- 1 Flux variations and vertical distributions of siliceous Rhizaria (Radiolaria and
- 2 Phaeodaria) in the western Arctic Ocean: indices of environmental changes

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#### Abstract

- 24 The vertical distribution of radiolarians was investigated using a vertical multiple
- 25 plankton sampler (100-0, 250-100, 500-250 and 1,000-500 m water depths, 62  $\mu$ m
- 26 mesh size) at the Northwind Abyssal Plain and southwestern Canada Basin in
- September 2013. To investigate seasonal variations in the flux of radiolarians in relation
- 28 to sea-ice and water masses, a time series sediment trap system was moored at Station
- NAP (75°00'N, 162°00'W, bottom depth 1,975 m) in the western Arctic Ocean during
- 30 October 2010-September 2012. We monitored species abundance changes in the
- 31 fourteen most abundant radiolarian taxa, and how they related to the vertical
- 32 hydrographic structure in the western Arctic Ocean. The radiolarian flux was
- 33 comparable to that in the North Pacific Ocean. Amphimelissa setosa was dominant

during the season with open water as well as at the beginning and at the end of the seasons with sea ice cover. Cold and well mixed water mass based on summer ice edge were essential for high reproduction and growth of *A. setosa*. Our data indicate that *A. setosa* might have a three months life cycle. During the sea-ice cover season, however, oligotrophic and cold-water tolerant actinommids were dominant, productivity of radiolaria was lower, and species diversity was greater. This might be associated with the seasonal increase of solar radiation stimulating the growth of algae on the ice and other phytoplankton species under the sea-ice, upon which the actinommids can feed on. This evidence suggests that the dynamics of sea-ice are a major factor affecting the general biological productivity, distribution, and composition as demonstrated in the radiolarian fauna.

Keywords: Radiolarians, Western Arctic Ocean, Sea-ice, Beaufort Gyre, Sediment trap

#### 1. Introduction

In recent years, summer sea-ice extent in the Arctic Ocean has decreased rapidly due to global climate change (Stroeve et al., 2007, 2012). The sea-ice in the Arctic Ocean reached its minimum extent in September 2012 since the beginning of satellite observation (NSIDC, 2012). The most remarkable sea-ice decrease was observed in the western Arctic Ocean, on the Pacific side (Shimada et al., 2006; Comiso et al., 2008; Markus et al., 2009). In the western Arctic Ocean, the advection of warm North Pacific water through the Bering Strait contributes to both sea-ice melt in summer and an inhibition of sea-ice formation during winter (Shimada et al., 2006; Itoh et al., 2013).

Biological CO<sub>2</sub> absorption is an important carbon sink in the ice-free regions of the Arctic Ocean (Bates et al., 2006; Bates and Mathis, 2009). Melting of sea-ice can both enhance and reduce the efficiency of the biological pump in the Arctic Ocean, depending on ocean circulation (Nishino et al., 2011). The Beaufort High, a high-pressure system over the Canada Basin in the Arctic Ocean, drives the sea-ice and the water masses anticyclonically, as the Beaufort Gyre (Fig. 1). In the Canada Basin, the Beaufort Gyre governs the upper ocean circulation (Proshutinsky et al., 2002), and it has strengthened recently due to the decreasing sea-ice (Shimada et al. 2006; Yang 2009). Melting of sea ice reduce the efficiency of the biological pump within the Beaufort Gyre because of deepening of the nutricline caused by freshwater

accumulation within the gyre (Nishino et al., 2011). Conversely, the efficiency of the biological pump is enhanced outside the gyre because of nutrient supply from shelves and improved light penetration (Nishino et al., 2011).

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Particle flux plays an important role in the carbon export (Francois et al., 2002). Based on sediment trap samples from the Canada Basin and Chukchi Rise, Honjo et al. (2010) found that the annual average of sinking particle flux was three orders of magnitude smaller than that in epipelagic areas where the particle flux was the main mechanism for carbon export to greater depths. However, Arrigo et al. (2012) observed a massive algal biomass beneath fully consolidated pack ice far from the ice edge in the Chukchi Sea during the summer, and suggested that a thinning ice cover increased light transmission under the ice and allowed blooming of algae. Boetius et al. (2013) also reported that the algal biomass released from the melting ice in the Arctic Ocean was widely deposited at the sea floor in the summer of 2012. Therefore, it is inferred that biomass of zooplankton also changed seasonally under the sea-ice in the Arctic Ocean, as a result of the variable sea-ice conditions. Microzooplankton are recognized as a key component of pelagic food webs (e.g., Kosobokova et al., 2002; Calbet and Landry, 2004), but the seasonal and interannual changes in their communities within sea ice regions are still poorly understood.

To understand the effect of sea ice reduction on marine ecosystems in the Arctic Ocean, we studied productivity, distribution, composition, and biological conditions of living radiolarians in both plankton tow samples and sediment trap samples.

In our study we have analyzed only the siliceous forms of class Rhizaria and herein we have used the definition of Radiolaria as defined by Suzuki and Aita (2011). In their taxonomic scheme they include the following orders: Collodaria, Nassellaria, Spumellaria, Acantharia and Taxopodia. In addition we do include order Entactinaria which Suzuki and Aita (2011) reported getting extinct during the Permian, but Bjørklund et al. (2008) demonstrated its presence also in recent plankton and sediment samples. In this study we have excluded order Acantharia as they have a skeleton of SrSO<sub>4</sub> and Collodaria, a group that normally do not possess a skeleton or only with loose spines. Therefore, our study only includes forms with a solid skeleton of SiO<sub>2</sub>. In this paper we have chosen to include data also on order Phaeodaria which have not been assigned to Radiolaria but to Cercozoa in recent studies using molecular biology (Cavalier-Smith and Chao, 2003; Nikolaev et al., 2004; Adl et al., 2005; Yuasa et al.,

2005). To make the text read well we therefore use Radiolaria, or radiolarians when appropriate, to also include Phaeodaria, this to make it possible for us to compare already published data from the north Pacific region (Okazaki et al., 2003, 2005; Ikenoue et al., 2010, 2012a).

Radiolaria are one of the most common microzooplankton groups, they secrete siliceous skeletons, and their abundance in a region is related to temperature, salinity, productivity and nutrient availability (Anderson, 1983; Bjørklund et al., 1998; Cortese and Bjørklund, 1997; Cortese et al., 2003). Their genus and family levels taxa also respond to various oceanographic conditions by altering their distribution patterns and compositions (Kruglikova et al., 2010, 2011). In recent studies, Ikenoue et al. (2012a, b) found a close relationship between water mass exchanges and radiolarian abundances based on a fifteen-year long time-series observation on radiolarian fluxes in the central subarctic Pacific. Radiolarian assemblages are also related to the vertical hydrographic structure (e.g., Kling, 1979; Ishitani and Takahashi, 2007; Boltovskoy et al., 2010), therefore variations in their abundance and proportion might be useful environmental proxies for water mass exchanges at each depth interval, especially as some of them occur in response to recent climate change (e.g., ocean circulation, expansion and decline of sea-ice, influx of water mass from other regions).

The radiolarian assemblages in the western Arctic Ocean has been studied mainly based on the samples collected by plankton tow at ice-floe stations (Hülsemann, 1963, Tibbs, 1967), and in the Beaufort Sea in summer of 2000 (Itaki et al., 2003) or in surface sediment samples, mainly over the Atlantic side of the Arctic Ocean (Bjørklund and Kruglikova (2003). Bernstein (1931, 1932, 1934) reported on six Polycystina, two Acantharia and two Taxopodia species, but did not give any information on abundance in the Barents Sea and Kara Sea for the Polycystina, but for the Acantharia and Taxopodia she reported them to be abundant, with a maximum occurrence in the deeper and warmer Atlantic water. Meunier (1910) also reported on Acantharia, Taxopodia and Nassellaria in the Kara Sea and the Arctic Ocean, but he stated (page 196) that his material was not rich in radiolarians. However, the knowledge of the geographical and the depth distribution of living radiolarians is still limited, and their seasonal and annual changes have not been studied in the western Arctic Ocean because of seasonal sea-ice coverage.

This is the first extensive study of the seasonal and interannual flux changes of

1 radiolarians in the western Arctic Ocean. We present radiolarian depth distributions and

2 flux variations in the western Arctic Ocean, and discuss their seasonality and species

3 associations in relation to the environmental conditions (temperature, salinity, depth,

sea-ice concentration, and downward shortwave radiation).

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#### 2. Oceanographic setting

7 The hydrography in the western Arctic Ocean has been discussed in several studies 8 (e.g., Aagaard et al., 1985; McLaughlin et al., 2011) and the upper 1,000 m of the water 9 column can be divided into five distinct water masses. The surface water is 10 characterized by low temperature and low salinity water (Aagaard et al., 1981) and can be subdivided into three layers, i.e. Surface Mixed Layer (SML), Pacific Summer Water 11 12 (PSW), Pacific Winter Water (PWW). The SML (0-25 m) is formed in summer by 13 sea-ice melt and river runoff and is characterized by very low salinities (less than 28). 14 The PSW (25-100 m) and PWW (100-250 m) are cold halocline layers originating from 15 the Pacific Ocean via the Bering Sea. The PSW flows along the Alaskan coast and 16 enters the Canada Basin through the Bering Strait and Barrow Canyon (Coachman and 17 Barnes, 1961) (Fig. 1). The PSW is relatively warmer and less saline (30-32 in the 18 1990s, 28-32 in the 2000s, according to Jackson et al., 2011) than the PWW. The PSW 19 is further classified into warmer and less saline Alaskan coastal water and cooler and 20 more saline Bering Sea water (Coachman et al., 1975), which originate from Pacific 21water that is modified in the Chukchi and Bering Seas during summer. The Alaskan 22coastal water is carried by a current along the Alaskan coast, and spread northwards 23 along the Northwind Ridge by the Beaufort gyre depending on the rates of ice cover and 24decay (Shimada et al., 2001). The PWW is characterized by a temperature minimum (of 25 about -1.7°C) and originates from Pacific water that is modified in the Chukchi and 26 Bering Seas during winter (Coachman and Barnes, 1961). The PWW is also 27 characterized by a nutrient maximum and its source is regenerated nutrients from the 28shelf sediments (Jones and Anderson, 1986). 29 The deep water is divided into Atlantic Water (AW) and Canada Basin Deep Water

The deep water is divided into Atlantic Water (AW) and Canada Basin Deep Water (CBDW). AW (250-900 m) is warmer (near or below 1°C) and saltier (near 35) intermediate water than the surface waters, and is originating from the North Atlantic Ocean, via the Norwegian Sea. The CBDW (below 900 m) is a cold (lower than 0°C) water mass located beneath the AW and has the same salinity as the AW. The CBDW is

- 1 formed by the brine formation on the shelves, which makes cold and saline water mass
- 2 sink over the continental margin into the deep basins (Aagaard et al., 1985).

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#### 3. Materials and methods

- 5 *3.1. Plankton tow samples*
- 6 Plankton tow samples were collected by vertical multiple plankton sampler (VMPS).
- 7 The instrument (mesh size: 62 μm, open mouth area: 0.25 m<sup>2</sup>) was towed from 4 layers
- 8 (100-0, 250-100, 500-250, and 1,000-500 m) at 2 stations (Station 32 in Northwind
- 9 Abyssal Plain, 74°32'N, 161°54'W; Station 56 in southwestern Canada Basin, 73°48'N,
- 10 159°59'W) (Fig. 1 and Table 1) in September 2013. Hydrographical data (temperature,
- salinity, dissolved oxygen, and chlorophyll a) down to 1,000 m water depth were
- simultaneously obtained from a CTD (Conductivity Temperature Depth profiler) cast.
- 13 The volume of seawater filtered through the net was estimated using a flow meter
- mounted in the mouth ring of the plankton net.
- The samples collected by VMPS were split with a Motoda box splitter and a rotary
- splitter (McLane<sup>TM</sup>WSD-10). The split samples were fixed with 99.5% ethanol for
- 17 radiolarian studies. Plankton samples were stained with Rose-Bengal to discriminate
- between living and dead specimens. The split samples were sieved through a stainless
- 19 screen with 45 µm mesh size. Remains on the screen were filtered through Gelman®
- 20 membrane filters with a nominal pore size of 0.45 µm. The filtered samples were
- desalted with distilled water. The edges of each filtered sample were cut according to
- slide size in wet condition and mounted on glass slides on a slide warmer. Xylene was
- added to the dried filters and samples, which were then permanently mounted with
- 24 Canada balsam. Radiolarian taxa were identified and counted with a compound light
- 25 microscope at 200 x or 400 x magnification. Plankton tow samples were stained with
- Rose-Bengal to discriminate between living and dead specimens. Specimens that clearly
- stained bright red were interpreted as living cells, while cells that did not stain red, or
- 28 just barely indicated a red shine, were interpreted as dead because of the lacking
- protoplasm. This is also in accordance to Okazaki et al. (2004). All specimens on a slide
- were identified and counted, and their individual numbers were converted to standing
- 31 stocks (No. specimens m<sup>-3</sup>).

