Acta Protozool. (2014) 53: 101–113
http://www.eko.uj.edu.pl/ap
doi:10.4467/16890027AP.14.010.1447

ACTA
PROTOZOOLOGICA

Special issue:
Marine Heterotrophic Protists
Guest editors: John R. Dolan and David J. S. Montagnes

Review paper

Microzooplankton in a Warming Arctic: A Comparison of Tintinnids and Radiolarians from Summer 2011 and 2012 in the Chukchi Sea

John R. Dolan[1, 2], Eun Jin Yang[3], Tae Wan Kim[3] and Sung-Ho Kang[3]

[1] Sorbonne Universités, UPMC Univ Paris 06, UMR 7093, LOV, Observatoire Océanologique, F-06230, Villefranche-sur-Mer, France; [2] CNRS, UMR 7093, LOV, Observatoire Océanologique, F-06230, Villefranche-sur-Mer, France; [3] Korea Polar Research Institute, KIOST, 213-3 Songdo-dong, Yeonsu-gu, Incheon, 406-840, Korea

Abstract. The Chukchi Sea was sampled in August of 2011, a year of near-normal sea ice among recent years, and again in August 2012, a year of all time record low sea ice. We exploited this sampling to test the hypothesis that different sea ice conditions are associated with differences in abundances or species composition of microzooplankton through an examination of tintinnids and radiolarians. From 18 stations in 2011, and 19 stations in 2012, organisms were enumerated in plankton net tow material, and chlorophyll determinations made (total and ≤ 20 μm) from discrete depth samples. We found that the low sea ice conditions of 2012 were associated with higher chlorophyll concentrations (both total and the ≤ 20 μm size fraction), compared to 2011. However, tintinnid ciliates and radiolarians were much lower in concentration, by about an order of magnitude, compared to 2011. In both years the radiolarian assemblage was dominated by *Amphiselma setosa*. The species composition of the tintinnid ciliates was similar in the two years, but there were distinct differences in the relative abundances of certain species. The 2012, low sea ice assemblage, was dominated by small forms in contrast to 2011, when large species were the most abundant. We present these findings in detail and discuss possible explanations for the apparent differences in the microzooplankton communities associated with distinct sea ice conditions in the Chukchi Sea.

Keywords: Climate change, plankton, rhizaria, sea ice, Tintinnina.

INTRODUCTION

Among all marine systems, the effects of climate change will likely be greatest in polar regions, as they will be directly impacted by loss of sea ice and subsequent shifts in species distributions (Doney *et al.* 2012). The recent dramatic declines in Arctic sea ice extent (total area containing zones of sea ice) and sea ice area (area actually occupied by sea ice) are evident (Fig. 1), and summers free of sea ice are expected within as little as 30 years from now (Wang and Overland 2009).

To date, the expected changes in the pelagic food webs of arctic seas have been assessed largely with models. Typically, models both conceptual (e.g., Wassman 2011) and quantitative (e.g., Zhang *et al.* 2010), point to marked increases in primary production, due to

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Address for correspondence: John R. Dolan, Sorbonne Universités, UPMC Univ Paris 06, UMR 7093, LOV, Observatoire Océanologique, F-06230, Villefranche-sur-Mer, France and CNRS, UMR 7093, LOV, Observatoire Océanologique, F-06230, Villefranche-sur-Mer, France; E-mail: dolan@obs-vlfr.fr.

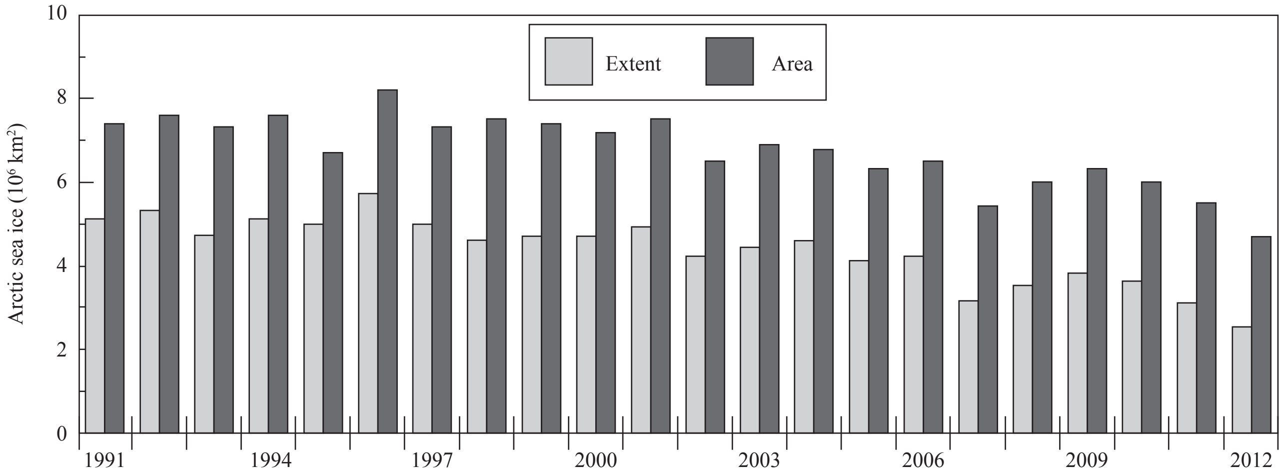

Fig. 1. Sea ice data for the month of August for 1991 to 2012. Data from the National Ice Data Center (nsdic.org). Note that sea ice was lower in 2012 than the previous record low of 2007.

both a longer ice-free season and larger area free of sea ice, leading to higher biomass of both phytoplankton and zooplankton as well increases in flux to the benthos. However, most food web models have virtually ignored possible changes in microzooplankton (i.e., protists) and have focused on shifts in the timing and duration of phytoplankton blooms and possible effects on the composition and abundance of metazoan zooplankton, because the latter are directly connected with certain exploited fish populations (e.g., Hunt *et al*. 2011, Rubao *et al.* 2013). This is despite the fact that microzooplankton are now generally recognized as a key component of pelagic food webs (e.g., Calbet and Landry 2004) and can potentially be a direct link to fish, via larval fish consumption of microzooplankton (Montagnes *et al.* 2010).

Some have hypothesized that increases in the ice-free period, following the spring bloom of phytoplankton, will lead to increases in the importance of microzooplankton grazing, compared to that of the mesozooplankton (e.g. Michel *et al.* 2012). However, in a recent review, Caron and Hutchins (2013) postulated that there may be 'non-intuitive' and 'counter-acting' effects of even small increases in temperature on the balance between phytoplankton and their microzooplankton grazers. Indeed, the effects of temperature increases on microbial food webs appear to be particularly unpredictable in both marine (Vazquez-Dominguez *et al.* 2012) and freshwaters (Montagnes *et al.* 2008). A recent mesocosm study of Baltic communities suggested that small increases in temperature will reduce the time-lag between blooms of phytoplankton and their protozoan grazers (Aberle *et al.* 2012). Such an effect may though not occur in Arctic systems. Rose and Caron (2007) specifically suggested that in polar communities phytoplankton growth could be less constrained by temperature than the growth of their protozoan grazers; recently this view has been contested (Sherr *et al.* 2013). Given such large uncertainties, there is a clear need for field observations of microzooplankton and the establishment of empirical relationships (Caron and Hutchins 2013). As it is widely acknowledged that microzooplanton are a key link in nearly every pelagic food web, the effects of changes in Arctic sea ice conditions on microzooplankton clearly merit examination.

