Spatial variability in valve morphology of Neodenticula seminae, an oceanic diatom in the subarctic North Pacific and the Bering Sea

Authors: SHIMADA, CHIEKO, and TANIMURA, YOSHIHIRO

Source: Paleontological Research, 10(1) : 79-89

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/prpsj.10.79

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Paleontological-Research on 04 Apr 2025
Terms of Use: https://bioone.org/terms-of-use

Paleontological Research, vol. 10, no. 1, pp. 79–89, April 30, 2006

Spatial variability in valve morphology of *Neodenticula seminae*, an oceanic diatom in the subarctic North Pacific and the Bering Sea

CHIEKO SHIMADA[1] AND YOSHIHIRO TANIMURA[2]

[1]*Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology, Tsukuba 305-8567, Japan (e-mail: c-shimada@aist.go.jp)*

[2]*Department of Geology and Paleontology, National Science Museum, Tokyo 169-0073, Japan*

Received 10 June 2005; Revised manuscript accepted 14 November 2005

Abstract. To gain basic insights into the marine pelagic diatom species *Neodenticula seminae*, and particularly the relationships between morphology, evolution and environment, we conducted a scanning electron microscopic image analysis using modern specimens collected in the subarctic North Pacific and Bering Sea during the summers of 1955 and 1996–2003. We recognized an apparent intraspecific variability between two biogeographic provinces in terms of morphology: (1) the Oyashio Region (in the northwestern margin of the Pacific Ocean) and (2) other oceanic regions. This variability may reflect spatial variation in the availability of nutrients such as silicate. Specimens from the Oyashio morphological province had thinly silicified valves, whereas those from the other oceanic provinces were extraordinarily rich in heavily silicified valves.

Key words: Bering Sea, Diatom, Morphology, North Pacific Ocean, Nutrient, Silicification

Introduction

Neodenticula seminae (Simonsen and Kanaya) Akiba and Yanagisawa, 1986 (Figure 1) is a species of planktonic marine diatom that is distributed throughout the subarctic North Pacific Ocean and the high-latitude seas along the margins of this ocean. This species is generally thought to be limited in its distribution to the Northern Hemisphere and first appeared in the fossil record around 2.4 Ma (million years ago) in the North Pacific Ocean (Simonsen and Kanaya, 1961; Akiba and Yanagisawa, 1986; Yanagisawa and Akiba, 1990, 1998). It often accounts for 40–50% or even more of the total diatom association in both the surface waters and the bottom sediments, particularly in the eastern part of the ocean, where it is endemic (Figure 2; Karohji, 1959; Kanaya and Koizumi, 1966; Sancetta, 1982; Sancetta and Silvestri, 1986; Takahashi, 1986, 1994). Although *N. seminae* has been reported in subtropical gyres in the Indian Ocean and the North Atlantic, its occurrences there seem to be quite sporadic and episodic. Semina (1981) reported fewer than 100 specimens/L from low latitudes in the North Atlantic (29°00′N, 71°16′W), in contrast with up to 3.3×10^7 specimens/L in surface seawaters from the subarctic North Pacific Ocean and its surrounding seas.

Given that the northern areas of the North Pacific Ocean and the surrounding seas have one of the greatest primary productivities in the world and that the phytobiota of this region serve as an efficient biological pump that drives nutrient cycling (Honjo, 1997; Honda, 2002), this predominant diatom species is likely to play a crucial role in the ocean-scale ecosystem and in biogeochemical cycles in these subarctic seas. In spite of this organism's importance, basic information on the species is quite limited because specimens can be difficult to obtain from their pelagic habitat. Thus, in the present paper, we perform more detailed spatial investigations to determine morphological variability in the species and provide basic insights into the ecological (physiological) and possible evolutionary relationships between morphology and environment.

The basionym originally given to the species was *Denticula seminae* for a dead specimen obtained from a surface sediment sample in the western part of the Bering Sea (Simonsen and Kanaya, 1961). No type specification (i.e., no holotype description) has ever been properly carried out for this species (but see

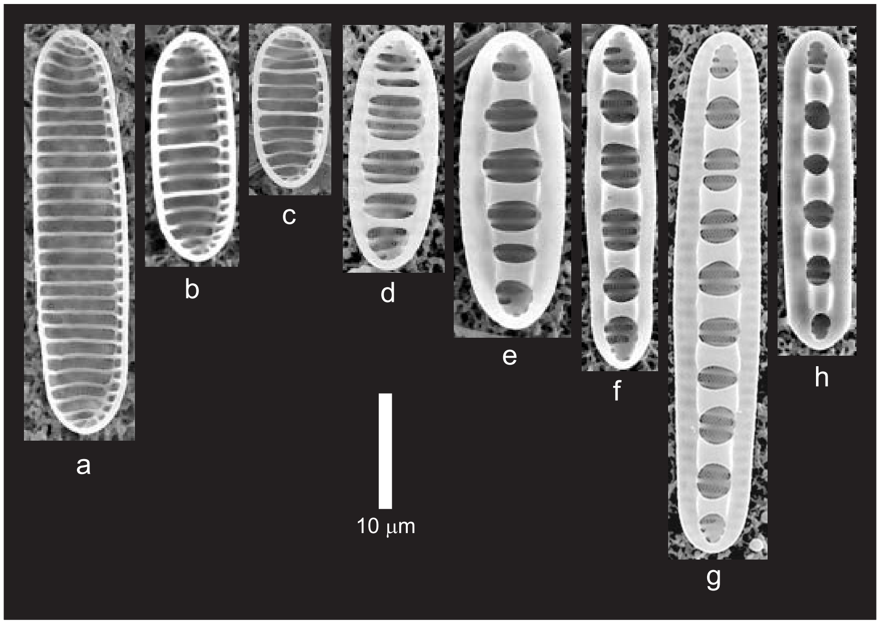

Figure 1. **a–h.** Scanning electron micrographs of the valvar appearance of various specimens of *Neodenticula seminae*. Note that the degree of silicification should be reflected in the morphology of the basal ridge. Specimens are from OS St. 88 (a), OS St. 33 (b), OS St. 50 (c), OS St. 88 (d), OS St. 17 (e), OS, St. 94 (f), OS St. 88 (g) and OS St. 94 (h), respectively.

