

The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: a first-attempt assessment

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Abstract Arctic marine unicellular eukaryotes are composed of microalgae and non-autotrophic protists. These eukaryotes comprise a well-diversified group of organisms that are either adapted to live in the upper water column of coastal and oceanic regions, here defined as phytoplankton/pelagic communities, or in bottom horizons of sea ice and known as sympagic/sea-ice-associated communities. There are approximately 5,000 recognized legitimate marine

phytoplankton species and an unknown number of sympagic eukaryotes. Although pelagic and sea-ice eukaryotes have been described since the exploration phase of the Arctic regions up to the early twentieth century, no synthesis regarding information from all Arctic seas have been undertaken, and no exhaustive current information provides the exact number and composition of species on a pan-Arctic scale. In a first attempt to assess the pan-Arctic diversity of pelagic and sea-ice eukaryotes, a wealth of data from various sources (e.g., scientific publications, unpublished reports, databases) were reviewed, while taxonomic data were confirmed with current nomenclature and classification. We report a total of 2,106 marine single-celled eukaryote taxa with 1,874 phytoplankton and 1,027 sympagic taxa from four grouped pan-Arctic regions, namely Alaska, Canada, Scandinavia including Greenland and the Russian Federation. Both phytoplankton and sympagic taxa were present in four of the six supergroups of eukaryotes described by Adl et al. (*J Eukaryot Microbiol* 52:399–451, 2005), which are Archaeplastida (chlorophytes and prasinophytes), Chromalveolata (e.g., chrysophytes, cryptophytes, diatoms, dictyochophytes, dinoflagellates and prymnesiophytes), Excavata (euglenids) and Opisthokonta (choanoflagellates). The bulk of this marine biodiversity of Arctic microorganisms consists of large cells (>20 μm) mainly due to examination at low magnification under light microscopy. Future efforts should focus enhancing our knowledge of the biological diversity of small cells (<20 μm), which represent less than 20% of our actual biodiversity assessment of pan-Arctic regions.

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Introduction

Polar regions, and more specifically the Arctic, have received a growing interest over the past decades due to the threatening impact of global warming (e.g., Johannessen et al. 1999; Moritz et al. 2002; Serreze et al. 2007; Thomas and Dieckmann 2010). Environmental changes are already observed at a pan-Arctic scale and include a decline in the volume and extent of the sea-ice cover (Comiso et al. 2008), an advance in the melt period (Comiso 2006; Markus et al. 2009), and an increase in river discharge to the Arctic Ocean (McClelland et al. 2006; Peterson et al. 2002) due to increasing precipitation and terrestrial ice melt (Peterson et al. 2006). Over the last decade, Arctic sea ice has undergone an unprecedented reduction in extent and thickness, exposing an ever growing fraction of the sea surface to solar radiation, therefore, increasing the phytoplankton production (Pabi et al. 2008). At the same time, increased stratification and nutrient depletion in the euphotic zone may cause shifts in the taxonomic composition of phytoplankton (Tremblay et al. 2009), as recently recorded by increasing abundances of small-sized (<2 μm in diameter) phytoplankton cells and decreasing nano-phytoplankton cells (Li et al. 2009). Increased ice-free conditions may also favor and extend northwardly the intrusion of Atlantic phytoplankton species, such as *Emiliania huxleyi* (Lohmann) Hay & Mohler, along the northern sector of the western Eurasian shelves (Hegseth and Sundfjord 2008). Similarly, a consequence of regional climate warming may explain the reappearance of the North Pacific plankton diatom, *Neodenticula seminae* (Simonsen & Kanaya) Akiba & Yanagisawa, in the North Atlantic through a pulse of Pacific water via the Canadian Arctic Archipelago and/or the Fram Strait (Poulin et al. 2010; Reid et al. 2007).

Ice algae constitute the second source of primary production in Arctic seas, with the highest relative contribution in the central Arctic Ocean (Gosselin et al. 1997). The increased freshening of surface waters underneath multi-year ice likely impacts the sea-ice biota (Melnikov et al. 2002). Increasing extent of annually formed sea ice over the Arctic Ocean, with vanishing and restricted multi-year ice limited to the northern regions of the Canadian Archipelago and Greenland (as reported for 2008 by the US National Snow and Ice Centre), may result in higher biomass of sympagic (i.e., sea-ice-associated) unicellular eukaryote taxa available for the upper trophic levels at the time of minimum irradiance reaching the polar surface waters. Higher likelihood of upwelling events along the transitional zone between ice-edge and coastal regions of the Arctic Ocean may contribute to enhance primary production and eukaryote biomass accumulation in annually formed

sea ice during the vernal season (Benoît Philippe, personal communication).

Through international agreements on the Convention on Biological Diversity and global initiatives, such as the Arctic Ocean Diversity component of the Census of Marine Life, there is a pressing need at documenting the current biodiversity of the Arctic Ocean at a pan-Arctic scale in order to assist the circumarctic countries in developing conservation strategies and monitoring plans of marine biodiversity. Not only had the United Nations declared 2010 the International Year of Biodiversity, but with the unprecedented rate of climate change affecting more specifically the Arctic, it is also becoming imperative to assess the biological diversity of all marine organisms across the entire Arctic region. Macroorganisms still remain the focal point of biodiversity issues because they are much easier to manage and more promptly significant to both decision-makers, Arctic peoples and the general public. Conversely, at the opposite end of the scale, microscopic organisms—and more precisely marine phytoplankton and sea-ice eukaryotes—are still puzzlingly without mention in the United Nations Convention on Biological Diversity (UNEP 1994).

Marine phytoplankton and sympagic algae comprise a group of photosynthetic, single-celled organisms that are acclimated to grow and develop in the upper water column of oceans and in polar sea ice, respectively. In the broader sense defined in this paper, this group also encompasses some non-autotrophic eukaryotes, excluding amoebae, ciliates, foraminiferans and radiolarians. These marine eukaryotic cells range in size from 0.2 to 200 μm and are further segregated into the pico- (<2 μm), nano- (2–20 μm) and micro-sized fractions (20–200 μm) of the scaling plankton nomenclature (Sieburth et al. 1978). Marine phytoplankton contribute more than 45% of the annual net primary production of the planet (Falkowski et al. 2004; Simon et al. 2009), while sympagic algae are contributing up to 57% of the total primary production in the central Arctic Ocean (Gosselin et al. 1997) and between 3 and 25% in Arctic shelf regions (Legendre et al. 1992).

It is, therefore, becoming imperative to increase our knowledge of the biodiversity of marine unicellular eukaryotes as climate change affects more severely and more rapidly the Arctic regions. There is no current inventory of marine phytoplankton and sea-ice unicellular eukaryotes at a pan-Arctic scale, and not even at regional scales. Large autotrophic diatoms have been recorded in Arctic regions for almost two centuries (Ehrenberg 1841, 1853), with the first studies on sea-ice diatoms focusing mostly on taxonomy (i.e., description of new taxa) and phytogeography (Cleve 1873, 1883, 1896; Cleve and Grunow 1880; Gran 1897, 1904; Grunow 1884; Østrup 1895, 1897; Vanhöffen 1897), whereas only a few

inventories have reported on the presence of other groups of phytoplankton (Grøntved and Seidenfaden 1938; Hsiao 1983; Lovejoy et al. 2002; Okolodkov and Dodge 1996; Ratkova and Wassmann 2005) and sympagic algae (Horner 1985; Hsiao 1983; Ilyash and Zhitina 2009; Okolodkov 1992; Ratkova and Wassmann 2005) from specific Arctic locations.

