, conclusive data on the effects on growth and physiological performance of primary producers are still lacking. Quantifying loads of freshwater and associated dissolved and suspended substances may be particularly challenging when most of the freshwater pathways have a diffuse nature through a complex seasonal network. Therefore, one possible approach is to define a sampling program in selected water pathways and model the overall hydrographic network with a hydrological model [e.g. SWAT (Soil Water Assessment Tool), Neitsch et al. 2002]. The model may be calibrated and validated with the help of available measurements. Thereafter, it may be used to quantify the loads mentioned above. Similarly, glacier water discharges may be simulated based on the glacier energy balance (Aas et al. 2016).

There are several tidewater glaciers in Kongsfjorden, as is also typical in many other Arctic coastal regions. The fronts of these glaciers have been identified as “ecological hotspots” due to their importance as feeding areas for seabirds and mammals (Fig. 14.3). The ice calving from these glaciers may provide suitable platforms for seal species, for resting, moulting, birthing and nursing. They may then also become important hunting areas for polar bears (Lydersen et al. 2014). The freshwater plumes from these glaciers transport a large load of suspended matter, contributing to the extremely high water turbidity near the glacier fronts, with direct implications for primary production and benthic deposition processes. The full extent of the contribution of these plumes to fjord biogeochemistry in terms of nutrients and organic matter is yet unknown. Tidewater glaciers in Svalbard are retreating but it is difficult to predict how long it will take for the glaciers in Kongsfjorden to retreat onto land and what consequences this will have on the fjord ecosystem (Kohler et al. 2007).

Furthermore, the transport, deposition and biological impact of pollutants are also dictated by the closely coupled continuum of atmosphere-land-sea. With respect to the deposition and bioaccumulation of contaminants, the relative importance of local sources (where there are or have been human activities) *vs.* distant transport has yet to be evaluated.

Fig. 14.3 Glacier fronts as ecological hotspots – Kittiwakes feeding in front of the Kongsvegen glacier, Kongsfjorden. (Photo: G.W. Gabrielsen)

Currently, also the trophic coupling of land and sea (and *vice versa*) is poorly understood. Climate change is not only likely to impact the terrestrial and marine ecosystems separately, but also their interaction (Stempniewicz et al. 2007). For example, seabirds nesting in the Kongsfjorden area may have to change their diet in response to potential shifts in the pelagic prey communities, with unknown consequences for pollutant uptake and energetics of birds (Hop et al. 2002b, Guzzo et al. 2014; Blévin et al. 2017). Reindeer, which can become deprived of terrestrial food sources after ice formation on the ground surface following more frequently occurring rain-on-snow events, may increasingly depend on access to marine shoreline food sources such as seaweeds (Hansen and Aanes 2012).

14.5 Primary Production

Primary production is one of the key processes for ecosystem function, but its utilization by the food web and its temporal trends are unresolved key questions in the face of environmental change. Furthermore, research on changes in primary production forms the basis of an understanding of environmental effects on higher trophic levels and food-web structure. As outlined above, there is large uncertainty with respect to the future radiation climate in Kongsfjorden, as a result of the balance between sea ice loss and sediment input. How the annually accumulated dose of photosynthetically active radiation and the distribution of light availability over the year may affect the timing of primary production and the community composition of primary producers needs to be evaluated. To tackle this question, coordinated plankton time series must be expanded further, in particular over seasonal cycles, for instance through weekly autonomous water sampling on moorings or regular sampling by station personnel. The timing of blooms is important to ecosystem function in Kongsfjorden. On the one hand, ongoing Atlantification may imply a reset of bloom initiation in the transition from an Arctic to a temperate regime and plankton succession patterns, with an earlier spring bloom and the potential for the occurrence of autumn blooms (Kahru et al. 2011; Ardyna et al. 2014). Alternatively, changes in advection patterns may delay re-seeding from the sediment, thus delaying spring bloom initiation (Hegseth and Tverberg 2013; Hegseth et al., Chap. 6). As, overall, the availability of macronutrients such as nitrate may limit primary production earlier in the season (Tremblay et al. 2015), the future balance between stronger surface stratification caused by warming and glacial melt with the increased input of nutrients from external sources (e.g. terrestrial run-off, advection of Atlantic water) could have beneficial or detrimental effects on annual net primary production. Thus, closer integration between physical, chemical and biological monitoring efforts will be the key to resolving questions of future primary production trends in Kongsfjorden. Furthermore, interactive effects between multiple drivers, including ocean acidification and warming, need to be considered (AMAP 2013; Riebesell and Gattuso 2015).

