

Review

The North Pacific Diatom Species *Neodenticula seminae* in the Modern and Holocene Sediments of the North Atlantic and Arctic

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Abstract: The paper presents micropaleontological information and observations of the North Pacific diatom species *Neodenticula (N.) seminae* (Simonsen and Kanaya) Akiba and Yanagisawa in the surface and Holocene sediments from the North Atlantic, Nordic, and Arctic Seas. The compilation of previously published data and new findings of this study on *N. seminae* in the surface sediments shows its broad occurrence as a usual element of the modern diatom microflora in the Nordic, Labrador, and Irminger Seas. The recent migration of *N. seminae* from its native area, the Subarctic Pacific, reflects the oceanographic shift in the late 1990s as greater transport of the warmer surface Pacific water to the Arctic causes Arctic sea-ice reduction. Micropaleontological studies of the Holocene sediments document the multiple events of *N. seminae* appearance in the Arctic during the latest Pleistocene and Holocene warming intervals. These observations can suggest the events of the increased influence of the North Pacific water on the Arctic environments in the past, not just during the recent warm climate amplification.

Keywords: micropaleontology; modern monitoring of climate change; Pacific water in the Arctic and North Atlantic; species migration; *Neodenticula seminae*; Arctic Holocene paleocology

1. Introduction

The Arctic Ocean and Subarctic North Atlantic areas have distinctive phytoplankton communities as a part of their marine ecosystems, which are now experiencing substantial change related to recent climate warming [1]. During the past 100 years, the average temperatures in the Arctic have increased significantly, by a factor of two compared to the average global rates [2]. The Arctic sea-ice volume and extent has decreased in the past 40 years by three-quarters and one half on average, respectively [3]. Changing marine environments can stress the subarctic/arctic ecosystems allowing the invasive non-native species to disrupt the local food chains and biodiversity [4]. Alien species can be a major component of recent global change transforming local marine ecosystems [5,6].

One of the examples of marine biological invasions in the Arctic, Nordic, and Labrador Seas is a recent occurrence of the native North Pacific diatom species *Neodenticula (N.) seminae* (Simonsen and Kanaya) Akiba and Yanagisawa [7–9]. Previous biostratigraphic studies of the Quaternary sediments from the Arctic and North Atlantic reported the disappearance of this species from the North Atlantic by the end of the Early Pleistocene, 0.84 million years ago (see literature summary in [8]). Now, it is a prominent component of the diatom assemblages in the Labrador and Nordic Seas (see following text). Micropaleontological studies have exhibited the events of interactions between the North Pacific and North Atlantic during the Pleistocene, e.g., based on radiolarian data [10,11]. The radiolarian species *Amphimelissa (A.) setosa* (Cleve) was dominant in the interglacial microfaunal assemblages of

the Subarctic Pacific during the last 1.1 million years, but disappeared there 72,000 years ago [10,11]. Appearance of *A. setosa* in the Middle to Late Pleistocene interglacial sediments of the Northern North Atlantic suggests the multiple connections between the North Pacific and Atlantic realms during the prominent warmings [11]. The final settling of *A. setosa* in the North Atlantic occurred in the Late Pleistocene; now, it is abundant in the Subarctic and Arctic Seas but does not occur in the North Pacific.

Recent studies of Miettinen et al. [9] and Sha et al. [12] exhibited a common to abundant occurrence of *N. seminae* in the surface sediments of the Fram Strait and Greenland Sea (1–5.7%), and Labrador Sea (2.18–18.21%), respectively. In addition to this information, we present new data on observations of *N. seminae* in the surface sediments of the Labrador and Irminger Seas and discuss the environmental changes which could favor its appearance there. In addition, we compile published reports on the occurrence of *N. seminae* in the Holocene sediments of the Arctic and Nordic Seas to exhibit the multiple events of its invasion from the North Pacific to the Arctic possibly during the Holocene warmings. As some of these reports are in Russian, we try to make them accessible to other specialists in this field of study.

