

Gegevens Bachelorscriptie:

Student: Floor Driessen

Studentnummer: s1766848

Begeleider: A. Buma – Ocean Ecosystems

Tweede beoordelaar: A. Piquet – Ocean Ecosystems

Startdatum Bachelorscriptie: 18.01.2012

Einddatum Bachelorscriptie: 12.02.2012

The effects of climate change on benthic communities in the Arctic Kongsfjordsystem, Svalbard

Abstract

Climate change is supposed to have an important effect on marine Arctic ecosystems. Increased temperatures will change the physical environment of northern fjords. Decreasing amounts of sea ice and sediment rich glacial run off affects light, nutrient and sedimentation conditions. These processes in turn will cause changes in primary production. The occurrence of benthic faunal life depends on the deposition of organic material for energy requirements. Changes in pelagic-benthic coupling will affect the entire ecosystem. In this thesis the various impacts of climate change on benthic communities in the Arctic Kongsfjordsystem are described. This system was chosen because it is an excellent natural model system for studying climate change related effects on marine communities. The structure and function of the benthic community suffers from high concentration and sedimentation rate of mineral suspensions, low levels of available organic matter and ice-berg scouring or sediment slides, as effects driven by climate change. Change in benthic communities is primarily caused by food supply and ice scouring.

KEYWORDS: *Arctic, benthic communities, climate change, ice cover, Kongsfjord, primary production, sedimentation*

Table of contents:

Abstract	1
Table of contents	2
1. Introduction	3
2. Physical environment of the Kongsfjordsystem, subjected to climate change	4
2.1 <i>General description of the Kongsfjordsystem</i>	4
2.2 <i>Temperature</i>	5
2.3 <i>Water masses & temperature</i>	5
2.4 <i>Arctic ice</i>	6
3. Benthic biota communities	7
3.1 <i>General description of the benthic community</i>	7
3.2 <i>Growth conditions</i>	9
3.3 <i>Food web dynamics</i>	10
4. Impact of climate change on benthic communities	13
4.1 <i>Changes in physical environment</i>	13
4.1.1 <i>Watermasses</i>	14
4.1.2 <i>Sea ice cover</i>	15
4.2 <i>Changes in food web dynamics</i>	17
Discussion and conclusions	19
References	20

1. Introduction

Climate change will have an impact on marine Arctic ecosystems. Temperature is increasing and causes melting of sea ice and glaciers. Arctic fjords are influenced by seasonal fluctuations in light, ice cover, freshwater inflow, surface salinities and temperatures (Fetzer *et al.*, 2002). The near-coastal zone varies from the rocky shores of exposed coasts, to sand and mud beds in sheltered areas of fjords and bays and is influenced to varying degrees by ice cover and scouring (ACIA, 2005). Ice scouring influences the diversity and structure of benthic communities and causes successional phases of community impoverishment (Holte *et al.*, 1996).

There is evidence for significant change in sea ice extent and thickness in the Arctic Ocean (ACIA, 2005; Clarke & Harris, 2003; Comiso *et al.*, 2008 as cited in Wassmann *et al.*, 2011; Førland *et al.*, 2009; IPCC, 2001; Svendsen *et al.*, 2002). In addition, coastal areas are strongly affected by glacier derived disturbances, mainly by the outflow of melt water produced by active tidewater glaciers (Ronowicz *et al.*, 2011). The inflow of sediment-rich glacial melt water on one hand is an input of minerals, which may supply essential nutrients for phytoplankton growth. On the other hand the melt water reduces transparency due to turbidity caused by sediments the glaciers picked up. Reduced sea ice increases the time period and areal extent of pelagic primary production, which may affect pelagic–benthic coupling (Cochrane *et al.*, 2009). In the Arctic, both ice algae and phytoplankton are readily consumed by the benthos (McMahon *et al.*, 2006), but the relative and actual amounts of each reaching the seafloor may be altered due to climate change. This is because any changes in the magnitude or timing of the respective blooms would affect how much of the material is consumed by grazers (Cochrane *et al.*, 2009).

Therefore, climate change might have an effect on the benthic community. Wassmann *et al.* (2010) found a total of 51 reports of documented changes in Arctic marine biota in response to climate change. The number of well-documented changes in planktonic and benthic systems was surprisingly low. Some factors that affect marine biota are known (e.g. high rates of inorganic sedimentation, large fresh-water inputs, high levels of concentrations of mineral suspensions in waters, and iceberg bottom-scouring) (Hop *et al.*, 2002; Włodarska-Kowalczyk & Pearson, 2004). The aim of this study was to find out the impact of climate change on benthic communities in the Arctic Kongsfjordsystem. The semi-open glacial fjord has a mouth to the open sea on the western coast of Svalbard. It is influenced by melt water of glacial origin as well as by mild temperatures mediated by the inflow of transformed Atlantic water (Piquet *et al.*, 2010). Therefore, the Kongsfjord is an excellent natural model system for studying climate change related effects on marine communities.

2. Physical environment of the Kongsfjordsystem, subjected to climate change

2.1 General description of the Kongsfjordsystem

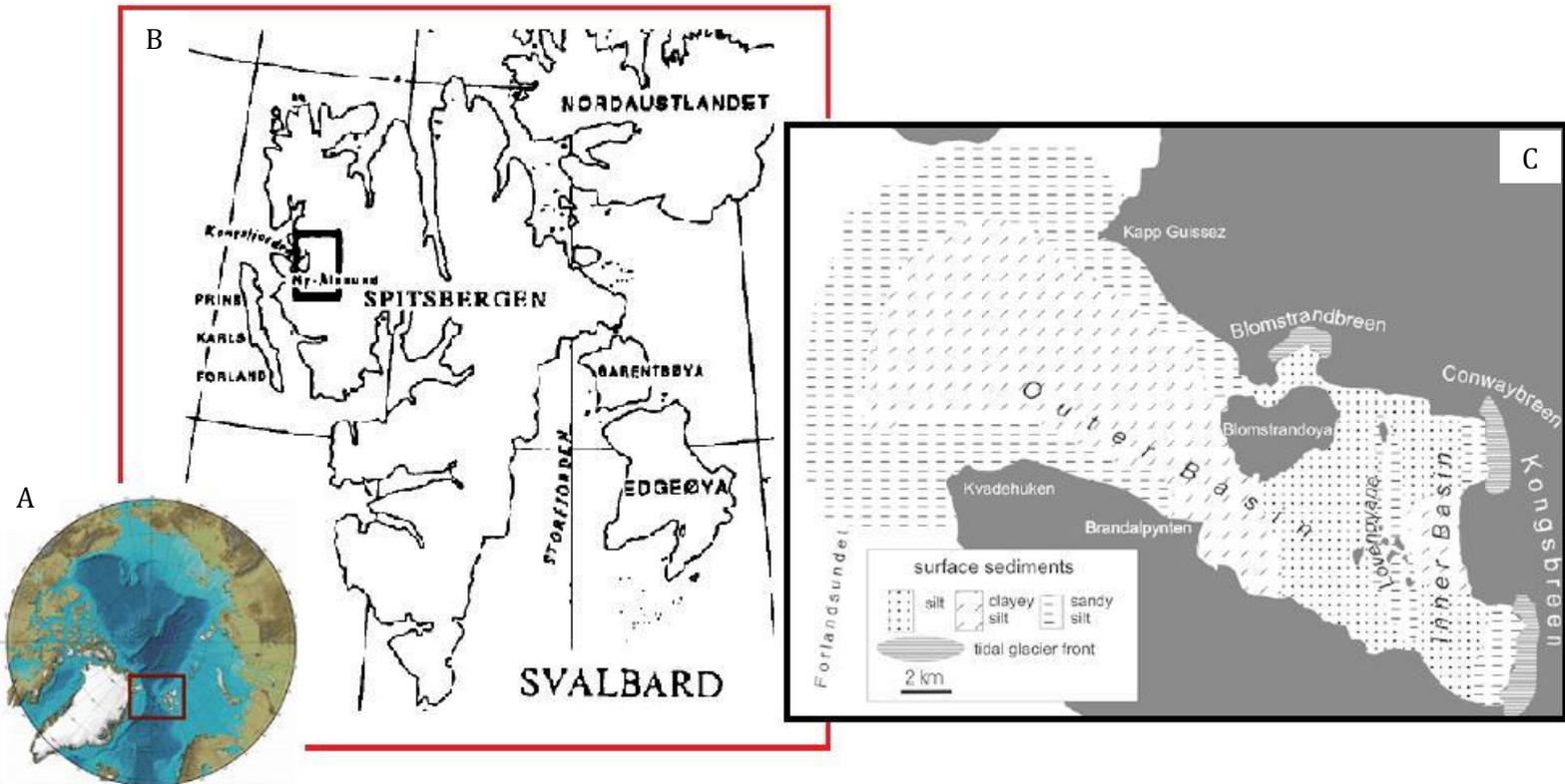


Figure 1. A The Arctic map indicating the location of Spitsbergen. B The Spitsbergen map indicating the location of the Kongsfjord system. C The Kongsfjord region indicating the surface sediments (modified from Hop *et al.*, 2006(A); Lefauconnier *et al.*, 1994(B); Wlodarska-Kowalczyk & Pearson, 2004 (C))

The coastline of Svalbard is surrounded by continental shelves broken by large fjord systems. The western archipelago experiences both seasonal ice cover and input from Atlantic-origin water carried by the West Svalbard current (McMahon *et al.*, 2006). The Kongsfjord system (78° 55'N, 11° 56'E, Svalbard) is an excellent natural model system for studying climate change related effects on marine communities (Hop *et al.*, 2006). The fjord is 20 km long and 4 to 10 km wide and covers an area of 209 km² (Fetzer *et al.*, 2002).