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1 Profiles of temperature, salinity, dissolved oxygen, and chlorophyll a down to 1,000 2 m depth at stations 32 (Northwind Abyssal Plain) and 56 (southwestern Canada Basin) 3 in September 2013 are from Nishino (2013) and shown in Fig. 2a and b, respectively. 4 At Station 32, temperature showed sharp decrease from the surface and down to about 5 25 m depth with a sharp increase at the base of SML. The PSW is generally cold (about 6  $-1^{\circ}$ C) with a maximum value (1.6°C) at about 50 m and shows a rapid decrease with 7 increasing depth. The PWW is the coldest water (minimum value -1.6°C) at about 200 8 m. Highest temperatures are found in the AW (near or below 1°C) at about 400 m with 9 a gradual decrease below 500 m. Salinity showed low values (25-28) in the SML, 10 increasing rapidly with depth from 28-32 in the PSW. In the PWW there is a gradual 11 increase of salinity from 32 to 35, while there is a slight decrease below the PWW/AW 12 boundary. Dissolved oxygen showed maximum value (405 µmol/kg) at the boundary 13 between SML and PWW, rapid decrease with increasing depth in the PSW and PWW, 14 minimum value (270 umol/kg) around the boundary between PWW and AW, and slight increase below that. Chlorophyll a higher than 0.1 mg m<sup>-3</sup> was observed in 0-80 m 15 16 depth. Temperature, salinity, dissolved oxygen, and chlorophyll a show almost similar 17 values at both Station 32 and Station 56 except for SML and PSW. In the SML, salinity 18 at Station 32 was slightly lower than at Station 56. In the PSW, a temperature peak at 19 Station 32 was about one degree higher, and a little deeper, compared to Station 56. In 20 0-80 m depth, chlorophyll a was a little higher at Station 56 than at Station 32.

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#### 3.3. Sediment trap samples

Particle flux samples were collected by a sediment trap (SMD26 S-6000, open mouth area 0.5 m<sup>2</sup>, Nichiyu Giken Kogyo, Co. Ltd.) rotated at 10–15-day intervals moored at 184 m (4th October 2010–28th September 2011)-260 m (4th October 2011–18th September 2012) and 1,300 m (4th October 2010–28th September 2011)-1,360 m (4th October 2011–18th September 2012) at Station NAP (Northwind Abyssal Plain, 75°00'N, 162°00'W, bottom depth 1,975 m) (Fig. 1; Table 2). The mooring system was designed to set the collecting instrument at approximately 600 m above the sea floor. This depth of the moored sediment traps was chosen in order to avoid possible inclusion of particles from the nepheloid layer, reaching about 400 m above the seafloor (Ewing and Connary, 1970). Recoveries and redeployments of the traps were carried out on the Canadian Coast Guard Ship I/B (ice breaker) "Sir Wilfrid

1 Laurier" and R/V "Mirai" of Japan Agency for Marine-Earth Science and Technology.

2 The sample cups were filled with 5% buffered formalin seawater before the sediment

3 trap was deployed. This seawater was collected from 1,000 m water depth in the

southern Canada Basin, and was membrane filtered (0.45 mm pore size). The seawater

in the sample cups was mixed with sodium borate as a buffer (pH 7.6-7.8) and 5%

formalin was added as a preservative.

The samples were first sieved through 1 mm mesh to remove larger particles, which are not relevant for the present study. The samples were split with a rotary splitter (McLane  $^{TM}$ WSD-10). At first, we used 1/100 aliquot size of the samples to make microslides for microscope work (species identification). We made additional slides in case of low radiolarian specimen numbers. In order to remove organic matter and protoplasm, 20 ml of 10% hydrogen peroxide solution are added to the samples in a 100 ml pyrex beaker, and heated (not boiling) on a hot plate for one hour. After this reaction was completed, Calgon® (hexametaphosphate, surfactant) solution was added to disaggregate the sample. The treated samples were then sieved through a screen (45  $\mu$ m mesh size). Both the coarse (>45  $\mu$ m) and fine (<45 $\mu$ m) fractions were filtered through Gelman membrane filters with a nominal pore size of 0.45 $\mu$ m and desalted with distilled water. The edges of each filtered sample were cut according to slide size in wet condition and mounted on glass slides on a slide warmer. Xylene was added to the dried filters and samples, which were then permanently mounted with Canada balsam.

We made slides of both the coarse (>45  $\mu$ m) and the fine (<45  $\mu$ m) fraction of each sample. For the enumeration of radiolarian taxa in this study, we counted all specimens of radiolarian skeletons larger than 45  $\mu$ m encountered on a slide. Each sample was examined under an Olympus compound light microscope at 200 x or 400 x magnification for species identification and counting. The radiolarian flux (No. specimens m<sup>-2</sup> day<sup>-1</sup>) was calculated from our count data using the following formula:

$$Flux = N*V/S/D \qquad (1)$$

where N is the counted number of radiolarians, V the aliquot size, S the aperture area of the sediment trap (0.5 m<sup>2</sup>), and D the sampling interval (day). Diversity indices using the Shannon-Weaver log-base 2 formula (Shannon and Weaver, 1949) were calculated for total radiolarians

 $32 H = -\sum P_i \log_2 P_i (2)$ 

where H is the diversity index, P is the contribution of species (relative abundance in

total radiolaria) and i is the order of species.

As supplemental environmental data, the moored sediment trap depth and the water temperature (accuracy of + 0.28°C) were monitored every hour (sensor type: ST-26S-T). Moored trap depth for the upper trap was lowered by about 80 m during the second year (about 260 m depth) than during the first year (about 180 m depth), caused by entanglement of the mooring ropes. During July-August in 2012, the moored trap depth was lowered to about 300 m, because of intensified water currents (Fig. S1). Time-series data of sea-ice concentration around Station NAP during the mooring period were calculated from the sea-ice concentration data set (http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn Smith OIv2/, cf. Reynolds et al., 2002).

#### 3.4. Taxonomic note

The species described by Hülsemann (1963) under the name of *Tholospyris gephyristes* is not a Spyridae. This species has been accepted as a Spyridae by most workers, but this species lacks the sagittal ring that is typical for the Spyridae. We have therefore assigned this species to the family Plagiacanthidae. We suggest this species be renamed to *Tripodiscium gephyristes* until a proper taxonomic analysis has been undertaken.

## 4. Results

#### 4.1. Radiolarians collected by plankton tows

A total of 43 radiolarian taxa (12 Spumellaria, 3 Entactinaria, 26 Nassellaria, and 2 Phaeodaria) were identified in the plankton tow samples (Table 3). We have observed taxopodians, but they have not been identified according to the two species as defined by Meunier (1910), nor have they been quantified. Furthermore, we have not been able to observe any collodarian individuals although we cannot exclude their presence in the Arctic Ocean (Lovejoy et al., 2006; Lovejoy & Potvin, 2011). The numbers of individuals for each radiolarian taxon are in Tables S1 (Station 32) and S2 (Station 56).

#### 4.1.1. Standing stocks and diversities of radiolarians

The abundance of living radiolarians at Station 32 was about two times higher than at Station 56 at each depth interval in the upper 500 m, the depth level at which the

1 abundance of living radiolarians decreased with increasing water depth at both stations 2 (Fig. 2a and b). The abundance of dead radiolarians also decreased with water depth at

3 both stations except for 100–250 m depth at Station 32 (Fig. 2a and b). The abundance

of dead radiolarians was generally higher than living radiolarians at both stations except

for in the 0–100 m depth at Station 32. The living radiolarian diversity index was low in

the 0-100 m depth interval, increased with depth, reached a maximum at about 400 m,

and then slightly decreased below 500 m depth at both stations.

8 At Station 32, Amphimelissa setosa (58%) and Amphimelissa setosa juvenile (22%) 9 were dominant, and Joergensenium sp. A (6%), Pseudodictyophimus clevei (4%), 10 Actinommidae spp. juvenile forms (3%), and Actinomma leptodermum leptodermum 11 (1%) were common (Fig 3a). At Station 56 the Actinommidae spp. juvenile forms 12 (38%) and Amphimelissa setosa (29%) were dominant, and Actinomma leptodermum 13 leptodermum (6%), Amphimelissa setosa juvenile (6%), Pseudodictyophimus clevei 14 (5%), and *Joergensenium* sp. A (4%) were common (Fig 3b). We defined the 2-shelled 15 forms of Actinommidae as juvenile. Then the 3 and 4 shelled forms will be adult. For 16 the Amphimelissa setosa we defined those with cephalis only as juveniles. Those with a 17 well developed cephalis and with a barely or well developed thorax are defined as adult. 18 Actinommidae spp. juvenile forms are mostly two-shelled juvenile forms of Actinomma 19 leptodermum leptodermum and Actinomma boreale, making it impossible to separate 20 between the two.

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4.1.2. Environmental significance of the vertical distribution of radiolarian species

We selected fourteen abundant radiolarian taxa to show their relation to the vertical hydrographic structure in the western Arctic Ocean (Fig. 4). The selected taxa were radiolarian taxa with 1% or higher relative abundance through the upper 1,000 m of the water column at either of the two stations and with high relative abundance in each water depth.

Adult and juvenile forms of Amphimelissa setosa were mainly distributed in the 0–250 m depth at both stations. In the 0-100 m depth, adult and juvenile stages were dominant (70% and 28%, respectively) at Station 32, and at Station 56 (23% and 7%, respectively) following the juvenile Actinomma spp. (56%). In the 100–250 m depth, A. setosa was the dominant species at both stations. At Station 32, the abundance of A. setosa in the 100–250 m depth interval was lower than in the 0–100 m depth, whereas at Station 56, the abundance in the 100-250 m depth was almost the same as in the 0-100 m depth.

Actinommidae spp. juvenile forms and *Actinomma l. leptodermum* were absent in 0–100 m depth at Station 32, but both, especially Actinommidae spp. juvenile forms (56%), were abundant at Station 56. Both were common in the 100-250 m depth at both stations (8% and 4%, respectively at Station 32; 14% and 7%, respectively at Station 56), and decreased in abundance in the 250–500 m depth. *Spongotrochus glacialis* was rare in the 0-100 m depth at Station 32 (0.4%) but with a slight increase at Station 56 (1.4%). In deeper layers *S. glacialis* was rare.

Joergensenium sp. A, Pseudodictyophimus clevei, and Actinomma boreale were abundant in the 100–250 m depth at both stations. Joergensenium sp. A was absent in the 0–100 m depth but abundant in the 100–250 m depth and rare in deeper depths. Pseudodictyophimus clevei was found throughout from the surface to 1,000 m depth, but was rare at Station 32 except for in 100-250 m. Actinomma boreale was rare and mainly found in the 100–250 m depth at both stations.

Ceratocyrtis histricosus was mainly found in the 250–500 m depth, and occurred also in the 100–250 m depth at both stations. Tripodiscium gephyristes was widely distributed below 100 m depth at Station 56, while at Station 32 this species was scarce at all depth layers. Pseudodictyophimus g. gracilipes occurred in very low numbers at both stations through the upper 1,000 m. Pseudodictyophimus plathycephalus, Plagiacanthidae gen. et sp. indet., and Cycladophora davisiana were most abundant below 500 m depth at both stations.

