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Impact of climate change on zooplankton communities, seabird populations and arctic terrestrial ecosystem—A scenario

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Abstract

Many arctic terrestrial ecosystems suffer from a permanent deficiency of nutrients. Marine birds that forage at sea and breed on land can transport organic matter from the sea to land, and thus help to initiate and sustain terrestrial ecosystems. This organic matter initiates the emergence of local tundra communities, increasing primary and secondary production and species diversity. Climate change will influence ocean circulation and the hydrologic regime, which will consequently lead to a restructuring of zooplankton communities between cold arctic waters, with a dominance of large zooplankton species, and Atlantic waters in which small species predominate. The dominance of large zooplankton favours plankton-eating seabirds, such as the little auk (*Alle alle*), while the presence of small zooplankton redirects the food chain to plankton-eating fish, up through to fish-eating birds (e.g., guillemots *Uria* sp.). Thus, in regions where the two water masses compete for dominance, such as in the Barents Sea, plankton-eating birds should dominate the avifauna in cold periods and recess in warmer periods, when fish-eaters should prevail. Therefore under future anthropogenic climate scenarios, there could be serious consequences for the structure and functioning of the terrestrial part of arctic ecosystems, due in part to changes in the arctic marine avifauna. Large colonies of plankton-eating little auks are located on mild mountain slopes, usually a few kilometres from the shore, whereas colonies of fish-eating guillemots are situated on rocky cliffs at the coast. The impact of guillemots on the terrestrial ecosystems is therefore much smaller than for little auks because of the rapid washing-out to sea of the guano deposited on the seabird cliffs. These characteristics of seabird nesting sites dramatically limit the range of occurrence of ornithogenic soils, and the accompanying flora and fauna, to locations where talus-breeding species occur. As a result of climate warming favoring the increase of ichthyiofagous cliff-nesting seabirds, we can expect that large areas of ornithogenic tundra around the colonies of plankton-eating seabirds situated far from the sea may disappear, while areas of tundra in the vicinity of cliffs inhabited by fish-eating seabirds, with low total production and supporting few large herbivores, will likely increase, but only imperceptibly. This may lead to habitat fragmentation with negative consequences for populations of tundra-dependent birds and mammals, and the possibility of a substantial decrease in biodiversity of tundra plant and animal communities.

Keywords: Arctic; Climate change; Nutrients; Seabirds; Terrestrial ecosystems

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1. Introduction

Polar regions are characterized by strong seasonality. The 24 h of darkness, low temperatures and snow and ice cover all make for extremely harsh living conditions during winter. In summer, the situation is reversed; there are excellent conditions for breeding and foraging (e.g., 24 h of daylight, little to no snow and, in many areas, reduced ice cover and high production in the sea). An abundance of land invertebrates appear, as well as thousands of migratory birds and mammals, which lead to heightened biological activity in the summer months (Sage, 1986).

Ecosystems in the contact zone of sea and land are unique in the Arctic. Because of the ocean's proximity, in the summer the temperature in the tundra remains a few degrees centigrade above zero, which causes the snow and surface soil to melt, enabling plants to grow. The arctic terrestrial ecosystem is usually characterized by low plant biomass and primary production, which are generally nitrogen- and/or phosphorus-limited (Ulrich and Gersper, 1978; Jonasson et al., 2000; Schmidt et al., 2002). Moreover, microbes and plants compete for nutrients (Shaver and Jonasson, 2001), and consequently a high proportion of biogenic salts is microbially fixed (Jonasson et al., 1999). In the conditions of reduced mineralization rate, some tundra plants (e.g., *Salix* and *Dryas* spp.) may utilize organic nitrogen in the soil directly through their mycorrhizae without previous mineralization of the organic compounds to inorganic nitrogen, and some even take up organic nitrogen without the aid of mycorrhizae (Michelsen et al., 1996). Low productivity is also a result of the relatively small area of tundra available, short growing season, low temperatures, permafrost, long-lasting snow cover, and considerable contribution of photosynthetically less efficient cryptogams in the communities, which usually form a thin vegetation layer (Alexandrova, 1980; Remmert, 1980; Sage, 1986; Stempniewicz, 1990a; Shaver and Jonasson, 2001).

