Protists of Arctic Sea Ice

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Abstract Sea ice not only shapes the global climate but is also an important background for a complicated ecosystem that is closely related to the littoral benthic ecosystem. This similarity is the reason why this formation is usually referred to as an "inverted bottom." In the deep central part of the Arctic Basin (which is 47% of its overall surface area), it is estimated that approximately 50% of the primary production comes from autotrophic protists (sympagic) related to sea ice. Global warming has caused changes in the range and time of sea ice occurrence, and the existence time of sea ice assemblages is also changing. After 173 years of ice-related microalgae studies, the appearance of 1027 taxa closely related to sea ice has been recorded.

Keywords Protists · Arctic · Sea ice · Primary production

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1 Introduction

During periods of maximum reach, sea ice covers approximately 12% of the global ocean surface (Weeks [2010\)](#page-13-0). The extensive structure of sea ice creates a type of "inverted bottom" system that is well suited for colonization by protists. The protists in the water column continuously grapple with gravity, the viscosity of the medium and the mixing of the water column. Substrate stability provided by sea ice is extremely important for autotrophic organisms, as they can develop in the sea ice without the risk of falling below the overexposed layer of the sea (the euphotic zone). On the other hand, ice cover acts as a "curtain" that weakens the transmission of light to the under-ice layers. Low values of photosynthetically active radiation (PAR) are compensated by relatively constant levels, which does not hinder the development of autotrophic protists adapted to low levels of PAR. Autotrophic microalgae can settle on the surface and within the porous structure formed by saltwater channels, which are characteristic of sea ice. In contrast to the seabed, movement by water currents or wind-driven ice serves as a vector for transferring coastal residents to the almost unproductive waters of the deep central Arctic Basin.

2 Sea Ice

The Arctic, unlike the Antarctic, is an environment dominated by the sea. The Arctic, surrounded by land is called by some Arctic Mediterranean Sea. The total area of the Arctic Ocean exceeds 14 million km^2 and represents approximately 4% of the global ocean surface. From the autumn to the late spring, the Arctic Sea is mostly covered with sea ice, and the maximum reach occurs in March.

In the age of progressing global warming, sea ice cover has decreased from decade to decade (Kwok and Rothrock [2009\)](#page-13-0). At the end of 2012, sea ice only had an area of 3.6 million km^2 (Fig. [1\)](#page-2-0). The area decreased by 36% from 2000, which represented approximately 5% of the northern hemisphere (Maykut [1985\)](#page-13-0). Ice cover is composed of 80–85% of the sea ice formed at the end of the astronomical winter. The remainder is perennial ice that has survived the melting period, which usually starts in May.

Qualitative changes are simultaneously observed with the loss of sea ice. In the 1980s, 40% of ice was composed of perennial ice, while it has dropped to just 10% in the current decade (Fig. [2\)](#page-3-0). Pessimistic prognoses assume that the perennial ice in the Arctic Basin will completely disappear by 2050 (Assessment [2009](#page-13-0)). The optimists, however, claim that this will occur at the end of the current century (Kwok et al. [2009\)](#page-13-0).

To understand the role of sea ice in the life of the communities associated with it, it is necessary to take a closer look at the processes of its formation. Sea ice begins to form only when sea water (at 35 PSU) cools to approximately −1.8 °C and to−1.3 °C at approximately 24 PSU. The density of sea water that is cooled at the surface in contact with air will increase and gradually fall to the deeper parts of the water column. That dense and cold water is replaced by warmer and lighter water masses at the

Fig. 1 Extent of Arctic sea ice. Source National snow and ice data center

surface, which also fall to deep layers after cooling. This process continues until the water in the top layer of the water column $(50-100 \text{ m})$ cools to the freezing point. First, tiny ice needles (frazil ice) are formed, which are lighter than the surrounding sea water. They flow to the surface and form a delicate, "oily", grease ice coating in windless weather, which thickens as it freezes. During windy weather, pancake ice is formed, consisting of more or less round, disc shaped ice pieces with diameters of 0.2–3 m. When floating to the surface, ice needles act as a plankton net, "scraping" suspended particles in the water. Some authors, e.g., Parker et al. [\(1985](#page-13-0)), believe that

