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Climate Change and Biological Oceanography of the Arctic Ocean

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Climate change and biological oceanography of the Arctic Ocean

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Polar environments are characterized by unique physical and chemical conditions for the development of life. Low temperatures and the seasonality of light create one of the most extreme habitats on Earth. The Arctic sea ice cover not only acts as an insulator for heat and energy exchange processes between ocean and atmosphere but also serves as a unique habitat for a specialized community of organisms, consisting of bacteria, algae, protozoa and metazoa. The primary production of sea ice algae may play a crucial role in the life cycle of planktonic and benthic organisms. Thus, a reduction of the sea ice extent due to environmental changes will influence the structure and processes of communities living inside the ice and pelagic realms.

1. Introduction

The Arctic Ocean is an enclosed sea area with two major connections to the surrounding seas, the shallow Bering Sea and the relatively deep Fram Strait. The Arctic marine environment is in its present state one of the most extreme habitats on Earth. Strong seasonal variations of some parameters, such as solar radiation, are in contrast to the relative stability of others, such as water temperature. Organisms living in polar oceans are well adapted to these environmental conditions. Climatic changes will therefore influence the structure of the Arctic marine communities, as already indicated by the geological record: the Pleistocene warming at approximately 1.5 Ma coincides with a drastic increase in North Atlantic species and calcareous organisms in the sediment record as a result of changes in the water mass exchange between the Arctic Ocean and its surrounding seas (Clarck 1990).

The emission of trace gases to the atmosphere by anthropogenic activities may lead to similar changes, but on much shorter time scales. Global models studying the effect of CO_2 increase in the Earth's atmosphere showed the largest temperature increase in the Arctic (Mitchell *et al.* 1990). Recent measurements from Alaska already demonstrate a temperature increase of approximately 1.5 °C during the past decade (Oechel & Vourlitis 1994).

An increase in atmospheric, and consequently sea surface, temperature will have a high impact on the Arctic marine epipelagic system. Based on present knowledge of the Arctic marine pelagic system, possible changes will be discussed in this contribution, but the developed scenario will be in no sense predictive. It is obvious that the response of the Arctic marine ecosystem will largely depend on the fate of its most characteristic realm, the permanent sea ice cover.

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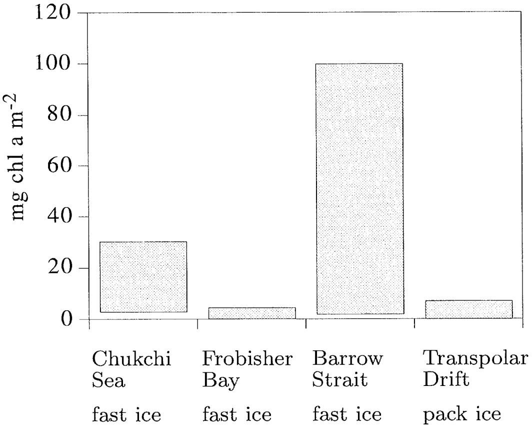

Figure 1. Algal biomass in Arctic sea ice. Data for Chukchi Sea from Clasby *et al.* (1973); Frobisher Bay from Grainger (1979); Barrow Strait from Smith *et al.* (1989) and Transpolar Drift from Gradinger (unpublished data).

2. The sea ice realm

Sea ice covers between 7 and 14 × 10^6 km^2 of the Arctic Ocean (Maykut 1985). Its existence largely influences the material and energy exchange between ocean and atmosphere and is therefore a crucial parameter in the modelling of environmental changes in polar areas. In contrast to Antarctica, about 50% of the Arctic sea ice floes survive summer melting and thus reach thicknesses of more than 2 m (for a detailed comparison between Arctic and Antarctic sea ice properties, see Spindler 1990).

