Pleistocene and Holocene distribution of the radiolarian
Amphimelissa setosa Cleve in the North Pacific and North
Atlantic: Evidence for water mass movement
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Abstract

The radiolarian Amphimelissa setosa is one of the prominent species of the Pleistocene radiolarian assemblages in the Sea of Okhotsk below the marine isotope stage (MIS) boundary 5/4, and it represents one of the most abundant radiolarian species in Holocene and modern environments of the Nordic Seas. We studied the \textit{A. setosa} distribution in six cores from the Sea of Okhotsk and established morphometric measurements on \textit{A. setosa} specimens from two cores of the Sea of Okhotsk and one core from the Labrador Sea. We further compared our data with other available studies from the Subarctic Pacific, the Labrador Sea, the North Atlantic, the Norwegian Sea, and the Iceland/Greenland Seas in order to discuss the possible settling of the species from the North Pacific via the Arctic Ocean into the Iceland/Greenland Seas. \textit{A. setosa} exhibits a stable abundant population in the Sea of Okhotsk during most of the last ca. 0.7 m.y. and might repeatedly extend its population into the North Atlantic through the Arctic Ocean during the Pleistocene interglacial optima. The species declines from the Sea of Okhotsk and from the Subarctic Pacific at the end of MIS 5. Its final documented settling into the North Atlantic is during MIS 5, when \textit{A. setosa} appears in low numbers in sediments of the Labrador Sea, however reaching significant percentages at the boundary of MIS 5/4. Based on the available information, we propose that \textit{A. setosa} could migrate from the North Pacific into the Arctic Ocean during the interglacial optimum MIS 5e and then through the channels of the Canadian Arctic Archipelago into the Baffin Bay and Labrador Sea. A further migration step of \textit{A. setosa} occurs at the boundary of MIS 5/4, when \textit{A. setosa} migrated from the Labrador Sea into the North Atlantic, probably related to a southward expansion of cold waters at the end of the MIS 5. During the warming at Termination I, \textit{A. setosa} moved from the North Atlantic into the Nordic Seas. The abundant occurrence of \textit{A. setosa} in sediments south of Iceland, the Norwegian and North Seas within the Younger Dryas period points to a marked cooling and a southward movement of polar water masses restricted to this time interval.

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1. Introduction

The northern North Pacific with its marginal seas is characterized by a different hydrographic regime in comparison to the northern North Atlantic. In the Subarctic Pacific, the prominent halocline (at depths of 75–200 m) inhibits water-mass exchange between the sea surface and the deep ocean, and thus isolates the upper mixed layer from the intermediate and deeper water masses (Uda, 1963; Warren, 1983). In contrast, the water column of the Subarctic Atlantic (the Greenland, Iceland, and Labrador Seas) is effectively isohaline and permits intense vertical deep mixing (Swift and Aagaard, 1981). Today, there is a very limited oceanographic and biological connection between the Subarctic domains of the Pacific and the Arctic Ocean. The only and very slow water-mass exchange (ca. 0.8 Sv) occurs through the shallow Bering Strait over a sill depth of about 50 m (Jones, 2001). Thus, the microplankton associations, in particular the radiolarian assemblages of the high-latitude North Pacific and North Atlantic, exhibit different assemblage compositions (Kruglikova, 1999). The Sea of Okhotsk, a Subarctic marginal sea of the North Pacific, is characterized by sediments rich in biogenic silica, composed of diatoms and radiolarians (Bezrukov, 1955; Kruglikova, 1975; Sancetta, 1981; Lisitzin, 1985; Abelmann and Nimmergut, 2005), and represents an ideal site to investigate these microfossil assemblages. In this study, we focus on the distribution of the radiolarian species Amphimelissa setosa Cleve (Fig. 1), which is one of the most prominent species in the Sea of Okhotsk below the Marine Isotope Stage (MIS) boundary 5/4. The species disappears from the Sea of Okhotsk and Subarctic Pacific at the end of MIS 5 (Kruglikova, 1976; Matul et al., 2002b). It occurs in relatively high percentages in the Labrador Sea during MIS 2–4 (Matul et al., 2002a) and in high numbers in the Nordic Seas (Molina-Cruz, 1991) and Greenland Sea (Schröder-Ritzrau, 1995) during MIS 1. We compare the distribution pattern of A. setosa in sediment core records from the Sea of Okhotsk with those from the Labrador Sea, North Atlantic and Norwegian Sea (Jansen and Bjørklund, 1985; Matul, 1995a, b, 2002a, b) to get information about regional changes in the A. setosa population during the Late Pleistocene and Holocene in relation to paleoceanographic aspects (Fig. 2).

