



The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway



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ABSTRACT

Approximately 60% of Svalbard's land areas are glaciated at the present time. The Archipelago has more than 1100 glaciers (>1 km²) and 163 of these are "tidewater glaciers" – that is glaciers that terminate (with their calving front) at the sea. It has been known for a long time that these glacier front areas are important feeding areas for seabirds and marine mammals. Herein, we review current knowledge regarding the importance of these areas for these animals and reflect upon the processes that create these apparent "hotspots". Kittiwakes *Rissa tridactyla*, routinely dominate avian assemblages in front of glaciers in Svalbard, but fulmars *Fulmarus glacialis*, ivory gulls *Pagophila eburnea* and glaucous gulls *Larus hyperboreus* also contribute to aggregations, which can sometimes comprise many thousands of individuals. The birds are often found in the so-called "brown zone", which is an area in front of tidewater glaciers that is ice-free due to currents and muddy due to suspended sediments. Animals at these sites typically have their stomachs full of large zooplankton or fish. These brown zones are also foraging hotspots for Svalbard's ringed seals (*Pusa hispida*) and white whales (*Delphinapterus leucas*). Prime breeding habitat for ringed seals in Svalbard occurs deep in the fjords where ice pieces calved from the glacier fronts become frozen into land-fast sea-ice, promoting the accumulation of snow to a depth suitable for ringed seal females to dig out birth lairs above breathing holes in the ice. These pupping areas are important hunting areas for polar bears (*Ursus maritimus*) in spring, especially female bears with cubs of the year during the period following emergence from the winter/birthing den. Glacier-ice pieces floating in coastal areas are also important for all seal species in the region as dry platforms during moulting and also as general resting platforms for both birds and seals. During the last decade there have been several years with a complete lack of spring sea ice in many of the fjords along the west coast of Spitsbergen. During the spring periods in these years, bearded seals (*Erignathus barbatus*) have replaced their regular sea-ice platform with glacier ice, using it as a solid substrate for both birthing and nursing as well as general resting. The mechanisms that create foraging hotspots at the fronts of tidewater glaciers are related to the massive subsurface plumes of freshwater discharged from the glacier fronts. As these plumes rise towards the surface they entrain large volumes of ambient water, tens to hundreds of times the original discharge volume. This water is drawn from all depth levels as the plume ascends. This entrainment ensures a continuous resupply of intermediate depth waters from the outer parts of the fjords towards the glacier front and greatly amplifies the general estuarine circulation. The intermediate water masses carry plankton from a broad area, including the outer fjord, into the glacier front area, where they get entrained in the plume rising towards the surface, and often become stunned or die from freshwater osmotic shock. These small animals fall as an easy prey to the surface feeding predators. Large, strong swimming marine zooplankton species can sometimes escape by swimming below the inflow of marine water. But, they then become concentrated in a water layer near the bottom, making them of interest and susceptible to predators. The intermediate water masses also bring nutrients towards the glacier fronts where they are transported up to the surface layer where they can subsequently be utilized for post-bloom primary production. However, this tends to have greatest influence some distance away from the glacier front, when much of the outflow sediment has settled out. Currently, the mass balance for Svalbard glaciers is negative and climate change predictions for the future suggest continued warming, and hence continued glacial retreat. This will result in a reduction in both the number of glaciers calving into the ocean in Svalbard and the total length of calving fronts around the Archipelago.

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Similar to the retraction of the northern sea-ice edge (which is another diminishing foraging hotspot for these same arctic vertebrates), the climate-warming-induced changes in glaciers will likely lead to substantial distributional shifts and abundance reductions for many arctic species.

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1. Introduction

The fact that seabirds concentrate in front of tidewater glaciers and near water outlets from grounded glaciers, in various places in the world, has been known for a long time. For example, Kittlitz's murrelets *Brachyramphus brevirostris* in Alaska are strongly associated with glacier fronts (Kuletz et al., 2003; Stenhouse et al., 2008) and so are blue-eyed shags *Phalacrocorax atriceps* and South American terns *Sterna hirundinacea* in South America (Brown, 1980). In the Atlantic Arctic, species including fulmars *Fulmarus glacialis*, kittiwakes *Rissa tridactyla*, ivory gulls *Pagophila eburnea* and glaucous gulls *Larus hyperboreus* have long been known to form large aggregations at glacier fronts (Hartley and Fisher, 1936; McLaren and Renaud, 1982; Mehlum, 1984; Renaud and McLaren, 1982). Arctic terns *Sterna paradisaea*, Brünnich's guillemots *Uria lomvia* and black guillemots *Cepphus grylle* are also commonly found in front of glaciers, though generally in smaller numbers.

Marine mammals also concentrate in areas in front of glaciers in Svalbard, Norway (Fig. 1), as first described by Hartley and Fisher in 1936. These authors frequently observed ringed seals *Pusa hispida* swimming in the so-called “bird zone” close to glacier fronts. More recent studies based on satellite tracking of various marine mammals in the Svalbard Archipelago have shown that these relatively restricted areas are used extensively by ringed seals (Freitas et al., 2008), white whales *Delphinapterus leucas* (Lydersen et al., 2001) and polar bears *Ursus maritimus* (Freitas et al., 2012).

The reason that glacier fronts are attractive to seabirds and marine mammals is mainly related to feeding. Animals collected at these sites typically have their stomachs filled with large zoo-plankton or fish (Hartley and Fisher, 1936; Weslawski et al., 1994). Older literature often refers to a so-called “brown zone” in front of glaciers being a hotspot for seabirds (Hartley and Fisher, 1936; Stott, 1936, 1990), which is an ice-free area in front of glaciers that is kept clear due to currents and is muddy, and hence brown, because of suspended sediment (Hartley and Dunbar, 1937–38; Fig. 2). Maximum densities of birds in the brown zones are sometimes so close to the glacier face that birds are reportedly killed by calving ice pieces (Stott, 1936). One explanation

for the high concentrations of food at glacier fronts is enhanced productivity through provision of nutrients from sub-glacial waters (Apollonio, 1973). Another reason might be that the freshwater entering the ocean at the bottom of glaciers causes an osmotic shock to the invertebrates and fish that subsequently are transported to the surface with the upwelling current, making them easily available to surface feeding birds (Hartley and Fisher, 1936; Stott, 1936; Weslawski and Legeżyńska, 1998; Zajaczkowski and Legeżyńska, 2001).

Whatever physical features creating these foraging hot spots, it is a fact that global warming is reducing these important foraging areas; they are becoming fewer and smaller as glacial melting proceeds (see f. inst. Kohler et al., 2007). In the present work we focus on the High Arctic Archipelago of Svalbard, Norway, where currently 60% of the land area is covered by glaciers and over 150 glaciers of the tidewater type terminate with their calving front in the ocean (Hagen et al., 1993; König et al., in press). Herein, we review current knowledge regarding the importance of glacier fronts for marine mammals and seabirds in Svalbard and also review current knowledge with regard to the underlying processes that create these foraging hotspots.

2. Importance of tidal glacier fronts for marine mammals and seabirds

2.1. Ringed seals

The ringed seal is the most abundant marine mammal in the Svalbard area (Lydersen, 1998). It is also the most tightly ice-associated seal, depending on very specific ice and snow-conditions for many important events in its annual cycle (see f. inst. Kovacs and Lydersen, 2008). In Svalbard many of the areas that fulfil the specific requirements for these critical life-history events are connected to fjords that have active glacier fronts that protrude into the ocean. For example, the preferred pupping habitat for ringed seals in Svalbard is land-fast sea-ice areas deep in the fjords where ice pieces calved from the glaciers have frozen into the sea ice. Around such pieces of entrapped glacier ice snow accumulates in drifts that are deep enough for ringed seals to dig out a lair in the snow over a breathing hole in the ice (Fig. 3). Such



Fig. 1. Map of Svalbard, with place names mentioned in the text.

lairs are constructed by adult ringed seals of both sexes and also by immature animals. The lairs provide shelter from harsh climate conditions (Smith et al., 1991) and also to some degree protection from predation. It takes some time for a predator to dig or smash through the snow roof of the lair and thus the seals have some chance to escape into the water (Lydersen and Gjertz, 1986). Ringed seal mothers give birth to their young in lairs, which provide shelter that is essential for the survival of the neonates that weigh only a few kilogrammes at birth. Each ringed seal has several breathing holes and lairs that it can move in between if one structure is attacked by a predator (Lydersen and Hammill, 1993; Lydersen and Kovacs, 1999). Polar bears and arctic foxes (*Vulpes lagopus*) are the main predators of ringed seals when they are in their lairs (Lydersen and Gjertz, 1986). But, if snow conditions are poor and the females are forced to give birth on the open ice, pups are also killed by glaucous gulls (*Larus hyperboreus*; Lydersen and Smith, 1989); without the protection of the lair mortality rates for the pups are very high.

When the pupping and breeding season is over, around late May, the ringed seals go through their annual moult, where they replace all their hair and the outer layers of the skin. The moulting period peaks in early June, with some temporal spread among the various age and sex groups (Carlens et al., 2006). Availability of an ice-platform is very important for this process to occur in an energetically efficient manner. Warm temperatures are beneficial for skin growth and the seals can circulate blood to the skin with much less heat loss taking place, when they are hauled-out, compared to when they are forced to be in the water. Under ideal conditions they spend most of their time on the ice resting during the moult (Carlens et al., 2006); they feed little during this time. The seals search out available sea ice for moulting and if there is sea ice remaining in their prime breeding habitat they simply complete the process here. Glacier ice is largely irrelevant for ringed seals during

this time of the year if annual land-fast ice is available. But, if there is no sea ice left at this time, in the late spring/early summer – as has been the case for several years in west-coast Spitsbergen fjords, then the ringed seal use glacier pieces to haul-out on as a substitute for sea ice (Lydersen and Kovacs, personal observations).

Satellite tracking has shown that when the moulting process is over ringed seals in Svalbard perform two very distinctive movement patterns (Freitas et al., 2008). Some seals move offshore seeking areas containing 40–80% ice coverage, while other individuals spread along the coasts of Svalbard concentrating their time near glacier fronts. Both tactics result in ringed seals being in areas with high concentrations of food and access to ice-platforms to rest (either in the form of sea ice or glacier ice, see Freitas et al., 2008). Offshore seals left the drifting pack-ice areas late in the autumn, even if ice conditions were still favourable, reflecting their need to return to the overwintering/breeding areas in the fjords of Svalbard before freeze-up. For ringed seals that remained close to the coast, habitat use intensities were influenced mainly by the distance to glacier fronts (and season). These animals were already close to their over-wintering/breeding habitat and simply became more sedentary as winter approached. In the study by Freitas et al. (2008) there was no statistical evidence for any association between sex or maturity status and the type of movement pattern individuals displayed. In an ongoing study of ringed seals in relation to changing sea ice conditions, satellite tagged animals from Kongsfjorden in 2011 showed extreme site fidelity during the post-moulting period (Lydersen and Kovacs, unpublished data). All of the tagged animals ($N = 11$) spent in excess of 90% of their time in the fjord where they were tagged, and six of them never left Kongsfjorden during the tracking period (average of 148 ± 35 SD, range 74–202 days). The animals spent most of their time affiliated with the various glacier fronts in this area (Fig. 4). The



Fig. 2. The “brown zone” in front of Kronebreen glacier in Kongsfjorden Svalbard (upper panel). The brown zone is the area in front of glaciers that is ice-free due to currents and muddy due to suspended sediment caused by the sub-surface plume of glacial meltwater. This area is a foraging hotspot for marine mammals and seabirds, here represented by kittiwakes (lower panel).

reason for the lack of offshore movements in the second study might be due to inter-annual differences in ice conditions or differences between the various tagging sites. But, it might also be attributable to the age of the tagged animals. Seals tagged in the Freitas et al. (2008) study had an average body mass of 48.7 ± 16.1 kg (range 31–89 kg, $N = 22$), while the ones in the ongoing study from Kongsfjorden were much larger, with an average body mass of 75.5 ± 15.7 kg (range 55–100 kg, $N = 11$). The Freitas et al. (2008) study might have had too few large, adult individuals to detect differences among age groups. Very few small seals were observed (or caught) in the ongoing Kongsfjorden study. This might be because large adult ringed seals stay close to glacier fronts where food is abundant and exclude smaller seals from these feeding “hot spots”. It makes no sense to leave the moulting area if it contains an abundance of food, given that their main predator, the polar bear, occurs only at very low density in Kongsfjorden. The seals that were caught during the Kongsfjorden study in July–August 2011 were in extremely good physical condition. Another factor that may play a role in the observed differences is that the recent study captured seals a few weeks later in the season than in the Freitas et al. (2008)

study, so ringed seals displaying the offshore strategy may have already left Kongsfjorden. Ringed seals shot in front of glaciers in Kongsfjorden in a study two decades ago fed mainly on krill, *Thysanoessa inermis* (Weslawski et al., 1994), although the ringed seal diet elsewhere in Svalbard is dominated by polar cod (Labansen et al., 2007).

