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Flow cytometric investigation and comparison of *Synechococcus* spp. pico-, nano- and microplankton in the Arctic and Antarctic polar regions during the summer period of 2019

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ABSTRACT

In the present study, *Synechococcus* spp. pico-, nano- and microplankton community compositions in the Arctic and Antarctic surface coastal waters were compared during the summer of 2019 using flow cytometry. The average surface water temperatures in Antarctica and the Arctic were -0.29 ± 0.28°C and 3.71 ± 0.71°C, respectively. While plankton abundance in Antarctica exhibited a relative increase with temperature, plankton abundance in the Arctic exhibited a relative decrease with temperature. However, no significant correlation was found between plankton abundance and temperature. *Synechococcus* spp. cell abundance dominated in both polar regions, followed by picoeukaryotes, microautotrophs and nanoeukaryotes. Overall, plankton abundance across sampling sites was highly variable. In Antarctica, the abundance of *Synechococcus* spp., picoeukaryotes, nanoeukaryotes and microautotrophs were the highest in S4 (151,400 cells/ml), S1 (2180 cells/ml), S2 (1080 cells/ml) and S4 (6100 cells/ml), respectively. On the other hand, the most abundant stations in the Arctic in terms of *Synechococcus* spp., picoeukaryotes, nanoeukaryotes and microautotrophs were N2 (19600 cells/ml), N3 (6400 cells/ml), N3 (500 cells/ml) and N4 (6100 cells/ml), respectively. While *Synechococcus* spp. and nanoeukaryote abundance were higher in Antarctica, only *Synechococcus* spp. abundance was significantly higher in Antarctica.

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Introduction

The polar regions, encompassing the Arctic and Antarctic, play a crucial role in the global climate system and marine ecosystems due to their unique physical, chemical and biological characteristics (Murphy et al. 2016; Screen et al. 2018). One of the key components of these ecosystems is the microbial assemblage, including phytoplankton, which forms the foundation of the marine food web and contributes significantly to primary production. Marine ecosystems are experiencing a set of unprecedented environmental changes with the increase of global temperature (Doney et al. 2012; Poloczanska et al. 2013; Constable et al. 2022). Among these, polar marine ecosystems are the most vulnerable (Parry 2007). Environmental changes in the polar regions are expected to change physical and chemical properties and create shifts in the community structure of living organisms and change species composition, especially those inhabiting the marine environment (Schofield et al. 2010; Murphy et al. 2016; Neukermans et al. 2018). Although there is extensive knowledge on melting rate of glaciers and changes in water in the polar ecosystems, how this process affects the marine biogeochemistry and biological productivity is unclear (Hopwood et al. 2020).

Primary producers in marine ecosystems have critical influence on the biological production and biogeochemical cycles (Flombaum et al. 2013). Cyanobacteria are the main primary producers in the polar regions (Kvíderová et al. 2019). *Synechococcus* spp. (0.8–1.5 µm) is the most common genera under the phylum and it is attributed to approximately 21% of global oceanic net primary production (Jardillier et al.

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2010). Temperature is the primary environmental factor driving global *Synechococcus* spp. distribution (Flombaum et al. 2013). Picoplankton is the smallest fraction of phytoplankton in marine ecosystems, including archaea, prokaryotic and eukaryotic unicellular organisms that are between 0.2–2.0 µm in size (Falkowski et al. 2008). The group is the most abundant autotrophic phytoplankton in most marine ecosystems as well as the Arctic and Antarctic (Degerlund and Eilertsen 2010; Gaulke et al. 2010; Zhang et al. 2015; Otero-Ferrer et al. 2018). Nanophytoplankton (2–20 µm) includes completely eukaryotic flagellates such as haptophytes, cryptophytes, prasinophytes, small diatoms and dinoflagellates (Wright et al. 2009; Vanzan et al. 2015). The group comprises more than 50% of chlorophyll-a biomass in Antarctic waters.

Due to the harsh environment and the complexity of food webs, the information gathered from polar studies is valuable for future studies on the impact of climate change and marine food webs. The summer is a crucial time in polar marine ecosystems, marked by extensive sunlight, ice melt and nutrient availability, which collectively drive primary production and support a range of trophic interactions (Arrigo 2014). Flow cytometry has been an important tool in plankton research thanks to allowing rapid quantitative observation of individual cells. The groups of plankton constitute the food source for unicellular or multicellular edible zooplankton. In this study, pico-, nano- and microplankton compositions of Antarctica and the Arctic coastal surface waters were compared and differences and similarities of size group and planktonic formation at both poles were assessed in the same year with the flow cytometric method. This comparison not only provided data for understanding the food chain but also allowed a comparison of the lower food layers at both poles in the same year.