Sea ice consists of a mixture of ice crystals and brine channels, which form a three-dimensional network of tubes and channels with typical diameters of 200 μm (Weissenberger *et al.* 1992) within the ice matrix. The brine salinity and the total volume of the brine channels as percentage of the ice volume are dependent on ice temperature and total salt content. For example, a decrease in the ice temperature from -4 °C to -10 °C leads to growth of ice crystals and thus an increase in brine salinity from 70 to 144 psu (Assur 1958), as well as a decrease in the brine volume.

Despite these harsh environmental conditions, a specialized community has developed and adapted to live within the brine channel system. Diatoms are the dominant primary producers and may contribute more than 90% of the total algal biomass (Poulin 1990). The seasonal development of the sea ice algae is mainly controlled by abiotic parameters. The onset of algal growth in spring is triggered by an increase in available light intensities after the dark polar winter. Sea ice, and especially its snow cover, reduces the incoming radiation by more than 90% due to high albedo. Therefore, ice algae are already adapted to start growing under extremely low light intensities (2–10 μmol m^{-2} s^{-1}; Horner & Schrader 1982). The biomass built up by sea ice algae during the Arctic summer varies between 1 and 100 mg Chl a m^{-2} (figure 1). Highest concentrations have been observed in fast ice areas of the Canadian shelf (Clasby *et al.* 1973; Smith *et al.* 1989), while the concentrations within the multiyear ice floes of the transpolar drift system are one or two orders of magnitude lower (Gradinger, unpublished data).

Large fluctuations in temperature, and therefore brine salinity, restrict life within the Arctic ice floes to the lowermost decimetres, and so-called sea ice bottom com-

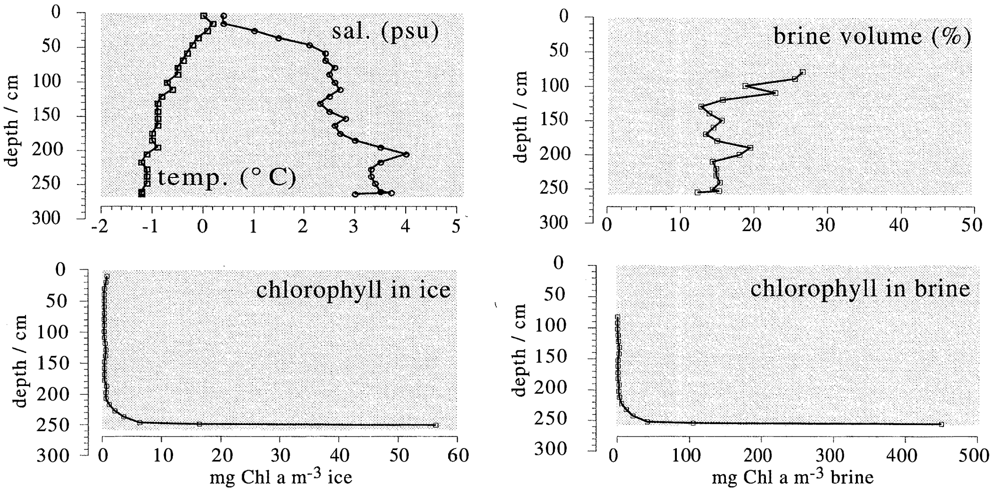

Figure 2. Temperature, salinity, brine volume and algal biomass in an Arctic multiyear ice floe (Gradinger, unpublished data).

munities are formed (Horner 1985). Figure 2 shows an example of the chlorophyll distribution in an Arctic multiyear ice floe, sampled in the East Greenland Current in August 1994 (Gradinger, unpublished data). Low salinities and relative high temperatures are idiosyncratic for Arctic summer sea ice. The calculated brine volume based on the equations by Frankenstein & Garner (1967) varies between 10 and 30% of the total ice volume. The chlorophyll profile clearly shows a well developed bottom community with concentrations above 50 mg Chl a m^{-3} ice in the lowermost centimetres. The actual algal concentration within the brine channel system is even higher exceeding values of 400 mg Chl a m^{-3} brine. This high algal biomass serves as the food source for a variety of proto- and metazoans (figure 3), which are mostly smaller than 1 mm. In shallow sea areas, nematoda and crustaceans are the dominating organism groups (Carey & Montagna 1982; Cross 1982; Kern and Carey 1983; Grainger *et al.* 1985), while a distinct community inhabits multiyear ice floes, with ciliates and turbellarians as most abundant taxa (Gradinger *et al.* 1991).

