

Characteristics and variations of the picophytoplankton community in the Arctic Ocean

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Abstract Picophytoplankton are responsible for much of the carbon fixation process in the Arctic Ocean, and they play an important role in active microbial food webs. The climate of the Arctic Ocean has changed in recent years, and picophytoplankton, as the most vulnerable part of the high-latitude pelagic ecosystem, have been the focus of an increasing number of scientific studies. This paper reviews and summarizes research on the characteristics of picophytoplankton in the Arctic Ocean, including their abundance, biomass, spatial distribution, seasonal variation, community structure, and factors influencing their growth. The impact of climate change on the Arctic Ocean picophytoplankton community is discussed, and future research directions are considered.

Keywords Arctic Ocean, picophytoplankton, climate change, review

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0 Introduction

The Arctic Ocean has been a semi-enclosed basin for 60–100 million years^[1-2], and throughout this period it has slowly exchanged surface waters with other oceanic regions^[3]. The special characteristics of physical isolation, perennially low water temperatures, and extreme cycles of polar day and night, mean that the Arctic Ocean provides a unique marine habitat for organisms, and is very sensitive to climate change^[4].

Climate change is already evident in the Arctic Ocean. The temperature of the Arctic system has been increasing over the past 100 years^[5], and as a result the extent of sea ice coverage has declined^[6]. Some models predict that the Arctic Ocean will be ice-free in summer by 2040^[7].

Picophytoplankton are photosynthetic plankton with a diameter <2 μm, including three cell types, cyanobacteria (*Synechococcus*), *Prochlorococcus*, and picoeukaryotes, although *Prochlorococcus* have not been reported in the Arctic Ocean. Picophytoplankton contribute substantially to

both total phytoplankton biomass and production in marine ecosystems, especially in oligotrophic waters where they can account for up to 90% of the total photosynthetic biomass and carbon production^[8-9]. Recent studies show that the Arctic Ocean has active microbial food webs that are often dominated by cells with a diameter <3 μm^[10-11], and that cells <5 μm in diameter are responsible for much of the carbon fixation over wide regions in the Arctic Basin^[12-13]. Picophytoplankton have a large surface-area-to-volume ratio, which facilitates effective acquisition of nutrient solutes and photons, and provides hydrodynamic resistance to sinking^[14]. As climate changes, these cells could be expected to increase in number in a regime of lower nitrate supply and greater hydrodynamic stability^[15]. Therefore, as one of the most sensitive components of high-latitude pelagic ecosystems, picophytoplankton could be viewed as both sentinels and amplifiers of global climate change^[16].

The aim of this paper is to summarize research on the characteristics and variation of picophytoplankton in the Arctic Ocean, including studies on picophytoplankton abundance, biomass, spatial distribution, seasonal variation, community structure and influencing factors, and the impact of climate change on picophytoplankton growth. We also discuss the prospects for future study in this field. It

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should be noted that picophytoplankton are defined as phytoplankton with a diameter $<2\ \mu\text{m}$, however, some of the reviewed studies focused on cells with a diameter $<5\ \mu\text{m}$, referred to as ultraphytoplankton. Therefore, for this paper, we reviewed studies on both picophytoplankton and ultraphytoplankton.

1 Abundance and biomass

1.1 Central Arctic Ocean

Recent studies have revealed a more dynamic carbon cycle in the surface waters of the Arctic Ocean^[12,17] than previously estimated^[18]. Research has also shown that picophytoplankton dominate the phytoplankton biomass and production in central Arctic waters^[12,19]. Booth and Horner^[19] discovered that picophytoplankton in the Canada and Makarov Basins contributed 93% to autotroph cell numbers ($1\ 300\text{--}10\ 020\ \text{cells}\cdot\text{mL}^{-1}$) and 36% to autotroph biomass ($1.0\text{--}7.1\ \mu\text{g}\cdot\text{C}\cdot\text{L}^{-1}$). Sherr et al.^[11] showed that autotrophic protists were numerically dominated by cells sized $<5\ \mu\text{m}$, which made up 44%–99% (average 95%) of cells in the phytoplankton assemblage during the growing season in the upper water column of the central Arctic Ocean. Lee and Whitlege^[13] found that small phytoplankton ($0.7\text{--}5\ \mu\text{m}$) represented about 70% of the total phytoplankton biomass in the upper mixed layer over all open-water stations during summer in the Canada Basin. However, the mean proportion decreased to 44.4% of the total biomass in the chlorophyll-maximum layer, in spite of high variability^[13]. Therefore, picophytoplankton are dominant organisms in the oligotrophic, strongly stratified central Arctic Ocean, especially in the upper layers.