Because of low temperatures and temperature-dependant activity of microorganisms, the rate of decay of dead organic matter is very slow in the terrestrial Arctic. This leads to an accumulation of organic matter (higher production than decomposition rate), and results in a high food supply for saprophagic arthropods (e.g., springtails and mites) and vertebrates (e.g., food-storing Arctic fox), and therefore, an increase of their role in the structure and functioning of the ecosystem (Seastedt, 1984; Sage, 1986; Jonasson et al., 1999). The number and role of poikilothermic herbivores (those that take on the temperature of their surroundings) in low temperatures is limited, as terrestrial plant food is difficult to decompose (because of difficulties in cellulose decomposition) and to assimilate, and therefore the energy transfer of these organisms is of low efficiency (Heal and French, 1974). However, in the ocean, the energy transfer efficiency is much greater because the cell walls of the phytoplankton do not contain cellulose (but alginians, hemicelluloses and polysaccharides) and the algae themselves have a high energy content, with lipids constituting up to 25–50% of their dry mass (Dunbar, 1982).

In polar seas, however, production is relatively high due to 24 h of sunlight in summer making continuous photosynthesis possible, high near-surface nutrient concentrations due to vertical mixing through a combination of wind-mixing and upwelling, and a predominance of diatoms that are very efficient producers (Dunbar, 1982; Stonehouse, 1989). The uneven spatial distribution of the mixing and upwelling regions results in patchy distributions of many marine organisms, especially pelagic species such as zooplankton, which has consequences for higher trophic levels such as fish, plankton- and fish-eating birds, seals and whales. In addition, regions where hydrographically different water masses mix, such as river estuaries, glacier fronts, and marginal ice zones, are often sites of rich feeding grounds (Dunbar, 1982). Plankton-eating seabirds depend on such feeding grounds situated close to breeding colonies to feed their chicks efficiently. However, below a certain level of zooplankton density, the birds can suffer starvation regardless of total biomass of food available. They are limited in their ability to "condense" plankton due to the limited volume of water that they can filter using structures in the mouth, and by the cost of transporting prey to their young at colonies (Croxall, 1987; Stempniewicz and Węsławski, 1992; Mehlum and Gabrielsen, 1993, 1995; Mehlum and Bakken, 1994; Lovvorn et al., 2001).

Because biochemical and physiological processes take place at high temperatures (~37–40 °C) in homeothermic vertebrates, these organisms play a very important role in arctic nutrient cycling. The high temperatures contribute to the effective activity of symbiotic microorganisms, thereby contributing to the digestion of plant cell walls and making food assimilation easier (Schmidt-Nielsen, 1983). The high number and role of warm-blooded animals is seen on all consumer levels. The breakdown of organic matter by homoeothermic vertebrates (mineralization, excrement and urine production) is rapid, particularly in comparison to the low rates of activity of free-living microorganism decomposers under cold conditions, which slows down matter cycling in polar ecosystems (Remmert, 1980). The biogenic salts produced by vertebrates are easily assimilated by plants, and may play a greater role in the fertilization of tundra and polar water bodies than in other terrestrial ecosystems Q1 (Golovkin, 1967; Zelickman and Golovkin, 1972; Golovkin and Garkavaya, 1975; Galkina, 1977; Krzyszowska, 1992; Bakker and Loonen, 1998; Wegener and Odasz-Albrigtsen, 1998; Jefferies and Rockwell, 2002; Juchnowicz-Bierbasz and Rakusa-Suszczewski, 2002; Stark et al., 2002; Rakusa-Suszczewski, 2003; Olofsson et al., 2004; Van der Wal and Brooker, 2004).

2. Importance of seabirds for the function of arctic terrestrial ecosystems

Seabirds, because they forage at sea and breed on land, transport organic matter from the nutrient-rich sea to the nutrient-poor land, and thereby help to sustain the terrestrial ecosystem. The flow of nutrients, energy, and material from one ecosystem to another can subsidize populations of terrestrial plants and animals and importantly influence the structure of communities and food webs (Tatur and Myrcha, 1984; Stempniewicz, 1990a; Stempniewicz and Węsławski, 1992; Węsławski and Stempniewicz, 1995; Croll et al., 2005). During one breeding season in Hornsund on Spitzbergen (see Fig. 2 for location), little auks (*Alle alle*) deliver ~60 t dry mass of guano km^{-2} to the colony area, ~25 t km^{-2} in the circular flight zone around the colony and ~0.6 t km^{-2} to the tundra between the colony and sea (Stempniewicz, 1990b, 1992).