14.6 Indicator Species

Changes in the physical environment will alter the performance of individual species in an ecosystem. Physiological fitness will affect reproduction and competitive strength in interactions with co-occurring species. Here, it is crucial to focus research on carefully selected species, either because of their ecological significance, for instance as ecosystem engineers, or because of their particular sensitivity or adaptive capacity to environmental changes. Such species have good potential as indicator species, and may be characterized by strict threshold levels for acclimation or adaptation. The following species and/or taxonomic and functional groups have been identified as being of specific interest in the evaluation of change in the Kongsfjorden system (and hence to extrapolate to changes across the Arctic):

First, it is striking that the significance of the entire microbial community to ecosystem function in Kongsfjorden has been largely neglected, although some studies have involved the microbial loop and production of microphytobenthos (Rokkan Iversen and Seuthe 2011; Seuthe et al. 2011; Karsten et al., Chap. 8). Changes in land runoff are likely to affect the efficiency, relative roles and identity of actors of microbial processes such as carbon, nitrogen and organic contaminant turnover (Dunton et al. 2006). New research activities in the fields of microbial ecology, biogeochemical cycling and contaminant biodegradation are desirable in the land-water interface associated with shallower marine areas. Soft sediment systems form the basis for the transfer of carbon, energy and persistent contaminant along benthic food chains, and hitherto monitoring in Kongsfjorden has largely focused on the deeper areas (below 20 m), which are readily accessible by larger research vessels (e.g. Miløovervåking Svalbard og Jan Mayen; www.MOSJ.no). This approach has left the sedimentary littoral and sublittoral zones largely unexplored regarding both biological and ecotoxicological processes. Coastal shallow waters represent areas of high productivity and are naturally intimately connected with biological and biogeochemical processes on land. Thus, in order to detect and understand the impact of climate change on Arctic systems, shallow water ecosystems need to be included.

In the hard-bottom benthic littoral and sub-littoral systems, the functional group of kelps (large brown seaweeds) comprises keystone species of great ecological significance to the overall system (Hop et al. 2016; Bartsch et al. 2016). Here the changing performance of polar (*Laminaria solidungula*) *versus* boreal-Arctic (*Saccharina latissima*) and boreal (*Laminaria hyperborea*) species should be compared.

With respect to benthic invertebrates, the group of amphipods has been proposed as key invertebrates to study in the intertidal/shallow subtidal fringe. *Gammarus setosus*, *Onissimus litoralis* and *Anonyx sarsi* represent commonly occurring species with different life strategies (Węsławski and Legeżyńska 2002). Amphipods are consumed by fish, seabirds and seals in the Arctic and therefore constitute a trophic link between water- and air breathers. Ecotoxicological assays related to reproductive success have for example already been developed both for temperate and Arctic amphipod species (Sundelin and Eriksson 1998; Bach et al. 2009).

In the pelagic realm, Atlantification may promote haptophytes such as *Phaeocystis* and coccolithophores, reducing the abundance of the currently dominant diatoms in the spring bloom phytoplankton assemblages (Hegseth and Tverberg 2013; Nöthig et al. 2015). The effects of changes in nutrient availability in Kongsfjorden may be best monitored by observing the abundance of picoeukaryotes (e.g. *Micromonas pusilla*) and dinoflagellates, which are indicators of nutrient-limited conditions and become increasingly important in nutrient-limited Arctic waters (Assmy and Smetacek 2009; Li et al. 2009). In terms of zooplankton community structure, the changing abundance of Arctic to boreal zooplankton species should be addressed by following the development of the plankton community composition, for example comparing abundances of the copepods *Calanus glacialis* and *C. hyperboreus vs. C. finmarchicus* (Kwasniewski et al. 2003, 2013; Walkusz et al. 2009).