In the Arctic, polynyas are open water regions surrounded by sea ice^[20]. Polynyas have been referred to as the oases of the Arctic because of their high productivity. Working on the Northeast Water Polynya, located in the permanent Arctic ice pack on the North East Greenland Shelf, Pesant et al.^[21] found that small phytoplankton cells ($<5\ \mu\text{m}$) dominated both the biomass and primary production in heavy ice-covered waters, while in open water, and in waters with mixed-ice conditions, the biomass was dominated by large ($>5\ \mu\text{m}$) phytoplankton, and primary production was shared between small and large cells. Size-fractionation experiments conducted by Legendre et al.^[22] in the marginal ice zone in the Greenland Sea also revealed that the phytoplankton biomass was dominated by small cells ($<5\ \mu\text{m}$), and the primary production was shared between small and large cells depending on the hydrographical conditions.

1.2 Arctic shelves and adjacent seas

The distribution of picophytoplankton in the waters of the Arctic shelves and adjacent seas has been studied extensively. The abundance and biomass on Arctic shelves varied greatly in response to differences in ice (e.g., concentration, thickness, duration), riverine input (e.g., nutrients, particles),

and ocean forcing (e.g., through flow, upwelling, wind, and tidal mixing)^[23].

Cottrell and Kirchman^[24] studied the coastal waters of the Chukchi and Beaufort Seas and found the abundance of Chl *a*-containing picoeukaryotes in summer was about $5.4\times 10^3\ \text{cells}\cdot\text{mL}^{-1}$. Not et al.^[25] discovered that the picoeukaryotic community at the boundary between the Norwegian, Greenland, and Barents Seas, was primarily composed of photoautotrophs in late summer (75% of the cells on average), and on average 44% of the Chl *a* biomass in this region could be attributed to picophytoplankton (including *Synechococcus* and picoeukaryotes). Schloss et al.^[26] found that picophytoplankton represented an average of 71% of total cells ($<20\ \mu\text{m}$) in the southeastern Beaufort Sea (Mackenzie Shelf and Amundsen Gulf regions). The highest concentration of picophytoplankton cells was $13\ 810\ \text{cells}\cdot\text{mL}^{-1}$ in the area influenced by the Mackenzie River, while the lowest concentration was $<1\ 500\ \text{cells}\cdot\text{mL}^{-1}$ in the vicinity of the Amundsen Gulf^[26]. Wang et al.^[27] found that autotrophic picoflagellate abundance in Kongsfjorden, Svalbard, ranged from $46\text{--}35\ 200\ \text{cells}\cdot\text{mL}^{-1}$, while autotrophic nanoflagellate abundance ranged from $40\text{--}4\ 600\ \text{cells}\cdot\text{mL}^{-1}$.

The above studies demonstrate that picophytoplankton are dominant organisms in the oligotrophic, strongly stratified waters of the Arctic Basin, and also in the coastal regions, and areas strongly influenced by inflows of fresh water.

2 Seasonal variation

In the Arctic, all groups of pelagic microbes respond strongly to the large annual variation in the amplitude of solar radiation, generally with lower biomass in spring, higher biomass during the short summer growing season (June–September), and decreasing biomass during autumn and winter. Among them, phytoplankton show the largest variation in seasonal abundance and biomass, and there is a rapid increase in phytoplankton stocks in June, after winter snow cover melts from the ice surface^[11]. Recent studies have shown that picophytoplankton play an increasingly important role in pelagic microbe systems, and that their abundance changes significantly with the seasons^[28–31].

In spring, the initial bloom takes place, and different stages of the spring bloom are dominated by phytoplankton of different sizes. The traditional view was that the pre- and post-bloom periods were dominated by small cells like picophytoplankton^[28–29], while the bloom period itself was dominated by larger cells. However, in a recent study, Hodal and Kristiansen^[30] investigated the phytoplankton in spring blooms at the marginal ice zone in the northern Barents Sea, and demonstrated that small cells dominated both biomass and primary production at the early- and late-bloom stages (71% and 63% of total Chl *a* concentrations, respectively), while within an ongoing bloom, large cells only dominated during the narrow period at the peak of the bloom. Hancke^[31] also found that the peak bloom group was dominated by diatoms while the early- and

late-bloom groups were more diverse and dominated by small cells like prymnesiophytes. Therefore, these recent studies have shown that, in some regions of the Arctic Ocean, picophytoplankton are dominant over more of the bloom period than previously reported.