A recent reassessment of the higher classification of eukaryotes based on ultrastructural and molecular approaches recognized six super-groups (Adl et al. 2005), and the marine phytoplankton and sympagic eukaryotes have representatives in four of these super-groups as previously reported for worldwide oceanic phytoplankton (Simon et al. 2009). Here, we followed the newly proposed classification of eukaryotes (Adl et al. 2005) in this collaborative effort to assess, for the first time, the biological diversity of marine phytoplankton and sea-ice unicellular eukaryotes at a pan-Arctic scale focusing, however, on Alaska, Canada, Scandinavia including Greenland, and the Russian Federation.

At the onset of this study, the main objectives were to (1) compile, for the first time, a comprehensive baseline study of the biodiversity of marine phytoplankton and sea-ice eukaryotes in the main coastal Arctic regions based only on presence/absence data, (2) compare the biological diversity of these marine eukaryotes between Arctic regions, and (3) update the nomenclature with the most current development in the systematics and classification of unicellular marine eukaryotes. Only the second objective of this study is discussed in this paper, because both the comprehensive data sets of Arctic marine eukaryotes and the updated nomenclatural information are still under revision.

Materials and methods

The biological diversity of marine, autotrophic and non-autotrophic pelagic and sympagic eukaryotes, excluding amoebae, ciliates, foraminiferans and radiolarians, was gathered from the main coastal circumarctic regions, namely Alaska, Canada, Scandinavia and Greenland (hereafter referred to only Scandinavia), and the Russian Federation. A wealth of taxonomic data was reviewed for presence/absence of marine eukaryotic cells flourishing in the pelagic waters of the northern polar seas, landfast and first and multi-year pack ice of the main Arctic regions. Various documentary sources were screened, such as scientific publications and books, MSc and PhD theses, published and unpublished government and industry reports, and personal databases (some of which are accessible through the internet). For the majority of the documents inventoried, the data acquisition was mainly based on species lists, which were rarely supplemented with illustrated drawings or light micrographs. However, old

taxonomic documents referring to the first descriptions of new taxonomic entities from polar regions were excluded from this survey (e.g., Cleve 1883, 1896; Gran 1904; Grunow 1884; Østrup 1895). Two major electronic spreadsheets, one for phytoplankton and one for sympagic eukaryotes, including recognized species (e.g., *Nitzschia frigida*), labeled species (e.g., *Navicula* sp. 1) and unidentified taxa (e.g., *Actinocyclus* spp.), based on presence/absence were generated for each of the main coastal circumarctic countries and are presently maintained, though still incompletely verified, at the Canadian Museum of Nature in Ottawa, Canada (mpoulin@mus-nature.ca). The taxonomic data file has not been entirely checked yet for author's authenticity, synonymy and spelling mistakes, but is available through the Arctic Register of Marine Species (ARMS: <http://www.marine-species.org/arms>) within the World Register of Marine Species (WoRMS) where it will be refined over time. Due to the urgency compiling a first biodiversity list of Arctic marine eukaryotes, we were unable to generate at this stage complementary data sets incorporating cell abundance values in relation to time and space, water depth and ice horizon sampled, ultimately appealing for pan-Arctic-scale mapping.

A total of 18 documentary sources were surveyed for the Alaskan Arctic, including the Bering Sea, the Arctic Ocean, and the continental shelf of Chukchi and Beaufort seas. For the Canadian Arctic, 78 documents were screened for the Hudson Bay system (i.e., Hudson Bay, Hudson Strait and Foxe Basin), the eastern Arctic (i.e., southern Davis Strait to northern Baffin Bay and Nares Strait), the western Arctic (i.e., Beaufort Sea to Amundsen Gulf and Franklin Bay), the Canadian Archipelago and the Canada Basin. In the Scandinavian Arctic, 71 documents were surveyed from the west coast of Greenland, the Norwegian and Greenland seas, Svalbard and the Norwegian Barents Sea. A total of 61 documentary sources were screened for the Russian Federation from the White Sea on the westernmost part of the country to the Far East Siberian Sea, Chukchi and Bering seas, and the Arctic Basin and Ocean.

All taxonomic information, still in progress, was confirmed with current nomenclature of the marine unicellular eukaryote taxa, while following the higher-level classification of eukaryotic protists proposed recently by Adl et al. (2005).

Results

The marine phytoplankton and sea-ice eukaryotes from the Arctic regions of Alaska, Canada, Scandinavia and the Russian Federation were classified into four super-groups: Archaeplastida (chlorophytes and prasinophytes), Chromalveolata (e.g., chrysophytes, cryptophytes, diatoms, dictyochophytes, dinoflagellates and prymnesiophytes), Excavata (euglenids) and Opisthokonta (choanoflagellates) (Table 1).

Table 1 Higher level classification of Arctic marine phytoplankton and sympagic unicellular eukaryote taxa following Adl et al. (2005)

AMOEBOZOA			
ARCHAEPLASTIDA	Chloroplastida		Chlorophyta, Prasinophytae
CHROMALVEOLATA	Stramenopiles		Bacillariophyta (diatoms), Bicosoecida, Chrysophyceae, Dictyochophyceae, Pelagophyceae, Raphidophyceae, Synurales, Xanthophyceae
	Cryptophyceae		
	Haptophyta		Prymnesiophyceae
	Alveolata		Dinzoa (dinoflagellates)
EXCAVATA	Euglenozoa (euglenids)		Euglenida, Kinetoplastea
OPISTHOKONTA	Choanomonada (choanoflagellates)		
RHIZARIA			

The Chromalveolata contain most of the marine microscopic taxa recorded from the pan-Arctic regions, with the Stramenopiles and Alveolata representing 62% and 21% of the total number of eukaryote taxa, respectively. A total of 2,106 marine single-celled eukaryote taxa (i.e., 1,874

phytoplankton and 1,027 sympagic taxa) were recorded at the pan-Arctic scale and the micro-sized fraction (i.e., 20–200 μm), mainly consisting of large-celled diatoms and dinoflagellates, accounted for 79% of all microscopic forms (Table 2). The Canadian and Russian Arctic showed the

Table 2 Total numbers of Arctic and Antarctic marine unicellular eukaryote taxa based on current pan-Arctic record inventory and from the literature, respectively