2.2. Bearded seals

The details of the annual cycle and the degree of ice dependence of bearded seals (*Erignathus barbatus*) are less well studied than for ringed seals. Peak pupping in this species in Svalbard occurs in the first half of May and the preferred birthing sites are small drifting floes of annual ice, broken off the landfast-ice edge in the fjords (Kovacs et al., 1996). Bearded seal pups are large at birth and are born directly on the ice, without any protective snow lair, and the pups are able to swim in the cold water from the day they are born (Lydersen and Kovacs, 1999; Lydersen et al., 1994). The lactation period is about three weeks long and pups are normally nursed on small ice floes or at the outer edge of the fast-ice (Gjertz et al., 2000; Kovacs et al., 1996). Bearded seals

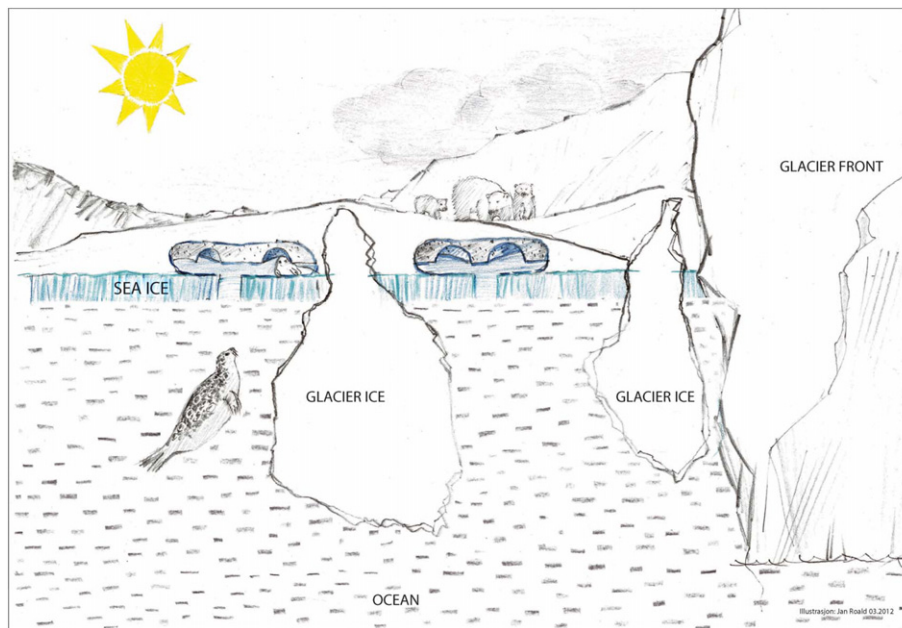


Fig. 3. A cross section of the fast-ice breeding habitat for ringed seals in Svalbard. The prime breeding habitat is land-fast sea-ice areas deep into the fjords where ice pieces calved from glaciers have frozen into the sea ice. Around such pieces of entrapped glacier ice snow accumulates in drifts that are deep enough for ringed seals to construct birth lairs. These areas are also very important hunting areas for polar bears in the spring when the females emerge from their dens with small cubs of the year.

have a tight coastal distribution; this is likely because of their shallow, benthic feeding habits (Hjelset et al., 1999; Krafft et al., 2000) in combination with their need for ice as a resting platform. If the spring ice-platforms used for nursing drift out over deeper waters, the animals actively leave them and move back into shallower areas (Hammill et al., 1994). In 2006 and 2007 there was no sea ice for pupping and nursing in Kongsfjorden. Bearded seals responded to this lack of their preferred sea ice habitat by using glacier ice pieces. Even the youngest pups were strong enough to pull themselves onto the high, irregularly shaped glacier-ice pieces using the well-developed claws on their fore-flippers, though it was clearly more challenging than flat annual ice (Kovacs and Lydersen unpublished data). The mothers nursed pups on large glacier-ice pieces and the pups rested alone on any glacier ice piece large enough to float with them on it. The growth rates of the pups were marginally higher during years with good sea ice conditions (3.1 ± 0.66 kg per day, $N = 43$) compared with years when glacial ice was used as a nursing platform (2.8 ± 0.69 kg per day, $N = 22$, $P = 0.05$, two-tailed t -test, Kovacs and Lydersen, unpublished data). Thus, as a short term solution to little available sea ice, glacier ice seems to provide a viable alternative for bearded seals.

Satellite tracking of bearded seal pups through their first year of life showed an initial dispersion from the areas where they are born and a subsequent exponentially decrease in monthly home range size as the pups get more and more sedentary with age (Kovacs et al., 2011a,b). Analyses of the determinants of space use show that distance to the nearest glacier plays a significant role in the attractiveness of a particular area (First-Passage Time analyses in combination with mixed-effects Cox-Proportional-Hazard models, Kovacs et al., 2011a).

During the bearded seal moulting period in July any available ice, whether it is sea ice or glacier ice, is used by bearded seals as a resting platform. In recent years in Svalbard, when little or no annual sea ice has formed in the fjords on the west coast of Spitsbergen, glacial ice pieces have been the exclusive moulting habitat for bearded seals, with no apparent negative consequences.

Very little is known about the whereabouts of bearded seals outside the breeding period. However, in an on-going study of bearded seals and their dependence on sea ice, five adult animals have been instrumented in Kongsfjorden in 2011 with GPS satellite transmitters (Lydersen and Kovacs, unpublished data). The data thus far collected

from these tags suggests that adult bearded seals have a very restricted, coastal distribution. However, they do not spend much time affiliating with glacier fronts, unlike the ringed seals, though they do haul out and rest on glacial ice through-out the year, including during the cold, dark winter months (Fig. 5). Although their feeding areas are sometimes far from the bottom of the fjord where the active glaciers are, the seals return to these areas to rest. So even though these animals can sleep in the water, they appear to have a strong preference for resting on ice, and take the time to swim a significant distance to find a suitable, dry resting platform.

2.3. White whales

White whales are the most common cetacean species in Svalbard. This species normally lives in tight association with sea ice and has “lost” the dorsal fin, which is considered to be an adaptation to swimming and diving in ice-covered waters. However, satellite tracking of white whales in Svalbard has shown that in the summer and early autumn the whales did not migrate to pack ice areas, they remained in coastal, largely ice-free areas (Lydersen et al., 2001). These tracking studies also showed that the whales spent 55% of their time actively diving (indicating foraging) in front of glaciers. When the whales changed location they did so in an apparently directed and rapid manner swimming very close to the shore-line until they arrived at a new glacier front (Fig. 6, Lydersen et al., 2001). Optimal foraging theory suggests that this type of prey-patch shifting behaviour may represent a long-term adaptation to a fluctuating environment. In such an environment, a good long-term strategy may be to visit different feeding areas with some regularity, spending the most time in areas that have the highest food abundance, but regularly evaluating other potential feeding areas. Animals can then monitor changes in food abundance between areas, and adjust their time according to temporal changes in food availability in each respective area. In this way the whales may exploit potential spatial variability in the timing of melt-water discharge and resulting pulses of upwelling and food aggregations. The reason for the extreme coastal movements could simply be that it is the shortest route between food hot spots, or it may be some sort of predator avoidance (see Lydersen Lydersen et al., 2001 for details). The little tracking that has been done outside the summer–autumn season in Svalbard shows

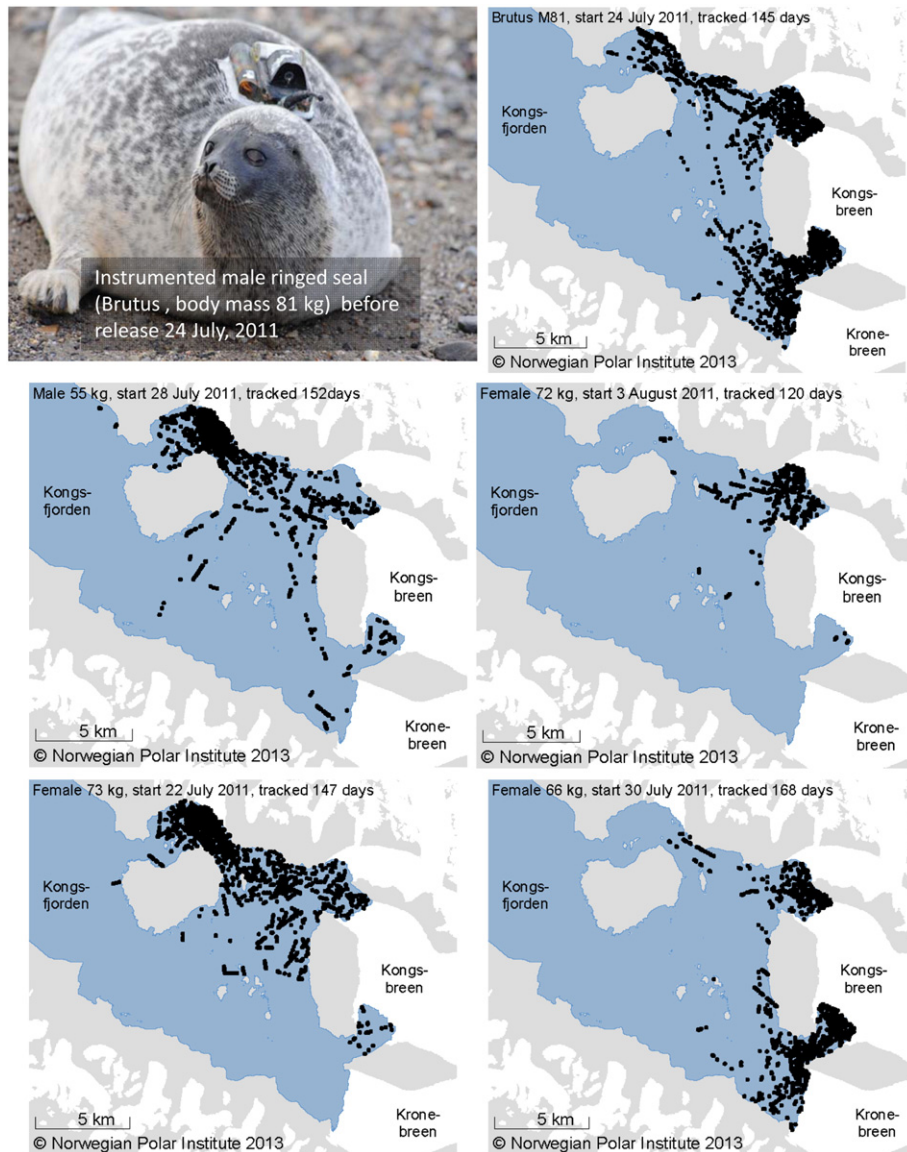


Fig. 4. Tracking results from five adult ringed seals caught in Kongsfjorden, Svalbard in the summer of 2011. Each black circle represents an Argos location. All seals were in extremely good condition (see upper left panel of a male 81 kg carrying a Conductivity–Temperature–Depth–Fluorometer–Satellite–Relay–Data–Logger CTD–fluoro–SRDL, for more details see: <http://www.npolar.no/en/research/ice/ecosystems/ringed-seals/fieldwork.html>). The tracks show that all animals spent the entire tracking period inside Kongsfjorden mainly close to glacier fronts (Lydersen and Kovacs, unpublished data).

that the whales are forced away from the coast as the fast-ice forms, but stay in areas close to shore within drifting pack-ice, with concentrations up to 90–100% ice cover (Lydersen et al., 2002).