Depths in the outer basin reach 428 m (on average 200–300 m), whereas the inner basin is considerably shallower, with a maximum depth of 94 m (on average 50–60 m) (Renaud *et al.*, 2011; Wlodarska-Kowalczyk & Pearson, 2004; Wlodarska-Kowalczyk *et al.*, 2005). There is a semidiurnal tide with a range of approximately 2m (Fetzer *et al.*, 2002) and the coast is bound by rocky shores. Three tidal glaciers terminate in the fjord water (Figure 1). Kongsbreen, situated in the innermost part of the fjord, is the most active glacier (Lefauconnier *et al.*, 1994). Soft sediments, such as sand and muds, dominate the subtidal sediments throughout the fjord (Renaud *et al.*, 2011) and are similar in terms of their granulometry in the inner and outer basins of the Kongsfjord (Denisenko *et al.*, 2003).

In the short summer, freshwater influx from glaciers and snowfields enters the shallow coastal areas at several places, where it overlies the marine water. During low tide this water spreads over the scarce sandy mudflats, so that these areas must cope with a wide salinity range reaching from freshwater to fully marine conditions on the sediment surface (Bick & Arlt, 2005). The fjord water is influenced by melt water of glacial origin as well as by mild temperatures mediated by the inflow of transformed Atlantic water (Piquet *et al.*, 2010). The Kongsfjord is covered by ice during the winter season from October to March/April (Buma, 2012 (pers. comm)).

2.2 Temperature

Open or seasonally upper-layer waters in the Arctic Ocean that are ice-free, experience seasonal fluctuations in temperature due to the annual cycle of atmospheric heating and cooling (ACIA, 2005). Higher atmospheric temperature in summer leads to more melting and discharge of icebergs (Ronowicz *et al.*, 2011; Svendsen *et al.*, 2002). The freshwater input to the Kongsfjord, due to melting, is mainly limited to summer and autumn and modifies the oceanographic conditions of the inner basin and the middle part of the fjord (Wlodarska-Kowalczyk & Pearson, 2004). Due to the significant freshwater input, the surface water in the fjord is characterized by lower salinity compared to the Arctic surface water of the coastal area and the subsurface is decreased in temperature (ACIA, 2005). Kongsbreen is responsible for the strongest glacier sediment discharge of turbid fresh water in the fjord (Sommerfield *et al.*, 2006). Sediment discharge can be measured as an inverse value of light beam attenuation (Piquet *et al.*, 2010). The main driving force for freshwater supply is related to variations in the calving rates of glaciers, precipitation and melting or freezing due to the seasonal variation in air temperature (Svendsen *et al.*, 2002).

The IPCC report (2007) predicts that annual Arctic surface temperatures north of 60°N will rise 0.5 to 1.6°C by 2030 and 1.1 to 6.4°C by 2100 (Fredersdorf *et al.*, 2009). Most of the observed increase in globally averaged temperatures since the mid-20th century is very likely due to the observed increase in anthropogenic greenhouse gas concentrations (IPCC, 2007 as cited in Wassmann *et al.*, 2011). The increase of temperature will lead to earlier sea ice melt and later freeze-up. The large difference in temperature between air masses of Arctic or Atlantic origin cause great fluctuations in weather conditions, especially during winter (Førland *et al.*, 2009). As air temperatures are very likely to increase more in winter (6°C increase in the central Arctic) than in summer (1 °C increase) there is likely to be an associated decrease in the amplitude of the seasonal cycle, as in warmer winters compared to summer (ACIA, 2005). Atmospheric warming has increased Arctic Ocean temperature and resulted in decreased extent and thickness of sea ice (Kwok & Rothrock, 2009 as cited in Wassmann *et al.*, 2011). By 2050, the CGCM2 model projects that the entire marine Arctic may be sea-ice free in summer (ACIA, 2005; Arzel *et al.*, 2006 as cited in Wassmann *et al.*, 2011) and therefore, more areas will be exposed to direct sunlight (ACIA, 2005).

2.3 Water masses & temperature

Relatively warm air and water masses circulate towards the Arctic from the lower latitudes, while colder Arctic air and water are transferred southwards (ACIA, 2005; Clarke & Harris, 2003). The distributions of water masses and ice are climate driven (Lippert & Iken, 2003; Renaud *et al.*, 2011; Svendsen *et al.*, 2002; Wlodarska-Kowalczyk *et al.*, 2005). The temperature and salinity levels of marine Arctic waters vary widely

and reflect the influence of the warm Pacific and Atlantic, heat exchange with the atmosphere, precipitation, inflow of freshwater and the melting and freezing of sea ice.

The Kongsfjord is strongly influenced by the West Spitsbergen Current (WSC) of Atlantic origin that transports relatively warm saline water northwards (Drinkwater, 2006; Hop *et al.*, 2006) and keeps the west coast of Spitsbergen generally free of ice (ACIA, 2005). Because of this influence, the fjord can be regarded as sub-Arctic rather than Arctic (Hop *et al.*, 2002) and is characterized by relatively mild temperatures when compared to other Arctic locations at similar high latitude (Piquet *et al.*, 2010). In the Arctic dominance period (autumn and winter), surface water that represents a mixture of glacial melt water and fjord water formed during late spring and summer, mixes with Atlantic water types (Hop *et al.*, 2006). Advection of warm water masses together with prevailing wind patterns and air temperatures, may prevent ice formation in the fjord. Now this happens only in summer, but due to climate change, there could be a chance this happens in other seasons, in future as well. Atmospheric warming has already increased the Arctic Ocean temperature (Kwok & Rothrock, 2009). Therefore the fjord can undergo an intense and rapid shift from an Arctic-water- to an Atlantic-water-dominated system (Hop *et al.*, 2006).

2.4 Arctic ice

Sea ice cover

Sea ice is a dominant physical feature for most of the Arctic areas, with year-round cover in the central Arctic Ocean, to seasonal cover in most of the remaining areas. It controls the exchange of heat and other properties between atmosphere and ocean and determines the penetration of light (Cochrane *et al.*, 2009; Hop *et al.*, 2006; McMahon *et al.*, 2006). Moreover sea ice provides a surface for particle deposition, a habitat for ice algae and contributes to stratification through ice melt. In winter, ice cover suppresses water column phytoplankton productivity and stimulates ice algae productivity.

The seasonal sea ice cycle has an inter annual variability both in maximum and minimum coverage. Due to annual increasing atmospheric temperatures, the sea ice starts retreating northward in March and April, into the central Arctic basins. By October, new sea ice forms in areas that are open in summer, especially for the Arctic coast. Between November and January there is a steady advance everywhere toward the winter peak (ACIA, 2005). Every year around 7 to 9 million km² of sea ice freezes and melts in the Arctic (Parkinson *et al.*, 1999 as cited in ACIA, 2005). An increase of 1°C in the atmospheric water temperatures slightly above 0°C prevents sea ice formation, which is limited to the edges and inner parts, whereas the central and outer parts of the fjord remain ice-free throughout most winters (Svendsen *et al.*, 2002). Førland *et al.* (2009), suggested that sea ice coverage will decrease more both in summer and winter, but changes in winter are generally projected to be much smaller than in summer.

Glaciers

In the Kongsfjord, summer temperature will induce a net balance of -0.7m and -0.55m for Austre Brøggerbreen and Midre Lovénbreen, two of the Kongsfjord glaciers. Iceberg scouring induces sedimentary instability in near-glacier marine basins. The effects of melting glaciers influences the nature and location of glacimarine sedimentation (Dowdeswell, 1987). The chronic physical disturbance of sediments is accompanied by low input levels of organic matter (Brown & Belt, 2012; Dowdeswell, 1987; Wlodarska-

Kowalczyk & Pearson, 2004; Włodarska-Kowalczyk *et al.*, 2005). Glacial melt-water is estimated to transport 2 million tons a year of mud, sand and gravel into the fjord. The main bulk is deposited in the inner basin, close (<0.5 km) to the glacier front (Denisenko *et al.*, 2003). The scale and magnitude of the impact depend on the activity of the glacier (Włodarska-Kowalczyk & Pearson, 2004).

