Appearance of the Pacific diatom *Neodenticula seminae* in the northern Nordic Seas – An indication of changes in Arctic sea ice and ocean circulation

Arto Miettinen a,⁎, Nalan Koç a,b, Katrine Husum b

a Norwegian Polar Institute, Fram Centre, N-9296 Tromsø, Norway
b Department of Geology, University of Tromsø, Dramsveien 201, N-9037 Tromsø, Norway

**A R T I C L E   I N F O**

Article history:
Received 30 April 2011
Received in revised form 30 May 2012
Accepted 4 June 2012

Keywords:
Neodenticula seminae
Diatoms
Pacific water
Arctic
Sea ice
Ocean circulation
The Nordic Seas

**A B S T R A C T**

The marine diatom *Neodenticula seminae* belongs to the present day planktonic assemblage of the subarctic North Pacific and its high-latitude marginal seas. In the middle and high-latitude North Atlantic, *N. seminae* occurred from the middle Pleistocene to the early–middle Pleistocene transition when it became locally extinct. After a long absence of 0.84 Ma, it was found again in the North Atlantic in the late 1990s (Reid et al., 2007). Here we show from sediment samples taken in 2006, 2007 and 2008 that *N. seminae* now has appeared in the Nordic Seas for the first time in geologic history, and it already has a widespread modern distribution in the northern Nordic Seas. The appearance of *N. seminae* in the Nordic Seas coincides with an increased influence of Pacific water via the Arctic Ocean due to diminished sea ice and/or changed ocean circulation in the Arctic Ocean. Our results show that trans-Arctic exchanges, which were first observed in the North Atlantic in the late 1990’s are still in motion, or possibly even accelerated during recent years. The appearance of *N. seminae* in the Nordic Seas might even suggest initiation of a unique climatic transition of the scale seen during the mid-Pleistocene transition. More trans-Arctic exchanges can be expected in the near future if the modern warming trend and reduction of sea ice continues in the Arctic.

© 2012 Elsevier B.V. All rights reserved.

**1. Introduction**

The ongoing episode of climate warming has drastic consequences for marine conditions especially in the northern oceans (Fig. 1). The Arctic Ocean responds more rapidly to global warming than most areas of the planet; observations document accelerating retreat and thinning of the Arctic sea ice cover over recent decades (e.g. Comiso et al., 2008). These changes in sea ice cover substantially affect atmospheric, hydrographic and ecological conditions at high latitudes (Spreen et al., 2009; Leu et al., 2010; Overland and Wang, 2010; Polyak et al., 2010), e.g. freshwater export from the Arctic may modify global- to basin-scale ocean circulation patterns and climate (Greene et al., 2008; de Steur et al., 2009), or earlier phytoplankton blooms in the Arctic Ocean may have consequences to the Arctic food chain and carbon cycling (Kahru et al., 2011).

*Neodenticula seminae* (Simonsen & Kanaya) Akiba & Yanagisawa is a pennate marine planktonic diatom which belongs to the modern assemblage of the subarctic North Pacific and its high-latitude marginal seas, where it commonly accounts for >40% of the diatom assemblage (Kanaya and Koizumi, 1966; Sancetta, 1982; Sancetta and Silvestri, 1986; Takahashi, 1986; Shimada et al., 2006). The species appeared in the fossil record around 2.4 Ma in the North Pacific (Akiba and Yanagisawa, 1986; Yanagisawa and Akiba, 1990, 1998). During the Holocene, *N. seminae* was the dominant diatom assemblage in the Bering Sea from 6.5 cal ka BP to the present (Caisse et al., 2010). Primary productivity in the subarctic North Pacific is among the highest in the world’s oceans with the phytoplankton serving as an efficient biological pump driving elemental cycles including the carbon content of the ocean (Honjo, 1997). The dominant diatoms (including *N. seminae*) in this highly productive region play an important role in ocean-scale ecosystem and biochemical dynamics (Shimada et al., 2006).