Semina, 1956; Simonsen and Kanaya, 1961; Akiba and Yanagisawa, 1986; Yanagisawa and Akiba, 1990).

Recently, we discovered significant morphological differences between the specimens obtained from the water columns of the northwestern Pacific margin and the central Bering Sea (Shimada *et al*., 2003) in terms of readily apparent thinly silicified basal ridges, an internal valvar structure. In the present paper, we report spatially extended results on the variability in the internal valvar morphology of the species using supplementary plankton net and surface water materials collected during the summers (June to August) of 1955 and 2003.

Material and methods

For the present study, we utilized plankton net samples taken during cruises of the 1955 NORPAC Expedition of the Oshoro-maru operated by Hokkaido University, and during the GH03 expedition of the Hakurei-maru No. 2, operated by the Geological Survey of Japan. We performed an image analysis of these materials and of those used in Shimada *et al.* (2003), for a total of 1525 valve specimens from 29 stations, widely distributed in the subarctic North Pacific Ocean and the Bering Sea (Table 1, Figure 3). In the NORPAC samples, contributed by Dr. Taro Kanaya to the National Science Museum in Tokyo, the siliceous shells of the microorganisms were well preserved.

As described in our previous work (Shimada *et al.*, 2003), all the samples collected during each cruise were filtered onto a membrane (HAWP04700, Millipore Co.) in appropriate concentration to recognize the important valve structures of the species, and prepared for observation with a scanning electron microscope (SEM). All valve specimens from each station were digitally photographed using the SEM (JEM5310, JEOL at the National Science Museum, Tokyo; S-2250N, Hitachi, at Hokkaido University) with an appropriate magnification: 2000× or 3500×. We performed a scaling calibration between the two SEMs before compiling the dataset. Subsequently, we biometrically analyzed the micrographs using the NIH Image1.62 software (http://rsb.info.nih.gov/nih-image/). We chose the most easily quantifiable characteristics of the internal valve morphology for our analysis and focused on the following morphometrics in our statistical analysis: the apical and transapical dimensions of the valve (Va and Vt) and of the central foramen (Fa and Ft) and basal ridge (Ba and Bt), the number of foramina per valve (Nf), and the width of the deck (D) (Figure 4). We also standardized the dimensions of Bt and D as Bt' ($= Bt/Vt$) and D' ($= D/Vt$), respectively, to support a more through

