New evaluation of species-specific biogenic silica flux of radiolarians (Rhizaria) in the western Arctic Ocean using microfocus X-ray computed tomography

Takahito Ikenoue, Katsunori Kimoto, Yuiko Nakamura, Kjell R. Bjørklund, Naoki Kuramoto, Masaaki Ueki, Eiji Watanabe, Motoyo Itoh, Shigeto Nishino, Takashi Kikuchi, Naoko Harada, Motoyo Ito, Kjell R. Bjørklund, and Katsunori Kimoto

Abstract

We studied time-series fluxes of radiolarian particles collected by two sediment traps deployed at the eastern (Sta. NAP12t) and western (Sta. CAP12t) sides of the Chukchi Borderland in the Chukchi Sea from 04 October 2012 to 18 September 2013. In order to elucidate the contribution of radiolarian skeletons to the biogenic silica flux, a three-dimensional (3D) imaging technique using microfocus X-ray computed tomography (MXCT) was applied to radiolarian siliceous skeletons. We calculated volumes of individual radiolarian skeletons accurately using a 3D model of them, thereby estimating the mass of silica for each radiolarian species. The time-series fluxes of radiolarian abundance were combined with the mass of radiolarian silica and were transformed to estimate fluxes of radiolarian silica. As a result, we found that the main carrier of radiolarian silica in the western Arctic Ocean was represented by only two species; that is, Amphimelissa setosa (averages: 55.2 wt% at Sta. NAP12t, 70.8 wt% at Sta. CAP12t) and Spongotorchus glacialis (averages: 36.7 wt% at Sta. NAP12t, 23.2 wt% at Sta. CAP12t). The total radiolarian silica flux was usually higher in the eastern side than that in the western side of the Chukchi Borderland. The contribution of radiolarian silica to the biogenic silica flux was less than 10 wt % in general during the sampling duration, but occasionally reached 19.6–34.8 wt% during the open water season. This suggests that not only diatoms but also radiolarians make a significant contribution in driving the silica cycle in the Arctic Ocean.

Microplankton are recognized as a key component of pelagic marine food webs (Calbet and Landry 2004). Microplankton

*Correspondence: ikenoue@kaiseiken.or.jp

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Additional Supporting Information may be found in the online version of this article.

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such as diatoms, silicoflagellates, phaeodarians, and radiolarians build up their skeletons by taking up silicic acid directly from seawater. The transfer of silicic acid from the marine hydrosphere to the biosphere initiates the marine biological cycle of Si; it is also a way to link the cycle of this element to that of carbon. Silicon exists in the ocean as silicate, which is an important component of the marine biogenic matter that accumulates in coastal and abyssal sediments (Sarmiento and Gruber 2006; Tréguer et al. 2021). Among microplankton, the importance of silicifying rhizarians to biogeochemical cycles has been suggested in previous studies (e.g., Takahashi et al. 1983; Bernstein et al. 1990; Takahashi 1991), but it has become re-recognized more quantitatively by recent advanced techniques (Biard et al. 2018; Ikenoue et al. 2019a; Llopis Monferrer et al. 2020). The major taxa of silicifying rhizarians are represented by the Radiolaria (Retaria) and Phaeodaria (Cercozoa, Thecofilosea) (Adl et al. 2019) and their skeletons are composed of amorphous silica SiO2·nH2O, which is referred to as biogenic silica or biogenic opal (Anderson 1983).
Radiolaria is a group of marine eukaryotic protists that includes the following five orders: Colloclaria, Nassellaria, Spumellaria, Acantharia, and Taxopodia (Suzuki and Not 2015). In this study, we have excluded the order Acantharia as they have strontium sulfate skeletons, as well as Colloclaria and Taxopodia that normally do not possess a skeleton, or only have loose siliceous spines. Our study only includes Nassellaria and Spumellaria that typically have a solid skeleton of SiO₂ and these two are the most important for the silica cycle among the Rhizaria in the western Arctic Ocean. To facilitate the reading of the text, we therefore use Radiolaria, or radiolarians, to encompass the Nassellaria and Spumellaria groups.

Radiolarian skeletons in sinking particles may concentrate at different depths and also act as ballast, carrying them to deeper waters, (Turner 2015) and are well preserved in marine sediments, either as complete skeletons, fragments, or particles. The biogenic silica in sinking particle flux is the sum of the specific contributions from diatoms, silicoflagellates, phaeodarians, and radiolarians, but the contribution of each estimated so far is preliminary. To better understand the global silicon and carbon cycles, it is important to elucidate the composition of the biogenic silica, since the flux and fate of biogenic silica and organic carbon differs depending on the taxonomic group (Takahashi 1991). However, there have been only a few studies to evaluate the amount of biogenic silica due to radiolarians (e.g., Takahashi 1991; Jacot Des Combes and Abelmann 2009; Llopis Monferrer et al. 2020). These authors used different evaluation methods, and it is therefore difficult to properly compare and quantify the amount of biogenic silica. There are a few ways to estimate the values of biogenic silica content of individual specimens. One way is by chemical analysis as performed by Llopis Monferrer et al. (2020, 2021), another way is by mass measurement of only a few large (> 400 μm) radiolarian species using an electronic precision balance and then take the average (Takahashi 1991) or using simple radiolarian skeleton models that combine geometrical shapes such as spheres, cones, cylinders, ellipsoids, and cuboids (Jacot Des Combes and Abelmann 2009). In fact, since the skeletons of radiolarians have a very complicated structure, they cannot be exactly reproduced with a simple geometric model. Also in many cases, the mass of a particular species of radiolarians is lighter than the limit of the world's highest precision electronic balance (Resolution: 0.1 μg), so the mass of such a radiolarian cannot be measured by mass. It has therefore been difficult until now to quantify the amount of silica of radiolarians.