2.4. Polar bears

The main prey species for polar bears in Svalbard are ringed seals. Thus, it is not surprising that fast-ice areas close to glacier fronts are very important hunting areas for polar bears in the spring, given that they are the prime ringed seal pupping areas (see above and Fig. 2). In a study of space use patterns of polar bears (of different reproductive status), females with cubs of the year were found to have significantly smaller home-ranges and spend more time close to glacier fronts in spring than females with older cubs or lone females (Freitas et al., 2012). Access to abundant and predictable prey (ringed seal pups and sometimes also their mothers), energy conservation and reluctance to cross large open water areas are possible reasons for the observed patterns. Satellite tracking of female polar bears later in the year shows that they generally display two different space-use strategies;

one is to stay close to the coast and the other is to go offshore onto the drifting ice when the sea-ice recedes during summer (Mauritzen et al., 2001). The shore-based females in Mauritzen et al.'s (2001) study were not “stranded”, they chose to stay in coastal areas. These bears have reproductive success rates that are as high as the females that opt to go onto the offshore ice (Aars, J., pers. comm.). Detailed space use patterns have not been explored for the “terrestrial” bears. But, diving sensors on some of these bears show that they spend up to 13% of their time (per month) in the water (Aars and Andersen, 2008). There are several records of polar bears in Svalbard successfully hunting seals that were hauled out on glacier ice pieces. The bears dive at some distance from the resting seal and emerge out of the water with great speed in front of the seals and kill them. Since seal density is higher in areas close to glacier fronts, and it is here that the bears can hunt seals in summer it is likely that the coastal bears spend most of their time in areas with tidal glacier fronts during the ice-free season. In addition, seals sleep in the water, and we have found bearded seals (both pups and adults) sleeping at the water surface in Kongsfjorden that were easily approached by boat (with the outboard engine

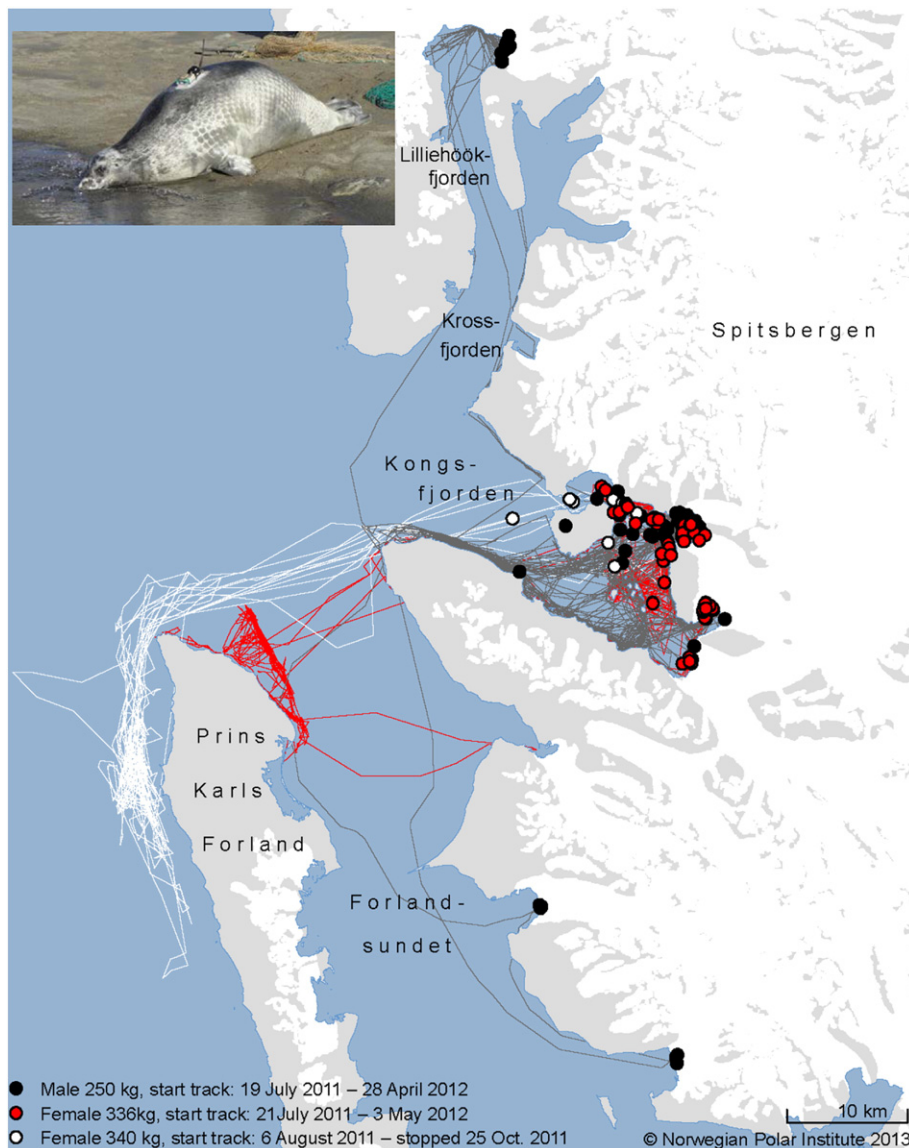


Fig. 5. Tracking results from three adult bearded seals caught in Kongsfjorden, Svalbard in the summer of 2011. Solid circles show places where the animals hauled out. Even if the seals swam out of the fjords to forage they returned into the fjords where they haul out on floating glacial ice pieces (Lydersen and Kovacs, unpublished data).

running) without waking the animals up (Lydersen and Kovacs, unpublished results). Such animals should be an easy prey for a polar bear; for more details on sleeping seals and predation, see Leclerc et al. (2012).

2.5. Seabirds

Several species of seabirds are reported to concentrate their foraging efforts in front of tidewater glaciers in various parts of Svalbard. Hartley and Fisher (1936) found that kittiwakes and fulmars in particular tended to concentrate in front of the glaciers in Billefjorden and Wijdefjorden. The birds flocked at the face of the glaciers, in the immediate vicinity of the melt-water outflow, in what the authors called the “brown zone” where the meltwater contained sediments (see Fig. 2). The number of birds feeding at the glacier fronts varied from some hundreds up to several thousands. Based on half-hour counts of the number of kittiwakes leaving a glacier front in Billefjorden, the daily number of birds feeding at the front in July was estimated to be ~16,000. The birds were mainly feeding on the euphausiid *Thysanoessa inermis*, which seemed to be the most common zooplankton in the “brown zone” during their study (Hartley and Fisher, 1936). The food was

captured by surface pecking (Hartley and Fisher, 1936). The turbid water would most likely prevent prey detection at depth – also explaining the general absence of diving birds in the brown zone area. Glaucous gulls, Arctic terns, black guillemots and ivory gulls were also seen near glacier fronts, but in much smaller numbers than kittiwakes and fulmars. Arctic skuas (*Stercorarius parasiticus*) were seen kleptoparasitizing kittiwakes and Arctic terns (Hartley and Fisher, 1936), using high glacial ice pieces as observation points and starting points for their attacks.

Norderhaug et al. (1977) reported concentrations of seabirds in front of the glaciers in northwest Spitsbergen and Mehlum (1984) reported concentrations of feeding seabirds, especially kittiwakes and fulmars in front of the Austfonna glacier on Nordaustlandet and at outflows of small freshwater rivers in Kongsfjorden. At Austfonna, concentrations of seabirds were found in two areas where the meltwater entered the sea under the surface. Some hundreds of kittiwakes and fulmars fed in each of these areas and birds rested on the glacier itself or on floating glacier ice pieces. Based on net hauls ca. 100 m outside the “brown zone”, it was assumed that the birds were feeding on pteropods (*Limacina helicina*). In Kongsfjorden, the amphipod *Themisto libellula* was very abundant in the “brown zone” and was found floating dead

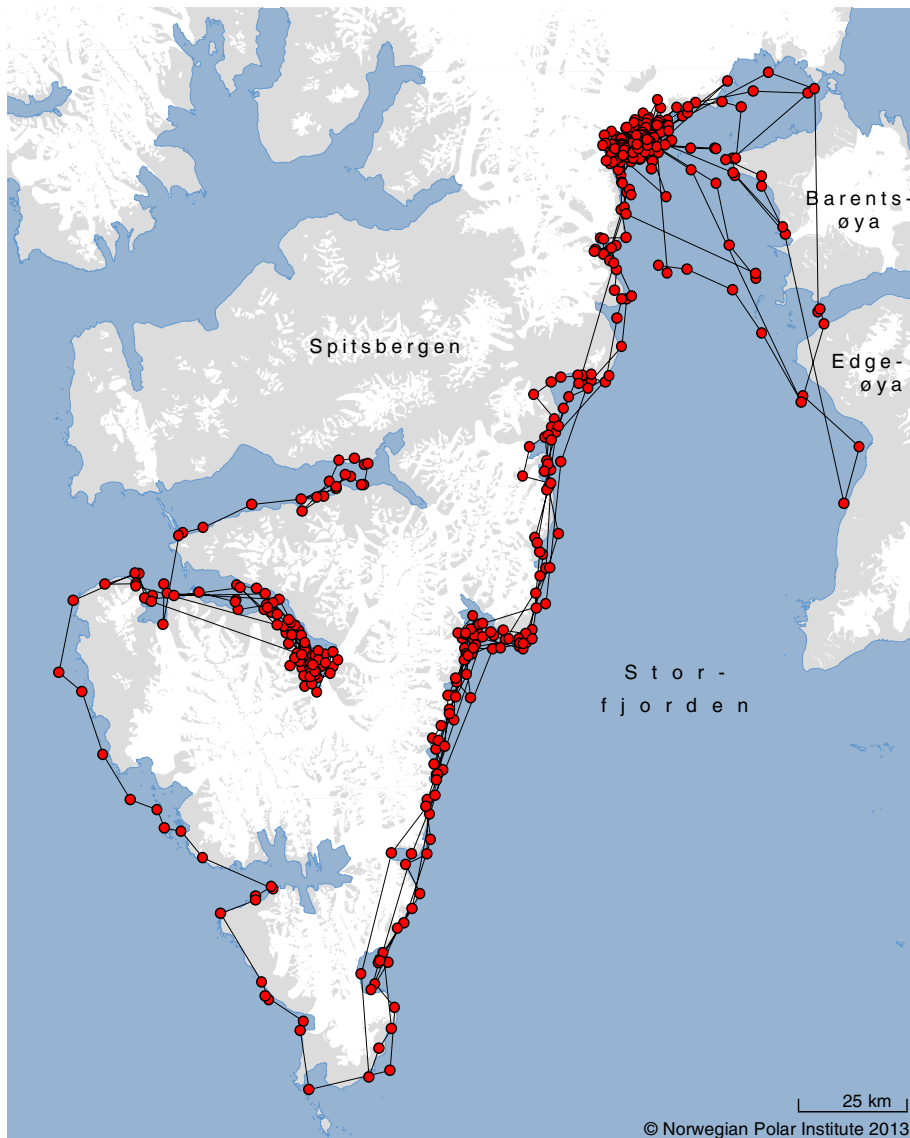


Fig. 6. Tracking results from 3 white whales caught in Van Mijenfjorden in the summer of 1997 showing whale species affiliation with glacier fronts. (Data from Lydersen et al., 2001).

at the sea surface and along the beach, probably killed by osmotic shock caused by the freshwater entering the sea (Mehlum, 1984).