There are good reasons to assume that changes in sea ice extent and duration as well as warmer waters will impact microzooplankton communities in some fashion. For example, changes in abundances or species compositions of a wide variety of Arctic protistan taxa have occurred with changes in sea ice conditions. Sediment core material from well-studied areas indicate distinct shifts in assemblages of diatoms (Weckström *et al.* 2013), dinoflagellates (Solignac *et al.* 2011), and benthic foraminifera (Polyak *et al.* 2013). However, such studies, while highly suggestive, are of limited value in predicting changes over the next decades, as sediment core material integrates conditions over long periods, and evidence from the gradual changes of the past may be of limited value in assessing the effects of contemporary rapid changes. The, perhaps, more appropriate sequencing-based studies have suggested that microbial communities (including eukaryotic forms) may be responding to recent polar changes in the form of shifts in species compositions; however, apparent changes are difficult to relate directly to abundance or compositions of functional groups (Comeau *et al.* 2011).

We examined certain protistan taxa of the microzooplankton in the Chukchi Sea as a preliminary attempt to assess the effect of changes in summer sea ice conditions. Among all the Arctic Seas, in the Chukchi Sea changes in sea ice have been perhaps the most marked over the past decade (Grebmeier 2012). A variety of climate change models concur in predicting ice-free summers in the Chukchi Sea in the coming decades (Wang *et al.* 2012). While these long-term trends are clear, there is considerable inter-annual variability. The Chukchi Sea was sampled extensively by the Korean icebreaker Araon in August of 2011, a year of near-normal sea ice among recent years, and again in August 2012, a new record summer of low sea ice (Fig. 1).

From plankton net samples we enumerated the tintinnids and radiolarians of the microzooplankton to test the hypothesis that different summer sea ice conditions of 2011 and 2012 are associated with differences in abundances or species composition of microzooplankton. We focused on tintinnid ciliates and radiolarians. In most systems, both groups are generally minor components of the microzooplankton, in terms of numerical concentrations or biomass, compared to oligotrichid ciliates or heterotrophic dinoflagellates, including the microzooplankton of the Bering and Chukchi Seas (Sherr *et al.* 2009, 2013). However, in contrast to oligotrichid ciliates or dinoflagellates, changes in community composition are relatively easy to assess because species identifications can be made (with certain caveats) on the basis of the lorica in tintinnids or the skeleton in radiolarians, by microscopic examination of preserved, but otherwise untreated, material. Notably, there exists a considerable literature on species occurrences and distributions of both tintinnids and radiolarians. Furthermore, in tintinnids, the morphology of the lorica, especially the diameter of the open, oral end of the lorica, the lorica oral diameter (LOD), is relatable to some ecological characteristics of the species, such as prey size exploited and maximum growth rate (Dolan 2010, Montagnes 2013). Consequently, changes in the morphological characteristics of a tintinnid assemblage correspond with changes in ecological characteristics (Dolan and Pierce 2013). Data on the resources exploited by microzooplankton were gathered in the form chlorophyll a concentrations, both total and the less than 20 µm size fraction corresponding to 'nano-pico sized phytoplankton'.

Here we present data on the communities of tintinnids and radiolarians found in the Chukchi Sea in August with the distinct sea ice conditions of 2011 and 2012. While limited in focus to tintinnids and radiolarians, this is the first study, to our knowledge, to attempt to directly examine the effects of disappearing summer sea ice in the Arctic on microzooplankton.

MATERIALS AND METHODS

Data and samples were collected in the Chukchi Sea from onboard the Korean Research Icebreaker Araon in August 2011 and in August/early September in 2012. Data presented here are from 18 stations from the 2011 cruise and 19 stations from the 2012 cruise. Station locations and sea ice concentrations in the Chukchi Sea during the cruise period (based on data from the NSDIC) are shown in Fig. 2. A Niskin bottle rosette equipped with CTD probes was used to obtain discrete depth samples for chlorophyll and nutrient measures and plankton net tows were performed to assess microplankton community composition. Samples for other biological, physical and chemical parameters were taken; however, sample and data analysis are in progress and data will appear later, elsewhere.

For chlorophyll *a* determinations, water samples of 0.3–1 l were obtained from 6–7 discrete depths between the surface and 100 m depth. Water samples were filtered through a 0.7 µm Whatman glass fiber filter (GF/F), directly for 'total chlorophyll' or first filtered through a 20 µm Nucleopore filter to estimate the size-fraction, '≤ 20 µm'. Chlorophyll concentrations were determined onboard using a Turner Designs Trilogy model fluorometer calibrated using commercial chlorophyll *a* standards. For details of the protocols see Lee *et al.* (2007).

Net tows were made with a 20-µm plankton net of 0.45 m diameter towed from 100 m depth to the surface. For direct microscopic examination, net tow material was fixed by standard methods (6% Bouin's or 2% Lugol's, final concentration). Aliquots were examined in settling chambers using an inverted microscope equipped with DIC optics. Multiple aliquots were examined until a net material sample volume representing material from at least 10–20 l was analysed. Tintinnid species identifications were made based on lorica morphology using the monographs of Kofoid and Campbell (1929, 1939). Radiolarians were overwhelming dominated by a single morphotype identified by Noritoshi Suzuki (Tohoku University) as *Amphimelissa setosa*.

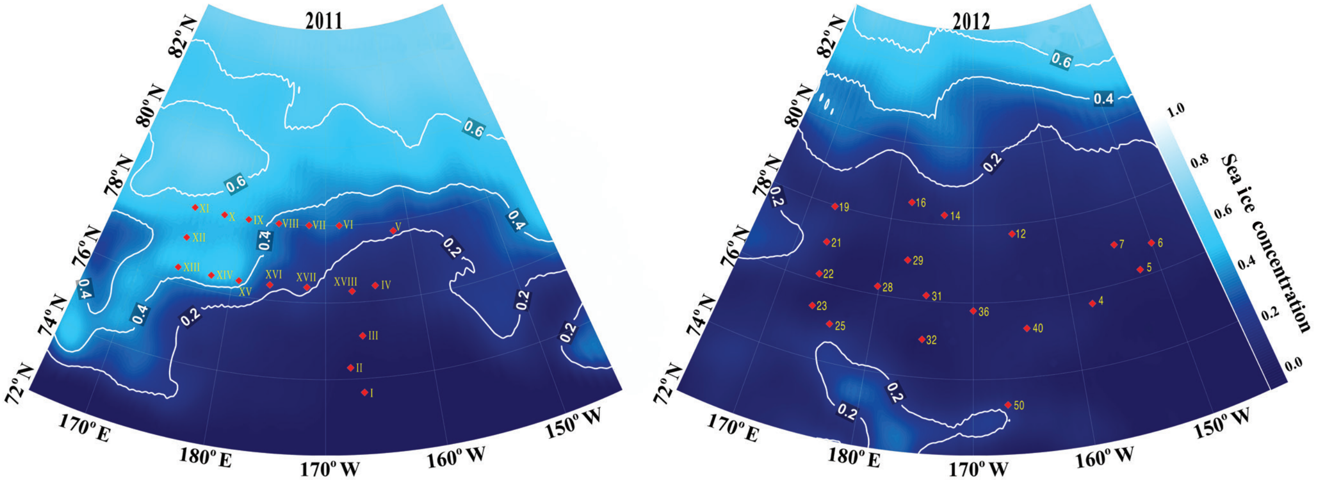

Fig. 2. Station locations and sea ice concentrations (fraction surface covered) in August 2011 and August 2012. For exact locations and sampling dates see Table 1.

