

# Tintinnid ciliates of the marine microzooplankton in Arctic Seas: a compilation and analysis of species records

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**Abstract** We set out to examine a postulated latitudinal trend in species richness within the Arctic Ocean. We compiled species records of tintinnid ciliates in the Arctic from the literature and added our own unpublished Chukchi Sea data to produce a database (available as an Online Resource data file) consisting of 1427 records of 89 species from 414 locations above 65°N sampled from 1885 to 2015. While there was no trend of species richness throughout the Arctic, there was a significant positive relationship between species richness and the number of sites sampled in a 2° band, suggesting a sampling effect. Plotting cumulative numbers of species and cumulative number of sites sampled by year, we found a linear relationship in log cumulative numbers of species and log sites sampled, and a lack of a plateau in the species accumulation trend. Species records are highly dominated by four species, accounting for 45% of the records: *Acanthostomella norvegica*, *Parafavella denticulata*, *Ptychocylis obtusa* and *Salpingella acuminata*, all of which, except *S. acuminata*, have long been suspected to be morphologically variable, with different morphotypes given undue

species status. Pooling all reported species of *Acanthostomella*, *Parafavella* and *Ptychocylis* yielded little qualitative differences but considerable quantitative differences. We found large discrepancies in geographic coverage. We conclude that many zones projected to experience large changes in sea ice coverage are under-sampled. Based on the historical trend, the list of Arctic tintinnid ciliate species will likely continue to grow with new sampling, regardless of changes in the Arctic Seas.

**Keywords** Biodiversity · Biogeography · Plankton · Zooplankton · Protist · Latitudinal diversity gradient

## Introduction

Microzooplankton are a key component of planktonic food webs as they are responsible for the consumption of most of the primary production in the plankton, including in the Arctic Seas (Nelson et al. 2014). The relative importance of microzooplankton as grazers in the Arctic Seas is predicted to increase due to the foreseen shifts towards smaller phytoplankters (Li et al. 2009) and changes in the timing of phytoplankton blooms (Michel et al. 2012). Tintinnid ciliates are a usually minority component in the microzooplankton (McManus and Santoferrara 2013). However, in the Arctic tintinnid ciliates can occasionally be a significant component of the grazer community (Sherr et al. 2009) and can seasonally dominate the biomass of the ciliate microzooplankton (Seuthe et al. 2011). Tintinnids are also a component of the sea ice fauna (e.g. Melnikov et al. 2002). Among the microzooplankton, they are unique in possessing a cylindrical or cup-shaped species-specific lorica (shell) permitting species identification with relative ease compared to most other taxa of the microzooplankton.

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Furthermore, an easily measured dimension of the lorica, the size of oral opening, is correlated with size of preferred prey and maximum growth rate (Montagnes 2013). Species with similar lorica oral diameters share then key ecological characteristics and can be considered as ecological redundants.

For tintinnids, global distribution patterns are, compared to most microzooplankton taxa, relatively well known. On a large scale, they display the most common global biogeographic pattern found among marine species, the bimodal diversity gradient, wherein species richness increases from high to low latitudes with a slight dip near the equator (Chaudary et al. 2016). Recently, we examined the latitudinal pattern in morphological diversity as well as species diversity in tintinnids along a Northern Hemisphere transect from the Sea of Japan/East Sea to the High Arctic sampled in late summer of 2012, the year of record low sea ice (Dolan et al. 2016). Both species richness and morphological diversity (as numbers of distinct oral diameters) declined dramatically to low levels in the High Arctic. We found just a few species in the High Arctic of very different morphologies suggesting a marked lack of ecological redundancy in the tintinnid assemblage. However, our sampling, as with all oceanographic campaigns and indeed any sampling, yielded only snapshots of certain locales and with generally large detection limits; hence, the generality of our finding for tintinnids in the Arctic Ocean overall required confirmation. Diversity gradients within the Arctic have been found previously for terrestrial plants (e.g. Jedrzejek et al. 2012) terrestrial vertebrates (Glig et al. 2012) and aquatic insects (Scott et al. 2011).

To our knowledge, there have been no studies of latitudinal gradients in diversity with regard to planktonic organisms of the Arctic. Following Longhurst (1998), the Arctic Ocean along with its marginal seas comprises the Boreal Polar Province. The latitudinal gradients (roughly) characterising the province between 65°N and the High Arctic, potentially influencing species richness, include water temperature, temporal and areal extent of sea ice, water column depth as well as areal extent of the Arctic Sea (Longhurst 1998).

It has been noted that Arctic data is unusually scattered, often in obscure journals, and generally not compiled (Wassmann 2011). Previous reviews of tintinnid species distributions (i.e. Pierce and Turner 1993; Dolan and Pierce 2013), with regard to the Arctic, relied on the few easily available Arctic records and concerned only the genus level. Furthermore, the analyses pre-dated several recent relatively large studies (i.e. Monti and Minocci 2013; Dolan et al. 2014; Feng et al. 2014; Matsuno et al. 2014; Li et al. 2016). To our knowledge, there is no inventory or checklist of tintinnid ciliates in the Arctic. It would be fair to say that tintinnid ciliates have been largely neglected. In

recent large synthesis reports concerning Arctic biodiversity (e.g. Meltotte 2013; Jorgensen et al. 2016) and reviews of microbes in the Arctic (Dickson et al. 2016) tintinnid ciliates are not mentioned.

To address questions of the magnitude of tintinnid species and morphological diversity in the Arctic and the possible existence of geographic patterns, it was necessary to construct de novo a database of species records for the Arctic. We combed the published literature for records of the presence of species in locations above 65°N. To published records, we added our own previously unpublished data from analysis of samples obtained in 2010, 2013, 2014 and 2015 from a large suite of stations in the Chukchi Sea. The questions we sought to address were as follows: (1) What is the known taxonomic diversity of tintinnids in the Arctic Seas, (2) What is the morphological diversity, in terms of distinct sizes of oral openings, of the tintinnids found in the Arctic Seas, and (3) Is there a latitudinal diversity gradient within the Arctic Sea? While the database was assembled to answer these questions, it may also serve as baseline data, often lacking and needed to detect possible distributional shifts (Jorgensen et al. 2016), as well as providing a checklist of known Arctic morpho-species against which emerging molecular data (e.g. Lovejoy 2014; Pedros-Alio et al. 2015; Stecher et al. 2016) may eventually be cross-referenced.

## Methods

Google Scholar (<https://scholar.google.com/>) was used to identify documents containing the name of a known Arctic tintinnid genus (i.e. *Acanthostomella*, *Leprotintinnus*, *Parafavella*, *Ptychocyllis*). Searches were run also for documents containing the term “arctic” as well the word “tintinnid” or “tintinnids” or “tintinnida”. Articles citing documents containing a species record and the reference list of the articles themselves were screened by title. For some publications that reported pooled data, e.g. species found in sets of stations, the authors were contacted with a request for their data on species by sampling location (see Acknowledgements for the authors who generously supplied data). Reports from the historic literature were obtained by searching the biodiversity Heritage Library (<http://www.biodiversitylibrary.org/>) for documents containing mentions of known Arctic species. It should be noted that sampling among the studies varied widely from coarse plankton nets to whole water examination. For many records, tintinnid species were noted as “by-catch” as the investigations were focused primarily on phytoplankton or metazoan zooplankton. Consequently no attempt was made to analyse data in terms of species per investigator publication. A species record was logged only when a binomial



species name was given and a location was given, or could be determined, with a sample date (at least the year). Data were entered into a spreadsheet containing eight columns by which records may be sorted: species, latitude, longitude, locality, reference, sample date, note (station or sample number), and system or sea (i.e. Baffin Bay, Barents Sea, Beaufort Sea, Canadian Archipelago, Chukchi Sea, Greenland Sea, Kara Sea, Laptev Sea, Norwegian Sea, White Sea). We have likely missed some of the Russian language literature not repeatedly cited. However, we have no reason to believe that such additional data would materially effect our conclusions.