Fig. 2 Qualitative changes to Arctic sea ice. Source National snow and ice data center

the suspension—along with the protist cells floating in the water column, acts as condensation nuclei, by which cooled sea water begins to freeze. Both sea ice forms (grease and pancake) combine into a larger compact coating that isolates the water column from the air and causes the ice to continue to grow only from below, thereby preserving the previously seized particles. After a few days, young ice (more than 10–30 cm thick) is formed. The ice development process lasts from late fall to May/ June. As a result of the insulating properties of ice and the snow layer accumulating on its surface, the rate of increase in the sea ice thickness declines over time. By the end of the spring in the Arctic (April/May), the average thickness of sea ice is up to 2 m (at most up to 3 m), and in warmer areas (e.g., West Spitsbergen), its thickness exceeds one metre.

The ice that has formed appears to be homogeneous at the surface and is similar to a pane of glass. However, it is not. During the formation of sea ice, water forms a crystal structure that does not leave any space for additives such as salt. This means that the salts dissolved in the water must be removed outside the ice. The salt that is pressed out of the ice forms higher salinity sea water with a lower freezing point. As a result, the apparently homogeneous sea ice is, in fact, a heterogeneous structure. Its porosity, which is calculated by the total surface of the unfrozen channels filled with brine, is from 0.6 to 4 m² kg⁻¹ (Krembs et al. [2000\)](#page-13-0). The salinity in brine channels may reach more than 100 PSU (Spindler [1996;](#page-13-0) Bartsch [1989\)](#page-13-0). Values of the 40 PSU (Schünemann [2004\)](#page-13-0), thus exceeding the salinity of the Dead Sea, are not extraordinary. Despite the high salt concentrations in brine, the general salinity in the core of one-year sea ice is relatively low, ranging from 2 to 14 PSU (Maykut [1985\)](#page-13-0), and the salinity is lower if the ice is older. This results in a strong stratification of the water column under ice, with a marked layer of low salinity water at the time of melting. The changes in the salt concentrations associated with the formation and melting of sea ice cause ice-dwelling organisms to face extremely high salinities in the autumn and low salinities in the spring and summer.

2.1 Factors Affecting the Development of Sea Ice Protists

2.1.1 Light

Ice cover is a surface that constitutes an effective barrier for the sun's rays. In circumpolar regions where the supply of light is limited even without the effects of ice, it is a factor that significantly affects the life under the sea. In the Arctic region, especially at high latitudes, extreme light seasonality occurs. This seasonality is noticeable above 60° latitude, where an imbalance between the lengths of day and night is clearly visible (from 6 "bright" hours in the winter to 19 in the summer), and the sun does not rise more than 53° above the horizon. Above the Arctic Circle, the length of the bright period varies from 100 to 200 days. For the remainder of the year, it is at least twilight except for a brief period of days and nights. For this reason, the average annual PAR dose is only 23% of the dose that reaches the surface of the equatorial region.

The low position of the sun over the horizon is, in other words, the acute angle of the sun rays, resulting in a strong reflection of light (albedo) from the surface of the sea, which is multiplied by the presence of ice and snow. The undisturbed sea surface reflects 4% of incident radiation at 40 $^{\circ}$ and approximately 42% at 5 $^{\circ}$ incidence (Jerlov [1968](#page-13-0)). Despite the shrinking sea ice cover in the Arctic, the covered area is still significant. Thus, ice reflects 15 to 90% of the incident radiation. The remaining non-reflected part of the radiation is further weakened as it passes through the snow layer and the ice column. In such a system, the snow dominates the weakening of the passing light. The value of the attenuation coefficient varies depending on the type of the snow (according to the Inuit—the indigenous people of the Arctic and Subarctic areas—there are more than 100 types). The attenuation coefficient varies from 1.5 to 45 m⁻¹ (Palmisano et al. [1987\)](#page-13-0), and the coefficient for the ice column does not exceed 1.6 m−¹ . Depending on the topography of the snow-ice cover, 0.15–7% of the PAR reaches the surface of the sea. The significant total light attenuation has a clear effect on the condition and abundance of sea ice protist (Fig. 3).