3. Benthic biota communities

3.1 General description of the benthic community

The Arctic sea and sea ice provides an extensive habitat for phytoplankton and ice algae as dominant primary producers. Sea ice algae are considered to be the main primary producers for ice-covered oceans and so is phytoplankton for open summer areas (Bauerfeind *et al.*, 2005; Birger *et al.*, 2004; Brown & Belt, 2012; Denisenko *et al.*, 2003; Horner & Schrader, 1982; McMahon *et al.*, 2006; Mundy *et al.*, 2009). Phytoplankton does not grow during ice covered periods. Ice algae live both attached to the bottom of sea ice and within the ice column as in blooms during spring, while phytoplankton lives in the water column and in blooms after the ice melts in early summer (Hsiao, 1992). Seafloor (benthic) faunal species are dependent on the deposition of organic material for their energy requirements (McMahon *et al.*, 2006). Benthic communities can be divided into an intertidal and a subtidal community and have high taxonomic diversity on most continental shelves. The benthos represents all major feeding groups, from shallow subtidal offshore filter- and suspension-feeders and intertidal surface deposit feeders (Bick & Arlt, 2005; Denisenko *et al.*, 2003; Renaud *et al.*, 2011) to predators and scavengers (Renaud *et al.*, 2011).

The benthic fauna of Svalbard varies with depth and habitat. The most common species in the rocky littoral zone include barnacles (*Balanus balanoides*), mobile gastropods (*Littorina saxatilis*) and amphipods (*Gammarus setosus* and *G. oceanicus*) (ACIA, 2005). The soft bottom fauna is dominated by the small polychaetes *Scoloplos armiger* and *Spio filicornis*, and oligochaetes (McMahon *et al.*, 2006; Weslawski *et al.*, 1993). Sublittoral organisms include the barnacle *Balanus balanus* that contributes a large proportion of the biomass of sessile species (Jørgensen & Gulliksen, 2001). The bivalve *Hiatella arctica*, the actinarians *Urticina eques* and *Hormathia nodosa*, bryozoans and *Ophiopholis aculeata* are other conspicuous sessile species. Many, small, motile amphipods (*Calliopidae* sp.), isopods (*Munna* sp. and *Janira maculosa*), snails (*Alvania* sp.) and barnacles (*Tonicella* sp.) are observed together with infaunal polychaetes, nematodes, bivalves (*Thyasira* sp.), and amphipods (*Harpinia* spp.). The infauna occurs in pockets of sediment on the rocky wall (ACIA, 2005).

In different studies, deposit feeding polychaetes are the dominant taxa in Arctic glacial fjords (Blanchard *et al.*, 2010; Cochrane *et al.*, 2009; Fetzer *et al.*, 2002; McMahon *et al.*, 2006). They comprise 88% of the total macrofaunal abundance and 62% of the total macrofaunal biomass. They are known for their high reproduction rates (Bick & Arlt, 2005). 75 Genera and 28 families of polychaetes are known to occur in the Kongsfjord, where Terebellidae, Ampharetidae, Maldanidae, Spionidae and Polynoidae are the dominant families in terms of species numbers (Włodarska-Kowalczyk *et al.*, 2007). The soft-sediment systems of sheltered areas of fjords are often dominated by deposit feeders (Table 1) (Denisenko *et al.*, 2003; McMahon *et al.*, 2006).

In the Kongsfjord, fourteen different taxa are found, of which mean abundance, biomass and feeding strategy of soft bottom benthic invertebrates are shown in Table 1 (McMahon *et al.*, 2006). Bryozoans and hydrozoans represent species-rich groups within kelp forests of the Kongsfjordsystem (Wlodarska-Kowalczyk *et al.*, 2009). Very little research has been done on the structuring effects of larval and postlarval processes on arctic macrobenthic communities. The supply of larvae and the distribution and survival of their juveniles also regulate, besides abiotic factors and predation, benthic communities (Fetzer *et al.*, 2002).

Table 1. Mean abundance (number of individuals per 78,5 cm² core ± SD), biomass (mg ash-free dry weight per 78,5 cm² core ± SD) and feeding strategies of benthic invertebrates from Thiisbukta (Ny Ålesund, Kongsfjord, Svalbard) in July 2004. N=5 replicate sediment cores. (as adjusted from McMahon *et al.*, 2006)

Taxon	Abundance	Biomass (mg)	Feeding strategy
Annelida	130.9 ± 56.4	290.0 ± 41.2	
Oligochaeta	92.6 ± 49.1		Deposit feeder
<i>Scoloplos armiger</i>	13.3 ± 9.1		Deposit feeder
<i>Travisia forbesii</i>	9.3 ± 7.2		Deposit feeder
<i>Spio filicornis</i>	9.3 ± 8.2		Deposit/suspension feeder
<i>Euchone analis</i>	5.6 ± 8.8		Suspension feeder
<i>Eteone longa</i>	0.9 ± 1.2		Predator
Mollusca	10.7 ± 2.6	162.3 ± 22.4	
<i>Liocyma fluctuosa</i>	8.6 ± 2.2		Suspension feeder
<i>Macoma calcarea</i>	1.0 ± 1.0		Deposit/suspension feeder
<i>Buccinum</i> sp.	0.9 ± 1.2		Predator
<i>Astarte borealis</i>	0.1 ± 0.4		Suspension feeder
<i>Mytilus</i> sp.	0.1 ± 0.4		Suspension feeder
Sipuncula	0.9 ± 0.9	15.9 ± 8.4	
<i>Phascolopsis gouldii</i>	0.9 ± 0.9		Deposit feeder
Arthropoda	0.9 ± 0.9	1.3 ± 1.1	
<i>Onisimus littoralis</i>	0.9 ± 0.9		Scavenger
Foraminifera	5.3 ± 2.1	<1.0	
<i>Psammosphaeridae</i>	5.3 ± 2.1		Detritivore

Fish fauna in the Kongsfjord consists of a mixture of boreal and Arctic species. The benthic fish community counts of about 30 species in total and only few are pelagic. Most of the benthic species are Arctic residents (Hop *et al.*, 2006). Polar cod (*Boreogadus saida*) is the most abundant fish species in the Kongsfjord (Hop *et al.*, 2002) and the main fish species associated with sea ice (Lønne & Gulliksen, 1989). Capelin (*Mallotus villosus*) and herring (*Clupea harengus*) occur in the Kongsfjord, presumably in larger numbers during warm years.

The upper trophic levels in the Kongsfjord is represented by a variety of marine mammals (seals, walruses, whales and polar bear) and seabirds. Many species are migratory and only reside in the Arctic during their breeding and subsequent feeding periods. The common eider (*Somateria mollissima*) is one of the most abundant bird species in addition to black-legged kittiwakes (*Rissa tridactyla*) (Hop *et al.*, 2002). Most bird species preys on pelagic fish and invertebrates. The common eider is a benthic feeder that forages in shallow waters on invertebrates, including molluscs (e.g.

Buccinum glacialis, *Hiatella arctica*) (Dahl *et al.*, 2003) and sea urchins (*Stongylocentrotus droebachiensis*) (Bustnes and Lønne, 1995 as cited in Hop *et al.*, 2006

3.2 Growth conditions

Many benthic faunal species are dependent on the deposition of organic material from the water column, for their energy requirements (McMahon *et al.*, 2006; Wlodarska-Kowalczyk *et al.*, 2005). The Kongsfjord has little organic input from the sparsely vegetated terrestrial habitats surrounding it. Glacial runoff doesn't provide considerable amounts of organic matter for use by benthic fauna (Renaud *et al.*, 2011). A relatively large proportion of the primary production in highly productive water columns could potentially reach the bottom (Fetzer *et al.*, 2002), so primary and benthic production tend to be coupled (ACIA, 2005; Bauerfeind *et al.*, 2005; Cochrane *et al.*, 2009; Hop *et al.*, 2006; McMahon *et al.*, 2006). The fraction of sinking matter that reaches the bottom is related to bottom depth; the shallower the water body, the greater the amount of material reaching the bottom (Brown & Belt, 2012) and the more potential food, the higher benthic biomass (Carroll *et al.*, 2008; Denisenko *et al.*, 2003). Benthic community respiration rates significantly increase shortly after algal blooms, due to the influx of organic matter (Goody, 2002, McMahon *et al.*, 2006; Renaud *et al.*, 2007).

Light, temperature, salinity, nutrient concentrations and ice or snow cover are parameters that determine primary production (e.g. relative contributions, distributions and productivity). Primary production occurs in the euphotic zone, when light and nutrient conditions allow (ACIA, 2005; Bauerfeind *et al.*, 2005). The Kongsfjord is on a high latitude, meaning that it is subjected to an extremely seasonal photoperiod (Clarke & Harris, 2003), but ice cover determines the penetration of light (Cochrane *et al.*, 2009; Hop *et al.*, 2006; McMahon *et al.*, 2006) and suppresses water column productivity (Figure 2) (Cochrane *et al.*, 2009; Grant *et al.*, 2002; Grebmeier *et al.*, 2006), involving a non steady-state ecosystem (Morata *et al.*, 2011). Primary production peaks are in spring and later in the year (Goody, 2002), due to seasonal ice-melting, causing vertical stratification and therefore developing a nutrient rich euphotic zone (Cochrane *et al.*, 2009).