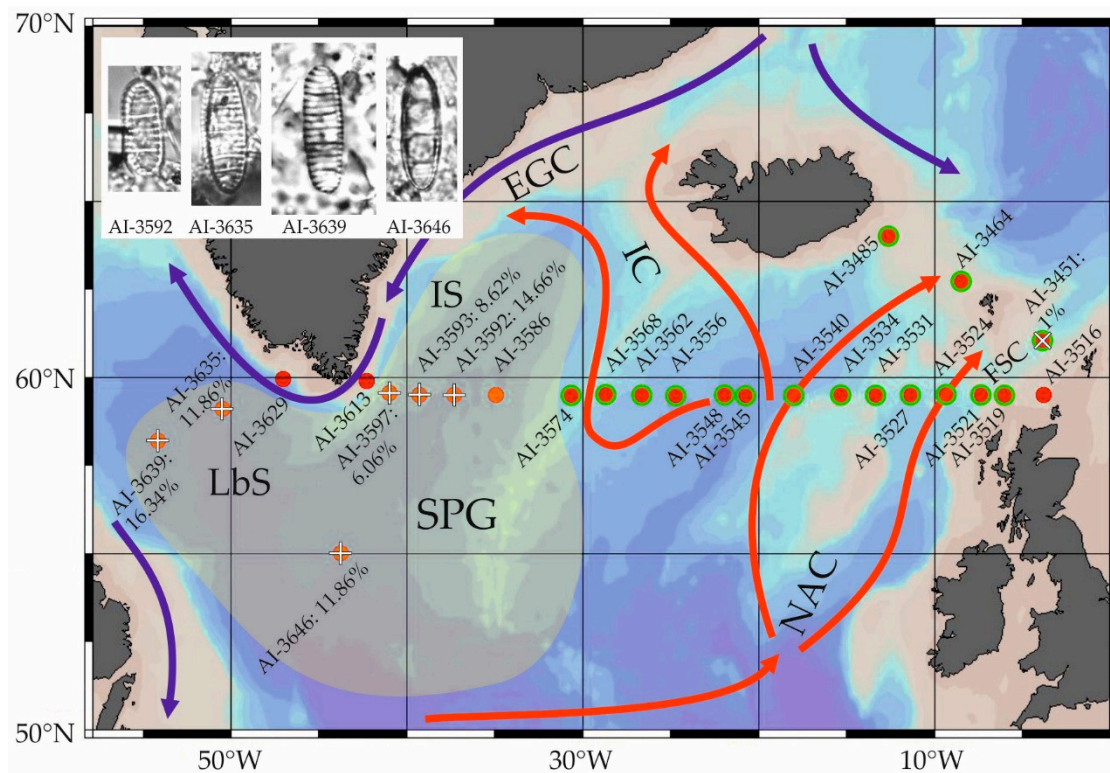


Figure 1. The map of analyzed surface sediment samples (red dots) on the North Atlantic transect at 59.5° N (Table A1). The name of the station follows the position of the sample. White crosses mark samples with *N. seminae*; percentages after the station name show *N. seminae* abundances. Green-framed red dots mark samples with warm-water subtropical diatoms. Red arrows mark warm surface currents, and blue arrows mark cold surface currents. SPG is Subpolar Gyre, LbS is Labrador Sea, IS is Irminger Sea, NAC is North Atlantic Current, IC is Irminger Current, EGC is East Greenland Current, FSC is Faroe-Shetland Channel. The source of the blank map is Ocean Data View software [13]. The microphotographs of *N. seminae* valves are presented.

We compiled data on *N. seminae* distribution in various sampling material and geographical areas: (1) marine plankton from the Northwestern North Atlantic [7,8,14] and Western Arctic Ocean between the Bering Strait and point of 85° N in the Arctic Ocean Basin [15]; (2) sediment trap on Station NAP, the Southern Northwind Abyssal Plain in the Western Arctic Ocean [16]; and (3) the Late Pleistocene and Holocene sediments from the Arctic Ocean and Nordic and Arctic Seas [17–23]. In addition, we report new data on *N. seminae* occurrence in 26 surface sediment samples from a 0–2 cm layer of

the grab samplers obtained during the 51st cruise of the Russian RV Akademik Ioffe in June–July 2016 on the North Atlantic transect at 59.5° N between the Labrador Sea and the Faroe-Shetland Channel (Figure 1; Table A1).

The map of *N. seminae* distribution in the surface sediments of the North Atlantic and Nordic Seas (Figure 2a) presents our data on the 59.5° N transect together with published data of Sha et al. [12] on the Labrador Sea and Miettinen et al. [9] on the Nordic Seas.