2. Material and methods

The distribution of the radiolarian species A. setosa Cleve was studied in six sediment cores from different areas and water depths of the Sea of Okhotsk (Figs. 2 and 3, Table 1). The cores were recovered during two cruises with R.V. Akademik M. A. Laurentyev (Nürnberg et al., 1997; Biebow and Hüttén, 1999). The 46 m long core MD01-2415 was taken during the cruise IMAGES VII with R.V Marion Dufresne from the central part of the Sea of Okhotsk (Bassinot et al., 2002). We compared the A. setosa distribution in the Sea of Okhotsk sediment records with the abundance variations of the species documented in cores from the northern North Atlantic (Figs. 2 and 3, Table 1). The radiolarian preparation was done according to methods described in Abelmann (1988) and Abelmann et al. (1999). Radiolarian counts were done routinely at a magnification of 160× or 320×. At least 350 specimens were counted per slide. In addition, the whole slide was scanned to document the presence or absence of A. setosa and biostratigraphic indicator species.

A. setosa counts are calibrated to the age models of Cores LV28-42-4 and MD01-2115 (Fig. 3; Matul et al., 2002b; Nürnberg and Tiedemann, 2004). Nürnberg et al. (1997), and Biebow and Hüttén (1999) show that changes in lithology, magnetic susceptibility as well as tephrastro- and biostratigraphic events occur synchronously in sediment cores of the Sea of Okhotsk. The age assignment of the other cores from the Sea of Okhotsk (LV27-8-4, LV 27-5-3, LV28-44-3) is therefore based on a correlation of these parameters to those recorded in Core LV28-42-4 (Nürnberg et al., 1997; Biebow and Hüttén, 1999; Matul et al., 2002b) by using the AnalySeries software (Paillard et al., 1996). The age models of the North Atlantic cores are based on a combination of radiocarbon, marine isotope stratigraphic as well as tephrastro- and biostratigraphic records (Table 1).

For a comparison with available morphometric data on A. setosa skeletons from plankton and surface sediments of the Nordic Seas (Björklund and Swanberg, 1987), we established a morphometric analysis on 210 A. setosa tests from seven interglacial sediment samples (30 per sample) of Cores LV28-42-4 and LV28-44-3 from the Sea of Okhotsk, where the species exhibits prominent abundance peaks. In addition, we measured the dimensions of 120 A. setosa tests in four samples.
(30 per sample) of Core P172 from the Labrador Sea where abundant numbers of *A. setosa* occur within the glacial time period MIS 2–4 (Matul et al., 2002a). The morphometric measurements were done on specimens from sediment intervals with highest *A. setosa* abundances to ensure optimal environmental and growth conditions. Only specimens with an intact thorax have been used. We registered those

Fig. 1. *Amphimelissa setosa* Cleve from the Pleistocene sediments of the Sea of Okhotsk. Photographs 1–6: Core LV28-42-4, sample 394–395cm. Photographs 7–12: Core LV28-44-3, sample 898–899cm. Scale bar is 50 μm.
A. setosa tests, which had the appropriate position on the slide to permit accurate measurements. The measurements, following those done by Bjørklund and Swanberg (1987), include: (1) heights of eucephalic, antecephalic and postcephalic chambers, (2) sagittal diameter, (3) width of cephalis in direction of the sagittal diameter, (4) the total height of the specimen, (5) for additional 5–6 specimens also the frontal diameter (Fig. 4A). Images of A. setosa specimens under the microscope were routinely transmitted through the video system to the display, and then measured there with a scaled micrometric liner. The accuracy of the measurements is about ±1 μm. The mean arithmetical value and the standard deviation from the mean value were calculated for the obtained variables.