Ocean acidification is an emerging driver of environmental change and affects many pH sensitive extra- and intracellular physiological functions (Pörtner 2008), and keystone Arctic species are shown to be affected (Thor and Oliva 2015; Thor et al. 2016). At present there are no suitable indicators of biological effects of ocean acidification, but the exposure to potential ocean acidification effects can be monitored by studies of pteropod shell degradation (Gannefors et al. 2005; Comeau et al. 2009, 2010; Lischka and Riebesell 2012; Fransson et al. 2016; Fig. 14.4). Future research on higher trophic levels needs to address species shifts in the fish fauna of Kongsfjorden, and the abundance of polar cod *versus* Atlantic fish species such as capelin and herring (Hop and Gjøsæter 2013; Dalpadado et al. 2016). Kittiwakes have been proposed as a representative bird species affected by climate change and pollutant impacts (Goutte et al. 2015; Tartu et al. 2015; Bustnes et al. 2017).

Globally, a “jellification” of coastal systems (an increased abundance of jellyfish species and other gelatinous zooplankton) is observed (see Gibbons and Richardson 2013), and this has also been noted in Kongsfjorden (Falk-Petersen et al. 2002; Lundberg et al. 2006). Research on the ecological functions of jellyfish (e.g. the genera *Cyanea*, *Mertensia*, *Beroë*) is urgently required, in particular with respect to their contribution to the trophic web through their impact on zooplankton standing stock and/or in providing food to the benthos.

For the indicator species mentioned, the assessment whether their responses (comprising regulatory, acclimatory or adaptive traits) can keep up with the pace of environmental change will be crucial to predictions of the future trajectory of the Kongsfjorden ecosystem. As a baseline for such studies, extended habitat and species distribution mapping are vital to improving data coverage for Kongsfjorden and enhancing the valuable information already provided by the Mareano database (www.mareano.no).

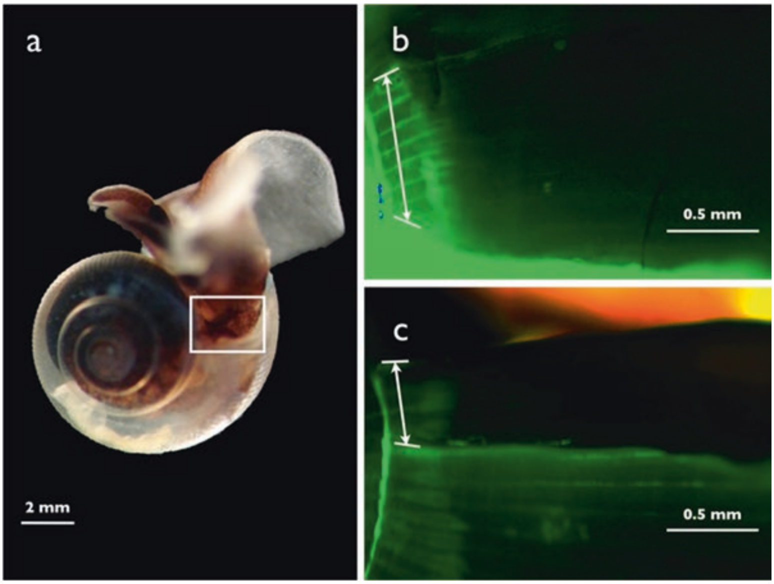

Fig. 14.4 The Arctic pteropod *Limacina helicina* **(a)**, stained with calcein (staining calcium carbonate depositions) and subsequently maintained at pH 8.09 **(b)** and 7.78 **(c)**, illustrating reduced calcification under reduced pH. The arrow indicates the linear extent of the shell over an incubation period of 5 days. (Figure from Comeau et al. 2009)