Group	Arctic					Antarctic ^{a, b, c}
	Alaska	Canada	Scandinavia	Russia	Total	
Archaeplastida						
Chlorophyta	12	34	3	17	55	1
Prasinophytae	1	42	25	18	60	7
Chromalveolata						
Centric diatoms	99	199	132	202	297	115
Pennate diatoms	232	604	251	563	930	80
Bicosoecida	0	7	5	1	10	1
Chrysophyceae	9	22	18	8	38	14
Dictyochophyceae	3	14	9	9	19	4
Pelagophyceae	1	0	0	0	1	0
Raphidophyceae	0	2	1	2	3	0
Synurales	0	3	3	0	6	1
Xanthophyceae	1	3	0	0	3	0
Cryptophyceae	0	23	10	9	30	3
Prymnesiophyceae	2	33	45	10	70	43
Dinoflagellates	74	266	183	257	441	66
Excavata						
Euglenida	3	14	4	10	20	3
Kinetoplastea	1	8	1	0	9	2
Opisthokonta						
Choanoflagellates	0	30	39	9	46	32
Cyanophyta	0	4	0	9	12	0
Incertae sedis	5	42	25	4	56	10
Total	443	1350	754	1128	2106	153 ^b –388 ^c

^a Horner (1985)^b Palmisano and Garrison (1993)^c Scott and Marchant (2005)

highest numbers of marine eukaryotes with 1,350 and 1,128 taxa, respectively, while pennate diatoms dominated in each of the four pan-Arctic countries, accounting for between 33% and 52% of all phytoplankton and sympagic eukaryote taxa. The marine Arctic phytoplankton were predominantly represented by Stramenopiles (60%), mostly diatoms (57%), followed by Alveolates with dinoflagellates (23%), while Arctic sympagic eukaryotes showed a strong dominance of Stramenopiles (74%) with diatoms (71%) and Alveolates with dinoflagellates (13%) (data not shown).

The lowest and highest diversity of Arctic marine phytoplankton were recorded for Alaska and Canada with 272 and 1,229 eukaryote taxa, respectively, with intermediate records for Scandinavia (including Greenland) and the Russian Federation with 686 and 954 taxa, respectively (data not shown). This low number of eukaryote taxa reported for the Alaskan Arctic is explained by the lowest number of investigations conducted in these regions. The Arctic phytoplankton communities are mainly represented by pennate diatoms, dinoflagellates and centric diatoms, except in Alaska where the latter group predominate in terms of number of taxa (Fig. 1). The contribution of small autotrophic and heterotro-

phic eukaryotes (<20 μm) accounted between 9% and 15% in the Russian and Alaskan Arctic, and up to 20% and 22% in Scandinavian and Canadian Arctic, respectively. The proportion of eukaryote taxa from a freshwater origin varied from 5% to a maximum of 18% of the marine phytoplankton recorded in the Canadian Arctic (data not shown).

At the pan-Arctic scale, landfast and pack ice are predominantly colonized by pennate diatoms, which accounted for 52% in the Scandinavian Arctic up to 77% in Alaska (Fig. 2). The highest diversity was recorded in the Russian Arctic with 697 sympagic taxa, followed by the Canadian, Scandinavian and Alaskan Arctic with 540, 276 and 275 taxa, respectively. The proportion of small-celled autotrophic and heterotrophic eukaryotes varied between 4% and 8% for Alaska and Russia, respectively, and 21% in Scandinavia, while freshwater taxa accounted for a maximum of 22% in the Scandinavian Arctic.

Further examination of the data set, still incompletely verified for nomenclature at present, of all marine phytoplankton and sympagic eukaryotes (data not shown) highlighted some taxa that were the most frequently reported in both environments for the whole Arctic (Table 3); the high

Fig. 1 Relative proportion (%) of marine phytoplankton taxa recorded from the Alaskan, Canadian, Scandinavian including Greenland and Russian Arctic. *A* centric diatoms; *B* pennate diatoms; *C* dinoflagellates; *D* other stramenopiles; *E* remaining groups; *F* incertae sedis + choanoflagellates (refer to Table 1)