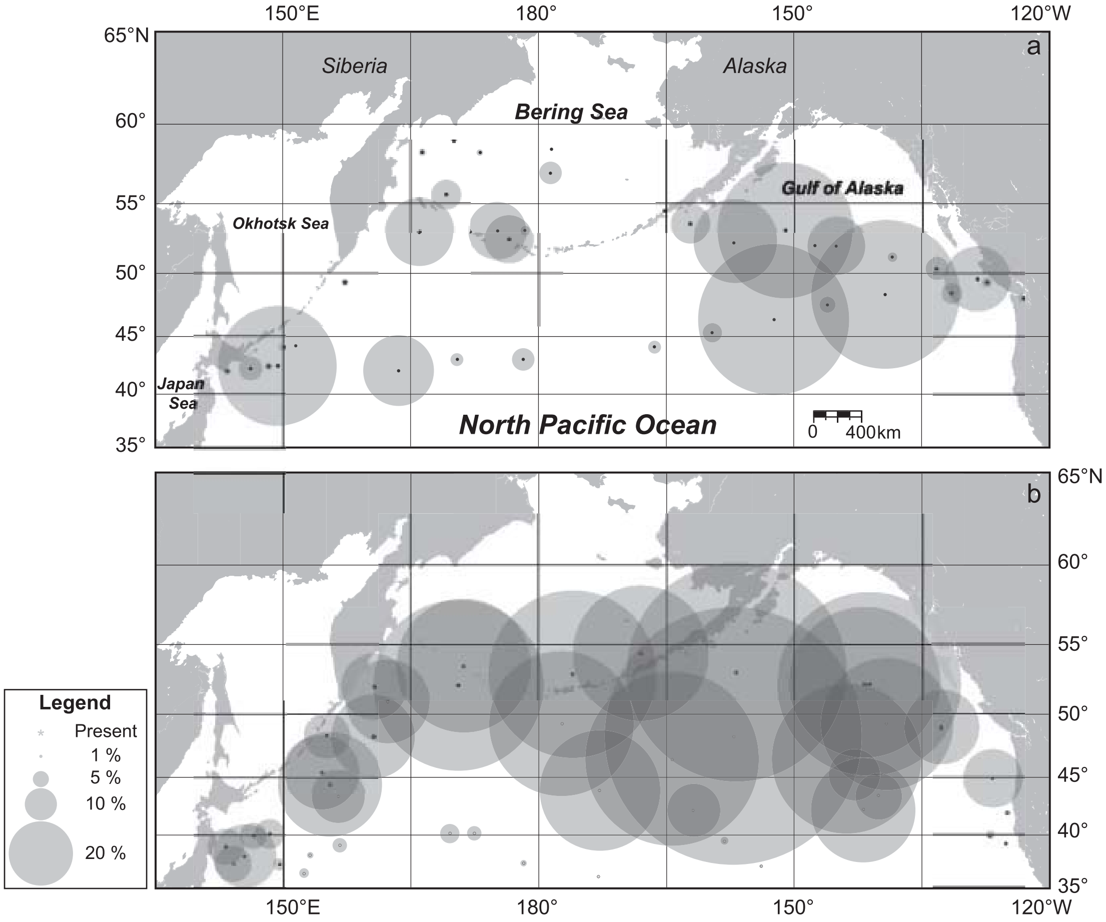

Figure 2. a. Percentage abundance of *Neodenticula seminae* in the total diatom assemblage in the plankton net samples that were analyzed in this study. These were taken during the NORPAC Expedition of the Oshoro-maru, 1955. Data after Karohji (1959). **b.** Percentage abundance of the species in the total diatom thanatocoenoses in the surface sediments (Kanaya and Koizumi, 1966).

morphometric investigation. During the image analysis, we excluded specimens with extraordinarily thin or entirely absent basal ridges, which would have prevented differentiation of the primary and secondary pseudosepta. Because the morphology of the foramina and basal ridges vary relatively little within a valve, we chose the larger one located in the central part as the representative sample for our measurements.

We grouped the sample stations geographically into five oceanic provinces based on Taniguchi (1999) which dealt with the hydrographic properties in the subarctic North Pacific and the Bering Sea: (1) the region around the subarctic Oyashio Current (OR), in the northwestern Pacific margin; (2) the western subarctic gyre (WSG); (3) the Bering Basin (BB); (4) the Gulf of Alaska (GA); and (5) the central gyre of the subarctic Pacific, south of the Aleutian Arc (SA).

Results

Neodenticula seminae exhibited great variability in its internal morphology in the samples examined from the North Pacific and the Bering Sea (Figure 1). We provide descriptive statistics for the biometric measurements as an overview of the differences among each population in Table 2. Apical and transapical valve lengths (*Va* and *Vt*) for the 1525 specimens ranged from 8.2 to 47.0 and 4.3 to 11.6 μm, respectively. The data for *Va* appear somewhat skewed toward lower values and those for *Vt* appear skewed toward higher values compared with previous values obtained by light microscopy (10 to 60 μm for *Va* and 4 to 9 μm for *Vt*; Simonsen and Kanaya, 1961; Yanagisawa and Akiba, 1990). This is probably because our SEM observations allowed a greater number of intact specimens measured.

Table 1. Profiles of the samples collected at each station. OR, Oyashio Region; WSG, Western Subarctic Gyre; BB, Bering Basin; GA, Gulf of Alaska; SA, South of the Aleutians. "Surface" indicates samples to a depth of several meters below the sea surface. Serial numbers given in the right column correspond to those used in all figures.

No.	Cruise	Station	Province	Latitude (N)	Longitude	Date	Mesh apperture (μm)	Wire out (m)	Haul
1	GH03	102	OR	42°22′	144°44′ E	June 9, 2003	10	200	Vertical
2	GH03	105	OR	42°48′	144°22′ E	June 3, 2003	10	200	Vertical
3	KT96-16	MC14	OR	41°06′	143°06′ E	September 5, 1996	—	100–200	—
4	HO71	36	OR	40°15′	154°59′ E	June 9, 1996	—	75–250	—
5	HO71	38	OR	41°45′	155°00′ E	June 10, 1996	—	75–250	—
6	HO71	40	OR	43°15′	154°59′ E	June 11, 1996	—	200–250	—
7	NORPAC (OS)	4	OR	44°06′	150°10′ E	June 23, 1955	94	Surface	Horizontal
8	NORPAC (OS)	5	OR	44°22′	151°50′ E	June 24, 1955	94	Surface	Horizontal
9	NORPAC (OS)	94	OR	42°57′	163°57′ E	August 24, 1955	94	Surface	Horizontal
10	NORPAC (OS)	100	OR	42°45′	149°35′ E	August 24, 1955	94	Surface	Horizontal
11	NORPAC (OS)	14	WSG	53°01′	166°00′ E	June 29, 1955	112	50	Vertical
12	NORPAC (OS)	17	WSG	53°02′	172°00′ E	July 1, 1955	112	50	Vertical
13	NORPAC (OS)	30	WSG	53°10′	175°24′ E	July 8, 1955	112	50	Vertical
14	NORPAC (OS)	31	WSG	52°50′	176°56′ E	July 9, 1955	112	50	Vertical
15	NORPAC (OS)	33	WSG	52°30′	178°54′ E	July 9, 1955	112	50	Vertical
16	NORPAC (OS)	34	WSG	53°14′	178°40′ E	July 10, 1955	112	50	Vertical
17	NORPAC (OS)	39	BB	57°00′	178°58′ W	July 11, 1955	112	50	Vertical
18	NORPAC (OS)	26	BB	58°30′	173°15′ E	July 6, 1955	112	50	Vertical
19	KH97-2	9	BB	57°26′	179°53′ W	July 27, 1997	—	50–200	—
20	NORPAC (OS)	50	GA	52°58′	162°19′ W	July 21, 1955	94	Surface	Horizontal
21	NORPAC (OS)	54	GA	53°13′	151°06′ W	July 23, 1955	94	Surface	Horizontal
22	NORPAC (OS)	55	GA	52°06′	147°56′ W	July 23, 1955	94	Surface	Horizontal
23	NORPAC (OS)	56	GA	52°01′	145°02′ W	July 24, 1955	94	Surface	Horizontal
24	NORPAC (OS)	67	SA	48°48′	131°50′ W	August 10, 1955	94	Surface	Horizontal
25	NORPAC (OS)	70	SA	48°38′	139°28′ W	August 11, 1955	94	Surface	Horizontal
26	NORPAC (OS)	73	SA	47°56′	146°05′ W	August 13, 1955	94	Surface	Horizontal
27	NORPAC (OS)	79	SA	45°31′	159°59′ W	August 16, 1955	94	Surface	Horizontal
28	NORPAC (OS)	82	SA	44°13′	166°36′ W	August 17, 1955	94	Surface	Horizontal
29	NORPAC (OS)	88	SA	43°08′	178°21′ E	August 20, 1955	94	Surface	Horizontal