Nominal concentrations of organisms were calculated based 100 m net hauls. In general, very few tintinnids are found below the chlorophyll maximum depth (e.g., Dolan and Marassé 1995) which was usually between 20–50 m depth. Consequently, the concentrations of tintinnids in the surface layer were likely several times higher than those reported here which represent the entire 100 m water column. With regard to the possibility of under-estimation of organismal concentrations due to net clogging, based on our experience, the density of particulate matter in the net tow material was relatively sparse, particularly in the 2012 samples. Thus, we believe that net clogging did not occur.

Correlation analysis was applied to investigate the relationships between concentrations (log transformed) of organisms and chlorophyll. Comparisons of data from 2011 to those of 2012 were made using the Mann-Whitney rank sum test, as data did not meet the requirements of normality. All differences noted in the results and discussion as "significant" refer to the Mann-Whitney U statistic with a probability level of $p < 0.001$.

RESULTS

Across the basin there were distinct differences in sea ice concentrations in 2011 and 2012 (Figs. 1, 2). In both years a wide variety of water column conditions were encountered (Tables 1, 2). For example, near surface salinity values varied between about 25–29 PSU among stations in both years. The temperature at 2 m depth averaged –1.0 ± 0.29°C at the 2011 stations, that included a wide range of sea ice concentrations, compared to –0.6 ± 0.40°C in 2012 when no sea ice was encountered.

The organismal concentrations were distinctly different in the two years. In 2011 chlorophyll *a* concentrations were low in the stations with sea ice (0.16 ± 0.02 $\mu g\ l^{-1}$) and peaked in the ice-free stations (Fig. 3). An inverse pattern characterized tintinnids and radiolarians all of which showed markedly lower concentrations in the ice-free stations (Fig. 3). The overall averages for the 2011 stations were 2.3 ± 4.41 tintinnids l^{-1} and 2.3 ± 1.89 radiolarians l^{-1}. Different organismal concentrations were encountered in the sea ice-free 2012 sampling. Average chlorophyll concentrations were distinctly and significantly higher (avg. 0.8 ± 0.75 $\mu g\ l^{-1}$), especially compared to the sea ice stations in 2011 (Fig. 3). However, concentrations of tintinnids (0.3 ± 0.42 cells l^{-1}) and radiolarians (0.2 ± 0.19 cells l^{-1}) were distinctly and significantly lower, by about an order of magnitude, compared to the concentrations encountered in 2011 (Fig. 3).

There was no significant correlation between log tintinnids and log chlorophyll *a* for either 2011 or 2012. However, the highest concentrations of tintinnids correspond to the low-chlorophyll, high sea ice stations of 2011. Log radiolarian concentrations (Fig. 4) were negatively, but weakly related to log chlorophyll concentrations in both 2011 ($r^2 = 0.20$, $p < 0.05$) and 2012 ($r^2 = 0.26$, $p < 0.05$). In both years there was a substantial portion of the chlorophyll stock in the size fraction ≤ 20 μm. Although the proportion of this "nano-pico-sized phytoplankton" was highest in the stations with sea ice in 2011, the absolute concentrations were

Table 1. Summary data from the August 2011 cruise. The concentrations of chlorophyll *a*, tintinnids and radiolarians are values per liter, integrated through the 0–100 m depth segment of the water column. Chlorophyll concentrations were determined in 6–8 discrete depth samples between 0 and 100 m. Organismal concentrations are from plankton net tow material obtained using a 20 µm net drawn from 100 to 0 m depth.

St	Lat, Long	Date	Salinity @2m	Temp @2m	Total Chlorophyll *a* µg l^{-1}	≤ 20 µm Chlorophyll *a* µg l^{-1}	Tintinnids l^{-1}	Radiolarians l^{-1}
I	73.6°N, 166.5°W	02	27.5	0.2	1.17	0.51	0.51	0.30
II	74.3°N, 167.6°W	03	26.6	–0.4	0.54	0.20	0.70	0.48
III	75.1°N, 166.3°W	04	25.9	–1.1	0.08	0.05	0.86	0.69
IV	76.4°N, 164.7°W	05	25.4	–1.1	0.07	0.07	0.73	6.07
V	77.7°N, 161.9°W	06	26.5	–1.1	0.12	0.11	0.88	4.54
VI	78.0°N, 168.3°W	09	27.7	–1.1	0.06	0.06	0.88	2.71
VII	78.0°N, 172.0°W	09	27.7	–1.2	0.10	0.10	2.51	4.07
VIII	78.0°N, 175.7°W	09	27.7	–1.3	0.14	0.14	1.29	1.23
IX	78.0°N, 179.3°W	10	28.2	–1.3	0.11	0.10	1.35	0.66
X	78.0°N, 177.7°W	11	28.3	–1.3	0.13	0.13	5.24	2.31
XI	78.0°N, 174.0°W	11	28.6	–1.3	0.14	0.14	7.82	3.51
XII	77.2°N, 174.0°W	13	28.3	–1.2	0.13	0.13	4.64	1.30
XIII	76.4°N, 174.0°W	13	29.0	–1.5	0.17	0.16	1.00	0.48
XIV	76.4°N, 177.7°W	14	27.3	–1.3	0.13	0.13	7.28	3.46
XV	76.4°N, 179.3°W	14	28.3	–1.4	0.09	0.09	3.81	1.06
XVI	76.4°N, 176.3°W	15	26.4	–1.0	0.09	0.09	0.93	1.88
XVII	76.4°N, 172.0°W	16	26.0	–0.8	0.10	0.10	0.62	5.58
XVIII	76.3°N, 167.2°W	16	25.2	–0.6	0.07	0.07	0.23	1.01

Table 2. Summary data from the August 2012 cruise. The concentrations of chlorophyll *a*, tintinnids, and radiolarians are values per liter, integrated through the 0–100 m depth segment of the water column. Chlorophyll concentrations were determined in 6–8 discrete depth samples between 0 and 100 m. Organismal concentrations are from plankton net tow material obtained using a 20 µm net drawn from 100 to 0 m depth.