3. Results

3.1. A. setosa records in the Sea of Okhotsk and northern North Atlantic

The earliest occurrence of A. setosa in Pleistocene sediments from the Subarctic areas at about 1.03 Ma is described from Core MD01-2415 located in the northern central Sea of Okhotsk (Fig. 3). A. setosa appears here during a relatively short time period (ca. 1.03–0.96 Ma) in numbers between 5–10% (Fig. 3). It is not recorded in the interval between ca. 0.96 and 0.78 Ma, although the radiolarian preservation is good (Matul et al., in prep).

A. setosa is one of the prominent species of the radiolarian fauna in the sediment cores from the Sea of Okhotsk between MIS 17 to the end of MIS 5 (ca. 0.71–0.09 Ma) (Fig. 3). The species generally occurs in moderate abundances of ca. 10–15% within glacial periods and reaches highest values of about 40–55% of the radiolarian fauna during interglacial intervals. Prominent peaks of A. setosa during interglacial periods are persistently accompanied by high radiolarian abundances and increased biogenic silica accumulation (Nürnberg and Tiedemann, 2004). A. setosa numbers decline abruptly (down to 0.2–1%) in the cores from the Sea of Okhotsk in the upper MIS 5, and the species disappears finally from the Sea of Okhotsk just above the boundary of MIS 5/4 at about 72 ka (Fig. 3, Matul et al., 2002b). The abundant interglacial occurrence of A. setosa also is recorded in cores from the Subartic Pacific since the last ca. 0.55 m.y. (Kruglikova, 1976, 1977). A. setosa disappears from the open Subarctic Pacific similarly as in the Sea of Okhotsk at the end of MIS 5 (Kruglikova, 1976, 1977, 1999).

The first persistent occurrence of A. setosa in Late Pleistocene sediments of the northern North
Atlantic is documented in Core P172 from the Labrador Sea (Fig. 3, Matul et al., 2002a). However, *A. setosa* also is noted to occur earlier at the base of MIS 10 and in MIS 8 in the Labrador Sea (Bjørklund, 2004, personal communication), but any quantitative and continuous information about this earlier distribution is not yet available. In Core P172, *A. setosa* appears in low numbers (1–2%) in the upper MIS 5. The abundances of *A. setosa* increase up to 15% in MIS 4 and vary between 2 and 20% within MIS 3–4. Highest numbers of 30–38% occur at the end of MIS 3 and in MIS 2, and decline to 1–2% in MIS 1 (Fig. 3).

In the other cores from the northern North Atlantic, *A. setosa* is documented since MIS 3 (Fig. 3). We cannot exclude an earlier occurrence of *A. setosa* in this area because the basal age of most of the investigated cores is not older than MIS 3 (Fig. 3). In Core MK316 from the Reykjanes Ridge (spanning the time interval MIS 5–1) increased radiolarian numbers are only recorded in MIS 3, whereas in the older and younger intervals the radiolarian abundances are very low (Fig. 3). However, the disappearance and sharp decline of *A. setosa* in the cores from the open North Atlantic (L254, MK340) and Labrador Sea (P172) at the MIS 2/1 boundary point to a change in the environmental conditions during this interval (Fig. 3). This change occurs later in Core MK340 from the Reykjanes Ridge area, where the last peak of *A. setosa* (>30%) is within the Younger Dryas section compared to 1–3% in the previous Allerød and following Preboreal sections. A similar pattern in the *A. setosa* distribution during the lower MIS 1 is documented in Core 28/18 G/P (Fig. 3) from southeastern Norwegian Sea (Jansen and Bjørklund, 1985) and also in a core from the Skagerrak area of the North Sea (Bjørklund, 1985).