Microfocus X-ray computed tomography (MXCT) is a non-destructive three-dimensional (3D) imaging technique. Recent development of micro-CT technology has made it possible to construct detailed 3D models of radiolarian skeletons, and therefore MXCT also enables volume estimates of the radiolarian skeletons. In a previous study, we have shown that MXCT is useful in representing 3D models of the radiolarian skeletons (Ikenoue et al. 2016). However, the volume of the 3D model of the radiolarian skeleton changes significantly depending on the boundary pixel value between the radiolarian skeleton and the air even for the same sample. In addition, boundary values also differ between specimens. Therefore, in this study, we have developed a method for determining the boundary pixel value for more accurate quantification of the volume of radiolarian skeletons.

The densities of the radiolarian fossils are known to be about 1.7–2.0 g cm⁻³ measured by the sink-float density determination (Hurd and Theyer 1977). However, it is unclear whether those silica density values can be applied to the modern radiolarian skeletons, as their density has never been accurately determined. Therefore, we estimated the density of a recently living radiolarian skeleton (Spongolithus glacialis), by calculating the volume of the large (100–485 μm, Hülseman 1963, based on 90 measurements) radiolarian skeleton by MXCT imaging and accurately measuring the mass with an electronic balance.

In the Pacific sector of the Arctic Ocean, a drastic reduction in the summer sea-ice extent has been observed (Stroeve et al. 2007; Comiso et al. 2008; Markus et al. 2009). Such sea-ice reduction is closely related to significant warming, freshening, and ocean acidification in the Arctic Ocean (Steele et al. 2008; Yamamoto-Kawai et al. 2009a, 2009b); and these changes are matters of concern for their possible effects on marine ecosystems and biogeochemical cycles of biophilic elements such as silicon (Grebmeier et al. 2010; Wassmann et al. 2011; Harada 2016).

We focus on the Chukchi Sea, where the most remarkable retreat of summer sea ice has been observed (Stroeve et al. 2012). The upper water column in the Chukchi Sea can be affected by three characteristic water types: Pacific water, East Siberian Shelf water, and Beaufort Gyre water (Fig. 1) (Nishino et al. 2011). In the Northwind Abyssal Plain of the eastern Chukchi Borderland, shelf waters entrained by surface eddies are derived via the Chukchi Sea shelf break. These surface eddies and the influx of oligotrophic water originating from the oceanic Beaufort Gyre (which are related to sea-ice reduction) occasionally have a major impact on the components and productivity of siliceous microplankton (radiolarians and diatoms) (Watanabe et al. 2014; Ikenoue et al. 2015; Onodera et al. 2015a). The biogenic silica collected in the Northwind Abyssal Plain mainly consists of diatoms and radiolarians based on microscopic observations (Ikenoue et al. 2015; Onodera et al. 2015a). Other siliceous skeletons (silicoflagellate skeletons, siliceous endoskeleton of the dinoflagellate genus Actiniscus, chrysophyte cysts, ehridian flagellates, and palmales) and phaeodarians were minor components in the same trap samples (Ikenoue et al. 2015; Onodera et al. 2015b). However, in the Chukchi Abyssal Plain of the western Chukchi Borderland, the quantitative and seasonal variation of microplankton has not been reported, previously.

In this paper, we report on biogenic silica fluxes due to radiolarians in the western Arctic Ocean based on the samples collected by two sediment traps moored in the
Chukchi Borderland from October 2012 to September 2013. Our study represents a new approach to quantify species-specific biogenic silica flux using the MXCT technique. We constructed skeletal models for each radiolarian species by using our MXCT technique. Here, based on these volume estimates, we are able to calculate a quantitative estimate of the biogenic silica flux due to radiolarians.

Materials and methods

Sediment trap samples

Sinking particles were collected by a time-series sediment trap (SMD26S-6000, open mouth area 0.5 m², Nichiyu Giken Kogyo, Co. Ltd.) at Sta. NAP12t on the Northwind Abyssal Plain (75.00°N, 162.00°W, seafloor depth of 1975 m) and at Sta. CAP12t on the continental slope adjacent to the Chukchi Abyssal Plain (75.21°N, 172.55°W, seafloor depth of 447 m) from 04 October 2012 to 18 September 2013 (Fig. 1). The traps at Stas. NAP12t and CAP12t were deployed at 260 and 240 m, respectively, and they collected sinking particles with 26 bottles rotating at intervals of 10–15 d. To preserve the trapped particles, each sample bottle was filled with pre-filtered deep-sea water with 4% pH-neutralized formalin before the sediment trap deployment. At Sta. CAP12t, temperature and salinity at 95 m were also measured hourly by a CTD Sensor (A7CT-USB, JFE Advantec) during the sampling periods. The mooring deployment and recoveries were operated by the Canadian Coast Guard Ship (CCGS) Amundsen and the research vessel Mirai of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC).

Time-series data of shortwave radiation and sea-ice concentration around Stas. NAP12t and CAP12t during the mooring period were obtained from the National Centers for Environmental Prediction (NCEP) data/Climate Forecast System Version 2 (CFSv2) data (Saha et al. 2014).

Chemical analysis of sinking particles

Sinking particles collected by the sediment traps were sieved through a 1-mm mesh to remove large swimmers, and the fine particle fraction (less than 1 mm) was equally split into appropriate aliquots for each analysis using a rotary splitter (1/10 for chemical analysis, and 1/100 for enumeration of radiolarian taxa). Biogenic silica of sinking particles was measured by a modified alkaline leaching method of Mortlock and Froelich (1989). Particulate organic and total carbon and nitrogen in the sinking particles were measured by a CHN Analyzer (NCS2500, Thermo Ques). Organic matter (OM) content was estimated by “Redfield ratio” (Redfield et al. 1963) and organic carbon content as described in Honda et al. (2002).
Inorganic carbon content was estimated by the difference of total carbon and organic carbon contents. CaCO₃ was calculated by multiplying inorganic carbon content by 100/12. The lithogenic material (LM) concentration was estimated using the following formula:

$$\text{LM (wt%) = Total mass} \times \text{OM} \times \text{CaCO}_3 \times \text{Biogenic silica}$$

Details of chemical analysis of sinking particles are described in Onodera et al. (2021).