Many studies have focused on picophytoplankton, and have found these organisms to be relatively abundant during summer and early autumn in different regions of the

Arctic Ocean (Table 1), with one or two blooms occurring regularly in summer. However, Sherr et al.^[11] studied the autotrophic microbes in the upper water column of the central Arctic Ocean and observed three distinct blooms over the summer. The initial bloom consisted of diatoms and phytoflagellates, mainly 2 μm -sized *Micromonas* sp., while the two subsequent blooms were dominated by the flagellated non-colonial *Phaeocystis* sp. (4–6 μm in diameter)^[11].

Table 1 Picophytoplankton and nanophytoplankton abundance in the Arctic Ocean

Regions	Groups	Abundance/ (10^3 cells·mL ⁻¹)	Method	Season	Reference
Central Arctic Ocean (Canada and Makarov Basins)	Pico-	1.3–10.02	EFM; LM	Late summer	[18]
Greenland Norwegian and Barents Sea (GNB)	Pico-	3–15	EFM; FCM	Late summer	[24]
Southeastern Beaufort Sea (Mackenzie Shelf and Amundsen Gulf)	Pico-	1.5–13.81	FCM	Autumn	[25]
	Nano-	0.003–2.90			
Coastal waters of the Chukchi Sea and the Beaufort Sea	Pico-	$5.37 \pm 1.83^*$	FCM	Summer	[23]
	Pico-	0.046–35.2			
Kongfjorden, Svalbard	Pico-	0.036–4.6	EFM	Late summer	[26]
	Nano-				

Note: “*”: on average; FCM: flow cytometry; EFM: epifluorescence microscopy; LM: inverted light microscopy.

In autumn, especially in the transition period from late summer to early autumn, some differences in picophytoplankton abundance have been observed. As shown in Table 1, in some regions, particularly the southeastern Beaufort Sea, picophytoplankton were as abundant (1.5×10^3 – 13.81×10^3 cells·mL⁻¹) in autumn as in summer in other regions. A lot of nutrients are consumed by algal blooms during summer, and nutrient concentrations are relatively low in autumn. Because of their large surface-area-to-volume ratio picophytoplankton take up nutrients efficiently even at low concentrations, which might explain their abundance at the surface layer in autumn^[26].

There has been little research on phytoplankton in winter because logistical support is challenging and limited. Sherr et al.^[11] found persistent stocks of heterotrophic and autotrophic microbes during winter months, but the cell abundance was low. The winter stocks consisted of pico- and nanoflagellates, mainly *Micromonas* sp., and unidentified haptophytes, with an abundance of hundreds of cells·mL⁻¹, and diatoms and pigmented dinoflagellates >20 μm in diameter, with an abundance of about 1 cell·mL⁻¹^[11]. Cottrell and Kirchman^[24] found Chl *a*-containing picoeukaryotes decreased 200-fold, from 5.4×10^3 cells·mL⁻¹ in summer to 0.02×10^3 cells·mL⁻¹ in winter, probably reflecting the cessation of primary production during winter darkness.

3 Community structure

3.1 Diversity

Lovejoy et al.^[32] analyzed microbial eukaryote diversity during the summer of 2002, focusing on picoeukaryotes (<3 μm -diameter cells) in the Beaufort Sea, the Greenland, Norwegian, and Barents Seas (GNB), and the Arctic Ocean,

using 18S rRNA gene clone libraries. The ribotypes were diverse and picophytoplankton mainly included phototrophic stramenopiles, with sequences related to dictyochophytes, diatoms and bolidophytes. Alveolates were also identified, with similarity to dinoflagellates, and sequences for other algae were recovered, including cryptophytes from the Beaufort Sea, a haptophyte from the GNB, and prasinophytes, including *Bathycoccus*, *Micromonas*, and *Mantoniella*^[32]. The diversity of picoprasinophytes was further discussed by Lovejoy et al.^[33] in 2007. Not et al.^[34] identified a novel group, picobiliphytes, within the photosynthetic stramenopiles, and proposed that it was an independent lineage, possibly with a weak sister relationship to the cryptophyte/katablepharid clade.