Fig. 3 Differentiation of snow-ice cover thickness and its effect on the autotrophic protists associated with ice. a View of a consolidated ice pack. Photo J. Wiktor **b** Measurement based on data from the CASES project (Patchiness experiment)

2.1.2 Hydrological Factors

Other important factors affecting protist development in sea ice are nutrient availability and metabolic activity in low temperatures. Although carbon fixation and the growth of ice protist communities are most efficient in temperatures ranging from 4 to 14 °C (Thomas and Dieckmann [2000\)](#page-13-0), these organisms develop the ability to survive in environments where the temperature may reach −16 °C. Sea ice protists do not freeze internally because of their ability to accumulate a special kind of proteins that prevent ice crystallization—antifreeze proteins (AFPs). It is assumed that the most stable and favourable physical and chemical conditions for protist development are in the lower—approximately 20 cm—layer of the ice, where the most abundant protist assemblages associated with sea ice dwell.

3 Protists

In 1841, Ehrenberg ([1841](#page-13-0)) initiated studies on ice protists and published a list of diatom species that he observed in the sea ice in the area of Spitsbergen and the Barrow Strait in 1853 (Ehrenberg [1853\)](#page-13-0). Therefore, protists have been studied for over 170 years. Three-quarters of a century later, Bursa ([1961\)](#page-13-0) described the ice diatom assemblages of Hudson Bay (Canada). The first studies were executed from ships frozen in sea ice, often for more than one year (sometimes forever). Since then, as the technology has advanced, studies on ice protists have increased. Currently, surveys are based from icebreakers, airplanes and helicopters landing on ice, and progress in materials technology has facilitated the participation in field work.

Despite such a long tradition of research, the question "where do microalgae come from in sea ice" remains, since ice is formed during the polar night or at the end of the polar day period.

To understand this, the "sea ice" section must be revisited, where the processes related to sea ice formation are described. As mentioned earlier, the initial stage of ice formation begins in the fall when few representatives of microalgae remain in the water as residue from the previous growing season. Autotrophs are inactive due to the lack of light but remain as living cells in the water. Tiny needles of frazil ice float to the surface and grab particles from the water column (Garrison [1991\)](#page-13-0), including bacteria, various nano- (smaller than 20 µm) and microplanktonic (larger than 20 µm), photo (autotrophic) and phagotrophic (heterotrophic) organisms. Their abundance usually is low, on the order of one thousand per square metre. In newly formed ice, the abundance of protists can be fifty times higher than in the surrounding sea water (Thomas and Dieckmann [2000](#page-13-0)).

The migration of frazil ice towards the surface is not the only reason for the concentration of protist in sea ice. Cells can also be caught even after ice cover has formed, which occurs via the comb-like structure of the lowermost layer of the sea

Fig. 4 Structures of the lower layer of the sea ice (a) and brine channels (b). *Photos J.* Wiktor

ice. In addition, due to waves and sea tides, the water pressure pushes the microalgae cells into the open saline channels (Fig. 4a, b). So far, studies have demonstrated that the incorporation of cells into the ice during formation is selective, and not all cells survive the drastic changes in the environment (Fig. 5).

Significant developments in sea ice studies have finally allowed the first panarctic list of ice taxa to be generated. So far, 1027 taxa of protists have been indicated,

Fig. 5 Cell concentration in the formed sea ice of Franklin Bay (based on data from Rozanska et al. [2009\)](#page-13-0)