**Enumeration of radiolarian taxa**

Sediment trap sample slides for light microscope observation were prepared using the methods described by Ikenoue et al. (2015). We counted all radiolarian skeletons from the 45 μm–1 mm fraction encountered on each slide with an Olympus BX43 transmitted light microscope at 200x or 400x magnification. The radiolarian flux (no. of specimens m⁻² d⁻¹) was calculated from count data using the following formula:

$$\text{Radiolarian flux} = \frac{N \times V}{S/D}$$

where \( N \) is the counted number of radiolarians, \( V \) the aliquot size, \( S \) the aperture area of the sediment trap (0.5 m²), and \( D \) the sampling interval (days). All skeletal fragments that could be allocated to a species, or a group of species, were included in our counts. Since skeletal fragments that cannot be identified at the species level were also counted as Spumellarida indet. or Nassellariida indet., the number of skeletal fragments that could not be counted is estimated to be negligible in 45 μm–1 mm fraction. Radiolarians from the < 45 μm fraction were not included in this study. Therefore, it should be noted that if there is a large amount of < 45 μm radiolarian debris in the sample, it may be underestimated.

We defined adult and juvenile forms of Actinommaidae, Amphimelissa setosa, and Pseudodictyophimus according to Ikenoue et al. (2015) as follows: the two-shelled forms of Actinommaidae were defined as juvenile. To be consistent, the three- and four-shelled forms were defined as adult. Actinommaidae spp. juvenile forms are mostly two-shelled juvenile forms of *Actinomma leptodermum* and *Actinomma boreale*, making it impossible to separate between the two. For the *A. setosa*, those with only a cephals were defined as juveniles. Those with a well-developed cephalis, and with a barely or well-developed thorax, were defined as adult. Pseudodictyophimus spp. juvenile forms were defined as *Pseudodictyophimus* with only a small cephalis and a short three-bladed apical spine. Nassellariida indet. was a part of Nassellarian cephalis (Supporting Information Plate S1) and could not be identified at the species level, but was considered juveniles of Nassellarians, including *A. setosa*.

**Quantification of individual radiolarian skeletal volume by MXCT**

We selected 13 radiolarian taxa for quantification of individual radiolarian skeletal volume. The selected 13 radiolarian taxa were major taxa with non-sporadic appearances, showing a relative abundance in total radiolarians of ≥ 9% in each sample during the sampling period. For taxa that were counted separately as adults and juveniles, if adults were the major taxon, even juveniles with low contribution were included in the 13 selected radiolarian taxa. The other radiolarian taxa were too rare, and therefore insignificant in the calculation of biogenic silica flux due to radiolarians.

The radiolarian skeletons in the sediment trap samples were cleaned of OM and protoplasm by hydrogen peroxide solution according to Ikenoue et al. (2015). Specimens of the selected 13 radiolarian taxa were picked out from the cleaned sediment trap samples where each taxon occurred abundantly; that is, from the samples of #2, 3, 4, 5, 11, 13, 22, and 26 collected at NAP12t. An average-sized specimen of each of the selected 13 radiolarian taxa was picked out from the specimens and observed by MXCT: ScanXmate-DF160TSS105 (Comscantechno Co. Ltd., Yokohama, Japan) with a high-resolution X-ray detector (Geometric resolution: 0.45 μm/voxel) equipped in JAMSTEC. A high-resolution setting (X-ray focus diameter: 0.8 μm; X-ray tube voltage: 80 kV; detector array size of 1024 x 1024 pixels; 1800 projections in 360° rotations) was applied for 3D quantitative densitometry of the individual skeleton. It took about 2 h to take a MXCT image of one individual. In order to achieve a high-contrast image as far as possible, we stacked images that were exposed four times in one projection. We used ConeCTexpress (White rabbit Corp., Tokyo, Japan) for correction and reconstruction tomography data; and the general principle of Feldkamp cone beam reconstruction.
was followed to reconstruct image cross sections based on filtered back projections.

The tomographic image was represented with a 16-bit (65,536 contrasts) grayscale. A 3D image of the interior of a radiolarian skeleton was obtained by collecting X-ray transmission images from all angles of the radiolarian skeleton and generating a series of two-dimensional (2D) cross-sectional images. These 2D images were stacked and a 3D image was built by 3D image visualization and processing software Molcer Plus (White Rabbit corp., Tokyo). The skeleton volumes for the 13 selected taxa from individual 3D images were also calculated using the software Molcer Plus.

Morphologic analysis by the MXCT method provides more accurate and quantitative parameters than ever recorded for individual radiolarian skeletons; therefore, it is a powerful tool for resolving evaluation of species-specific biogenic silica flux by siliceous microplankton in the seawater. An established methodology for estimation of radiolarian skeletal volume has not previously been reported until now. Here, we propose the most recent and accurate quantitative method to define skeletal volume based on a histogram of radiolarian images.

X-ray CT acquisitions are typically done in the air, and the reconstructed images consist of the following components: (1) object (radiolarian skeleton), (2) partial volumes that are associated with the object, and (3) surrounding air. In this study, the peak frequencies of the 16-bit grayscale amorphous silica histogram itself were closer to the air and it partly overlapped each other (Fig. 2); therefore, it was difficult to identify the boundary between them. We calculated the grayscale value of the surrounding air, which was located adjacent to the specimen in the same field of view, in order to know the distribution of the histogram of the air. In this case, it meant that the highest grayscale value of the air was indicated as the threshold value between the air and the material (Fig. 2). Therefore, it can be considered that the whole histogram above this threshold is derived from the radiolarian skeleton.