In the middle and high-latitude North Atlantic, *N. seminae* occurred from the Middle Pleistocene at 1.26 Ma to the early–middle Pleistocene transition at 0.84 Ma ago (Baldauf, 1986; Koç and Flower, 1998; Koç et al., 1999). Baldauf (1986) interpreted that the occurrence of *N. seminae* in the North Atlantic indicates the presence of cool and low-salinity surface waters originated from the Arctic Ocean in the early Pleistocene, and that this suggests that the Arctic Ocean was partially ice free allowing the transportation of the species between the Bering Sea and the North Atlantic. The time interval when *N. seminae* was present in the North Atlantic straddles the transition from the dominance of 41 ka cycles in the climate record to the dominance of 100 ka cycles. It is possible that the first occurrence of *N. seminae* in the North Atlantic is an indicator of the cooling, which started at 1.26 Ma, leading to the establishment of the 100 ka cycles

[doi:10.1016/j.marmicro.2012.06.002]
and intensified Northern hemisphere glaciations. Conditions in the North Atlantic were too warm for subarctic \textit{N. seminae} before 1.26 Ma, after which conditions cooled to subarctic environment favorable for the species. \textit{N. seminae} thrived in the North Atlantic the next ca. 0.4 Ma until conditions turned too severe with perennial sea ice cover leading to the disappearance of the species at 0.84 Ma. A closure of the connection between the Pacific and the Bering land bridge due to the growth of ice and falling sea level (Head and Gibbard, 2005) could be another reason for the disappearance at this time, but more likely the colder conditions in the North Atlantic led to the extinction of \textit{N. seminae} in this area (e.g. Reid et al., 2007). The presence of \textit{N. seminae} in North Atlantic sediments may therefore be attributable to the unique conditions related to the mid-Pleistocene transition (Koç et al., 1999).

After a long absence, re-occurrence of \textit{N. seminae} was reported in the Labrador Sea (Fig. 1) during the late 1990s as the first record in the North Atlantic for more than 0.8 Ma (Reid et al., 2007). They suggested that \textit{N. seminae} was carried in a pulse of Pacific water in 1998/early 1999 via the Canadian Arctic Archipelago and/or Fram Strait, and that the event coincided with modifications in Arctic hydrography and circulation, the increased flows of Pacific water into the Northwest Atlantic and the exceptional occurrence of extensive ice-free water to the North of Canada in the previous year 1998. It appears therefore that the appearance of \textit{N. seminae} is an indicator of the speed of the change that is taking place in the Arctic and North Atlantic Oceans as a consequence of regional climate warming and marks a change in the circulation between the North Pacific and North Atlantic Oceans via the Arctic (Reid et al., 2007, 2008).

Although \textit{N. seminae} was found at one site north of Iceland in 2002 (Reid et al., 2007), this species has never been found elsewhere in the Nordic Seas (the Greenland, Iceland and Norwegian Seas). In this paper, we report the appearance of the Pacific diatom \textit{N. seminae} in surface sediment samples recovered in 2006–2008 from the northern Nordic Seas. This discovery represents a considerable expansion of its subarctic range since its appearance in the plankton of the northern North Atlantic in 1999. We also discuss the causes of this appearance and the significance of the findings as evidence of the trans-Arctic migration of planktonic organisms from the North Pacific to the North Atlantic.

2. Material and methods

During the International Polar Year 2007–2008 (IPY), 36 stations were sampled for surface sediments from the East Greenland and West Spitsbergen margins, Greenland Basin and Fram Strait during cruises by the R/V \textit{Jan Mayen} in October 2006, September 2007, and August 2008.

Undisturbed surface sediment samples were taken by multi corer and/or box corer. As an original aim, a total of 25 surface sediment samples were studied for diatoms in order to extend the existing training data set of Andersen et al. (2004b) for diatom transfer functions for quantitative sea surface temperature (SST) reconstructions (Miettinen and Koç, in preparation).

The diatom samples were prepared using the method described by Koç et al. (1993), which consists of HCl and H$_2$O$_2$ treatment to remove calcium carbonate and organic matter, clay separation and preparation of quantitative slides. A Leica Orthoplan microscope with 1000× magnification was used to identify and count the diatoms. The counting procedure described by Schrader and Gersonde (1978) was followed. A minimum of 300 diatom frustules (in addition to Chaetoceros resting spores) were identified for each sample.