Seabirds eat a protein-rich diet and produce nitrogen-rich excrement. Guano deposited in large seabird colonies is the only known abundant source of ammonia volatilization in polar regions, and probably makes a highly significant contribution to the local nitrogen budget (Wilson et al., 2004). Moss- or lichen-dominated arctic ecosystems are particularly sensitive to increased levels of nitrogen deposition (van der Wal et al., 2003; van der Wal and Brooker, 2004). Increased atmospheric nitrogen deposition therefore contributes to the large-scale changes in plant species composition by facilitating the invasion of grasses and grass-like plants in a wide range of habitats.

For the reasons mentioned above, large seabird colonies play a crucial role in initiating local concentrations of plants and animals and in ecosystem function. They increase the primary and secondary production and species diversity (Eurola and Hakala, 1977; Dubiel and Olech, 1992; Gaston and Donaldson, 1995). They also serve as nuclei around which dense vegetation creates sites of foraging, hiding and breeding for herbivores. Besides the excreta that seabirds deposit near the colony, they also contribute considerable amounts of organic matter (lost prey items, eggs, chicks and adults) constituting easy source of food for scavengers and predators. In addition to changes in the nearby tundra plant communities (Croll et al., 2005), seabird excrement may fuel local increases in phytoplankton production in coastal waters neighbouring large seabird colonies (Zelickman and Golovkin, 1972). In some cases geomorphologic changes are observed, such as the stabilization of rock debris on mountain slopes and talus where the little auks breed, as a result of the development of a rich vegetation due to intensive fertilization (Stempniewicz, 2005).

The Arctic has no long-term guano deposits, in contrast to the Antarctic. In the Antarctic, penguins concentrate large amounts of excreta in colonies situated on flat coastal terraces. Due to the small amounts of snow-melt and rainfall in the Antarctic, guano deposits accumulate and return to sea in limited amounts (Tatur and Myrcha, 1984; Rakusa-Suszczewski, 2003). Arctic seabird colonies, on the other hand, are usually situated on cliffs and mountain slopes and are subject to melt water flows across the tundra between the seabird colonies and the sea. Thus, the guano is dissolved and is carried across the tundra where it can be absorbed by plants throughout the summer (Pulina et al., 1984, 2003). The mossy tundra, which efficiently stores water, is also a microhabitat with a rich bacterial flora and invertebrate (coprophagic) fauna that recycles nutrients (Klekowski and Opaliński, 1984; Seastedt, 1984).

The amount of biogenic salts deposited per unit time and per unit area of tundra depends on the daily rate excrement production, which is a function of colony size, the length of time the birds remain in the colony, bird species and their body size. Guano composition is related to bird diets, with different

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proportions of organic and non-organic fractions and composition of the different mineral salts observed in the excrements of plankton-, fish- and bivalve-eating birds (Galkina, 1974; Bedard et al., 1980). It may be that different bacterial communities develop on different types of excreta resulting in different biochemical transformations that ultimately produce a different composition, amount and proportion of nutrients available to tundra plants. While this, in turn, could favour development of different plant and animal communities on the different ornithogenic soil types, this hypothesis has not been tested experimentally.

The rate at which nutrients delivered to the colony area as guano reach the sea depends on the distance between breeding colonies and the sea, as well as topography (altitude of the colony, inclination, ground type, ridges, ponds, etc.) and runoff. Also vegetation type, plant species composition, coverage level, thickness of the vegetation layer, water absorption and amount of salts dissolved in the water are important (Pulina et al., 1984; Stempniewicz, 1990a, b). The two colony types, coastal rocky cliffs inhabited by guillemots and little auk breeding aggregations situated in rock debris on mild mountain slopes far from the seashore, differ substantially in these respects. The time the guano deposited in the colony remains on the tundra is crucial for the microorganisms decomposing it and determines the proportions of biogenic salts being assimilated by plants before the salts reach the sea (Heal and French, 1974; Stempniewicz, 2005).

3. Climate variability and seabird biology and ecology

Ongoing climate warming will have significant effects on all aspects of avian life cycles (Stevenson and Bryant, 2000; Ainley and Divoky, 2001). There is some evidence of climate impact on the timing of reproduction, breeding success and population changes (e.g., Järvinen, 1994; Forchammer and Stenseth, 1998; McCleery and Perrins, 1998; Gjerdrum et al., 2003; Dunn, 2004; Fredriksen et al., 2004). Egg-laying dates are influenced by factors such as feeding conditions during the pre-laying period, female body size and condition, age and number of times the bird has bred. Sea-ice extent and sea-surface temperature (SST) fluctuations may severely influence timing and success of breeding (Barbraud and Weimerskirch, 2001; Gaston et al., 2005a, b). Arctic seabirds exhibit flexible patterns of phenology, reflecting the timing of optimal prey availability. Adjustment to food requirements and prey availability is crucial for their reproductive success, and climate fluctuations may disrupt trophic relationships as has been observed in Atlantic puffins (*Fratercula arctica*) (Durant et al., 2003).