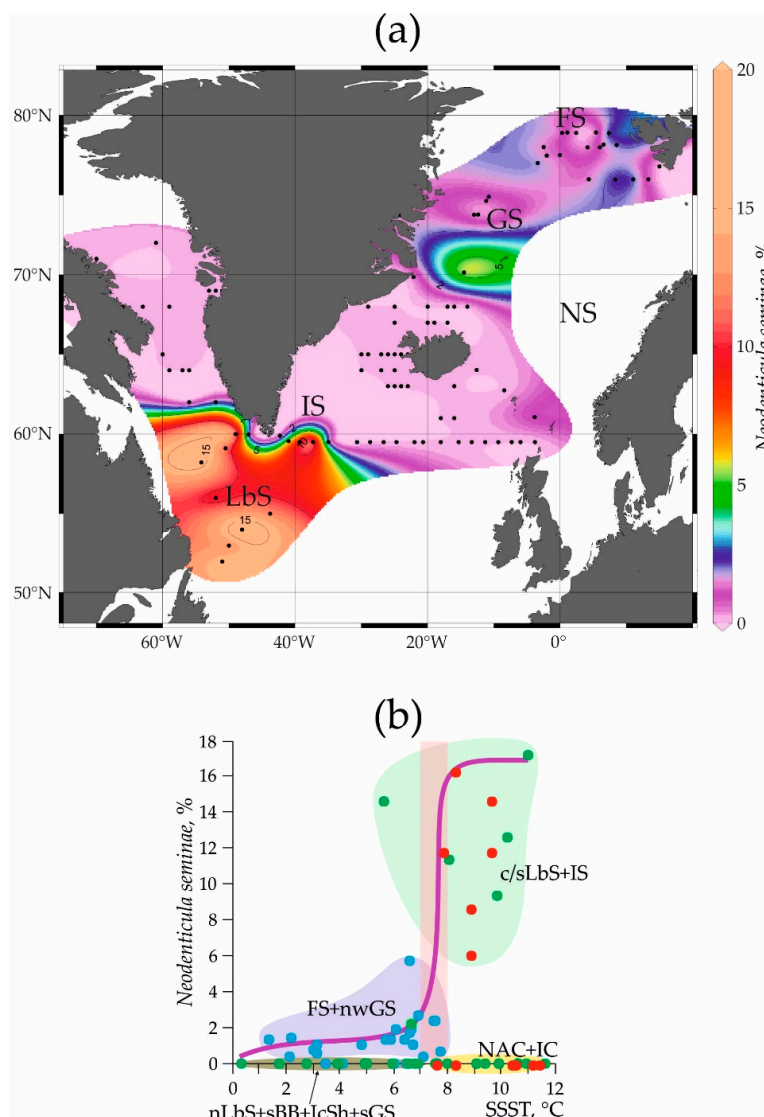


Figure 2. (a) is the distribution of *N. seminae* in the surface sediment samples of the Nordic and Labrador Seas, data from [9,12] and this study (Table A1). Black dots mark diatom samples. (b) is a plot of *N. seminae* percentages in the surface sediments, data from [9,12] and this study (Table A1), versus SSST (Summer Sea Surface Temperature). SSST for the period of 2007–2017 is extracted from the World Ocean Atlas 2018 [24]. Purple line approximates distribution of *N. seminae* greatest percentages. Transparent red vertical bar marks a rapid change of *N. seminae* abundances. Colored fields mark geographical areas: LbS is Labrador Sea, c/sLbS is central/southern Labrador Sea, nLbS is northern Labrador Sea, IS is Irminger Sea, GS is Greenland Sea, nwGs is northwestern Greenland Sea, sGs is southern Greenland Sea, sBB is southern Baffin Bay, NS is Norwegian Sea, FS is Fram Strait, IcSh is Iceland Shelf, NAC is North Atlantic Current, IC is Irminger Current. Blue, green, and red dots mark data from [9,12], and this study (Table A1), respectively. The map is created by Ocean Data View software [13].

Plot “*N. seminae* percentages in the surface sediments versus SSST (Summer Sea Surface Temperature)” in Figure 2b provides a view of the temperature impact on the distribution of this species based on data from [9,12] and this study (Table A1). Data on SSST for the period of 2007–2017 are from the World Ocean Atlas 2018 [24].

2. Diatom Species *Neodenticula seminae* in the Modern Ocean

Figures 1, 2a and 3 present visual information on the occurrence of *N. seminae* in the modern Subarctic North Atlantic and Arctic Seas.

The native area of the modern distribution of the diatom species *Neodenticula seminae* (Simonsen and Kanaya) Akiba and Yanagisawa is the Subarctic Pacific with its marginal Bering, Okhotsk, and Japan seas. Semina [25] found *N. seminae* (= *Denticula marina*) to be common in the plankton of the Bering Sea and the open Northwestern Subarctic Pacific. Karohji [26] documented its high abundances (as *Denticula* sp.) up to 37–47% in the living diatom associations from the Bering Sea, Gulf of Alaska, and Northwestern Subarctic Pacific. The work of Taniguchi et al. [27] presented similar data. Alexander and Cooney [28] summarized the available information on the plankton studies in the Bering Sea and, based on the report of Phifer [29], noted *Denticula seminae* was present in the Bering Sea and Bering Strait plankton samples. However, the original work of Phifer [29] does not provide such data. Recent publications of, e.g., Aizawa et al. [30] and Wang et al. [31] confirm the abundant occurrence of *N. seminae* in the North Pacific plankton.