### 3.2. Morphometric measurement

*A. setosa* specimens from Pleistocene sediments of the Sea of Okhotsk fit basically in the type-species description given by Petrushevskaya (1981) and that of Bjørklund and Swanberg (1987) for the non-fjord cold-water morphotype of *A. setosa* from the Nordic Seas. On a first view, the only visible difference between the *A. setosa* tests from the Sea of Okhotsk and northern North Atlantic is that *A. setosa* tests from the Sea of Okhotsk sediments (SO specimens) are more robust compared to those from the Labrador Sea sediments (LS specimens) and plankton and modern sediments of the Nordic Seas (NS specimens). The morphometric study also exhibits apparent statistical deviations in basic dimensions of the species tests from the Sea of Okhotsk and North Atlantic areas (Fig. 5). We constructed the outline of an *A. setosa* skeleton by using the mean morphometric values measured on specimens from the Sea of Okhotsk, Labrador Sea and Nordic Seas (Fig. 4B). The mean morphometric values for the NS specimens were taken from Bjørklund and Swanberg (1987) and additional measurements of the height of ante- and post-cephalic chambers, and cephalis width were extracted from the photographs of *A. setosa* presented in Bjørklund and Swanberg (1987).
are (1) persistently larger in the height of the cephalis and in the total height of the shell, and (2) larger in some other dimensions if compared with the LS specimens from MIS 4-3 (Fig. 4). However, the SO specimens from the uppermost MIS 5 section appear to be smaller than the tests from the lower sediment sections, and exhibit a transitional stage between LS and older SO specimens. The LS specimens, being the smallest within the MIS 4 to lower MIS 3, increase in size toward MIS 2, where they have almost the same sagittal diameter as the SO specimens. The cephalis of the NS specimens seems to be squeezed from its apex, and stretched in a direction of the sagittal diameter, compared to the LS and SO specimens (Fig. 4). The morphological deviations between the specimens of the different areas and time intervals are within the range of the basic dimensions documented in the A. setosa-type descriptions and thus do not affect the species definition. The morphological differences may reflect different kind of ecological influences, such as silica availability, hydrographic conditions, and productivity regime.

4. Discussion

4.1. Modern A. setosa distribution

Comprehensive plankton and surface sediment studies in northern high-latitude areas show that A. setosa lives in a cold-water environment with temperatures ranging from <0 to 9°C (Petrushkevskaya, 1969, 1974; Petrushevskaya and Bjørklund, 1974; Swanberg and Eide, 1992; Schröder-Ritzrau, 1995; Itaki et al., 2003).

Recently accomplished plankton investigations in the Chukchi-Beaufort Seas show that maximum standing stock of A. setosa occurs during September between 50 and 150 m, which is in the temperature minimum layer with temperatures close to the freezing point (Itaki et al., 2003). High numbers of A. setosa (40–70%) also are reported from plankton samples in the upper 300–400 m located close to the summer ice edge during June–July in the Greenland Sea (Swanberg and Eide, 1992). Sediment trap investigations in the Greenland Sea (Schröder-Ritzrau, 1995) indicate that highest abundances of
*A. setosa* occur in a sediment trap from 500 m depth between July and September. The plankton and sediment trap studies in the Nordic Seas and Arctic Ocean show that maximum *A. setosa* numbers arise during the productive period in summer, when coccolithophores, diatoms and radiolarians exhibit highest fluxes (Kohly, 1994; Samtleben et al., 1995; Schröder-Ritzrau, 1995; Itaki et al., 2003).

*A. setosa* dominates the radiolarian assemblages in surface sediments of the Iceland/Greenland Seas (Petrushevskaya, 1969, 1974; Petrushevskaya and Björklund, 1974; Björklund et al., 1998; Cortese et al., 2003) and in some areas of the Arctic Seas along Eurasia (Kruglikova, 1988, 1989, 1999; Björklund and Kruglikova, 2003; Itaki et al., 2003), but it is not abundant in the Labrador Sea today (Petrushevskaya and Björklund, 1974). Highest percentages of the species are recorded from surface sediments of the eastern Barents Sea (73%), Beaufort and Chukchi Seas (54–93%), on the Iceland Plateau (76%) and southwest of Jan Mayen Island (52–61%) (Molina-Cruz and Bernal-Ramirez, 1996; Björklund et al., 1998; Björklund and Kruglikova, 2003; Cortese et al., 2003; Itaki et al., 2003).