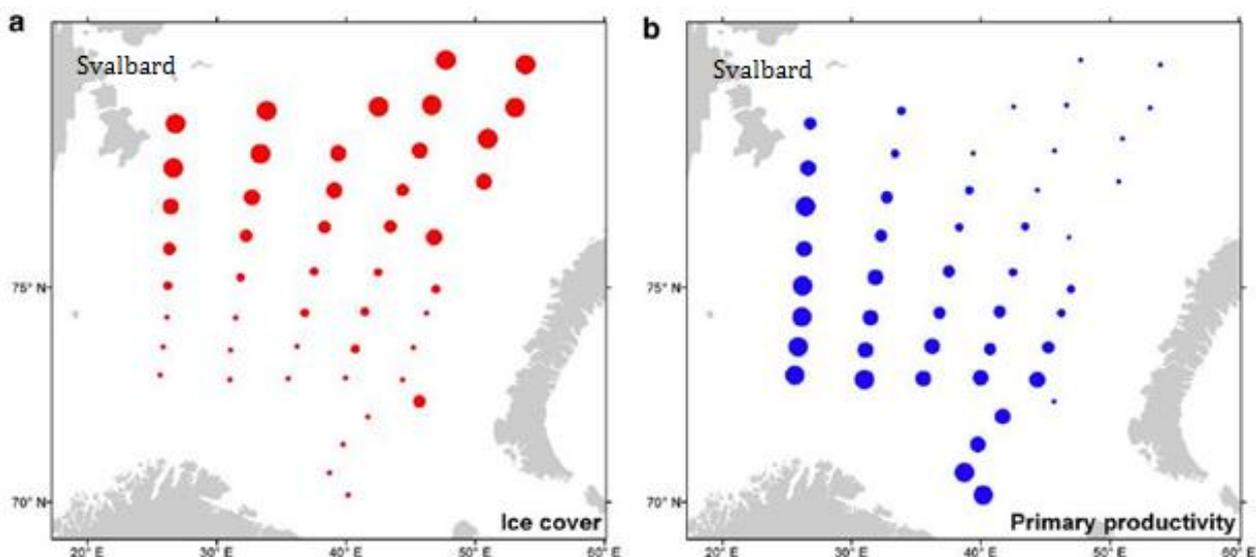


Figure 2. Graphic representation of selected results at sampling stations in the Barents Sea: **A.** Averaged annually ice cover during the period July 2002–August 2003; values from 0–57%. **B.** Modelled integrated water column productivity; averaged for 2002–2003; values from 17–134 g C m² y⁻¹. (modified from Cochrane *et al.*, 2009)

Soft-sediment benthic communities on Arctic shelves are dominated by deposit feeding groups, with few obligate filter feeders compared to other habitats (Cochrane *et al.*, 2009). In contrast, hard-substrate communities are characterized by large filter feeding taxa (anemones, bivalves, ascidians, bryozoans) (Beuchel & Gulliksen, 2008). The benthic community structure in the area shows large inter-annual and long-term variability (Denisenko, 2001 as cited in Cochrane *et al.*, 2009), this likely is a result of fluctuations in temperature, water masses, food quality, quantity and timing, as well as biological competition and recruitment success (Cochrane *et al.*, 2009). Deposit feeders, for example, may be preferentially selecting ice algae for its essential fatty acids (EFA) content (quality) rather than relying solely on phytoplankton (quantity) (McMahon *et al.*, 2006).

A huge amount of the benthic invertebrates occur in the top 4 cm of the sediment (McMahon *et al.*, 2006), busy reworking or mixing the bottom sediments, particularly in areas with low sedimentation rates (Clough *et al.*, 1997; Dowdeswell, 1987). It is common for large quantities of ice algae to resurface due to active sediment mixing (Mincks *et al.*, 2005). The concentration of carbon in the sediment has a strong influence on the diversity of the benthic communities, while both carbon and water depth affect the distribution of communities and the feeding mode of the dominant species (Denisenko *et al.*, 2003). The importance of deposit feeders and carnivores increases towards the outer shelf (Figure 3)(Fetzer *et al.*, 2002). The small amount of organic carbon in the sediments, as a dilution effect caused by the heavy sedimentation of inorganic matter, may constrain the presence of deposit feeders at the innermost station of the fjord, because carbon is an important food source them (Piepenburg *et al.*, 1996). The density distribution of polychaetes for example, follows the same pattern as the mean total abundance and total organic carbon, indicating that most of them are deposit feeders (Horner & Schrader, 1982). The food web system is build upon this feeding group.

3.3 Food web dynamics

Food-web structure does not vary significantly in the fjord area between May and October. It may vary on small spatial scales due to variability depending on nutritional sources, assimilation of dominant groups, primary carbon sources and seasonal activity levels. Renaud *et al.* (2011) suggested little spatial difference between within the fjord and on the shelf outside the fjord. Many benthic organisms feed on multiple prey items and at multiple trophic levels throughout the year, but the fjord act as a single system with one main source of food, e.g. primary production (Renaud *et al.*, 2011).

Carbohydrates (organic matter) produced in primary production is primarily consumed by herbivorous animals, which later may be eaten by fish. The fish are then consumed by seabirds and mammals. In terms of food webs, the carbon that successfully reaches the seafloor is important, since many benthic faunal species are dependent on the deposition of this organic material from the water column for their energy requirements (Clough *et al.*, 1997; McMahon *et al.*, 2006; Sweetman & Witte, 2008). The main loss of organic matter between one trophic level and the next, results in the release of CO₂ or nutrients. Only a small fraction of the organic matter reaches the seabed (e.g. the deeper the water column, the smaller the fraction) (ACIA, 2005), because the material is consumed by grazers (Cochrane *et al.*, 2009). The remineralization of organic matter at the seafloor is a source of nutrient release to the water column (Grebmeier *et al.*, 2006).

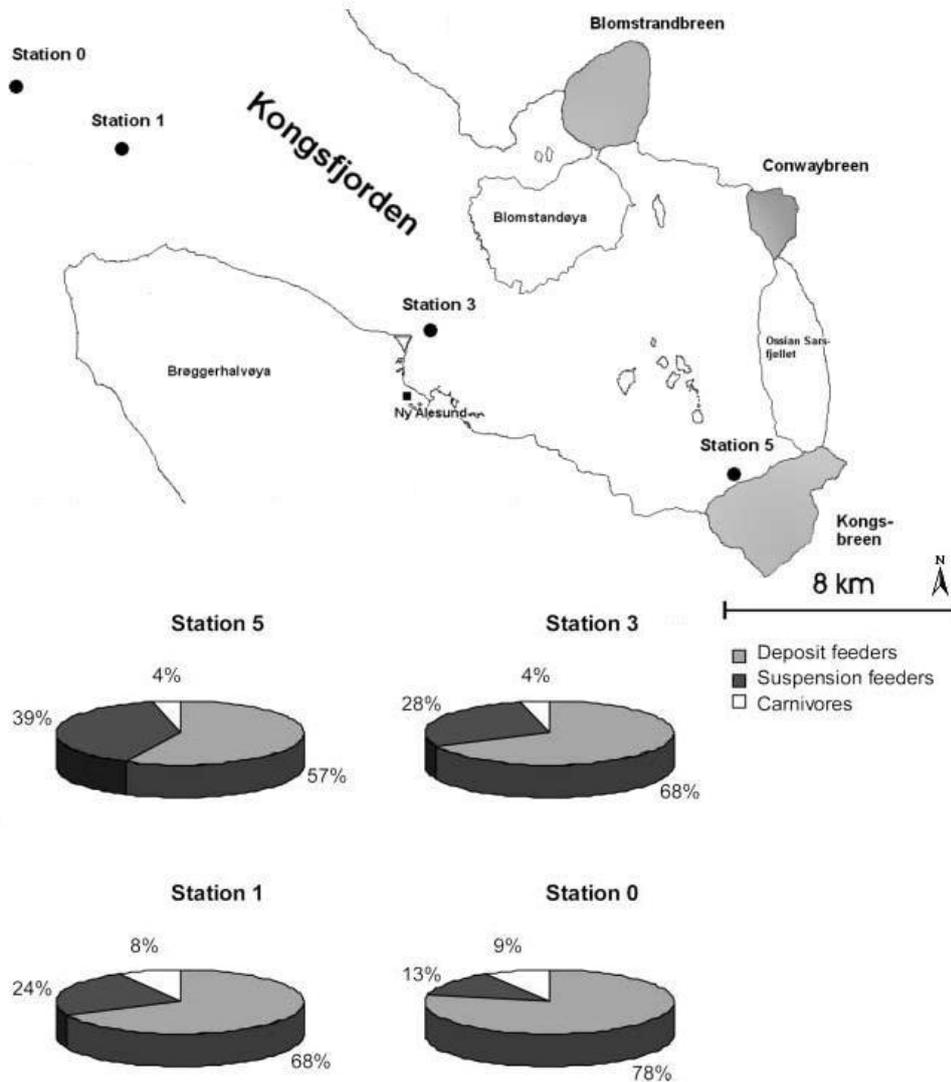


Figure 3. Location of benthic sampling stations in the Kongsfjord with relative abundance of juvenile deposit feeders, suspension feeders and carnivores of all species, as adjusted from Fetzer *et al.*, 2002

It can be driven by micro- and meiobenthic communities in spring and by macrobenthic communities in summer (Grant *et al.*, 2002). Following the ice melt during the spring-to-summer transition, the mismatch between peak primary production and zooplankton grazing allows for an enhanced export of organic material to the seafloor (ACIA, 2005; Wassmann *et al.*, 2006 as cited in Link *et al.*, 2011) but on the other hand, it is a match when grazers are located in the same space and time as where primary production occur (ACIA, 2005), and therefore the export could be reduced. Remineralization is thus an important food input to benthic communities and significantly increases benthic activity (Link *et al.*, 2011). Polar cod, the most abundant fish species, feeds on pelagic zooplankton (e.g. *Themisto libellula* and *Apherusa glacialis*) (ACIA, 2005) therefore its presence doesn't affect the benthos.