Seabirds regularly face short-term fluctuations in food availability during chick rearing, and weather conditions can influence the growth of chicks (Braun and Hunt, 1983; Konarzewski and Taylor, 1989). Ongoing global changes may enlarge fluctuations in oceanic conditions in the arctic seas, including the timing and amount of prey available in the marine environment. Seabirds are relatively well adapted to a variable environment, as they are long-living *k*-strategists with low annual mortality and reproductive output, capable of maintaining stable population numbers even though there is breeding failure for many years (e.g., Durant et al., 2003). Chicks can modify slightly their pattern of energy use and allocation as a response to short-term diet restrictions, while adult birds have rather flexible foraging strategies. However, in periods where parents cannot adequately provision their young, the degree of developmental plasticity of the growing young will be a crucial determinant for the reproductive outcome and over the long run lack of prey may lead to population decline (Øyan and Anker-Nilssen, 1996; Kitaysky, 1999).

Seabirds, such as auks, exhibit an energetically costly way of life due to their flapping flight, distant foraging trips and pursuit diving. Consequently, their energy budgets are expected to be highly sensitive to climate fluctuations. This is of special concern for small auks, which exhibit one of the highest mass-specific daily energy expenditure (DEE) among all seabirds measured (Gabrielsen et al., 1991). Climate change could alter oceanic prey distribution, thereby forcing seabirds to fly longer distances to reach feeding areas where their preferred prey is most abundant, causing increased energetic demands (Bech et al., 2002). Weather variations, sea-ice cover and water temperature have been found to affect summer fish distributions in arctic seas. For example, in the Bering Sea the polar cod (*Boreogadus saida*), which constitutes an important diet item for many arctic seabirds, is only present within the “cold pool” waters. In warm years, the “cold pool” shrinks causing low abundance of polar cod (Wyllie-Echeverria and Warren,

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1998). Similarly, the little auks breeding in Hornsund, in southwestern Spitzbergen, feed mainly on the large copepod *Calanus glacialis*. They restrict their foraging activity to Arctic Water and avoid Atlantic Water that contains the smaller copepod, *Calanus finmarchicus*. Little auks breeding in Spitzbergen may consequently be impacted by climate change because during years when the flow of Atlantic water increases, they may be forced to forage in areas with sub-optimal conditions (Węsławski et al., 1999a, b; Karnovsky et al., 2003).

Breeding success of seabirds is also determined by predation rates (Øro and Furness, 2002). It has been found that large gulls increase their predation intensity on seabird eggs and chicks in years with low fish availability, and in some instances they may be totally dependent on eggs (Massaro et al., 2000). Glaucous Gulls (*Larus hyperboreus*) in Hornsund have their highest energy demands during the feeding of chicks near the time of fledging, and they have adjusted this period to coincide with when the little auks are fledging their young, a period when there is an abundant and easily available supply of young little auks leaving the colony. A shift in the timing of little auk egg laying will have significant consequences for glaucous gull breeding success (Stempniewicz, 1995; Wojczulanis et al., 2005). Low food availability to the little auks will affect their breeding success directly (decisions to breed, adult body condition and chick feeding rate) and indirectly (changes in risk of predation by glaucous gulls).

4. Climate change and ecosystem functioning—a scenario

Climate variability in the polar regions in the North Atlantic and vicinity, both near-decadal (e.g., related by the North-Atlantic Oscillation or NAO) and longer-term, leads to changes in large-scale circulation patterns and the hydrologic regime of the northern North Atlantic (Hurrell, 2003). A crucial oceanographic consequence of a positive NAO index is an increase in the flow of warm Atlantic water into the Arctic Ocean (Dickson et al., 2000). This in turn influences the distribution, abundance, composition and size structure of zooplankton communities (Beaugrand et al., 2002a). Changes in the size and energy content of key zooplankton prey affect energy transfer in the pelagic food web. Along with the increased influx of Atlantic waters, Arctic zooplankton communities, dominated by large coldwater species, retreat to be replaced with small plankters associated with warmer waters during a positive NAO (Fig. 1) (Beaugrand et al., 2002b). Such shifts in zooplankton communities have important consequences for the animal species that tap into this food base (Węsławski et al., 1999a, 2000; Karnovsky et al., 2003). Because of differences in the anatomy and functioning of the feeding apparatus in birds and fish, domination of large crustaceans in zooplankton favours the feeding of plankton-eating seabirds, such as the little auk, while the dominance of small forms redirects the food chain to plankton-eating fish, and only then to fish-eating birds (e.g., guillemots *Uria* sp.) (Węsławski et al., 1994, 1999a, b, 2000). Thus, plankton-eating birds should dominate Arctic avifauna in cold periods and recess in warmer periods, when fish-eaters dominate (Kitaysky and Golubova, 2000).