Strøm et al. (2012) conducted aerial surveys around Svalbard in August and September 2010 and 2011 to document post-breeding distribution of seabirds. During these surveys large flocks of fulmars and kittiwakes (Fig. 7), but also aggregations of glaucous gulls and ivory gulls were observed feeding at many glacier fronts. The aggregations were especially evident in front of the large tidewater glaciers in east Svalbard, such as the Negribreen, Hochstetterbreen and Hinlopenbreen on the east coast of Spitsbergen, Stonebreen on Barentsøya and Austfonna on Nordaustlandet. The birds were concentrated at the face of the glaciers, in the immediate vicinity of the sub-surface meltwater river outlets, and numbered from several hundred up to several thousand individuals (Fig. 7). At Austfonna, concentrations of more than 200 ivory gulls and about 200 glaucous gulls were found in the same area where Mehlum (1984) reported large groups of kittiwakes and fulmars some decades ago. With an estimated breeding population of 1000–1500 pairs of ivory gull in Svalbard (Gilchrist et al., 2008), as much as 5–10% of the breeding population was likely feeding in front of the Austfonna glacier at the time of the survey. In an ongoing study

of ivory gulls in relation to changing sea ice conditions, satellite tagged birds breeding on Barentsøya frequently used the Austfonna glacier front as a foraging area; this appears to be an annual event (Strøm et al., unpublished data, Fig. 8).

In addition to being important as feeding areas, the glacier pieces that calve off the glacier fronts are used as resting platforms for many of the feeding seabirds. Kittiwakes are rarely seen resting on the water, they prefer to rest on ice pieces or on shore in the vicinity of tidewater glaciers. The reason for this resting out of water could be related to reducing predation risks, but it has been shown that kittiwakes have a much higher resting metabolic rate when resting on water compared to in air (40% higher when water and air temperatures both were 12.5 °C, (Humphreys et al., 2007)), so energetic savings might also be an issue in their preference for resting on ice or land. Similar findings have been documented for alcids, cormorants and penguins, but not for diving ducks (Richman and Lovvorn, 2011). Thus, having glacier ice pieces to rest on reduces heat loss and since these resting platforms are located where an abundance of food is found there are minimal transport costs involved in moving between key foraging sites and the places where the bird can rest and process the ingested food.

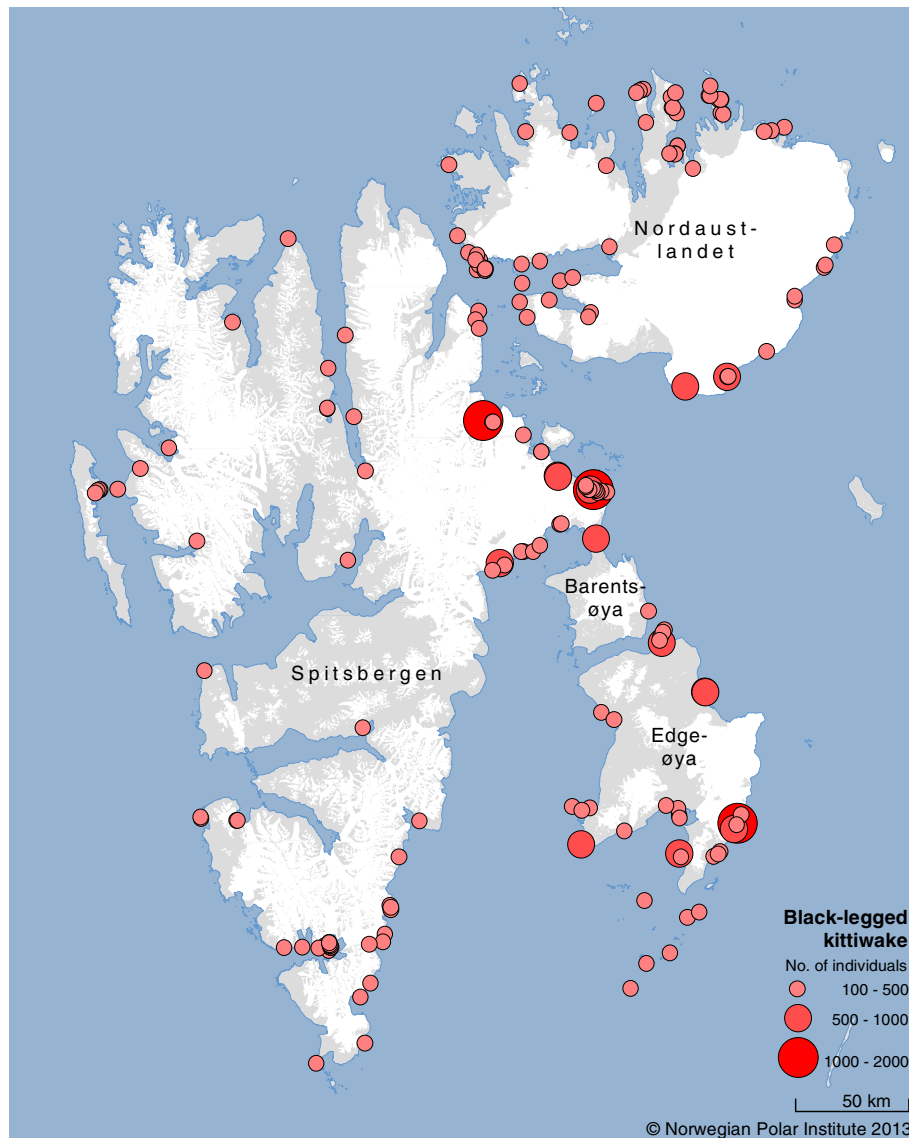


Fig. 7. Results from an aerial survey of kittiwakes conducted in Svalbard in August and September 2010 and 2011 to document their post-breeding distribution. Largest concentrations are found close to various glacier fronts such as the Negribreen, Hochstetterbreen and Hinlopenbreen on the east coast of Spitsbergen, Stonebreen on Barentsøya and Austfonna on Nordaustlandet (Strøm et al. unpublished data).

3. Glaciers in Svalbard

The Svalbard Archipelago has a total land area of $\sim 60,000 \text{ km}^2$ of which $\sim 35,000 \text{ km}^2$ (60%) is glaciated at present (Hagen et al., 1993; König et al., in press). In total there are more than 1100 glaciers larger than 1 km^2 on Svalbard (König et al., in press), and of these, 163 (15%) are tidewater glaciers (Fig. 9). In terms of area, more than 60% of all glacier fronts terminate at the sea (Błaszczuk et al., 2009). This means that a significant portion of surface melt and precipitation in Svalbard is delivered to the ocean at calving glacier fronts.

Positions of tidewater glacier fronts are variable, on both seasonal time scales, during which frontal positions are modulated chiefly by calving rates, and over longer time scales, when geometry of the fronts are influenced by long-term changes in the mass balance of the glaciers. Using satellite imagery acquired in the period 2000–2006, Błaszczuk et al. (2009) estimated the total length of calving ice-cliffs around Svalbard to be approximately 860 km. This is a shorter total length than the 1030 km found by Dowdeswell (1989), which was based on older data (i.e. Norwegian Polar Institute maps made during the period 1936–1990). The difference between the two estimates likely reflects

changes in the seaward margins of tidewater glaciers during the intervening years, although the actual lengths and hence the amount of change depends on geometry of the calving front. Retreat of glaciers with a convex front, such as Bråsvellbreen in Nordaustlandet, will result in a decrease in the length of the calving front, whereas retreat of the glaciers in the innermost part of the fjord Hornsund has increased due to the constriction of the calving fronts when the glaciers were at their greatest extent. However, basin geometry is not the only factor influencing the calving front extent; some glaciers have retreated out of the fjords entirely and now terminate on land. Błaszczuk et al. (2009) compared their inventory to that of Hagen et al. (1993) and found that 14 glaciers retreated from the sea to land over a 30–40 year period in Svalbard.

A complicating factor for studying tidal glacier fronts in Svalbard in the context of climate change is its many surge-type glaciers (Hamilton and Dowdeswell, 1996; Jiskoot et al., 2000; Murray et al., 2003). Surging glaciers alternate long periods of relative quiescence with periods of dynamic advance (lasting 1–3 years). During advances glacier speeds increase dramatically and the glacier front moves forward, often by a kilometre or more. Estimates of the number of surging glaciers vary a lot (ranging from 13 to 90%, see Jiskoot et al., 2000), but

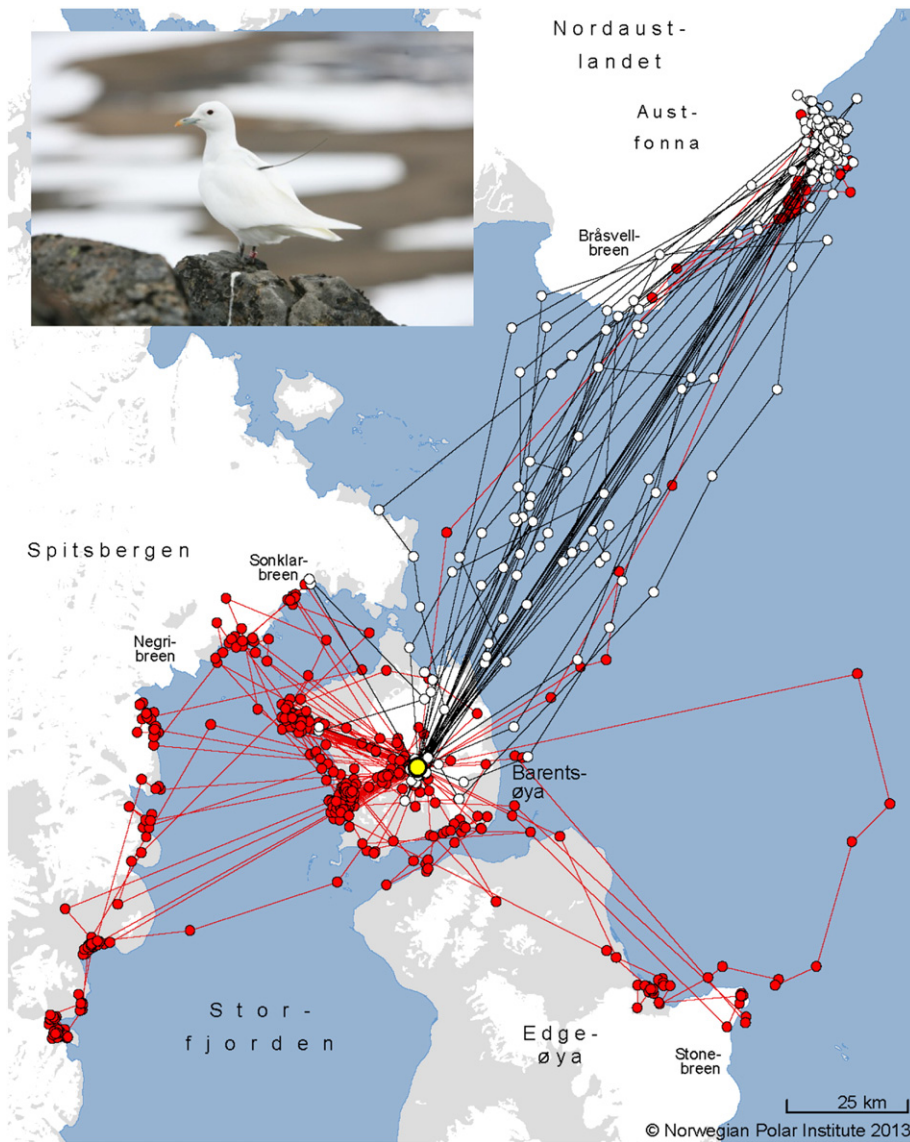


Fig. 8. Tracking results of ivory gulls breeding on Barentsøya conducted in 2011 show that these birds frequently use the Austfonna glacier front as a foraging area (Strøm et al. unpublished data).

regardless of the precise number, it is not surprising that [Błaszczuk et al. \(2009\)](#) found 11 formerly land-based glaciers now terminating in the sea. While surging undoubtedly complicates the assessment of the availability and marine system influences tidal glaciers, it is clear that glaciers have been thinning and retreating in Svalbard for some time ([Kohler et al., 2007](#)). On the long time-scale, Svalbard glaciers retreated following the end of the Ice Age and the collapse of the Fennoscandian ice sheet around 12,000 BP. Climate during the Holocene is thought to have been quite stable overall, but with a few relatively warm periods, the Holocene Thermal Maximum (HTM) at the beginning of the Holocene ([Miller et al., 2010](#)), and two more recent warming during the past decades.