We included previously unpublished data from cruises in the Chukchi Sea area in 2010, 2013, 2014, and 2015. Sampling and sampling analysis followed methods described in detail in Dolan et al. (2013, 2016). Briefly, for most stations a 20- $\mu\text{m}$  mesh plankton net was towed from approximately 100 m to the surface. Net material was fixed with either Acid Lugol's solution or Bouin's fixative, and in the lab sample aliquots were examined with an inverted microscope. Our previously unpublished species records were entered under "reference" as ARA 01 Cruise for 2010, ARA 03 Cruise for 2013, ARA 05 Cruise for 2014, and ARA 06 Cruise for 2015 (see the Online Resource data file containing all species records).

To examine morphological characteristics of the Arctic species pool, each species was assigned lorica dimensions. We used the average of the range of lorica dimensions for the species given in the text descriptions by Kofoid and Campbell (1929) as many investigators relied on the monograph for species identification. For species depicted in Kofoid and Campbell (1929) but unaccompanied by a text description, we assigned dimensions of forms with text descriptions depicted in the plates as having very similar dimensions. For species described after 1929, the dimensions given in the original descriptions were assigned. We realise that dimensions and scales of depictions in Kofoid and Campbell (1929) contain errors compared to the preferred authority of the original description or re-descriptions (e.g. Dolan 2016b; Santoferrara et al. 2016). However, the dimensions given in the text, or implied in the illustrations of Kofoid and Campbell, are likely to correspond to those of the organism observed by individual investigators compared to a more authoritative description. The final species list was cross-checked against GenBank to identify taxa for which sequence data have been deposited as of July 25th 2016.

We also distinguished some possibly doubtful species identities. Some of the tintinnid species commonly found in sub-Arctic and Arctic waters have long been suspected to form variable loricas with the morphological variants given undue status as distinct species. These suspected polymorphs are species of *Acanthostomella* (our own observations), *Parafavella* (Schulz and Wulff 1927; Burkovsky

1973; Cardinal et al. 1977; Davis 1978) and *Ptychocylis* (Davis 1981).

## Results

### Qualitative and quantitative characteristics of the species records

We extracted data from 39 publications published between 1900 and 2015 containing records of species from locations from 65° to 82°N. Including our own new data for the Chukchi Sea, the database contains 1427 records of 89 species from 414 locations sampled from 1885 (Gran 1900) to 2015 (this report). The vast majority of records are from single time point sampling of unique localities from oceanographic cruises in summer months. Few reports gave time-series data and only two had data from winter sampling, which interestingly yielded species similar to those found in summer sampling at the same site (Gaarder 1938; Tibbs 1967).

Table 1 summarises the contents of the database giving the list of species, the number of records by "Sea", for each species, as well as the first year the species was reported from the Arctic. Taxa for which one or more nucleotide sequences have been deposited in GenBank are shown in bold. Of the 19 tintinnid genera, 13 are represented in GenBank and of the 89 tintinnid species GenBank contains sequence data for 23 species. The complete database of species records is supplied as a Online Resource data file. Figure 1 shows the locations of all sampling points revealing large discrepancies in the geographic coverage of the data. Notably, there are no data for the Eastern Siberian Sea and there is very little data available for the Laptev Sea as well as the Canadian Archipelago.

The four most often reported species, in order of the number of records, were *Ptychocylis obtusa*, *Parafavella denticulata*, *Acanthostomella norvegica* and *Salpingella acuminata*, species of quite distinct morphologies (Fig. 2). The four species accounted for 45% of the species records (Fig. 3). These species were also the most widely distributed in terms of the number of seas from which they were reported (Table 1) and their apparent latitudinal range (Fig. 3). Remarkably, no species has been reported from all of the Arctic Seas. The number of potentially questionable records, the "oncens" that is species recorded but once, represent 20 out of the 89 species. The suspected "polymorphs", possibly morphological variants of the most common species of *Acanthostomella*, *Parafavella* and *Ptychocylis*, represent 21 of the 89 species. Thus, even after subtracting potentially dubious records, the Arctic tintinnid fauna is substantial, consisting of 48 species in 16 genera. The morphological diversity, in terms of numbers

**Table 1** List of species recorded from Arctic Seas

Species	GS	BB	CA	Be S	C S	LS	KS	Ba S	WS	NS	References	First year
<i>Acanthostomella conicoides</i>					5						27, 35	2010
<i>Acanthostomella gracilis</i>		1	3								20, 34	1988
<i>Acanthostomella norvegica</i>	35	2			63		12	16		25	1, 2, 3, 4, 5, 11, 12, 13, 15, 16, 17, 18, 19, 23, 24, 26, 27, 28, 29, 35, 36, 37, 38, 39	1899
<i>Bursaopsis vitrea</i>					1						10	2012
<i>Canthariella pyramidata</i>					2						35	2010
<i>Codonellopsis frigida</i>					10						14, 22, 35	2010
<i>Codonellopsis lagunela</i>										2	28, 30	1945
<b><i>Codonellopsis morchella</i></b>					1						35	2010
<i>Codonellopsis ovata</i>									1		3	1970
<i>Codonellopsis pusilla</i>									1		3	1970
<i>Codonellopsis schabi</i>					1						35	2010
<i>Eutintinnus apertus</i>					1						9	2011
<i>Eutintinnus tenuis</i>	2										13	1994
<b><i>Favella azorica</i></b>					10						35	2010
<i>Helicostomella fusiformis</i>										1	12	1930
<b><i>Helicostomella subulata</i></b>					2				2	6	12, 22, 3, 24, 30, 14	1898
<i>Leprotintinnus bottnicus</i>						1	1		1		3, 33	1927
<b><i>Leprotintinnus pellucidus</i></b>	2	4		6	24		12	14		8	1, 2, 3, 4, 9, 11, 12, 14, 17, 19, 22, 30, 32, 36, 39	1907
<i>Metacylis vitreoides</i>	1				3		3				1, 3, 22, 32	1907
<i>Ormosella trachelium</i>					1						35	2010
<i>Parafavella acuta</i>							7				1, 3	1925
<i>Parafavella cylindrica</i>								17		1	1, 8, 36	1921
<i>Parafavella denticulata</i>	76	9	1		1	1	9	10	2	20	1, 2, 3, 24, 8, 30, 29, 12, 13, 15, 23, 16, 17, 18, 19, 27, 25, 32, 33, 34, 36, 37, 38	1895
<i>Parafavella dilatata</i>										1	8	1975
<i>Parafavella edentata</i>	3									2	5, 11, 12, 30	1898
<i>Parafavella elegans</i>	1	1	9	2	2					1	7, 14, 15, 26, 34	1975
<i>Parafavella faceta</i>					3						14	2014
<i>Parafavella gigantea</i>	24	2		8	1		18	5	13		22, 6, 8, 11, 29, 26, 15, 16, 17, 18, 31, 21	1907
<i>Parafavella hemifusus</i>								3			1	1925
<i>Parafavella jorgensi</i>					15						14, 35	2010
<i>Parafavella media</i>	3										5	1898
<i>Parafavella obtusa</i>									1		3	1970
<i>Parafavella obtusangula</i>	1									1	8, 26	1975
<i>Parafavella parumdentata</i>					9		2		9	1	8, 10, 22, 39	1975
<i>Parafavella promissa</i>					1						14	2014
<i>Parafavella robusta</i>	14						9			1	1, 9, 18	1906
<i>Parafavella rotundata</i>							6			1	1, 30	1925
<i>Parafavella subrotundata</i>					1		10				1, 6, 22	1921
<i>Parafavella tenuis</i>							2				1	1925