3. Results

\textit{N. seminae} was found in most of the surface sediment samples (21/25 = 84%) taken from the northern Nordic Seas in 2006, 2007

![Fig. 1. The northern oceans. FS = Fram Strait, BS = Bering Strait, CAA = Canadian Arctic Archipelago, GST = Gulf of St. Lawrence. The study area is outlined.](image-url)
4. Discussion

4.1. Stratigraphic and biogeographical distribution of N. seminae in the North Atlantic and Nordic Seas

*N. seminae* is found in the North Atlantic from 1.26 to 0.84 Ma (Baldauf, 1986; Koç and Flower, 1998; Koç et al., 1999). However, it is not present in the Nordic Seas, not even during the middle Pleistocene when it is common in the North Atlantic (e.g. Koç and Scherer, 1996). *N. seminae* was not found in a set of surface samples from the Nordic Seas collected for the training data set of Andersen et al. (2004b) for quantitative sea surface temperature (SST) reconstructions. It is not observed either in any Holocene paleoceanographic records based on diatoms from the North Atlantic (e.g. Andersen et al., 2004a,b; Berner et al., 2008). *N. seminae* has first been reported in the plankton of the North Atlantic subpolar gyre (Labrador Sea) in 1999. Its geographic distribution has been extended to the Irminger Sea one year later (Reid et al., 2007), and to the Gulf of St. Lawrence in 2001 and 2002 (Starr et al., 2002, 2003). In addition, it has been reported at one station to the north of Iceland in 2002, and at two stations south of Iceland in 2002 and 2003 (Reid et al., 2007). Despite the dominance of this species in phytoplankton assemblages and its high abundance in the Gulf of St. Lawrence in 2001 (Starr et al., 2002), it is not widely distributed, e.g. it is only observed in 0.2% of the samples of the Continuous Plankton Recorder survey (Reid et al., 2007). Except at one site north of Iceland in 2002 (Reid et al., 2007), *N. seminae* has never been observed in the Nordic Seas prior to the current study of samples from 2006 to 2008. The species is not recorded in the core-top sample of a high-resolution sediment core from the Iceland Basin of the subpolar North Atlantic which represents the year 2004 (Miettinen et al., 2011, 2012). Neither is *N. seminae* observed in a high-resolution diatom study of core MD99-2322 from the East Greenland shelf, covering the last 2800 years (the core-top sample is from the 19th century), even though the core site is directly influenced by the East Greenland Current which carries water outflowing from the Arctic Ocean (Miettinen and Koç, in preparation). Together these observations indicate that the recent appearance of *N. seminae* in the Nordic Seas is the first time in geological history, and likely to be linked to recent changes in the Arctic Ocean.

4.2. Causes of the expansion of *N. seminae* into the Nordic Seas

Trans-Arctic exchanges of boreal plankton between the Pacific and Atlantic are affected by changes in sea level, (sea) ice cover, and ocean circulation (Greene et al., 2008). The Bering Strait is a gateway between the Pacific and the Arctic Ocean. During the periods of continental ice sheets during the Pleistocene, and thus lower global sea level, the Bering Strait can be completely blocked. Once Pacific organisms have reached the Arctic Ocean, sea ice cover and circulation patterns determine whether or not they can encroach on the North Atlantic through the Canadian Archipelago and/or Fram Strait (Greene et al., 2008). As the journey of organisms across the Arctic Ocean takes several months, their survival is also dependent on their physiological ability to survive low temperatures and light levels.

The observed frequency of *N. seminae* in surface sediment samples across the northern Nordic Seas indicates a widespread modern distribution of the species in this region. This suggests a higher influence of the Pacific waters arriving through the Fram Strait during the last few years. One cause for the stronger freshwater fluxes and introduction of a Pacific component into the diatom assemblages of the Nordic Seas in 2006–2008 may be the recorded reductions in the extent of sea-ice cover in 2005 and 2007 (Fig. 3).