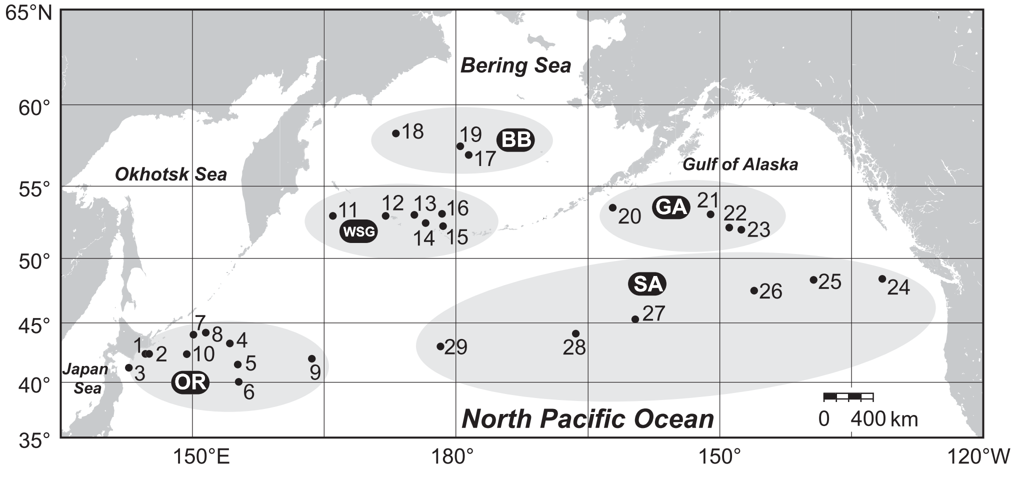

Figure 3. Sources of materials analyzed in the present study: OR, Oyashio Region; WSG, Western Subarctic Gyre; BB, Bering Basin; GA, Gulf of Alaska; SA, South of the Aleutians. Groups were based on Taniguchi (1999). See Table 1 for detailed profiles of the stations and samples identified by the sample numbers given in the Figure.

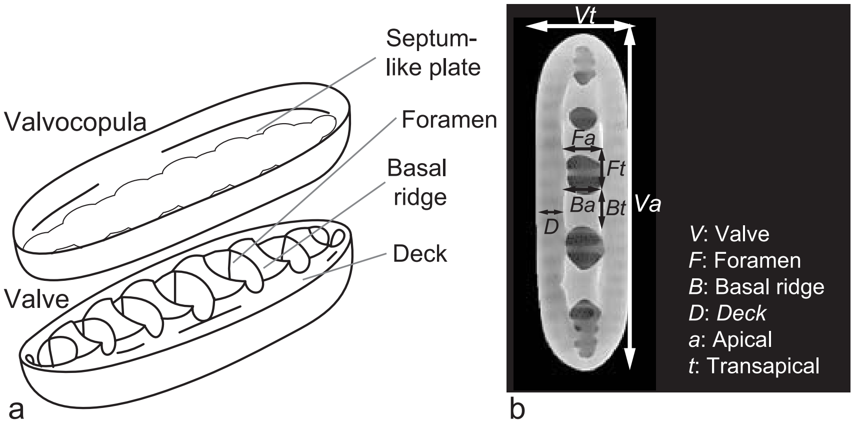

Figure 4. Morphometric dimensions of the intervalvar anatomy of *Neodenticula seminae*. **a.** Schematic illustration of a theca (part of a frustule). **b.** Morphometric dimensions assessed in our digital measurements of the SEM micrographs.

Table 2. Basic statistics for *Neodenticula seminae* valve morphometrics in the five study populations. *V*, valve; *F*, foramen; *B*, basal ridge; *a*, apical; *t*, transapical; *Nf*, no. of foramina in a valve. Valves represent mean ± S.D.