St	Lat, Long	Date	Salinity @2m	Temp @2m	Total Chlorophyll *a* µg l^{-1}	≤ 20 µm Chlorophyll *a* µg l^{-1}	Tintinnids l^{-1}	Radiolarians l^{-1}
4	75.7°N, 157.8°W	9/2	24.7	–0.1	0.35	0.12	0.17	0.14
5	76.3°N, -155.4°W	9/1	25.5	–0.1	0.31	0.09	0.13	0.25
6	77.0°N, 154.0°W	31	25.5	0.1	0.22	0.07	0.35	0.31
7	77.3°N, 157.2°W	8	25.7	–1.1	0.24	0.07	0.32	0.64
12	77.8°N, 165.4°W	9	26.7	–1.2	0.43	0.12	0.11	0.43
14	78.3°N, 173.6°W	10	28.3	–1.3	0.40	0.12	0.23	0.17
16	78.5°N, 177.8°W	11	28.0	–1.1	0.45	0.12	0.17	0.23
19	78.0°N, 173.0°W	17	28.0	–1.1	0.77	0.41	0.13	0.52
21	80.1°N, 173.2°W	18	27.4	–0.8	1.60	0.17	0.09	0.39
22	76.2°N, 173.5°W	19	27.4	–0.6	2.42	0.70	0.30	0.00
23	75.3°N, 173.8°W	19	27.5	–0.3	2.38	0.21	0.06	0.03
25	48.0°N, 175.9°W	21	27.5	–0.9	1.82	0.48	0.02	0.04
28	76.2°N, 179.8°W	22	26.7	–0.5	0.80	0.17	1.55	0.02
29	77.0°N, 177.4°W	24	26.6	–0.4	0.28	0.11	1.38	0.49
31	76.2°N, 174.9°W	26	25.9	–0.3	0.25	0.10	0.58	0.37
33	75.0°N, 178.0°W	27	26.7	0.3	0.61	0.18	0.13	0.19
36	75.8°N, 170.0°W	29	25.3	–0.4	0.43	0.26	0.32	0.09
40	75.3°N, 164.7°W	5	26.0	–0.8	0.22	0.06	0.11	0.38
50	73.3°N, 166.9°W	9/6	28.8	–1.2	1.63	0.45	0.02	0.00

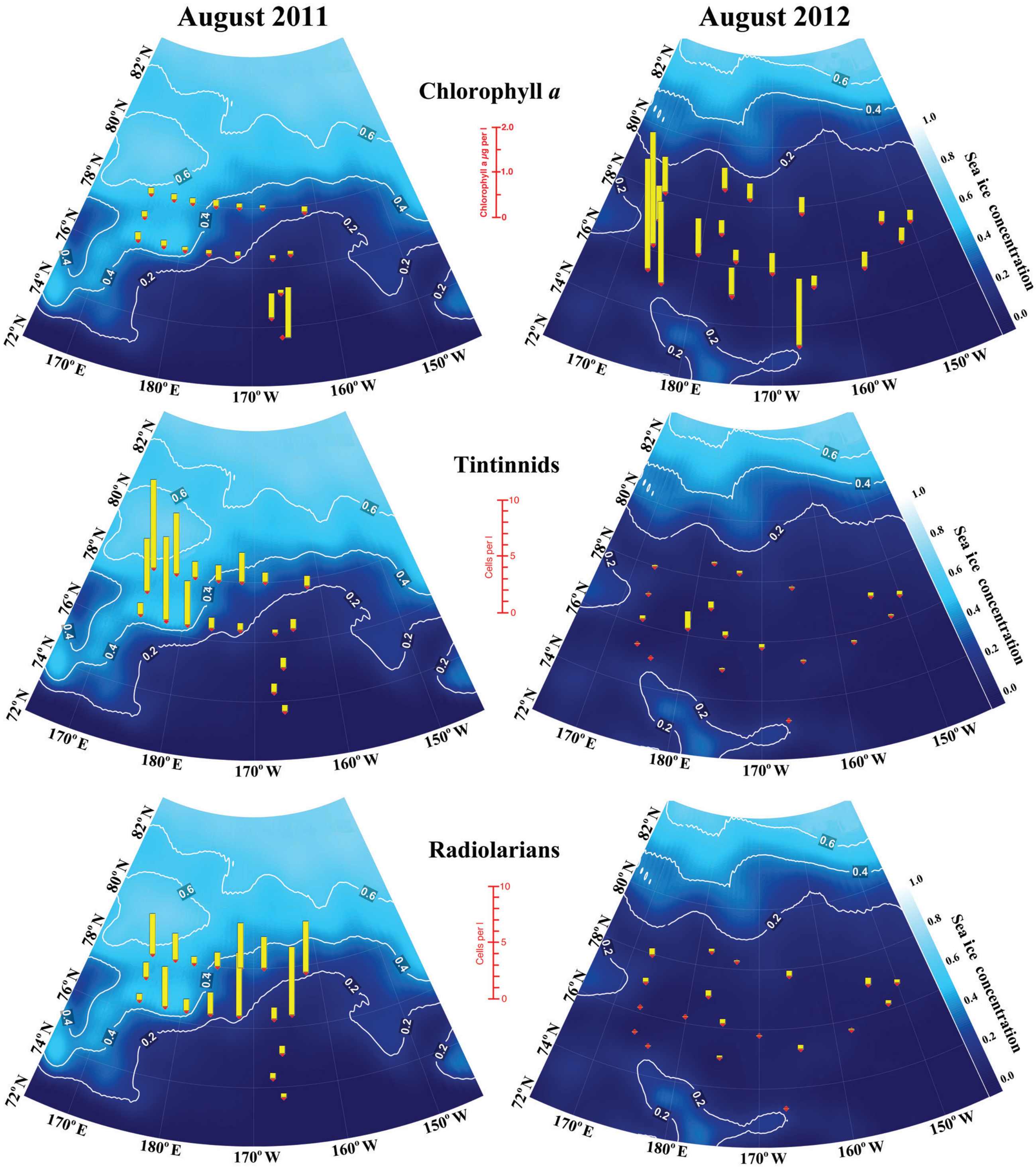

Fig. 3. Spatial distribution of concentrations of chlorophyll *a*, tintinnid and radiolarian abundances (values per liter, integrated through the 0–100 m depth segment of the water column) in August 2011 and 2012. Station numbers are shown in Fig. 1 and exact values are given in Table 1.