Our results suggest that during the sea ice minima of the last few years, there has been a single pulse or several pulses of Pacific surface

---

**Table 1**

<table>
<thead>
<tr>
<th>Site no.</th>
<th>Station number</th>
<th>Area</th>
<th>Latitude</th>
<th>Longitude</th>
<th><em>N. seminae %</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>JM06-WP-07-BC</td>
<td>West Spitsbergen</td>
<td>78 52.620 N</td>
<td>007 20.459 E</td>
<td>2.6</td>
</tr>
<tr>
<td>2</td>
<td>JM06-WP-10-BC</td>
<td>Fram Strait</td>
<td>78 56.176 N</td>
<td>005 24.075 E</td>
<td>–</td>
</tr>
<tr>
<td>3</td>
<td>JM06-WP-12-BC</td>
<td>Fram Strait</td>
<td>78 54.461 N</td>
<td>002 24.919 E</td>
<td>–</td>
</tr>
<tr>
<td>4</td>
<td>JM06-WP-14-BC</td>
<td>Western Fram Strait, sea-ice edge</td>
<td>78 55.888 N</td>
<td>001 06.460 E</td>
<td>1.0</td>
</tr>
<tr>
<td>5</td>
<td>JM06-WP-16-MC</td>
<td>Western Fram Strait, sea-ice edge</td>
<td>78 53.767 N</td>
<td>016 06.16 E</td>
<td>1.3</td>
</tr>
<tr>
<td>6</td>
<td>JM06-WP-19-MC</td>
<td>Western Fram Strait, sea-ice edge</td>
<td>78 50.077 N</td>
<td>002 30.173 W</td>
<td>1.4</td>
</tr>
<tr>
<td>7</td>
<td>JM06-WP-21-MC</td>
<td>Western Fram Strait, sea-ice edge</td>
<td>77 00.204 N</td>
<td>003 23.662 W</td>
<td>1.9</td>
</tr>
<tr>
<td>8</td>
<td>JM06-WP-24-MC</td>
<td>Western Fram Strait, sea-ice edge</td>
<td>74 38.00 N</td>
<td>011 11.21 W</td>
<td>0.5</td>
</tr>
<tr>
<td>9</td>
<td>JM06-WP-26-MC</td>
<td>Western Fram Strait, sea-ice edge</td>
<td>74 53.49 N</td>
<td>010 46.10 W</td>
<td>1.0</td>
</tr>
<tr>
<td>10</td>
<td>JM07-WP-168-MC</td>
<td>Greenland Sea</td>
<td>70 09.00 N</td>
<td>014 31.00 W</td>
<td>5.7</td>
</tr>
<tr>
<td>11</td>
<td>JM07-WP-170-MC</td>
<td>East Greenland Margin</td>
<td>73 44.873 N</td>
<td>024 11.956 W</td>
<td>1.5</td>
</tr>
<tr>
<td>12</td>
<td>JM07-WP-171-MC</td>
<td>East Greenland Margin</td>
<td>73 46.138 N</td>
<td>013 03.603 W</td>
<td>0.7</td>
</tr>
<tr>
<td>13</td>
<td>JM07-WP-172-MC</td>
<td>East Greenland Margin</td>
<td>73 47.080 N</td>
<td>012 21.640 W</td>
<td>–</td>
</tr>
<tr>
<td>14</td>
<td>JM07-WP-176-MC</td>
<td>Scoresby Sound Shelf</td>
<td>69 51.585 N</td>
<td>022 07.008 W</td>
<td>0.3</td>
</tr>
<tr>
<td>15</td>
<td>JM07-WP-180-MC</td>
<td>Greenland Basin, western side</td>
<td>77 28.610 N</td>
<td>002 02.540 W</td>
<td>1.3</td>
</tr>
<tr>
<td>16</td>
<td>JM07-WP-182-MC</td>
<td>Greenland Basin</td>
<td>77 30.540 N</td>
<td>000 02.270 W</td>
<td>1.3</td>
</tr>
<tr>
<td>17</td>
<td>JM08-WP-337-MC</td>
<td>West Spitsbergen Slope</td>
<td>78 08.130 N</td>
<td>006 30.411 E</td>
<td>1.9</td>
</tr>
<tr>
<td>18</td>
<td>JM08-WP-338-MC</td>
<td>West Spitsbergen Slope</td>
<td>78 10.029 N</td>
<td>006 32.731 E</td>
<td>1.7</td>
</tr>
<tr>
<td>19</td>
<td>JM08-WP-339-MC</td>
<td>Fram Strait</td>
<td>77 59.731 N</td>
<td>005 58.354 E</td>
<td>1.0</td>
</tr>
<tr>
<td>20</td>
<td>JM08-WP-341-MC</td>
<td>Fram Strait</td>
<td>77 59.720 N</td>
<td>004 07.442 E</td>
<td>0.3</td>
</tr>
<tr>
<td>21</td>
<td>JM08-WP-342-MC</td>
<td>Fram Strait</td>
<td>75 59.752 N</td>
<td>004 19.589 E</td>
<td>1.3</td>
</tr>
<tr>
<td>22</td>
<td>JM08-WP-344-MC</td>
<td>Fram Strait</td>
<td>75 58.938 N</td>
<td>008 19.364 E</td>
<td>2.3</td>
</tr>
<tr>
<td>23</td>
<td>JM08-WP-345-MC</td>
<td>Fram Strait</td>
<td>75 59.682 N</td>
<td>011 01.013 E</td>
<td>2.3</td>
</tr>
<tr>
<td>24</td>
<td>JM08-WP-348-MC</td>
<td>Storfjord Through</td>
<td>75 59.737 N</td>
<td>013 17.892 E</td>
<td>0.6</td>
</tr>
<tr>
<td>25</td>
<td>JM08-WP-350-MC</td>
<td>Hornsund Deep</td>
<td>76 47.888 N</td>
<td>014 58.809 E</td>
<td>–</td>
</tr>
</tbody>
</table>
waters which has transported _N. seminae_ into the Nordic Seas. The fluxes of Pacific water through the Arctic Ocean have occurred at least since the 1970s (e.g. Belkin, 2004) but they have not been found able to transport _N. seminae_ into the Nordic Seas previously. We point out that the recent appearance of _N. seminae_ could suggest the occurrence of larger ice free areas in the Arctic and conditions (e.g. enough light for the photosynthesis of diatoms and maybe also warmer sea surface) enabling _N. seminae_ to survive the long journey across the Arctic Ocean. In earlier pulses, since the 1970s, Pacific water has probably flowed under ice with too severe conditions for diatoms.