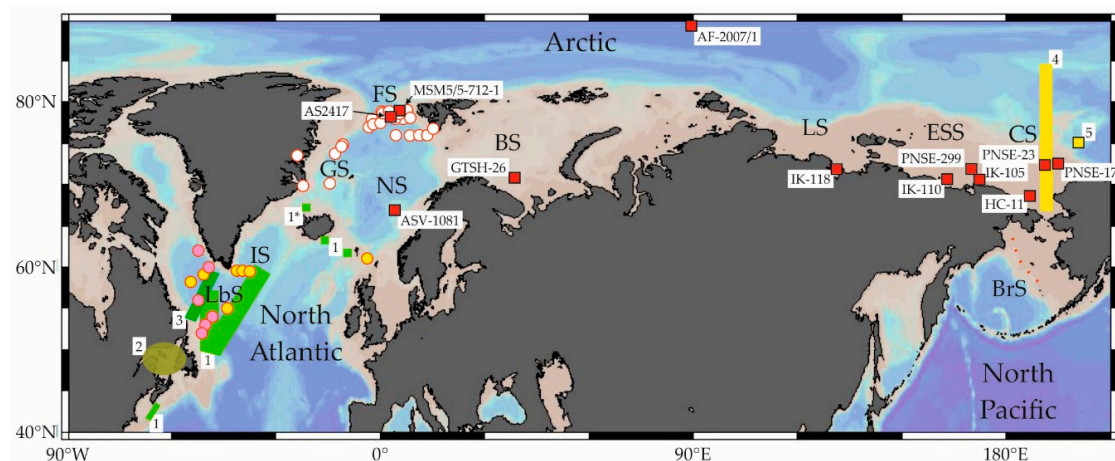


Figure 3. Observations of *N. seminae* in the plankton, sediment trap, surface, and Holocene sediment samples in the Arctic Ocean and North Atlantic. Plankton samples: 1 as green bars and squares, 1* as green square, 2 as a greenish oval, 3 as a dark-green bar, and 4 as yellow bar [7,8,14,15]. Sediment trap NAP samples: 5 as black-framed yellow square [16]. Surface sediment samples: red-framed white-, yellow-, and rose dots [9,12] and this study (Table A1). Holocene sediment cores: black-framed red dots with names on the white background [17–23,32]. LbS is Labrador Sea, IS is Irminger Sea, GS is Greenland Sea, NS is Norwegian Sea, FS is Fram Strait, BS is Barents Sea, LS is Laptev Sea, ESS is East-Siberian Sea, CS is Chukchi Sea, BrS is Bering Sea. Red arrows in Bering Sea show the northeastern limit of *N. seminae* permanent occurrence in surface sediments of the North Pacific (data mostly from the 1970s) [33]. The source of the blank map is Ocean Data View software [13].

In the mid-1980s, Takahashi [34] first documented the abundant fluxes of *N. seminae* in the sediment traps of the Subarctic Pacific. Various studies of the diatom samples from 18 sediment traps in the Subarctic and transitional (Subarctic/Subtropical) Pacific exhibited massive occurrence of this species in the phytoplankton during the most productive seasons [35–41]. Following the publication by Semina [25], in numerous reports published during the period of 1960s–2010s, *N. seminae* was referred to as either a common or dominant species in the diatom assemblages from the surface sediments of the Subarctic Pacific [42–50].

As concluded by Takahashi [36], *N. seminae* is an indicator species of primary productivity in the nutrient-rich and well-mixed surface waters of the Subarctic Pacific showing both spring and autumn peaks of its highest development in the siliceous phytoplankton communities.

Reid et al. [8] reported the first abundant occurrence of *N. seminae* in Labrador Sea plankton in May 1999. Another case of *N. seminae* appearance in the North Atlantic was the dominance of this species among the planktic diatoms in the Gulf of St. Lawrence, Eastern Canada, in April 2001 [7]. Later, Fragoso [14] documented *N. seminae* from plankton studies in the Labrador Sea in May–June 2011–2014. Studies of Poulin et al. [51] revealed no significant morphological and phylogenetic differences between *N. seminae* populations in the Subarctic Pacific and Gulf of St. Lawrence. Miettinen et al. [9] first published data on the observations of *N. seminae* in abundances of 0.3–5.7% from the surface sediments of the Fram Strait and Nordic Seas based on the study of samples collected during 2006–2008. Sha et al. [12] next reported the abundant occurrence of 2–18% *N. seminae* in the surface sediments of the Labrador Sea sampled in 2008. In our new surface sediment samples, which were collected in 2016, the abundance of *N. seminae* reached 6–16% at six stations in the Labrador and Irminger Seas (Figures 1 and 2a; Table A1). In the same area, Sha et al. [12] found *N. seminae* with abundances of 2% to 18% at seven stations. All stations with *N. seminae* observations are within the Subpolar Gyre west of ca. 35°W in the Northwestern North Atlantic. *N. seminae* occurs in the assemblages with both abundant and non-abundant, well-preserved cold-water north-boreal diatom flora dominated by *Rhizosolenia hebetata* Bailey, *Thalassiosira antarctica* Comber var. *borealis*, *Thalassiosira gravida* Cleve, *Actinocyclus curvatus* Janish, and *Coscinodiscus marginatus* Ehr. In samples with *N. seminae*, sporadic specimens of the warm-water or sea-ice diatoms occur. Overall, we find no clear relationship between *N. seminae* occurrences in the North Atlantic surface sediments and the appearance of particular diatom taxa. There are no indications of the redeposition of the older diatom forms. Diatom assemblages in surface sediments east of approximately 35° W on the North Atlantic transect at 59.5° N (in Figure 1, green-framed red dots) contain the warm-water subtropical species *Hemidiscus cuneiformis* Wallich., *Rhizosolenia bergonii* Perag., *Roperia tessellata* (Roper) Grun., *Shionodiscus oestrupii* (Ostenf.) Alverson, Kang and Terriot. The observations of these species reflect an influence of warmer waters of the North Atlantic and Irminger Currents. *N. seminae* does not occur in surface sediments east of approximately 35° W on the North Atlantic transect at 59.5° N with the warmer temperate surface waters.