Southern and western Spitsbergen are influenced by different ocean currents (Fig. 2). The Sørkapp Current brings cold, arctic waters from the northeast with a zooplankton community represented by large planktonic crustaceans (e.g., *C. glacialis*) while the warm-water West and South Spitsbergen Currents (branches of the North Atlantic Current that itself is an extension of the Gulf Stream) carry small calanoids, e.g., *C. finmarchicus* predominates (Fig. 2). The extension of each current and hence proportions of arctic and Atlantic water masses around South Spitsbergen varies depending on the NAO phase. Total zooplankton biomass is similar in the two water masses, however, the deficiency of large (>3 mm) crustaceans in Atlantic water dramatically decreases the feeding efficiency of planktivorous seabirds (Węsławski et al., 1999b). For example, the average percentage of large *C. glacialis* found in the little auk diet resembled that found in net tows in water masses influenced by the cold Sorkapp Current and was approximately 8-fold higher than that found in warm West Spitsbergen Current (Fig. 3). In the years with a large influx of Atlantic water (positive NAO index), feeding conditions and the energy budget of little auks would markedly deteriorate, and over the long-term would probably cause a population decrease. Southernmost little auk populations in south Greenland and Iceland have already collapsed due to change in ocean circulation there, and a northward shift of the species' breeding range is expected with further climate warming in Arctic (Stempniewicz, 2001).

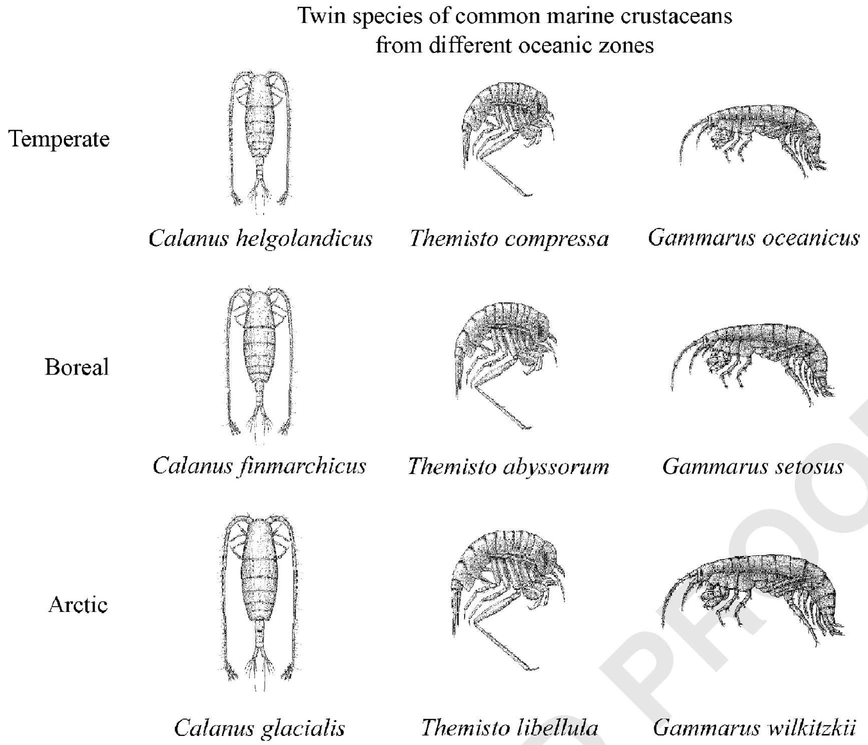

Fig. 1. Closely related species are represented by larger forms in cold Arctic waters and by smaller ones in warmer boreal and temperate oceanic zones (Węsławski, unpublished materials).