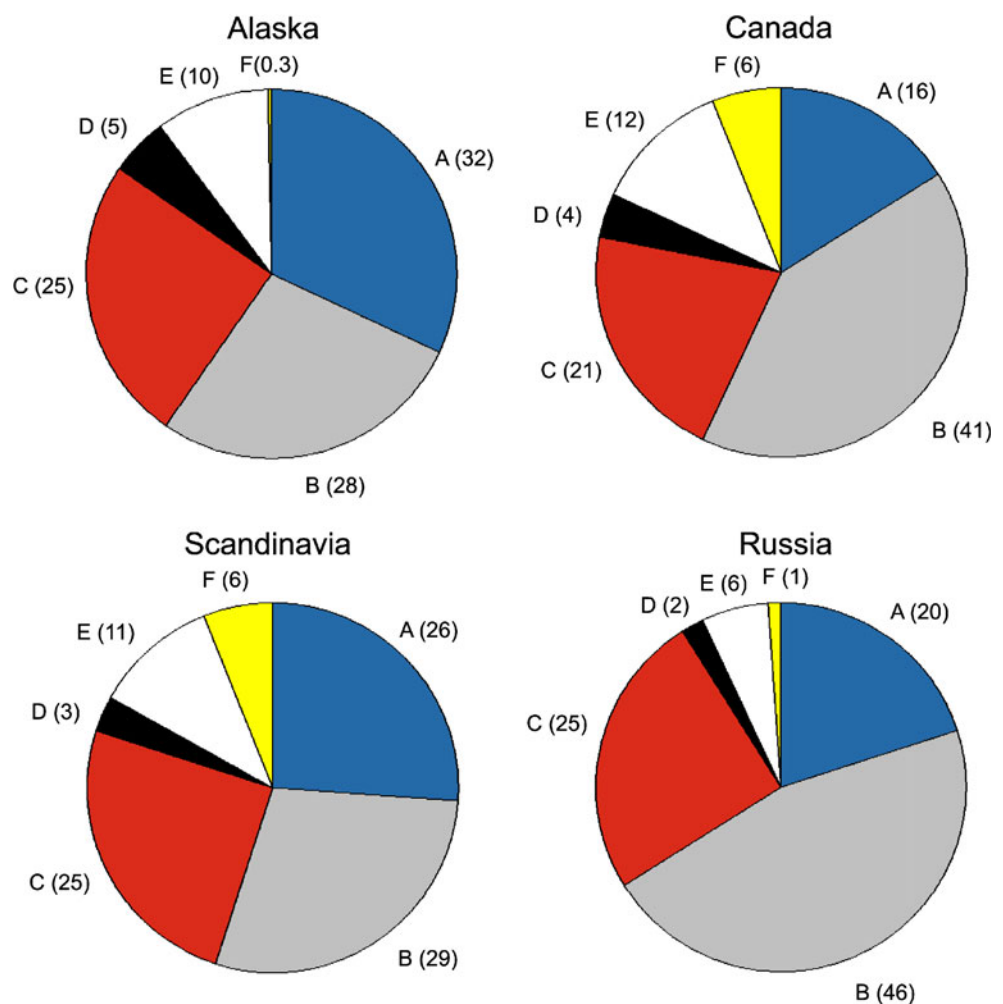
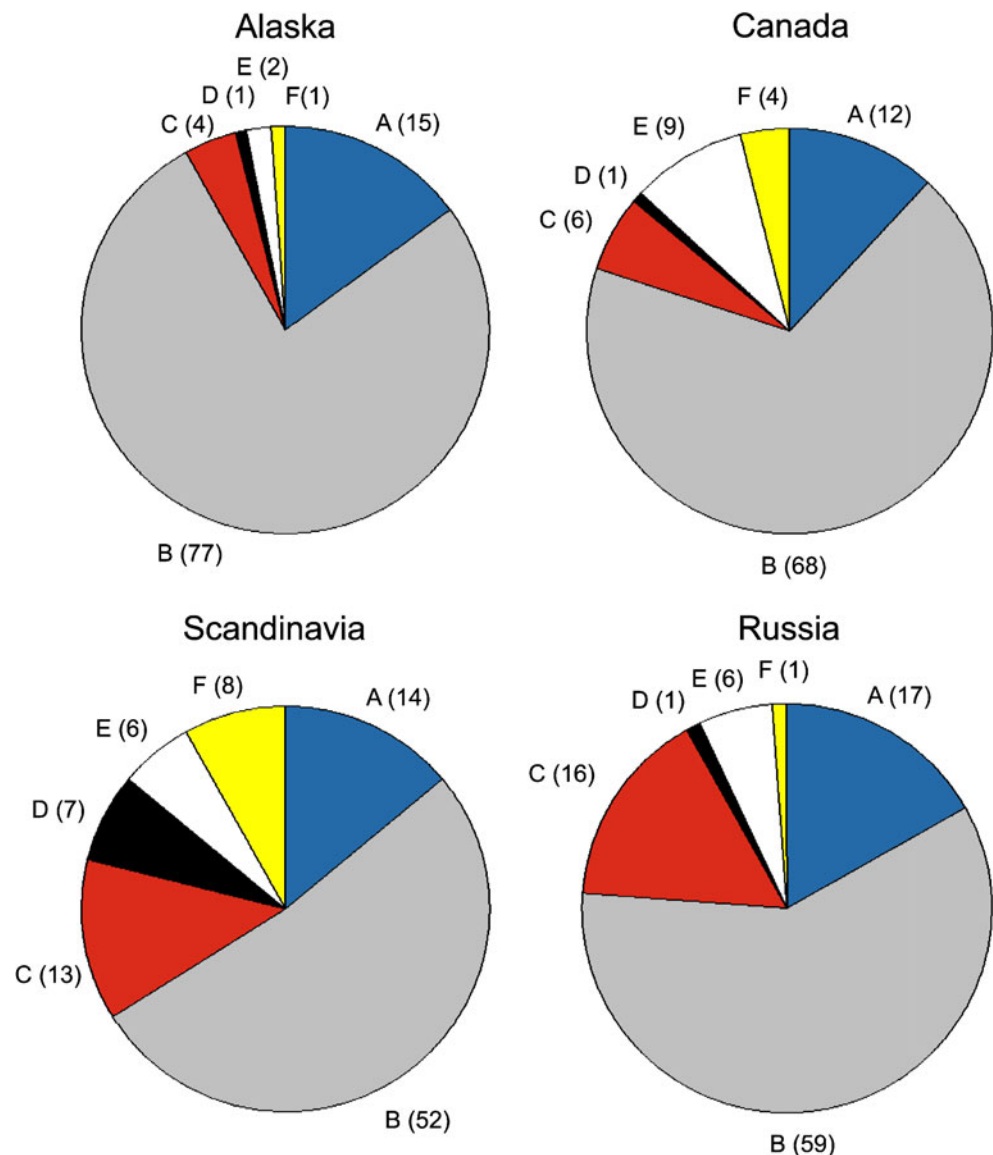


Fig. 2 Relative proportion (%) of marine sea-ice eukaryote taxa recorded from the Alaskan, Canadian, Scandinavian including Greenland and Russian Arctic. *A* centric diatoms; *B* pennate diatoms; *C* dinoflagellates; *E* remaining groups; *F* incertae sedis + choanoflagellates (refer to Table 1)



frequency of recorded taxa listed for Alaska may result from the low number of recorded inventories. Some colonial centric (*Chaetoceros furcillatus* [new name following Peterson et al. (1999)], *Thalassiosira gravida*, *T. nordenskiöldii*) and pennate (*Fragilariopsis oceanica*) diatoms, and the solitary pennate diatom *Cylindrotheca closterium* and the heterotrophic dinoflagellate *Protoperdinium pellucidum* are characterized by being marine cold-water phytoplankton taxa widespread across the northern polar seas, except for the latter taxon more omnipresent in warm to temperate regions. In landfast and pack ice, some colonial (*Entomoneis kjellmanii*, *Fragilariopsis cylindrus*, *F. oceanica*, *Nitzschia frigida*, *Pauliella taeniata*) and solitary (*Cylindrotheca closterium*, *Navicula directa*) pennate diatoms, and the colonial centric *Melosira arctica* and solitary, epiphytic *Atheya septentrionalis* can be considered sympagic and/or strikingly associated with northern polar sea ice, while *N.*

frigida can be regarded as the sentinel species endemic of sympagic communities.

Mostly ubiquitous in northern marine environments, the cold-adapted pelagic diatoms *Thalassiosira gravida* (probably with some records corresponding to misidentified *T. antarctica* var. *borealis* Fryxell et al.; see Discussion) and *T. nordenskiöldii* are typically occurring underneath the ice or in ice-free waters throughout the Arctic. Depicted as truly sympagic taxa from Arctic sea ice, *Melosira arctica*, *Fragilariopsis cylindrus*, *F. oceanica* and *Nitzschia frigida* are always present in annually formed sea ice. Another interesting pennate diatom is the solitary *Cylindrotheca closterium*, which occurred both in pelagic waters as well as in polar sea ice throughout the entire Arctic regions.

Two pelagic diatoms, *Manguinea rigida* (M. Peragallo) Paddock and *Membraneis challengerii* (Grunow) Paddock, known to occur in southern polar Antarctic waters have

Table 3 List of the most frequently reported marine phytoplankton and sea-ice eukaryote taxa from the four main pan-Arctic regions. **Bold characters** highlight taxa present in at least three regions; habitat characteristics from the literature are presented once when taxa are first mentioned