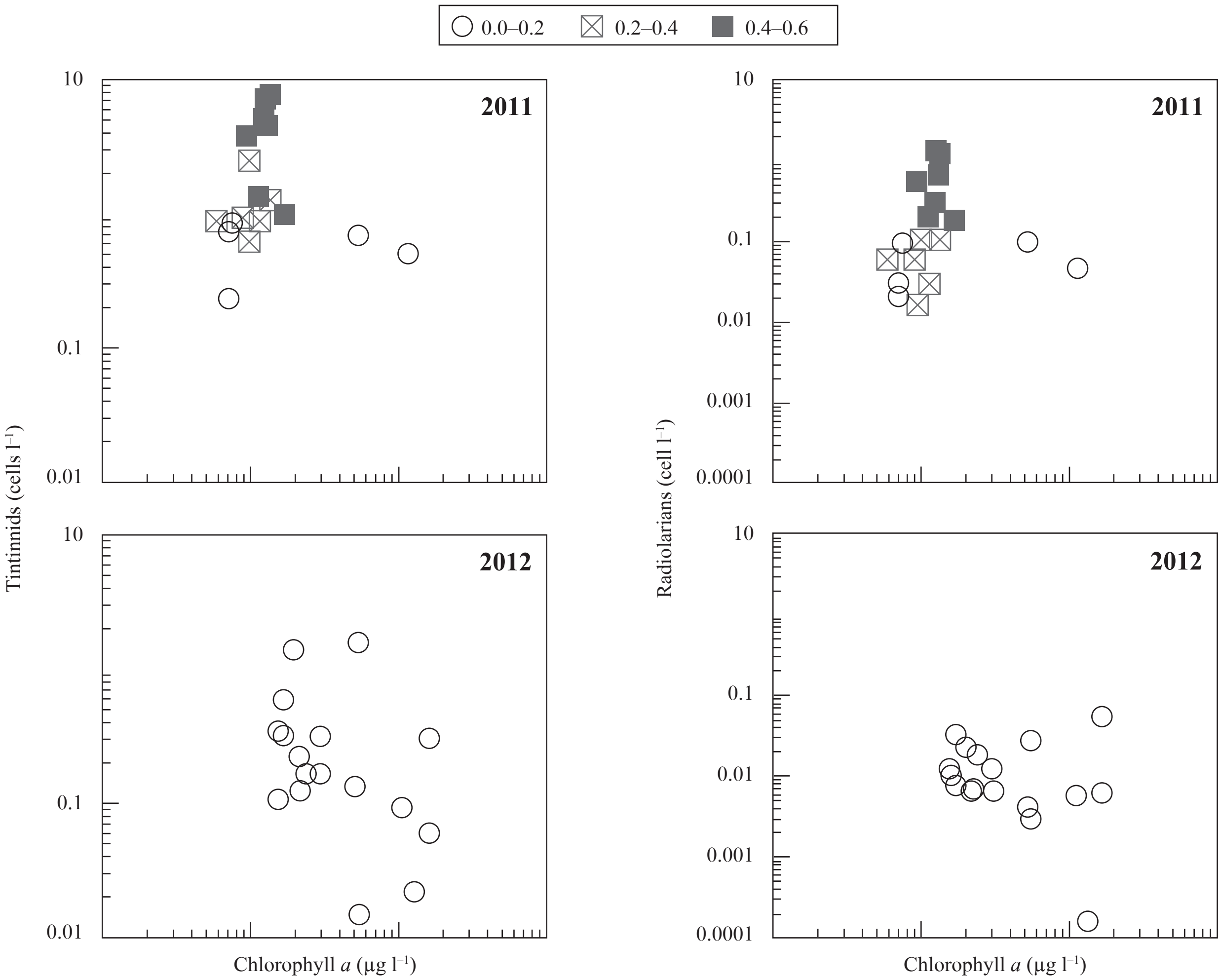

Fig. 4. Scatterplots of tintinnid and radiolarian abundances as a function of chlorophyll *a* concentration (values per liter, integrated through the 0–100 m depth segment of the water column) in the samples from 2011 and 2012. The symbols denote different concentrations of sea ice (see Figs. 2 and 3).

significantly greater in the ice-free stations sampled in 2012 (Tables 1, 2, Fig. 5).

The tintinnid species assemblages encountered in 2011 and 2012 were nearly identical in terms of the identities of the dominant species but differed considerably not only in overall concentrations but also in the relative importance of individual species. Table 3 gives the overall average concentrations, the number of stations at which each species was found, and the average concentrations at the stations in which it occurred. In 2011 with an extensive zone of sea ice, the most abundant species was the relatively large *Ptychocylis urnula*. It was found in significantly higher concentrations in 2011 compared to 2012, at 1.4 ± 1.50 cells l^{-1} in 2011 and only 0.06 ± 0.039 cells l^{-1} in 2012. In the samples from the ice free 2012, the small tintinnid *Salpingella faurei* was the most abundant form. Concentrations of *S. faurei* were not significantly different in the two years. Thus, the dominance of *S. faurei* in 2012 was due to the near absence of *P. urnula* in 2012. The two species that characterised the assemblages of 2011 and 2012 are distinct in lorica oral diameter (LOD), the anterior open end of the lorica. The 2011 dominant, *P. urnula*, has an LOD of ~75 µm, while the 2012 dominant, *S. faurei,* has an LOD of only ~10 µm (Figs. 6, 7). With regard to the radiolarian fauna, in both years a single species *Amphimelissa setosa* was overwhelming dominant, accounting for about 90% of all individuals.

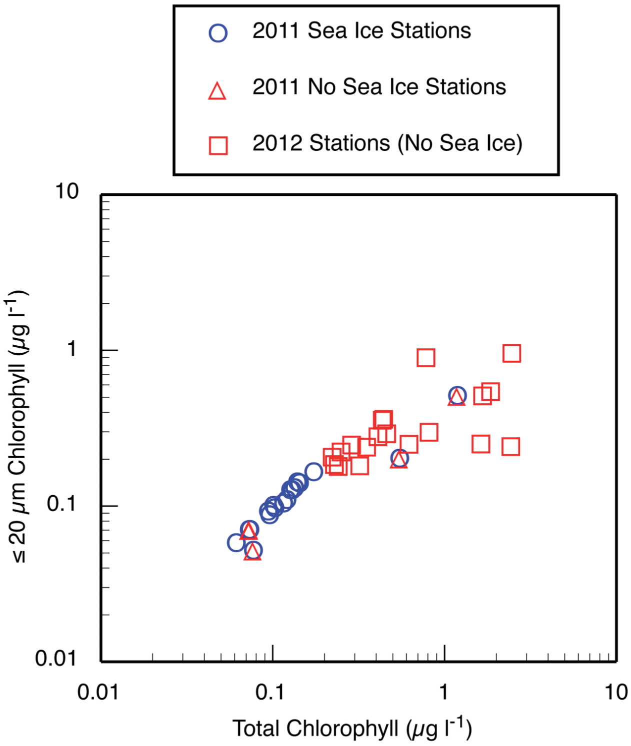

Fig. 5. Scatterplot of chlorophyll values (average integrated concentrations 0–100 m depth stratum), total vs. the fraction ≤ 20 µm. While the portion of the chlorophyll crop in 2012, without sea ice, was lower, the absolute concentrations of 'nano-pico-sized' phytoplankton was substantially greater.