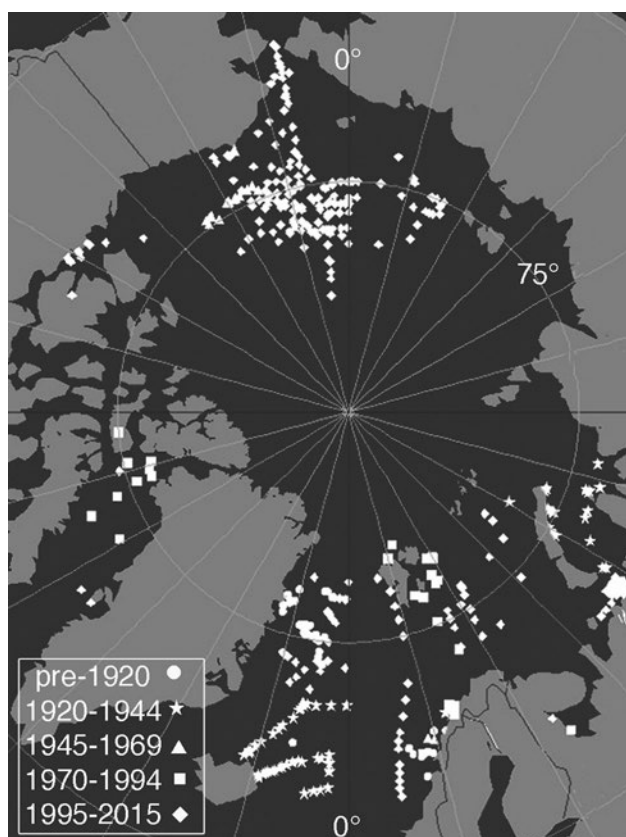
Table 1 continued

Species	GS	BB	CA	Be S	C S	LS	KS	Ba S	WS	NS	References	First year
<i>Parafavella ventricosa</i>					2						14	2014
<b><i>Ptychocyclus acuta</i></b>	1	1						3		1	7, 29, 26, 15	1975
<i>Ptychocyclus arctica</i>					1				1	4	3, 4, 7, 12, 30	1926
<i>Ptychocyclus cylindrica</i>										3	12, 30	1930
<i>Ptychocyclus drygalski</i>	9			10							16, 21	1935
<i>Ptychocyclus minor</i>										1	7	1975
<i>Ptychocyclus obtusa</i>	71	5	9	1	116		20	9	13	13	22, 9, 10, 1, 2, 3, 4, 5, 7, 11, 12, 30, 29, 13, 14, 15, 16, 17, 18, 25.32, 35, 36, 39	1898
<i>Ptychocyclus urnula</i>	31				1		7			8	4, 12, 16, 30, 36, 38	1921
<i>Salpingacantha perca</i>					1						35	2010
<i>Salpingacantha simplex</i>					14						22	2010
<b><i>Salpingella acuminata</i></b>	18			23	66		2	2	1	11	2, 3, 4, 9, 10, 12, 16, 21, 22, 28, 30, 36, 37, 38	1921
<i>Salpingella curta</i>										2	17	2008
<i>Salpingella faurei</i>					65						9, 10, 22	2010
<i>Salpingella secata</i>							3	3			29	1925
<i>Salpingacantha unguiculata</i>								1			29	1993
<i>Schmidingerella serrata</i>										5	12, 30, 38	1930
<b><i>Schmidingerella taraiakensis</i></b>									1		3	1970
<b><i>Steenstrupiella robusta</i></b>									1		3	1970
<b><i>Stenosemella nivalis</i></b>					8		1			1	14, 17, 35, 36	1921
<i>Stenosemella olive</i>								1	1	2	3, 29, 12	1930
<b><i>Stenosemella steinii</i></b>		2									15	1988
<b><i>Stenosemella ventricosa</i></b>					4		9			1	1, 22, 23, 35, 36	1921
<b><i>Tintinnidium mucicola</i></b>					17						35	2010
<i>Tintinnopsis acuminata</i>					17						14, 22	2010
<i>Tintinnopsis amphora</i>								1			40	2002
<i>Tintinnopsis angusta</i>								5			40	2002
<b><i>Tintinnopsis baltica</i></b>					5						14, 22	2014
<b><i>Tintinnopsis beroidea</i></b>	2	1			6		9	5	1	9	1, 2, 3, 4, 9, 12, 15, 30, 36, 37, 38	1899
<i>Tintinnopsis campanula</i>									1	5	3, 12, 30, 38	1898
<b><i>Tintinnopsis elongata</i></b>								7			40	2002
<b><i>Tintinnopsis fimbriata</i></b>					1	1	1		1		3, 22, 33	1927
<i>Tintinnopsis japonica</i>					2						3, 14	2014
<i>Tintinnopsis karajacensis</i>	1				5		10				4, 22, 32, 36	1907
<i>Tintinnopsis kofoidi</i>					1						14	2014
<b><i>Tintinnopsis lata</i></b>					9		3				1, 22	1925
<b><i>Tintinnopsis major</i></b>										1	12	1930
<i>Tintinnopsis mayeri</i>					4						14	2014
<i>Tintinnopsis meuneri</i>							3				1	1925
<b><i>Tintinnopsis nana</i></b>					1				1		3, 22	1970
<i>Tintinnopsis nitida</i>							4				1, 36	1921
<b><i>Tintinnopsis parvula</i></b>	1				1				1	3	3, 4, 11, 12, 30	1930
<i>Tintinnopsis plagiostoma</i>								2			40	2002
<b><i>Tintinnopsis rapa</i></b>					16						3, 9, 14, 22	2011

**Table 1** continued

Species	GS	BB	CA	Be S	C S	LS	KS	Ba S	WS	NS	References	First year
<i>Tintinnopsis subacuta</i>					2						9	2012
<i>Tintinnopsis tubulosa</i>							4		1		3, 36	1921
<i>Tintinnopsis turbo</i>					2			1		2	22, 2	1988
<i>Tintinnopsis undella</i>						1	1				3, 33	1927
<i>Tintinnopsis urnula</i>					2					2	9, 12	1930
<i>Tintinnopsis vasculum</i>								14			40	2002
Species	GS	BB	CA	Be S	C S	LS	KS	Ba S	WS	NS	References	First year

Number of records for the Greenland Sea (GS), Baffin Bay (BB), Canadian Archipelago (CA), Beaufort Sea (Be S) Chukchi Sea (CS), Laptev Sea (LS), Kara Sea (KS), Barents Sea (BS), White Sea (WS) and Norwegian Sea (NS). References given in Table 2. Taxa in bold denote sequence data present in GenBank as of July 25 2016



**Fig. 1** Map of the locations sampled from 1885 to 2015 from which one or more tintinnid species was reported. Note that there does not appear to be any historical bias with regard to a dominance of nearshore compared to open water sampling