Materials and method

Sampling

Turkish Arctic and Antarctic expeditions took place during the summer of 2019 at both poles. Antarctica sampling was performed during the third Turkish Antarctic expedition (TAE-III), supported by the Ministry of Industry and Technology (Türkiye), in the austral summer between 4–28 February 2019. Surface water samples (5 m depth) were collected by Betanzos R/V from 8 sampling sites located on the western Antarctic Peninsula using 5 l Niskin bottles operated with the messenger (Table I, Figure 1A).

Arctic sampling was performed during the Turkish Arctic scientific expedition supported by the Türkiye İş Bankası, in the summer between 14–20 July 2019. Surface water samples (5 m depth) were collected by Anakena R/V from 7 sampling sites located on the western coasts of the Svalbard archipelago (Table I, Figure 1B) using 5 l Niskin bottles operated with the messenger. Seawater temperature and salinity in all the stations were measured using Sea Bird SBE-37-SMP-ODO CTD (Sea Bird Scientific, USA).

Flow cytometry

For the cell analysis in the flow cytometer, water samples (1.5 ml) were fixed with glutaraldehyde (1% final concentration). The samples were kept at 4°C for at least 30 min for completing the fixation procedure. The samples were then flash-frozen in liquid nitrogen and stored at −80°C. Samples were thawed at room temperature prior to analysis. Autotroph prokaryotic and eukaryotic plankton were enumerated using a flow cytometer (BD Accuri C6, BD Biosciences, USA). Before analysing the samples BD Spherotech 6 and 8 peak validation beads were used to check and monitor the cytometer performance. After validation,

Table I Geographic locations of sampling stations in the West Antarctic Peninsula (Antarctica) and Svalbard archipelago (Arctic)

Region	Station	Locality	Sampling date	Latitude	Longitude	Water temp. (°C)
Antarctica	S1	King George Island	4-Feb-19	62°12′22,91″S	58°56′39,85″W	1.0
	S2	Livingston Island	7-Feb-19	62°38′06,64″S	60°23′11,93″W	0.7
	S3	Nansen Island	28-Feb-19	64°30′07,02″S	62°00′12,54″W	−0.8
	S4	Argentina Island	8-Feb-19	65°13′46,12″S	64°23′11,93″W	0
	S5	Adelaide Island	25-Feb-19	66°20′04,04″S	68°07′29,88″W	−0.8
	S6	Horseshoe Island	18-Feb-19	67°49′09,62″S	67°11′35,55″W	−1.0
	S7	Horseshoe Island	12-Feb-19	67°50′27,5″S	67°21′43,99″W	−0.4
	S8	Marguerite Bay	24-Feb-19	68°04′40,76″S	68°42′43,64″W	−1.0
Arctic	N1	Svalbard archipelago	20-Jul-19	80°10′34″N	09°40′14″E	2.0
	N2	Svalbard archipelago	20-Jul-19	79°55′48″N	10°52′00″E	2.0
	N3	Svalbard archipelago	20-Jul-19	79°05′37″N	07°42′24″E	2.0
	N4	Svalbard archipelago	19-Jul-19	79°00′38″N	11°22′50″E	3.0
	N5	Svalbard archipelago	14-Jul-19	78°07′16″N	13°46′39″E	6.0
	N6	Svalbard archipelago	14-Jul-19	77°37′58″N	14°28′30″E	6.0
	N7	Svalbard archipelago	15-Jul-19	76°59′56″N	15°34′17″E	5.0