As Kazarina and Yushina [47] and Ren et al. [33] proposed, the sea surface temperature of the highest *N. seminae* abundances in its native Pacific area ranges between 6 and 11 °C (mean annual sea surface temperature), and 8 and 15 °C (summer sea surface temperature). In the Subarctic Pacific, the species disappears from the diatom assemblages at places where sea surface temperature decreases below 5–6 °C. Figure 2b shows the same pattern of the temperature impact on *N. seminae* distribution in the North Atlantic samples. In addition to the temperature, the habitat in the subarctic deep-sea basins and on the continental slopes, but not on the shelf, can be preferable for *N. seminae* as, e.g., maps in [33] demonstrate. The coldest-water and shallow-water environments in the northernmost Beringia, Northern Labrador Sea, and on the Greenland/Iceland shelves seem to be not suitable for *N. seminae*: its percentages drop there to zero ([33]; Figure 2a in this study).

In addition to the Nordic, Labrador, and Irminger Seas, *N. seminae* now appears in the Chukchi Sea. Wang et al. [15] found it (without reporting its specific abundance) in the plankton samples to the north of the Bering Strait up to the point of 85° N. The species sporadically appeared in the sediment trap samples of 2010–2012 at station NAP in the Southern Northwind Abyssal Plain in the Western Arctic Ocean [16].

3. Diatom Species *Neodenticula seminae* in the Holocene Sediments of the Nordic and Arctic Seas

From the summary of Reid et al. [8], *N. seminae* was a usual component of the Quaternary microfossil assemblages in the North Atlantic within the time interval of 1.2 to 0.84 million years ago before its disappearance in this region. Many publications on the Late Pleistocene and Holocene micropaleontology of the North Atlantic and Nordic Seas did not report *N. seminae* in the sedimentary

records, e.g., Koç Karpuz and Schrader [52] and Koç Karpuz and Jansen [53] for the Greenland, Iceland, and Norwegian Seas; Andersen et al. [54] for the Reykjanes Ridge and the North Iceland and East Greenland shelves; Witak et al. [55] for the Reykjanes Ridge and the Faroe Skjalafjord; Witon et al. [56] for the Faroe fjords; Ran et al. [57] for the North Iceland shelf; Krawczyk et al. [58] and Li et al. [59] for Disco Bay of West Greenland; and Oksman [60] for the Baffin Bay and Isvika Bay on the Northern Svalbard. However, some studies undertaken during the past two decades document observations of this species in the latest Pleistocene and Holocene sediments from various places in the Nordic and Arctic Seas.

Figure 3 shows stations in the Nordic and Arctic Seas with *N. seminae* observations in the Late Pleistocene and Holocene sediments. Polyakova [17] made extensive studies of the diatoms in the Late Cenozoic (including the Late Pleistocene and Holocene) sediments of the Eurasian Arctic Seas. She observed sporadic specimens of *N. seminae* in the early Holocene sediments on the Kanin Rise in the Southern Barents Sea and in the middle to late Holocene sediments on the shelf of the East Siberian and Chukchi Seas. Obrezkova and Tsoy [32] and Tsoy and Obrezkova [21] documented the appearance of the species in the middle to late Holocene units of the sediment cores from the Southern Laptev and Southern East Siberian Seas. The late Holocene sediments on the North Pole [18] contain *N. seminae* alongside the species-rich boreal coccoliths and planktic foraminiferas. Mukhina and Dmitrenko [19] found *N. seminae* in the abundant diatom assemblages, composed of the arctic, boreal, and some subtropical species, from the supposed Bølling-Allerød sediments on the Vøring Plateau, the Norwegian Sea. All these authors propose the appearance of *N. seminae* within the intervals of warmer environmental conditions. However, the authors mentioned above do not provide a reliable age model, supported by direct radiocarbon dating; the sediment core chronology is based on the litho- and biostratigraphy combined with a correlation with the well-dated paleoclimatic archives.