The Arctic has proved to be a rich source of microbes with novel genetic sequences. In the study conducted by Lovejoy et al.^[32], 42% of sequences recovered had less than 98% similarity to any sequences in GenBank. Furthermore, 15% of these sequences had less than 95% similarity to any previously recovered sequences. These results indicate the existence of endemic or under-sampled taxa in the Arctic Ocean environment^[32].

3.2 Cyanobacteria

Synechococcus and *Prochlorococcus* are two main representative groups of marine cyanobacteria. The almost complete absence of *Prochlorococcus* in the Arctic Ocean might be a result of the ecological differentiation caused by the low temperature of the Arctic waters. It is likely that geographical isolation and natural selection also contribute to the lack of *Prochlorococcus* in the Arctic Ocean^[24,35].

Synechococcus abundance was lower in the Arctic Ocean than in temperate and tropical waters, and this group was also absent in the central region of the Arctic Ocean^[36].

Their poor performance in the Arctic might be caused by their temperature-depressed growth rates, and a resulting inability to keep up with grazing by nanoflagellates, ciliates and other fine-particle collectors^[35,37]. Studies have shown a higher abundance of *Synechococcus* in the Beaufort Sea coastal waters ($3.503\text{--}6.713\times 10^3$ cells·mL⁻¹) than other Arctic waters, including the Chukchi Sea ($4\text{--}80$ cells·mL⁻¹), the Greenland Sea ($0\text{--}1.079\times 10^3$ cells·mL⁻¹), and the Canada Basin ($0\text{--}6.0\times 10^2$ cells·mL⁻¹)^[24,33,36,38]. The discharge of the warmer, fresher, nutrient rich waters from the Mackenzie River might explain the higher abundance in the Beaufort Sea coastal waters.

Research into the diversity of the Arctic *Synechococcus* is still very limited. One study using 16S ribosomal gene sequencing of *Synechococcus* showed that a *Synechococcus* rich in phycocyanin, sampled from the Canada Basin, was most similar (98%–99%) to *Microcystis elabens*, a common species of freshwater phytoplankton^[35], while Waleron et al.^[38] found that *Synechococcus* from the coastal waters of the western Canadian Arctic Ocean were closely related to freshwater and brackish *Synechococcus*. No typically marine *Synechococcus* sequences were recovered^[38]. These findings support the hypothesis of an allochthonous origin of cyanobacteria in the coastal regions of the Arctic Ocean, from the Mackenzie River and other nearby inflows, and are also consistent with the survival but little net growth of cyanobacteria under present conditions in northern high-latitude seas^[38].

3.3 Picoprasinophytes

Slapeta et al.^[39] studied the *Micromonas* ecotype and its global dispersal, and Lovejoy et al.^[33] examined and summarized the biogeography, diversity, and growth characteristics of picoprasinophytes, especially the *Micromonas* ecotype, in the Arctic. In combination with records from earlier research on Arctic Ocean phytoplankton, these studies provided broad evidence that picoprasinophytes are spatially and temporally prevalent throughout the Arctic region^[11,19,25,40].

A widely accepted oceanographic paradigm is that photosynthetic picoplanktonic cyanobacteria are continuously abundant in the ocean, while larger-celled eukaryotes including diatoms, prymnesiophytes, and dinoflagellates rise above this phototrophic background and produce seasonal blooms under specific hydrographic conditions^[41]. An unusual feature of Arctic marine ecosystems is that the background population of cyanobacteria is conspicuously absent or sparse. Therefore, in the Arctic Ocean picoprasinophytes have replaced cyanobacteria in the baseline community and persist throughout all seasons. Lovejoy et al.^[33] determined that the Arctic Ocean *Micromonas* ecotype was a unique pan-Arctic form that differed genetically, and in terms of growth characteristics, from *Micromonas pusilla* clades collected elsewhere in the world.

Bathycoccus also form part of the baseline picophytoplankton community in the Arctic, replacing cyanobacteria.

Not et al.^[25] first reported their existence in the GNB, and Lovejoy et al.^[33] found they were widely distributed in northern waters. Furthermore, the genetic variability of *Bathycoccus* was much less than for *Micromonas*^[33,42].