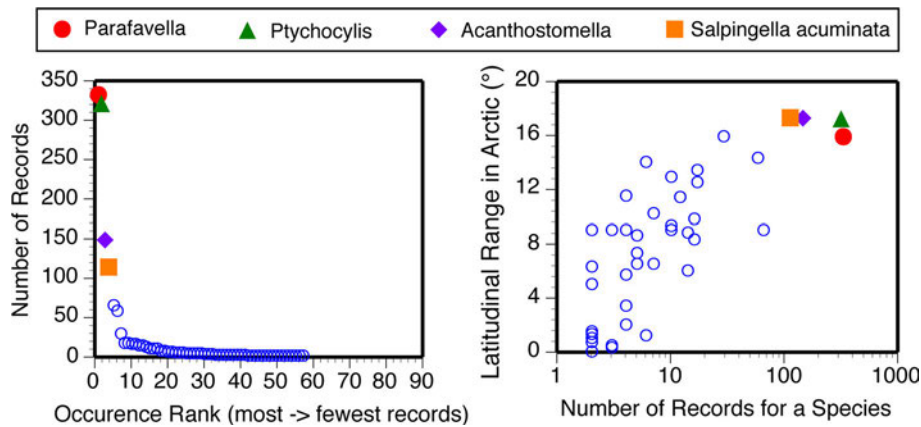
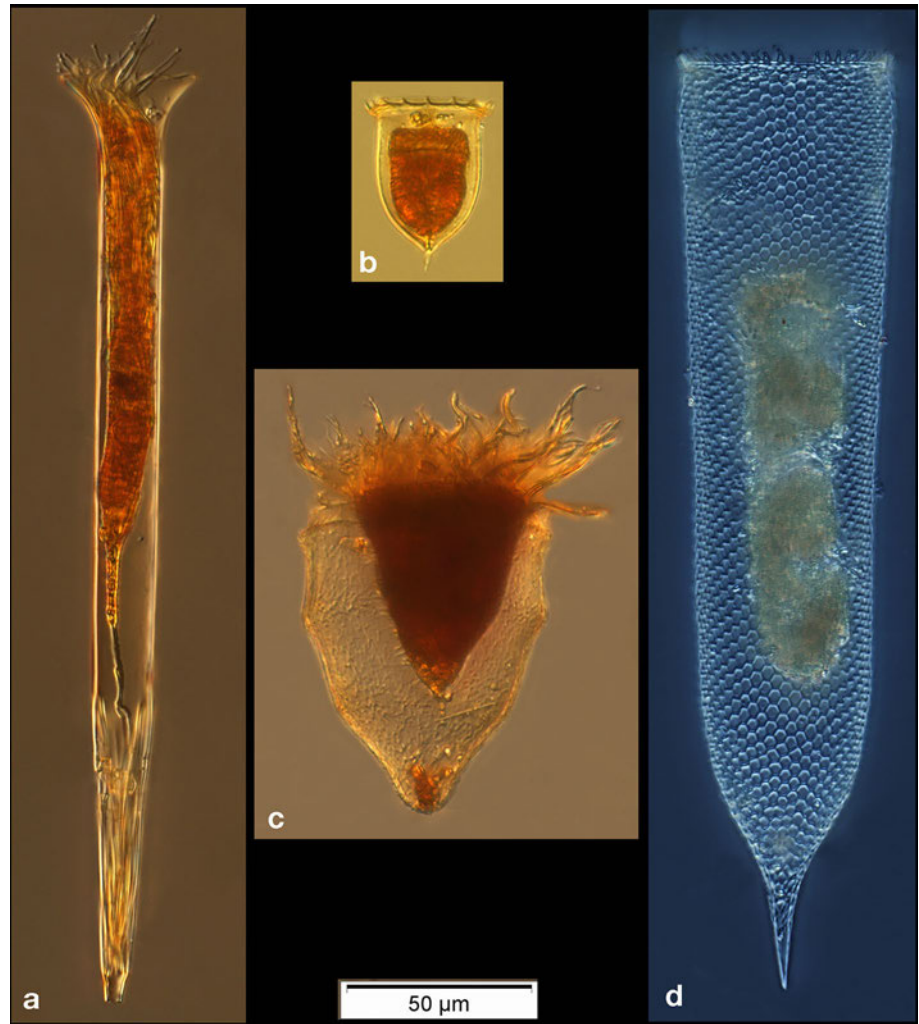
of species in different size classes of lorica oral diameter, is large as well, considering the entire species pool recorded, or the species pool remaining after removing “oncercs” and “polymorphs” (Fig. 4). Most size classes contained several species. Notably, the size classes containing, or neighbouring, the four most commonly recorded species were the size classes containing the largest numbers of species (Fig. 4).

### Latitudinal and historical patterns

We pooled species records in bands of 2° latitude and plotted species richness against latitude. The resulting graph (Fig. 5) showed large differences in species richness among bands of latitude with perhaps a linear decline from 74° to 82°, but no overall gradient of species diversity with latitude. The heterogeneity in species richness among bands led us to examine the relationship between the number of sites sampled within a 2° band of latitude and the number of species recorded as occurring in the band. We found a significant positive relationship between species richness of a 2° latitudinal band and the number of sites sampled in the band (Fig. 5). The lack of a latitudinal gradient and the apparent positive relationship of species richness with sampling effort held when excluding “polymorphs”, the species recorded which are suspected of being morphological variants of another species recorded from the same latitudinal band. Examination of data concerning the Chukchi Sea, arguably the most sampled and with a large latitudinal gradient, revealed the same patterns (data not shown). The Arctic Seas vary considerably in basic characteristics of latitudinal range, area, average depth, importance of freshwater input, etc. (see the online resource figure Arctic Ocean bathymetric map). However, plotting the apparent species richness of the Arctic Seas as a function of sampling effort revealed the same positive relationship (Fig. 6). The apparent strong effect of sampling effort on apparent species richness led us to examine the large-scale (over the past 120 years) historical trends.

We found strikingly similar patterns plotting accumulated sites sampled with time from 1895 to 2015 and accumulated apparent species richness from 1985 to 2015 (Fig. 6). A simple linear correlation characterised the historical data cumulative sampling effort (log cumulative sites) and (log) cumulative number of species recorded (inset graph in Fig. 6). The relationship resembles a typical species-area curve of a census of contiguous habitats

**Fig. 2** Micrographs of the four most commonly reported tintinnids from Arctic waters: **a** *Salpingella acuminata*, **b** *Acanthostomella norvegica*, **c** *Ptychocyclus obtusa*, and **d** *Parafavella denticulata*. All Lugol's fixed specimens except for **d**, a Bouin's fixed cell

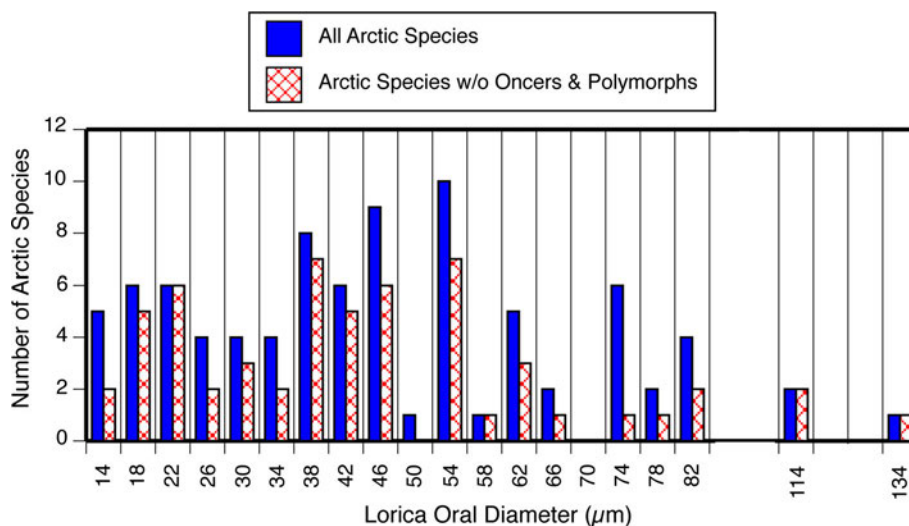


**Fig. 3** Plot of occurrence rank (*left panel*) and apparent latitudinal range versus the number of records for the species (*right panel*). Remarkably, four species account for a large fraction of the species records and these most frequently recorded forms are also those with

(Preston 1962). It is important to note that temporal increases in the Arctic species inventory do not represent increases in the number of species new to science but rather

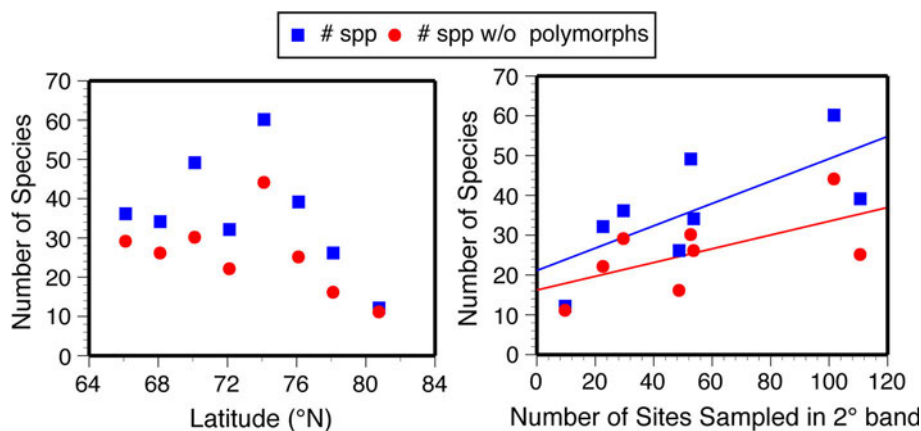
the largest apparent latitudinal range (species with but a single record were excluded). Note that while a species recorded but once will by definition have no latitudinal range, species with multiple records may or may be recorded across a range of latitudes

new to the Arctic. There was no indication of a plateau in the relationship suggesting that further increasing sampling effort in the Arctic, that is simply by continuing to sample,



**Fig. 4** Morphological characteristics of tintinnid species found in the arctic, frequency distribution of lorica oral diameters, or mouth sizes. Species were binned in size classes of 4  $\mu\text{m}$ . Data shown for all reported species (all Arctic Species) and the reduced pool of species remaining after removing species recorded only once and suspected

morphological variants of a main species (Arctic Species w/o Oncers & Polymorphs). The size classes containing the most frequently recorded species are shown with an asterisk. Note that x axis breaks used to include the large size classes omitting empty intermediate size categories



**Fig. 5** Species richness as a function of latitude, pooling data in bands of 2° latitude (*left panel*) and species richness as a function of the number of sites sampled within the 2° band of latitude (*right panel*). For both plots total numbers of species as recorded in publications are shown as well numbers of species without suspected polymorphs, morphological variants of the other species also recorded

in the band of latitude. Note the lack of consistent latitudinal gradient in species richness throughout the Arctic and the correlation of species richness within a band of latitude with the number of sites sampled within the band. For total species (# spp)  $r = 0.70$ ; for species excluding records of suspected morphological variants (w/o polymorphs)  $r = 0.63$

will likely yield increases in the number of tintinnid species known from Arctic waters (Fig. 7).