Ecological responses to climate fluctuations have been documented in many marine and terrestrial animal populations for different trophic levels (Coulson et al., 2000; Ainley and Divoky, 2001; Hunt and Stabeno, 2002; Stenseth et al., 2002; Walther et al., 2002; Durant et al., 2003). Climate change will certainly affect also arctic tundra, which is dominated by functional plant groups of low nutrient requirements, making the system vulnerable to future temperature and nutrient variability (Jonasson et al., 1999). The productivity of vascular plants, particularly grasses and grass-like vegetation, generally increases strongly after even small additions of N and P (e.g., Shaver and Jonasson, 2001). This suggests that any changes in the input or cycling of these nutrients, for instance from increased rate of nutrient mineralization caused by climate warming (Cattle and Crossley, 1995), or from fertilization level by seabirds and ammonia volatilization from the colonies (Wilson et al., 2004), most likely will change the community structure and increase plant productivity. Croll et al. (2005) showed that the introduction of arctic foxes (*Alopex lagopus*) to the Aleutian archipelago induced strong changes in tundra plant productivity and community structure. By preying on seabirds, foxes considerably reduced nutrient transport from the ocean to the land, affecting soil fertility and transforming more productive grasslands to less productive maritime tundra ecosystems. The powerful indirect response of the ecosystem was different from that of the classic trophic cascade.

The climate warming presently observed and predicted for the future in Polar Regions will result in serious consequences for the structure and functioning of the terrestrial part of ecosystem, in part due to probable changes in the arctic avifaunal composition (Fig. 4). Large colonies of plankton-eating little auks are located on mild mountain slopes and talus, usually a few kilometres off the shore (Stempniewicz, 2001). They strongly influence large adjacent areas by enriching the tundra with great amounts of guano deposited per time and area unit. Nutrients stay in the tundra for a long time, and are accessible for plants, which show a high biomass and number of taxa near little auk colonies (Dubiel and Olech, 1992). As a result, the number of herbivores (geese, Svalbard Reindeer *Rangifer*

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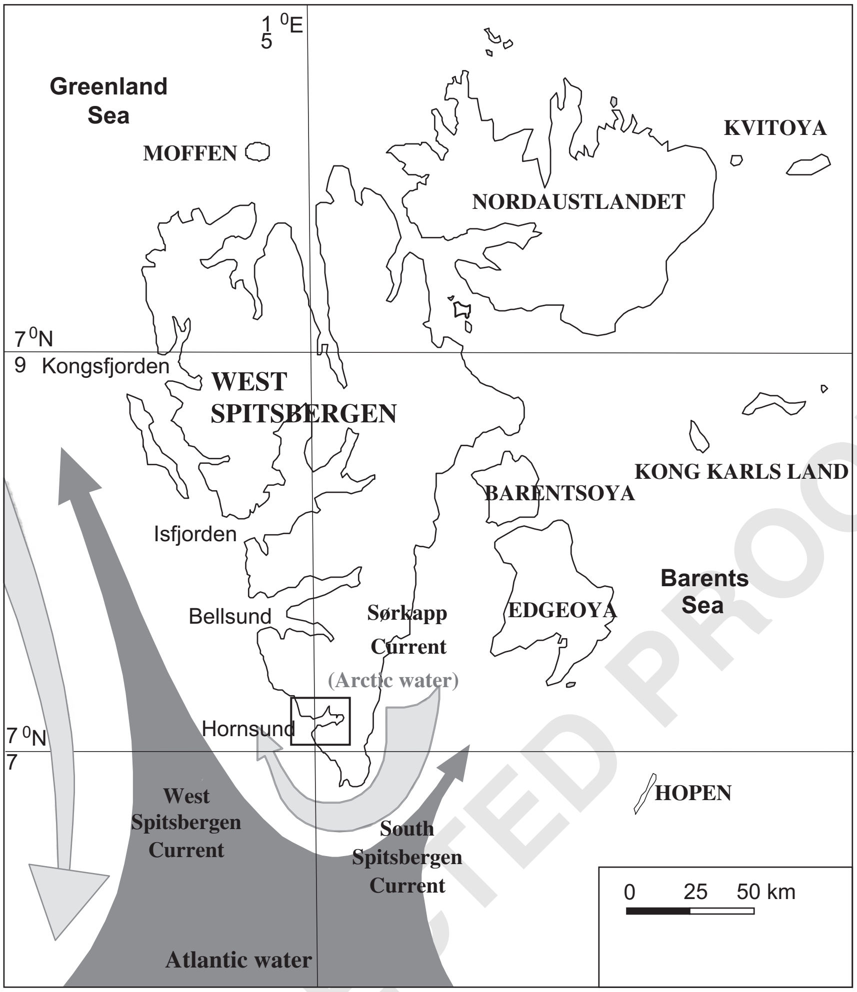

Fig. 2. Schematic map of sea currents influencing South and West Spitsbergen (light-grey: Arctic Water; dark-grey: Atlantic Water).

tarandus platyrhynchus), scavengers and predators (arctic fox) supported, as well as density of tundra-nesting birds, is high (Stempniewicz, 1990a, b, 1992).