The high algal biomass inside Arctic ice floes is used by pelagic and benthic organisms during parts of their life cycle. Carey & Montagna (1982) observed larvae of benthic polychaetes and molluscs inside Arctic sea ice, and Kurbjeweit *et al.* (1993) made a similar observation for the Antarctic pelagic copepod, *Stephos longipes*. For these organisms, ice floes serve as a kind of 'kindergarten' to the juveniles, providing both food and shelter against possible predators.

3. The under-ice realm

The boundary-layer between Arctic ice floes and the water column forms the habitat for a specific community of organisms. Diatoms, mainly the species *Melosira arctica*, may grow to long, macroscopic visible bands, reaching lengths of more than 15 m and widths of 1–2 m, hanging down from the underside of the floes into the water column (Melnikov & Bondarchuk 1987). Amphipods of the genera *Gammarus*, *Apherusa* and *Onisimus* (Lønne & Gulliksen 1991) are permanently living at the boundary between ice floes and the pelagic realm in densities of up to 60 individuals per m^2 of ice (Carey 1985). These organisms, which are partially endemic to the

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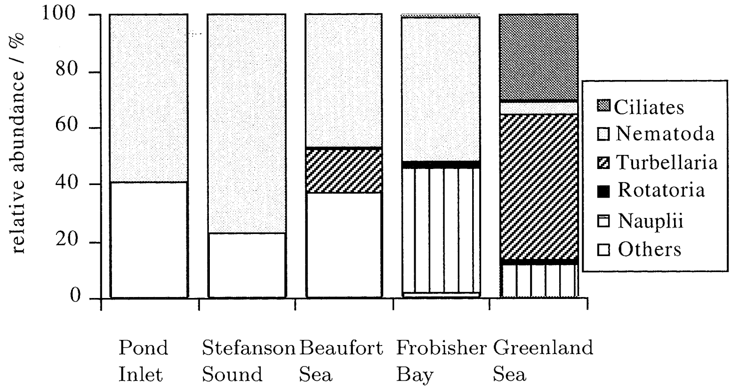

Figure 3. Relative composition of sea ice meiofauna in various parts of the Arctic Ocean. Data for Pond Inlet from Cross (1982); Stefanson Sound from Carey & Montagna (1982); Beaufort Sea from Kern & Carey (1983); Frobisher Bay from Grainger *et al.* (1985) and Greenland Sea from Gradinger *et al.* (1991).

Arctic Ocean, use the high algal biomass formed both directly at the underside and by the bottom community as a food source (Carey & Boudrias 1987). Besides the availability of food, they use the ice underside as a refuge to find shelter in the three-dimensional structure of, for example, pressure ridges.

Beside the autochthonous under-ice fauna, pelagic zooplankton, like the copepod species *Calanus glacialis* and *Pseudocalanus* spp. (specially *P. minutus*), temporarily ascend from deeper water layers to the underside of the ice floes to feed on ice algae (Runge *et al.* 1991). The under-ice fauna forms the link between the ice based primary production and the pelagic animals. These feed on ice algae and are important prey organisms for higher trophic levels like the polar cod (*Boreogadus saida*; Bradstreet & Cross 1982).