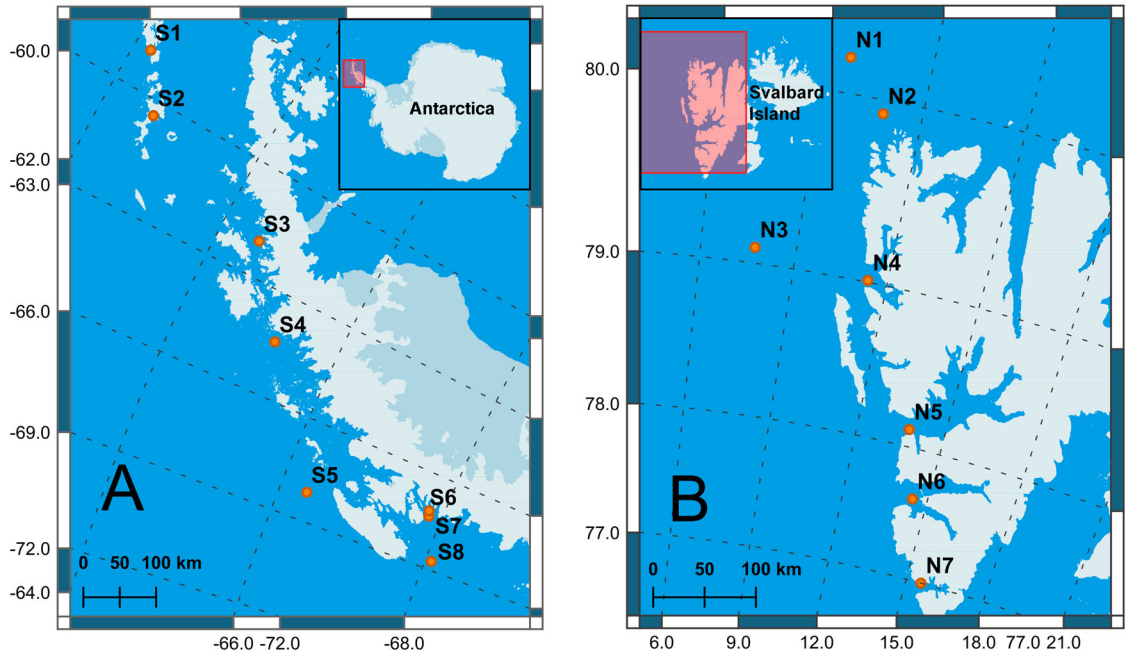

Figure 1. Sampling stations along the coast of the western Antarctic Peninsula (A) and along the western coasts of the Svalbard archipelago (B).

50 µl of seawater was used per sample for analysis. Samples were analysed at a nominal flow rate of 35 µl min-l and a core of 16 µm. Thresholds were 2000 and 1000 on FSC-H and 1000 on FL3-H, respectively. Chlorophyll fluorescence (FL3, CHL. > 670 nm) and phycoerythrin fluorescence (FL2, PE. 585 ± 20 nm) were also measured by flow cytometer (Supplementary Figure 1) using the BD Accuri C6 plus software. The results are given in cells/ml (Cumulative events = 4711, Average event/s = 55, event/ml = 94). The size fractions for the cells were between 0.2–2 µm for picoplankton (including *Synechoccus* spp.), 2–20 µm for nanoplankton and 20–50 µm for microplankton.

Data analyses

The raw data failed the normal distribution assumption after a Shapiro–Wilk test. Thus, the abundance data were log10 transformed to satisfy normal distribution. The plankton abundance and Shannon diversity indices in Antarctica and the Arctic were compared using the t-test. Spearman rank correlation was used to determine the relationship between phytoplankton abundance and temperature. A non-metric multidimensional scaling (NMDS) procedure was run to visually distinguish the picoplankton community compositions of Antarctica and the Arctic. The community composition was statistically compared using analysis of similarities (ANOSIM). Following a significant difference in ANOSIM, the similarity percentages breakdown (SIMPER) procedure was used to determine the contribution of individual variables to the dissimilarity. Bray–Curtis dissimilarity was used in NMDS, ANOSIM and SIMPER analyses. The data are presented as mean±standard error of the mean. The analyses and visualizations were performed in R (v. 4.1.3) (R Core Team 2022).

Results and discussion

In this study, pico-, nano- and microplankton community abundance in Antarctica and the Arctic in the summer of 2019 were investigated using flow cytometry. The results demonstrate that the overall average phytoplankton composition was dominated by *Synechococcus* spp. (95.6% in Antarctica and 71.7% in the Arctic), which was the most abundant group in all the stations in both Antarctica (67,957.5 ± 16,086.9 cells/ml) and the Arctic (12,768.6 ± 1683.7 cells/ml). The rest was composed of picoeukaryotes (1235 ± 222.6 cells/ml in Antarctica and 2854.3 ± 733.6 cells/ml in the Arctic), microautotrophs (1350 ± 685.3 cells/ml in Antarctica, 1900 ± 792.8 cells/ml in Arctic), and nanoeukaryotes (512.5 ± 143.5 cells/ml in Antarctica, 294.3 ± 54.3 cells/ml in Arctic). Plankton abundance in the sampling stations was highly variable (Table II). The stations where the highest abundances of *Synechococcus* spp., picoeukaryote, nanoeukaryote and microautotroph were found in Antarctica were S4 (151,400 cells/ml), S1 (2180 cells/ml), S2 (1080 cells/ml) and S4 (6100 cells/ml),

Table II Temperature and plankton abundance by stations in the Antarctica and Arctic plankton abundance (cells/ml)