Alaska	Canada	Scandinavia	Russia
Phytoplankton taxa			
Centric diatoms			
<i>Attheya septentrionalis</i> ^{I, m, p} (Østrup) Crawford	<i>A. septentrionalis</i>	<i>C. decipiens</i>	<i>C. contortus</i>
^a <i>Chaetoceros contortus</i> ^{P, m, p} Schütt	<i>C. decipiens</i> ^{P, m, c} Cleve	<i>C. furcillatus</i>	<i>T. gravida</i>
<i>C. furcillatus</i> ^{P, m, p} Bailey	<i>C. furcillatus</i>	<i>C. socialis</i>	<i>T. nordenskiöldii</i>
<i>C. socialis</i> ^{P, m, p} Lauder	<i>C. wighamii</i>	<i>T. gravida</i>	
<i>C. wighamii</i> ^{P, b-m, p} Brightwell	<i>E. groenlandica</i>	<i>T. nordenskiöldii</i>	
<i>Eucampia groenlandica</i> ^{P, m, p} Cleve	<i>T. gravida</i>		
<i>Thalassiosira gravida</i> ^{P, m, p-t} Cleve	<i>T. nordenskiöldii</i>		
<i>T. nordenskiöldii</i> ^{P, m, p-t} Cleve			
Pennate diatoms			
<i>Cylindrotheca closterium</i> ^{I-P, m, c} (Ehrenberg) Reimann & Lewin	<i>C. closterium</i>	<i>F. oceanica</i>	<i>C. closterium</i>
<i>Fragilariopsis cylindrus</i> ^{I-P, m, p-t} (Cleve) Frenguelli	<i>F. cylindrus</i>		<i>T. nitzschioides</i>
<i>F. oceanica</i> ^{P, m, p-t} (Cleve) Hasle	<i>F. oceanica</i>		
<i>Nitzschia frigida</i> ^{I, m, p} Grunow	<i>N. frigida</i>		
<i>Pseudo-nitzschia seriata</i> ^{P, m, p-t} (Cleve) H. Peragallo	<i>P. seriata</i>		
<i>Thalassionema nitzschioides</i> ^{P, m, p-t} (Grunow) Mereschkowsky			
Dinoflagellates			
<i>Protoperidinium brevipes</i> ^{P, m, p} Paulsen & Balech		<i>P. pellucidum</i>	<i>P. brevipes</i>
<i>P. pellucidum</i> ^{P, m, w-t} Bergh			<i>P. pellucidum</i>
Prymnesiophyte			
<i>Phaeocystis pouchetii</i> ^{P, m, p} (Hariot) Lagerheim		<i>P. pouchetii</i>	
Sea-ice taxa			
Centric diatoms			
<i>A. septentrionalis</i>	<i>A. septentrionalis</i>	<i>A. septentrionalis</i>	<i>M. arctica</i>
<i>Melosira arctica</i> ^{P, m, p} Dickie	<i>M. arctica</i>	<i>M. arctica</i>	
Pennate diatoms			
<i>C. closterium</i>	<i>C. closterium</i>	<i>C. closterium</i>	<i>C. closterium</i>
<i>Entomoneis kjellmanii</i> ^{I, m, p} (Cleve) Poulin & Cardinal	<i>E. kjellmanii</i>	<i>F. cylindrus</i>	<i>E. kjellmanii</i>
<i>F. cylindrus</i>	<i>F. cylindrus</i>	<i>F. oceanica</i>	<i>F. cylindrus</i>
<i>F. oceanica</i>	<i>F. oceanica</i>	<i>N. pelagica</i>	<i>F. oceanica</i>
<i>Navicula directa</i> ^{I-B, m, p-t} (W. Smith) Ralfs	<i>N. directa</i>	<i>N. frigida</i>	<i>N. directa</i>
<i>N. pelagica</i> ^{I, m, p} Cleve	<i>N. transitans</i>	<i>P. taeniata</i>	<i>N. transitans</i> v. <i>derasa</i>
<i>N. transitans</i> ^{I, m, p} Cleve	<i>N. frigida</i>		<i>N. frigida</i>
<i>N. transitans</i> v. <i>derasa</i> ^{I, m, p} (Grunow) Cleve	<i>N. longissima</i>		<i>N. polaris</i>
<i>Nitzschia frigida</i>	<i>P. taeniata</i>		<i>P. delicatissima</i>
<i>N. longissima</i> ^{B-P, m, p-t} (Brébisson) Ralfs			
<i>N. polaris</i> ^{I, m, p} Grunow			
<i>Pauliella taeniata</i> ^{I-P, m, p} (Grunow) Round & Basson			
<i>Pseudo-nitzschia delicatissima</i> ^{P, m, p-t} (Cleve) Heiden			

^a Specimens most probably erroneously recorded as tropical, warm water *Chaetoceros compressus* Lauder

^I Sea-ice taxa, ^P phytoplankton taxa, ^B benthic taxa; ^m marine, ^b brackish, ^c cosmopolitan, ^p polar (cold) water, ^t temperate water, ^w warm water

been recorded scarcely in the Canadian Arctic. *Manguinea rigida* occurred once in the phytoplankton of Amundsen Gulf, southeast Beaufort Sea in the western Arctic and in sea ice in both Franklin Bay, southeast Beaufort Sea and in northern Baffin Bay in the eastern Arctic, while *Membraneis challengerii* was recorded only once in sea ice from the northern Baffin Bay.

A certain number of known harmful eukaryotes have also been recorded in the marine phytoplankton and sympagic communities across the entire Arctic regions, which are more widespread in tropical to temperate coastal waters, forming massive bloom events, causing not only public health threats but also fish, aquatic bird and mammal kills (Table 4). A total of 37 potentially toxic species were recorded, including 25

Table 4 List of potentially harmful/toxic marine unicellular eukaryote taxa recorded in phytoplankton and sea-ice communities across the whole Arctic regions

Taxon	Phytoplankton	Sea ice
Diatoms		
<i>Amphora coffeaeformis</i> (Agardh) Kützing	2, 3, 4	1, 2, 4
<i>Pseudo-nitzschia australis</i> Frenguelli	3, 4	3, 4
<i>P. calliantha</i> Lundholm et al.	np	4
<i>P. delicatissima</i>	1, 2, 3, 4	1, 2, 3, 4
<i>P. fraudulenta</i> (Cleve) Hasle	3	4
<i>P. multiseriata</i> (Hasle) Hasle	3	np
<i>P. pungens</i> (Cleve) Hasle	1, 2, 3, 4	1, 2, 4
<i>P. seriata</i>	1, 2, 3, 4	1, 2, 3, 4
<i>P. turgidula</i> (Hustedt) Hasle	2, 3	2
Raphidophytes		
<i>Heterosigma akashiwo</i> (Hada) Hara & Chihara	2, 4	4
Prymnesiophytes		
<i>Chrysochromulina leadbeateri</i> Estep et al.	3	np
<i>Phaeocystis pouchetii</i>	1, 2, 3, 4	2, 3, 4
Dinoflagellates		
<i>Alexandrium hiranoi</i> Kita & Fukuyo	1	np
<i>A. minutum</i> Halim	3, 4	4
<i>A. monilatum</i> (Howell) Taylor	2, 3	2
<i>A. ostenfeldii</i> (Paulsen) Balech & Tangen	2, 3, 4	4
<i>A. tamarense</i> (Lebour) Balech	1, 2, 3, 4	2, 3, 4
<i>Amphidinium carterae</i> Hulbert	2, 4	4
<i>A. operculatum</i> Claparède & Lachmann	1, 2, 3	4
<i>Cochlodinium polykrikoides</i> Margalef	3	np
<i>Coolia monotis</i> Meunier	2	2
<i>Dinophysis acuminata</i> Claparède & Lachmann	1, 2, 3, 4	2, 4
<i>D. acuta</i> Ehrenberg	1, 2, 3, 4	4
<i>D. caudata</i> Saville-Kent	2	2
<i>D. fortii</i> Pavillard	2, 3, 4	np
<i>D. norvegica</i>	1, 2, 3, 4	4
<i>D. rotundata</i> Claparède & Lachmann	4	np
<i>Gonyaulax spinifera</i> (Claparède & Lachmann) Diesing	1, 2, 3, 4	4
<i>Karenia brevis</i> (Davis) Hansen & Moestrup	2	4
<i>K. mikimotoi</i> (Oda) Hansen & Moestrup	2	np
<i>Karlodinium veneficum</i> (Ballantine) Larsen	3, 4	3, 4
<i>Lingulodinium polyedrum</i> (Stein) Dodge	1, 2, 3, 4	np
<i>Phalacrocoma rotundatum</i> (Claparède & Lachmann) Kofoid & Michener	1, 2, 3	np
<i>Prorocentrum lima</i> (Ehrenberg) Dodge	2, 4	4
<i>P. minimum</i> (Pavillard) Schiller	2, 3, 4	4
<i>Protoceratium reticulatum</i> (Claparède & Lachmann) Bütschli	1, 2, 3	3, 4
<i>Protoperdinium crassipes</i> (Kofoid) Balech	1, 2, 4	np