Phytoplankton can remain in the water column for a long time (1 to 2 months) due to slow sedimentation rates and frequent resuspension (Van der Loeff *et al.*, 2002). Ice algae sink rapidly to the sea floor after the spring ice melts (Ambrose *et al.*, 2005).

Therefore, phytoplankton may be a more accessible food source for suspension feeders during summer (McMahon *et al.*, 2006). Deposit feeders might feed on ice algae in the sediment in summer, because ice algae are often buried deep in the sediment by infauna (Mincks *et al.*, 2005). The high diversity of infaunal organisms in Arctic soft sediments suggests a complex food web where many organisms feed at a variety of trophic levels (Iken *et al.*, 2010). For example, benthic amphipods like *O. littoralis* provide a link between higher trophic level consumers, such as bottom feeding fish and birds, and deposit feeding primary consumers, which in turn rely on ice algae (Hop *et al.*, 2002). The complex food web is supported by the finding of many species from different taxonomic groups occupying each feeding group (Renaud *et al.* 2011).

4. Impact of climate change on benthic communities

4.1 Changes in physical environment

In the Kongsfjord, there is a change in biomass, species richness, species diversity and taxonomic diversity between places that are exposed to glacial disturbance and different depths (Figure 4). Bottom-dwelling organisms may be buried, larval settlement may be hindered, filtering appendages of suspension feeders may become clogged by inorganic particles and the tubes of tube-building organisms may be buried thereby impeding irrigation and leading to suffocation (Moore, 1977 and Hall, 1994 as cited in Wlodarska-Kowalczyk *et al.*, 2005). Besides, an increased influence of Atlantic water, in time, caused a northward shift of benthic species along the Svalbard coast. Drinkwater (2006), for example compared the benthos prior to 1931 with that of the 1950s and indicated that Atlantic species had spread northward by approximately 500 km (Figure 5).

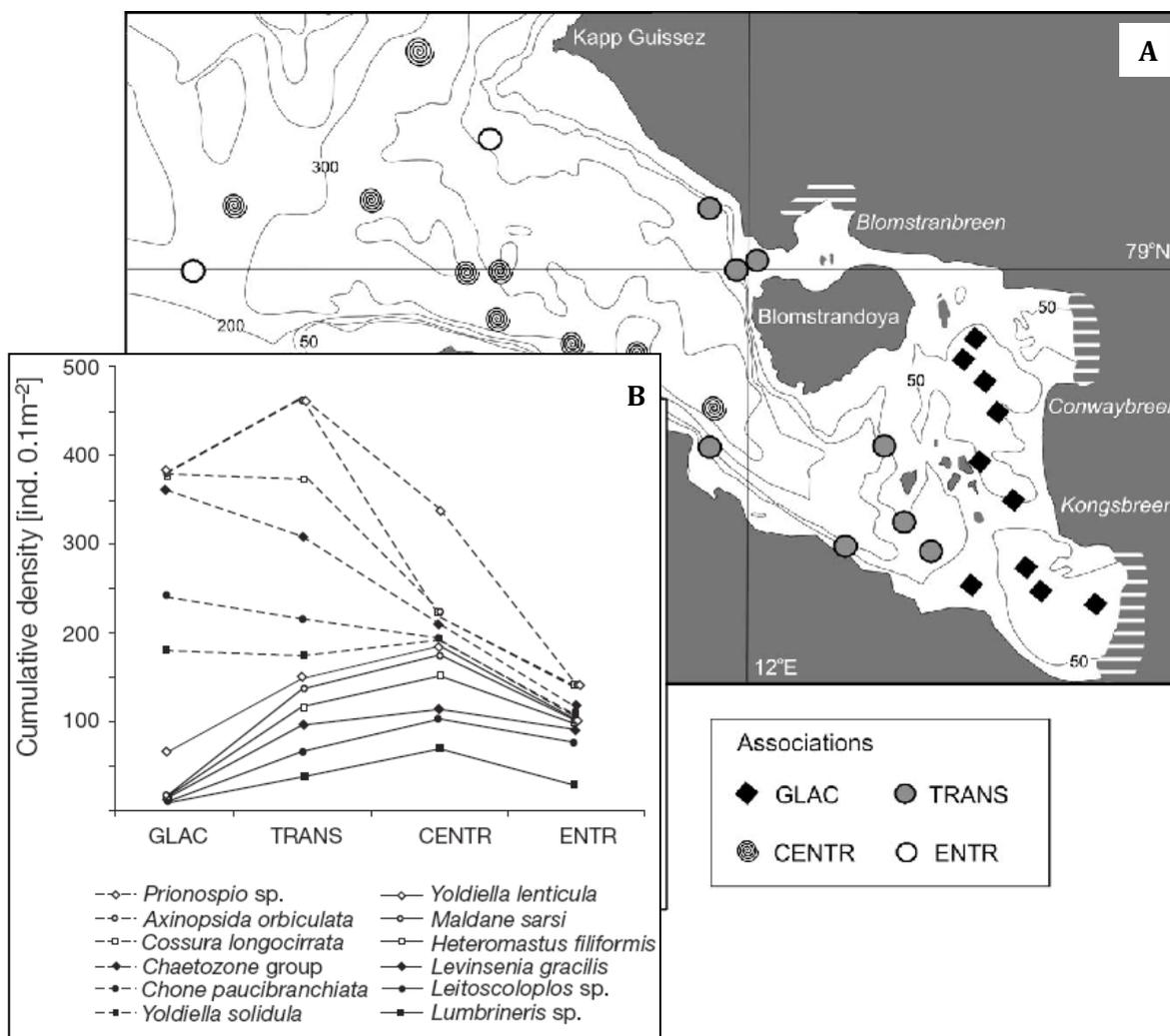


Figure 4. A. Location of sampling stations in the Kongsfjord. The symbols represent 4 associations over a range of depth (GLAC (38 to 83 m), TRANS (72 to 125 m), CENTR (258 to 380 m) and ENTR (155 to 258 m), based on multiple samples taken at sampling stations. **B.** Cumulative mean densities (ind. 0.1 m⁻²) in each association of the most abundant species in the fjord. Species with a dominance exceeding 2% are presented. (modified from Wlodarska-Kowalczyk *et al.*, 2005)