## Discussion

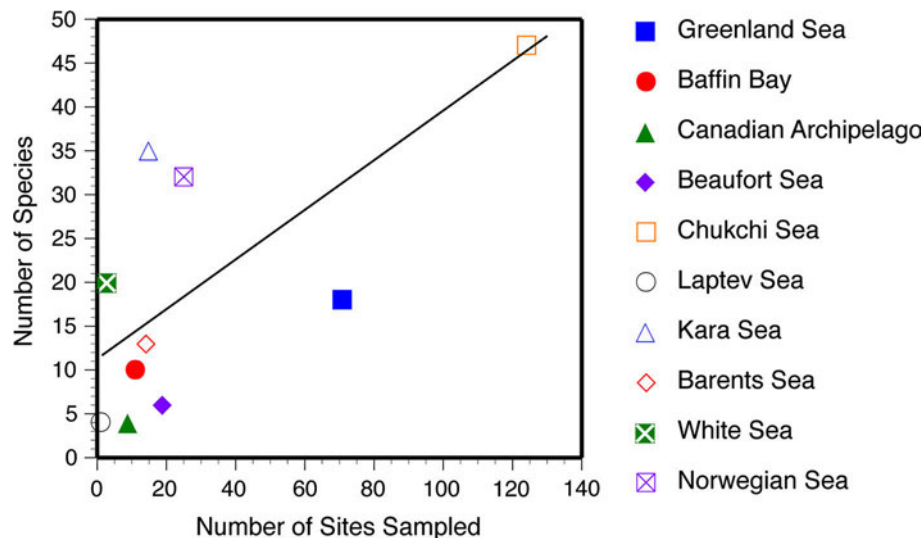
### Qualitative and quantitative characteristics of the species records

To put the magnitude of tintinnid species diversity in the Arctic, 89 species, in perspective, one can compare the number with total known diversity of living forms. The

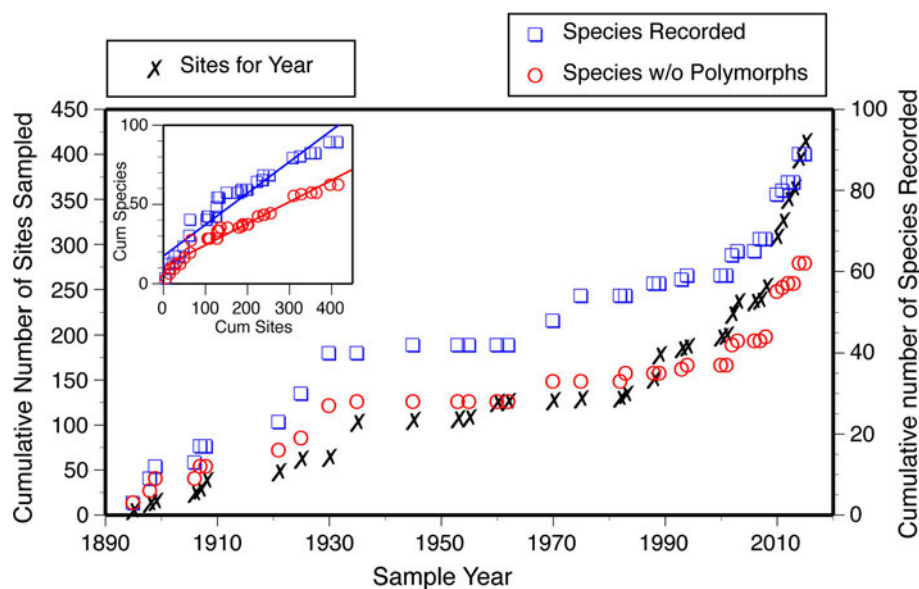
standard taxonomic monograph of Kofoid and Campbell (1929) lists and illustrates about 750 species. In a more recent compendium, the list extends to over 900 species (Zhang et al. 2012). Although many catalogued “species” are likely to be synonyms (e.g. Dolan 2016b), the forms reported from the Arctic Seas appear to represent a considerable fraction of described tintinnid species not restricted to warm waters, which number about 500, based on genus characterisation (Pierce and Turner 1993; Dolan and Pierce 2013). A majority of the Arctic genera are represented in GenBank with at least one nucleotide sequence deposited (Table 1). Of those genera without any



**Fig. 6** Species richness of the Arctic Seas as a function of the number sites sampled within the sea. The seas differ considerably in basic characteristics of area, latitudinal range, average depth, freshwater input, ice cover, etc., (see Online Fig. 1). Note the positive relationship of species richness with sampling effort,  $n = 10$ ,  $r^2 = 0.66$ ,  $p < 0.05$



**Fig. 7** Temporal changes in the cumulative number of sites sampled and species recorded (all reported and excluding suspected morphological variants of other species) in the Arctic from 1895 to 2015. Note the close correspondence in temporal trends. A simple linear correlation of log cumulative number of sites and log cumulative number of species is shown in the *inset graph* resembling the Preston species area curve for contiguous habit sampling (Preston 1962)



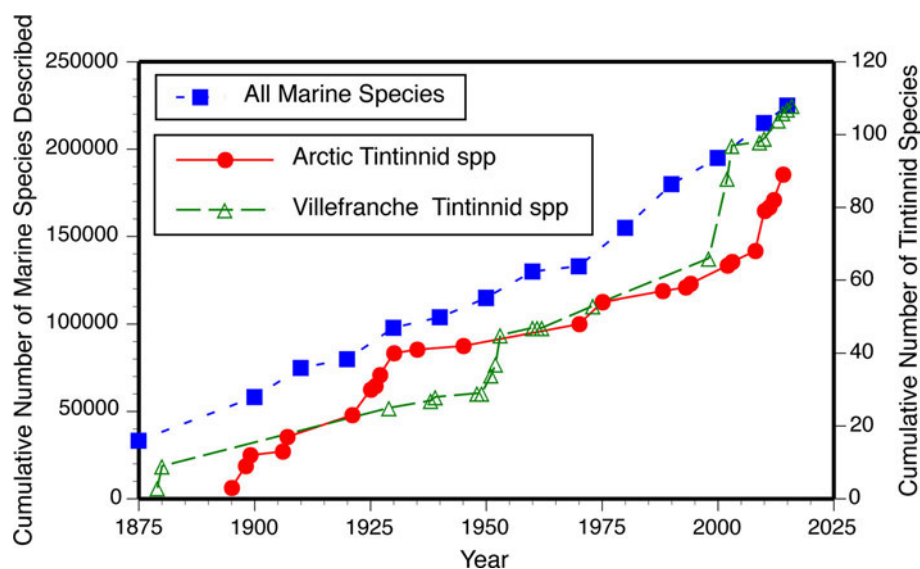
GenBank record, most have been recorded only a few times. However, of two the most abundant and long-known taxa, *Acanthostomella* and *Parafavella*, are completely absent from GenBank.