1 Alaska, 2 Canada, 3 Scandinavia including Greenland, 4 Russia, np not present

dinoflagellates mainly of the genera *Alexandrium* Halim and *Dinophysis* Ehrenberg, nine diatoms mostly of the genus *Pseudo-nitzschia* H. Peragallo, two prymnesiophytes, including *Phaeocystis pouchetii*, and the raphidophyte *Heterosigma akashiwo*. The most frequently recorded taxa throughout the four Arctic regions were the planktonic diatoms *Pseudo-nitzschia delicatissima*, *P. pungens* and *P. seriata*, the dinoflagellates *Alexandrium tamarense*, *Dinophysis acuminata*, *D. acuta*, *D. norvegica*, *Gonyaulax spinifera* and *Protoceratium reticulatum*, and the prymnesiophyte *Phaeocystis pouchetii*.

Discussion

Both Arctic phytoplankton and sea-ice eukaryote communities are controlled by a suite of environmental variables (e.g., nutrients, irradiance, snow and sea-ice cover, water stratification, salinity, temperature) that will determine their abundance, biomass and taxonomic composition through time, region, water depth and ice thickness. Unfortunately, this study reports only data based on the presence/absence of marine microscopic eukaryotes, neglecting geographical coordinate data, abundance values, water depth and ice horizon sampled. This simplified data set prevents us from drawing stronger conclusions about hot spots, knowledge gaps and the autecology of characteristic northern polar microorganisms. The high variability in the number of marine unicellular eukaryotes observed across the Arctic is closely related to the sampling effort, which is strongly dependent on the funding support from the various circum-arctic countries for these remote oceanographic expeditions and the strategic orientation of research programs (Figs. 3 and 4). In the broad sense, without targeting any specific circumarctic regions, a high frequency in the number of inventory records for phytoplankton was observed in the Hudson Bay system, the Norwegian Barents Sea and Laptev Sea (Fig. 3), while for sea-ice eukaryotes, a moderately-high number of inventory records was noticed for the Beaufort/Chukchi seas, Hudson Bay, Baffin Bay and the Norwegian Barents Sea (Fig. 4). Finally, lower numbers of inventory records for both phytoplankton and sea-ice eukaryotes were distributed throughout the other surveyed circumarctic regions.

Since the first report of 114 marine phytoplankton taxa in the northern polar seas between the Canadian Ellesmere and Baffin islands and Greenland (Grøntved and Seidenfaden 1938), the last three decades have been successful in generating new information about these marine single-celled eukaryote species for the whole Arctic regions (Table 5). Lovejoy et al. (2002) recorded a total of 178 taxa, with twice the number of small-sized autotrophic and heterotrophic cells compared with the 65-

year-old study of Grøntved and Seidenfaden (1938) conducted in the same Arctic region. Hsiao (1983) was the first to compile all taxonomic entries for the whole Canadian Arctic, recording 354 phytoplankton and 205 sea-ice eukaryote taxa. In the Russian Arctic which extends across 160° of longitude, phytoplankton and sea-ice eukaryotes accounted for 156 taxa in the Chukchi, East Siberian and Laptev seas (Okolodkov 1992), while Ratkova and Wassmann (2005) recorded 237 phytoplankton and 230 sympagic taxa from the Barents and White seas. It would seem that the taxonomic composition of sea-ice eukaryotes decreased in the westward direction in the Russian Arctic (Ilyash and Zhitina 2009). Only Horner (1985) was the first to report a total of 23 phytoplankton and 290 sympagic eukaryote taxa for the entire Arctic regions, which surprisingly turned out to be much less than the previous species inventory by Hsiao (1983) for the whole Canadian Arctic, including the Hudson Bay system. Only recently, Ikävalko (2003) reported the presence of 863 sympagic eukaryote taxa for the whole Arctic with, however, several questionable records. Now this first list of marine single-celled phytoplankton and sea-ice eukaryotes with 1,874 and 1,027 taxa, respectively, for the whole Arctic regions (i.e., Alaska, Canada, Scandinavia including Greenland, Russian Federation) represents the base line data that will be useful in future monitoring plan.

The most frequently recorded marine phytoplankton diatom taxa at the pan-Arctic scale consist of the cold water centric *Chaetoceros furcillatus*, *Thalassiosira gravida* and *T. nordenskioeldii*, and pennate *Cylindrotheca closterium* and *Fragilariopsis oceanica*, which are characteristic of northern polar seas (Degerlund and Eilertsen 2010; Hegseth and Sundfjord 2008; Sakshaug et al. 2009; Tremblay et al. 2009) but also extending their distribution to temperate waters where they can be abundant in the spring blooms (Bérard-Therriault et al. 1999; von Quillfeldt 2000a). Another frequently reported taxon across the Arctic is the warm to temperate water armoured heterotrophic dinoflagellate *Protoperidinium pellucidum*. In the northern polar regions, the most commonly recorded pennate diatoms *Cylindrotheca closterium*, *Entomoneis kjellmanii*, *Fragilariopsis cylindrus*, *F. oceanica*, *Navicula directa*, *Nitzschia frigida* and *Pauliella taeniata* are always strongly associated with the bottom horizon of landfast and pack ice (Melnikov et al. 2002; Rózańska et al. 2009; von Quillfeldt et al. 2009). Most of these diatom species form long ribbon-shaped and arborescent colonies, except for the solitary *C. closterium* and *N. directa*. The consistent occurrence of the sympagic diatom *N. frigida* across the whole Arctic and its high adaptation to a wide range of light regimes make it a key species of the northern polar sea ice (Hegseth 1992; Rózańska et al. 2009). Two centric diatoms, *Attheya septentrionalis* and *Melosira arctica*, are also very commonly associated with polar sea