				Plankton abundance (cells/ml)			
Region	Station	Temperature (°C)	Salinity (‰)	*Synechococcus* spp.	Picoeukaryote	Nanoeukaryote	Microautotroph
Antarctica	S1	1	33.7	61960	2180	60	440
Antarctica	S2	0.7	33.8	45140	860	1080	660
Antarctica	S3	−0.8	32.8	43920	1140	80	340
Antarctica	S4	0	31.9	151400	840	1060	6100
Antarctica	S5	−0.8	32.8	70620	920	720	760
Antarctica	S6	−1	32.2	32480	1940	420	500
Antarctica	S7	−0.4	32.3	119700	340	220	1220
Antarctica	S8	−1	32.0	18440	1660	460	780
Arctic	N1	2	34.6	12400	1620	340	3340
Arctic	N2	2	34.1	19600	3340	300	1220
Arctic	N3	2	33.9	15380	6400	500	780
Arctic	N4	3	34.2	15720	3700	360	6100
Arctic	N5	6	33.6	9840	3060	160	760
Arctic	N6	6	33.8	10060	1160	340	440
Arctic	N7	5	33.8	6380	700	60	660

respectively. On the other hand, in the Arctic, the highest abundance of *Synechococcus* spp., picoeukaryote, nanoeukaryote and microautotroph were found in N2 (19,600 cells/ml), N3 (6400 cells/ml), N3 (500 cells/ml) and N4 (6100 cells/ml), respectively (Table II).

Higher abundances of microautotrophs (1900.00 ± 792.81 cells/ml) and picoeukaryotes (2854.29 ± 733.56 cells/ml) were recorded for the Arctic compared with Antarctica (1350 ± 685.2 cells/ml microautotrophs and 1235 ± 223.5 cells/ml picoeukaryotes) but these differences were not significant (t-test, $P > 0.05$). *Synechococcus* spp. and nanoeukaryote abundances were higher in Antarctica, however, only *Synechococcus* spp. abundance was significantly higher in Antarctica (t-test, $P < 0.05$) (Figure 2A). *Synechococcus* spp. is an abundant and widespread genus, especially in coastal areas, and can tolerate a broad range of temperatures, light and nutrient levels (Varkey et al. 2016). Previous studies suggested that cold waters with low salinity can be more suitable for *Synechococcus* spp. (Gradinger and Lenz 1995; Rodríguez et al. 2002). The Antarctica coastal waters are comparatively less saline than the Arctic (Durack 2015). Thus, the significantly higher *Synechococcus* spp. abundance in Antarctica can be attributed to lower salinity.

Experimental studies on different *Synechococcus* strains indicate that the optimum growth temperature is 20–27°C (Mackey et al. 2013) and low temperature can result in decrease or no effect on growth (Varkey et al. 2016). On the other hand, under an average water temperature of 14°C, there was a positive relationship between annual average *Synechococcus* spp. abundance and temperature. Above that point, the relationship was not significant and appeared to be related with other factors and highly variable among different types of habitats (Li, 1998).

There are controversial results on *Synechococcus* spp. abundance in polar regions. *Synechococcus* spp. were generally thought to be absent in polar regions due to low temperatures (Pedrós-Alió et al. 2015). Sea ice loss in the Arctic Ocean and extent in the open water surface resulted in an increase of phytoplankton abundance over recent decades (Lewis et al. 2020). The cell concentration falls below 102 cells/ml in oceanic waters, however, higher abundances are reported on sea ice (Walker and Marchant 1989), lakes and rivers in the Arctic and Antarctica

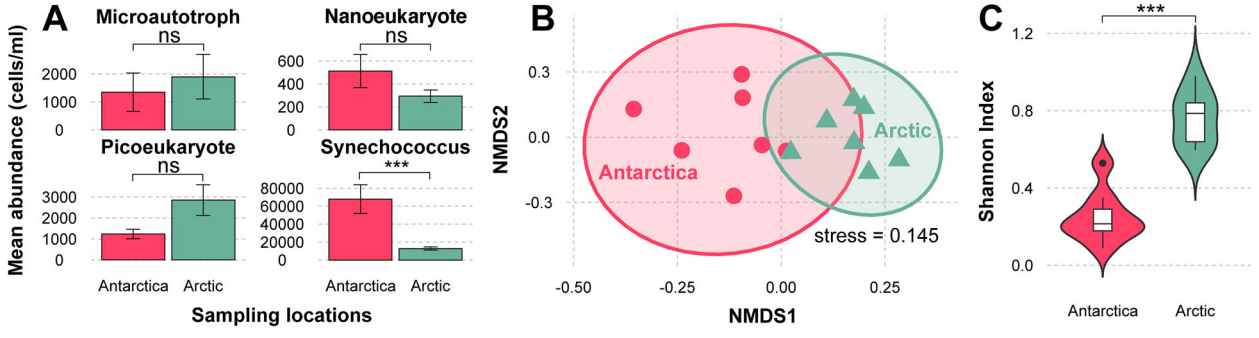

Figure 2. The comparison of plankton abundance in Antarctica and the Arctic (A). Non-metric multidimensional scaling (NMDS) showing significant separation of picoplankton composition (B). Comparison of Shannon diversity in Antarctica and Arctic (C). (ns: indicates no significant difference, *** indicates $P < 0.05$ according to t-test).