The range of impacts of the fish-eating Brunnich's guillemots (*Uria lomvia*) colonies, which are situated on rock cliffs close to the shore, is much smaller because of the short distance to the sea and rapid washing-out of the biogenic salts (guano) deposited on the land by birds back to the sea (Eurola and Hakala, 1977). This dramatically limits the area and range of occurrence of ornithogenic soils with the accompanying flora and fauna communities (Fig. 4).

The two colony types may also differ in the rate of volatilization of ammonia. In general, the conditions for ammonia emission are thought to be less favourable in the colonies of burrow-nesting seabirds, which are usually covered by vegetation, comparing to those of the open-nesting species (Wilson et al., 2004). However, in case of the little auk and guillemot colonies the situation is equivocal. Although the little auk chicks leave part of their excreta in the nests situated under the boulders (Stempniewicz, 1990b), which hampers volatilization rate, the colonies have a rather small inclination and a large uncovered (not overgrown) evaporating area. In the cliff-inhabiting guillemots, the nests are open and are also not overgrown but since the colony wall is almost vertical, the majority of guano falls down into dense vegetation at the foot of colony, thus substantially reducing the volatilization rate. Additionally, because of the close proximity of the nesting cliffs to the sea,

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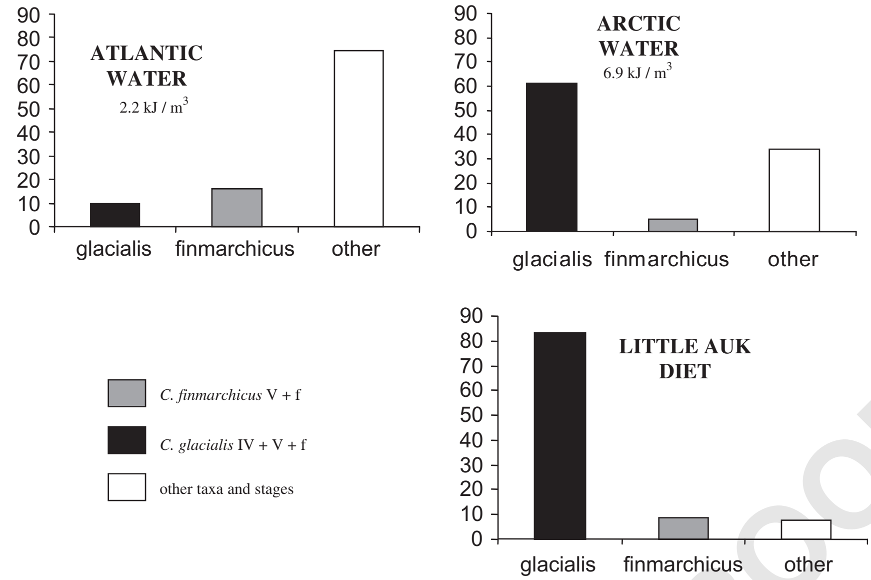

Fig. 3. Average % of *Calanus glacialis* and *C. finmarchicus* (stages CIV–VI + females) found in net tows (ind m^{-3}) in water masses influenced by cold Sorkapp Current (Arctic Water), by warm West Spitsbergen Current (Atlantic Water) and in the Little Auk diet (diagram based on data from Karnovsky et al., 2003).

much of the guano is washed to the sea before ammonia volatilization can take place.

Under future climate warming and assuming increased inflow of Atlantic waters, we can expect a rise in ichthyiofagous cliff-nesting seabird populations and a decline in the plankton feeding seabirds in the Spitzbergen area. As a result, large areas of tundra supplied with nutrients of marine origin, delivered to plankton-eating seabird colonies situated far from the sea, may disappear. In contrast, small areas of ornithogenic tundra in the vicinity of cliffs inhabited by fish-eating seabirds, with low total production and unable to support large herbivores may predominate. We hypothesize that this would lead to negative consequences for populations of tundra-related birds and mammals and a substantial decrease in biodiversity of tundra plant and animal communities. This result, in part, is because increases in populations of cliff-nesting seabirds take place mainly by increases of nest density and to a lesser extent by increases of colony size, whereas in case of little auks, their local population size is generally correlated with colony area and surrounding colony-fuelled tundra area. Thus, taking into account short distance to seashore and rapid washing out of the excreta, ornithogenic tundra developing near cliff-nesting seabird colonies remains small in spite of an increase in the number of breeding birds. Additionally, the small and widely separated areas of ornithogenic tundra that develop near this type of colonies, even though numerous, cannot support local populations of avian and mammalian herbivores (e.g., geese and reindeer). These animals live in groups and need larger areas of tundra (e.g., such as in the vicinity of little auk colonies) to survive and breed successfully.