			Mean ± S.D. (μm)						
No.	Province	No. valves	*Va*	*Vt*	*Fa*	*Ft*	*Ba*	*Bt*	*Nf*
1	OR	52	23.54 ± 6.48	7.37 ± 0.46	5.24 ± 1.88	5.85 ± 0.66	0.39 ± 0.18	4.46 ± 0.65	4.19 ± 0.97
2	OR	53	25.43 ± 6.34	7.29 ± 0.67	4.84 ± 1.54	5.27 ± 0.95	0.53 ± 0.23	4.50 ± 0.88	4.77 ± 1.07
3	OR	16	20.59 ± 4.85	6.39 ± 1.12	3.87 ± 1.18	4.11 ± 1.26	1.04 ± 0.45	3.52 ± 1.16	4.50 ± 0.97
4	OR	39	23.65 ± 4.63	6.65 ± 1.10	3.58 ± 1.33	3.55 ± 1.06	1.20 ± 0.50	3.22 ± 0.90	5.05 ± 1.12
5	OR	18	25.09 ± 3.97	6.45 ± 0.92	4.10 ± 1.19	3.51 ± 0.65	1.16 ± 0.42	3.04 ± 0.64	4.94 ± 0.87
6	OR	24	24.66 ± 4.28	6.75 ± 0.86	4.12 ± 1.54	4.06 ± 1.07	0.99 ± 0.48	3.45 ± 0.90	5.21 ± 1.36
7	OR	51	23.52 ± 5.24	6.65 ± 0.74	2.73 ± 0.96	3.30 ± 0.89	1.28 ± 0.47	3.19 ± 0.67	5.57 ± 1.33
8	OR	29	24.72 ± 5.27	7.13 ± 0.90	3.61 ± 1.52	4.05 ± 0.95	1.01 ± 0.52	3.72 ± 0.86	5.28 ± 1.46
9	OR	50	19.82 ± 5.30	5.87 ± 0.72	3.18 ± 1.14	3.39 ± 0.75	0.99 ± 0.51	2.97 ± 0.68	4.76 ± 1.56
10	OR	53	14.59 ± 2.02	6.32 ± 0.47	2.63 ± 1.28	3.47 ± 0.82	1.08 ± 0.52	2.95 ± 0.76	3.74 ± 0.84
11	WSG	61	27.23 ± 4.52	7.14 ± 0.80	3.44 ± 1.24	4.08 ± 1.20	1.08 ± 0.54	3.74 ± 0.92	5.64 ± 1.20
12	WSG	52	20.33 ± 3.65	6.74 ± 0.67	3.38 ± 1.14	3.80 ± 1.05	1.19 ± 0.60	3.51 ± 0.82	4.38 ± 0.77
13	WSG	51	22.02 ± 5.21	6.55 ± 0.77	3.08 ± 1.08	3.33 ± 0.74	1.32 ± 0.55	3.04 ± 0.58	5.04 ± 1.37
14	WSG	60	22.00 ± 4.37	6.62 ± 0.64	3.41 ± 1.52	3.62 ± 1.03	1.43 ± 0.63	3.30 ± 0.84	4.68 ± 1.17
15	WSG	13	21.20 ± 5.37	6.24 ± 0.70	2.52 ± 0.89	2.85 ± 0.82	1.71 ± 0.55	2.73 ± 0.62	4.69 ± 1.03
16	WSG	57	22.35 ± 4.38	6.35 ± 0.74	2.75 ± 0.84	2.93 ± 0.66	1.62 ± 0.42	2.84 ± 0.54	5.21 ± 1.08
17	BB	54	22.09 ± 4.91	6.20 ± 0.77	3.09 ± 1.13	3.20 ± 0.95	1.24 ± 0.61	2.88 ± 0.74	5.13 ± 1.24
18	BB	55	25.25 ± 4.54	6.80 ± 0.77	3.36 ± 0.98	3.51 ± 0.81	1.35 ± 0.47	3.23 ± 0.57	5.35 ± 1.11
19	BB	221	21.59 ± 3.62	6.55 ± 0.77	2.79 ± 0.80	3.08 ± 0.53	1.50 ± 0.37	2.72 ± 0.47	5.13 ± 1.05
20	GA	50	14.64 ± 2.23	5.80 ± 0.53	2.68 ± 0.97	3.33 ± 0.83	0.92 ± 0.52	2.78 ± 0.74	3.90 ± 0.79
21	GA	56	15.65 ± 2.80	6.42 ± 0.55	2.81 ± 1.19	3.59 ± 0.83	1.22 ± 0.53	3.03 ± 0.87	3.79 ± 0.82
22	GA	51	16.09 ± 2.17	6.59 ± 0.70	2.65 ± 1.20	3.49 ± 0.92	1.19 ± 0.42	3.09 ± 0.92	3.90 ± 0.81
23	GA	50	16.19 ± 4.60	6.39 ± 0.62	2.56 ± 1.00	3.25 ± 0.67	1.20 ± 0.41	2.98 ± 0.61	4.04 ± 1.16
24	SA	52	21.17 ± 4.78	6.62 ± 0.85	2.87 ± 0.81	3.29 ± 0.66	1.40 ± 0.42	3.13 ± 0.54	4.94 ± 1.35
25	SA	50	21.93 ± 11.36	5.70 ± 1.17	2.89 ± 1.18	3.04 ± 0.88	1.24 ± 0.55	2.79 ± 0.67	5.54 ± 2.97
26	SA	51	16.83 ± 6.18	5.50 ± 0.69	2.59 ± 0.72	2.84 ± 0.50	1.23 ± 0.45	2.38 ± 0.46	4.39 ± 1.77
27	SA	50	15.15 ± 5.89	6.17 ± 0.63	2.47 ± 0.91	3.44 ± 0.89	1.09 ± 0.50	3.02 ± 0.81	3.78 ± 1.20
28	SA	54	16.89 ± 4.49	6.29 ± 0.61	2.90 ± 1.13	3.34 ± 0.69	1.19 ± 0.48	2.89 ± 0.58	4.07 ± 1.21
29	SA	52	26.30 ± 10.00	6.30 ± 0.89	2.60 ± 0.94	3.12 ± 0.98	1.20 ± 0.49	2.93 ± 0.76	6.63 ± 2.89

Based on these internal valvar structures, the data obtained in the present study strongly support our previously reported results (Shimada *et al*., 2003). When we concentrated on the basal ridge morphology, we noted that its appearance varied dramatically among specimens (Figure 1). The specimens obtained from samples in the OR province tended to possess more delicate basal ridges (less elongated apically

Table 3. Correlation matrix among the measured parameters. V, valve; F, foramen; B, basal ridge; a, apical; t, transapical; Nf, no. of foramina in a valve.