This method can define the air/material boundary in every analysis; therefore, it is useful for quantitative analysis of radiolarian morphology. On the other hand, however, very thin and small skeletal structures of radiolarians under the geometric resolution of MXCT cannot be detected. This is because structures below geometric resolution are buried in the noise of surrounding air, making it difficult to separate air and material. This problem is a common issue that occurs in all microfocus X-ray CT methods. However, such a tiny structure of radiolarian skeleton below geometric resolution is sufficiently small compared to volume of the entire radiolarian skeletons. Therefore we ignored the volumes below geometric resolution in this study, but we still claim that our technique provides the most detailed and accurate volume measurements in currently available technology.

**Fig. 3.** Time-series data at Sta. NAP12t from 04 October 2012 to 18 September 2013. (a) Climate Forecast System Version 2 (CFSv2) reanalysis data of downward shortwave radiation at the surface of sea ice and ocean (after sea-ice opening); (b) CFSv2 reanalysis data of sea-ice concentration; (c) total mass flux and bulk components of sinking particles; (d) total radiolarian fluxes; and (e) radiolarian faunal compositions. Blank (white) areas in bulk component data indicate no analysis because of limited sample volume.

**Mass measurement of radiolarian skeleton and estimation of radiolarian skeleton density**

*S. glacialis* is probably the largest spumellarian species in the western Arctic Ocean with an average size of 410 μm (the diameter of the disk without the spine ranged from 253 to 497 μm in this study) in the selected 13 radiolarian taxa, and
Table 1. List of the 33 radiolarian taxa encountered in the sediment trap samples.

| Phylum | Taxa | References |
|--------|------|------------|
| Rhizaria, Cavalier-Smith (2002) | | |
| Radiolaria, Müller (1858) | | |
| Polycystina, Ehrenberg (1838); emend. Riedel (1967) | | |
| Spumellaria, Ehrenberg (1875) | | |
| 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 | Ikenoue et al. (2015), plate 1, figs. 11–14
| Actinomma leptodermum, Jørgensen (1900); longispinum, Cortese and Bjørklund (1998) | Cortese and Bjørklund (1998), plate 2, figs. 15–22
| Actinomma leptodermum longispinum juvenile | Ikenoue et al. (2015), plate 1, figs. 17 and 18
| Actinomma spp. juvenile forms* | Ikenoue et al. (2015), plate 1, figs. 19–24
| Actinomma morphogroup B | Ikenoue et al. (2015), plate 2, figs. 1–4
| Drymyomma elegans, Jørgensen (1900) | Dolven et al. (2014), plate 1, figs. 5–7
| Spongiscidae, Haeckel (1862) | Bjørklund et al. (1998), plate I, fig. 3
| Spongotrochus glacialis, Popofsky (1908)* | Ikenoue et al. (2015), plate 3, fig. 12
| Styloclyta sp. | |
| Quinquecapsulariidae Dumitrica (1995) | Ikenoue et al. (2016), plate 2, figs. 4–8; plate 3, figs. 1–7
| Joergensenium arcticum, Ikenoue, Dumitrica and Bjørklund (2016)* | Ikenoue et al. (2016), plate 2, figs. 1–3
| Joergensenium arcticum juvenile* | |
| Nassellaria, Ehrenberg (1875) | | This study, Supporting Information Plate S1, figs. 1–19
| Nasserellida indet.* | |
| Sethophormididae, Haeckel (1881); emend. Petrushevskaya (1971) | Petrushevskaya (1971), fig. 31, I–III
| Enneaphoropsis rotula, Haeckel (1881) | Petrushevskaya (1971), fig. 32, IV, V
| Enneaphoropsis enneastrum, Haeckel (1887) | Bjørklund et al. (2014), plate 9, figs. 15–17
| Protosclera simplex, Cleve (1899) | |
| Plagiacanthidae, Hertwig (1879); emend. Petrushevskaya (1971) | Petrushevskaya (1971), fig. 52, II–IV
| Ceratocystis hirsutus, Jørgensen (1905) | Petrushevskaya (1971), fig. 57, 1
| Lophofoa clevei, Petrushevskaya (1971) | Dolven et al. (2014), plate 6, figs. 20–24
| Phormacantha histrius, Jørgensen (1900)* | Bjørklund et al. (1998), plate II, figs. 26 and 27
| Peridium longispinum, Jørgensen (1900) | Dolven et al. (2014), plate 7, figs. 7–9
| Plectacantha oikos, Jørgensen (1905) | Bjørklund et al. (2014), plate 9, figs. 5–7
| Pseudodictyophimus clevei, Jørgensen (1900)* | Bjørklund et al. (1998), plate II, figs. 7 and 8
| Pseudodictyophimus gracilipes gracilipes, Bailey (1856)* | Ikenoue et al. (2015), plate 6, figs. 14–19
| Pseudodictyophimus gracilipes, Bailey (1856); multispinus, Bernstein (1934) | Bjørklund and Kruglikova (2003), plate V, figs. 11–13
| Pseudodictyophimus phalcycephalus, Haeckel (1887) | |
| Tripodiscium (Tholospyris) geyphysitis, Hülsman (1963) | |
| Eucyrtidiidae, Ehrenberg (1847); emend. Petrushevskaya (1971) | Petrushevskaya (1971), fig. 92, VIII–IX
| Artostobus joergensi, Petrushevskaya (1967) | Bjørklund et al. (1998), plate II, figs. 1 and 6
| Cycladophora davisiara, Ehrenberg (1862) | Bjørklund et al. (1998), plate II, figs. 23–25
| Lithocampe platyccephala, Ehrenberg (1873) | Petrushevskaya (1967), fig. 74, I–IV
| Lithocampe aff. Furuscipula, Popofsky (1908) | Bjørklund et al. (2014), plate 9, figs. 10 and 11
| Sethocornus tabulatus, Ehrenberg (1873) | |
| Cannobotryidae, Haeckel (1881); emend. Riedel (1967) | Bjørklund et al. (1998), plate II, figs. 30–33
| Amphimelissa setosa, Cleve (1899)* | Ikenoue et al. (2015), plate 9, figs. 34–39
| Amphimelissa setosa juvenile* | |