(Waleron et al. 2007; Vincent and Hobbie 2019). Yet, in certain periods of the year high *Synechococcus* spp. abundance (higher than 1000 cells/ml) was reported in Arctic surface waters around Svalbard archipelago even in water temperatures colder than 2°C (Paulsen et al. 2016). The result of this study also presents evidence that *Synechococcus* spp. can be found in the polar regions with high abundance at water temperatures below 6°C. Experimental studies on growth of tropical ecotypes of *Synechococcus* showed that temperatures below 10°C inhibit growth. Yet, in nature, presence of *Synechococcos* spp. have been reported at low temperatures (Gradinger and Lenz 1995; Mackey et al. 2013). Presence of *Synechococcus* spp. populations in polar regions might support existence of different thermotypes of *Synechococcus* spp. suggesting a physiological adaptation to cold waters.

Moreover, high density of cold-adapted eukaryotic picophytoplankton was observed in the Arctic (Sherr et al. 2003; Lovejoy et al. 2007; Tremblay et al. 2009; Zhang et al. 2015) and Antarctica (Doolittle et al. 2008). Gradinger and Lenz (1995) reported varying concentrations of *Synechococcus* spp. in the west of Svalbard. While there were no observations in the polar water samples below 0°C, a maximum of 5470 cells/ml was observed in Atlantic water samples with water temperature below 4°C (Gradinger and Lenz 1995). In August 2002, about 25,000 cells/ml *Synechococcus* spp. was observed in surface waters of the Norwegian and Barents seas (Not et al. 2005). In addition, the stations close to the polar front which were warmer and saltier had higher abundance. Although temperature is an important factor affecting the distribution and growth of plankton in the marine environment (Varkey et al. 2016), a seasonal

Table III Similarity percentage (SIMPER) result for the average dissimilarity of picoplankton community in Antarctica and the Arctic

Antarctica vs the Arctic	Avg. dis. = 59.48%	Contribution (%)	Cumulative (%)
	Synechococcus spp.	91.82	91.82
	Picoeukaryote	4.08	95.90
	Microautotroph	3.33	99.23
	Nanoeukaryote	0.77	100