Arctic species diversity appears to be lower than that reported for the Southern Ocean, reviewed recently in Dolan et al. (2013). The records from the Southern Ocean are roughly comparable in quantity (2000 records from 402 locations) but contain 192 species. However, it is important to recall that the Southern Ocean is a much larger system as its northern border is usually taken as 40°S. Even using a northern border of 60°S, the surface area of the Southern Ocean is 21,000 km<sup>2</sup> compared to the Arctic Ocean's 15,000 km<sup>2</sup> (Eakins and Sharman 2010). Among the 89 species recorded from Arctic Seas, 20 have only been found once from one locality and possibly represent stray species

rather than resident forms. In comparison, among the Southern Ocean species, over a third appear to be strays, that is with only one recorded presence (Dolan and Pierce 2013). While many species have been found in the Arctic, the records mirror early reports of tintinnid assemblages being overwhelmingly dominated by just a few species (Gran 1900) as nearly half the records concern only four species (Fig. 3). In the size class of each these frequently recorded species are several other species of similar mouth size or lorica oral diameter (Fig. 4).

If we consider species of similar mouth size to be ecologically similar, then the pattern of several species in each size class suggests that there is considerable ecological redundancy overall in the pool of Arctic tintinnid species based on the inventory pooling all historical records. This is in contrast to findings of little ecological redundancy

**Fig. 8** Cumulative number of marine species described from 1875 to 2015 and cumulative number tintinnid species reported from the Arctic from 1885 to 2015 as shown in Fig. 6. Data on the temporal changes in the species inventory of the Bay of Villefranche (NW Mediterranean Sea) are from Dolan (2016a). Data for total marine species (benthic, nekton, planktonic, parasitic, free living, etc.) described from WoRMS Editorial Board (2016)



from our recent study which was based on samples from a transect of stations across the western Arctic to 82°N (Dolan et al. 2016). The discrepancy likely reflects the fact the overall species pool described here sums a large number of samplings conducted over a long period of time. However, both the single transect data and the overall pooled data suggest that the High Arctic is apparently species-poor. The High Arctic, characterised by a smaller areal extent and extensive sea ice coverage relative to lower latitude Arctic Seas, may indeed be species-poor. However, it is also poorly sampled and actually may harbour more species than known at present.

Interestingly, among the four species which dominate species records of the Arctic, two are also found in the Antarctic. *Acanthostomella norvegica* appears to be a bipolar species found in high-latitude waters of both hemispheres but absent from tropical, subtropical and temperate systems (Dolan and Pierce 2013). However, it is rarely abundant in Antarctic waters. The other Arctic dominant found also in Antarctic assemblages is *Salpingella acuminata*. It is an apparently cosmopolitan species found as a dominant form in assemblages from tropical waters (Dolan et al. 2007) to the Chuckchi Sea (Dolan et al. 2014). However, like *A. norvegica* it is not known to be dominant form in Antarctic waters.

### Latitudinal and historical patterns

Our study began with a desire to confirm or refute the existence of a latitudinal diversity gradient in the Arctic Ocean. Geographic distribution of species records showed no gradient throughout the Arctic Ocean, only a decline from 74° to 82°. While the highest latitudes do harbour a lower number of species, the highest latitudes are also the

least sampled. We found a positive relationship between apparent species richness of a latitudinal zone and the number of sites sampled within the zone. This led us to examine the historical trends of species records and sampling effort. Additions to the species inventories closely corresponded with cumulative sampling effort in the crude form of the number of sites sampled. Based on our findings, we predict that the species inventory will continue to grow simply as a result of increased cumulative sampling effort. There appears also to be a lack of baseline data on the distribution and composition of phytoplankton taxa (Daniëls et al. 2013). This considerably complicates diagnosis of the effects of changes in the Arctic for both microzooplankton and phytoplankton because baseline data is necessary to detect shifts (Jorgensen et al. 2016). In contrast, a similar situation does not appear to be the case for metazoan taxa of the zooplankton. Zooplankton diversity has been described as well characterised except for taxa restricted to the bathypelagic layer where increased sampling is expected to reveal species new to science (Kosobokova et al. 2010). Changes in circulation in the Arctic are predicted to yield major changes in the composition of metazoan zooplankton (Wassmann et al. 2015) that in contrast to phytoplankton and microzooplankton may be detectable. In reality, the lack of long time-series data such as that available for Mediterranean zooplankton (e.g. Berline et al. 2012) prevents rigorous examination of temporal changes in the species composition at any one particular site, much less the Arctic Sea overall (Table 2).

The historical species accumulation curve for tintinnid species recorded from the Arctic is difficult to assess as comparative data for other taxa are unavailable, as far we know. There are data for another locality. A recent study examined increases with time in the species inventory of

**Table 2** Sources of Arctic records of tintinnids, References numbers as noted in Table 1

Reference #	Citation (for full reference see "References")
1	Bernstein (1931)
2	Boltovskoy et al. (1991)
3	Burkovsky (1976)
4	Bursa (1963)
5	Cleve (1899)
7	Davis (1981)
8	Davis (1978)
9	Dolan et al. (2014)
10	Dolan et al. (2016)
11	Feng et al. (2014)
12	Gaarder (1938)
13	Levinsen et al. (1999)
14	Li et al. (2016)
15	Lovejoy et al. (2002)
16	Meschkat (1939)
17	Monti and Minocci (2013)
18	Ostenfeld and Paulsen (1911)
19	Paranjape (1987)
20	Smayda (1958)
21	Tibbs (1967)
22	Present study: Chukchi Sea data 2010, 2013, 2014, 2015
23	Lutter et al. (1998)
24	Chernova and Primako (2011)
25	Yokoi et al. (2016)
26	Kubiszyn et al. (2014)
27	Piontek et al. (2014)
28	Braarud et al. (1985)
29	Jensen and Hansen (2000)
30	Heimdal (1974)
31	Ratkova et al. (1998)
32	Ostenfeld (1910)
33	Burkovsky et al. (1974).
34	McLaughlin et al. (2009)
35	Matsuno et al. (2014)
36	Rossolimo (1927)
37	Boltovskoy et al. (1995)
38	Gran (1900)
39	Yang et al. (2004)
40	Lee et al. (2003)

tintinnid ciliates in the Bay of Villefranche in the NW Mediterranean Sea (Dolan 2016a) and data do exist for the discovery of species new to science as species described with time. Figure 8 shows data retrieved from the WoRMS database for all marine biota catalogued showing accumulated number of species with time from 1880 to 2015

along with the species accumulation curve for Arctic tintinnids from this study and the Bay of Villefranche from Dolan (2016a). Increases in inventory of described marine species worldwide with time can be attributed to sampling effort directed towards novel or previously under-sampled environments (rather than re-examining archived samples) and thus increases in cumulative sampling effort. There is a striking similarity in the slopes reflecting close correspondence in the relative rates of increases over time in the number of described species in marine biota overall and the number of tintinnid species known from sampling in the Arctic as well as a bay in the Mediterranean Sea. We suggest that this indicates that sampling effort in the Arctic has remained roughly proportional to sampling for new marine species world-wide since the beginning of the twentieth century. Unfortunately, testing such a hypothesis would be quite challenging and well beyond the scope of the present study.

## Conclusion

We found large discrepancies in geographic coverage of tintinnid species records with data. Many areas likely to experience large changes in sea ice coverage are under-sampled. While we found no clear trend of species richness with latitude through out the Arctic, there was a significant positive relationship between species richness reported and the number of sites sampled in a 2° band, suggesting a sampling effect. Examination of temporal trends in sampling effort and changes in the species inventory revealed a near-linear relationship in cumulative numbers of species recorded and sites sampled with time, and a lack of a plateau in the species accumulation trend. Species records are highly dominated by four species, accounting for 45% of the records: *Acanthostomella norvegica*, *Parafavella denticulata*, *Ptychocyliis obtusa* and *Salpingella acuminata*, all of which, except *S. acuminata*, have long been suspected to be morphologically variable, with different morphotypes given undue species status. Pooling all reported species of *Acanthostomella*, *Parafavella* and *Ptychocyliis* yielded little qualitative differences but considerable quantitative differences. The list of Arctic tintinnid ciliate species will likely continue to grow with new sampling, regardless of changes in the Arctic Seas. A perhaps more useful harbinger of change in the micro-zooplankton community of the Arctic would be shifts in the occurrences and ranges of the four historically dominant species or replacement of one the dominants by another species.