3.4 Other dominant picoeukaryotes

After prasinophytes, prymnesiophytes (haptophyta) are the second most dominant picoeukaryotes in the Arctic Ocean. During the 1994 AOS expedition across the polar cover, Booth and Horner^[19] found maximum abundances for flagellated *Phaeocystis pouchetii* and 2 μm phytoflagellates (tentatively identified as *Micromonas pusilla*) of 470 and 10 000 cells·mL⁻¹ respectively. The importance of haptophyta pigment signatures in the pico-size fraction has been demonstrated in many oceanic regions^[43]. Among the three blooms observed by Sherr et al.^[11] in the upper water column of the central Arctic Ocean, the last two were dominated by flagellated non-colonial *Phaeocystis* sp. (4–6 μm in size) with a peak abundance of 18 000 cells·mL⁻¹. Haptophyta have also been found in the GNB^[25,32].

4 Influencing factors

4.1 Nutrients and light

In the oligotrophic waters of high-latitude Arctic seas, low levels of nutrients have been considered to be the limiting factor for phytoplankton blooms^[44–45]. However, according to the resource competition theory, small cells, with large surface-area-to-volume ratios, are more effective in the acquisition of nutrient solutes and photons^[46]. Therefore, they are likely to be predominant in oligotrophic waters, and their dominant biomass and cell abundance in the central Arctic Ocean supports this viewpoint. In both the Northeast Water Polynya and the North Water (NW), *Micromonas* was found in ice-free areas when nitrate was at a low concentration (0.83 μM in the Northeast Water Polynya, and 0.1–0.7 μM in the NW)^[47].

Phytoplankton blooms in summer consume a large amount of nutrients, and therefore picophytoplankton might predominate at the surface layer in autumn or late summer. When NO₃⁻ was almost depleted in the upper mixed layer of open-water stations in the Canada Basin, small phytoplankton (0.7–5 μm) represented 69.3% (SD = ±10.6%) of the total phytoplankton biomass at the surface^[13]. Schloss et al.^[26] found that picophytoplankton were the most abundant phytoplankton during the autumn season, probably reflecting low nitrate concentrations (surface waters average = 0.65 μM). In all the transects sampled by Not et al.^[25], abundance of picoeukaryotes greater than 4 000 cells·mL⁻¹ was always restricted to the uppermost 30 m of the water column.

There have been some studies on light intensity and ultraviolet radiation, and their influence on the phytoplankton community and growth in the Arctic Ocean^[48–49], but few have focused on picophytoplankton.

4.2 Temperature and salinity

Phytoplankton community composition is influenced by the stable cold temperature of high-latitude waters, which selects for specific species in polar seas. Picophytoplankton in Arctic waters are mainly composed of psychrotrophics and psychrophilics, and as typical representatives of picophytoplankton, cyanobacteria were found to be psychrotrophic rather than psychrophilic^[37]. They were tolerant to cold water conditions, with low growth rates under cold ambient temperatures, while their optimum temperature for growth was higher than 15°C^[37]. In contrast, *Micromonas*, the dominant species in the high-latitude waters, preferred lower temperatures (optimal growth at 6–8°C), showed impaired growth rates at 12.5°C, and failed to grow at 15°C in laboratory tests^[33].

Within the temperature range of Arctic waters, the distribution of picophytoplankton indicated a preference for warmer and less saline waters, typically surface layers and areas of fresh water discharge. Schloss et al.^[26] reported that the environmental variable salinity was well correlated with phytoplankton abundance, especially with the most abundant phytoplankton group, the picophytoplankton. They found picophytoplankton abundance was significantly higher in low-salinity and high-temperature surface waters (above 10 m) than in deeper waters^[26]. Significantly higher picophytoplankton abundances were also found in water masses with relatively higher temperatures and lower salinity, such as the Mackenzie River (MR) plume and ice melt waters, as compared to all other water masses^[26]. Waleron et al.^[38] studied the input of cyanobacteria and picoeukaryotes to coastal waters of the Arctic Ocean from the Mackenzie River, and found them to be allochthonous, and typically land-derived, and consequently cyanobacteria and picoeukaryotes were more abundant in surface waters.

4.3 Water masses

The Arctic Ocean is a semi-enclosed basin, and various water masses with different chemical and physical characteristics flow into it. As a result, the picophytoplankton community structure and distribution may be influenced by the factors discussed above.