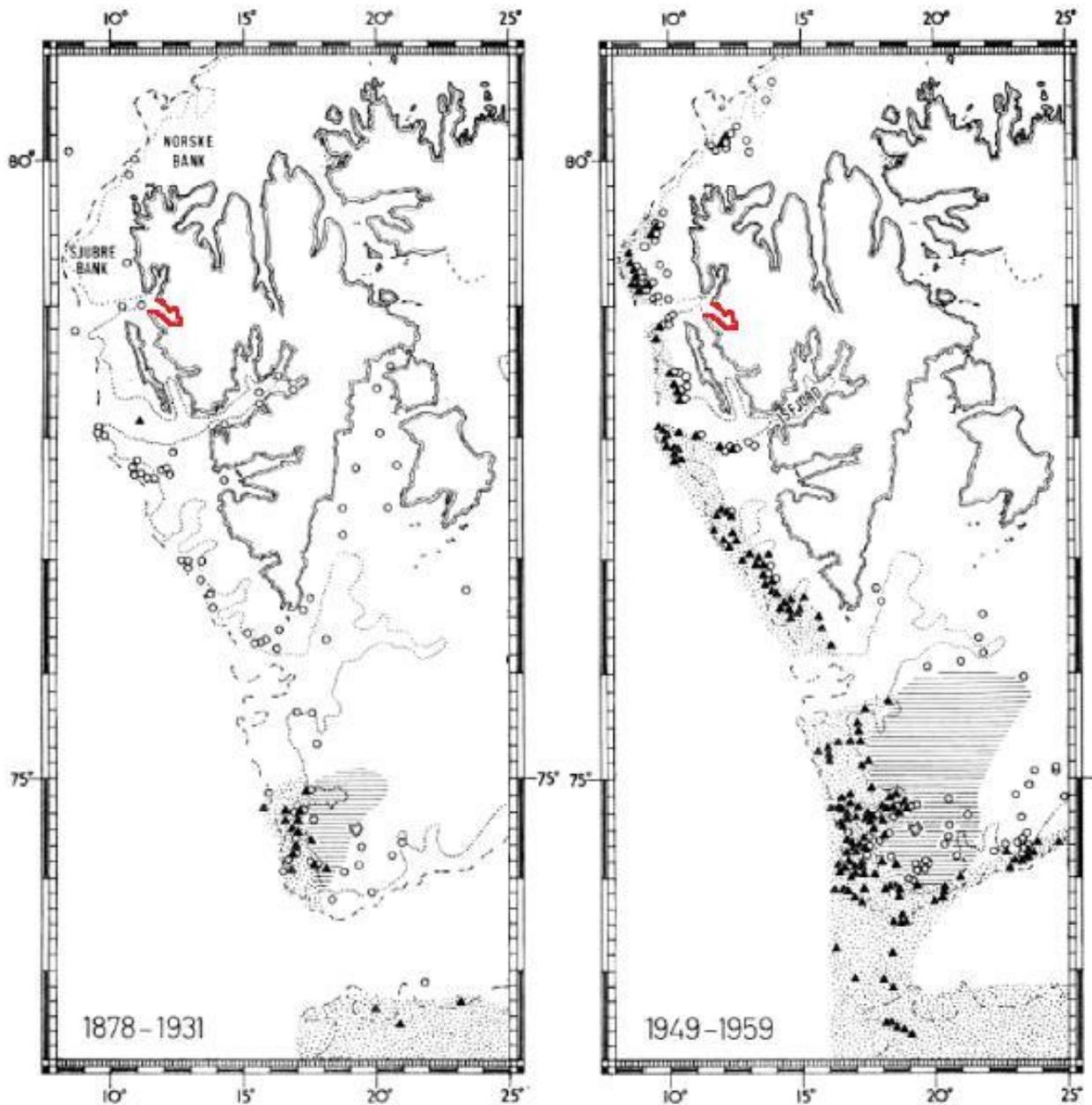


Figure 5. The changes in the benthic species near Svalbard. The open circles represent Arctic species and the triangles Atlantic species. The stippled area indicates where Atlantic species dominate and the hatched area where conditions can vary from extreme Atlantic to extreme Arctic conditions (+5 °C to near -2 °C). The red line indicates the location of the Kongsfjord. (modified from Drinkwater, 2006)

4.1.1 Water masses

Relatively warm saline water of Atlantic origin, transported northwards, influences the Kongsfjord (Drinkwater, 2006; Hop *et al.*, 2006). Due to increasing temperatures and sea cover changes, the influx of Atlantic water could result in the establishment of boreal species in the fjord, including benthic organisms with pelagic life stages. Changes in species composition are between a state of Atlantic dominance (warm and saline) and one of Arctic dominance (cold and fresh). Arctic species prefer habitats influenced by cold water currents, while boreal species predominate in areas affected by warmer coastal waters. For example, Bick & Arlt (2005), identified the polychaeta to species level in the Kongsfjord. Seven species (54%) were classified as cosmopolitan, three as

arctic-boreal (23%) and three as arctic-boreal-Mediterranean (23%). In time, the fjord may undergo an intense shift from an Arctic-water- to an Atlantic-water-dominated system concerning species composition, due to climate change.

Cochrane *et al.* (2009), investigated patterns in the abundance and composition of benthic faunal assemblages in the Barents Sea in relation to water mass. Three main faunal groups were identified, based on similarity of numerical faunal composition. The northern and southern faunal groups were separated by the northernmost penetration of Atlantic Water. The northern faunal group was characterized by a relatively low faunal abundance and low taxon dominance, giving a generally high relative faunal diversity. Within the southern group, the faunal abundance showed some variation across the area, but on average was 48% higher than that of the northern group.

4.1.2 Sea ice cover

Light

Due to increasing temperature, the sea ice extent and thickness will decrease more in summer and winter. Increasing temperature will cause earlier breakup and later freeze-up of ice. Therefore a shorter period of sea-ice cover will show up. Longer ice-free periods will significantly increase sub-surface light availability (ACIA, 2005; Brown & Belt, 2012) in advantage of phytoplankton. Removal of light limitation in areas presently covered by multi-year sea ice is likely to result in a two- to fivefold increase in primary production, provided wind mixing is sufficient to ensure adequate nutrient supply (ACIA, 2005). The longer ice-free periods will cause earlier and longer spring to summer activity. It might be possible that increasing light intensity resulting from reduced ice cover thickness, may favor more light-adapted species (Horner & Schrader, 1982). Ice algae live attached to sea ice and within the ice column and therefore the amount of habitat of ice algae will get lost with decreasing sea ice cover. During the winters of 2006/7 and 2007/8 there was little ice in the fjord, which largely eliminated ice algae as a potential food source for local food webs (Renaud *et al.*, 2011). Changes in ice cover, due to climate change, therefore, control changes in amount, composition, timing and dispersal of primary producers.

In winter, deposit feeding primary consumers rely on ice algae. Deposit feeders often dominate Arctic soft-sediment systems (Denisenko *et al.*, 2003), and thus a climate change-mediated reduction in their preferred food source could significantly affect their distribution and abundance (McMahon *et al.*, 2006). Arctic warming will likely cause a decrease in ice algae and may cause an increase in phytoplankton reaching the seafloor. McMahon *et al.* (2006), found that ice algae may be preferentially selected by some benthic species, such as the bivalve *Macoma calcaria*. Reduced sea ice cover may result in a shift from a 'sea ice-benthos' to 'phytoplankton-zooplankton' dominance in terms of carbon fluxes (Piepenburg, 2005). Thus global warming may increase the quantity, but reduce the quality of food input to the Arctic benthic food web.

Nutrients and sediments

Fetzer *et al.* (2002), expected heavy discharge of inorganic sediments to be one of the main structuring factors of benthic communities. The Kongsfjord frequently experiences high turbidity due to glacial runoff. The sediment-rich glacial melt water on one hand is an input of minerals, which are nutrients needed for phytoplankton growth. On the other hand the melt water reduces transparency due to turbidity caused by the

inorganic material the glaciers picked up (ACIA, 2005; Grant *et al.*, 2002; Grebmeier *et al.*, 2006; Hop *et al.*, 2006; Ronowicz *et al.*, 2011). Reduced transparency will work out in reduced light availability for different micro-eukaryotic species (Piquet *et al.*, 2010). By changing transparency and the input of nutrients, melt water can cause changes in phytoplankton characteristics and in turn change benthic life.

Sedimentation is expected to increase exponentially with decreasing distance from the glacier (Fetzer *et al.*, 2002), but sampling by Weslawski (unpublished work) suggested that the basin was faunistically homogeneous, perhaps as a result of the heavy glacial sedimentation (Piquet *et al.*, 2010). Renaud *et al.*, (2011) suggested that faunal zonation, being dominated by 'opportunist' taxa, is mainly due to communities immediately adjacent to the glacier, because food-web structure is largely invariant in the rest of the Kongsfjord, but they have not sampled from this narrow zone. Increasing sedimentation rates of inorganic material may cause elevated problems for suspension feeders and the resulting soft and unstable sediments may also create difficulties for tube-building organisms (Wlodarska-Kowalczyk *et al.*, 2011). Besides, for the suspension-feeding bryozoan *Alcyonidium disciforme*, for example, the high inorganic sedimentation is not a limiting factor. Moreover, quite some suspension feeders are epifaunal and motile species (crabs, hermit crabs, basket stars and brittle stars (Brown & Belt, 2012; Grebmeier *et al.*, 2006). Table 2 shows that a relatively huge amount of the GLAC species (range of depth is 38 to 83 m) are mobile.

Table 2. Percentage of functional types in total number of animals in each association. Functional groups are designated by codes: first letter(s) = feeding type: f: suspension feeders, s: surface detritus feeders, b: subsurface detritus feeders, c: carnivores, o: omnivores; last letter = mobility type: m: mobile, d: discretely mobile, s: sedentary; u: unknown functional type

Functional type	GLAC	TRANS	CENTR	ENTR
fs	0.3	1.5	2.3	0.4
fd	0.1	–	0.1	–
fm	0.3	0.4	–	4.7
f/ss	–	0.1	1.0	–
f/sd	13.1	4.9	1.3	0.6
f/sm	6.7	11.1	0.1	1.4
ss	0.7	8.7	1.6	8.4
sd	–	0.4	30.2	1.7
sm	66.6	32.4	9.2	12.2
bs	–	4.0	10.3	3.9
bm	4.4	21.7	22.0	34.4
cm	3.5	7.4	17.0	14.9
c/bm	–	1.1	0.8	1.3
s/cm	1.4	1.3	1.1	9.4
om	–	0.1	0.2	0.6
u	2.9	4.9	2.7	6.3

Even though young oligochaetes are exclusively found near the glacier, no species seem to be well adapted to the high sedimentation rate close to the glacier. Juvenile suspension-feeding bivalves seem to be less disturbed but appear to be more vulnerable to currents on the more exposed sites. Coupling biotic data to abiotic factors reveals that hydrographic factors are more responsible for the structuring of the benthic juvenile community (Fetzer *et al.*, 2002). When sedimentation establishes tremendous change, due to enforced glacier run off by climate change, settlement of the benthic community will be troubled more.

Ice scouring

The coast of the Kongsfjord is bound by rocky shores. The presence of sediment in the water column is regarded as a severe stress agent for hard-bottom macro organisms, living on the shores, especially suspension feeders (Airoldi, 2003 as cited in Ronowicz *et al.*, 2011). Suspension-feeding organisms in sediment stressed environments are observed to experience reduced survival and mortality as a consequence of both burial and scouring. This can cause changes in species composition and diversity in communities. Due to ice scouring, the macro fauna of intertidal and subtidal areas consists mainly of polychaetes and motile species, which are apparently well adapted to the disturbances in progress. The high reproduction rates of polychaetes may favor their colonization of such areas. Ice scouring removes 'late successional species' and creates opportunities for colonization by 'early successional species' (Lenihan & Oliver, 1995). Therefore, ice scouring by melting ice, prevents sessile animals on glacier termini from settling (Gutt, 2001), but is not likely to influence the benthos when located deeper than the depth at which icebergs can have an effect.