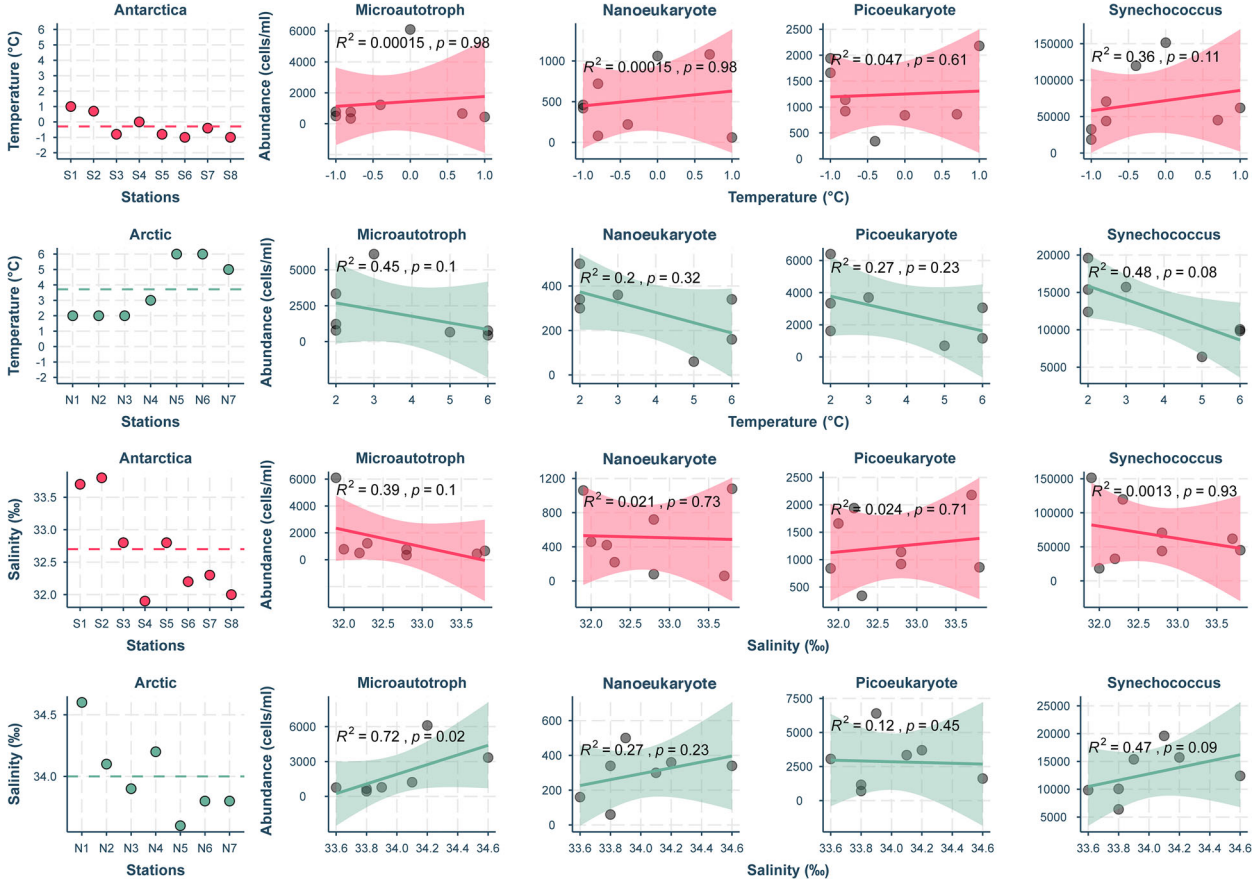

Figure 3. Seawater temperature at each station and the relationship between temperature and plankton abundance in Antarctica (top row), and Arctic (bottom row).

change in *Synechococcus* spp. abundance was observed which was attributed to changes in salinity rather than temperature (Gradinger and Lenz 1995). The river and lake ecosystems constituting *Synechococcus* spp. were considered as the main source of the Arctic Ocean (Waleron et al. 2007). In some cases, the *Synechococcus* spp. were restricted in brackish water and there was a decline in abundance with increasing salinity (Moreira-Turcq and Martin 1998). Similarly higher concentrations of picoplankton were observed in warmer and diluted patches in Gerlache Strait (Rodríguez et al. 2002). However, it was assumed that some species can tolerate a wide range of salinity levels resulting in wide dispersion in the marine environment (Waterbury et al. 1986). Our results indicate no relationship between *Synechococcus* spp. abundance and temperature; however, it is not sufficient to explain environmental factors on abundance since other water parameters and the strains at the sampling stations are unknown.

The NMDS ordination illustrates the split between Antarctica and Arctic phytoplankton community composition (Figure 2B), which is also expressed in the ANOSIM results ($R = 0.67$, $P < 0.01$). Similarity percentage (SIMPER) presented that the difference in picoplankton community composition between Antarctica and the Arctic (59.48%) is mainly driven by *Synechococcus* spp. (91.82%) followed by picoeukaryotes (4.08%) and microautotrophs (3.33%) (Table III). The Shannon diversity index in the Arctic was significantly higher (Figure 2C) since the composition in Antarctica was highly dominated by *Synechococcus* spp. (Table III).

The average seawater temperatures collected from sampling stations in Antarctica and the Arctic were -0.29 ± 0.28°C and 3.71 ± 0.71°C, respectively (Figure 3). Plankton abundance in the Antarctica and Arctic exhibited a relative increase and decrease with temperature, respectively. However, no significant correlation between the abundance and temperature was found (Spearman rank correlation, $P > 0.05$) (Figure 3). The average salinity was ‰32.7 ± 0.26 and ‰34.0 ± 0.13 in Antarctica and the Arctic, respectively. No significant correlation except for microautotrophs in the Arctic was found between abundance and salinity (Figure 3). However, there was a relative increase in the phytoplankton abundance in the Arctic with the salinity.

Conclusions

Increasing ocean temperature optima at high and low latitude marine ecosystems will unarguably affect the marine organism composition. Our results provide substantial data on the composition of microplanktonic organisms in the Arctic and Antarctic polar regions in the summer period of 2019. *Synechococcus* spp. dominated the composition in both polar regions and was significantly more abundant in the Antarctic. With increasing temperatures, melting ice in the polar regions might decrease the water salinity and affect the community composition. Therefore, the role of phytoplanktonic organisms in the polar food chain should be a priority for future research. Moreover, regular comprehensive monitoring studies will help to better understand the effects of changing climate on phytoplankton dynamics and their effect on the polar food chain.

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Disclosure statement

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Author contribution

AMF: Conceptualization, Funding Acquisition, Methodology, Investigation, Writing – Original Draft. YT: Formal analysis, Data curation, Visualization, Writing – Original Draft, Writing – Review & Editing. RÇÖ: Writing – Original Draft, Writing – Review & Editing. EB: Investigation. İY: Investigation, EA: Investigation.

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References

Arrigo KR. 2014. Sea ice ecosystems. Annual Review of Marine Science. 6:439–467. doi:10.1146/annurev-marine-010213-135103.

Constable AJ, Harper S, Dawson J, Holsman K, Mustonen T, Piepenburg D, Rost B. 2022. Cross-chapter paper 6: polar regions. In: Pörtner H-O, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B, editors.Climate change 2022: impacts, adaptation and vulnerability. contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change. Cambridge (UK): Cambridge University Press; p. 2319–2368. doi:10.1017/9781009325844.023.