Fig. 6 Taxa associated with Arctic sea ice—Nitzschia frigida (a), N. pelagica (b). Photos J. Wiktor

among which diatoms are the most dominant group (71%) (Poulin et al. [2011\)](#page-13-0), which are most commonly represented by Pennales. Criopelagic taxa are present in ice assemblages, such as shrubby colonies of Nitzschia frigida (Fig. 6a) that are associated with ice and are capable of living in the pelagic environment, band-like colonies of Navicula pelagica (Fig. 6b), Fragilariopsis cylindrus, and F. oceanica. Pauliella taeniata has also been recorded during the spring in the Baltic Sea. Moreover, "heavier", poorly floating representatives belonging to benthic genera such as Pleurosigma (Fig. [7a](#page-8-0)) and *Navicula transitans* have also been found in brine channels. Melosiraceae M. arctica (Fig. [7](#page-8-0)b) has also been associated with ice, which in the summer forms large, branched garlands of algae mats under the sea ice that can reach 3 m in length (Melnikov [1997\)](#page-13-0). Diatoms inhabiting the sea ice are usually relatively large (more than $20 \mu m$); hence, single cells, as well as colonies, are important food bases for the higher trophic levels. The most common species of the centric (Centrales) diatoms is Attheya septentrionalis; however, because of the small size (even for protist), these diatoms rarely dominate the biomass of ice communities. Other representatives of Centrales are mainly taxa belonging to the genus Thalassiosira sp. In addition, Chaetoceros sp. occur only in young ice.

In contrast to pelagic areas, where the biomass and proportion of higher taxonomic groups of autotrophic protists can be roughly estimated from satellite observations (Comiso [2010](#page-13-0)), researchers must rely on field work to determine the

Fig. 7 Taxa associated with ice—Pleurosigma sp. (a), Melosira arctica (b). Photos J. Wiktor

composition of ice algae. It is not possible to take samples without time-consuming and labourious ice cores collection, which is so burdensome that the number of samples is usually limited. The most common tools used to sample ice are cores. This method has advantages as well as disadvantages. Sampling cores sometimes cause damage to the lower, brittle, inhabited layer of the ice, and the quality of the sample depends on the operator's precision. Sea ice sampling can also be conducted by a diver. This is a more onerous method (especially for the diver) and has greater logistical challenges, especially because during the most intensive development of the surveyed communities, the air temperature does not exceed—1 °C. The diver takes samples using cores or pumps, which are similar to underwater vacuum cleaners with a plankton net instead of a bag. Then, the collected ice must be melted. As the sea ice column is characterized by low salinity, considerable amounts of low saline water is released during thawing, exposing the collected organisms to osmotic shock. To prevent this, ice core samples are melted in pre-filtered (to remove planktonic organisms) marine water to maintain the salinity typical for the natural environment. Then, the prepared samples are ready for further analysis. The whole ice sample preparation process is often very invasive and often affects the quality of the results.

Figure [3](#page-4-0) illustrates how variable the ice and snow cover are, and how they result in a patchy distribution of ice communities, which causes uncertainty in the estimations of the protist abundance and biomass. The distribution of sea ice protist communities also depends on the history of the formation of the sea ice, consumer pressure, and the movement of the drifting ice with the currents, which differentiates the density of the assemblages. It causes unpredictable results that are impossible to extrapolate from one area to another—even to the nearest region. Despite the difficulties in the accurate estimation of the abundance of ice protists, we are able to determine that the numbers fluctuate by at least five orders of magnitude $(<10⁴$ to $>10⁹$ under one square metre of ice) (Fig. [8](#page-10-0)). In general, lower values are characteristic of young ice or the upper layer, while high values refer to the ice-water contact layer and the internal spaces in ice that are filled with marine water (Thomas and Dieckmann [2000](#page-13-0)). A high abundance of protists is often visible from the colour of the sea ice (Fig. [4](#page-6-0)).