14.7 Trophic Interactions

Trophic interactions within Kongsfjorden have been characterized by Hop et al. (2002a), and divided into a benthic and pelagic food web, however, with a hitherto only fragmented understanding of their interactions (bentho-pelagic coupling processes). Research on trophic interactions needs to move towards the quantification of energy budgets and flows between the different nodes within the trophic web (Paar et al. 2016; Duarte et al., Chap. 12). In particular, the top-down control of the system with respect to the impacts of seabirds and mammals has only been addressed to a limited extent in Kongsfjorden (but see estimates in Hop et al. 2002a). With progressing Atlantification, large predators could enter the system and cause cascading effects (e.g. tuna, dolphins, killer whales, baleen whales, and Atlantic cod) with potential interaction with the Greenland shark, which is already a significant, large predator in the system (Lydersen et al. 2016). Furthermore, there is only very fragmentary knowledge about predator-parasite/pathogen-relationships (Maat and Brussard 2016). Microbial pathogens and the significance of marine viruses have been largely overlooked. As previously mentioned, our understanding of the microbial ecology and biogeochemical cycling is still in its infancy, and those need to be further explored in order to understand the effects of anticipated environmental changes on nutrient- and contaminant cycling related to ecosystem services.

Approaches in metagenomics indicate that there are many – currently unidentified – organisms that may be important in the system and which should be studied with high priority, such as viruses and fungi that infect phytoplankton, or prokaryotes that facilitate nutrient recycling (Piquet et al. 2016). Here, adaptive processes may occur through an arms race between host and pathogen, and be further modulated by environmental changes. Furthermore, classical questions in biological oceanography remain to be answered for the Kongsfjorden system (and for most other Arctic coastal systems) concerning match-mismatch situations in the dynamics of phytoplankton blooms *versus* grazer abundance (Søreide et al. 2010). Loss rates of primary producers and the fate of the organic carbon have only been determined to a limited extent for Kongsfjorden (Hop et al. 2006). This approach has to be applied for the pelagic and benthic realms, and their connections, including vertical flux of both phytoplankton and faecal pellets. The energy flow within food webs depends on how much of the organic matter is retained in the pelagic system relative to sinking to the benthos. With ocean warming and acidification, it is expected that more organic matter will be retained in the pelagic system, particularly above the mixed layer depth, because of smaller phytoplankton species, increased activity of the microbial loop, and more intense grazing by zooplankton (Wassmann et al. 2006; Riebesell et al. 2013). The complex trophic web might become rearranged as the environment changes, for instance due to key species becoming rarer (e.g. pteropods) and the arrival of new predators and grazers or their increased abundance, such as sea urchins grazing down kelp forests, and increased predation on sea urchins by eiders. A thorough analysis of current ecosystem structure and functions is thus central to facilitate ecosystem modelling, prediction of future conditions and extrapolation in a pan-Arctic perspective.

Changes in food web structure directly affect the fate of contaminants and thus their concentrations in higher organisms (Rasmussen et al. 1990; Borgå et al. 2001; Hallanger et al. 2011). Intricate equilibria exist between environmental contaminant concentrations, transport patterns, biodegradation, bioavailability, bioaccumulation and biomagnification, which are partly determined by thermodynamic principles (Mackay and Fraser 2000). Thermodynamics is therefore one key to understanding the fate and effects of contaminants, driven primarily by temperature and contaminant affinities to environmental matrixes such as sediment, water, air, ice, organisms and tissues within organisms. Climate change is thus predicted to act directly on these dynamics.

In the Arctic, higher trophic levels are dominated by migrating species, which move seasonally across large distances and inhabit different geographical regions. This means that species like seabirds, marine mammals and polar bears are only temporarily connected to a specific geographical location such as Kongsfjorden or a certain area within Kongsfjorden. These populations are consequently also only temporarily exposed to the environmental conditions or stressors specific to that location, which makes adaptive responses to local contamination unlikely. Increased release of contaminants from local land based sources (e.g. old dumps and industrial sites) to coastal waters is predicted in a warmer Arctic (Noyes et al. 2009). Several such sources have been identified on Svalbard and some in the Kongsfjord area (Granberg et al. 2017 and references therein). Lower trophic level populations including planktonic species have shown rapid adaptation to local conditions related to both contaminant and climate change factors despite a potential for extensive distribution of pelagic larvae and thus genetic exchange (Vidal and Horne 2003; Whitehead et al. 2012; Peijnenburg and Goetze 2013; Thor and Dupont 2015; De Wit et al. 2016). When a population adapts the trophic link represented by the particular species remains intact. This prevents food chains from being disrupted, but it also allows for continued food chain transfer of contaminants to higher trophic levels at polluted sites. Likewise, when populations fail to adapt the link is broken and contaminant transfer is stopped. It is thus important to understand adaptive responses on several trophic levels and to a multitude of stressors in concert. Integrated approaches where ecological and ecotoxicological aspects are considered simultaneously are needed in order to fully comprehend the impact of climate change on Arctic biological systems.