However, except of the Iceland Plateau, radiolarian abundances in surface sediments of the Arctic Seas and most of the Greenland Sea are generally

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**Fig. 4.** (A) Measurements of *A. setosa* tests: 1, height of eucaphalic chamber; 2, height of antecephalic chamber; 3, height of postcephalic chamber; 4, width of cephalis; 5, frontal diameter; 6, total height; 7, sagittal diameter. (B) Graphic simulation of *A. setosa* tests from the different areas.

**Fig. 5.** Morphometric data on *A. setosa* tests from the Sea of Okhotsk and the North Atlantic.
low, ranging between several hundreds to few specimens per gram bulk sediment (Björklund and Kruglikova, 2003; Cortese et al., 2003; Itaki et al., 2003). A really massive accumulation of *A. setosa* is centered on the Iceland Plateau, where maximal percentages (>50%) together with highest radiolarian abundances (>50,000 individuals per gram bulk sediment) occur in surface sediments of the western part (Cortese et al., 2003). The Iceland Plateau is an area of intricate mixing of cold and relatively fresh polar waters with warmer and saline Atlantic waters (Swift and Aagaard, 1981) and high-chlorophyll concentrations (up to 2 µg/l) during summer (July–September, World Ocean Atlas 2001 in Conkright et al., 2002). Summer sea-surface temperatures in the area are below 10°C and salinity varies from 34.3 to 35.1 psu (Björklund et al., 1998). The information gathered from several investigations in the Arctic Ocean and Nordic Seas shows that *A. setosa* lives in a cold-water environment (Petrushevskaya, 1969, 1974; Petrushevskaya and Björklund, 1974; Swanberg and Eide, 1992; Schröder-Ritzrau, 1995; Itaki et al., 2003). However, the mass accumulation of the species on the Iceland Plateau, an area of strong vertical mixing of the water column, leads us to conclude that besides temperature food supply also is a controlling factor for the high accumulation of the species in the sediment record.

In order to understand the effect of the hydrography on the abundant accumulation of *A. setosa* in the Iceland Sea, we extracted temperature, salinity and oxygen data from the upper 500 m of this ocean area, averaged over the time period July–September (World Ocean Atlas 2001 in Conkright et al., 2002) and compared the data with those from the Sea of Okhotsk (Fig. 6A). In contrast to the Arctic Ocean and Nordic Seas, *A. setosa* does not occur in the modern environment of the Sea of Okhotsk (Kruglikova, 1975; Nimmergut and Abelmann, 2002; Abelmann and Nimmergut, 2005). The comparison shows that there are some distinct environmental differences between the Iceland Sea and the Sea of Okhotsk. The latter is covered by sea-ice during winter whereas the Iceland Sea is generally ice-free year-round but affected by cold waters originated from the Greenland Current (Swift and Aagaard, 1981; Parkinson, 2000).

In the Iceland Sea, subsurface waters below the shallow non-steep thermocline are characterized by rather uniform conditions with low temperatures (between −0.5 and +2°C), high salinity (between 34.7 and 35 psu), and high-dissolved oxygen (between 7 and 7.5 × 10^{-6} mol/l) values (World Ocean Atlas 2001 in Conkright et al., 2002), which point to intensive mixing and ventilation of the water column from the sea surface (Fig. 6A). The hydrographic conditions of the Sea of Okhotsk are distinctly different from those of the Iceland Sea, and are characterized by a steep thermocline, caused by strong freshening and warming of the uppermost sea surface during summer and by distinctly lower salinity and oxygen values in surface and subsurface waters (Kitani, 1973; Yang and Honjo, 1996). The pronounced sea-surface stratification during summer inhibits strong vertical mixing of the water column. The evident difference between the vertical water structures of the Iceland Sea and Sea of Okhotsk is illustrated in the temperature/salinity diagrams (Fig. 6B): the water column of the Iceland Sea exhibits no pronounced sea surface stratification whereas the Sea of Okhotsk water column is strongly stratified. The comparison supports our suggestion that *A. setosa* prefers environmental conditions characterized by well-mixed, cold and saline surface/subsurface waters, which increases the food supply into the upper ocean.