#### 4.2. Radiolaria collected by sediment trap

A total of 51 radiolarian taxa (15 Spumellaria, 3 Entactinaria, 31 Nassellaria, and 2 Phaeodaria) were identified in the upper and lower sediment trap samples at Station NAP during 4th October 2010–18th September 2012 (Table 3). We have observed taxopodians, but they have not been identified nor quantified. Furthermore, we have not been able to observe any collodarian individuals. The number of radiolarians counted in each sample ranged from 8 to 1,100 specimens in the upper trap, and from 0 to 2,672 specimens in the lower trap (Tables S3 and S4). There were 15 samples with fewer than 100 specimens (2 samples in upper trap, 13 samples in lower trap). Most of the species recognized in our sample materials are shown in Plates 1-9.

4.2.1. Radiolarian flux and diversity in the upper trap

The highest total radiolarian fluxes in the upper trap were observed during the beginning of sea-ice cover season (November in 2010 and 2011, >10,000 specimens  $m^{-2}$  day<sup>-1</sup>) (Fig. 5). The fluxes were higher during the open water season (August–October in 2011, average, 5,710 specimens  $m^{-2}$  day<sup>-1</sup>) and around the end of sea-ice cover season (July–August in 2011, >4,000 specimens  $m^{-2}$  day<sup>-1</sup>) than during the sea-ice cover season (December–June, average in 2011, 944 specimens  $m^{-2}$  day<sup>-1</sup>; average in 2012, 723 specimens  $m^{-2}$  day<sup>-1</sup>). The fluxes varied from 114 to 14,677 specimens  $m^{-2}$  day<sup>-1</sup> with an annual mean of 2,823 specimens  $m^{-2}$  day<sup>-1</sup>. The diversity of radiolarians, however, was higher during the sea-ice cover season (>3) than during the open water season (<2) (Fig. 5). The diversity indices were negatively correlated with the total radiolarian fluxes (r = -0.91) (Fig. 6).

Species composition varied seasonally. Adult and juvenile Amphimelissa setosa were most dominant (90%) during the sea-ice free season, and the beginning and the end of sea-ice cover season. The juvenile and adult forms were abundant in earlier and later seasons, respectively (Fig. 7). During the sea-ice cover season, however, Actinommidae spp. juvenile forms (range, 0-51%; average, 18%), Actinomma leptodermum leptodermum (range, 0–14.6%; average, 4%), Actinomma boreale (range, 0-33%; average, 4%) were dominant. Relatively high percentages Pseudodictyophimus clevei, Pseudodictyophimus gracilipes, Tripodiscium gephyristes were also observed during the sea-ice cover season.

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## 4.2.2. Radiolarian flux and diversity in the lower trap

Total radiolarian flux in the lower trap varied from 0 to 22,733 specimens m<sup>-2</sup> day<sup>-1</sup> with an annual mean of 4,828 specimens m<sup>-2</sup> day<sup>-1</sup> (Fig. 5). The fluxes were high during November–December both in 2010 and 2011 and during March in 2011 (>10,000 specimens m<sup>-2</sup> day<sup>-1</sup>), while extremely low (average, 21 specimens m<sup>-2</sup> day<sup>-1</sup>) during May-September in 2012. Diversity did not change greatly, and increased slightly during May-July 2011, and in April 2012 when the radiolarian fluxes were low. The diversity indices were weakly negatively correlated with the radiolarian fluxes (r = -0.52) (Fig. 6).

Adult and juvenile stages of Amphimelissa setosa were dominant throughout the

sampling periods (range, 66–92%; average, 82%). The relative abundance of A. setosa

2 juvenile was slightly increased in 2012 in comparison to 2010 and 2011.

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#### 5. Discussion

5.1. Comparison between Arctic and North Pacific Oceans

6 Biogenic particle flux into the deep sea in the Canada Basin was generally assumed 7 to be low due to the low productivity of siliceous and calcareous microplankton, which 8 plays an important role in the biological pump process (Honjo et al., 2010). However, 9 we observed high radiolarian fluxes (14,677: upper trap, 22,733: lower trap) at Station 10 NAP during the open water season and around the beginning and the end of sea-ice 11 cover season in 2011-2012. The annual means (2,823: upper trap, 4,823: lower trap) 12 were comparable to those observed in several areas of the North Pacific Ocean (Fig. 8, 13 Table S5). However the radiolarian fluxes in the upper trap showed an apparent 14 abundant season (July-November) and a sparse season (December-June) in a year, and 15 that the lower trap also showed an extremely low flux during May-September 2012. 16 Therefore we regarded the period when radiolarian fluxes were higher than  $1\sigma$  (3,489: 17 upper trap; 5,675: lower trap) as a contributing period. As a result, the mean of 18 radiolarian fluxes during the contributing period in the western Arctic Ocean showed a 19 higher value (7,344: upper trap; 11,871: lower trap) than at any other stations in the 20 North Pacific Ocean (Table S5). The biogenic opal collected in this study mainly 21consisted of radiolarians and diatoms based on our microscopic observations. Other 22siliceous skeletons (silicoflagellate skeletons, siliceous endoskeleton of dinoflagellate 23 genus Actiniscus, chrysophyte cysts, ebridian flagellate, and palmales) are minor 24components in the same trap samples (Onodera et al., 2014), therefore siliceous 25 skeletons of radiolarians and diatoms might play an important role to export biogenic 26 silica to the deep Arctic. Onodera et al. (2014) also estimated the diatom contribution to 27 POC flux at station NAP, but more than half of the contribution to total POC has not 28been explained yet. Relatively high flux of radiolarians in arctic microplankton might 29 contribute to a substantial part of the POC flux.

- 5.2. Characteristic and ongoing morphogenesis and speciation of radiolarians in the
- 32 western Arctic Ocean
- The radiolarian fauna observed in this study was characterized by high dominance of

1 two families, the Cannobotryoidae and the Actinommidae (Fig. 3). Amphimelissa setosa 2 is the dominant species, while the actinommids make a species association with a close 3 affinity to the Norwegian Sea fauna. Amphimelissa setosa first appeared in the North 4 Pacific and migrated into the North Atlantic through the Arctic Ocean during the 5 Pleistocene interglacial optima (Matul and Abelmann, 2005). This species became 6 extinct in the North Pacific close to the MIS 4/5 boundary (Kruglikova, 1999; Matul et 7 al., 2002; Ikenoue et al., 2011), and has not been observed in recent materials in the 8 North Pacific (Ikenoue et al., 2012a). Petrushevskaya (1979) pointed out that the 9 arctic-boreal radiolarian species known from the Arctic Ocean basins had been 10 originated from the early Postglacial Norwegian Sea polycystine radiolarian fauna. 11 Bjørklund and Kruglikova (2003) also concluded that the modern radiolarian fauna in 12 the Arctic Ocean had a close affinity to the Norwegian Sea radiolarian fauna. This is 13 also supported by the species listed in Table 3, they all occur in the Norwegian Sea, 14 except for the taxa that we at present classify as endemic to the Arctic Ocean. Inflow of 15 radiolarians with waters from the northern part of the Bering Sea is probably negligible 16 since the most abundant and typical radiolarian species in the recent Bering Sea such as 17 Stylochlamydium venustum, and Ceratospyris borealis are absent in the western Arctic 18 Ocean. These two species are surface dwellers in the North Pacific (Tanaka and 19 Takahashi, 2008) and are major species in the recent Bering Sea (Ikenoue et al., 2012a). 20 Our results suggest that the radiolarian fauna in the western Arctic Ocean was 21characterized by a wide morphologic variability in the skeletons within the family 22Actinommidae and high standing stock of *Joergensenium* sp. A in the PWW (Table S6). 23 Actinomma morphogroup A (58 specimens), Actinomma morphogroup B (57 24specimens), Joergensenium sp. A (1,401 specimens), has so far only been observed in 25 the western Arctic Ocean in our study. We have not seen this species outside the Arctic 26 Ocean, neither in the North Pacific or in the North Atlantic. Actinomma morphogroup A 27 and B and Joergensenium sp. A might be new species endemic for the western Arctic. 28 Kruglikova et al. (2009) described two new species Actinomma georgii and A. turidae, 29 and suggested the possibility of endemism for these two species. They also indicated a 30 fifth group Actinomma indet. (their fig. 5, p. 32) which probably consists of still several 31 undescribed species. Their argument was that the endemism arose as radiolarians had 32 been rapidly evolving under the stressful conditions in the Arctic Ocean, and that 33 speciation or morphogenesis within the family Actinommidae might be ongoing in the

1 central Arctic Basin. Our results support this hypothesis, and suggest that local 2 speciation or morphogenesis took place not only in the central Arctic basin, but also in 3 the western Arctic Ocean. This is demonstrated by the occurrence of what we interpret 4 as new and still undescribed *Actinomma* species. These new forms are very similar to A. 5 boreale, but with a different structure of the medullary shells. Also within the 6 radiolarian group Entactinaria, in the genus Joergensenium, one or two undescribed 7 species are found. The reason for radiolarian species speciation in this area is still not 8 understood but we can only speculate that this can be controlled by the harsh 9 environmental stress (Allen and Gilooly, 2006; Kruglikova et al., 2009), particularly the 10 extremely cold water masses under the sea-ice (-1.7°C) and the always-changing 11 quality of the water masses, affected by the inflowing Pacific water.

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## 5.3. Vertical distribution of species and hydrographic structure

## 14 5.3.1. PSW and PWW association

Amphimelissa setosa and its juvenile stages were found in shallow cold-water in both stations 32 and 56. Specifically, they were more abundant in the SML and PSW (0-100 m) at Station 32 than Station 56. At Station 32, these two water masses exhibited warmer temperature (about one degree higher at the temperature peak) than Station 56; indicating that cold to moderately warm (-1.2 to 1.6 °C), and well mixed water mass were more favorable for this species than perennial cold water masses such as PWW (100-250 m). According to Dolan et al. (2014), A. setosa showed significantly lower abundances with higher chlorophyll a concentrations of 2012, the low sea ice year, compared to the year of 2011 with higher sea ice and lower chlorophyll a concentrations. Thus, the abundance of phytoplankton protoplasm with the remains of chlorophyll a is not related with the abundance of A. setosa. This is harmonious with our result that chlorophyll a was a little higher at Station 56 but the abundance of A. setosa at Station 56 was fairly lower than that at Station 32 in contrast to Actinommidae spp. juvenile forms, Actinomma l. leptodermum. Therefore the favorable condition for A. setosa is related to cold and well mixed water mass and any other organisms except for those from phytoplankton near the summer sea-ice edge. The vertical and geographic distribution of A. setosa has been described in several previous studies. This species dominated (60-86%) the radiolarian assemblage through the upper 500 m of the water column in the Chukchi Sea and the Beaufort Sea and so can be an indicator of cold

- 1 Arctic surface water (Itaki et al., 2003). Bernstein (1931) noted that this species live in
- 2 the cold (-1.68°C to -1.29°C) and saline (34.11 to 34.78) waters in the Arctic Ocean.
- 3 Matul and Abelmann (2005) also suggested that A. setosa prefers well-mixed, cold and
- 4 saline surface/subsurface waters. Bjørklund et al. (1998) reported its distribution in the
- 5 western part of the GIN Seas, being dominant (up to 76%) at the Iceland Plateau and
- 6 common (>20%) just north of the Iceland-Faeroe Ridge. In the eastern part of the
- 7 Barents Sea, west of Novaja Zemlya, Bjørklund and Kruglikova (2003) reported
- 8 Amphimelissa setosa as the dominant (77%) species.
- 9 Actinommidae spp. juvenile forms, Actinomma l. leptodermum, Spongotrochus
- 10 glacialis were mainly distributed in the PSW and PWW and preferred different water
- 11 masses from Amphimelissa setosa. Actinomma l. leptodermum and Actinomma boreale
- 12 had been reported as a group (e.g., Samtleben et al., 1995), due to identification
- problems, particularly of the juvenile stages, but the adult stages can be separated into
- two species following Cortese and Bjørklund (1998). Actinomma l. leptodermum were
- absent in the water masses of SML and PSW at Station 32, but they were abundant in
- these water masses at Station 56. At Station 56, SML and PSW water masses were
- 17 colder (-1.2 to 0.6 °C) and more homogeneous than at Station 32; indicating that
- Actinommidae spp. juvenile forms and A. l. leptodermum preferred slightly warmer
- water than PWW (-1.6 °C). Our results show that Actinommidae spp. juvenile forms
- and A. l. leptodermum are most abundant in the upper water layers where phytoplankton
- 21 also prevails (Fig. 2). It is most likely that the juvenile actinommids and A. l.
- 22 leptodermum may be bound to the euphotic zone, and so can be herbivorous.
- 23 Spongotrochus glacialis, showing a similar vertical distribution as Actinommidae spp.
- juvenile forms and Actinomma l. leptodermum, also preferred warmer water than PWW.
- 25 This species inhabited surface water in the Okhotsk Sea, and is well adapted to low
- temperatures and low salinities (Nimmergut and Abelmann 2002). Okazaki et al. (2004)
- 27 reported S. glacialis as a subsurface dweller with abundance maximum in the 50–100 m
- interval in the Okhotsk Sea, associated with the phytoplankton production.