4.2 Changes in food web dynamics

Renaud *et al.*, 2011, provided evidence that Arctic marine food chains are not shorter than marine food chains from lower latitudes. Changes in sea ice cover have important implications for Arctic marine biota. All levels of the food web are likely to be affected, ranging from primary production to higher mammals (Clarke & Harris, 2003; McMahon *et al.*, 2006). Sea ice plays an important role in production of ice algae and phytoplankton, which in turn supplies nutrients to organisms such as copepods (Clarke & Harris, 2003). Besides, sea ice is also required as a solid substrate on which both seals pup and bears hunt, at the top of the food pyramid (Renaud *et al.*, 2011).

Late retreat leads to an early, ice-associated bloom in cold water, whereas no ice, or early retreat, leads to an open water bloom in warm water (ACIA, 2005). In years when the spring bloom occurs in cold water, low temperatures limit the production of zooplankton. This will lead to bottom-up limitation and a decreased biomass of piscivorous fish, over decadal scales. When the bloom occurs in warm water, zooplankton populations should grow rapidly, providing prey for larval and juvenile fish. Abundant zooplankton will lead to abundant predatory fish. Sinking of faecal pellets is, besides organic matter from primary production, an important component of organic carbon for benthic communities (Hop *et al.*, 2006), and their sedimentation is higher in summer than in spring, presumably because of high grazing activity due to higher zooplankton abundance and biomass in bloom periods (Walkusz *et al.*, in review, as cited in Hop *et al.*, 2006).

Polar cod forms a major link in the transfer of energy from zooplankton to top carnivores. Polar cod is a top predator in the regional food chain of the Kongsfjord and feeds on copepods and amphipods. Species of seals or whales rely on Polar cod and in turn, predators such as polar bears depend on seals (ACIA, 2005). Because benthic communities in the Barents Sea are an important food source for a range of top predators, changes in pelagic-benthic coupling will affect the entire ecosystem (Cochrane *et al.*, 2009).

Investigating food web dynamics can help predict the relative stability of the system when confronted with species introductions/extinctions, altered productivity patterns, and other natural or human-induced system changes (Renaud *et al.*, 2011).

5. Discussion & Conclusion

The above described impacts are interconnected and separation of their effects on benthic communities is difficult. The effects of seasonal fluctuations in temperature can be used to predict changes in environment due to increasing temperature. Temperature rise leads to a shift in primary production by earlier ice melt and later freeze-up and this in turn will affect the composition and quantity of food transported to the benthos. This shift could significantly impact the structure and function of the benthic community.

The Kongsfjordsystem (78° 55'N, 11° 56'E, Svalbard) is an excellent natural model system for studying climate change related effects on marine communities. Fjord water is influenced by melt water of glacial origin as well as by mild temperatures mediated by the inflow of transformed Atlantic water. The distributions of ice and water masses are climate driven, and advection of warm water masses prevents ice formation in the fjord. Besides, the influx of Atlantic water could result in the establishment of boreal species in the fjord, including benthic organisms with pelagic life stages.

Benthic organisms are directly and indirectly affected by seasonal glacier activity. High concentration and sedimentation rate of mineral suspensions, low levels of available organic matter, which is diluted by the sedimentation of inorganic material and catastrophic events such as ice-berg scouring or sediment slides. Stronger changes in ice characteristics and glacier activity, due to climate change, will even harm them more.

Future climate scenarios for the Arctic must be treated with great caution. We know that there is a tight pelagic-benthic coupling, which influences the entire ecosystem. The area is highly sensitive due to interactions between atmosphere, oceans and sea ice, which are strongly influenced by climate variations. Melting ice and sedimentated glacial run off, already has tremendous effects on both primary production and benthic life. Fetzer *et al.*, 2002 found that the importance of deposit feeders and carnivores increased towards the outer shelve of the Kongsfjord. In time, the communities within the fjord will be totally impoverished in species richness, and the food web might fall apart.

Most of the changes described in reports, were range shifts and changes in abundance, growth/condition, behaviour/phenology and community/regime shifts concerning marine mammals and fish. More research on benthic life should be developed. This thesis indicates some changes that have already been documented, and also signals at changes that may occur. Research should be stirred up, to be more able to make suggestions on where efforts should be focused to ensure that regime shift in the Arctic Ocean ecosystem does not happen unnoticed.

References

1. Airolidi L (2003) The effect of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology: Annual Review* 41:161-236
2. Arctic Council and International Arctic Science Committee (2005). Arctic climate impact assessment, Scientific report. Cambridge University Press: 453-538 (Available at <http://www.acia.uaf.edu>)
3. Ambrose Jr W.G, von Quillfeldt C, Clough L.M, Tilney P.V.R, Tucker T (2005) The sub-ice algal community in the Chukchi sea: large- and small-scale patterns of abundance based on images from a remotely operated vehicle. *Polar Biology* 28:784-795
4. Arzel O, Fichfet T, Goosse H (2006) Sea ice evolution over the 20th and 21st centuries as simulated by current AOGCMs. *Ocean Modelling* 12:401-415
5. Bauerfeind E, Leipe T, Ramseier R.O (2005) Sedimentation at the permanently ice-covered Greenland continental shelf (74°57.7'N/12°58.7'W): significance of biogenic and lithogenic particles in particulate matter flux. *Journal of Marine Systems* 56:151-166
6. Berner K.S, Koç N, Godtliobsen F (2010) High frequency climate variability of the Norwegian Atlantic Current during the early Holocene period and a possible connection to the Gleissberg cycle. *The Holocene* 20(2):245-255
7. Beuchel F, Gulliksen B (2008) Temporal patterns of benthic community development in an Arctic fjord (Kongsfjorden, Svalbard): Results of a 24-year manipulation study. *Polar Biology* 31:913-924
8. Bick A, Arlt G (2005) Intertidal and subtidal soft-bottom macro- and meiofauna of the Kongsfjord (Spitsbergen). *Polar Biology* 28:550-557
9. Birgel D, Stein R, Hefter J (2004) Aliphatic lipids in recent sediments of the Fram Strait/Yermak Plateau (Arctic Ocean): composition, sources and transport processes. *Marine Chemistry* 88:127-160
10. Blanchard A.L, Howard M, Feder H.M, Hoberg M.K (2010) Temporal variability of benthic communities in an Alaskan glacial fjord, 1971–2007. *Marine Environmental Research* 69:95-107
11. Brown A.T, Belt S.T (2012) Identification of the sea ice diatom biomarker IP25 in Arctic benthic macrofauna: direct evidence for a sea ice diatom diet in Arctic heterotrophs. *Polar Biology* 35:131-137
12. Bustnes J.O, Lønne O.J (1995) Sea ducks as predators in northern kelp forest. In: Skjoldal H.R, Hopkins C, Erikstad K.E, Leina H.P (Eds.), *Ecology of Fjords and Coastal Waters*, Elsevier Science BV Amsterdam:599-608
13. Carroll M.L, Denisenko S.G, Renaud P.E, Ambrose Jr W.G (2008) Benthic infauna of the seasonally ice-covered western Barents Sea: Patterns and relationships to environmental forcing. *Deep-Sea Research II* 55:2340-2351
14. Clarke A, Harris C.M (2003) Polar marine ecosystems: major threats and future change. *Environmental Conservation* 30 (1):1-25
15. Clough L.M, Ambrose Jr W.G, Kirk J, Cochran J.K, Barnes C, Renaud P.E, Aller R.C (1997) Infaunal density, biomass and bioturbation in the sediments of the Arctic Ocean. *Deep-Sea Research II* 44(8):1683-1704
16. Cochrane S.K.J, Denisenko S.G, Renaud P.E, Emblow S.C, Ambrose Jr W.G, Ellingsen I.H, Skarðhamar J (2009) Benthic macrofauna and productivity regimes in the Barents Sea - Ecological implications in a changing Arctic. *Journal of Sea Research* 61:222-233