During the HTM, Svalbard glaciers were likely reduced in extent. [Oerlemans et al. \(2011\)](#) proposed that at least part of Hansbreen, a medium-sized tidewater glacier in southern Spitsbergen, disappeared during the early Holocene. [Svendsen and Mangerud \(1997\)](#) concluded that there were no glaciers in the valley Linnédalen, on the western coast of Spitsbergen during the HTM, though [Hald et al. \(2004\)](#) concluded that central Spitsbergen was never completely deglaciated during the Holocene, based on evidence from sediment cores. Modern patterns of ice loss indicate that the highest mass losses are currently occurring

in the western and southern parts of Svalbard (e.g. [Moholdt et al., 2010](#); [Nuth et al., 2010](#)). During the HTM these parts of Svalbard likely experienced dramatic retreat and possibly even loss of small, low-lying glaciers. However, while larger glaciers, which tend to be tidewater types, may have also retreated during the HTM, they likely did not disappear completely. Northern and eastern parts of Svalbard were likely least affected during the HTM similar to today; modern retreat rates are much less in these areas compared to southern parts of Svalbard ([Moholdt et al., 2010](#)).

Little is known about glacial history for the period between the HTM and the time of early exploration of Svalbard. Temperature proxy records from Svalbard ice cores suggest a gradual cooling from about 800 AD, culminating in the so-called Little Ice Age (LIA). The coldest period during the LIA appears to be sometime in the mid-1850s. The most recent period warming began at the end of the LIA, during the second half of the 1800s. Svalbard glaciers attained their maximum recent extents following the peak of the LIA, more or less in the first two decades of the 1900s, after which time they began to retreat (e.g. [Plassen et al., 2004](#)).

The post-LIA warming featured a marked temperature increase in the 1920s and -30s, followed by some cooling in the 1960s and then a steady warming over the last four decades, similar to what has been



Fig. 9. Map of Svalbard where all glacier covered areas ($\sim 35,000 \text{ km}^2$) are shown in white. All fronts that calve into the ocean are coloured in red. Names of glaciers mentioned in the text are also shown.

seen across the Arctic (Overland et al., 2004). The most significant trend in the recent warming has been for the summer months; since summer temperature has the strongest influence on Svalbard glacier mass balance (LeFauconnier et al., 1999), this summer warming has led to increasing rates of mass loss (Kohler et al., 2007).

The current overall mass balance for Svalbard glaciers is negative (Dowdeswell et al., 1997; Hagen et al., 2003a,b; Moholdt et al., 2010; Nuth et al., 2010; Wouters et al., 2008), although the estimated rates of decline vary depending on the method used: current estimates range from -5 to $-15 \text{ km}^3 \text{ yr}^{-1}$, which are equivalent to a drop in the average surface elevation of -0.14 to -0.40 m per year. Careful geodetic analyses have shown that the rate of ice loss has accelerated in the recent decades (Kohler et al., 2007), a finding that is consistent with a strong warming trend in summer temperatures on Svalbard (Nordli and Kohler, 2004), as well mass balance observations made elsewhere around the globe (Kaser et al., 2006; Zemp et al., 2009). Further warming of the Arctic is predicted in the context of global climate warming and we can expect continuing retreat of Svalbard glaciers, and concomitant declines in the number of tidewater calving glaciers and the total length of calving fronts around the Svalbard Archipelago.

4. Hydrology and ocean dynamics of glacial fjords

Circulation in fjords ending at a glacier front is strongly influenced by the way in which the glacier's drainage system interfaces with the ocean. Glacial outputs can result in some characteristic differences from "normal" fjords where surface drainage enters via rivers. Glaciers contribute freshwater in the form of: i) direct surface runoff at the

front (a very minor source, representing surface melting of ice at the glacier front); ii) subaqueous melting at the glacier face, where the ice is in contact with relatively warm fjord water; and iii) most significantly, through en- or subglacial drainage (from within or beneath the glacier, respectively). Glaciers that meet the sea typically drain relatively large areas and summer melt in combination with rain can lead to large discharges of freshwater at the glacier front. While this freshwater can flow out from the glacier at intermediate depths, it has likely travelled a significant distance through the subglacial drainage system.

Glacier drainage begins once there is sufficient surface melt to warm the glacier snowpack to the melting point, allowing water to make its way downward through the englacial drainage network and ultimately to the subglacial drainage network. Subglacial drainage can vary between two qualitatively distinct flow systems, a channelized or "fast" system, typical for the summer season and a distributed or "slow" system, which is widespread during the winter months (Fountain and Walder, 1998). In the latter case, the subglacial drainage system is distributed over a wide area of the bed, with a large number of cavities connected haphazardly. As surface water enters this slow system, overpressure occurs, leading to lift-up and entrainment of basal sediments. As a result, the first water to come out of the glacier at the beginning of the melt season tends to be especially sediment-laden (e.g. Hodgkins et al., 1999).

Because there is an inverse relation between steady-state discharge and the pressure gradient required to move the discharge through basal ice tunnels as the melt season progresses, those parts of the drainage system transporting more water have lower pressures. This tends to concentrate discharges into ever-larger channels. Gradually, the

subglacial drainage network undergoes a transition from a distributed system into a discretely channelized system, comprising an arborescent network of distinct tunnels (the fast system) that connects to water input points. An important facet of this summertime transition from a slow to a fast drainage system is that the volume of flow in the individual drainage channels can change throughout the melt season, and thus plumes can potentially change location at the glacier front during the course of a summer. Furthermore, a more highly channelized system has less contact with the glacier bed, and therefore less sediment will be entrained. Sudden water influxes can over-pressurize the fast flow system, establishing temporary connections to the slow system and further sediment entrainment, but in general sediment levels decline through the melt season. Finally, as the drainage system evolves, it becomes progressively more efficient, and thus surface water influxes tend to come out more rapidly at the glacier front.

Towards the glacier front, local pressure geometry can force subglacial waters upward, creating outflows at intermediate depths. In fjords where glacial water enters the ocean at or near the ocean surface, outflow dynamics will be similar to those seen at river mouths. However, the norm is for glacier water to discharge below the surface; the low relative density of these waters – in cases where the sediment load is not exceptionally high – forces them to rise rapidly towards the surface, thus entraining large volumes of ambient fjord water. The outflow velocity will force additional entrainment, and it is the sum of buoyancy and momentum-driven entrainment that determines the overall dilution of the plume (Mugford and Dowdeswell, 2011). If a fjord is weakly stratified, as is usually the case in the early summer season in the Arctic, the meltwater plumes can protrude to the surface. Once the meltwater plume reaches the surface it tends to flow towards the mouth of the fjord, further entraining subsurface water at a rate depending on its relative density and flow velocity. Later in the summer season, if the ambient fjord water becomes strongly stratified and the glacier discharge rate decreases, the plume may entrain enough ambient water to become neutrally buoyant at some intermediate depth, impeding ascension and protrusion at the surface.

Subsurface plumes have two distinct effects on the local environment. Firstly, any organisms that are entrained in the rising plume will be brought towards the surface where they will be more easily accessible for surface feeding animals (Fig. 10). If plume salinity is sufficiently low, some marine zooplankton species may be stunned or even killed from osmotic shock if exposure occurs rapidly and lasts for some period of time (Zajaczkowski and Legeżyńska, 2001). Secondly, as the plume rises it will entrain large volumes of ambient water, tens to hundreds of times the original discharge volume. This water will be drawn from all depths that the plume passes through. This entrainment ensures a continuous resupply of intermediate depth waters, including zooplankton and nutrients, to the glacier front area. These nutrients can support post-bloom primary production. However, this production usually occurs some distance away from the actual glacier front, where a significant proportion of the outflow sediments has settled out (Etherington et al., 2007).

There are also other factors that are important for the circulation of the system, both near the glacier front and in the fjord as a whole. Winds generally influence surface circulation, and persistent katabatic winds blowing “down” the glacier towards the fjord (Fig. 10) may enhance upwelling effects of the glacial meltwater discharge. Wind-driven vertical mixing influences stratification and thus affects both the primary productivity and the circulation dynamics driven by horizontal density gradients. Density differences between fjord water and coastal and off-shelf water masses, on seasonal and inter-annual time scales, will lead to both intermittent and large scale exchange events. Tidal currents drive local mixing and to some extent net exchange of water between the different fjord basins and between the fjord and the coast. Fjord geometry also strongly influences circulation; the width of a fjord determines the effect of the earth’s rotation on circulation. The presence (location and depth) of sills will limit deep

exchange in the interior basins, while at the same time introducing enhanced mixing at the sill depth. For an overview of typical effects of these main forcing mechanisms on an Arctic glacial fjord, see Svendsen et al. (2002).

Circulation, stratification and water mass properties vary substantially through the annual cycle (Cottier et al., 2010). In winter there is little freshwater input, the water column is cooled by heat loss through the surface, and where sea ice is formed there will be release of brine (salt-enriched water) into the underlying water column. Altogether this results in deep mixing; in many high-latitude fjords convection reaches all the way to the sea floor. In spring increased freshwater input from land, and solar heating of the surface layer increase stratification significantly. This development continues through summer, modulated by wind mixing events and exchange with the outer coastal water masses. In autumn, the freshwater flux ceases, and the surface begins cooling again, decreasing the upper-column stratification.

5. Sedimentology in glacial fjords

Tidewater glaciers terminate directly in the sea and thus have significant influence on sea water properties, circulation and sedimentation (Görlich et al., 1987; Powel, 1990; Syvitski, 1989). The contact between sediment- and mineral-laden glacier melt-water and seawater leads to strong environmental gradients at tidewater glacier fronts.

Climate warming during the last 100 years has caused the retreat of many of Svalbard’s glaciers (see above), possibly leading to an increase in sediment supply and accumulation (Zajaczkowski et al., 2004). While glacier-derived material is comprised mostly of minerals, Hood et al. (2009) suggest that glacier outflows can also provide a quantitatively significant amount of fossil/subfossil bioavailable carbon since glaciers may be eroding ancient peatlands; during the warmer parts of Holocene many of Svalbard’s glaciers retreated onto land and proglacial areas were covered by tundra. Finally, Stubbins et al. (2012) have shown that aerosols derived from fossil fuel burning are conserved in glaciers and exported in glacier outflows.

Field investigations with water-column monitoring and sediment traps have revealed significant spatial differences in suspension loads and sedimentation rates, varying according to the distance from glacier fronts. The most intensive settling, which controls mud deposition (tens of centimetres per year) occurs from melt-water plumes when they are still near the glacier front (Elverhoi et al., 1983; Görlich et al., 1987). The largest settling results from turbulent flow of dense suspension (up to 1000 g m^{-3}) and flocculation of clay minerals, occurring during the mixing of fresh and sea water (Zajaczkowski, 2008). Seasonal sedimentation rates vary greatly since most of the terrigenous matter carried by glacial outflows is delivered during the relatively short summer season. At increasing distances from the glacier front the glacier suspension load, and thus sedimentation rates, falls resulting in significant decreases of sediment accumulation (Görlich et al., 1987).

Western Spitsbergen glaciers are highly susceptible to climatological and hydrological fluctuations, due to their proximity to the West Spitsbergen Current, which transports warm Atlantic water northward, as well as the colder East Spitsbergen Current, flowing from the Barents Sea. Past changes in the relative inflows of Atlantic and Arctic waters has resulted in significant variability of environmental condition along the western Spitsbergen shelf (Majewski et al., 2009). Furthermore, recent warming has led to increases in melt-water fluxes from Svalbard’s glaciers, influencing fjord hydrology, sea ice conditions and local biota. Decreasing amounts of land-fast ice in numerous west Spitsbergen fjords, and a concurrent increase in turbid water fluxes, have many implications including timing of the productive season, earlier appearance of mesozooplanktonic organisms, increases in the dissolved organic carbon pool in the water and decreases in organic fluxes to the sediment in the spring (Zajaczkowski et al., 2010).