## 30 5.3.2. PWW association

- 31 Joergensenium sp. A, Pseudodictyophimus clevei, and Actinomma boreale, were
- mainly distributed in the PWW. Joergensenium sp. A and P. clevei might prefer cold
- water (-1.7°C) with low turbulence. The depth distribution of *Joergensenium* sp. A was

1 restricted to the PWW (100-250 m) and the upper AW (250-500 m), but P. clevei was 2 more widely distributed. Joergensenium sp. A has not yet been described from recent 3 radiolarian assemblages, so it can be suggested that this species might occur only on the 4 Pacific side of the Arctic Ocean and might serve as an indicator for the PWW layer. 5 Standing stocks of A. boreale were lower than Actinommidae spp. juvenile forms and A. 6 l. leptodermum at both stations, and mainly occurred in the PWW. In the surface 7 sediments of the Greenland, Iceland and Norwegian Seas, A. boreale is associated with 8 warm (Atlantic) water, whereas A. l. leptodermum seems to have broader environmental 9 tolerance, as it is associated with both the cold East Greenland Current and the warm 10 Norwegian Current water (Bjørklund et al., 1998). Other environmental factors such as 11 salinity, food availability, or seasonal differences of their growth stages due to the 12 sampling period might influence the standing stocks of A. boreale.

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## 5.3.3. Upper AW association

15 Ceratocyrtis histricosus occurred commonly in the upper AW (250-500 m) and 16 rarely in the PWW. This species is a species interpreted as being introduced from the 17 Norwegian Sea, most likely during the early Holocene, by the warm Atlantic water drifting through the Arctic Ocean (Kruglikova, 1999). Itaki et al. (2003) first noticed 18 19 that Ceratospyris histricosus had not been observed in the Canada Basin during the 20 1950s and 1960s and he pointed out that the common occurrence of this species in the 21Chukchi and Beaufort seas in 2000 might be an effect of the recent warming of the AIW. 22Itaki et al. (2003) also introduced that the temperature of the AIW in 1994 at the 23 Chukchi-Mendeleyev boundary was higher by at least 0.2°C than in the 1950s and 241960s, from Swift et al (1997). Differing from Itaki et al. (2003), we first found this 25 species in the PWW. According to McLaughlin et al. (2011), the mean temperature of 26 the PWW within the Canada Basin increased slightly (~0.05°C) from 2003 to 2007 and 27 then remained constant until 2010. According to Itaki et al. (2003), C. histricosus can survive in the temperature range of 0.5–4°C. Although our data on the temperature of 28 29 the PWW is apparently lower than the lower limit for survival of this species (Fig. 2), 30 the rare existence of this species in the PWW may be caused by unobserved warming in 31 the PWW or by appearance of other optimistic conditions for C. histricosus. However, 32 the warming in the AIW has already been recognized in 1994 (Swift et al., 1997) and a 33 warming in the PWW is also reported by McLaughlin et al. (2011), suggesting that the

- 1 recent warming of the PWW and AW might induce the expansion of the habitat of C.
- 2 histricosus into the PWW. It is not so much the effect of the temperature itself that is
- 3 causing the expanding distribution of C. histricosus, but the general temperature
- 4 increase indicates that larger volumes of warmer AW is entering the Arctic Ocean. The
- 5 increasing volumes of inflowing AW will therefore increase the chances for more exotic
- 6 radiolarians to reach further and further into the Arctic Ocean and the Chukchi Sea.
- Bjørklund et al. (2012) reported 98 tropical-subtropical radiolarian taxa in the area
- 8 north of Svalbard in the eastern Arctic Ocean. They stated that there are always pulses
- 9 of warm Atlantic water that do reach the Arctic Ocean, transporting warmer water fauna.
- We did not observe any tropical and subtropical radiolarian taxa in the western Arctic
- Ocean. However, future, continuous monitoring of the annual changes in the radiolarian
- 12 fauna, including C. histricosus, in the western Arctic Ocean might be able to pick up
- this type of signal.

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- 5.3.4. Lower AW association
- 16 Pseudodictyophimus plathycephalus, Plagiacanthidae gen. et sp. indet. (Pl. 8, Figs.
- 17 11-18), and Cycladophora davisiana were abundant in the cold and oxygenated lower
- AW at both stations. However, their distribution patterns in PWW and upper AW water
- masses were slightly different between Station 32 and Station 56 whereas temperature,
- salinity, and dissolved oxygen have similar values at both stations. Their standing
- 21 stocks might therefore reflect the influence of other variables than hydrographic
- 22 conditions alone. Pseudodictyophimus g. gracilipes is widely distributed in the World
- Ocean, and known to inhabit the surface layer at high latitudes, while living at greater
- depth at low latitudes (Ishitani and Takahashi, 2007; Ishitani et al., 2008). Itaki et al.
- 25 (2003) reported that the maximum depth P. g. gracilipes occurred at 0-50 m in the
- 26 Chukchi Sea and 25-50 m in the Beaufort Sea. However, in our results, P. g. gracilipes
- did not show any specific vertical distribution, and its standing stocks were low.

- 29 5.4. Seasonal and annual radiolarian flux
- 30 5.4.1. Radiolarian fauna and seasonal sea-ice concentration
- 31 Seasonal radiolarian fluxes at Station NAP were characterized by the high
- dominance of a few species and the changes of their ratios in the upper trap with the
- 33 seasonal changes in sea-ice concentration. Amphimelissa setosa adult and its juvenile

1 forms were dominant during the open-water season and around the beginning and the 2 end of ice-cover seasons, while the actinommids (Actinommidae spp. juvenile forms, 3 Actinomma l. leptodermum, Actinomma boreale) were dominant during the ice-cover 4 season (Fig. 5). These observations might explain the regional difference in the 5 radiolarian species distribution in the Arctic Ocean. Amphimelissa setosa were 6 dominant in Arctic marginal sea sediments (Iceland, Barents, and Chukchi Seas) where 7 sea-ice disappeared in the summer but Actinommidae were dominant in the central 8 Arctic Ocean (Nansen, Amundsen, and Makarov Basins) where the sea surface was 9 covered by sea-ice throughout the year (Bjørklund and Kruglikova, 2003). Zasko et al. 10 (2014) also reported that A. setosa was essentially absent in the plankton samples in the 11 central polar basins. The summer ice edge hosts well-grown ice algae and ice fauna 12 (Horner et al., 1992; Michel et al., 2002; Assmy et al., 2013) and its presence causes an 13 alternation between stable water masses and deep vertical mixing where the nutrients 14 are brought to the surface (Harrison and Cota, 1991), with both conditions being 15 favorable for primary productivity. Swanberg and Eide (1992) found that abundance of 16 A. setosa and its juveniles was correlated well with Chlorophyll a and phaeopigments 17 along the ice edge in summer in the Greenland Sea. Dolan et al. (2014), however, 18 reported that the abundance of A. setosa was not entirely related to high Chlorophyll a 19 with low sea-ice concentration as we have said in section 5.3.1. Therefore we 20 interpreted that cold and well mixed water mass based on summer ice edge and maybe 21also other ice fauna elements were essential for high reproduction and growth of A. 22setosa.

From the upper trap, a flux peak of *A. setosa* juvenile occurred at the end of the sea-ice season, and that the flux peak of adult *A. setosa* occurred at the beginning of the sea-ice season (Fig. 7). The time interval between these peaks might indicate that *A. setosa* has a three months life cycle. *Pseudodictyophimus clevei* also shows flux peaks during the beginning of the sea-ice season (November-December) (Fig. 7). These two species seem to prefer to live under a cold water mass with sea-ice formation. On the contrary, juvenile stages of actinommids were dominant during the ice-cover season (Fig. 5). Therefore, we interpreted the actinommids to be tolerant of oligotrophic and stratified cold water masses. Itaki and Bjørklund (2007) reported that reproduction could occur even at the juvenile stage in at least some actinommids since they frequently found conjoined juvenile Actinommidae skeletons in the Japan Sea

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1 sediments. Furthermore, the flux of Actinommidae spp. juvenile forms increased

2 towards the end of the sea-ice cover season, accompanied by an increase in downward

3 shortwave radiation (Fig. 5 and 7). This might indicate that Actinommidae spp. juvenile

4 form can feed on algae growing on the ice or other phytoplankton under the sea-ice.

5 Therefore, A. setosa and the juvenile actinommids might have different nutritional

6 niches.

This study showed that the productivity of radiolarians was high, but diversity was low, during summer season with low sea-ice concentration in the western Arctic Ocean (Fig. 5 and 6). In contrast, radiolarian fauna in the sediment trap set in the Okhotsk Sea showed high diversity during summer season (Okazaki et al., 2003). The maximum total radiolarian flux during the summer season around the sea-ice edge and the open water is characterized by high dominance of *A. setosa* (>90%) in our area. Such high dominance of a single species does not occur in the Okhotsk Sea, where the main nine taxa contributed with more than 60 % of the radiolarian assemblage (Okazaki et al., 2003). *Amphimelissa setosa*, which has a small and delicate siliceous skeleton, might respond to water mass conditions near summer ice edge both more directly and more rapidly. The contrast of seasonal diversity between these two areas was due to the difference of species composition and their response to water mass changes with low sea-ice.

Actinomma boreale, Spongotrochus glacialis, Joergensenium sp. A were probably related to food supply to the PWW during the sea-ice free season. Relatively higher fluxes of these three species in the upper trap in summer 2012 compared to summer 2011 might be due to an effect of the deeper mooring depth of the trap after October 2011 (Fig. 7 and S1). This might be caused by their vertical distribution patterns, as they are more abundant at depths lower than the first upper trap depth (about 180 m) (Fig. 3a). On the other hand, Ceratocyrtis histricosus and Tripodiscium gephyristes in the upper trap showed increase in their fluxes from May to September in summer 2012. The water temperature at the upper trap depth also increased during the same period (Fig. 7 and S1), we therefore interpreted their increase to be related to the mixing of nutrient and warm upper AW and lower PWW, rather than a decrease in sea ice concentrations due to their preference for the warm, upper AW.

1 Intensification of geostrophic currents on the periphery of Beaufort Gyre (Fig. 1) has 2 been reported in recent years (Nishino et al., 2011; McPhee, 2013). This intensification 3 is caused by increasing volume of water from sea-ice melt associated with the reduction 4 of arctic summer sea-ice and the river runoff to the basins (Proshutinsky et al., 2009; 5 Yamamoto-Kawai et al., 2008). The total radiolarian flux showed lower production 6 during summer (July-September) in 2012 than in 2011 in both the upper and, especially, 7 lower traps (Fig. 5). Most radiolarian taxa also showed lower flux during summer of 8 2012 (Fig. 7). On the other hand, fluxes of the actinommids (Actinommidae spp. 9 juvenile forms, Actinomma l. leptodermum, Actinomma boreale), possibly adapted to 10 cold and oligotrophic water, showed higher values during December 2011-September 11 2012 than during December 2010-September 2011. Actinommidae spp. juvenile forms 12 and A. l. leptodermum were most abundant in the depth interval of 0-100 m at Station 13 56 in the southwestern Canada Basin. Therefore, we interpreted these data to mean that 14 cold and oligotrophic water in the Canada Basin began to spread to Station NAP in the 15 Northwind Abyssal Plain from December 2011 and continued to affect the radiolarian 16 fluxes at least until September 2012. McLaughlin et al. (2011) reported that the position 17 of the center of the Beaufort Gyre shifted westwards and that the area under the 18 influence of the gyre spread northwards and westwards in recent years. Moreover, 19 high-resolution pan-Arctic Ocean model results also showed that the Beaufort Gyre 20 expanded by shifting its center from the Canada Basin interior to the Chukchi 21Borderland in 2012 compared with 2011, and the ocean current direction in the surface 22100 m layer switched northwestward to southwestward in December 2011 (E. Watanabe, 23 personal communication, 2014). Thus, recent intensification of Beaufort Gyre currents 24associated with sea-ice reduction, would have affected the surface water mass 25 conditions and as well as the ecological conditions in the western Arctic Ocean.