Number of inventory records

- < 6
- 6-10
- 11-15
- > 15

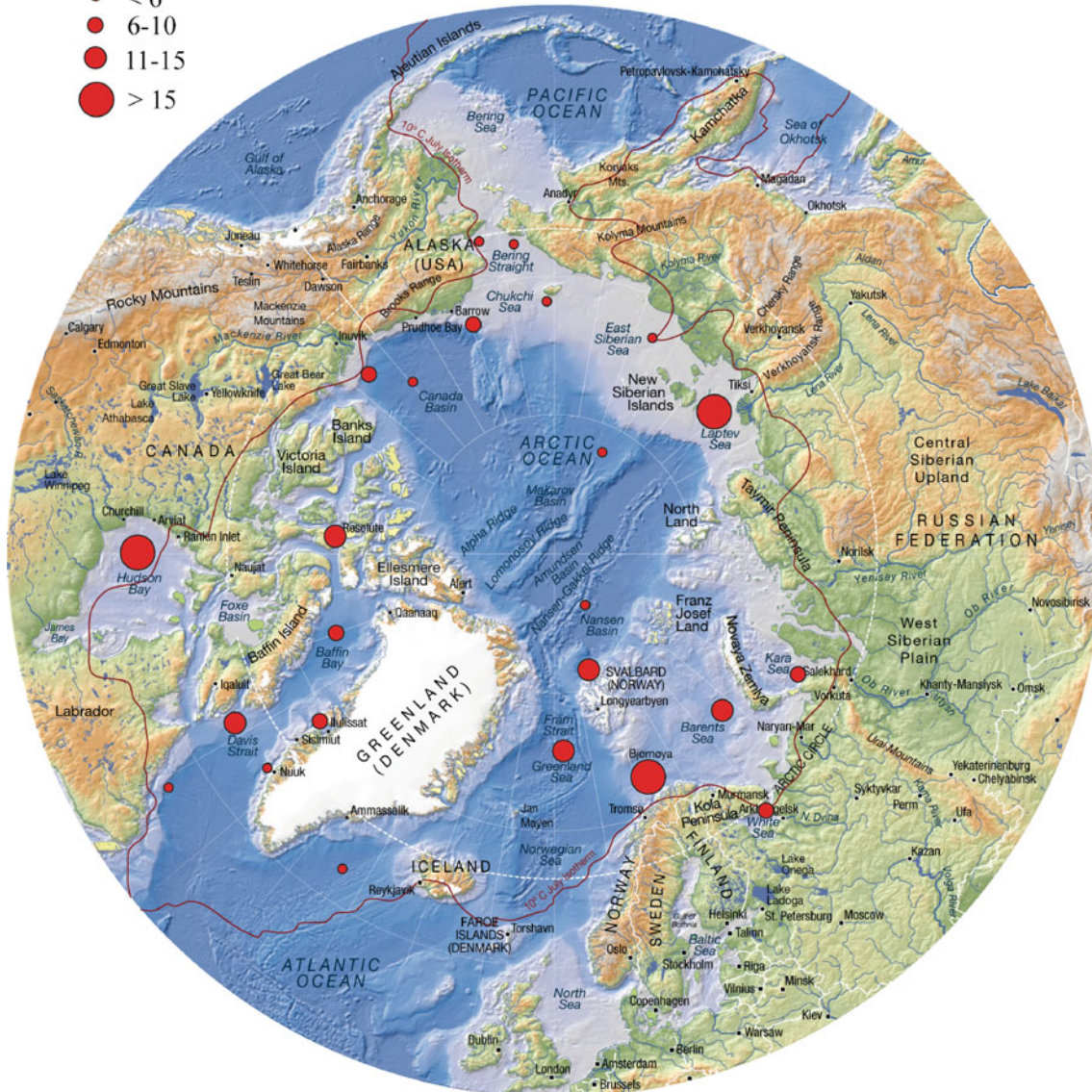


Fig. 3 Number of phytoplankton inventory records throughout the Arctic regions

ice; the former usually being epiphytic on large diatom cells (e.g., *Entomoneis* spp., *Nitzschia* spp.), while the latter is characteristically a sub-ice colonial species. *Melosira arctica* is unique in that it is free-floating or loosely attached to the under-ice forming very long curtains that trail into the water column attached to the underside of Arctic sea ice (Ambrose et al. 2005; Gradinger 1998; von Quillfeldt 1997).

Comparison to other regions

At the global scale, the marine Arctic unicellular eukaryotes display a rather high taxonomic diversity compared with the classic portrayal of this northern cold environment as

being biologically poorly diversified (Archambault et al. 2010). If the number of worldwide recognized microscopic algae, recently estimated at 24,300 taxa (Poulin and Williams 2002), including some 5,000 phytoplankton taxa in the world oceans (Sournia et al. 1991; Tett and Barton 1995), then our number of pan-Arctic phytoplankton and sea-ice unicellular eukaryotes at 2,106 taxa is a respectable fraction. Our estimate is considerably higher than 153 to 388 taxa reported for its Antarctic counterpart (Table 2; Horner 1985; Palmisano and Garrison 1993; Scott and Marchant 2005). This low species richness of marine Antarctic unicellular eukaryotes may be explained by historical scientific interests, less effort spent identifying

Number of inventory records

- < 6
- 6-10
- > 10



Fig. 4 Number of sea-ice eukaryote inventory records throughout the Arctic regions

species and more on experimental studies (Horner 1985), but more likely represents an underestimation of the real diversity of Antarctic protists.

There are only some 200 unicellular eukaryote taxa, corresponding approximately to 75% large cells ($>20 \mu\text{m}$) versus 25% small cells ($<20 \mu\text{m}$), that have been reported from both Arctic and Antarctic phytoplankton and sea-ice communities with, however, unanswered questions regarding their truly bipolar nature. There are several questionable occurrences, such as the sea-ice diatoms *Navicula glaciei* Van Heurck or *Nitzschia frigida* recorded in Hudson Bay in the Canadian sub-Arctic and in Antarctic, respectively, that are very likely due to misidentifications (Palmisano and Garrison 1993; Poulin et al. 1983; Scott and Marchant 2005). There are a suite of small naviculoid diatoms closely

related to *N. glaciei* (Poulin and Cardinal 1982), while in the Antarctic sea ice *Nitzschia stellata* Manguin is known to form arborescent colonies similar to *N. frigida*, but the two species are morphologically different (Medlin and Hasle 1990). This is especially the case for the hard to differentiate *Thalassiosira antarctica* var. *borealis* from *T. gravida* (von Quillfeldt 2000a, 2001), or the recently described *Nitzschia promare* Medlin and *Fossula arctica* Hasle et al., which may have been previously recorded as *Nitzschia*, *Fragilariopsis* and *Fragilaria* species (Hasle et al. 1996; Medlin and Hasle 1990; Sakshaug et al. 2009; von Quillfeldt 2001).