4. The pelagic realm

The biomass of pelagic organisms in the permanently ice-covered central regions of the Arctic Ocean is extremely low. The permanent ice cover reduces the incoming radiation, significantly suppressing algal growth to a degree already recognized by the early studies of Braarud (1935) and Steemann-Nielsen (1935). Concentrations of inorganic nutrients are relatively high throughout the year, and oxygen concentrations are in near equilibrium with the atmosphere, in agreement with the general idea of very low primary productivity in the central Arctic regions (Jones *et al.* 1990). The low algal biomass under the permanent pack ice is formed by small flagellates (Braarud 1935; Horner & Schrader 1982) in contrast to the diatom-dominated ice algal community. Investigations in the permanently ice-covered western part of the Greenland Sea (Gradinger & Baumann 1991) revealed an average algal biomass of 7 mg Chl m^{-2} in the upper 40 m of the water column under dense pack ice (figure 4), a value similar to the biomass observed inside the ice brine channel system. Thus, algal biomass has almost the same total value in sea ice and in the water column below, but the ambient concentrations (sea ice brine channels: greater than 400 mg Chl a m^{-3}; euphotic zone: less than 0.2 mg Chl a m^{-3}) are extremely different.

High phytoplankton concentrations, with integrated chlorophyll concentrations above 40 mg Chl m^{-2}, are restricted to marginal ice zones (MIZ) and polynyas. The

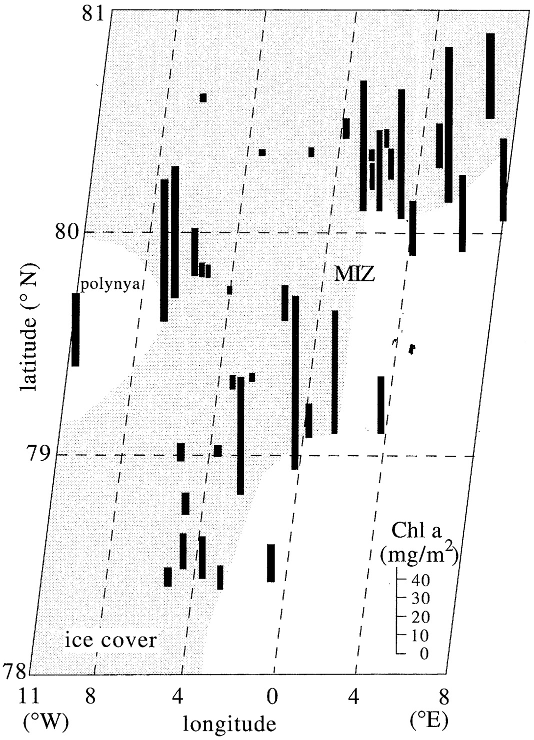

Figure 4. Distribution of algal biomass in the upper 40 m of the Greenland Sea (modified after Gradinger and Baumann (1991)).

significance of MIZ as regions of enhanced pelagic productivity was first shown for Arctic shelf areas (Rey & Loeng 1985; Alexander & Niebauer 1981), where melting of ice floes leads (i) to an enhanced water column stratification and (ii) to increasing radiation. These conditions allow an even earlier onset of the phytoplankton growth in the MIZ than in the adjacent open water. Plankton blooms in MIZ are mainly formed by *Phaeocystis pouchetii* and pelagic diatom species (Gradinger & Baumann 1991). During the Arctic summer, nutrients become depleted in the upper layers of the water column (Spiess *et al.* 1988; Kattner & Becker 1991). Mesoscale processes like eddies and local wind-induced upwelling events (Buckley *et al.* 1979; Johannessen *et al.* 1983) lead to spatial patchiness in nutrient and algal concentrations and permit a prolongation of the algal growth period throughout the Arctic summer until the months September/October (Heimdal 1983).

Other areas of enhanced primary productivity in the Arctic Ocean are polynyas. The North East Water polynya, as one example, opens each year on the Greenland shelf, starting in late spring (May–June), and reaching its maximum extent of 44 000 km^2 in late summer (Wadhams 1981). Investigations in the polynya revealed similar biological characteristics to those described for marginal ice zones, since improved light availability and water column stratification enhance phytoplankton growth (Gradinger & Baumann 1991). The gradual increase in algal biomass is related to a decrease in nutrient concentrations until nitrate becomes depleted in the surface layer (Lara *et al.* 1994).