After arriving at the Nordic Seas, _N. seminae_ has maintained viable standing stocks in the area, i.e. most probably, the species belongs now to the recent diatom assemblage of the Nordic Seas. Thus, the recent occurrence of _N. seminae_ does not necessarily indicate a persistent input of Pacific water although this was the original source.

The observed distribution suggests that Fram Strait is the main transport route for these Pacific diatoms into the Nordic Seas. However, a somewhat higher occurrence of _N. seminae_ in the NE sector of the Nordic Seas is difficult to explain by the ocean current system, since the area influenced by the East Greenland Current (which originally carried the species into the Nordic Seas) is not so rich in _N. seminae_. We think that the cause for the recent distribution of the species is the stimulating effect of the warm Atlantic waters on the growth of _N. seminae_ in this area. _N. seminae_ is a subarctic species (not an arctic species, which are common in the area controlled by the East Greenland Current) and therefore the NE sector offers more favorable conditions for its growth and blooming. In principle, _N. seminae_ in the Nordic Seas could have originated from the Canadian Archipelago, which was probably the source for the species in the Labrador Sea (Reid *et al.*, 2007). Later, it could have migrated via the North Atlantic main stream into the Nordic Seas. However, _N. seminae_ in the Nordic Seas is heavily silicified, corresponding to the silicification level of this species in the North Pacific, thereby differing clearly from less

---

**Fig. 2.** Percentage occurrence of _N. seminae_ in the surface sediment samples. Site numbers in Table 1. Arrows show a modern surface circulation pattern in the Nordic Seas (solid lines = cold Arctic waters, dashed lines = warm Atlantic waters, EGC = East Greenland Current) (modified from Blindheim and Østerhus, 2005).