*Major 13 radiolarian taxa.
it was selected for this specific radiolarian skeleton’s mass measurement and for its density estimation. The mass of the specimen was measured at the National Metrology Institute of Japan using an electronic balance UMX5 (Mettler Toledo K.K., Switzerland). The maximum capacity and the resolution of the electronic balance are 5.1 g and 0.1 μg, respectively, and the electronic balance was calibrated with a mass standard weight traceable to the national mass standard of Japan. To accurately measure the mass of the specimen, the measurement was carried out under a stable environment (room temperature: 24.3–24.4 °C, relative humidity: 43–44%, atmospheric pressure: 1014.4–1014.7 hPa). Because the specimen was extremely small, it was not possible to load it onto the electronic balance directly. A container on which the specimen can be mounted was therefore used.

The mass of the specimen was measured using the balance by the following procedures. At first, only the container was loaded onto the balance and the balance reading was recorded. The container was unloaded from the electronic balance, and the specimen was mounted on the container. The specimen and container were loaded onto the balance, and the balance reading was recorded. The specimen and container were unloaded, and the specimen was removed from the container. Finally, the empty container was loaded onto the balance and the balance reading was recorded. From the three balance readings, the mass of the specimen was determined. This measurement sequence was repeated three times, and the average of the three mass values was used as the average mass of the specimen. The uncertainty of the average mass of the specimen was determined from the standard deviation of three mass measurements of the specimen. The density of a specimen was obtained by combining the results of the mass and volume measurements using the following equation:

$$\text{Skeletal density of } S.\text{ glacialis} = \frac{\text{mass (μg/specimen)}}{\text{volume (mm}^3\text{)}}.$$  

**Estimation of radiolarian biogenic silica flux**

We defined the biogenic silica flux due to the selected 13 radiolarian taxa as radiolarian silica flux (RSi flux), and the sum of them was defined as total RSi flux. According to Hurd and Theyer (1977), the density of radiolarian skeletons did not differ significantly between samples from different time periods, ranging from 1.7 to 2.0, and was approximately 2.0 in most samples. Since all the samples used in this study are of recent living specimens, the density of radiolarian siliceous skeletons was assumed to be constant regardless of species or specimens. The silica mass for each radiolarian taxa is obtained by multiplying the density of weighed S. glacialis by the calculated skeleton volume using the following equation:

$$\text{RSi mass} = \text{Radiolarian skeletal volume (mm}^3\text{)} \times \text{skeletal density of } S.\text{ glacialis}$$

Finally, we calculated the RSi flux (mg m$^{-2}$ d$^{-1}$) using the following equation:

$$\text{RSi flux} = \text{Radiolarian flux} \times \text{RSi mass}$$

**Results**

**Mooring conditions of sediment traps**

The Chukchi Borderland is in polar night from late October to early February (Figs 3a, 4a). The shortwave radiation at the sea surface (or surface of sea ice) at Sta. NAP12t ranged from...
0 to 362 W m$^{-2}$ (Fig. 3a) and that at Sta. CAP12t ranged from 0 to 374 W m$^{-2}$ (Fig. 4a). Stas. NAP12t and CAP12t are located in a seasonal sea-ice zone and were covered by sea ice from late October through July (Figs. 3b, 4b). The ice-cover period at CAP12t began about 1 week earlier than it did at NAP12t, but the shortwave radiation (light environment) at the sea surface is comparable between the two stations. Pressure and temperature sensors attached to the sediment traps recorded that the sediment traps were moored stably at a water depth of 235–236 m (median, 235 m) for Sta. NAP12t, and at 263–267 m (median, 264 m) for Sta. CAP12t.

**Particle fluxes**

Total mass (TM) flux and bulk components (Biogenic silica, OM, CaCO$_3$ and LM) at Stas. NAP12t and CAP12t are summarized in Figs. 3c, 4c, respectively (Onodera et al. 2021). The TM flux mainly consisted of LM at both stations throughout the sampling periods (median percentage: 56.7 wt% LM, followed by 26.7 wt% OM at Sta. NAP12t; 45.1 wt% LM, followed by 23.3 wt % biogenic silica at Sta. CAP12t). At Sta. NAP12t, the biogenic particles (Biogenic silica, OM, CaCO$_3$) and LM fluxes began to increase at the end of July in 2013, with summer peaks in mid-August. At Sta. CAP12t, however, the biogenic particles and LM fluxes increased during the period from March to May in 2013; with peaks in March in spite of this being in the sea-ice cover season. The significantly low TM flux during August–September 2013 at Sta. CAP12t was presumably due to clogging of the funnel part of the sediment trap and is underestimated.

**Radiolarian fluxes**

A total of 33 radiolarian taxa (10 Spumellaria, 21 Nassellaria) were identified at Stas. NAP12t and CAP12t from 04 October 2012 to 18 September 2013 (Table 1). The number of radiolarians counted in each sample ranged from 6 to 879 specimens at Sta. NAP12t, and from 10 to 597 specimens at Sta. CAP12t (Supporting Information Tables S1, S2). There were 33 samples with fewer than 100 specimens (14 samples at Sta. NAP12t, and 19 samples at Sta. CAP12t).
S. glacialis

CAP12t

juvenile (only with the two medullary shells), and J. arcticum leptodermum (August–September): Actinommidae spp. juvenile forms (only with the two medullary shells), Actinomma leptodermum leptonarium, Actinomma boreale, Joergensenium arcticum, J. arcticum juvenile (only with the two medullary shells), and S. glacialis.