Future studies are planned to test the above scenarios. Comparisons of the impact of two different seabird colonies (the little auks and Brunnich's guillemots) in Hornsund in southwest Spitsbergen on the surrounding tundra will be carried out. The comparison will include the area of ornithogenic tundra, amount of seabird excreta deposited per unit time and per unit area, ammonia volatilization rate, quantity and quality of nutrients available to plants, and the degree to which nitrogen-based nutrients ($\delta^{15}N$) in the soil, plants and diverse groups of terrestrial consumers are marine derived. Also the structure and biomass of the soil microorganisms, plants and invertebrates, as well as number of vertebrate herbivores and common tundra-nesting birds in the two areas will be studied.

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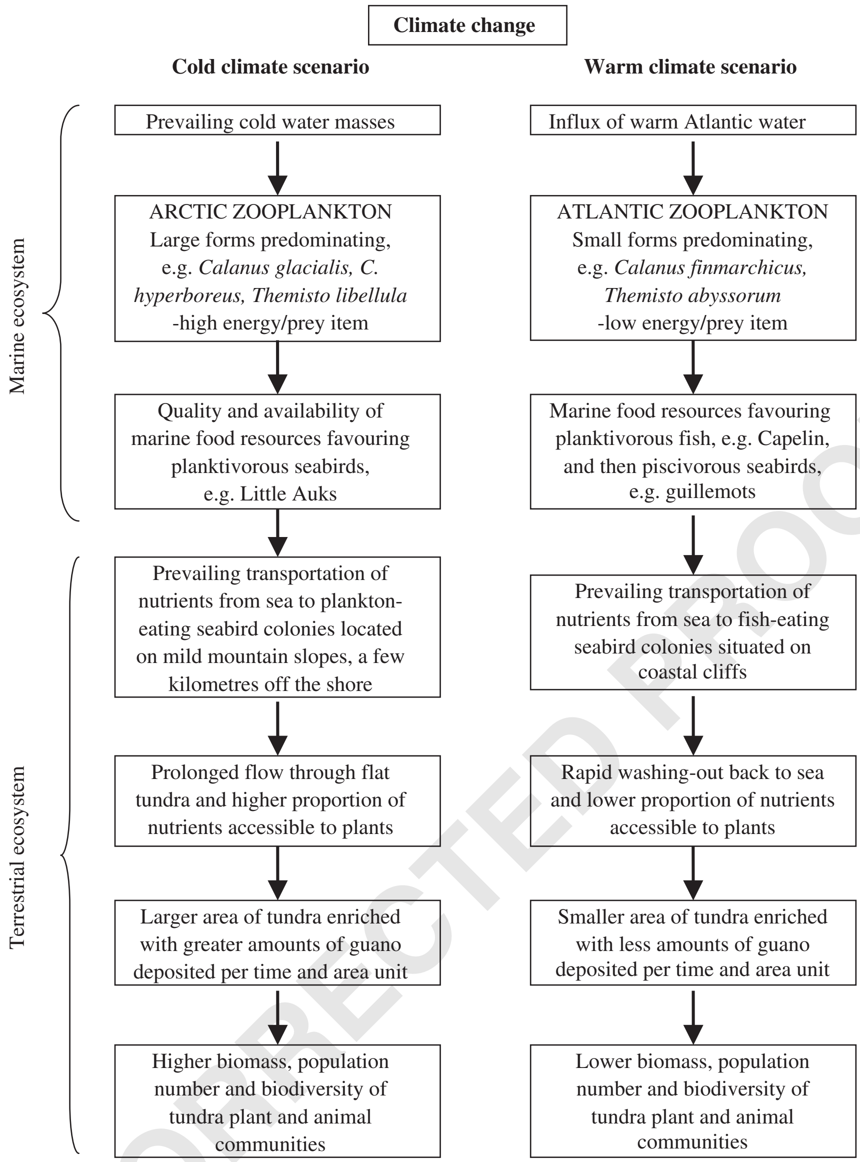

Fig. 4. Impact of climate change on zooplankton communities, seabird populations and arctic terrestrial ecosystem—a scenario.

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