Near glacier fronts, poor light transmission through the turbid glacier water disrupts primary production, lowering the organic flux;

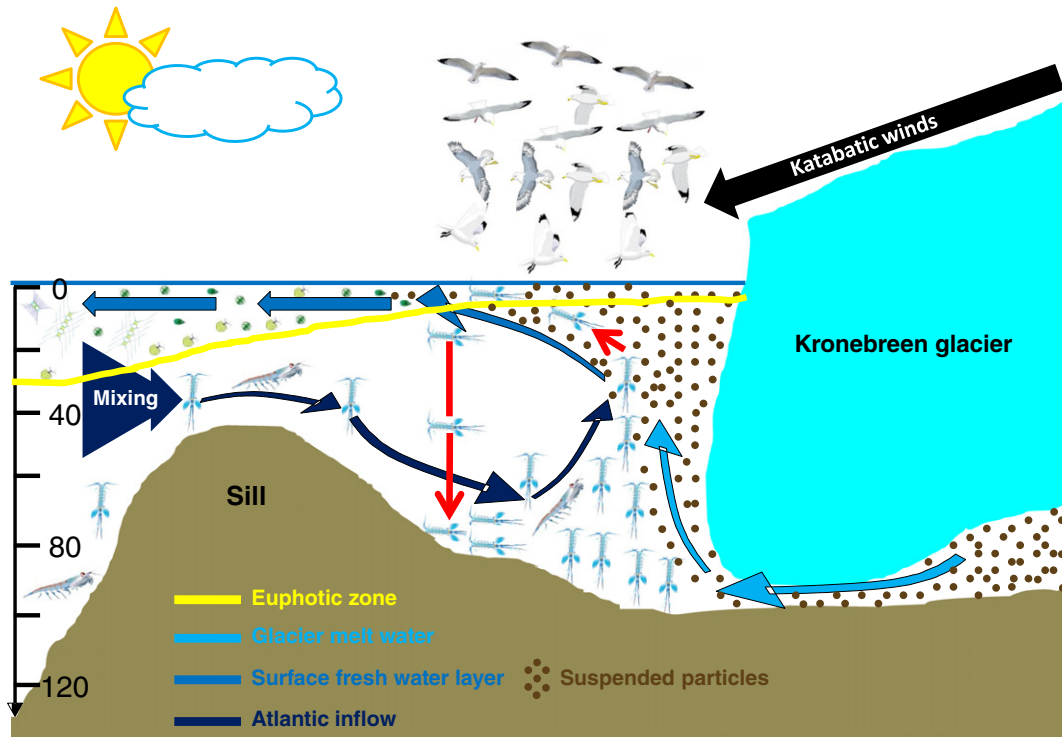


Fig. 10. Physical forcing of biological processes in the inner part of Kongsfjorden during summer. Kongsfjorden is lined by tidewater glaciers (e.g. Kronebreen) that discharge large amounts of freshwater (light blue arrows) and sediments (brown dots) into its inner part. The inner part is separated from the deeper, outer part by a shallow sill. The prevailing down-fjord katabatic winds (black arrow) favour an outflow of surface freshwater (“medium” blue arrows) along the northern shore which is compensated by the inflow of deeper, saline shelf waters (dark blue arrows) along the southern shore of Kongsfjorden. This estuarine circulation is the characterising hydrographical feature during summer. Primary productivity (depicted by different phytoplankton taxa) and depth of the euphotic zone (yellow line) are strongly reduced in the inner part due to turbidity resulting from glacier derived sediment discharge and increase with distance from the glaciers. Advected zooplankton is either stunned or killed by osmotic shock (red arrows) upon entrainment into glacier meltwater and serve as an important food source for benthic communities and sea birds foraging near the glacier front.

this, combined with high rates of inorganic deposition (reaching up to $200 \text{ g m}^{-2} \text{ d}^{-1}$), leads to low organic content in the sediment near glacier fronts (Fig. 11). These proximal sediments therefore provide poor condition for supporting settled benthic organisms, due to the very low levels of biologically active matter (Włodarska-Kowalczyk et al., 2005).

Seasonal cycles in the suspension load and sedimentation lead to a time lag between peaks in organic sedimentation and peaks in mineral sedimentation. Mineral sedimentation rates are at a maximum in the summer–autumn season, while organic productivity peaks occur earlier on, yielding dark and light laminations in the mud near glacier fronts. Control of the time lag is exerted by settling of primary production products from the euphotic zone, burial of organic matter and trapping of nutrients in sediment (Görlich et al., 1987).

The distribution of turbid surface water, and therefore sedimentation patterns, vary across the various Svalbard fjords, likely in association with the magnitude of activity and erosion of the glaciers and the hydrology of the fjords. For example, two relatively well-studied fjord systems, Kongsfjorden and Hornsund, have quite different hydrological/sedimentological regimes. Kongsfjorden is connected to the outer shelf and broader ocean through a submarine trough. Thus, the inflow of Atlantic water can be limited by stratification of the water column, which decreases in midsummer (Svendsen et al., 2002). Hornsund differs from most of the other western Spitsbergen shelf sites by being more influenced by Arctic water. Shelf water mixes slowly with Atlantic water, forming strong density gradients along the SW shelf of Spitsbergen (Saloranta and Svendsen, 2001), resulting in decreased warm water inflow into Hornsund. In addition, the fjord and adjacent shelf receive multiyear pack ice transported from the Barents Sea around Sørkapp. These differences influence fjord hydrology, sediment flux and fjord biota.

6. Plankton and benthos in glacial fjords

6.1. Phytoplankton

Generally, there are two main physical forcing factors affecting fjord ecosystems along the west coast of Svalbard: 1) advection of warmer Atlantic water masses and 2) massive freshwater discharges from glacier run-off during the summer months. This is particularly true for Kongsfjorden since it lacks a sill at its opening allowing a relatively unhindered inflow of Atlantic water and it is surrounded by large tidewater glaciers in its inner parts (Svendsen et al., 2002, Fig. 12). The production and transfer of organic material, as well as plankton species composition, vary along gradients induced by the seasonality of freshwater discharge in conjunction with fluctuations in advective processes, solar radiation, wind patterns, tidal currents and topographical steering (Basedow et al., 2004; Willis et al., 2006).

The pattern of phytoplankton seasonal succession in Kongsfjorden is similar to temperate and boreal marine ecosystems with the main biomass accumulation occurring in spring and a low biomass regenerating system predominating during summer. Neritic diatom species (in particular *Chaetoceros socialis* and *Thalassiosira nordenskiöldii*) and the haptophyte *Phaeocystis pouchetii* dominate the phytoplankton assemblage in spring and are replaced by a regenerating community dominated by smaller flagellates, dinoflagellates and the chrysophyte *Dinobryon balticum* in summer (Eilertsen et al., 1989; Hasle and Heimdal, 1998; Keck et al., 1999). Protozoan (ciliates and heterotrophic/mixotrophic dinoflagellates) biomass peaks in conjunction with the phytoplankton spring bloom and is controlled by copepod grazing during the summer months, while food availability constrains population size in winter (Seuthe et al., 2011). In winter, a heterotrophic system dominated by bacteria, pico- and nanoflagellates is sustained by elevated levels of

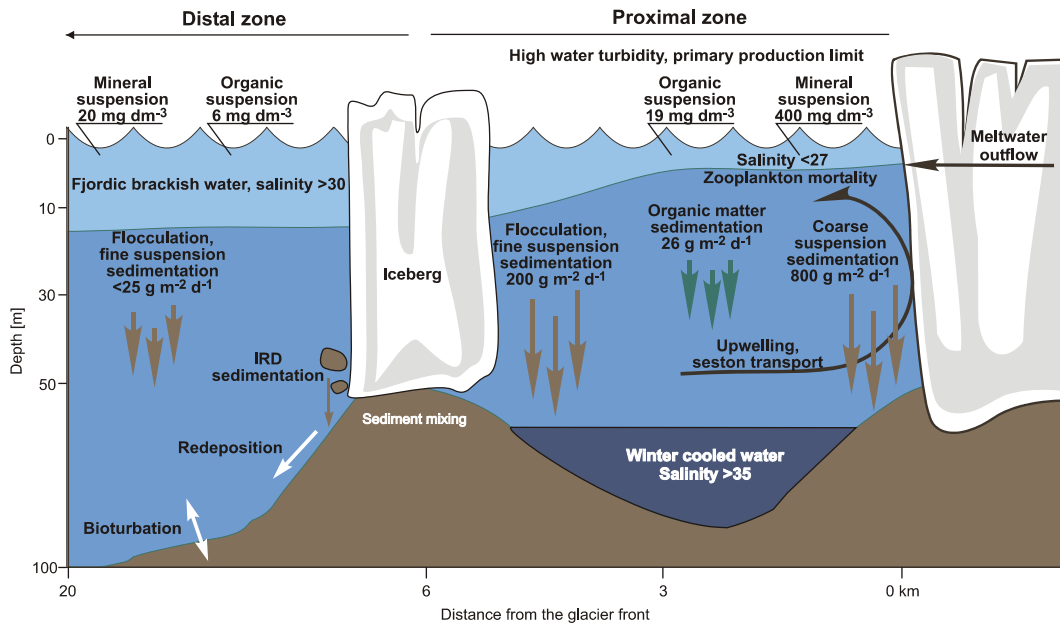


Fig. 11. Model of sediment supply and sedimentation in the glacial bay of Kongsfjorden. Data are based on Svendsen et al. (2002) and measurements were done in July 2003 (Zajaczkowski, M. unpublished results).

dissolved organic matter (Iversen and Seuthe, 2011). In summer, diatom biomass is low and often restricted to the subsurface layers (Piwosz et al., 2009). Motile species such as dinoflagellates that are capable of migrating between the sunlit surface layer and the nutricline are favoured during the strongly stratified summer months (Hop et al., 2002; Piquet et al., 2010). Differences in the susceptibility to coagulation with suspended particles and subsequent sedimentation between the colonial *D. balticum* and solitary flagellates could explain the low abundances of the former and persistence of the latter in the inner part of Kongsfjorden (Keck et al., 1999). The ability of *D. balticum* to supplement autotrophy by ingesting particles (McKenrie et al., 1995) could explain its dominance in the outer parts of the fjord during the

nutrient limited summer months. On the other hand, high concentrations of fine mineral particles might also directly deter this filter-feeding species in the inner parts of the fjord.

While the spring bloom starts well before the onset of the melt season and is thus not influenced by meltwater discharge, phytoplankton productivity is strongly reduced in the inner fjord basin due to light limitation resulting from glacier-derived sediment discharge during summer. This is reflected in the steep decrease in phytoplankton standing stocks (Piwosz et al., 2009) and chlorophyll concentrations (Fig. 13e) in the inner parts of the tidal glacier fjords. The summer phytoplankton community has to cope with strong gradients in light availability that can fluctuate rapidly in time and space and strongly depend on external

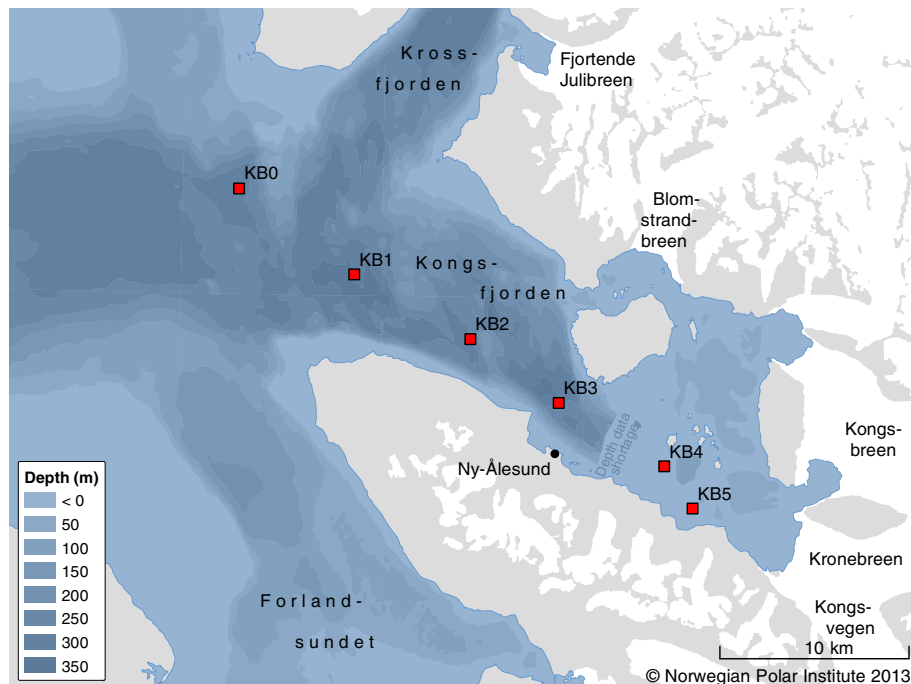


Fig. 12. Bathymetry of Kongsfjorden, Svalbard. Adapted from Svendsen et al. (2002). Also shows location of transect stations where data is collected for Fig. 13.