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## 5.4.3. Vertical and lateral transport

Flux peaks of total radiolarians in the lower trap are delayed by about two weeks in comparison to the upper trap (Fig. 5). Therefore, the sinking speed of the aggregated radiolarian particle flux between these depths were averaged to 74 m day<sup>-1</sup> during November-December 2010, 86 m day<sup>-1</sup> during July-August 2011, and 73 m day<sup>-1</sup> during November 2011. Watanabe et al. (2014) simulated movement of cold and warm eddies using a high-resolution pan-Arctic Ocean model, and suggested that the high total mass

flux during October-December 2010 at Station NAP, as we determined using sediment samples, was mainly due to the enhancement of the marine biological pump by an anti-cyclonic cold eddy. Shelf-break eddies induce the lateral transport of resuspended bottom sediments composed of old carbon, and enhance the biological pump (O'Brien et al., 2013; Watanabe et al., 2014). Actually, the passage of a cold eddy was observed as a cooling and a deepening of the moored trap depth in the corresponding period (Fig. S1). Amphimelissa setosa was the most dominant species (>90%) and showed the highest flux (13,840 specimens m<sup>-2</sup> day<sup>-1</sup>) during November 2010 in the upper trap. The flux of this species was about 3.500 specimens m<sup>-2</sup> dav<sup>-1</sup> higher and kept the highest value half a month longer than that in 2011. The cold eddy passage would transport a cold and well mixed water mass, conditions favorable for A. setosa. Therefore the cold eddy passage in addition to seasonal water mass variations with sea ice formation would enhance the high radiolarian flux.

Radiolarian fluxes in the lower trap were generally higher than in the upper trap except for May-September 2012 (Fig. 5). The extremely low fluxes in the lower trap during this interval might be due to a decrease of aggregate formation. The latter process, which helps rapid sinking of biogenic particles, would be suppressed by influx of oligotrophic surface water originating from the Beaufort Gyre in the Canada Basin. In the southwestern Canada Basin (Station 56), high standing stock of dead radiolarian specimens (Fig. 2) might indicate an inefficient biological pump in this area. In addition, fluxes of Actinommidae spp. juvenile forms were lower in the lower trap, in spite of their high abundance in the upper trap since December 2011. We speculate that the disappearance of fluxes of Actinommidae spp. juvenile forms in the lower trap might be due to lack of aggregate formation.

Higher abundance in the lower trap of species having a wider vertical distribution (*Pseudodictyophimus g. gracilipes*, *P. plathycephalus*) or intermediate to deep water distribution (*Ceratocyrtis histricosus*, *Tripodiscium gephyristes*, Plagiacanthidae gen. et sp. indet., and *Cycladophora davisiana*) might be attributed to the reproduction of these species at a depth level situated between the upper and lower traps. The seasonal changes in the fluxes of intermediate and deep dwellers to the lower trap would reflect the availability of food supply. The flux of *Pseudodictyophimus g. gracilipes*, *P. plathycephalus*, Plagiacanthidae gen. et sp. in det. and *Cycladophora davisiana* in the lower trap was high during July-August 2011. This probably indicates that decomposing

1 material from the primary production during the sea-ice free season was transported to 2 great depths and might also act as a substrate for bacterial growth, providing the deep 3 water radiolarians with sufficient food elements. We have no data to support this but in 4 the Chukchi Sea, moderately high rates of bacterial production at the end of the growing 5 season (July-August) have been found (Cota et al., 1996; Wheeler et al., 1996; Rich et 6 al., 1997). Most of the radiolarian species in the lower trap also peak during March 7 2011, a period of heavy ice cover and low downward shortwave radiation. In addition, 8 in the lower trap the flux peak during March in 2011 was made up of more than 80% of 9 A. setosa, a definite surface water species. However, during this period a similar peak 10 was not found in the upper trap. Therefore, the flux peaks during March 2011 could be 11 derived from some lateral advection at a depth lower than 180m or a re-suspension of 12 shelf sediments.

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- polycystine Radiolaria based on the 18s rDNA sequences of the Spumellarida and
- 24 the Nassellarida, Eur. J. Protistol., 41, 287–298, 2005.

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## 27 Table captions

- Table 1. Logistic and sample information for the vertical plankton tows for radiolarian
- standing stock (S. S.) at two stations during R/V Mirai Cruise MR13-06
- Table 2. Locations, mooring depths, standard sampling interval, and sampled duration
- of sediment trap station in the western Arctic Ocean. \*Details of the exact durations for
- and S4.
- Table 3. List of 51 radiolarian taxa encountered in the plankton tow and sediment trap

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## Supplement table captions

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- 5 tows at Station 32
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- Fig. 1. Map of the Chukchi and Beaufort Seas showing the locations of sediment trap
- 17 (solid triangle) and plankton tows (solid circles). Gray arrows indicate the cyclonic
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- 21 (b) in comparison to vertical profiles of temperature, salinity, dissolved oxygen, and
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- 33 Sea-ice concentration data are from Reynolds et al. (2002)

- 1 (http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn SmithOIv2/). (b)
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Fig. S1. Moored trap depth and the water temperature in the upper trap.

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- 32 Scale bar= 100 µm for all figures.

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- same specimen. NAP10t Deep #12. 15, 16. Plagiacanthidae gen. et sp. indet., same
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- 14 (Cleve, 1899), same specimen. NAP10t Deep #14. 42–43. *Protocystis harstoni* (Murray,
- 15 1885), same specimen. NAP10t Deep #18.
- 16 Scale bar= 100 μm for all figures.

Table 1. Logistic and sample information for the vertical plankton tows for radiolarian standing stock (S. S.) at two stations during R/V Mirai Cruise MR13-06

Station ID		Sampling	Depth	Flow	Aliquot	Living	Dead	Total
		time	interval	water mass	size	radiolarian	radiolarian	radiolarian
		(UTC)	(m)	(m3)		S. S. (count)	S. S. (count)	S. S. (count)
Station 32	74°32' N, 161°54'W	1:24	0-100	20.4	1/4	247 (1257)	75 (381)	322 (1638)
		1:22	100-250	27.2	1/4	96 (654)	116 (790)	212 (1444)
Date	09 Sep 2013	1:18	250-500	39.7	1/2	11 (215)	20 (397)	31 (612)
		1:10	500-1000	79.3	1/2	12 (462)	17 (665)	29 (1127)
Station 56	73°48' N, 159°59'W	17:36	0-100	15.8	1/4	499 (1968)	677 (2671)	1176 (4639)
		17:34	100-250	23.8	1/2	265 (3156)	480 (5711)	745 (8867)
Date	27 Sep 2013	17:30	250-500	40.8	1/2	55 (1125)	276 (5627)	331 (6752)
		17:22	500-1000	81.8	1/2	25 (1034)	83 (3381)	108 (4415)

Table 2. Locations, mooring depths, standard sampling interval, and sampled duration of sediment trap station in the western Arctic Ocean

Trap station	Latitude	Longitude	Water depth Mooring depth (m)		Standard sampli Sampled interval		
NAP10t	75°00' N	162°00'W	1975	184 (upper), 1300 (lower)	10-15	4 October 2010–28 September 2011	
NAP11t	75°00' N	162°00'W	1975	260 (upper), 1360 (lower)	10-15	4 October 2011–18 September 2012	

<sup>\*</sup> Details of the exact durations for each sample are shown in tables S3 and S4.

Table 3. List of 51 radiolarian taxa encountered in the plankton tow and sediment trap samples

n	Taxa	References				
Phylum	Rhizaria, Cavalier-Smith (2002)					
Class	Radiolaria, Müller (1858)					
Sub-class Order	S Polycystina, Ehrenberg (1838); emend. Riedel (1967) Spumellaria, Ehrenberg (1875)					
Family	Actinommidae, Haeckel (1862); emend. Riedel (1967)					
-	Actinomma boreale, Cleve (1899)	Cortese and Bjørklund (1998), Plate 1, Figs. 1–18				
	Actinomma leptodermum leptodermum, Jørgensen (1900)	Cortese and Bjørklund (1998), Plate 2, Figs. 1–14				
	Actinomma morphogroup A					
	Actinomma leptodermum, Jørgensen (1900); longispinum, Cortese and Bjørklund (1998)	Cortese and Bjørklund (1998), Plate 2, Figs. 15-22				
	Actinomma leptodermum longispinum juvenile					
	Actinommidae spp. juvenile forms					
	Actinomma turidae, Kruglikova and Bjørklund (2009)	Kruglikova et al. (2009), Plate 5, Figs. 1–35, Plate 6, Figs. 1–26				
	Actinomma morphogroup B					
	Actinomma morphogroup B juvenile *Drymyomma elegans, Jørgensen (1900)	Delven et al. (2014). Ploto 1. Figs. 5.7				
	*Actinomma friedrichdreyeri, Burridge, Bjørklund and Kruglikova (2013)	Dolven et al. (2014), Plate 1, Figs. 5-7 Burridge et al. (2013), Plate 6, Figs. 7-15, Plate 7, Figs. 3-15				
	Arachnosphaera dichotoma, Jørgensen (1900)	Dolven et al. (2014), Plate 1, Figs. 1-4				
Family	Litheliidae, Haeckel (1862)	Doiven et al. (2011), 1 late 1, 1 155. 1				
	* Streblacantha circumtexta? Jørgensen (1905)					
Family	Spongodiscidae, Haeckel (1862)					
	Spongotrochus glacialis, Popofsky (1908)	Bjørklund et al. (1998), Plate I, Fig. 3				
	Stylodictya sp.					
Order	Entactinaria, Kozur and Mostler (1982)					
	Cleveiplegma boreale, Cleve (1899)	Dumitrica (2013), Plate 1, Figs. 1-9				
	Joergensenium sp. A					
0.1	Joergensenium sp. B					
Order	Nassellaria, Ehrenberg (1875) Sethophormididae, Haeckel (1881); emend. Petrushevskaya (1971)					
Family	Enneaphormis rotula, Haeckel (1881)	Petrushevskaya (1971), Fig. 31, I-III				
	Enneaphormis rotata, Hacckel (1887)	Petrushevskaya (1971), Fig. 31, I-III				
	Protoscenium simplex, Cleve (1899)	Bjørklund et al. (2014), Plate 9, Figs. 15-17				
Family	Plagiacanthidae, Hertwig (1879); emend. Petrushevskaya (1971)	_,				
	*Arachnocorys umbellifera, Haeckel (1862)	Welling (1996), Plate 14, Figs. 24-27				
	Ceratocyrtis histricosus, Jørgensen (1905)	Petrushevskaya (1971), Fig. 52, II–IV				
	Ceratocyrtis galeus, Cleve (1899)	Bjørklund et al. (2014), Plate 8, Figs. 1 and 2				
	*Cladoscenium tricolpium, Haeckel (1887)	Bjørklund (1976), Plate 7, Figs. 5-8				
	Cladoscenium tricolpium?	D . 1 . 1 . (10E4) E: . EE .				
	Lophophaena clevei, Petrushevskaya (1971)	Petrushevskaya (1971), Fig. 57, I				
	Phormacantha hystrix, Jørgensen (1900) *Peridium longispinum?, Jørgensen (1900)	Dolven et al. (2014), Plate 6, Figs. 20-24 Bjørklund et al. (1998), Plate II, Figs. 26 and 27				
	Plectacantha oikiskos, Jørgensen (1905)	Dolven et al. (2014), Plate 7, Figs. 7-9				
	Pseudodictyophimus clevei, Jørgensen (1900)	Bjørklund et al. (2014), Plate 9, Figs. 5-7				
	Pseudodictyophimus gracilipes gracilipes, Bailey (1856)	Bjørklund et al. (1998), Plate II, Figs. 7 and 8				
	Pseudodictyophimus spp. juvenile forms	, , , , , , , , , , , , , , , , , , , ,				
	Pseudiodictyophimus gracilipes, Bailey (1856); bicornis, Ehrenberg (1862)	Bjørklund and Kruglikova (2003), Plate V, Figs. 16-19				
	Pseudodictyophimus gracilipes, Bailey (1856); multispinus, Bernstein (1934)	Bjørklund and Kruglikova (2003), Plate V, Figs. 11-13				
	Pseudodictyophimus plathycephalus, Haeckel (1887)	Bjørklund and Kruglikova (2003), Plate V, Figs. 1-5				
	Tetraplecta pinigera, Haeckel (1887)	Takahashi (1991), Plate. 24, Figs. 1-5				
	Tripodiscium (Tholospyris) gephyristes, Hülsemann (1963)	Bjørklund et al. (1998), Plate II, Figs. 20 and 21				
F:1	Plagiacanthidae gen. et sp. indet.					
Family	Eucyrtidiidae, Ehrenberg (1847); emend. Petrushevskaya (1971) Artostrobus annulatus, Bailey (1856)	Digwlyhand et al. (2014). Plate 0. Figs. 1.4				
	Artostrobus joergenseni, Petrushevskaya (1967)	Bjørklund et al. (2014), Plate 9, Figs. 1-4 Petrushevskaya (1971), Fig. 92, VIII–IX				
	*Cornutella stylophaena, Ehrenberg (1854)	Petrushevskaya (1967), Fig. 52, VIII–IX				
	*Cornutella longiseta, Ehreneberg (1854)	Petrushevskaya (1967), Fig. 62, I–II, Fig. 58, VIII				
	Cycladophora davisiana, Ehrenberg (1862)	Bjørklund et al. (1998), Plate II, Figs. 1 and 6				
	Lithocampe platycephala, Ehrenberg (1873)	Bjørklund et al. (1998), Plate II, Figs. 23–25				
	Lithocampe aff. furcaspiculata, Popofsky (1908)	Petrushevskaya (1967), Fig. 74, I–IV				
	Sethoconus tabulatus, Ehrenberg (1873)	Bjørklund et al. (2014), Plate 9, Figs. 10 and 11				
Family	Cannobotryidae, Haeckel (1881); emend. Riedel (1967)					
	Amphimelissa setosa, Cleve (1899)	Bjørklund et al. (1998), Plate II, Figs. 30–33				
CI.	Amphimelissa setosa juvenile					
Class	Cercozoa, Cavalier-Smith (1998); emend. Adl et al. (2005)					
Order	Phaeodaria, Haeckel (1879) Lirella melo, Cleve (1899)	Digglyland at al. (2014). Plata 11. Figs. 5 and 6				
	Protocystis harstoni, Murray (1885)	Bjørklund et al. (2014), Plate 11, Figs. 5 and 6 Takahashi and Honjo (1981), Plate 11, Fig. 11				
	1 roweysus nursion, municipy (1005)	rakanasin ana monjo (1701), mate 11, mg. 11				