DISCUSSION

Despite remarkable differences in sea ice conditions, we found a largely similar set of species of microzooplankton in the Chukchi Sea in 2012, the record year of low sea ice, compared to the more normal, in terms of sea ice, summer season of 2011. The radiolarian assemblage was dominated in both years by *Amphimelissa setosa*. It is very common across the entire Arctic and known to be the dominant species in the Chukchi Sea based on analysis of surface sediments (Bjørklund and Kruglikova 2003). The tintinnid species encountered (Table 3), similar in the two years, are quite typical for Arctic seas and form the bulk of the tintinnid communities in other systems, for example, the western coast of Greenland (Levinson *et al.* 1999), the Greenland Sea (Boltovskoy *et al.* 1995) and the Barents Sea (Boltovskoy *et al.* 1991, Jensen and Hansen 2000).

Overall, the tintinnid and radiolarian species found in both ice-free and more normal August conditions were largely the same set of taxa and not unexpected nor unusual. We found no evidence of incursions of forms new to the Arctic as has been reported for other areas (i.e., Bjørklund *et al.* 2013). What was unexpected were significantly lower abundances of tintinnids and radiolarians associated with higher chlorophyll

Table 3. Average concentrations (± SD) of microzooplankton species enumerated in the samples from 2011 (n = 18 stations) and 2012 (n = 19 stations).

Species	2011 Overall Avg Conc	2011 Avg Conc in Stations Present (# Stations)	2012 Overall Avg Conc (cells l⁻¹)	2012 Avg Conc in Stations Present (# Stations)
Acanthostomella norvegica	0.5 ± 0.57	0.8 ± 0.69 (11)	0.1 ± 0.14	0.2 ± 0.20 (9)
Eutintinnus apertus	0.001 ± 0.003	0.03 (1)	0	0
Leprotintinnus pellucidus	0.05 ± 0.080	0.3 ± 0.12 (3)	0.0001	0.0001 (1)
Ptychocylis urnula	1.4 ± 1.5	1.6 ± 1.65 (15)	0.06 ± 0.039	0.06 ± 0.039 (19)
Salpingella acuminata	0.1 ± 1.36	0.3 ± 0.07 (10)	0.03 ± 0.030	0.05 ± 0.0251 (11)
Salpingella faurei	0.2 ± 0.022	0.3 ± 0.23 (18)	0.13 ± 0.146	0.15 ± 0.16 (15)
Tintinnopsis acuminata	0.03 ± 0.13	0.3 ± 0.07 (2)	0.0001	0.0001 (1)
Tintinnopsis urnula	0.01 ± 0.018	0.1 ± 0.03 (2)	0.0001	0.0001 (1)
Amphimelissa setosa	2.30 ± 1.523	2.30 ±1.523 (18)	0.25 ± 0.164	0.25 ± 0.164 (19)

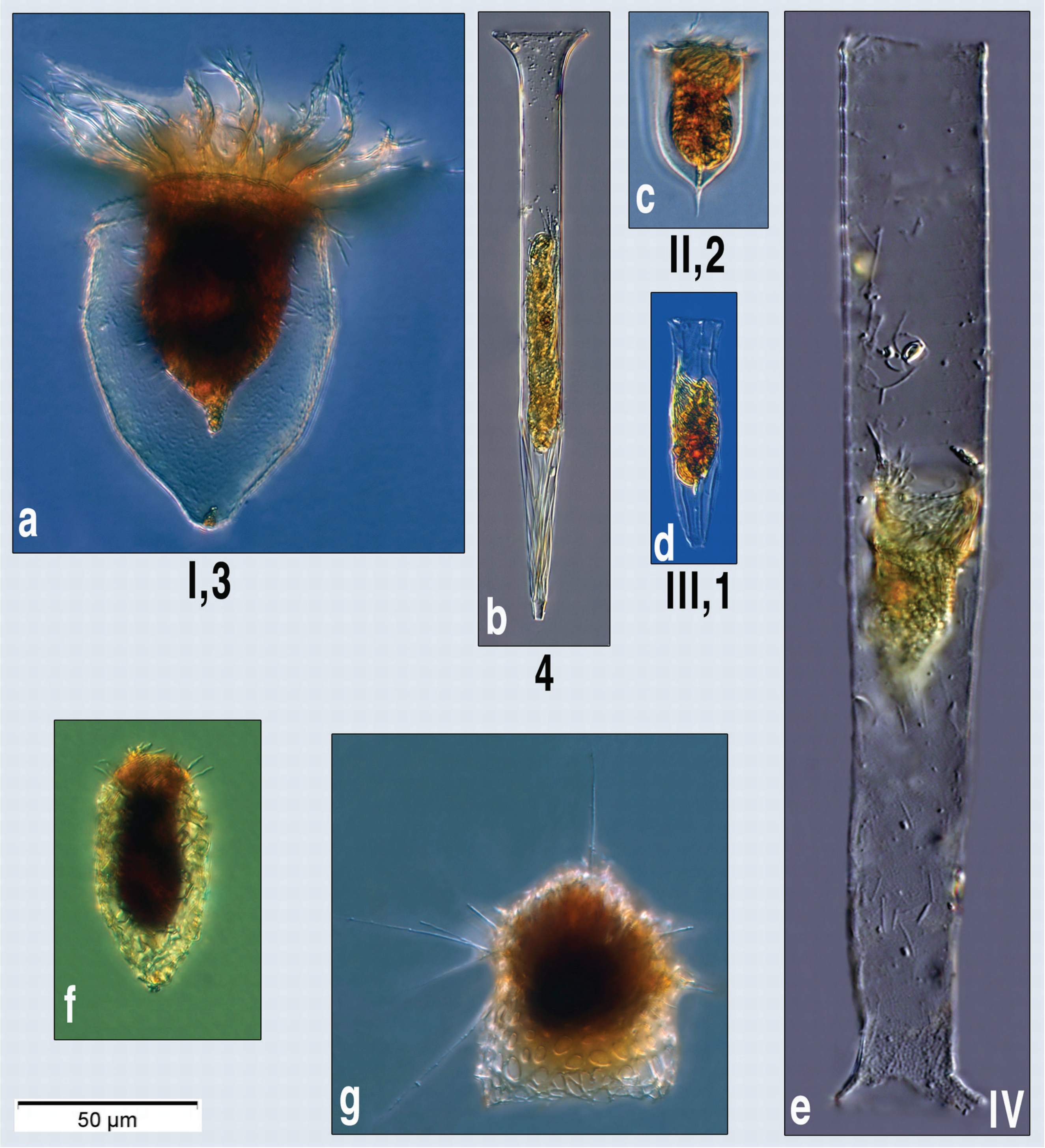

Fig. 6. The dominant species of tintinnids and radiolaria of the Chukchi Sea: **a** – *Ptychocylis urnula*; **b** – *Salpingella acuminata*; **c** – *Acanthostomella norvegica*; **d** – *Salpingella faurei*; **e** – *Leprotintinnus pelludicus*; **f** – *Tintinnopsis acuminata*; **g** – *Amphimelissa setosa*. The roman numerals denote the rank abundance of the top 4 species in the 2011 samples and the arabic numerals the rank abundance of the top 4 species in the 2012 samples. Note that the difference in the morphologies of the most abundant species in 2011 'I' , *P. urnula* compared to the dominant species in samples from the ice free year of 2012 "1", *S. faurei*. See Fig. 7 for the relative abundance of all the tintinnid species.