The lack of authenticated taxonomic reports prevented accurate species level identification to access bipolarity, even though some efforts resulted in a better circumscrip-

Table 5 Number of diatom and flagellate taxa in marine phytoplankton and sea-ice communities recorded from various circumarctic locations. Annually formed landfast and pack ice were considered under the sea-ice habitat

Region	Habitat	Number of diatom taxa	Number of flagellate taxa	Total number of taxa	Reference
Smith Sound to Labrador Sea	Phytoplankton	63	51	114	Grøntved and Seidenfaden (1938)
East to west Canadian Arctic	Phytoplankton	244	110	354	Hsiao (1983)
	Sea ice	197	8	205	
Whole Arctic	Phytoplankton	22	1	23	Horner (1985)
	Sea ice	271	19	290	
Chukchi, East Siberian and Laptev seas	Sea ice	148	8	156	Okolodkov (1992)
East Siberian Sea	Sea ice	115	6	156	Okolodkov (1993)
Arctic Ocean	Phytoplankton	30	10	40	Booth and Horner (1997)
	Sea ice	31	7	38	
Baltic Sea	Phytoplankton	20	56	76	Ikävalko and Thomsen (1997)
	Sea ice	22	58	80	
Laptev Sea	Phytoplankton	28	19	47	Tuschling et al. (2000)
	Sea ice	19	1	20	
Kara Sea	Phytoplankton	8	8	16	Druzhkov et al. (2001)
	Sea ice	11	5	16	
Smith Sound to Baffin Bay	Phytoplankton	70	108	178	Lovejoy et al. (2002)
Canada Basin	Phytoplankton	28	24	52	Melnikov et al. (2002)
	Sea ice	25	6	31	
Chukchi Sea	Phytoplankton	42	7	49	von Quillfeldt et al. (2003)
	Sea ice	199	1	200	
Barents and White seas	Phytoplankton	134	103	237	Ratkova and Wassmann (2005)
	Sea ice	143	87	230	
Whole Arctic	Phytoplankton	1059	815	1874	This study
	Sea ice	731	296	1027	

tion of mostly large-celled eukaryotes, namely diatoms (Hasle et al. 1996; Medlin and Hasle 1990; Medlin and Priddle 1990; Poulin 1990, 1991, 1993; von Quillfeldt 2000b). The situation is even more problematic for small-sized autotrophic and heterotrophic eukaryote cells which have been often neglected from Arctic inventories. Over the last decades only a few studies contributed to a better recognition and circumscription of these small eukaryote taxa (Daugbjerg 1996; Daugbjerg and Moestrup 1993; Daugbjerg and Vørs 1994; Ikävalko 1998; Ikävalko and Gradinger 1997; Thomsen et al. 1997; Vørs 1993). Some species have been characterized as being bipolar like *Fragilariopsis cylindrus* and *Porosira glacialis* (Grunow) Jørgensen. Recently, Lundholm and Hasle (2008) confirmed the bipolarity of *F. cylindrus*, a cold-adapted pennate diatom, based on morphological data, but this was not corroborated by nucleotide sequence data. A recent examination of the bipolar issue for marine invertebrates suggests bipolarity is exceedingly rare (Allcock et al. 2010). Further studies with specific molecular probes will contribute to further assess the existence of morphological differences between labelled-bipolar species of marine single-celled eukaryotes.

Unfortunately, there are too few exhaustive current inventories of marine phytoplankton eukaryotes from tropical and temperate regions; only some reported on the phytoplankton diversity in the St. Lawrence ecosystem in Eastern Canada, the North Sea and coastal Norwegian waters with 499, 288 and 502 fully illustrated taxa, respectively (Bérard-Therriault et al. 1999; Hoppenrath et al. 2009; Throndsen et al. 2007), while Horner (2002) described and illustrated the most common 134 phytoplankton species recorded from the Washington coast in the Pacific Ocean.

Other biodiversity assessments of marine phytoplankton have focused mainly on large-celled eukaryotes (>20 µm), neglecting totally or almost the contribution of small autotrophic and heterotrophic eukaryotes. For example, Villac et al. (2008) listed 572 phytoplankton taxa, consisting mainly of diatoms (82%) and dinoflagellates (16%) along the coast of São Paulo in Brazil. Moreno et al. (1996) and Okolodkov and Gárate-Lizárraga (2006) reported the occurrence of 418 planktonic and benthic diatoms, and 605 dinoflagellates from the Gulf of California and the Mexican Pacific Ocean, respectively, while Kravesky et al. (2009) and Steidinger et al. (2009) recorded 948 planktonic and

benthic diatoms, and 633 planktonic dinoflagellates from the Gulf of Mexico, respectively. Globally, Gómez (2005) reported 1,555 species of free-living marine dinoflagellates in the world's oceans, while Young et al. (2003) illustrated some 260 extant coccolithophorid taxa and Jordan et al. (2004) presented a revised classification scheme of 309 extant prymnesiophytes. There is a pressing need to improve the knowledge of small-celled autotrophic and heterotrophic eukaryotes by increasing biodiversity inventory and monitoring, particularly now at times of global warming threatening not only the polar regions but also all coastal and oceanic regions of the earth.

Perspectives and recommendations

In addition to well-established, cold-adapted marine eukaryote taxa throughout the whole Arctic, there are several known to be harmful or toxic species that are extending their distribution range or simply entering the northern polar seas (Table 4). No studies have been conducted yet for testing the potential toxicity of these 37 marine planktonic eukaryote taxa. This research avenue should be pursued before further development and exploitation of the Arctic's biological resources, particularly knowing the detrimental effects of species like *Alexandrium tamarense*, *Dinophysis acuminata*, *Protoceratium reticulatum* and *Pseudo-nitzschia seriata*.

Moreover, the large range in cell-size of Arctic marine pelagic and sympagic eukaryotes has obviously resulted in a strong bias towards large cells (>20 µm) being recorded more often. Additionally, cells exhibiting a rigid and robust casing exterior, like the siliceous frustules of diatoms and the cellulosic plates of thecate dinoflagellates, can explain why these eukaryote taxa are relatively better preserved in fixed samples and, therefore, more represented in species inventories from Arctic marine ecosystems. To account for such a bias, future studies need to address the diversity of the pico- and nano-sized fraction (<20 µm) of marine eukaryotic cells. Such studies will benefit greatly if based on a combination of traditional light and electron microscopy, and molecular methods such as clone libraries or pyrosequencing of environmental samples. Real-time PCR based on sequence information obtained from PCR clone libraries or pyrosequencing can then be used to get abundance estimates of dominant or harmful/toxic species (Doucette et al. 2009; Scholin et al. 2009). Such an initiative will require that the field of taxonomy be better financially supported by the pan-Arctic countries and works in close collaboration with other disciplines like molecular biology in an international consortium-like network. It would also be imperative to develop some training of the next generation of expert scientists in the field of phytoplank-

ton taxonomy and systematics, which has been entirely neglected at present (Archambault et al. 2010).

This first attempt to inventory the biodiversity of marine Arctic unicellular eukaryotes did not allow us to validate the accurate identification of the various taxa reported because all records, with only a few exceptions, were merely listing of the species present in a given polar region without the existence of voucher collections or micrographs documenting species identification. However, this first inventory of the basic trophic level of the marine food web is crucial for future monitoring planning of the Arctic. It highlights that a greater effort is still needed to better circumscribe the marine Arctic eukaryotes, especially the small-sized autotrophs and heterotrophs, including molecular analyses.

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