	Va	Vt	Fa	Ft	Ba	Bt	Nf	D	Bt'	D'	Ba/Bt'
Va	1	—	—	—	—	—	—	—	—	—	—
Vt	0.43	1	—	—	—	—	—	—	—	—	—
Fa	0.23	0.26	1	—	—	—	—	—	—	—	—
Ft	0.13	0.56	0.64	1	—	—	—	—	—	—	—
Ba	0.05	−0.23	−0.49	−0.74	1	—	—	—	—	—	—
Bt	0.23	0.61	0.59	0.90	−0.66	1	—	—	—	—	—
Nf	0.75	0.26	−0.20	−0.14	0.14	−0.05	1	—	—	—	—
D	0.22	0.44	−0.38	−0.39	0.49	−0.45	0.35	1	—	—	—
Bt'	0.03	0.16	0.57	0.78	−0.69	0.88	−0.21	−0.81	1	—	—
D'	−0.03	−0.16	−0.57	−0.78	0.69	−0.88	0.21	0.81	−1	1	—
Ba/Bt'	0.02	−0.22	−0.49	−0.75	0.96	−0.73	0.14	0.58	−0.79	0.79	1

and wider transapically). Specimens with considerably larger foramina and thinner basal ridges (*i.e.*, different morphs) were predominantly found in samples from the stations in the OR region around the subarctic Oyashio Current off northern Japan, in the northwestern Pacific (see Table 2 for the data for sites 1 and 2, which correspond to stations 102 and 105 in the GH03 survey).

We paid great attention to the Ba/Bt' ratio, which we have introduced here because it seems to be the most visually recognizable parameter. Note that intervalvar dimensions correlate well with each other (Table 3). Considering the appearance of the deck, it is apparent that D also reflects width, that is, robustness of the valvocopula, one of the cingulum structures of the species' frustule (Figure 4). This fact strongly suggests that the Ba/Bt' ratio could serve as an index of the overall level of silicification of the frustule. Therefore, it appears reasonable to adopt Ba/Bt', which reflects the appearance of the basal ridge, as an index of the degree of silicification of the whole cell in this species. We also noticed a clear bimodal distribution in Ba/Bt' (Figure 5), which highlights the difference in morphology of the basal ridges between the OR specimens and those from the other provinces (Figure 6).

This newly obtained data for the parameters of each population strongly supports the results of Shimada *et al.* (2003) and suggests a spatial (geographic) bias in basal ridge morphology (*i.e.*, regional variation in the degree of silicification of the valves). These results also suggest the existence of at least two morphological provinces: (1) one in the margin of the northwestern Pacific, roughly west of 160°E and south of the westernmost part of the Aleutian Arc (*ca.* 55°N), which corresponds to the OR province; and (2) an ensemble of the rest of the oceanic provinces in the subarctic oceans. However, the details of this morphological variability are unknown because few specimens of the species in the NORPAC samples were collected off the eastern end of the Kurile Arc and inside the Okhotsk and Japan Seas.

Discussion

What factors are responsible for the observed geographic variability in diatom morphology? In general, the ratios of elements in a diatom cell seem to be both species specific and dependent on temperature, salinity, light intensity, availability of macro- and micronutrients, and the life history and size of the cell (Brzezinski, 1985). In addition, it has been proposed that an undamaged diatom cell will typically have an intracellular Si : N ratio (molar basis) of approximately 1 : 1, despite strong control by the above-mentioned environmental properties (Brzezinski, 1985). However, it has also been proposed that cells growing under certain stresses, such as an iron deficiency, will increase that ratio (Takeda, 1998).

Empirically, more thinly silicified or smaller diatoms have been observed in natural populations during phytoplankton blooms that progressively develop a silicate limitation (Darley, 1982). Harrison *et al.* (1977) also reported that *Skeletonema costatum* reduced its intracellular Si content under silicate-limited conditions. Of the several macronutrients in the ocean, nitrate and phosphate are used by all phytoplanktonic organisms. However, silicates are essential only for siliceous-shelled phytobiotic taxa such as the Bacillariophyceae (diatoms) and some Chrysophyceae (Parmales and Dictyochales), even though nitrate and phosphate are also important for certain vital activities such as metabolic and organelle functions. Since silicate is crucial for siliceous microorganisms to form rigid shells, its availability might have a more direct impact on diatom silicification and thus on frustule morphology. Therefore, we focused on spatial (geographical) varia-