The life cycles of the Arctic zooplankton species are strongly adapted to the extreme seasonality and patchiness of food availability. During the short Arctic summer, Arctic mesozooplankton, mainly consisting of copepods (*Calanus glacialis*, *Calanus hyperboreus*, and *Metridia longa*) feed and grow as young stages in the euphotic zone and accumulate energy-storage products, especially lipids, to survive the long starvation periods. They overwinter using a diapause-like strategy in deep waters, and again ascend to the euphotic layer in early or late spring (Smith & Schnack-Schiel 1990). The high algal biomass in polynyas and MIZ is used by the herbivorous zooplankton to sustain themselves in the Arctic Ocean. While the mesozooplankton may only have a minor impact on the algal production in the polynya and the marginal ice zone (Barthel 1986; Hirche *et al.* 1994) these regions are of special importance as areas of successful reproduction for the Arctic zooplankton (Hirche *et al.* 1991).

Due to the availability of food, marginal ice zones and polynyas are of major importance to the higher trophic levels of the Arctic marine ecosystem, as mesozooplankton species (*Calanus* spp.) are central to the pelagic food web (Bradstreet & Cross 1982). Various species of birds and marine mammals use marginal ice zones as migration routes due to the reliable availability of food (Ainley & DeMaster 1990). The breeding success of Arctic seabirds is dependent on the development of marginal ice zones at an accessible distance from the breeding grounds (Bradstreet 1988). Bird densities in marginal ice zones may be one to three orders of magnitude higher than in the adjacent ice-covered or open water area (Divoky 1979). Polynyas are for the same reasons attractors for both predators and their prey (Dunbar 1981). Large sea bird rookeries in the Canadian Arctic are located in the bird's flight range to a recurring polynya (Brown Nettleship 1981). The distribution of marine mammals is to a large extent determined by the position of polynyas as well (Stirling *et al.* 1981). Changes in the extent and distribution of polynyas, marginal ice zones and permanent ice cover will consequently directly influence recruitment success, migration behaviour and, in the long term, life cycle strategy of Arctic marine birds and mammals.

5. Effects of climate change on the Arctic marine system

The atmospheric CO_2 concentration has increased from a pre-industrial level of 280 ppm to a current level of approximately 360 ppm with an annual rate of about 1.5%. The concentration of methane, which is an even more effective greenhouse gas than CO_2, is increasing at a similar rate. These changes in the composition of the Earth's atmosphere have the potential to affect the global climate and increase the surface temperature. Predictions for the global climate in the next century using general circulation models indicate an enhanced warming of Arctic areas relative to lower latitudes, making the Arctic one of the most sensitive areas in the world.

Evidence of warming in high latitudes has already been gathered. Temperature in certain parts of northern Alaska has increased over the last decade, and will largely affect the conditions for terrestrial ecosystems (Oechel & Vourlitis 1994). The expected warming of the Arctic atmosphere will cause the permanent pack ice to shrink or even disappear in the next century.

A reduction in the extent of the permanent ice cover and a shift to a more seasonal ice regime will greatly affect the structure of the Arctic marine ecosystem (figure 5). Polynyas and marginal ice zones will occur in regions which until now have been characterized by a permanent ice cover and an extremely low biological productivity (Manak & Mysak 1989). Today, there is still uncertainty about the role of the biological CO_2 pump in relation to physical processes in general (Longhurst 1991) and in