Bylinskaya et al. [20] presented the distribution of the microfossils in the Late Pleistocene sediments of the Eastern Fram Strait. They used the AMS (Accelerated Mass Spectrometry) radiocarbon dating and the oxygen-isotopic data for the core chronology and detected *N. seminae* within the uppermost glacial marine oxygen-isotope stage 2 just prior to the onset of the Holocene. The ^{210}Pb and AMS ^{14}C -data allowed Tsoy et al. [22] to make a detailed microfossil study of the last 2300 years on the Southwestern Chukchi Sea shelf. *N. seminae* was not abundant or dominant, but a stable component of the diatom assemblages during this time interval and disappeared just within the coldest intervals, such as the Little Ice Age and Dark Ages Cooling.

Matul et al. [23] documented the appearance of *N. seminae* in the well-dated sediment core MSM5/5-712-1 from the Eastern Fram Strait. The paleoenvironmental record of the core covers the past 2000 years with time resolution of studied sediment samples between 37 and 54 years. Sporadic *N. seminae* specimens occurred at time levels of 173 CE (within the Roman Warm Period (RWP)) and 1989 CE (within the Recent Warming (RW)). The later part of the RWP between 0 and 440 CE in the core MSM5/5-712-1 is marked by the abundant occurrence (from 25–30% to 70–90%) of the warm-water diatom *Coscinodiscus radiatus* Ehr. and presence (1–4%) of the subtropical species *Roperia tessellata* (Roper) Grunow, *Shionodiscus oestrupii* (Ostenfeld) Hasle, and *Ethmodiscus rex* (Wallich) Hendeby. Compared to the RWP, the RW interval (from 1730 CE) contains the abundant diatom assemblages with a prevalence of the cold-water productivity taxa *Thalassiosira gravida* Cleve/*Thalassiosira antarctica* Comber resting spores (up to 40–45%) and warmer-water *Thalassiosira gravida* Cleve/*Thalassiosira antarctica* Comber vegetative cells (up to 40%). *N. seminae* appeared in the core MSM5/5-712-1 during both RWP and RW warmings but RWP was more pronounced in the Eastern Fram Strait. The late Holocene dinocyst-based paleoreconstructions for the Fram Strait close to the core MSM5/5-712-1 show an obvious maximum of the sea surface temperature during RWP 0–200 CE; sea-ice cover was similar to that during RW [61]. Werner et al. [62], for the core MSM5/5-712-1, described higher subsurface temperatures and greater advection of the warmer water in the area during the time interval of 100 to 300 CE. Such data can support our conclusion on the appearance of *N. seminae* in the Fram Strait during the prominent warming of the Roman time. Occurrence of *N. seminae* in the core MSM5/5-712-1

at the time level of 1989 CE precedes a major hydrological shift in the Northern Hemisphere at the end of the 1990s which initiated the species migration to the North Atlantic (see discussion in the next section). The most recent observation of *N. seminae* in the core MSM5/5-712-1 is from time level of 1989 CE. The age model of this core was developed by Spielhagen et al. [63] on AMS ^{14}C -datings with the best 1σ error to be as high as ± 23 calendar years. Thus, true age assignment of sample with *N. seminae* (1989 CE) can be different, and a strong relationship between this *N. seminae* occurrence and a definite climatic event within RW should be questioned. However, *N. seminae* observation at 1989 CE is very close to the event of clear negative anomalies of Arctic sea-ice extent in 1990 (Figure 4a). As model simulations show [64], the trend in negative anomalies of the Arctic sea-ice extent started from 1979–1980 and increased between 1986 and 1992 both in warm and cold seasons. Anthropogenic signals in the Arctic ice change became stably detectable from the early 1990s [64,65].

4. Migration of the Native North Pacific Diatom Species *Neodenticula seminae* to the North Atlantic as a possible Reflection of the Global Climate Change

Publications on the diatom assemblages from the surface sediments of the subarctic North Atlantic, Nordic, and Arctic Seas, which were obtained before the 2000s, did not report observations of *N. seminae* (e.g., [52,54,66–69]). The appearance of *N. seminae* in the plankton and modern sediment records followed an oceanographic shift in the Northern Hemisphere from the end of the 1990s (Figure 4a).