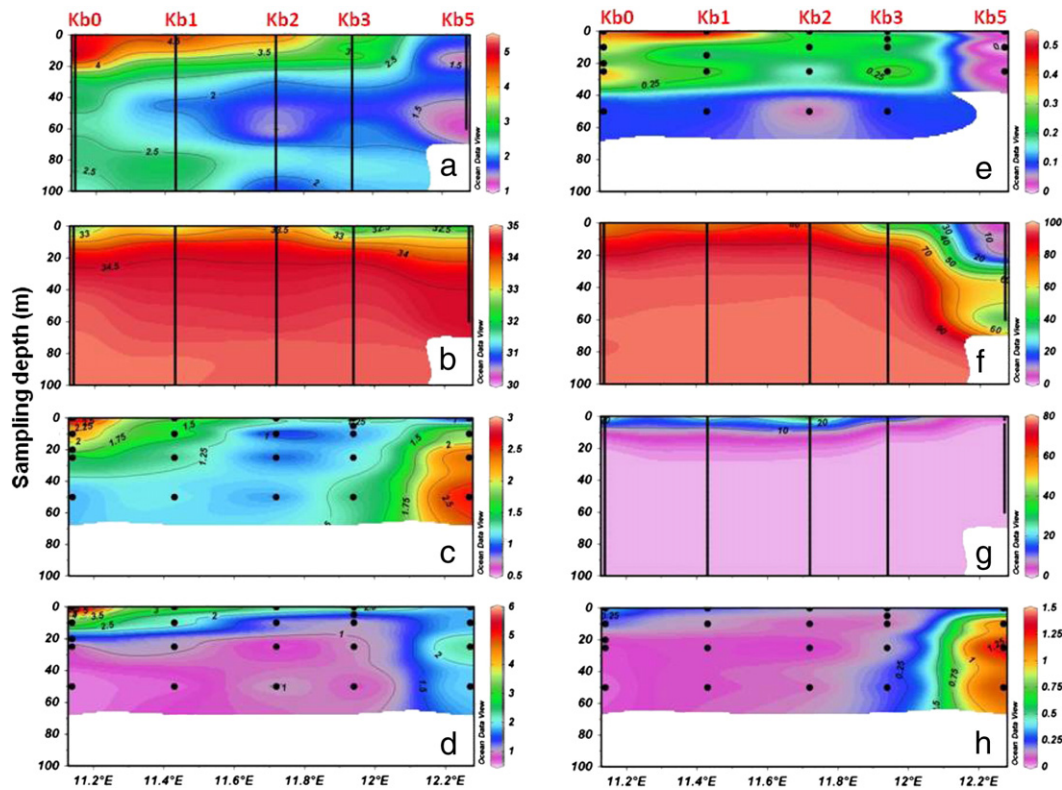


Fig. 13. Oceanographic transect from the inner basin (station Kb5) to the mouth (station Kb0) of Kongsfjorden from 15 July 2011 including a) temperature in °C, b) salinity in PSU, c) silicate concentration in $\mu\text{mol l}^{-1}$, d) dissolved inorganic nitrogen (DIN) in $\mu\text{mol l}^{-1}$ corresponding to the sum of nitrite, nitrate and ammonium, e) chlorophyll *a* concentration in $\mu\text{g l}^{-1}$, f) transmissometer derived beam transmission in %, g) % surface photosynthetically active radiation (PAR) and, h) nitrite concentration in $\mu\text{mol l}^{-1}$. (Assmy et al. unpublished data).

forcing factors. In a study from Glacier Bay, Alaska has shown high and sustained chlorophyll *a* levels throughout the summer and in the fall over the bay's shallow entrance sill due to a combination of two processes: 1) enhanced vertical mixing and nutrient renewal caused by strong tidal currents and 2) freshwater stratification in conjunction with high light levels (Etherington et al., 2007). This is in contrast to the chlorophyll spring peak followed by lower levels throughout the summer in Kongsfjorden (Fig. 13). In Kongsfjorden, increased mixing and associated entrainment of nutrients into the shallow surface layer are likely to have little effect on phytoplankton productivity close to the sill due to its proximity to the tidewater glaciers and resulting light limitation caused by the high sediment loads (Fig. 13f). However, the entrained nutrients can have a positive effect on phytoplankton productivity once they are advected further out into the outer parts of Kongsfjorden where light becomes available. Residual concentrations of silicate and dissolved inorganic nitrogen (Fig. 13c and d) in the summer stratified surface layer (Fig. 13a and b) suggest fresh water discharge at the glacier front, or lateral advection from other fronts in Kongsfjorden, as possible sources of nutrients during summer.

An additional source of nitrite and nitrate during summer could be due to shallow nitrification by nitrifying bacteria. Nitrifying bacteria oxidize ammonium (NH_4^+) to nitrite (NO_2^-) and NO_2^- subsequently to nitrate (NO_3^-). In the ocean this process is usually most pronounced at the bottom of the euphotic zone due to inhibition of nitrification by light and because phytoplankton outcompetes nitrifying bacteria for ammonium uptake in the euphotic zone (Ward, 2008). However, high sediment loads in the inner basin of Kongsfjorden cause aphotic conditions at shallow depths (Fig. 13f and g), which prevents phytoplankton growth (Fig. 13e) and could favour nitrifying bacteria. Both elevated ($>1 \mu\text{M}$) nitrite concentrations (Fig. 13h) and identification of nitrifying bacteria (*Nitrosomas* and *Nitrospira*) in Kongsfjorden (Piquet et al., 2010) suggest that this process is relevant in providing oxidized forms of nitrogen to the surface layer during summer.

Most ice algal biomass is restricted to the lowermost 20 cm of the ice. Ice algae start to accumulate in late March as far north as Rijpfjord (80°N), but usually bloom between late April and mid June (Hop et al., 2002; Leu et al., 2011). However, due to high levels of interannual variation in the position of the ice edge and the timing of ice melt and break-up (Svendsen et al., 2002), the timing and growth conditions for ice algae can vary considerably from year to year and between different locations (Leu et al., 2011; Søreide et al., 2010). Diatoms dominate the sympagic community, particularly species of the pennate genera *Nitzschia* and *Navicula*. Although of lesser importance vegetative cells and cysts of dinoflagellates have also been observed in sea ice. As a general rule, species diversity declines with distance to the bottom of ice cores. Ice algae growth is sensitive to snow cover, as attenuation of light is high in snow. Particulate material frozen into the ice near glacier fronts might similarly increase light attenuation and create sub-optimal conditions for ice algal growth.

6.2. Zooplankton

Generally, fjords have a consistent pattern of zooplankton occurrence with large, oceanic forms dominating in the outer parts and smaller, neritic, brackish species in the inner basins (Matthews and Heimdal, 1980). This pattern is present in glaciated fjords as well. Svalbard's glacial fjords have a high frequency of occurrence and density of small copepods such as *Pseudocalanus* and *Oithona similis* species (up to 60% of all zooplankton density in summer) in their inner parts and larger copepods such as *Calanus* spp. in the outer fjords and shelf waters (Walkusz et al., 2009; Table 1). Small copepods are able to complete their life cycles in shallow coastal waters and are typical inhabitants of the inner parts of glacial fjords.

Estuarine circulation, typical of glacial fjords during summer, transports various marine zooplankton species with near-bottom currents towards the glacier front. Here stenohaline oceanic species might be

Table 1

Zooplankton – selected species in the glacial bays of Svalbard (compilation from Weslawski et al., 1991, 2000; Walkusz et al., 2009).

Species	Description	Density (n/100 m ³) in glacial bay	Density n/100 m ³ in outer fjord part
<i>Thysanoessa inermis</i> , <i>Thysanoessa raschii</i>	Euphausiids, often in swarms, concentrated and killed in glacial bays	100–200	1–50
<i>Pseudocalanus minutus</i> , <i>Oithona similis</i>	Small copepods, micrograzer, natural inhabitant of glacial bays	400,000	2200
<i>Themisto libellula</i> , <i>Themisto abyssorum</i>	Large pelagic amphipods, carnivorous, often in swarms, concentrated & killed in glacial bays	200–400	10–100
<i>Calanus finmarchicus</i> , <i>Calanus glacialis</i>	Large copepods, grazers, concentrated and killed in glacial bays	18,300	11,800
<i>Limacina helicina</i>	Winged snail, herbivorous	400–600	20–100

found – like euphausiids, chaetognaths, sea snails, pelagic amphipods and large copepods. Those species are not part of the local fauna and most of them cannot cope with the high turbidity and low salinity of the water found here, resulting in the well-documented osmotic shock and sinking of dead plankton in areas close to glacier fronts (Hartley and Fisher, 1936; Weslawski and Legeżyńska, 1998). In Kongsfjorden, the concentration of dead plankton on the sea bed in these areas can reach over 500 individual copepods and over 100 individual euphausiids per m² (Weslawski and Legeżyńska, 1998), which is estimated to constitute about 15% of the summer zooplankton standing stock in this fjord (Zajaczkowski and Legeżyńska, 2001). The outflow of brackish, cold water at the surface causes the larger, better swimmers among the marine zooplankton to escape and dive below this layer, into the inflow of marine water associated with local upwelling. This creates a “death trap” as described by early observers of this phenomenon (Dunbar, 1951; Hartley and Fisher, 1936), where animals are trapped and concentrated in a water layer near the bottom caused by the system of currents, that brings them towards the glacier, killing them if they are swept into the fresher surface waters (Weslawski et al., 2000). The larger zooplankton species such as krill, *Calanus* copepods and *Themisto* species “trapped” in the plum at the glacier front are all very lipid rich (Falk-Petersen et al., 2000, 2009; Scott et al., 1999), and are valuable high energy food (Falk-Petersen et al., 1990) for fish, seabirds and mammals (Dahl et al., 2000, 2003; Wold et al., 2011) that are found foraging at the tidal glacier fronts.

6.3. Zoobenthos

Tidewater glaciers add specific stress factors to the environment of the sea bed in fjords where they occur. These stressors include increased sedimentation, iceberg scouring and often very low water temperatures associated with high salinity (i.e. the presence of winter-cooled water). Mechanical disturbance of the sea bed via ice scouring inhibits the development of long-lived sessile organisms, and promotes small, active nektobenthic or mobile species (Table 2). The pattern of zoobenthos occurrence in glacial bays resembles the pattern known from polluted sediments (Pearson–Rosenberg model; Włodarska-Kowalczyk and Pearson, 2004). However, there are also factors that are beneficial for some animals living in the sea bed near glacier fronts, such as the constant and abundant supply of sinking organic matter in the form of dead plankton, which ended up in turbid surface waters (see above). This creates good living conditions for specialized carnivore/necrophage lysianasoid amphipods that feed on dead copepods (Zajaczkowski and Legeżyńska, 2001). Another advantage is the stability of temperature and salinity, in the deep, isolated basins that are sometimes found in the inner parts of glacial fjords (see Fig. 11) that sometimes change less than 1 °C and 1 PSU over the course of tens of years (Kędra et al.,

2010; Weslawski et al., 2010). The presence of such water masses provides good conditions for cold water, marine species of arctic origin. Some cold water “relicts” are known to survive in the inner fjord basins of mainland Norway (Brattegard, 1980) and in glacial bays within Svalbard (Włodarska-Kowalczyk et al., 1998). One such species is the bryozoan *Alcyonidium disciformae*, which is the only sessile, colonial species that is typical for glacial fjords (Table 2). This circular, o-ring-shaped species is known to withstand heavy sedimentation, provided that there is enough sea bottom current to allow it to turn upside down and shake the sediment off the colony intermittently (Kuklinski and Porter, 2004).