3.1 Primary Production

Protist biomass is estimated during microscopic analysis or from measured chlorophyll α concentrations with the assumption that most of the unicellular organisms associated with the sea ice are autotrophs. Protist biomass expressed in chlorophyll a concentrations has ranged from 0 to 300 mg m⁻² in the Arctic. While considering the amount of organic carbon, the annual production of autotrophs inhabiting sea ice ranged from 6 to 73 TgC year⁻¹ (Thomas and Dieckmann [2000\)](#page-13-0), and constitutes from 1 to 12.5% of the total primary production in the Arctic (data refer to pelagic primary production estimated by Arrigo et al. [2008\)](#page-13-0). Although compared to pelagic organisms, the amount of organic carbon assimilated by autotrophic ice protists is relatively small. In areas covered with sea ice, they are the exclusive source of organic carbon available for higher trophic levels (Thomas and Dieckmann [2000](#page-13-0)). Although diatoms are the most abundant group in sea ice assemblages and have major contributions to the primary production, the significant role of other organisms in the functioning of sea ice communities has been discovered, including small autotrophic flagellates such as Prymnesiophyceae, Dinoflagellata, Chlorophyta (particularly Prasinophyceae), Chrysophyceae and Cryptophyceae.

Fig. 8 Distribution and abundance of *Nitzschia frigida* in different Arctic regions (Wiktor [2015\)](#page-13-0)

3.2 Beneficiaries of Primary Production

Recently, more attention has been paid to the role of the microbiological loop in the function of communities associated with sea ice. Phagotrophic protists (feeding on previously produced organic matter) control the abundance of bacteria and other unicellular organisms. Through the decomposition of organic matter, simple inorganic compounds are recycled in the environment and become available again for autotrophs. The most important contributors to the total biomass of phagotrophs are flagellates (cells with one or more flagella), including euglenids, *dinoflagellates*, ciliates and tiny nanoflagellates whose taxonomic affiliations have not been determined. Phagotrophic flagellates are a very diverse group of organisms that includes six distinct 'supergroups' of protists, of which the best known are dinoflagellates because of their significant abundance in the environment, considerable size and characteristic morphological features. In the sea ice, dinoflagellates are most often represented by the species of the Protoperidinium sp., Gymnodinium sp., Gyrodinium sp. and Polykrikos sp. genera. These species constitute an important food base for the multicellular organisms associated with the sea ice—from tiny crustaceans (including *Calanoida*, *Amphipoda*) to fish feeding on them (e.g., polar cod Boreogadus saida).

Apart from the fact that ice-associated communities function as a food base, the biological pump also plays an important role in the binding and deposition of excess carbon dioxide. During the melting period, protists are released to the marine water column. Under light, thermal and osmotic stress, cells die (Fig. 9) and fall to the bottom (e.g., Central Arctic Basin where the bottom depth reaches over 2000 m), where are deposited in the sediments without the possibility of return to the surface.

Fig. 9 Aggregates of dead sea ice protists during the ice melting period. Photo J. E. Ross

4 What Is Next?

In the time of shrinking sea ice cover, we have to face the question of what comes next for the sea ice associated protists. It could be said that since the ice will disappear, there will also be fewer protists. However, the answer to this question may not be so simple. The answer is complicated because the most severe loss of sea ice has been recorded in the summer. It is often said that the record (usually the minimum) extent of sea ice is recorded at the end of the season in September when the ice begins to form again. Sea ice formation, which is often late, continues in the spring during the time of autotroph blooms. Therefore, protists will not lose too much of their "favourite" habitat.

However, the substrate itself is not everything. The analysis of ice sheet anomalies indicates a decrease compared to the 1979–2000 average (NSIDC). Ice decline is greatest in the most productive Arctic shelf areas. Lower compactness of the ice cover results in a higher total surface area of the crevasses (windows). Although sea ice associated autotrophic organisms may have more light available, excess light can destroy shade-loving organisms. Dead diatom cell aggregates have been observed near crevasses by the authors. An example of how light adversely affects the abundance of autotrophs is presented as the temporary variability of protist obtained during studies in northern Svalbard (Fig. 10). Another scenario of climate change predicts the appearance of a thicker layer of snow on thinner ice; thus, the amount of light reaching the lower layer of the sea ice will decrease.

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Fig. 10 Temporal variation the number of cells in sea ice associated assemblages (a) and PAR doses in Ripfjorden (Nordaustlandet) (b) (Source Data based on database of Cleopatra project)

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