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## References

- Berline L, Siokou Frangou I, Marasovic I, Vidjak O, Fernandez de Puelles ML, Mazzocchi MG, Assimakopoulou G, Zervoudaki S, Fonda Umani S, Conversi A, Garcia Comas C, Ibanez F, Gasparini S, Stemmann L, Gorsky G (2012) Intercomparison of six Mediterranean zooplankton time series. *Prog Oceanogr* 97:100–76–91
- Bernstein T (1931) Protist plankton of the North West part of the Kara Sea. *Trans Arct Inst* 3:1–23 (in Russian with English summary)
- Boltovskoy D, Vivequin SM, Swanberg NR (1991) Vertical distribution of tintinnids and associated microplankton in the upper layer of the Barents Sea. *Sarsia* 76:141–151
- Boltovskoy D, Vivequin SM, Swanberg NR (1995) Tintinnids and other microplankton from the Greenland Sea: abundance and distribution in the marginal ice zone (May–June 1989). *PSZNI: Mar Ecol* 16:117–131
- Braarud T, Gaarder KR, Nordli O (1985) Seasonal changes at various points off the Norwegian west coast. 1958. *Fisk Skr Ser Havunders* 12:1–77
- Burkovsky IV (1973) Variability of *Parafavella denticulata* in the White Sea. *Zool Zhurnal* 52:1277–1285 (in Russian with English summary)
- Burkovsky IV (1976) New data on tintinnids (Ciliata) of the Arctic and revision of fauna. *Zool Zhurnal* 55:325–336 (in Russian with English summary)
- Burkovsky IV, Zamyshlyak YY, Poskryakova NP (1974) Revision of the fauna of tintinnida (Ciliata) of the White Sea. *Zool Zhurnal* 53:1757–1776 (in Russian with English summary)
- Bursa A (1963) Phytoplankton in coastal waters of the Arctic Ocean at Point Barrow Alaska. *Arctic* 16:239–262
- Cardinal A, Laffleur P E, Bonneau E (1977) Les tintinnides (Ciliata: tintinnida) des eaux marines et saumâtres du Québec. I. Formes hyalines. *Acta Protozool* 16:15–22
- Chaudary C, Saeedi H, Costello MJ (2016) Bimodality of latitudinal gradients in marine species richness. *Trends Ecol Evol* 31(9):670–676 in press
- Chernova EN, Primako EM (2011) Distribution of zooplankton in the estuary of Keretskaya Guba (White Sea). *Rus J Mar Biol* 37:104–110
- Cleve PT (1899) Plankton collected by the Swedish expedition to Spitzbergen in 1898, vol 32. *Kongl Svenska Vetenskaps Akademiens Handlingar*, 51 pp
- Daniëls FJA, Gillespie LJ, Poulin M et al (2013) Plants. In: Meltofte H (ed) Arctic biodiversity assessment. Status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna, Akureyri, pp 311–353
- Davis CC (1978) Variations of the lorica in the genus *Parafavella* (Protozoa: tintinnida) in northern Norway waters. *Can J Zool* 56:1822–1827
- Davis CC (1981) Variations of lorica shape in the genus *Ptychocylis* (Protozoa: tintinnina) in relation to species identification. *J Plank Res* 3:433–443
- Dickson I, Walker G, Pearce DA (2016) Microbes and the Arctic Ocean. In: Hurst CJ (ed) Their world: a diversity of microbial environments. *Advances in environmental microbiology* 1, Springer, Zurich, pp 341–381
- Dolan JR (2016a) Historical trends in the species inventory of tintinnids (ciliates of the microzooplankton) in the Bay of Villefranche (NW Mediterranean Sea): shifting baselines. *Eur J Protistol*. doi:10.1016/j.ejop.2016.10.004
- Dolan JR (2016b) Planktonic protists: little bugs pose big problems for biodiversity assessments. *J Plank Res* 38:1044–1051. doi:10.1093/plankt/fbv079
- Dolan JR, Pierce RW (2013) Diversity and distributions of tintinnid Ciliates. In: Dolan JR, Agatha S, Coats DW, Montagnes DJS, Stocker DK (eds) *Biology and ecology of tintinnid ciliates: models for marine plankton*. Wiley Blackwell, Oxford, pp 214–243
- Dolan JR, Ritchie MR, Ras J (2007) The neutral community structure of planktonic herbivores, tintinnid ciliates of the microzooplankton, across the SE Pacific Ocean. *Biogeosciences* 4:297–310
- Dolan JR, Yang EJ, Kim TW, Kang S H (2014) Microzooplankton in a warming Arctic: a comparison of tintinnids and radiolarians from summer 2011 and 2012 in the Chukchi Sea. *Acta Protozool* 52:101–113
- Dolan JR, Yang EJ, Kang S H, Rhee TS (2016) Declines in both redundant and trace species characterise the latitudinal diversity gradient in tintinnid ciliates. *ISME J* 10:2174–2183. doi:10.1038/ismej.2016.19
- Eakins BW, Sharman GF (2010) *Volumes of the World's Oceans from ETOPO1*. NOAA National Geophysical Data Center, Boulder. [https://www.ngdc.noaa.gov/mgg/global/etopo1\\_ocean\\_volumes.html](https://www.ngdc.noaa.gov/mgg/global/etopo1_ocean_volumes.html)
- Feng M, Zhang W, Xiao T (2014) Spatial and temporal distribution of tintinnid (Ciliophora: tintinnida) communities in Kongsfjorden, Svalbard (Arctic), during summer. *Polar Biol* 37:291–296
- Gaarder KR (1938) Phytoplankton studies from the Tromsø district 1930–31. *Tromsø Mus Arsh Nat Avd NR* 11(55):1–159
- Glig O, Kovacs KM, Aars J et al (2012) Climate change and the ecology and evolution of Arctic vertebrates. *Ann NY Acad Sci* 1249:166–190
- Gran HH (1900) Hydrographic biological studies of the North Atlantic Ocean and the coast of Nordland. *Rep Nor Fish Mar Investig* 1:1–137
- Heimdal B (1974) Composition and abundance of phytoplankton in the Ullsfjord area, North Norway. *Astarte* 7:17–42
- Jedrzejek B, Drees B, Daniëls FJA, Hörtzel N (2012) Vegetation discontinuities and altitudinal indicator species in mountain of West Greenland: finding the best positions and traits to observe the impact of climate warming in the Arctic. *Appl Veg Sci* 15:432–448
- Jensen F, Hansen BW (2000) Ciliates and heterotrophic dinoflagellates in the marginal ice zone of the central Barents Sea during spring. *J Mar Biol Assoc UK* 80:45–54
- Jorgensen LL, Archambault P, Armstrong C et al (2016) Chapter 36G. Arctic Ocean. In: Inness L, Simcock A (joint coordinators) *The group of experts of the regular process. The first global integrated marine assessment*. United Nations, New York, 47 pp
- Kofoed CA, Campbell AS (1929) A conspectus of the marine and freshwater ciliata belonging to the suborder tintinnoinea, with descriptions of new species principally from the Agassiz Expedition to the Eastern Tropical Pacific 1904–1905. *Univ Calif Publ Zool* 34:1–403