Lovejoy et al.^[32] found that pico-size phototrophic stramenopiles from the Arctic Ocean were mostly araphid diatoms, while centric diatoms and bolidophytes were recovered from the GNB. They proposed that the difference was likely a consequence of the histories of the water masses^[32]. The GNB cuts across southward-flowing Arctic water and northward-flowing Atlantic water, which is relatively low in silicic acid required for diatom growth^[25]. In contrast, Pacific water, which is the source of the upper mixed layer of the western Arctic Ocean, is high in silicic acid^[50-51].

Even on small scales, water masses can have an influence on picophytoplankton community structure and distribution^[52]. Mostajir et al.^[53] reported that a surface current

flows northward along the western coast of Greenland in autumn, bringing warmer, more saline water to the eastern part of the NOW, while surface Arctic water (colder, less saline) coming from the Kane Basin flows southward along the western part of the NOW. These two distinct water masses, with their different physical and chemical characteristics, govern picophytoplankton and nanophytoplankton distributions in the NOW during the autumn^[53]. The findings of Schloss et al.^[26], on abundance in ice melt waters as discussed above, also supports the influence of small scale water masses on picophytoplankton community structure and distribution^[26].

The inflow of fresh water from several rivers also contributes significantly to production over the Arctic shelves. The Mackenzie River, the largest input to the Beaufort Sea-Mackenzie Shelf region, introduces a great deal of fresh water, dissolved organic matter (DOM), particulate organic matter (POM), and planktonic cells to the Beaufort Sea^[32-33,38,54-56]. Schloss et al.^[26] also found maximum pico- and nanophytoplankton cell concentrations in the area influenced by the Mackenzie River.

4.4 Biotic factors

In addition to abiotic factors, biotic factors also have an important influence on picophytoplankton in the Arctic Ocean. As primary producers in the microbial loop, picophytoplankton play an important role in the conversion of POM and DOM, but they are also influenced by the presence and activities of other microbes, including grazing by herbivorous protozoa, interactions with bacteria, and lysis by viruses.

To date, few studies have focused on the influence of bacteria and viruses on picophytoplankton, but there has been some research on the grazing of picophytoplankton by herbivorous protozoa in the Arctic Ocean. In the central Barents Sea, phytoplankton growth and microzooplankton grazing rates were closely coupled during early summer^[57]. Dilution experiments showed that grazing losses ranged from 64%–97% of daily Chl *a* production, and were greater for smaller size fractions^[57]. Sherr et al.^[58] conducted the first study of microzooplankton grazing impact on phytoplankton in the western Arctic Ocean during spring and summer, in an area encompassing parts of the Chukchi Sea, the Beaufort Sea, and the Canada Basin. Their dilution experiments revealed that, on average, microzooplankton grazing consumed only 22±26% of phytoplankton daily growth^[58]. The lower grazing rates found by Sherr et al.^[58] might be explained by the low temperature limitation to the growth of herbivorous heterotrophic protists, because the abundance variation of phytoplankton and heterotrophic bacteria is always coupled. In the central Arctic Ocean, when algal blooms were dominated by small-sized cells, the stocks of bacteria and heterotrophic protists also increased, with no time delay^[11].

5 Community and climate change

5.1 Ecological winners in the central Arctic Ocean

Climate change is already evident in the Arctic Ocean, with the retraction of sea ice, higher water temperatures, increased input of riverine waters, and other physical characteristics^[5-7]. These changes have been accompanied by variations in phytoplankton communities.

As global climate changes, conditions will favor some organisms more than others, and there will be ecological winners and losers. Melting sea ice, combined with increasing input from large river runoff, is affecting the physical characteristics of the Arctic Ocean. Li et al.^[14] carried out environmental monitoring of the Canada Basin during 2004—2008, and observed warming, freshening, decreasing density, and decreasing nutrient levels in the upper water layer. In contrast, the density and nutrient levels in the deep water layer were maintained, resulting in stronger stratification and greater hydrodynamic stability of the water column^[14]. These changes were accompanied by a shift in phytoplankton size structure towards small microbial eukaryotes, and cold-adapted picoprasinophytes^[14]. The fossil record suggests that, over the past 34 million years, the average size of diatoms has decreased by almost a factor of triple^[59]. Isotopic analyses of benthic and planktonic foraminifera have indicated that this decline in size was correlated with an increase in thermal stratification or stability, similar to the changes currently taking place in the central Arctic Ocean.