4.2. Pleistocene and Holocene *A. setosa* distribution

The abundant occurrence of *A. setosa* in sediments of the Sea of Okhotsk, Subarctic Pacific and North Atlantic makes the species a potential stratigraphic and paleoecological indicator. In the Sea of Okhotsk and Subarctic Pacific, prominent peaks of *A. setosa* are generally found within the interglacial intervals below the MIS boundary 5/4 (Fig. 3) whereas in the open North Pacific *A. setosa* occurs in distinct lower numbers (Kruglikova, 1976, 1977, 1999; Matul et al., 2002b).

Interglacial intervals in the Sea of Okhotsk are marked by increased radiolarian and biogenic silica accumulation (Nürnberg and Tiedemann, 2004; Matul et al., 2002b). In contrast to the Subarctic Pacific, *A. setosa* is one of the most prominent species of the glacial radiolarian assemblages in the Labrador Sea during MIS 2–4, although the relatively low absolute radiolarian numbers may imply reduced productivity during this time period (Matul et al., 2002a). Reduced biological productivity during MIS 2–4 is also recorded from ODP Site 646 in the central Labrador Sea (Aksu et al., 1992). The magnitude of biological productivity is strongly influenced by the duration of the sea-ice cover (Scharek et al., 1994). The recently established
last glacial sea-surface reconstruction in the northern North Atlantic and Nordic Seas show that the area was ice-free during summer (Pflaumann et al., 2003). This was also suggested by earlier studies, which imply a northward transport of warmer air and water masses during MIS 2 and 4 that have caused ice-free conditions in the Labrador Sea during summer (Alam et al., 1983; Aksu and Mudie, 1985). We suggest that the high percentages of *A. setosa* but low-radiolarian accumulation during MIS 2 and 4 reflect environmental conditions comparable to those of the Arctic Ocean today, where the biological productivity is restricted to the short ice-free summer (Bjørklund and Kruglikova, 2003; Itaki et al., 2003). The other limiting factor that could have lowered glacial productivity in the Labrador Sea might be the reduced inflow of nutrients (e.g., silica) from the ice-covered Arctic Ocean (Aksu and Mudie, 1985). We suggest that the high percentages of *A. setosa* but low-radiolarian accumulation during MIS 2 and 4 reflect environmental conditions comparable to those of the Arctic Ocean today, where the biological productivity is restricted to the short ice-free summer (Bjørklund and Kruglikova, 2003; Itaki et al., 2003). The other limiting factor that could have lowered glacial productivity in the Labrador Sea might be the reduced inflow of nutrients (e.g., silica) from the ice-covered Arctic Ocean (Aksu and Mudie, 1985). This could explain why the *A. setosa* tests recorded in Labrador Sea Core P172 are thinner walled than those from the Sea of Okhotsk, North Atlantic and Nordic Seas. *A. setosa* is suggested to be less resistant against dissolution in the Nordic Seas, where its abundances correlate with biogenic opal preservation (Cortese et al., 2003). As the species in our material from the Labrador Sea exhibits (1) high numbers in glacial sediments, and (2) significant abundance changes at major paleoclimatic boundaries (increase at MIS 5/4 boundary and drop at MIS 2/1 boundary), we assume that not dissolution but environmental changes are the main factors controlling the *A. setosa* distribution in the Labrador Sea during MIS 1–5.

The co-occurrence of high percentages of *A. setosa* and radiolarian abundances in interglacial sediments of the Sea of Okhotsk below MIS 4 may reflect hydrographic conditions similar to those of the Iceland Sea today, marked by cold but ice-free conditions during winter, longer high-productivity periods and enhanced supply of nutrients through vertical mixing of the water column. The disappearance of *A. setosa* from the Sea of Okhotsk and from the Subarctic Pacific is difficult to explain yet. It may be ascribed to the establishment of a strongly developed sea-surface stratification during summer, induced by seasonal changes in the monsoon system. The oceanic system of the Sea of Okhotsk and northwestern Pacific today are strongly influenced by the large-scale atmospheric circulation (Uda, 1963). The winter monsoon leads to strong cooling and sea-ice formation in the northwestern Pacific and in the Sea of Okhotsk. The southeast Asian summer monsoon transports warm and