14.8 Ecosystem Modelling

Modelling will be one of the primary tools to address the impact of environmental change on the structure and function of Arctic marine ecosystems and the performance of their component species, again by using Kongsfjorden as a model site. Overall, there is a multitude of potential goals that can be achieved through modelling. These include evaluating the effects of Atlantification and glacier retreat on fjord circulation, on primary and secondary production, on potential shifts in species distribution and abundance and on community composition. Future modelling efforts should build on existing, or currently developing, models for meteorology, ice mass balance, hydrology, hydrodynamics and biogeochemistry. Ideally, a coupled physical-biogeochemical modeling platform should be built integrating most of these models/processes to properly take into account the feedbacks between the physical and the biogeochemical realms (Duarte et al., Chap. 12).

Different modeling approaches should be developed in parallel, aiming at their integration once the adequate level of maturity is reached. A powerful tool to quantify how species ranges will be altered under different climatic change scenarios are species distribution models (SDM), that statistically link spatial data of environmental variables to species presence/absence or abundance data. These models are now widely used to forecast the effects of climatic change on biodiversity (Pearson and Dawson 2003; Araujo et al. 2005; Buckley et al. 2010; Elith et al. 2010) and to guide management policies, such as to track the invasion of alien species (e.g. Kearney et al. 2008). SDMs are typically based on correlations between distributional and environmental data and, thus, they do not explore the physiological and biotic causal mechanisms underlying species distributions. This potentially limits the accuracy of predictions for species at non-equilibrium state with the physical environment, in particular non-indigenous spreading organisms. In this context, the potential applicability of physiological limits to increase the robustness of SDM projections has been suggested, as well as the need to include biological factors, but both approaches have been rarely performed to date (but see Martínez et al. 2015). These major gaps should be addressed by developing new tools to integrate knowledge on the physical and biotic mechanisms underlying species biogeography. This may partly be achieved by integrating the predictions of coupled physical-biogeochemical models (see above) with the physiology and population dynamics of target species: changes in the physical and the biogeochemical environment forecasted by the former will drive changes in species abundances and distributions.

Other approaches that may be developed in parallel and possibly feedback to those described include dynamic energy budget (DEB) models of selected species, potentially allowing prediction of changes in physiological traits in response to a changing environment and/or different pollutant loads. The coupled models mentioned above focus on biogeochemistry and lower trophic level interactions. However, there is growing interest in end-to-end models, combining physicochemical oceanographic descriptors and organisms across all trophic levels in a single modeling framework. End-to-end models result from the need to have quantitative tools for ecosystem-based management, dealing with bottom-up and top-down controls, varying in time and space as a result of global climate change among other possible environmental changes (Fulton 2010; Rose et al. 2010). Another argument in favor of this type of model is the need to properly account for the feedbacks between high trophic level organisms and biogeochemical cycles (Duarte et al., Chap. 12).