- Kosobokova KN, Hopcroft RR, Hirche H J (2010) Patterns of zooplankton diversity through the depths of the Arctic's central basins. *Mar Biodiv*. doi:10.1007/s12526-010-0057-9
- Kubiszyn AM, Piwosz K, Wiktor JM, Wiktor JM Jr (2014) The effect of inter annual Atlantic water inflow variability on the planktonic protist community structure in the West Spitsbergen waters during the summer. *J Plank Res* 36:1190–1203
- Lee K H, Chung K H, Soh H Y, Lee W (2003) On the distribution of zooplankton in the southeaster Barents Sea during July 2002. *Korean J Environ Biol* 21:392–399
- Levinsen H, Nielsen TG, Hansen BW (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. II. Heterotrophic dinoflagellates and ciliates. *Aquat Microb Ecol* 16:217–232
- Li WKW, McLaughlin FA, Lovejoy C, Carmack EC (2009) Smallest algae thrive as the Arctic Ocean freshens. *Science* 326:539
- Li H, Xu Z, Zhang W, Wang S, Zhang G, Xiao T (2016) Boreal tintinnid assemblage in the Northwest Pacific and its connection with the Japan Sea in summer 2014. *PLoS ONE* 11:e0153379. doi:10.1371/journal.pone.0153379
- Longhurst A (1998) Ecological geography of the sea. Academic Press, San Diego, pp 101–108
- Lovejoy C (2014) Changing views of Arctic protists (marine microbial eukaryotes) in a changing Arctic. *Acta Protozool* 53:91–100
- Lovejoy C, Legendre L, Martineau M J, Bacle J, von Quillfeldt CH (2002) Distribution of phytoplankton and other protists in the north water. *Deep Sea Res II* 49:5027–5047
- Lutter S, Taasen J, Hopkins CCE, Smetacek V (1998) Phytoplankton dynamics and sedimentation processes during spring and summer in Balsfjord, Northern Norway. *Polar Biol* 10:113–124
- Matsuno K, Ichinomiya M, Yamaguchi A, Imai I, Kikuchi T (2014) Horizontal distribution of microprotist community structure in the western Arctic Ocean during late summer and early fall of 2010. *Polar Biol* 37:1185–1195
- McLaughlin F, Carmack E, O'Brien M et al (2009) Physical and chemical data from the Beaufort Sea and Western Canadian Arctic Archipelago, September 2–16, 2000. Canadian data report of hydrography and ocean science, vol 180, 167 pp
- McManus GB, Santoferrara LF (2013) Tintinnids in microzooplankton communities. In: Dolan JR, Montagnes DJS, Agatha S, Stoecker DK (eds) *The biology and ecology of tintinnid ciliates: models for marine plankton*. Wiley Blackwell, Oxford, U.K., pp 198–213
- Melnikov IA, Kolosova EG, Welch HE, Zhitina LS (2002) Sea biological communities and nutrient dynamics in the Canada Basin of the Arctic Ocean. *Deep Sea Res. I* 49:1623–1649
- Meltofte H (2013) Arctic biodiversity assessment: status and trends in Arctic biodiversity. *Conservation of Arctic Flora and Fauna, Akureyri*
- Meschkat A (1939) Untersuchung über das herbstplankton im Bereich des "Ostlandstromes". *Int Rev Hydrobiol Hydrogr* 38:285–352
- Michel C, Bluhm B, Gallucci V et al (2012) Biodiversity of Arctic marine ecosystems and responses to climate change. *Biodiversity* 13:200–214
- Montagnes DJS (2013) Ecophysiology and behavior of tintinnids. In: Dolan JR, Montagnes DJS, Agatha S, Stoecker DK (eds) *The biology and ecology of tintinnid ciliates: models for marine plankton*. Wiley Blackwell, Oxford, UK, pp 85–121
- Monti M, Minocci M (2013) Microzooplankton along a transect from northern continental Norway to Svalbard. *Polar Res* 32:19306. doi:10.3402/polar.v32i0.19306
- Nelson RJ, Ashjian CJ, Bluhm B, Conlan KE et al (2014) Biodiversity and biogeography of the lower trophic taxa of the Pacific Arctic region: sensitivities to climate change. In: Grebbmeier JM, Maslowski W (eds) *The Pacific Arctic region: ecosystem status and trends in a rapidly changing environment*. Springer, Dordrecht, pp 269–336
- Ostenfeld H (1910) Marine plankton from the East Greenland Sea (W. of 6°W. Long. and N. of 73°30'Lat.) collected during the Danmark Expedition" 1906–1908. II. Protozoa. *Danmark Ekspeditionen til Gronlands Nordostkyst 1906–1908 under ledelse af I. Mylius Erichsen* 3:288–299
- Ostenfeld CH, Paulsen O (1911) Marine plankton from the East Greenland Sea (W. of 6° W. Long. and N. of 73°30'Lat.) collected during the Danmark Expedition" 1906–1908. IV. General remarks on the microplankton. *Danmark Ekspeditionen til Gronlands Nordostkyst 1906–1908 under ledelse af I. Mylius Erichsen* 3:319–336
- Paranjape MA (1987) The seasonal cycles and vertical distribution of tintinnines in Bedford Basin, Nova Scotia, Canada. *Can J Zool* 65:41–48
- Pedros Alio C, Potvin M, Lovejoy C (2015) Diversity of planktonic microorganisms in the Arctic Ocean. *Prog Oceanogr* 139:233–243
- Pierce RW, Turner JT (1993) Global biogeography of marine tintinnids. *Mar Ecol Prog Ser* 94:11–26
- Piontek J, Sperling M, Nöthig E M, Engel A (2014) Regulation of bacterioplankton activity in Fram Strait (Arctic Ocean) during early summer: the role of organic matter supply and temperature. *J Mar Syst* 132:83–94
- Preston FW (1962) The canonical distribution of commonness and rarity: part 1. *Ecology* 43:185–215
- Ratkova TN, Wassmann P, Verity PG, Andreassen IJ (1998) Abundance and biomass of pico-, nano-, and microplankton on a transect across Nordvestbanken, north Norwegian shelf in 1994. *Sarsia* 84:213–225
- Rossolimo LL (1927) Planktonic ciliates of the Kara Sea. *Tr. Plavuch. morsk. n. i. in ta* 2:63–77 (in Russian with German summary)
- Santoferrara LF, Bachy C, Alder VA et al (2016) Updating biodiversity studies in loricate protists: the case of the tintinnids (Alveolata). *J Eukaryot Microbiol, Ciliophora, Spirotrichea*. doi:10.1111/jeu.12303
- Schulz B, Wulff A (1927) Hydrographische und planktologische Ergebnisse der Fahrt Des Fischereischutzbootes "Zeiten" in das Barentsmeer im August–September 1926. *Ber Dtsch Wiss Komm Meeresforsch* 3:211–280
- Scott RW, Barton DR, Evans MS, Keating JJ (2011) Latitudinal gradients and local control of aquatic insect richness in a large river system in northern Canada. *J N Am Benthol Soc* 30:621–634
- Seuthe L, Iversen KR, Narcy F (2011) Microbial processes in a high latitude fjord (Kongsfjorden, Svalbard): II. Ciliates and dinoflagellates. *Polar Biol* 34:751–766
- Sherr EB, Sherr BF, Hartz AJ (2009) Microzooplankton grazing impact in the Western Arctic Ocean. *Deep Sea Res II* 56:1264–1273
- Smayda TJ (1958) Phytoplankton studies around Jan Mayen Island. March–April, 1955. *Nytt Mag Botanikk* 6:75–96
- Stecher A, Neuhaus S, Lange B, Frickenhaus S, Beszteri A, Kroth PG, Valentin K (2016) rRNA and rDNA based assessment of sea ice protist biodiversity from the central Arctic Ocean. *Eur J Phycol* 51:31–46
- Tibbs JF (1967) On some planktonic protozoa taken from the track of drift station ARLISI, 1960–61. *Arctic* 20:247–254
- Wassmann P (2011) Arctic marine ecosystems in an era of rapid climate change. *Prog Oceanogr* 9:1–17
- Wassmann P, Kosobokova KN, Slagstad D et al (2015) The contiguous domains of Arctic Ocean advection: trails of life and death. *Prog Oceanogr* 139:42–65

- WoRMS Editorial Board (2016) World register of marine species. doi:10.14284/170; <http://www.marinespecies.org> at VLIZ. Accessed 2016 07 14
- Yang EJ, Choi JK, Kim SY, Chung KH, Shin H C, Kim Y (2004) Spatial distribution and community structure of heterotrophic protists in the Central Barents Sea of Arctic Ocean during Summer. *Ocean Polar Res* 26:567–579
- Yokoi N, Matsuno K, Ichinomiya M et al (2016) Short term changes in a microplankton community in the Chukchi Sea during autumn: consequences of a strong wind event. *Biogeosciences* 13:913–923. doi:10.5194/bg-13-913-2016
- Zhang W, Feng M, Yu Y, Zhang C, Xiao T (2012) An illustrated guide to contemporary tintinnids in the world. Science Press, Beijing, p 499