17. Comiso J.C, Parkinson C.L, Gersten R, Stock L (2008) Accelerated decline in the Arctic sea ice cover. *Geophysical Research Letters* 35
18. Denisenko S.G (2001) Long-term changes of zoobenthos biomass in the Barents Sea. *Proceedings of the Zoological Institute of the Russian Academy of Sciences* 289:59-66
19. Denisenko S.G, Denisenko N.V, Lehtonen K.K, Andersin A.B, Laine A.O (2003) Macrozoobenthos of the Pechora Sea (SE Barents Sea): community structure and spatial distribution in relation to environmental conditions. *Marine Ecology Progress Series* 258:109-123
20. Dowdeswell J.A (1987) Processes of glacial marine sedimentation. *Progress in Physical Geography* 11:52-89
21. Drinkwater K.F (2006) The regime shift of the 1920s and 1930s in the North Atlantic. *Progress in Oceanography* 68:134-151
22. Fetzer I, Jørgen Lønne O, Pearson T (2002) The distribution of juvenile benthic invertebrates in an arctic glacial fjord. *Polar Biology* 25:303-315
23. Førland E.J, Benestad R.E, Flatøy F, Hanssen-Bauer I, Haugen J.E, Isaksen K, Sorteberg A, Ådlandsvik B (2009) Climate development in North Norway and the Svalbard region during 1900–2100. *NorACIA Report* 128
24. Fredersdorf J, Müller R, Becker S, Wiencke C, Bischof K (2009) Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp *Alaria esculenta* (Phaeophyceae). *Oecologia* 160:483-492
25. Gooday A.J (2002) Biological Response to Seasonally Varying Fluxes of Organic Matter to the Ocean Floor: A Review. *Journal of Oceanography* 58:305-332
26. Grant J, Hargrave B, MacPherson P (2002) Sediment properties and benthic-pelagic coupling in the North Water. *Deep-Sea Research II* 49:5259-5275
27. Grebmeier J.M, Cooper L.W, Feder H.M, Sirenko B.I (2006) Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Progress in Oceanography* 71:331-361
28. Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. *Polar Biology* 24:553-564
29. Hall S.J (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology: Annual Review* 32:179-239
30. Holte B, Dahle S, Gulliksen B, Næs K (1996) Some macrofaunal effects of the local pollution and glacier-induced sedimentation, with indicative chemical analyses, in the sediments of two Arctic fjords. *Polar Biology* 16:549-557
31. Hop H, Pearson T, Hegseth E.N, Kovacs K.M, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalczyk M, Lydersen C, Weslawski J.M, Cochrane S, Gabrielsen G.W, Leakey R.J.G, Lønne O.J, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S. Å, Bischof K, Voronkov A.Y, Kovaltchouk N.A, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. *Polar Research* 21:167-208
32. Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide J.E (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. *Progress in Oceanography* 71:182-231
33. Horner R, Schrader G.C (1982) Relative Contributions of Ice Algae, phytoplankton, and Benthic Microalgae to Primary Production in Nearshore Regions of the Beaufort Sea. *Arctic* 35(4):485-503

34. Hsiao S.I.C (1992) Dynamics of ice algae and phytoplankton in Frobisher Bay. *Polar Biology* 12:645-651
35. Iken K, Bluhm B, Dunton K (2010) Benthic food web structure under differing water mass properties in the southern Chukchi Sea. *Deep-Sea Research II* 57:71-85
36. IPCC (2001) Intergovernmental panel on climate change. *Climate change 2001: the scientific basis. Contribution of Working Group I to the third assessment.* Cambridge University Press, Cambridge:881
37. IPCC (2007) Intergovernmental panel on climate change. *Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment.* Cambridge University Press, Cambridge:996
38. Jørgensen L.L, Gulliksen B (2001) Rocky bottom fauna in arctic Kongsfjord (Svalbard) studied by means of suction sampling and photography. *Polar Biology* 24: 113-121
39. Kwasniewski S, Hop H, Falk-Petersen S, Pedersen G (2003) Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *Journal of Plankton Research* 25(1):1-20
40. Kwok R, Rothrock D.A (2009) Decline in Arctic sea ice thickness from submarine and ICES at records: 1958–2008. *Geophysical Research Letters* 36
41. Lefauconnier B, Hagen J. O, Rudant J.P (1994) Flow speed and calving rate of Kongsbreen glacier, Svalbard, using SPOT images. *Polar Research*:59-65
42. Lenihan H.S, Oliver J.S (1995) Anthropogenic and natural disturbances to marine benthic communities in Antarctica. *Ecological Applications* 5:311-326
43. Lippert H, Iken K (2003) Palatability and nutritional quality of marine invertebrates in a sub-Arctic fjord. *Journal of the Marine Biological Association of the United Kingdom* 83:1215-1219
44. Link H, Archambault P, Tamelander T, Renaud P.E, Piepenburg D (2011) Spring-to-summer changes and regional variability of benthic processes in the western Canadian Arctic. *Polar Biology* 34:2025-2038
45. Lønne O.J, Gulliksen B (1989) Size, Age and Diet of Polar Cod, *Boreogadus saida* (Lepechin 1773), in Ice Covered Waters. *Polar Biology* 9:187-191
46. McMahon K.W, Ambrose Jr W.G, Johnson B.J, Sun M, Lopez G.R, Clough L.M, Carroll M.L (2006) Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. *Marine Ecology Progress Series* 310:1-14
47. Mincks S.L, Smith C.R, DeMaster D.J (2005) Persistence of labile organic matter and microbial biomass in Antarctic shelf sediments: evidence of a sediment 'food bank'. *Marine Ecology Progress Series* 300:3-19
48. Moore P.G (1977) Inorganic particulate suspensions in the sea and their effects on marine animals. *Oceanography and Marine Biology: Annual Review* 15:225-363
49. Morata N, Poulin M, Renaud P.E (2011) A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor. *Polar Biology* 34:101–112
50. Mundy C.J, Barber D.G, Michel C (2005) Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae biomass during spring. *Journal of Marine Systems* 58:107-120
51. Parkinson C.L, Cavalieri D.J, Gloersen P, Zwally H.J, Comiso J.C (1999) Arctic sea ice extents, areas, and trends, 1978–1996. *Journal of Geophysical Research* 104:20837-20856

52. Piepenburg D, Chernova N.V, von Dorrien C.F, Gutt J, Neyelov A.V, Rachor E, Saldanha L, Schmid M.K (1996) Megabenthic communities in the waters around Svalbard. *Polar Biology* 16:431-446
53. Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. *Polar Biology* 28:733-755
54. Piquet A.M.T, Scheepens J.F, Bolhuis H, Wiencke C, Buma A.G.J (2010) Variability of protistan and bacterial communities in two Arctic fjords (Spitsbergen). *Polar Biology* 33:1521-1536
55. Renaud P.E, Riedel A, Michel C, Morata N, Gosselin M, Juul-Pedersen T, Chiuchiolo A (2007) Seasonal variation in benthic community oxygen demand: A response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? *Journal of Marine Systems* 67:1-12
56. Renaud P.E, Tessmann M, Evenset A, Christensen G.N (2011) Benthic food-web structure of an Arctic fjord (Kongsfjorden, Svalbard). *Marine Biology Research* 7:13-26
57. Ronowicz M, Wiodarska-Kowalczyk M, Kuklijski P (2011) Patterns of hydroid (Cnidaria, Hydrozoa) species richness and distribution in an Arctic glaciated fjord. *Polar Biology* 34:1437-1445
58. Somerfield P.J, Cochrane S.J, Dahle S, Pearson T.H (2006) Free-living nematodes and macrobenthos in a high-latitude glacial fjord. *Journal of Experimental Marine Biology and Ecology* 330: 284-296
59. Svendsen H, Beszczynska-Møller A, Hagen J.O, Lefauconnier B, Tverberg V, Gerland S, Ørbaek J.B, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther J.G, Dallmann W (2002) The physical environment of Kongsfjorden- Krossfjorden, an Arctic fiord system in Svalbard. *Polar Research* 21(1):133-166
60. Sweetman A.K, Witte U (2008) Macrofaunal response to phytodetritus in a bathyal Norwegian fjord. *Deep-Sea Research I* 55:1503-1514
61. Van der Loeff M.M.R, Meyer R, Rudels B, Rachor E (2002) Resuspension and particle transport in the benthic nepheloid layer in and near Fram Strait in relation to faunal abundances and ²³⁴Th depletion. *Deep-Sea Research I* 49:1941-1958
62. Walkusz W, Kwasniewski S, Falk-Petersen S, Hop H, Tverberg V, Wiczorek P, Weslawski J.M, in review. Seasonal and spatial changes in the zooplankton community in Kongsfjorden, Svalbard. *Journal of Marine Systems*
63. Wassmann P, Reigstad M, Haug T, Rudels B, Carroll M.L, Hop H, Gabrielsen G.W, Falk-Petersen S, Denisenko S.G, Arashkevich E, Slagstad D, Pavlova O (2006) Food webs and carbon flux in the Barents Sea. *Progress in Oceanography* 71:232-287
64. Wassmann P, Duarte C.M, Agustí S, Sejr M.K (2011) Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology* 17:1235-1249
65. Weslawski J.M, Wiktor J, Zajaczkowski M, Swerpel S (1993) Intertidal zone of Svalbard 1. Macroorganism distribution and biomass. *Polar Biology* 13:73-79
66. Włodarska-Kowalczyk M, Pearson T.H (2004) Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biology* 27:155-167
67. Włodarska-Kowalczyk M, Pearson T.H, Kendall M.A (2005) Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. *Marine Ecology Progress Series* 303:31-41

68. Włodarska-Kowalczyk M, Kukliński P, Ronowicz M, Legeryjska J, Gromisz S (2009) Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). *Polar Biology* 32:897-905
69. Włodarska-Kowalczyk M, Siciński J, Gromisz S, Kendall M.A, Dahle S (2007) Similar soft-bottom polychaete diversity in Arctic and Antarctic marine inlets. *Marine Biology* 151:607-616