All taxa are found in the trap, and \* refer to taxa found in trap only.

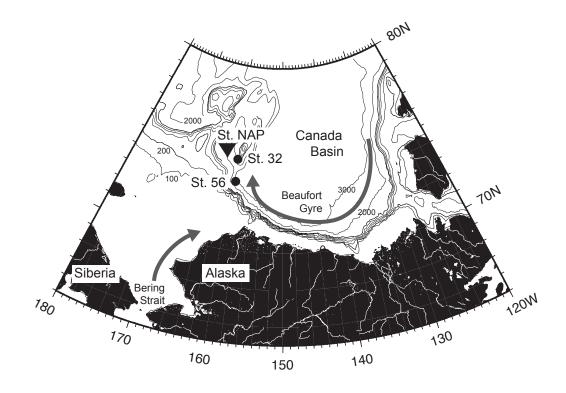


Fig. 1

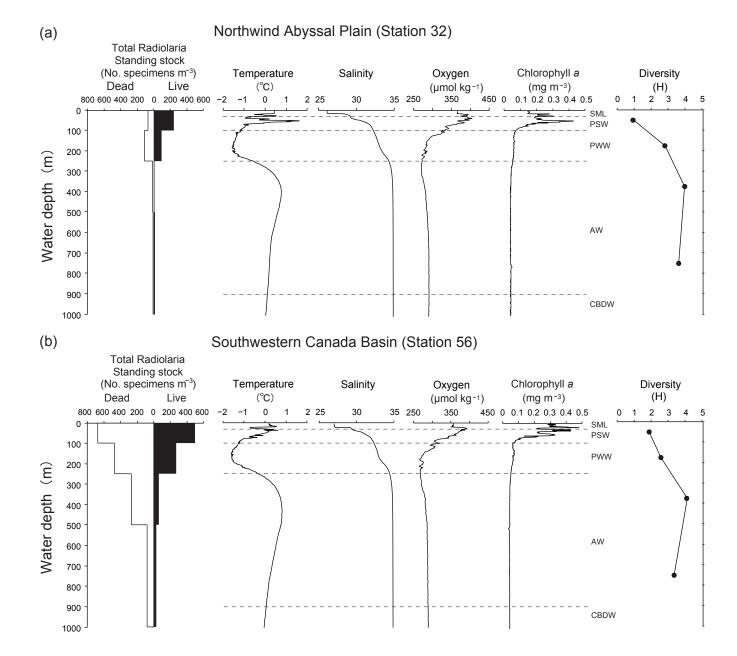


Fig. 2

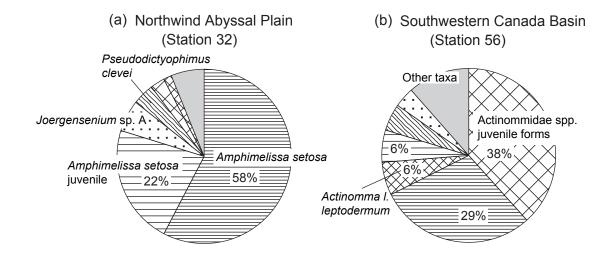


Fig. 3

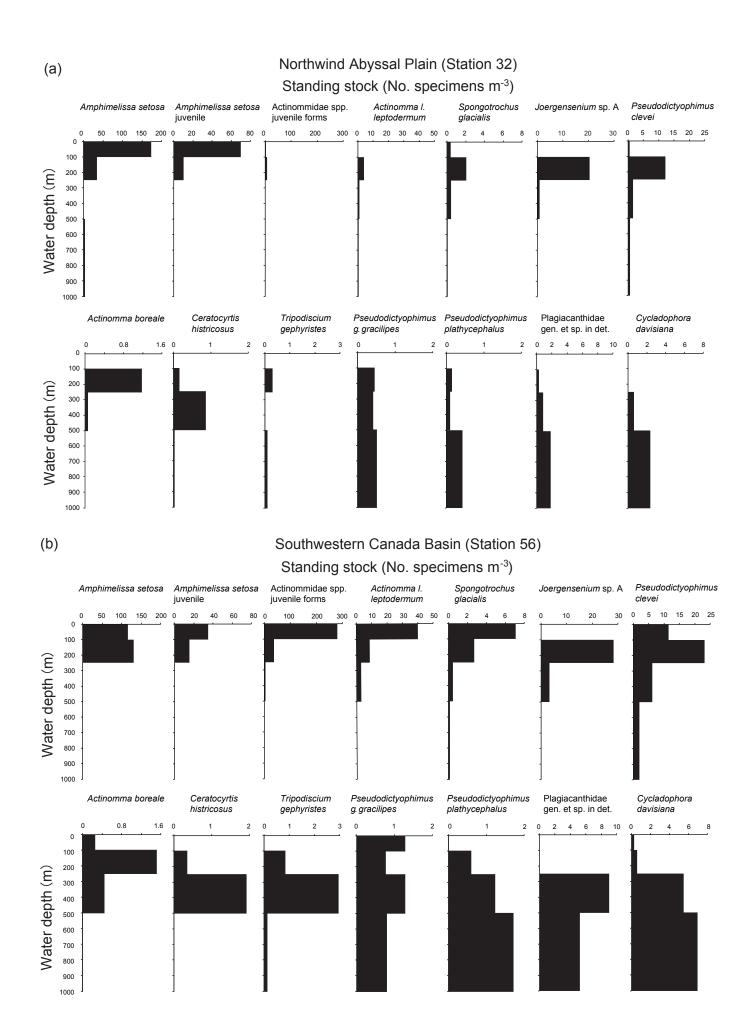


Fig. 4

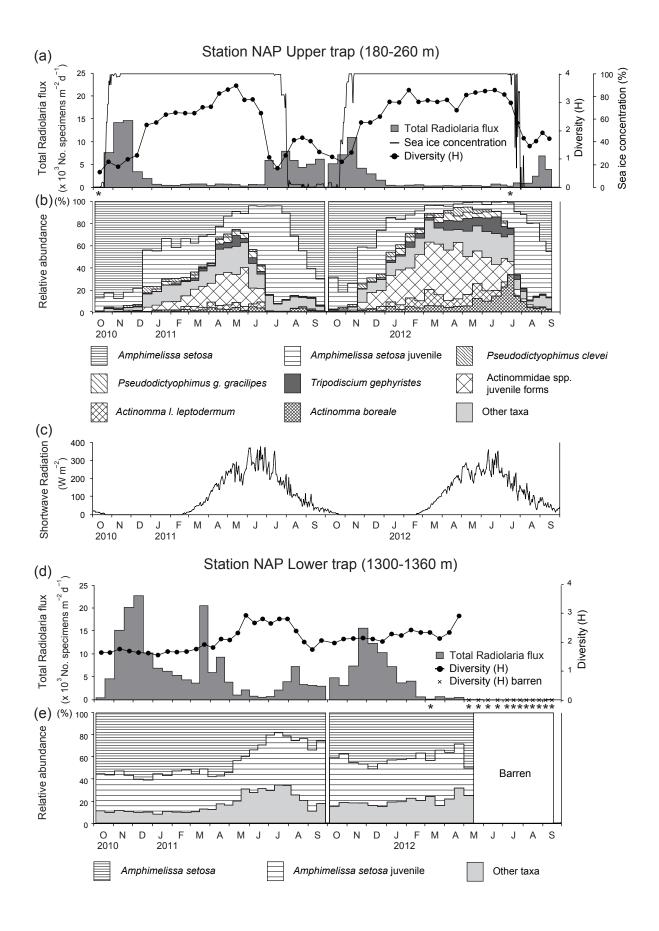


Fig. 5

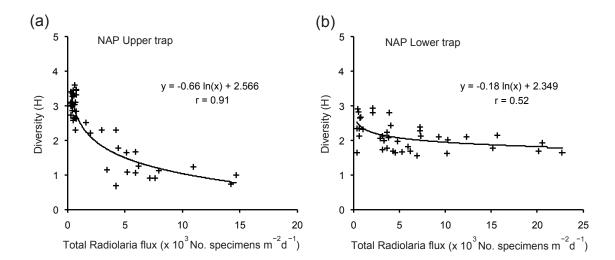


Fig. 6

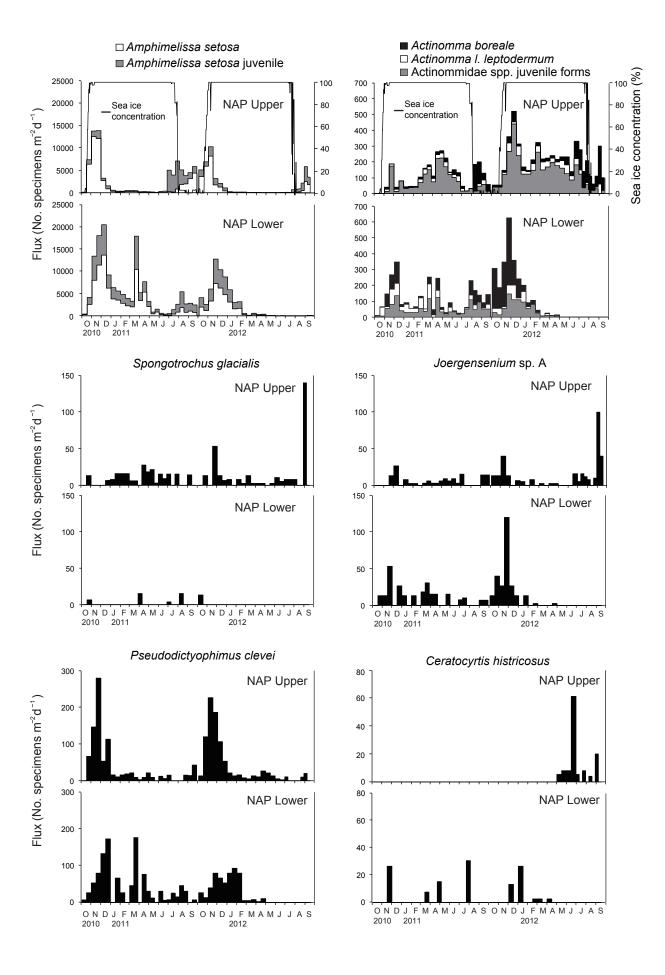


Fig. 7

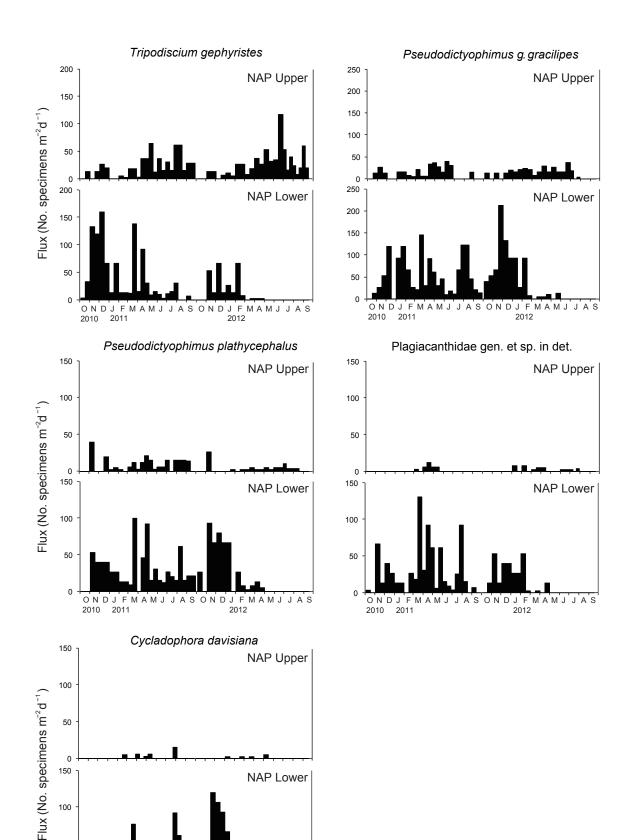


Fig. 7 (continued)