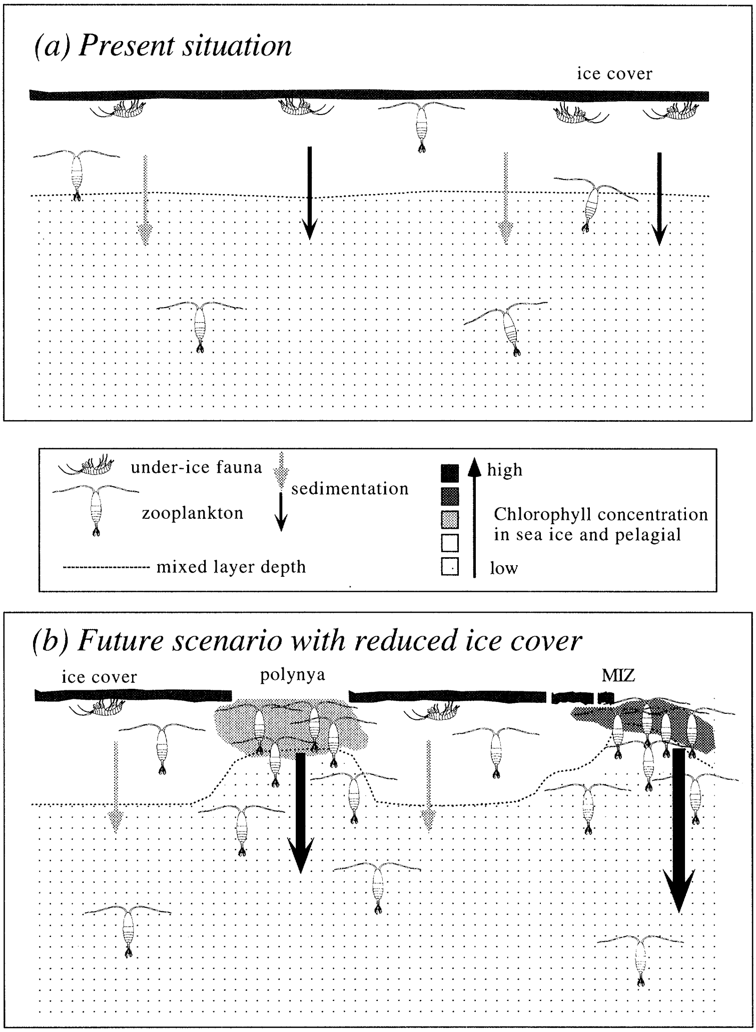

Figure 5. Structure of the marine ecosystem of the Arctic Ocean: (*a*) present state; (*b*) changes due to a reduction in the ice cover

polar oceans in particular, due to the scarcity of information (Legendre *et al.* 1992). Nevertheless, Anderson *et al.* (1990) have stated that the Arctic Ocean will be an active part of the biological pump transferring atmospheric CO_2 into the biogenic food web. An increase in the extent of polynyas and marginal ice zones further north will increase the biological productivity of the Arctic Ocean and the transfer of carbon from the atmosphere to the sea floor. Thus, the Arctic Ocean, despite its relatively small contribution to the world's ocean surface area, may play an important role in the global carbon cycle through enhancement of biological carbon fixation and subsequent sedimentation.

Besides the effects on total biological productivity, a reduction of the sea ice cover and changes in the location of polynyas and the marginal ice zones will have severe impact on several Arctic animals. Endemic ice-related species like the under-ice amphipod *Gammarus wilkitzkii*, or sea ice meiofauna species which are restricted in their distribution to the permanently ice-covered regions, will be diminished. Sea bird rookeries, located at present in the vicinity of polynyas and marginal ice zones, will either follow the receding ice extent, or the breeding success will decrease due to a higher energy consumption of the adults as a result of longer flight distances between feeding source and breeding area.

Endemic pelagic species like *Calanus glacialis* or *Calanus hyperboreus* will come into interspecific competition with sub-Arctic species like *Calanus finnmarchicus*, and the distribution boundaries of high-Arctic species may shift northward as sea-surface warming occurs. These changes in the composition of communities in the various habitats of the Arctic marine environment can be expected at timescales of years to decades and will largely depend on variations in the hydrographical regime, like, for example, the inflow of warm water from the North Atlantic.

The expected warming of the Arctic Ocean will change the structure of the marine communities into a more productive scenario. Harmful effects may be restricted to the flora and fauna living in close association to the Arctic multiyear ice floes. Greater danger to the Arctic marine environment on shorter timescales must be expected through pollution by oil, chlorinated hydrocarbons and radioactive waste, already introduced into the Arctic environment through human activity (Sakshaug & Skjodal 1989).

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