A migration of *N. seminae* to the Arctic and North Atlantic must proceed with the surface waters via the shallow Bering Strait. Although the total transport of the North Pacific water in the Arctic is generally not high, it increased in volume between 2002 and 2015 up to 1.2 Sv [70] compared to the previous rates of 0.78 to 0.83 Sv between 1946 and the late 1990s [71,72]. The hydrological observations in the Chukchi Sea, Beaufort Sea, and Canadian Basin exhibited an increase of the regional surface sea temperature starting from the late 1990s [73]. In the 2000s, the temperature of the surface Pacific Summer Water and Pacific Winter Water, entering the Chukchi Sea via the Bering Strait, reached values of 4–6.5 °C and 3 °C, respectively, causing a sharp reduction of the seasonal sea ice in the Western Arctic [74]. At the same time, primary productivity in the Pacific sector of the Arctic increased by factor of eight from 1959–1960 to 2000–2014 [75]. The Eastern Arctic areas also experienced a major oceanographic shift in the late 1990s. The temperature and salinity anomalies in the water layer of 10–200 m in the Nordic, Barents, and Labrador Seas became stably positive [76]. During the past 40 years, the sea-ice volume in the Arctic dropped by three-quarters, which means a decrease in the sea-ice extent by one half on average [3]. From 1998, the sea-ice extent anomalies are progressively negative from –5% to –30% and sometimes –50% compared to the multidecadal average (Figure 4a).

A hydrological consequence of the recent climatic changes is an increase in the inflow of the Pacific water in the Arctic. Based on the nitrate/phosphate ratio, ~90% of the upper mixed layer in the Northeast Water Polynya at the Northeastern Greenland has a North Pacific origin [77]. Almost all water in the passages of the Canadian Arctic Archipelago toward the North Atlantic (including Hudson Bay, Western Baffin Bay, along Labrador, and in the Grand Bank area), and some water in the Fram Strait and along East Greenland down to 66° N originates from the Pacific [9,78,79]. Therefore, we could suggest the main path of the modern dispersal *N. seminae* is from the Bering Sea via the Bering Strait along the Canadian shore, then through the Canadian Archipelago passages toward the Labrador Sea, and with the East Greenland Current toward the Fram Strait and the Northwestern Greenland Sea.