ONDJFMAMJJASONDJFMAMJJAS 2010 2011 2012

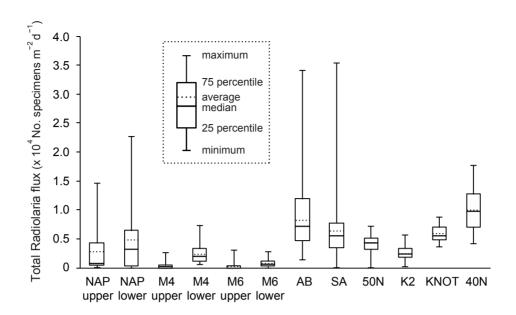


Fig. 8

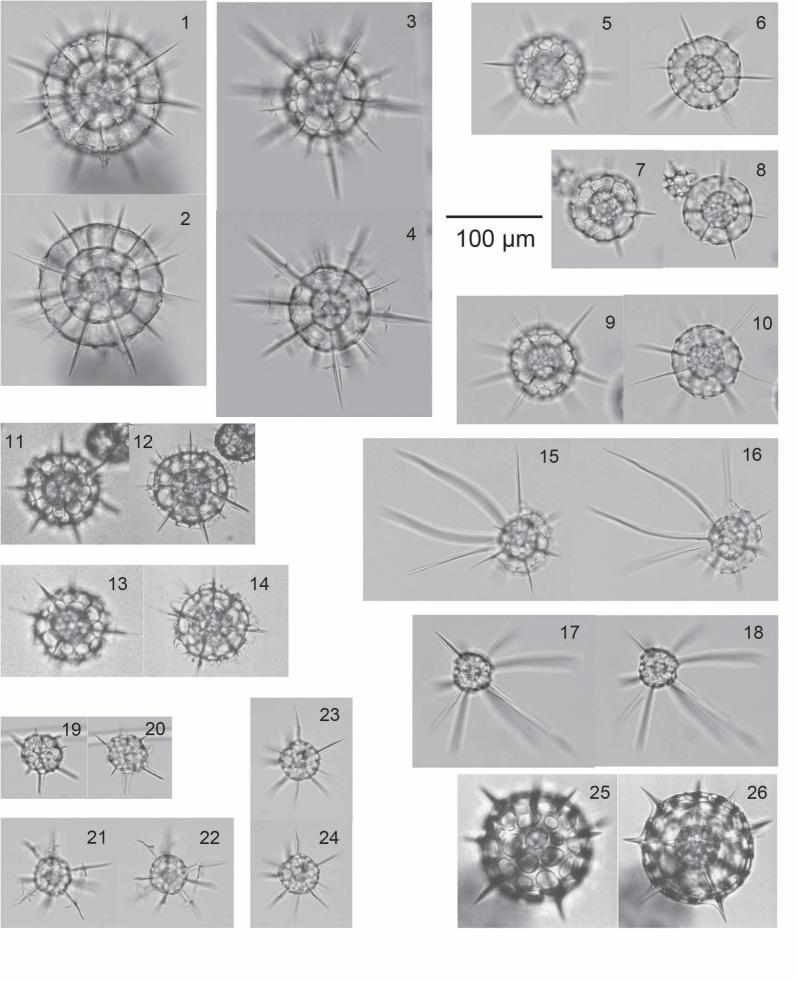


Plate 1

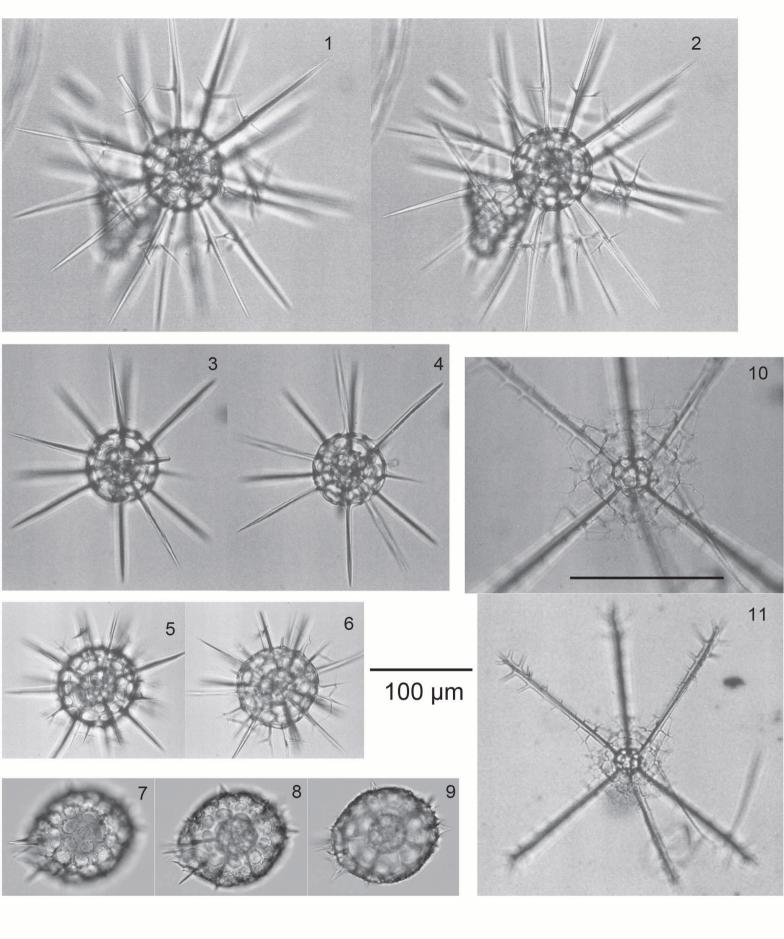


Plate 2

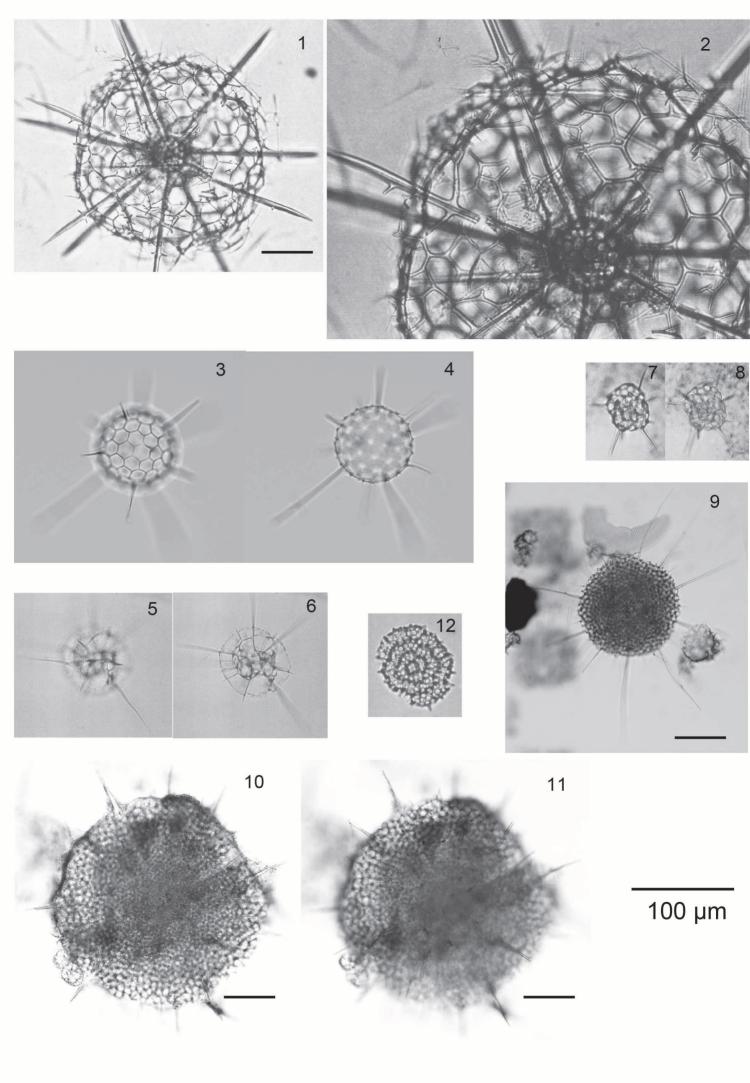


Plate 3

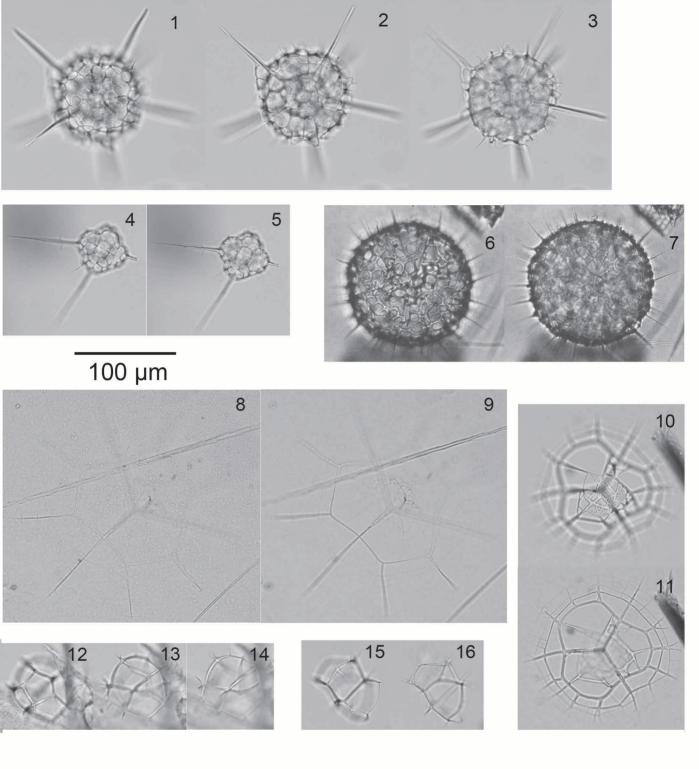