Small cells are much less efficiently transferred within marine food webs relative to larger phytoplankton, and they are also less subject to sinking losses in stratified, nutrient poor conditions. Consequently, it is possible that less biogenic carbon will be exported either for extraction (e.g., harvest), or for sequestration (e.g., burial), and the organic carbon export to fish communities and benthic ecosystems will be altered. Such effects could be enhanced by warmer temperatures that speed up respiration and microbial loop processes^[14,16]. However, the exact extent of these proposed shifts is unknown and further monitoring is required. Moreover, in eukaryotic phytoplankton, cell size is positively correlated with genome size and genome-size evolution. Consequently, climate-driven changes potentially alter the genomic structure and the evolution tempo of marine eukaryotic microorganisms^[60].

5.2 Competition between cyanobacteria and *Micromonas*

The unique pan-Arctic ecotype, *Micromonas*, displays a narrow thermal niche in keeping with the stable cold-temperature regime of high-latitude seas^[33,61]. However, polar cyanobacteria tend to be cold tolerant rather than psychrophilic, with slow growth rates under cold ambient temperatures and a preference for warmer temperatures^[37]. Many lakes and ponds melt out over the ice shelves in

summer, and these waters contain bottom sediments and benthic microbial mats. The main biomass constituents of the mats are oscillatorian cyanobacteria^[62]. As discussed above, cyanobacteria have already been identified in estuaries and continental shelf regions of the Arctic Ocean. As the Arctic Ocean warms it becomes more susceptible to invasive species from the south. Cyanobacteria may eventually replace picoprasinophytes, and the arrival of harmful algal bloom species may result in the modification of dinoflagellate assemblages. Cyanobacteria are still absent or sparsely distributed in Arctic waters, but their abundance is likely to increase with increasing water temperatures.

5.3 Lack of biodiversity

The uniquely polar phylotypes are a vulnerable component of global genetic diversity. Lovejoy et al.^[32] found a surprising lack of picoeukaryote diversity in the Arctic Ocean compared with other waters. The Arctic has historically been covered with thick multiyear ice, but in 2002 warm conditions caused a retraction of the ice cover over the western Arctic, exposing the underlying waters to high surface irradiance for the first time^[50]. The depauperate microbial assemblages, rare colonizers of marine species, may reflect the limitation of nutrient supply in this region^[32]. This phenomenon is similar to primary succession on land following glacial retreat. With the continued decline in annual sea ice, and the ongoing effects of climate change, such conditions may be increasingly common in this region, and the variations and adaptations of these colonizers in response to the new environment warrant further study.

6 Conclusions and prospects for future research

As discussed above, picophytoplankton are widely distributed in the Arctic Ocean, and display obvious seasonal variation, with relatively high abundance in hydrodynamically stable waters and areas of fresh water discharge. Generally, they prefer oligotrophic waters with relatively higher temperature and lower salinity. An unusual feature of the Arctic marine ecosystems is that Arctic Ocean picoprasinophytes replace cyanobacteria, and form the basis of the picophytoplankton community throughout all seasons. Compared with other regions, the biodiversity of picoeukaryotes in the Arctic Ocean is quite low. However, the Arctic Ocean has proved to be a rich source of novel sequences. With changing climate, the natural selectivity of picophytoplankton as ecological winners has already taken place in the central Arctic Ocean, further confirming that this pelagic ecosystem is very sensitive to change, and indicating that picophytoplankton can serve as both sentinels and amplifiers of global climate change.

Current studies on picophytoplankton community structure in the Arctic Ocean have focused on the North Atlantic sector, with little research on the Pacific sector. Therefore, there is a lack of information on the temporal

and spatial variation and community structure of picophytoplankton across the whole Arctic Ocean. Further studies on the association between the ecological functions of picophytoplankton and biodiversity are warranted. Climate change has already occurred in the Arctic, and some regions, including the central Arctic Ocean, show evidence of marked and rapid changes. More research is needed to determine the contribution of picophytoplankton to ecological change, and to clarify their role in carbon fixation, and in carbon and energy cycles. The response of picophytoplankton to climate change, especially physiological readaptation strategies to light, temperature, salinity, and nutrient variations, needs to be better understood. The influence of these changes on other members of the microbial loop, the impact on species at higher trophic levels, and effects on the entire marine environment over time, are also areas for further study.

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