Degerlund M, Eilertsen HC. 2010. Main species characteristics of phytoplankton spring blooms in NE Atlantic and Arctic Waters (68–80° N). Estuaries and Coasts. *33*(2):242–269. doi:10.1007/s12237-009-9167-7.

Doolittle DF, Li WKW, Wood AM. 2008. Wintertime abundance of picoplankton in the Atlantic sector of the Southern Ocean. Nova Hedwigia. 133:147–160.

Doney SC, Ruckelshaus M, Duffy E, Barry J, Chan JP, English F, Galindo CA, Grebmeier HM, Hollowed JM, Knowlton AB, et al. 2012. Climate change impacts on marine ecosystems. Annual Review of Marine Science. 4(1):11–37. doi:10.1146/annurev-marine-041911-111611.

Durack PJ. 2015. Ocean salinity and the global water cycle. Oceanography. 28:20–31. doi:10.5670/oceanog.2015.03.

Falkowski PG, Fenchel T, Delong EF. 2008. The microbial engines that drive earth's biogeochemical cycles. Science. 320(5879):1034–1039. doi:10.1126/science.1153213.

Flombaum P, Gallegos JL, Gordillo RA, Rincón J, Zabala LL, Jiao N, Karl DM, et al. 2013. Present and future global distributions of the marine Cyanobacteria Prochlorococcus and Synechococcus. Proceedings of the National Academy of Sciences of the United States of America. 110(24):9824–9829.doi:10.1073/pnas.1307701110.

Gaulke AK, Wetz MS, Paerl HW. 2010. Picophytoplankton: a major contributor to planktonic biomass and primary production in a eutrophic, river-dominated estuary. Estuarine, Coastal and Shelf Science. 90(1):45–54. doi:10.1016/j.ecss.2010.08.006.

Gradinger R, Lenz J. 1995. Seasonal occurrence of picocyanobacteria in the Greenland Sea and central Arctic ocean. Polar Biololgy. 15:447–452. doi:10.1007/BF00239722/METRICS.

Hopwood MJ, Carroll D, Dunse T, Hodson A, Holding JM, Iriarte JL, Ribeiro S, Achterberg EP, Cantoni C, Carlson DF, et al. 2020. Review article: How does glacier discharge affect marine biogeochemistry and primary production in the Arctic? The Cryosphere. 14(4):1347–1383. doi:10.5194/tc-14-1347-2020.

Jardillier, L., Zubkov, M. V., Pearman, J., Scanlan, D. J. (2010). Significant CO_2 fixation by small prymnesiophytes in the subtropical and tropical northeast Atlantic Ocean. The ISME Journal, 4, 1180–1192. doi:10.1038/ismej.20.

Kvíderová J, Elster J, Komárek J. 2019. Ecophysiology of cyanobacteria in the polar regions. Cyanobacteria: From Basic Science to Applications. 277–302. doi:10.1016/B978-0-12-814667-5.00014-3.

Lewis KM, Van Dijken GL, Arrigo KR. 2020. Changes in phytoplankton concentration now drive increased Arctic Ocean primary production. Science. 369(6500): 198–202. doi:10.1126/science.aay8380.

Li WKW. 1998. Annual average abundance of heterotrophic bacteria and Synechococcus in surface ocean waters. Limnology and Oceanography. 43:1746–1753. doi:10.4319/lo.1998.43.7.1746.

Lovejoy C, Vincent WF, Bonilla S, Roy S, Martineau M, Terrado R, Potvin M, et al. 2007. Distribution, phylogeny, and growth of cold-adapted picoprasinophytes in Arctic seas. Journal of Phycology. 43:78–89. doi:10.1111/j.1529-8817.2006.00310.x.

Mackey KRM, Paytan A, Caldeira K, Grossman AR, Moran D, Mcilvin M, Saito MA. 2013. Effect of temperature on photosynthesis and growth in marine *Synechococcus spp.*. Plant Physiololgy, 163, 815–829. doi:10.1104/pp.113.221937.

Moreira-Turcq PF, Martin JM. 1998. Characterisation of fine particles by flow cytometry in estuarine and coastal Arctic waters. Journal of Sea Research. 39:217–226. doi:10.1016/S1385-1101(97)00053-1.

Murphy EJ, Cavanagh RD, Drinkwater KF, Grant SM, Heymans JJ, Hofmann EE, Hunt GL, et al. 2016. Understanding the structure and functioning of polar pelagic ecosystems to predict the impacts of change. Proceedings of the Royal Society B: Biological Sciences. 283(1844):20161646. doi:10.1098/rspb.2016.1646.

Neukermans G, Oziel L, Babin M. 2018. Increased intrusion of warming Atlantic water leads to rapid expansion of temperate phytoplankton in the Arctic. Global Change Biology 24(6):2545–2553. doi:10.1111/gcb.14075.