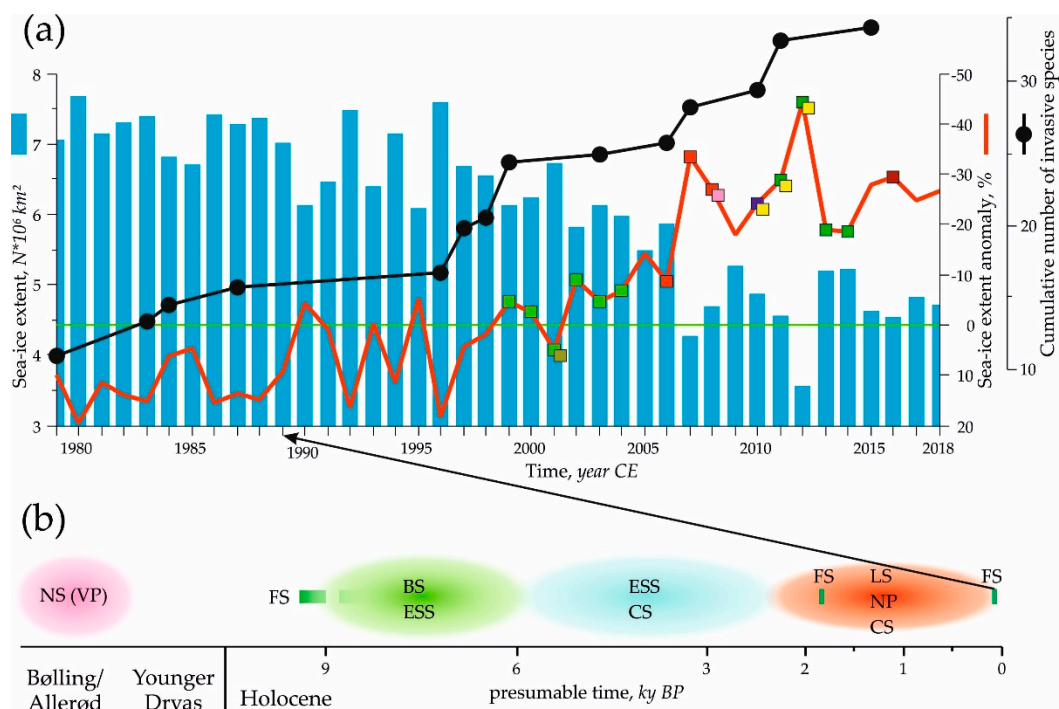


Figure 4. Records of *N. seminae* in the modern Arctic and North Atlantic and the Holocene sediments of the Arctic and Nordic Seas (see references in the Figure 3 caption). (a) *N. seminae* in the modern Arctic and North Atlantic: black-framed green and blue squares mark observations of *N. seminae* in the plankton, black-framed yellow squares mark observations of *N. seminae* in sediment trap NAP, black-framed red, brown, and rose squares mark observations of *N. seminae* in surface sediments. The Arctic sea-ice extent (vertical blue bars) and its anomalies (red line) are from [80]. Cumulative number of the invasive species (black dots and line) in the marine Arctic is from [81]. (b) *N. seminae* in the latest Pleistocene and Holocene sediments: green bars, green, blue, red, and pink ovals mark observations of *N. seminae* in the different areas within the different time intervals. NS(VP) is Norwegian Sea (Vøring Plateau), FS is Fram Strait, BS is Barents Sea, LS is Laptev Sea, ESS is East Siberian Sea, CS is Chukchi Sea, NP is North Pole.

Reid et al. [8] and Poulin et al. [51] note the unprecedented ice-free conditions in the Canadian Archipelago in 1998/1999 which could have been favorable for *N. seminae* dispersal to the Greenland Sea. Phylogenetic studies of *N. seminae* by Poulin et al. [51] do not support a long separation of the native North Pacific and newly established North Atlantic populations of the species. This can suggest a presumably recent migration of *N. seminae* to the subarctic areas of the North Atlantic. Invasion of species, both terrestrial and marine, has become one of main focuses of the ecosystem studies in recent decades; the number of publications on this topic has dramatically increased since the mid-2000s [82]. Chan et al. [81] provided data on invasions in the arctic and subarctic areas of the Atlantic realm from 1960 to 2015. The number of invasions increased sharply between 1996 and 1999 (Figure 4a). Appearance of *N. seminae* in the North Atlantic is within this event.

In summary, from the hydrological studies above, we could propose the oceanographic shift in the late 1990s, manifest as the higher transport of the warmer surface Pacific water to the Arctic together with a reduction of the Arctic ice (Figure 4a), may create a possibility for the native Subarctic Pacific diatom species *N. seminae* to settle in the subarctic areas of the Labrador Sea and Nordic Seas. Observations of *N. seminae* in the Holocene sediments of the Arctic and Nordic Seas (Figure 4b) can suggest the multiple events of the increased influence of the North Pacific water in the Arctic during the Holocene, not just during the recent Arctic warm climate amplification. However, additional high-resolution studies of the Holocene paleoenvironments are needed to prove a conclusion that *N. seminae* can appear in the North Atlantic and Arctic during such warm events.

Another means for *N. seminae* to migrate into the Arctic and North Atlantic can be via ballast water discharge by ships routing from the North Pacific. Several studies have discussed such a possibility for phyto- and zooplankton, as well as zoobenthos [83,84]. Regarding the recent appearance of *N. seminae* in the Labrador Sea and Gulf of St. Lawrence, Reid et al. [8] and Poulin et al. [51] noted low shipping volumes through the Canadian Archipelago Passages and in the Labrador Sea at the end of 1990s; thus, it was unlikely to expect a substantial ballast water exchange there. We cannot exclude such a possibility but the *N. seminae* occurrence in the pre-industrial time may point to the preferably natural migration of the species during oceanographic/environmental changes, which possibly have connections with warming events.

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Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A

Table A1. Distribution of diatom species *Neodenticula seminae* in surface sediment samples from the North Atlantic, the 51st cruise of the Russian research vessel Akademik Ioffe in 2016.

Latitude	Longitude	Station	<i>N. seminae</i> , %
55.0021	−43.7569	AI-3646	11.86
58.2180	−54.1686	AI-3639	16.34
59.1116	−50.5108	AI-3635	11.86
59.9664	−47.0353	AI-3629	0
59.8962	−42.3150	AI-3613	0
59.5627	−41.0077	AI-3597	6.06
59.5028	−39.3311	AI-3593	8.62
59.4926	−37.3242	AI-3592	14.66
59.5039	−34.9820	AI-3586	0
59.5062	−30.6606	AI-3574	0
59.5009	−28.6663	AI-3568	0
59.4988	−26.6601	AI-3562	0
59.4977	−24.7053	AI-3556	0
59.4931	−21.9865	AI-3548	0
59.4984	−20.6946	AI-3545	0
59.5004	−18.0003	AI-3540	0
59.5028	−15.3330	AI-3534	0
59.5009	−13.3339	AI-3531	0
59.4991	−11.3338	AI-3527	0
59.4988	−9.3336	AI-3524	0
59.5001	−7.3344	AI-3521	0
59.4996	−6.0041	AI-3519	0
59.5001	−3.8321	AI-3516	0
61.0679	−3.8666	AI-3451	sporadic specimen, but accepted as 1% to draw Figure 2a
62.7388	−8.4601	AI-3464	0
64.0252	−12.6182	AI-3485	0

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