![Fig. 6. The vertical structure of the surface and subsurface waters in the modern Sea of Okhotsk and Iceland Sea: (A) distribution of main hydrographic parameters, (B) temperature/salinity diagrams. The hydrological data are extracted from the World Ocean Atlas 2001 (Conkright et al., 2002).](image-url)
moisture-laden air masses to the Sea of Okhotsk that leads to a warming (up to 14 °C) and freshening (≤ 32.8 psu) of the upper sea surface (50 m) during summer (Kitani, 1973; Yang and Honjo, 1996). The thin, warm and low-salinity upper sea surface, in combination with the near-freezing temperature minimum below, leads to a pronounced stratification within the upper 200 m (Kitani, 1973; Yang and Honjo, 1996). We speculate that the development of such shallow halocline and warming of the upper sea surface may explain the disappearance of A. setosa from the northwestern North Pacific at the end of MIS 5. Evidence for an abrupt change in the Asian monsoon system at the transition of MIS 5/4 is given by data obtained from the Chinese Loess plateau (Porter, 2001; Xiong et al., 2002; Xiao et al., 1995). Changes in winter/summer monsoon conditions at that time could have evoked the development of such shallow halocline.

The persistently abundant occurrence of A. setosa during interglacial periods is recorded from the Sea of Okhotsk since 750 k.y. (Fig. 3) and from the Subarctic Pacific since about 550 k.y. (Kruglikova, 1976, 1977). The first occurrence in the North Atlantic is described from cores of the Labrador Sea where the species occurs commonly in MIS 10 and 8 (ODP Leg 105 sites, K.R. Bjørklund, personal communication), but high-quantitative numbers are only documented from MIS 4 to 2 (Core P172), yet (Fig. 3). Based on this information, we assume that the species migrated during periods with high sea-level stands such as MIS 11 and 5e from the Subarctic Pacific area into the Arctic Ocean and then into the Labrador Sea (Shackleton, 1987; Zazo, 1999; Gallup et al., 2002; Cutler et al., 2003). The possibility of the Pleistocene migrations of A. setosa is supported by the detection of similar faunistic movements during the Late Pliocene when a large portion of shallow-water molluscs migrated from the North Pacific northward through the Bering Strait into the North Atlantic (Taldenkova, 1998; Marincovich, 2000).

During the MIS 5e warming, the environmental conditions in the Arctic areas of northwest America and northeast Asia were milder than now. Pollen analyses show that the forests on Chukotka (north-east Asia) extended up to 1000 km to the north in comparison to the present (Lozhkin and Anderson, 1995; Shilo et al., 2001). The climatic warming during this period is also indicated in the reduced sea-ice extent in the Arctic Ocean. The study of benthic foraminifera and molluscs from the north-western Alaskan coast and shallow Beaufort Sea, suggests that during MIS 5e, the Bering Sea and the Arctic Ocean along Alaska were not perennially covered by sea-ice and that the winter sea-ice boundary in the Arctic Ocean was at least 800 km north of the Bering Strait (Brigham-Grette and Hopkins, 1995). Considering that even today modified Pacific water flow slowly via the Canadian Archipelago and Fram Strait into the northern North Atlantic (Dickson, 1999; Jones, 2001; Falck, 2001), one might expect that the climatic warming such as MIS 5e and MIS 11 have favored the water-mass transfer from the North Pacific via the Arctic Ocean into the North Atlantic.