CAP12t

The total radiolarian fluxes varied from 73 to 7960 specimens m⁻² d⁻¹ throughout the sampling period (Fig. 4d), with a mean daily flux of 982 specimens m⁻² d⁻¹. Relatively high fluxes were observed during 04 October 2012–18 November 2012 and during 31 May 2013–30 July 2013; while extremely low fluxes (range 73–640, average, 202 specimens m⁻² d⁻¹) were observed during 18 November 2012–31 May 2013, and 30 July 2013–18 September 2013. The highest total radiolarian

Table 2. Calculated skeleton volumes and mass of individual specimens of the major 13 radiolarian taxa in the Arctic Ocean.

| Taxa                                | Skeleton volume (mm³) | Silica mass (μg)* | Silica concentration (nmol Si/skeleton)† |
|--------------------------------------|-----------------------|------------------|-----------------------------------------|
| Actinomma boreale                    | 7.0E-05               | 1.5E-01 ± 3.5E-03| 2.1E+00 ± 5.0E-02                        |
| Actinomma leptodermum leptonarium    | 3.7E-05               | 7.9E-02 ± 1.9E-03| 1.1E+00 ± 2.7E-02                        |
| Actinomnidae spp. juvenile forms     | 1.3E-05               | 2.8E-02 ± 6.6E-04| 4.0E-01 ± 9.4E-03                        |
| Spongotrochus glacialis†             | 2.7E-03               | 5.8E-00 ± 1.4E-01| 8.3E-01 ± 2.0E-00                        |
| Joergensenium arcticum               | 7.5E-05               | 1.6E-01 ± 3.8E-03| 2.3E+00 ± 5.4E-02                        |
| Joergensenium arcticum juvenile      | 1.1E-05               | 2.3E-02 ± 5.5E-04| 3.3E-01 ± 7.9E-03                        |
| Phormacantha hystrix                 | 1.6E-05               | 3.4E-02 ± 8.1E-04| 4.9E-01 ± 1.2E-02                        |
| Pseudodictyophimus clevei           | 2.1E-05               | 4.5E-02 ± 1.1E-03| 6.4E-01 ± 1.5E-02                        |
| Pseudodictyophimus gracilipes graciipes | 1.4E-05             | 3.0E-02 ± 7.1E-04| 4.3E-01 ± 1.0E-02                        |
| Pseudodictyophimus spp. juvenile forms | 1.1E-05            | 2.3E-02 ± 5.5E-04| 3.3E-01 ± 7.9E-03                        |
| Amphimelissa setosa                  | 5.2E-05               | 1.1E-01 ± 2.6E-03| 1.6E-00 ± 3.7E-02                        |
| Amphimelissa setosa juvenile         | 2.6E-05               | 5.5E-02 ± 1.3E-03| 7.9E-01 ± 1.9E-02                        |
| Nassellarida indet                   | 4.0E-06               | 8.5E-03 ± 2.0E-04| 1.2E-01 ± 2.9E-03                        |

*The mass of silica (SiO₂·nH₂O) for each taxa was obtained by multiplying the density of S. glacialis by the calculated skeleton volume. The uniformity of the density among the 13 radiolarian taxa was assumed to be much better compared to the uncertainty of the density of S. glacialis. On the basis of this assumption, the mass uncertainties of the other 12 taxa were calculated from the density uncertainty of S. glacialis.

†The silica concentration was calculated for RSi as SiO₂·0.55H₂O (70.0 g mol⁻¹).

‡The mass of S. glacialis was measured by the electronic balance. The density of S. glacialis (2.1 ± 0.1 mg mm⁻³) was calculated from the mass and skeleton volume. The density uncertainty was determined from the mass measurement uncertainty and volume uncertainty of 0.

Fig. 6. Time-series data at Sta. NAP12t from 04 October 2012 to 18 September 2013. (a) Total radiolarian silica flux and (b) composition of radiolarian silica flux.
Radiolarian silica flux

The CT-scanned 3D images of the 13 selected radiolarian skeletons are shown in Fig. 5 and their cross-sectional images are also shown in Supporting Information Data S1–S13. The mass of *S. glacialis* was determined to be 5.8 μg with an uncertainty of 0.1 μg. The uncertainty was determined from the standard deviation of three mass measurements of the *S. glacialis* specimen. The uncertainty contributions from the other sources such as resolution and sensitivity of the balance were much smaller than the standard deviation and were therefore not considered in the estimation of the uncertainty. The calculated skeleton volume of *S. glacialis* from its CT-scanned 3D model was 0.0027 mm³. Assuming that the uncertainty of volume determination was 0, the skeleton density of *S. glacialis* derived from the mass and skeleton volume was 2.1 ± 0.1 mg mm⁻³. The specimens in this study are recent siliceous skeletons and have not undergone post-depositional diagenesis. The uniformity of the density among the 13 radiolarian taxa was assumed to be much better compared to the uncertainty of the density determination of *S. glacialis*. On the basis of this assumption, the masses and their uncertainties of the other 12 taxa were calculated based on the density and its uncertainty of *S. glacialis*. The skeleton volume and the corresponding silica mass for individual radiolarian taxa are shown in Table 2. The calculated silica mass of radiolarian taxa ranges from 0.0085 to 5.8 μg. Temporal variation of total RSi flux and its composition at Sta. NAP12t, and those at Sta. CAP12t are also shown in Fig. 7. The total RSi flux varied from 0.0071 to 1.0 mg m⁻² d⁻¹ at Sta. NAP12t, and from 0.0054 to 0.72 mg m⁻² d⁻¹ at Sta. CAP12t during the sampling period. The average value of total RSi flux at Sta. NAP12t over the sampling period was 0.26 mg m⁻² d⁻¹, which was 3.7 times higher than that of 0.070 mg m⁻² d⁻¹ at Sta.