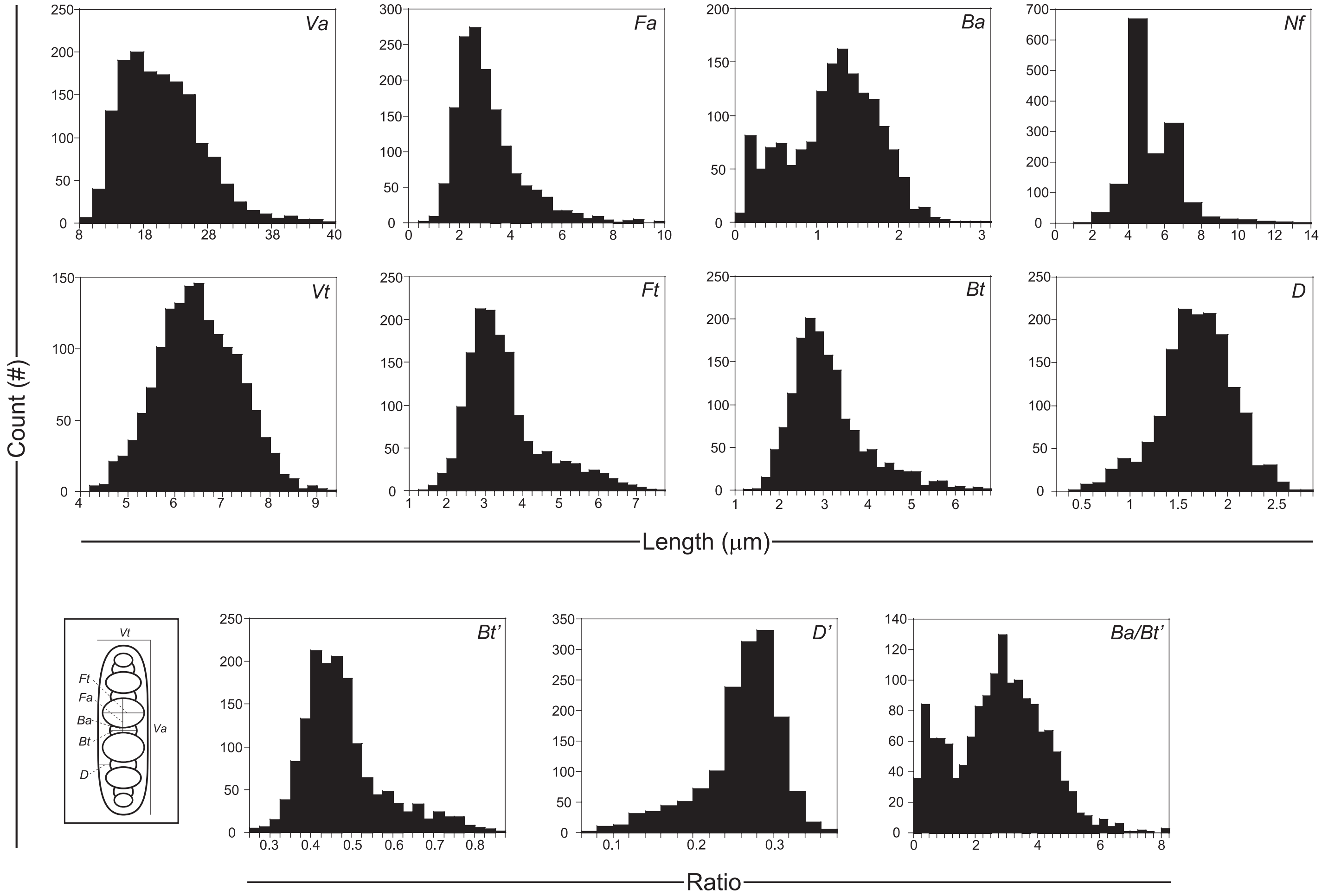

Figure 5. Histograms for each morphometric dimension for all specimens. V, valve; F, foramen; B, basal ridge; a, apical; t, transapical; Nf, no. of foramina in a valve; Bt' and D', standardized values of Bt and deck width, respectively.

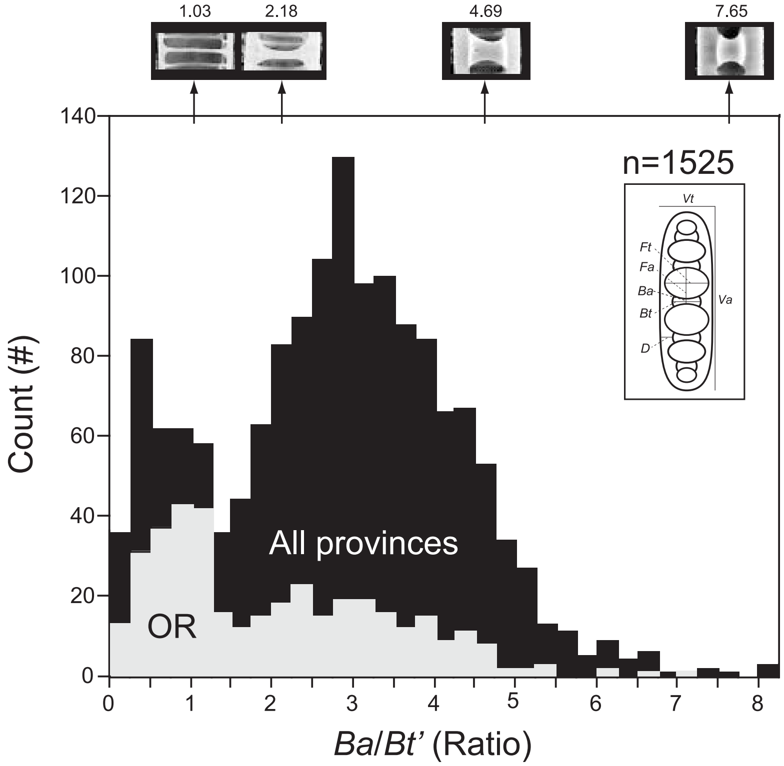

Figure 6. Histogram of the *Ba*/*Bt*′ ratio for all specimens other than those from the OR province and for specimens only from the OR province. Note that a clear threshold is recognizable. *V*, valve; *F*, foramen; *B*, basal ridge; *a*, apical; *t*, transapical; *Nf*, no. of foramina in a valve; *Bt*′, standardized value of *Bt*.