**Fig. 3.** Mean September sea ice extent in millions of km² for the northern hemisphere since 1978 (data from National Snow and Ice Data Center). This is a measure comparable to annual minimum sea ice extent. The blue (gray) line indicates the decreasing trend in September sea ice extent. The years 2006, 2007 and 2008 are highlighted.
silicified species from the Gulf of St. Lawrence in the NW North Atlantic (cf. Poulin et al., 2010). This supports the interpretation of Fram Strait as the source for N. seminae in the Nordic Seas.

Earlier results from the Labrador Sea and the North Atlantic indicate a major reorganization of circulation patterns in the Arctic and Atlantic Oceans during the last three decades (Reid et al., 2007; Greene et al., 2008; Overland and Wang, 2010), possibly in relation with diminished Arctic sea ice. Sea ice level pressure dropped precipitously in the central Arctic and led to the emergence of a strongly cyclonic atmospheric circulation in 1899 (Dickson, 1999). This cyclonic atmospheric circulation resulted in the increased transport of relatively warm, high-salinity Atlantic water into the Arctic Ocean primarily through the Barents Sea (Dickson, 1999; McLaughlin et al., 2002). Associated with the cyclonic atmospheric circulation and enhanced inflow of Atlantic water, an extensive reorganization of upper-ocean circulation patterns occurred in the Arctic Ocean (Dickson et al., 2000). The Pacific water export through the Canadian Archipelago is mainly affected by large-scale atmospheric forcing resembling the Arctic Oscillation (AO) or the North Atlantic Oscillation (NAO). In contrast, the variability of the Pacific water inflow through Fram Strait is controlled by changes in Pacific water storage in the Beaufort Gyre, with an increased export during years with a cyclonic circulation anomaly over the central Arctic Ocean (Jahn et al., 2010). The reorganization of circulation patterns caused several changes in the central Arctic Ocean: a) a shift in the front separating Atlantic and Pacific water masses from the Lomonosov Ridge to the Mendeleyev Ridge, b) a weakening and deflection of the Transpolar Drift, c) a weakening and shrinking of the Beaufort Gyre, d) an intensification and thickening of the Arctic Ocean Boundary Current, and e) a significant redirection of the shallow Arctic Ocean outflow entering the North Atlantic (McLaughlin et al., 2002; Steele et al., 2004).

The appearance of N. seminae in the Nordic Seas could suggest a unique climatic transition of the scale seen during the mid-Pleistocene transition (Koç et al., 1999), which finally led to the disappearance of the species from the North Atlantic at 0.84 Ma due to the severe conditions with perennial sea ice cover. The present appearance of N. seminae suggests that the trend is reversing, i.e. it is getting warmer again and the sea ice cover is becoming seasonal. Therefore it is possible for N. seminae to be transported from the Pacific again, and to survive and bloom in the Nordic Seas as a subarctic species. The appearance of N. seminae in the Nordic Seas could suggest a unique climatic transition of the scale seen during the mid-Pleistocene transition, where its occurrence in the North Atlantic indicated a transition to cold conditions. Today, however, it would rather indicate a transition to warmer conditions.

Our results show that trans-Arctic migrations, which were first observed from the North Atlantic in late the 1990's are still in motion and may have accelerated in recent years. It is likely that further trans-Arctic exchanges of Pacific species can be expected in the near future if the warming trends and sea ice reduction continue in the Arctic. Changes of this nature may pose high risks for the ecology of the Nordic Seas and the North Atlantic.

Acknowledgments

We are grateful to the editor and two anonymous reviewers for their constructive comments and suggestions. This paper is a contribution to the two International Polar Year (IPY) projects “Arctic Ocean warming in the Past” (WARMPAST, IPY 786) and “Arctic Natural Climate and Environmental Changes and Human Adaption: From Science to Public Awareness” (SciencePub, IPY 39) funded by the Research Council of Norway, the University of Tromsø and the Norwegian Polar Institute.

References