Not F, Massana R, Latasa M, Marie D, Colson C, Eikrem W, Pedrós-Alió C, et al. 2005. Late summer community composition and abundance of photosynthetic picoeukaryotes in Norwegian and Barents Seas. Limnology and Oceanography. 50:1677–1686. doi:10.4319/lo.2005.50.5.1677.

Otero-Ferrer JL, Cermeño P, Bode A, Fernández-Castro B, Gasol JM, Morán XAG, Marañon E, et al. 2018. Factors controlling the community structure of picoplankton in contrasting marine environments. Biogeosciences (online). 15(20):6199–6220. doi:10.5194/bg-15-6199-2018.

Parry ML. 2007. Climate change 2007-impacts, adaptation and vulnerability: working group II contribution to the fourth assessment report of the IPCC (Vol. 4). New York: Cambridge University Press.

Paulsen ML, Dore H, Garczarek K, Seuthe L, Müller O, Sandaa R-A, Bratbak G, Larsen A. 2016. Synechococcus in the Atlantic Gateway to the Arctic Ocean. Frontiers in Marine Science. 3:191. doi:10.3389/fmars.2016.00191.

Pedrós-Alió C, Potvin M, Lovejoy C. 2015. Diversity of planktonic microorganisms in the Arctic Ocean. Progress in Oceanography. 139:233–243. doi:10.1016/j.pocean.2015.07.009.

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, et al. 2013. Global imprint of climate change on marine life. Nature Climate Change. 3(10):919–925. doi:10.1038/nclimate1958.

R Core Team. 2022. R: A Language and Environment for Statistical Computing.

Rodríguez J, Jiménez-Gómez F, Blanco JM, Figueroa FL. 2002. Physical gradients and spatial variability of the size structure and composition of phytoplankton in the Gerlache Strait (Antarctica). Deep Sea Research Part II: Topical Studies in Oceanography. 49:693–706. doi:10.1016/S0967-0645(01)00119-9.

Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR. 2010. How do polar marine ecosystems respond to rapid climate change? Science. 328 (5985):1520–1523. doi:10.1126/science.1185779.

Screen JA, Bracegirdle TJ, Simmonds I. 2018. Polar climate change as manifest in atmospheric circulation. Current Climate Change Reports. 4(4):383–395. doi:10.1007/s40641-018-0111-4.

Sherr EB, Sherr BF, Wheeler PA, Thompson K. 2003. Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. Deep Sea Research Part I: Oceanographic Research Papers. 50:557–571. doi:10.1016/S0967-0637(03)00031-1.

Tremblay G, Belzile C, Gosselin M, Poulin M, Roy S, Tremblay J-É. 2009. Late summer phytoplankton distribution along a 3500 km transect in Canadian Arctic waters: strong numerical dominance by picoeukaryotes. Aquatic Microbial Ecology. 54:55–70. doi:10.3354/ame01257.

Vanzan M, Barrera-Alba JJ, Tenório MMB, Tenenbaum DR. 2015. Picoplankton and nanoplankton variability in an Antarctic shallow coastal zone (Admiralty Bay) during the austral summer of 2010/2011. Polar Biology. 38:1267–1284. doi:10.1007/s00300-015-1692-1.

Varkey D, Mazard S, Ostrowski M, Tetu SG, Haynes P, Paulsen IT. 2016. Effects of low temperature on tropical and temperate isolates of marine Synechococcus. The ISME Journal. 10:1252–1263. doi:10.1038/ismej.2015.179.

Vincent WF, Hobbie JE. 2019. Ecology of Arctic lakes and rivers. In: Ives JD, Barry RG, editors. The Arctic. Routledge; p. 197–232.

Waleron M, Waleron K, Vincent WF, Wilmotte A. 2007. Allochthonous inputs of riverine picocyanobacteria to coastal waters in the Arctic Ocean. FEMS Microbiology Ecology. 59:356–365. doi:10.1111/j.1574-6941.2006.00236.x.

Walker TD, Marchant HJ. 1989. The seasonal occurrence of chroococcoid cyanobacteria at an Antarctic coastal site. Polar Biology. 9:193–196. doi:10.1007/BF00297175.

Waterbury JB, Watson SW, Valois FW, Franks DG. 1986. Biological and ecological characterization of the marine unicellular cyanobacterium Synechococcus. In: Platt T, Li WKW, editors. Photosynthetic picoplankton. Vol. 214; p. 71–120.

Wright SW, Ishikawa A, Marchant HJ, Davidson AT, van den Enden RL, Nash GV. 2009. Composition and significance of picophytoplankton in Antarctic waters. Polar Biology. 32:797–808. doi:10.1007/s00300-009-0582-9.

Zhang F, He J, Lin L, Jin H. 2015. Dominance of picophytoplankton in the newly open surface water of the central Arctic Ocean. Polar Biology. 38:1081–1089. doi:10.1007/s00300-015-1662-7.