Plate 4

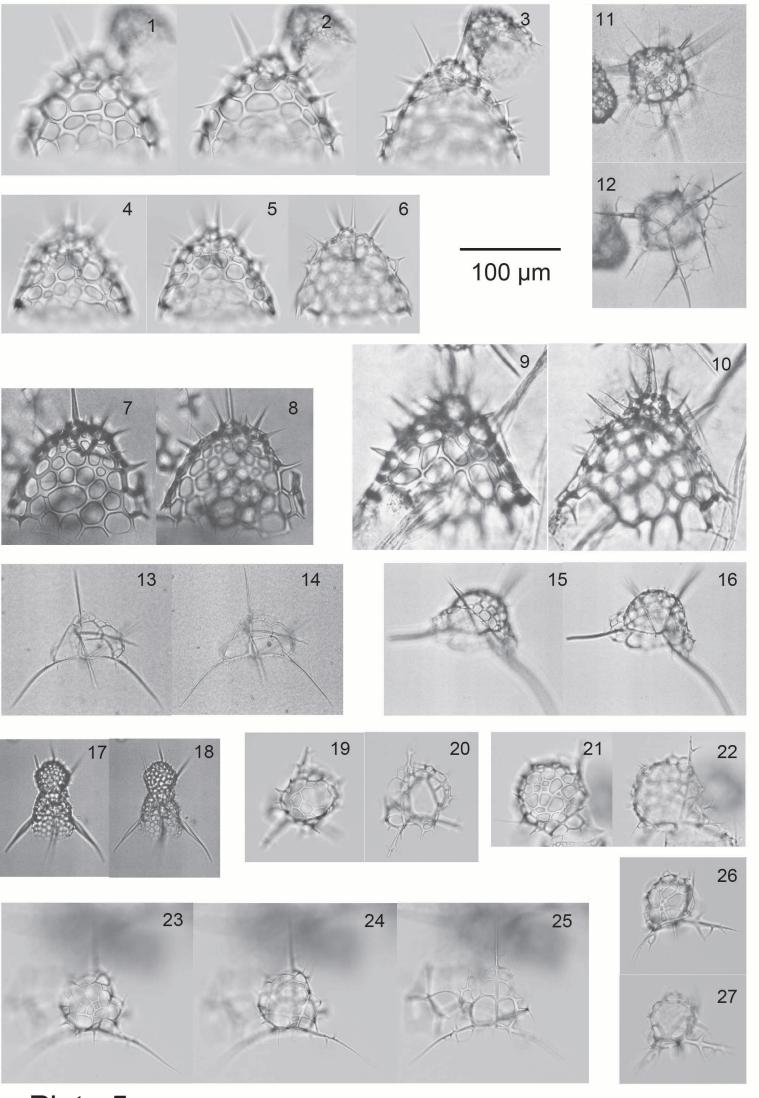


Plate 5

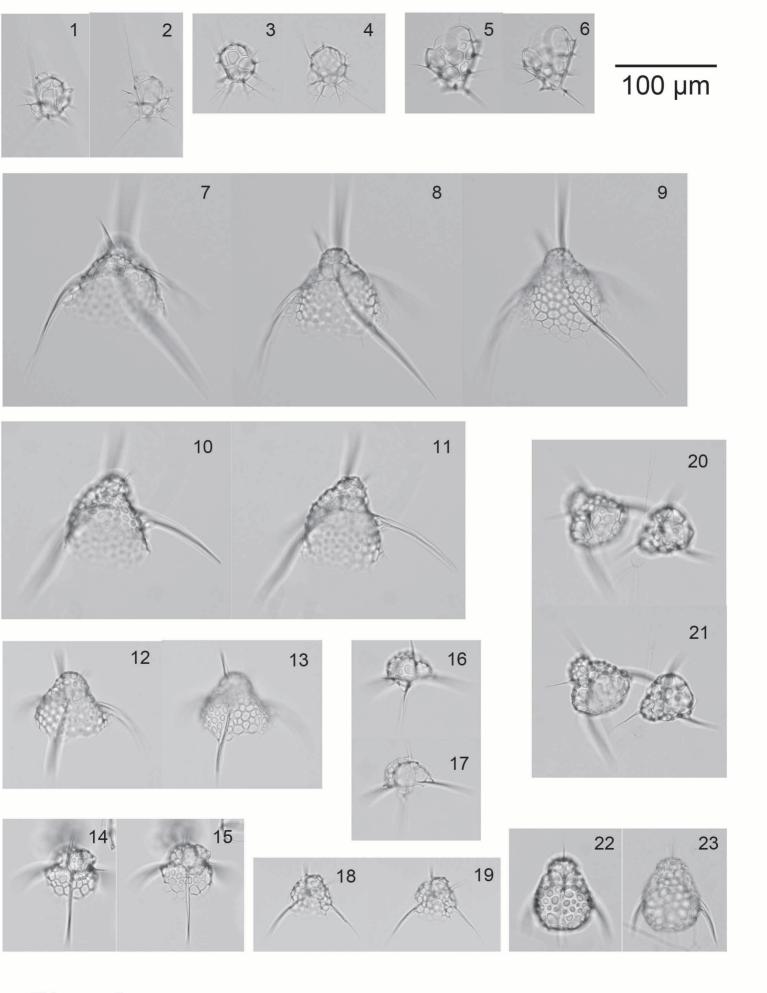


Plate 6

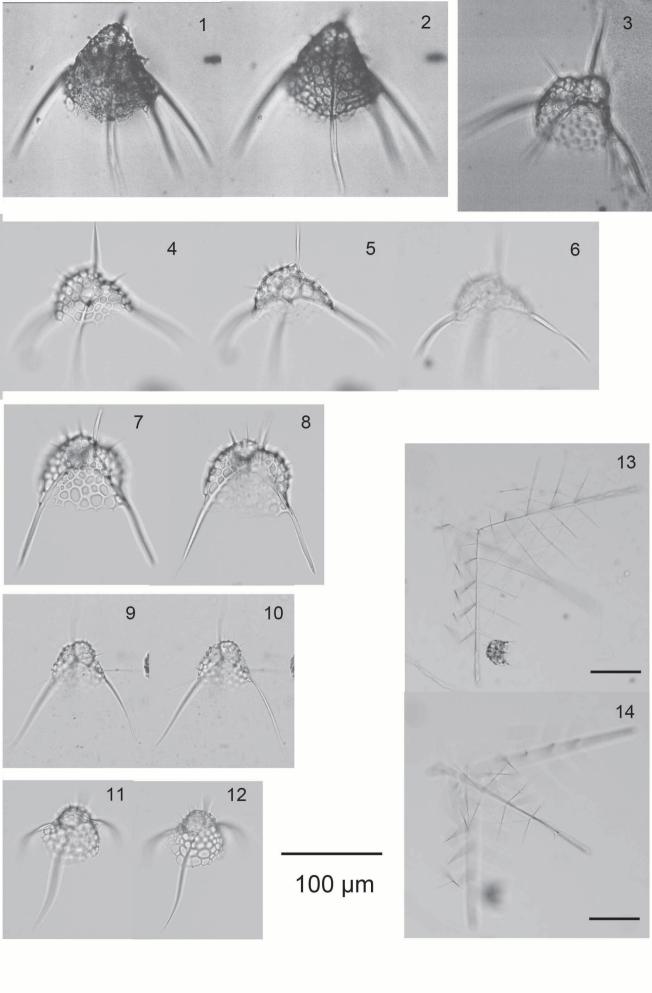


Plate 7

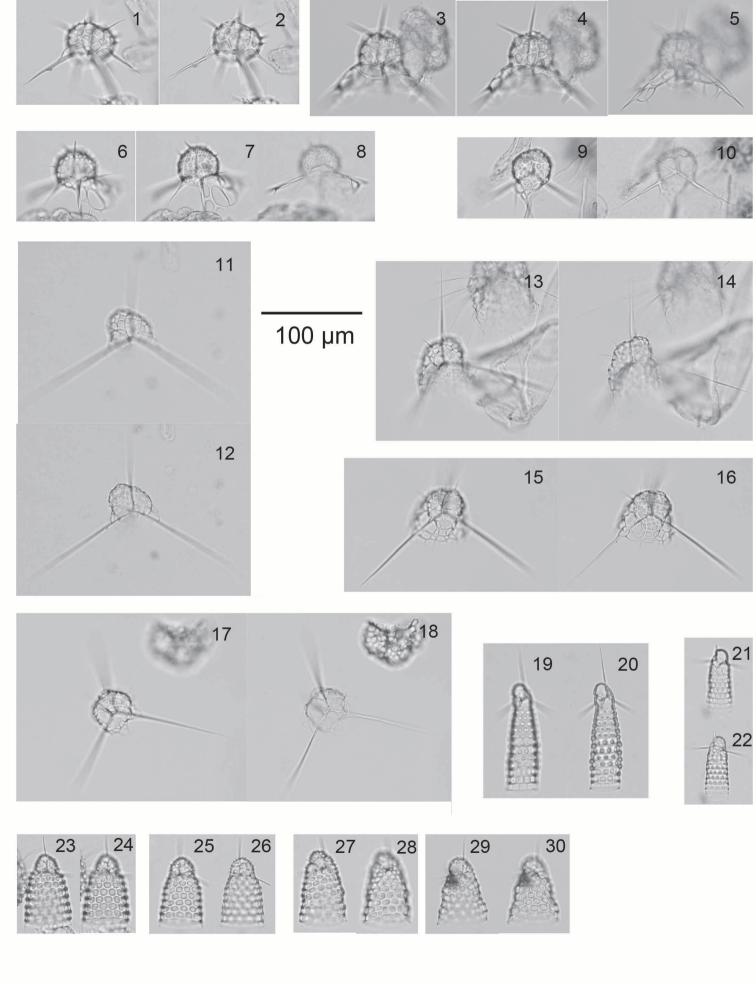


Plate 8

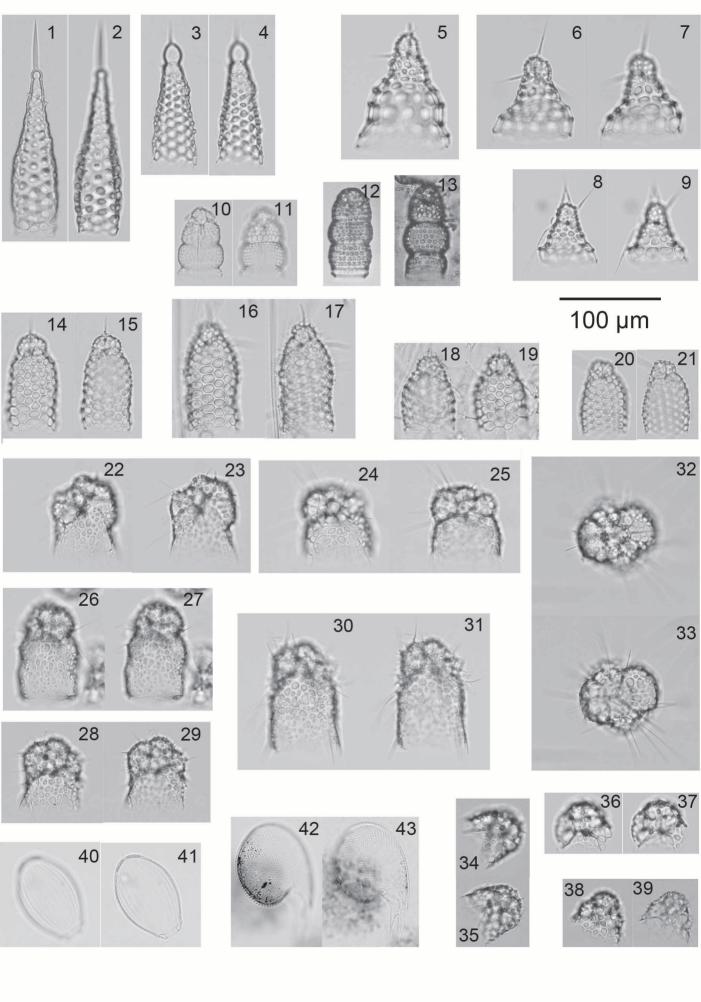


Plate 9