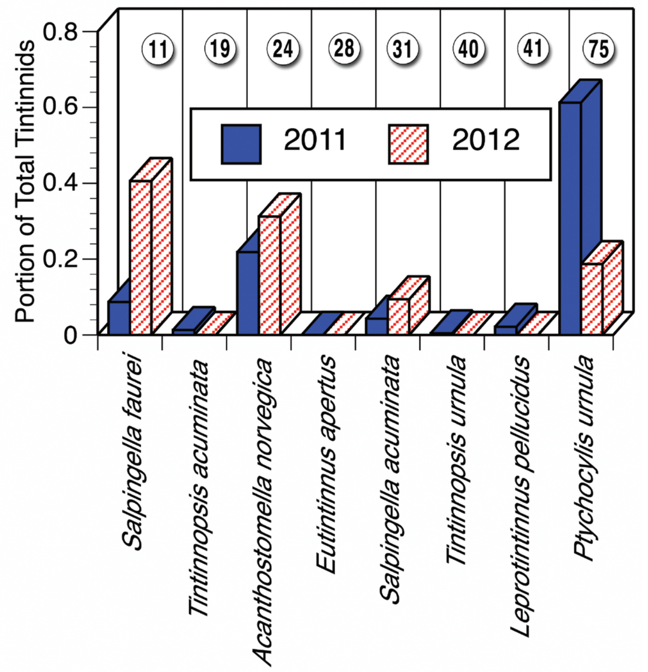

Fig. 7. Relative abundances (portion of the overall population) of each tintinnid species found in August 2011 with extensive sea ice and August 2012 with no sea ice. The numbers in circles show the lorica oral diameter in μm of the species. Note that the 2011 assemblage was dominated by the large-mouthed *Ptychocylis urnula* (LOD = 75 μm) and 2012 assemblage was dominated by the small-mouthed *Salpingella faurei* (LOD = 11 μm).

concentrations of 2012, the low sea ice year, compared to the preceding year of significant sea ice presence and lower chlorophyll concentrations (Figs. 2, 3, 5, Tables 1, 2). The differences of about an order of magnitude in abundance were accompanied by differences in the relative importance of tintinnid species of distinct morphologies.

The 2011 tintinnid assemblage, with relatively high abundances, was dominated by the large-mouthed (LOD = 75 μm) *Ptychocylis urnula*. The sparse 2012 population was dominated by the small-mouthed (LOD = 11 μm) *Salpingella faurei*. Given that tintinnid species feed most efficiently on prey about 25% of their LOD (Dolan 2010, Montagnes 2013), these differences in dominant species suggest that most of the tintinnid assemblage was feeding on prey of about 20 μm in size in 2011 and prey of about 3 μm in size in 2012. It should be recalled that tintinnids are usually a small part of the microzooplankton and so are unlikely to exert a significant impact on the prey they exploit; rather, the size spectrum of available prey (exploited by tintinnids and other taxa) is more likely to determine the composition of the tintinnid assemblage, in terms of the identity of the dominant morpho-types (Dolan *et al.* 2013).

It is tempting to link the higher microzooplankon concentrations of 2011, and larger on average larger tintinnid forms, to the presence of a distinct phytoplankton assemblages associated with summer sea ice. Unfortunately, we have no data other than chlorophyll concentrations concerning the phytoplankton. The concentrations of chlorophyll *a* in the ≤ 20 μm size fraction, presumably corresponding with prey exploited by tintinnids and radiolarians, were significantly higher in the sea ice-free sampling of 2012 compared to the preceding year, respectively 0.2 ± 0.17 μg l^{-1} and 0.1 ± 0.10 μg l^{-1}, as well as concentrations of total chlorophyll. Thus, the low abundances of tintinnids and radiolarians appear paradoxical. Studies in other systems have shown that high concentrations of tintinnids are indeed associated with the presence of sea ice, corresponding with diatoms dominating the phytoplankton. Bolotovskoy *et al.* (1995) found peak concentrations of total tintinnids (dominated by *Ptychocylis* and *Acanthostomella* also found in the Chukchi Sea) associated with the ice edge in the Greenland Sea in spring. However, while the stations in 2011 without sea ice (Fig. 2: I, II, III, IV, XVIII) did have lower concentrations of tintinnids, the stations did not clearly differ from those with sea ice in terms of species composition, nor the identity of the dominant species (data not shown) which argues against a distinct phytoplankton assemblages in the ice-free, compared to sea ice stations. Furthermore, the concentrations of total chlorophyll and ≤ 20 μm showed no consistent differences in the two sets of 2011 stations (Table 1). The radiolarian fauna provide no clear indications of possible differences in microzooplankton prey abundances or composition as very little is known concerning their diet. The dominant species, *Amphimelisa setosa*, is a nassellarian whose skeleton is composed of spicular elements and two chambers, a morphology associated with species who feed using a sort of an axopodial membrane to capture microflagellates and bacteria (Matsuoka 2007).

Qualitative differences in the compostion of the phytoplankton, not evident based on chlorophyll *a* concentrations, might explain the lower abundances of tintinnids and radiolarians we found comparing 2011 and 2012. However, an alternative (but not exclusive) explanation is a difference in predation pressure. We found largely similar declines in the concentrations of tintinnids and radiolarians comparing 2011 to 2012, of about an order of magnitude. These similar declines were unexpected as there is no reason *a priori* to assume that tintinnids and radiolarians should show similar trends and there was no correlation between the abundances among stations within either year (data not shown). To our knowledge, the only existing data on both tintinnids and radiolarians in an Arctic Sea or sub-Arctic sea is that of Bathman *et al*. (1990) based on the sedimentation of material from a site in the Norwegian Sea. The data show distinct temporal trends of tintinnids and radiolarians in the summer (Fig. 8) and have been taken as evidence that the two assemblages of microplankters have distinct patterns of seasonal abundance (Bathman *et al.* 1990, Wassmann *et al.* 1991).

The lower abundances of both tintinnids and radiolarians in 2012, and in similar proportions of about an order of magnitude relative to 2011, might have been due to a higher predation pressure on microzooplankton. We have no data to directly evaluate this possibility, only indications from other studies. A comprehensive study of mesozooplankton grazing conducted by Campbell *et al.* (2009) included experiments run in August in our study area in the years 2002 and 2004, years in which sea ice cover was similar to that found in 2011 (Fig. 1). Predation on microzooplankton was examined, and in most experiments a dietary preference for microzooplankton was documented. However, aggregate grazing rates gave estimates of impact equal to clearing only about 2–10% of the water column per day (Campbell *et al.* 2009, Table 4). If microzooplankters grow very slowly in polar waters as suggested by Rose and Caron (2007) and Rose *et al.* (2013), such low aggregate clearance rates might have a considerable impact. However, there seems to be no reason to assume that growth rates are low in arctic waters. Experimental data shows that tintinnids at least can grow at high rates (1.7–0.44 d^{-1}) in the marginal ice zone of the central Barents Sea (Jensen and Hansen 2000). Consequently, it is likely that mesozooplankton in 'normal' sea ice years is unlikely to exert a strong control on microzooplankton. However, low sea ice years might be distinctly different. A recent study reported that in July–August of 2007, the previous low sea ice year, copepod abundances were about twice that of the more normal years of 1991, 1992, and 2008; furthermore, sea ice reduction appears to correspond with the presence of large Pacific species (Matsuno *et al.* 2011).