There might be two possible migration pathways of A. setosa within the surface and subsurface water masses from the Arctic Ocean into the North Atlantic. One would be via the deepest channels of the Canadian Archipelago (e.g., via Parry Channel) through the Baffin Bay into the Labrador Sea (Fig. 2). The other would be via the Fram Strait into the Nordic Seas. However, the occurrence of A. setosa in the Nordic Seas before the last deglaciation is not finally approved yet. Jansen and Björklund (1985) attribute the first appearance of A. setosa, together with diatoms and coccoliths, in the southeastern Norwegian Sea to the beginning of the Allerød chronozone, at 12 ka, when Atlantic waters flowed into the area. The only available information that the species occurred earlier in the Nordic Seas also is based on a biostratigraphic study of DSDP Leg 38 sites where the species is described to be present in one sample of the uppermost, “Glacial” sediment unit (Björklund, 1976). The uncertainty of the latter age interpretation and the early occurrence of A. setosa in Core P172 from the Labrador Sea lead us to conclude that the pathway through the Canadian Archipelago channels into the Labrador Sea is the most likely one or at least the best documented one. The morphometric study shows that closest morphological similarities of A. setosa tests occur between the Sea of Okhotsk and Labrador Sea specimens within the upper MIS 5 (Fig. 5) and would support the pathway via the Canadian Archipelago channels. Alternatively, the species is not recorded in Pleistocene sediments of the Nordic Seas due to selective dissolution, as described from sediment trap and surface sediment studies in the Greenland Sea (Schröder-Ritzrau, 1995; Cortese et al., 2003), or to the lack of well-preserved radiolarian records in this area.
The first documented appearance of *A. setosa* in the North Atlantic is in the upper MIS 5 of Core P172 from the Labrador Sea, where the species occurs in very low numbers. A possible explanation why *A. setosa* did not occur earlier and in higher abundances during MIS 5 in the Labrador Sea might be that the surface water temperatures were simply too warm, caused by the extension of warm Atlantic water into this Subarctic area. This is supported by the occurrence of subtropical/tropical radiolarian species (*Botryococcus auritus-australis*, Collosphaeridae spp., *Didymocystis tetrathalamus*, *Tetrapyle quadriloba*) in the warm intervals of MIS 5 in Core P172 (Matul et al., 2002a). The significant surface water warming during MIS 5 in the Labrador Sea also is exhibited in sharp accumulation peaks of warm-water microfossils (e.g., the subtropical coccolith species *Gephyrocapsa oceanica*, and the temperate/subtropical planktic foraminifers *Neogloboquadrina pachyderma* dextral, *Globigerina quinqueloba* and *oceanica*) (e.g., the subtropical coccolith species *Gephyrocapsa oceanica*, and the temperate/subtropical planktic foraminifers *Neogloboquadrina pachyderma* dextral, *Globigerina quinqueloba* and *oceanica*) during the Younger Dryas in these areas.

Moreover, the reconstruction of the glacial sea-surface circulation of the northwest Atlantic (Sarnthein et al., 2003; Pflaumann et al., 2003) points to advection of warmer water up to the area west of Iceland and southward flow of polar waters that might have forced enhanced convection in the northwestern Atlantic, making this area an ideal site for the formation of the glacial upper North Atlantic Deep Water (Duplessy et al., 1991; Sarnthein et al., 2003; Pflaumann et al., 2003).

The onset of the last deglaciation, which forced the northward retreat of glacial cold waters (Ruddiman and McIntyre, 1981), limited the extension of *A. setosa* within the northern North Atlantic. High numbers of *A. setosa* (up to 40%) are only documented during the Younger Dryas cooling in cores located south of Iceland, in the North Sea, and in the southeastern Norwegian Sea (Jansen and Björklund, 1985; Björklund, 1985; Matul, 1995b). Sarnthein et al. (1995, 2001) suppose that the North Atlantic thermohaline circulation during the Younger Dryas was little different from the modern mode, leading to the same level of deep-water formation as during the Holocene. However, sea-surface conditions at that time differed from the modern ones. A strong cooling of the sea surface especially during winter, which could result in the extension of winter sea-ice and in a marked cooling of the Norwegian Sea and of the area south of Iceland (Ruddiman and McIntyre, 1981; Sarnthein et al., 1995, 2001), might have favored the abundant occurrence of *A. setosa* during the Younger Dryas in these areas.

At the beginning of the Holocene, the modern-type of circulation in the North Atlantic and Norwegian Sea was established (Jansen and Björklund, 1985). Subarctic waters retreated to the area of the Iceland/Greenland Seas, providing optimal environmental conditions for the final abundant settlement of *A. setosa* as indicated in the Holocene records from the northern Iceland Plateau (Molina-Cruz, 1991), and from the Greenland Sea (Schröder-Ritzrau, 1995).

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