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**Table 3.** Ranges of molar concentration of silica in individual radiolarian skeletons.

| Silica concentration (nmol Si/cell) | Spumellaria | Nassellaria | Reference |
|-----------------------------------|-------------|-------------|-----------|
| 0.33–83                           | 0.12–1.6    | This study  |
| 4.9–26                            | 0.63–15     | Takahashi (1981)* |
| 0.81–12.64                        | 1.08–3.23   | Llopis Monferrer et al. (2020) |
| –                                 | 1–4.8       | Llopis Monferrer et al. (2021) |

*Conversion from μg Si/cell to nmol Si/cell assuming a molecular weight of 70 g mol⁻¹ for SiO₂·0.5H₂O (Mortlock and Froelich 1989).*
CAP12t. Among 13 radiolarian taxa, A. setosa (adult and juvenile) and S. glacialis were the highest contributors to total RSi flux at both stations. The average contribution of A. setosa (adult and juvenile) of the total RSi flux throughout the sampling period was 55.2 wt% at Sta. NAP12t; and for Sta. CAP12t it was 70.8 wt%. The silica contribution of S. glacialis was 36.7 wt% at Sta. NAP12t, while at Sta. CAP12t it was 23.2 wt%. Compositions of biogenic silica flux at both stations are shown in Fig. 8. The contribution of RSi to the biogenic silica flux at Sta. NAP12t varied from 0.1 to 34.8 wt%, while at Sta. CAP12t it varied from 0.02 to 5.1 wt%.

**Discussion**

**Comparison of radiolarian fluxes in the Northwind Abyssal Plain and Chukchi Abyssal Plain regions**

The mean radiolarian flux at Sta. NAP12t was at about the same level as that of the past 2 yr at Stas. NAP10t and NAP11t (Ikenoue et al. 2015) and was 2.4 times as high as at Sta. CAP12t. The high flux at Sta. NAP12t was caused by higher fluxes of A. setosa than at Sta. CAP12t. Sta. CAP is more susceptible to warm, low-salinity water masses from the shelves and the shelf origin water would reduce the habitat range of A. setosa, inhibit its growth, and reduce its flux at Sta. CAP.

Radiolarian faunal compositions at Stas. NAP12t and CAP12t were similar during the open water season, but differed during the sea-ice cover season; that is, relative abundance of actinommds (Actinommdidae spp. juvenile forms, Actinomma l. leptodermum, and Actinomma boreale), S. glacialis, and J. arcticum increased at Sta. NAP12t during the sea-ice cover season (Figs. 3e, 4e). The actinommds, S. glacialis, and J. arcticum seem to prefer surface-subsurface water mass in the deep Arctic Ocean basins and are not so common in the shallow marginal arctic seas (Ikenoue et al. 2015, 2016, 2019b). Sta. CAP12t was located on the continental slope in the western side of the Chukchi Borderland; while Sta. NAP12t was located more on the inside of the basin area, on the eastern side of the Chukchi Borderland (Fig. 1). Thus, the radiolarian faunal composition at Sta. NAP12t indicated the characteristics of the radiolarian fauna in the Arctic basin area (Figs. 3e).

The difference in the radiolarian faunal compositions at both stations during the sea-ice cover season was largely due to the difference in the geographic position of the two stations. The eastern side of the Chukchi Borderland is occasionally influenced by relatively oligotrophic waters originating from the oceanic Beaufort Gyre (Nishino et al. 2011; Ikenoue et al. 2015; Onodera et al. 2015a). The actinommds can account for 60% of the radiolarian abundance in the western Arctic Ocean due to oligotrophic water (Ikenoue et al. 2015). However, at Sta. NAP12t no significant oligotrophic water effect was observed on the radiolarian faunal composition (Fig. 3e). The East Siberian Sea water occasionally appears on the western side of the Chukchi Borderland (Nishino et al. 2011), but signals of East Siberian Sea water were not detected by the multi-year bottom-tethered mooring data at Sta. CAP12t during the sampling period (Watanabe et al. 2017).

**Lateral advection of shelf-origin water over the Chukchi Abyssal Plain**

Remarkable high LM flux was observed in March 2013 at Sta. CAP12t. At the same time, biogenic silica flux and OM flux also peaked, in spite of being in the sea-ice cover season, although the total radiolarian flux was very low (Fig. 4). The moored CTD detected a spring subsurface warming (> −1.0°C) and a low salinity (< 32.2 psu) at 95-m water depth in March 2013 at Sta. CAP12t (Supporting Information Fig. S1). Watanabe et al. (2017) demonstrated that the warming and low salinity were caused by the Barrow Canyon throughflow and the subsequent Chukchi Slope Current toward the Chukchi Borderland by using a pan-Arctic high-resolution sea-ice–ocean model. Therefore, we interpreted that the remarkable high LM flux at Sta. CAP12t resulted from the lateral advection of shelf-origin water, and the accompanying biogenic silica and OM is therefore interpreted to be allochthonous. In fact, during our microscope observations of the fine fraction (< 45 µm) of the sediment trap sample slides, a substantial amount of siliceous fragments of diatom valves was found. In the Bering Strait and southern Chukchi Sea shelf, radiolarians were scarce or absent, probably due to the low salinity water mass (< 28 psu) and the shallow water depth (< 50 m) (Ikenoue et al. 2016, 2019b). Therefore, the shelf origin water should as expected include very few siliceous radiolarian skeletons. At Sta. CAP12t, the flux of Nassellaria indet., that is, immature nassellarians, increased in June, after March–May 2013, when LM originating from the shelf increased (Fig. 4). That may also be related to the extremely low flux of radiolarians in August–September 2013 during the open water season.