It appears possible that top-down control might account for the low concentrations of tintinnids and

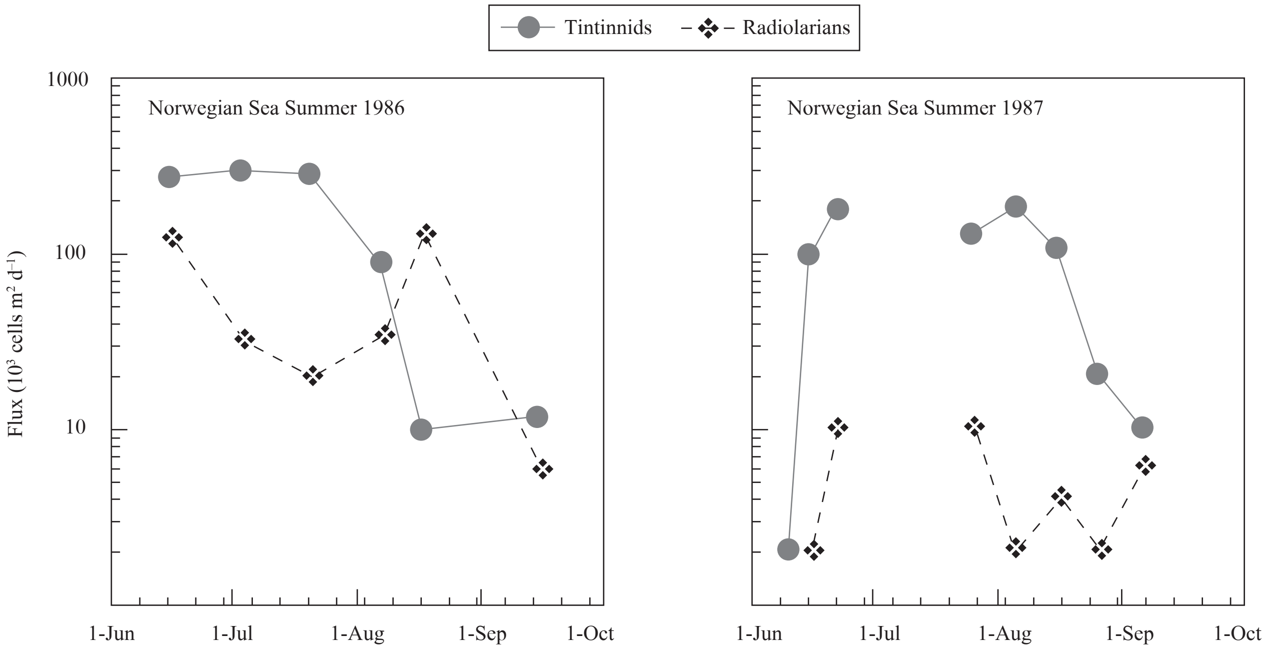

Fig. 8. Sedimentation rates of tintinnid loricas and radiolarian skeletons at 500 m on the Voering Plateau in the Norwegian Sea based on data from Bathman *et al*. (1990). Note that the flux of tintinnids and radiolarians, presumably reflecting concentrations of living cells in the surface waters, appear distinct. The apparent distinct temporal trends of tintinnids and radiolarians in the Norwegian Sea contrasts with the Chukchi Sea data showing largely parallel trends in concentrations (Fig. 3).

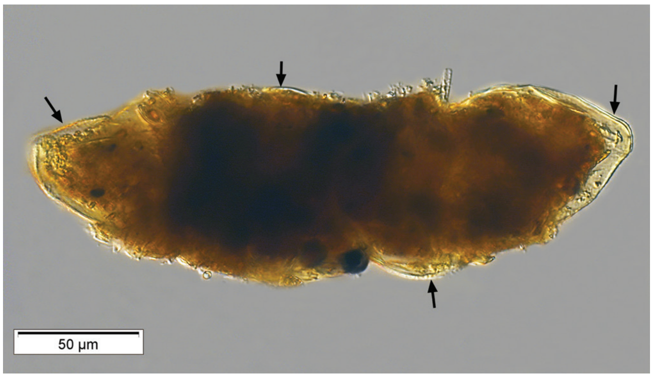

Fig. 9. Fecal pellet containing loricas of *Ptychocylis urnula* (arrows) found in material from the 2012 Station 40. The pellet is possibly from a large calanoid copepod according to J. T. Turner (University of Massachusetts Dartmouth).

radiolarians we found in the record year of 2012 compared to 2011 with sea ice conditions more like the past years. Perhaps co-incidently, in a 2012 sample we did find direct evidence of predation on *Ptychocylis urnula*: a fecal pellet identified by J. T. Turner as possibly from a large calanoid copepod which contained multiple loricas (Fig. 9). Similar to what we describe for 2012, apparently anomously low abundances of large protistan microplankters despite high prey concentrations, was also noted in the Norwegian Shelf waters in spring and summer samplings in 1994 and was attributed to top-down control on large protistan grazers (Verity *et al.* 1999). It is worth recalling that while top-down control of tintinids and radiolarians would likely extend to the entire microzooplankton community, we have no evidence that the abundance trends we documented do indeed extend across all microzooplankton taxa.

CONCLUSIONS

We found differences in the microzooplankton communities of the contrasting years, the differences were in the form of overall concentrations as well as relative abundances of certain species, with low abundances in the year of low sea ice. The differences we documented may have been related to the composition of the summer phytoplankton bloom. The large differences in the size of the dominant tintinnid species suggests a difference in the size-spectrum of phytoplankton prey. However, the markedly lower concentrations of both tintinnids and radiolarians, which likely exploit different prey, suggests a top-down control of microzooplankton may have occurred in the record low sea ice summer of 2012. Our data concern only the tintinnids and radiolarians. However, the trends documented do support the notion that the marked changes which have been reported in the abundance and composition of the mesozooplankton community of the Chukchi Sea associated with sea ice declines (Matsuno *et al.* 2011) likely extend to the microzooplankton.

Acknowledgements. The comments and suggestions of Ev Sherr, Dave Montagnes, and 2 reviewers on previous versions led to significant improvements in the paper. Financial support for this work was provided by the CNRS, the Université Paris 6 and Korea Polar Research Institute, KIOST, through project PM12020. We thank Mi Sa Jeon for her great help with sampling and data collection. The samples for 2011 were obtained through her efforts.

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Received on 28th May, 2013; revised on 15th June, 2013; accepted on 15th June, 2013