14.9 Upscaling and Comparison in a Pan-Arctic Perspective

From the foregoing, it is apparent that research conducted in the marine Kongsfjord Flagship program needs to become more integrated by also involving expertise from the other Flagship programs (Atmosphere, Cryosphere, Terrestrial Ecology). Furthermore, research conducted in Kongsfjorden must be placed in a broader geographic perspective. Identifying exchange processes between Kongsfjorden, neighboring fjords (Krossfjorden) and the open ocean will be a key task for further monitoring programs. However, the scope of research conducted in Kongsfjorden and the Ny-Ålesund Research and Monitoring facility should not be limited to the environmental setting of West Spitsbergen, but has to be placed in perspective of the entire Svalbard Archipelago and the Arctic as a whole. Thus, in a first step, research conducted at Ny-Ålesund and the other research facilities on and around Spitsbergen (Longyearbyen, Hornsund, Barentsburg, Hausgarten observatory in Fram Strait) should become more integrated, and up-scaling modelling is needed. The impacts of environmental changes are already being observed on western Svalbard. It therefore seems to be justified to regard Kongsfjorden as a harbinger for environmental changes of Arctic fjord systems in general. However, in order to enable more comprehensive predictions, comparative research on fjord systems that are currently less dramatically impacted than Kongsfjorden yet needs to be considered, for instance in northern and eastern Svalbard, Greenland, and also Hornsund (Piwosz et al. 2009). It is therefore recommended that options for establishing some research infrastructure at such sites with significantly lower Atlantic signals are evaluated.

14.10 Outlook

The Kongsfjorden system is one of the best-studied fjord systems across the entire Arctic region, with cutting-edge science being conducted at the highest international level. However, there remain important gaps in knowledge, which need to be addressed with high priority in order to give robust foundation for predictions on the future trajectory of Arctic coastal ecosystems in the face of environmental change. In addition to the above-mentioned and more specific research topics, some overarching fields for improvement have been identified. Overall, the links between the physical environment and key ecological processes need to be strengthened, in particular with respect to the drivers of primary and secondary production. The overriding factor of seasonality needs to be addressed by increasing research activity throughout the year (including winter observations and experiments) and reducing the emphasis on research at the height of summer. Perturbation experiments need to be up-scaled from individuals to consider integrated community responses, from short- to long-term incubations and manipulations, and from single to incorporate multiple drivers. Such experiments could be performed in large-scale mesocosm systems (Fig. 14.5).

It will further be crucial to expand research activities in the field of microbiology to address the fundamental role of microbes in ecological processes. These aspects are crucial to identify the losers and winners of environmental change, and how community composition and ecosystem functions will be affected. Furthermore, revealing the mechanisms of adaptation in key organisms will require intensified efforts in the rapidly developing molecular field, including population genetics, epigenetics and transcriptomics. In the longer term, consideration is required as to if and how the on-site infrastructure in Ny-Ålesund could be upgraded to facilitate such future research activities.

The diverse monitoring activities already underway generate extensive but often independent databases, and greater integration is required. A first, but critical, step forward would be to provide a facilitated and integrated accessibility to existing knowledge, to allow available data and information to be obtained more easily through a single source, rather than being scattered in various data repositories. Future research on the links between the physical and chemical environment and key ecological processes will benefit from improved access to existing datasets.

Ny-Ålesund and its surrounding area provide a unique study site to document and understand ongoing changes and to predict future Arctic ecosystem trajectories. The long research background across multiple systems (atmosphere, glaciers,

Fig. 14.5 One of the large-scale pelagic mesocosms of the EPOCA (European Project on Ocean Acidification) experiment 2010 deployed in Kongsfjorden. (Photo: J.-P. Gattuso)

tundra ecosystems) and multidisciplinary knowledge on Kongsfjorden and adjacent marine systems is a great strength and resource that is available nowhere else in the Arctic. It is important and increasingly urgent to use this knowledge to give foundation to robust and reliable predictions. The research carried out here must become increasingly multidisciplinary, encompassing climate, physics, chemistry and response of the biota. The approach must be integrative, including key polar and boreal species, populations and communities in order to make predictions about the continued delivery of ecosystem services. This special edition of studies on the Kongsfjorden ecosystem represents an important contribution towards the achievement of this goal.

Acknowledgements The authors are grateful to the Svalbard Science Forum for providing funding for the workshop "Adaptation to environmental changes in the Arctic" that took place in Tromsø, 10–12 October 2016, and formed the basis of the present contribution. Authors are also thankful to the Norwegian Polar Institute to be the host and providing additional financial support to the workshop. KB is grateful for the financial and logistical support provided by the Alfred Wegener Institute. PC is supported by NERC core funding to the British Antarctic Survey 'Biodiversity, Evolution and Adaptation' Team. JPG is supported by IPEV, the French Polar Institute. CJ is supported by research project CGL2015-67014R of the Ministry of Economy and Competitiveness of Spain.

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