7. Fishes in glacial fjords

Very little information exists in the primary literature on fish ecology or distribution in the fjords of Svalbard. A notable exception is a study by Falk-Petersen et al. (1986) on polar cod (*Boreogadus saida*) in the coastal waters of Spitsbergen. In this study Falk-Petersen et al. found high concentrations of polar cod in many of the fjords. These authors reported a marked size/age versus depth segregation in the area, with smaller and younger individuals occurring in shallower waters and older, larger individuals occurring in deeper waters often close to the bottom. Additionally, Renaud et al. (2012) have studied the diet of polar cod from glacial fjords. Because of the paucity of information on Svalbard's fish fauna in glacial fjords, dietary information from seabirds and marine mammals occupying these areas are provided below in an attempt to provide some insight into fish community composition. The degree to which this reflects the real composition of the fish community is uncertain, since many predators are selective with regard to what they choose to eat, but these data are likely to be somewhat representative.

Polar cod has been shown to be the most important fish species in the diet of various seal species collected at several locations in the fjords of Svalbard (Gjertz and Lydersen, 1986; Hjelset et al., 1999; Labansen et al., 2007; Lydersen et al., 1989; Weslawski et al., 1994). Many of the ringed seals collected for diet studies have been shot in the fast ice habitat in the inner parts of various glacial fjords. These seals feed primarily on young age classes of polar cod with adult female ringed seals feeding on the smallest fishes (Labansen et al., 2007). Adult females are generally found in the innermost, stable areas of the fjords (see section above) which are closest to the glaciers. They experience a very energy demanding period in the spring during their lactation period and during this time they need to eat at least 2.2 kg of polar cod daily to balance their energy budgets (Lydersen, 1995). The composition of fish in the stomachs of ringed seals varies geographically, but polar cod was always well represented and must be present in large numbers during the period when the fjords are covered with sea ice. Polar cod was also

Table 2

Zoobenthos – abundances and occurrence of typical species in Svalbard glacial bays (compilation from Kędra et al., 2010; Włodarska-Kowalczyk et al., 1998).

Species	Niche	Zoogeogr	Density	Remarks
<i>Onisimus caricus</i> (Amphipoda)	Carnivore, necrophagous, feeds on copepods in summer	Arctic	Up to hundreds per m ²	Mobile, active, may form swarms
<i>Alcyonidium disciformae</i> (Bryozoa)	Filter feeder	Arctic	5–20/m ²	Sessile, able to roll
<i>Yoldiella solidula</i> (Bivalvia)	Surface deposit feeder	Arctic	Above 100/m ²	Discretely motile
<i>Chaetozone</i> sp. (Polychaeta)	Surface deposit feeder	Cosmopolitan	Above 100/m ²	Discretely motile

found to be the most common food item for bearded seals, which were collected from late spring to early fall (May to September), on broken sea ice in front of glaciers (Hjelset et al., 1999). These polar cod were generally large individuals (average 150 mm). Based on data from Falk-Petersen et al. (1986), these fishes likely belong to the demersal fraction of the polar cod population in the fjords. Both this bearded seal study and several other studies (e.g. Lydersen et al., 1989; Weslawski et al., 1994) where seals were collected during summer and autumn, suggest that polar cod is also present during these seasons in large numbers in glacial fjords in Svalbard. A study by Weslawski et al. (1994) attempted to do a resource survey in Kongsfjorden in order to study prey selectivity by the ringed seals. However, these authors found that the seals found prey species that were not accessed using various nets and dredges. The authors did discover that 0-group polar cod was found in seals shot in the outer fjord basin in spring, while older fish were found in seal samples taken in summer from the central and inner fjord basins. An assessment of the diet of white whales in Svalbard, based on fatty acid analyses of the blubber of the whales, also indicated that polar cod is a major food item for this marine mammal species (Dahl et al., 2000).

Young redfish (*Sebastes* sp.) were found in high numbers (3782 specimens, in 53% of 134 collected stomachs) in the stomachs of ringed seals collected in the outer basins of Kongsfjorden by Weslawski et al. (1994). This species was not found in ringed seals from Kongsfjorden in earlier studies by Gjertz and Lydersen (1986, N = 284 ringed seals) or in latter work by Labansen et al. (2007, N = 99 ringed seals), though this latter work did report *Sebastes* sp. being found in some few seal stomachs in Forlandssundet–St. Jonsfjorden. The occurrence of this prey species appears to vary with the presence/absence of Atlantic water masses on the west coast of Spitsbergen. Other typically Atlantic (as opposed to Arctic) fish species have been found in seal stomachs from glacial fjords of Svalbard including Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*), haddock (*Melanogrammus aeglefinus*) and coalfish (*Pollachius virens*) (Hjelset et al., 1999; Labansen et al., 2007; Lydersen et al., 1989; Weslawski et al., 1994). However, they have not been recorded in high numbers in these studies, and similar to the *Sebastes* sp. the occurrence of these other fishes appears to be related to variations in the influx of Atlantic water masses into these glacial fjords.

Several Arctic species of fish have been found in seal stomachs from the glacial fjords of Svalbard. They include mainly benthic species such as American plaice (*Hippoglossoides platessoides*), various sculpins (mainly *Myoxocephalus scorpius*), various seasnails (mainly *Liparis liparis*), eelblennies (mainly *Lumpenus medius* and *Lumpenus lampretaeformis*) and various eelpouts *Lycodes* spp. (Gjertz and Lydersen, 1986; Hjelset et al., 1999; Labansen et al., 2007; Lydersen et al., 1989; Weslawski et al., 1994). In addition, more pelagic fish such as the Arctic char *Salvelinus alpinus* have been consumed by ringed seals in Kongsfjorden (Gjertz and Lydersen, 1986). Weslawski et al.'s (1994) Kongsfjorden resource survey documented four species of benthic fish, three of which have not been found in seal stomachs. They were all small specimens (60–80 mm) of Atlantic poacher (*Agonus decagonus*), sea tadpole (*Careproctus reinhardtii*) and daubed shanny (*Leptoclinius maculatus*).

Hartley and Fisher (1936) collected 227 kittiwakes feeding at the front of the Nordenskiöldbreen glacier on Spitsbergen. They recorded fish in four stomachs out of the 159 stomachs that contained food, but the remains could not be identified to species. They concluded that the fish was not abundant in the area, and that the fish were not a significant part of the kittiwake's diet (Hartley and Fisher, 1936). Several subsequent studies have looked at the diet of seabirds in glacier fjords on Spitsbergen in the breeding or post-breeding period (e.g. Lydersen et al., 1989; Mehlum and Gabrielsen, 1993; Mehlum and Gjertz, 1984). For fulmar and kittiwake the main piscivorous prey documented in all studies has been the polar cod. However, it must be noted that sampling has not taken place close to glacier fronts in any of these avian diet studies.

8. Conclusion and future research

Tidewater glacier fronts are clearly important foraging areas for many arctic sea birds and marine mammals. In addition, fast-ice areas close to glacier fronts are the most important breeding areas for ringed seals in Svalbard and therefore also very important foraging areas for polar bears, particularly females with young cubs during their first week after emerging from their winter dens. However, we lack quantitative information with regard to what fractions of the various bird and mammal populations utilize these hotspots and the temporal use of these areas across seasons (i.e. on an annual basis). For instance, the existing white whale data only encompasses a few months during the summer and much of the seabird information only relates to the breeding periods of the various species. But, recent aerial surveys around Svalbard in the post-breeding period (August and September 2010 and 2011) suggest that at least 70,000 kittiwakes remained in the area; most of these birds were observed feeding at glacier fronts (Strøm et al., 2012). This demonstrates that this habitat is also important for at least some species outside the breeding period. Thus, more tracking studies of birds and mammals are needed in order to gain further insight into the importance of glacier front areas. More detailed in situ studies of predators at glacier fronts would also be useful. Hartley and Fisher (1936) showed that the number of birds actually feeding at a specific glacier front during a day is many times higher than what can be recorded at any specific time of the day; this is also likely to be the case for mammals.

There is a notable lack of distribution information for fish species in glacial fjords in Svalbard, compared for instance with detailed investigations of glacial fjords in Alaska (Arimutsu et al., 2012). However, diet studies of seabirds and marine mammals suggest that various age groups of polar cod are present on a year-round basis. Pelagic, Atlantic species appear to occur in glacial fjords more erratically, with large interannual variance and perhaps also seasonal variation, depending on hydrography; perhaps especially depending on variation in the influxes of Atlantic water masses along the west coast of Spitsbergen. In addition, the fjords seem to have a variety of benthic fish species that likely reside quite locally on a year-round basis. Future studies of fishes in glacial fjords should include investigations of standing stocks of fish close to and at glacier fronts. As described above, large quantities of zooplankton are trapped in front of glaciers that likely attract significant numbers of polar cod that again attract the polar cod-eating marine mammals. However, visually searching fish predators may have problems detecting prey in the most turbid parts of the glacier fronts. No investigations of fish have been conducted in these areas due to the danger of operating close to active glacier fronts. But, use of various remote underwater vehicles, combined with acoustic and other detecting and capturing devices, should be encouraged to address this gap in our understanding of these ecosystem components.

The risk involved in sampling near calving glaciers, has resulted in knowledge regarding lower trophic animals and geophysics being extremely limited, few actual measurements from been collected in these areas. No measurements have ever been made by scientists in the plume of freshwater streaming out from the glaciers, where the upper trophic animals concentrate their foraging. However, ringed seals instrumented with satellite relayed data loggers with incorporated CTDs have recently performed many dives directly at glacier fronts and even through the plumes, providing novel data from these areas (Lydersen and Kovacs, unpublished data). "Extrapolated knowledge" on plankton and benthos, from areas "close" to the glacier fronts occur in the literature. But, even the huge amount of dead plankton found near glacier fronts as reported by Weslawski and Legeżyńska (1998) were in fact collected a minimum of several hundred metres away from the actual front of the glaciers being studied. So, new studies are needed in geophysics, lower trophic biology, fish community ecology and top trophic animal use of these areas in order to achieve a fuller understanding of the importance of glacier front areas in Svalbard and

elsewhere. New technology, including animal-borne instruments and other remotely controlled sampling devices is now available to conduct studies that would permit us to test theories regarding biological and physical processes of glacier front ecosystems. For example, effects of the aphotic conditions created by the high sediment loads from the glaciers on nitrifying bacteria could be explored.

It is clear that marine areas close to tidal-glacier fronts in Svalbard represent foraging hotspots for seabirds and marine mammals. It is also clear that the overall mass balance for Svalbard glaciers is negative and the predicted climate warming scenarios suggest that the glaciers will continue to retreat. This will lead to a reduction in both the number of glaciers calving into the ocean and the total length of calving fronts around the Archipelago. Similar to the retraction of the northern ice edge (which is another foraging hot-spot for these same arctic vertebrates), changes in tidewater glaciers in the coming decades will likely lead to substantial distributional shifts and for many species reduction in abundance (see Kovacs et al., 2011b). The behavioural plasticity that these seabirds and mammals might display in relation to climate change is difficult to assess. But, the extraordinarily fast rate at which environmental change is taking place in the Arctic is a cause for concern. The lack of spring sea ice in front of glaciers in the fjords of western Spitsbergen during the last decade has likely resulted in near-zero production of ringed seals. Changes in this one keystone predator have the potential to produce cascading effects through this arctic marine ecosystem.

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