**Contribution of radiolarian silica to biogenic silica flux in the western Arctic Ocean**

We established a new approach to estimate the amount of biogenic silica flux that is due to radiolarians using the MXCT technique. Estimation of the amount of biogenic silica from radiolarian species abundance data is important for determination of the main RSi carriers. There is a discrepancy between abundant radiolarian species data and the main RSi carrier since the radiolarian silica mass varies greatly with species (Jacot Des Combes and Abelmann 2009). In addition, the main RSi carrier changes when the composition of the radiolarian assemblage varies spatially and temporally. In this study, we found that the main RSi carrier in the western Arctic Ocean was represented by only two species (> 90 wt% in RSi); that is, A. setosa (average: 55.2 wt% at Sta. NAP12t, 70.8 wt% at Sta. CAP12t) and S. glacialis (average: 36.7 wt% at Sta. NAP12t, 23.2 wt% at Sta. CAP12t) (Figs. 6, 7). A. setosa was the main RSi carrier during the open water season due to its
explosive increase in abundance, although its skeleton size is fairly small among arctic radiolarians. On the other hand, *S. glacialis* was also the main RSi carrier during the sea-ice cover season. This is due to its large skeleton size in spite of a general low abundance.

Although our radiolarian skeleton volumes are not directly comparable to the cell volumes of Biard et al. (2018) and Llopis Monferrer (2020 and 2021), they can be compared by converting to molar concentrations of silica. The water content of radiolarian skeletons in this study is not clear, but radiolarians typically display higher water contents (about 14%) than diatoms (about 10%) (Mortlock and Froelich 1989). The chemical formula of silica when the water content is 14% is SiO$_2$–0.55H$_2$O (70.0 g mol$^{-1}$). The molar concentrations of individual radiolarian skeletons calculated for RSi as SiO$_2$–0.55H$_2$O are shown in Table 2. The ranges of silica molar concentrations of radiolarian skeletons reported in the previous studies are shown in Table 3. Although the molar concentrations of silica in this study varied depending on the species, they were in agreement with the range of values reported in previous studies (Table 3). The maximum molar concentration of silica in the Arctic radiolarians in this study tended to be higher in *Spumellaria* than *Nassellaria*, with the highest molar concentration of silica in *S. glacialis*, a spumellaria with a spongy skeleton (Tables 2, 3). High molar concentrations in species with spongy skeletons (e.g., *Dictyocoryne profunda*) are also observed in Takahashi (1981). On the other hand, the molar concentration of silica calculated from silica mass of *S. glacialis* in Takahashi (1981) is 4.9 (nmol/skeleton), which is one order of magnitude lower than the value in this study. This may be related to the fact that the size of *S. glacialis* in Takahashi (1981) (236 μm on average) is half the size of *S. glacialis* in this study (446 μm).

The contribution of RSi to the biogenic silica flux in the Chukchi Borderland was less than 10 wt% during most of the sampling period; but high contributions, which reached 19.6–34.8 wt%, were observed at Sta. NAP12t during the open water season in October–November 2012 and August–September 2013 (Fig. 8). The main component of siliceous plankton other than radiolarians is diatoms. (Ikenoue et al. 2015; Onodera et al. 2015a). Takahashi (1991) reported that the contribution of RSi at Sta. PAPA in the eastern Pacific Ocean usually has spring and fall peaks, which could reach more than 40 wt%. The lower RSi flux at Sta. NAP12t than that at Sta. PAPA would be related to the much longer sea-ice cover season in the Arctic Ocean and the difference in the species composition, as well as differences in the ecosystems at the two stations. In general, during the sampling period, the total RSi flux at Sta. NAP12t in the eastern side of the Chukchi Borderland was higher than that at Sta. CAP12t in the western side of the Chukchi Borderland (Figs. 6, 7). The low contribution of RSi in the biogenic silica flux at CAP12t would be accounted for not only by the low RSi flux due to the shallow water depth but also by the lateral advection of water originating on the shelf.

**Conclusion**

We have established a new method to quantify individual radiolarian skeletal volume by using the MXCT technique. This method allows us to calculate the volume of complex radiolarian skeletons, which cannot be reproduced accurately enough by simple geometric models, and to estimate for the first time the amount of radiolarian-derived biogenic silica flux in the seasonal sea-ice extent of the Arctic Ocean. As a result, the contribution of radiolarians to biogenic silica flux in the subsurface Arctic Ocean was estimated to be less than 10 wt% during the sea-ice cover season but reached 20–35 wt% during the open water season. The MXCT technique also allows us to identify the species of radiolarians that are the major carriers of radiolarian-derived biogenic silica. This has not been possible with population-based fluxes. In recent studies, the measurement of stable oxygen and silicon isotopes in tests of siliceous microplankton has been developed as a new tool to serve as paleoceanographic proxies (Chapligin et al. 2011; Abelmann et al. 2015). Therefore, the determination of the main RSi carrier can be useful information in the interpretation of the isotopic signals obtained from radiolarian skeletons.

The disadvantage of our MXCT technique is that the number of researchers who can use it is very limited because MXCT itself is a very expensive device at present. The advantage of our MXCT technique is that it can be applied to fossils in sediments because we are measuring the volume of silica skeletons, not the biovolume of cells. The laser confocal microscope (LCM) is one of the methods used to estimate the 3D morphology for microorganisms, but it is not suitable for volume and density measurements because it does not provide the same resolution in three dimensions. In addition, the LCM is not applicable to a dead skeleton because it requires fluorescence observation. Therefore, our MXCT technique is the most suitable method for the measurement of microscopic skeletons, including fossils. The application of our new method to waters other than the Arctic Ocean and sediments will lead to the elucidation of the role of siliceous shell plankton in the silica cycle from the past to the present.

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Conflict of Interest

None declared.