tions in silicate availability and in related factors to examine the relationship between *N. seminae* morphology and environmental variability. Unfortunately, we had difficulty obtaining some of this data because our study included historical samples taken five decades ago. As a result, we examine and discuss the background for this morphological diversity based on the statistical climatic information for some environmental variables obtained from the on-line database (World Ocean Atlas 2001; http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NODC/.WOA01/).

Most of the material analyzed in our study was recovered during the summer (except for the sample with serial number 3, from the KT96-16 cruise at station MC14, which was taken in early September). Clearly, it is important to understand the seasonal dynamics of nutrient availability in the subarctic North Pacific. For the Oyashio Region (OR), *in situ* oceanographic observations were made for 8 years (1990–1998) by the Hokkaido National Fisheries Research Institute (Saito *et al.*, 1998; Kasai *et al.*, 2001; Saito *et al.*, 2002). According to their observations, the region around the Oyashio Current represents one of the most fertile areas in the world's oceans, with the greatest level of primary productivity mainly contributed by diatoms. In general, higher concentrations of nutrients are brought to the surface from deeper layers by vertical mixing during the winter and early spring. Silicate levels are estimated to reach 50 μmol/L, which is comparable to levels recorded in the Southern Ocean (Saito *et al.*, 2002). Even though silicate levels may vary temporally and spatially, concentrations of this nutrient in surface waters in January and March are reported to shift to the same degree in both months or reach a maximum in March, suggesting that the nutrient supply remains high just before the spring phytoplankton bloom. Subsequently, as the phytoplankton bloom begins and expands, concentrations of nutrients in the surface water decrease, accompanied by increasing chlorophyll concentrations. This eventually results in a deficiency in both silicate and nitrate at many stations from June to August, when stratification of the surface water develops.

Accordingly, specimens from the OR province (the northwestern Pacific) in our study can be assumed to have developed during the spring phytoplankton

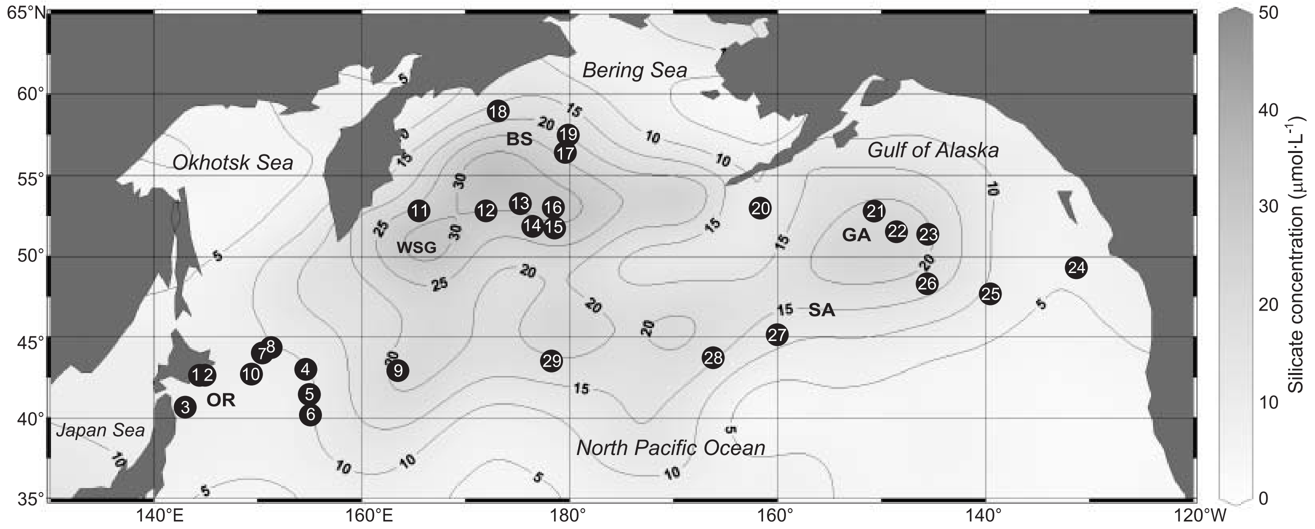

Figure 7. Spatial distribution of summer silicate concentrations. Illustrated by Ocean Data View (http://www.awi-bremerhaven.de/GEO/ODV/).

bloom, then subsequently grown in waters with a low concentration and availability of nutrients. This contrasts with the less pronounced seasonality in nutrient and plankton dynamics in the pelagic provinces of the subarctic Pacific Ocean (Banse and English, 1999; Harrison *et al.*, 1999). Unfortunately, this difference makes it somewhat difficult to strictly specify the timing for when the specimens we analyzed were produced. According to time-series sediment trap experiments carried out in the subarctic Pacific and the southern Bering Sea, higher productivity is reported from March to October, with spring phytoplankton blooms unstable in both their timing and magnitude (Takahashi *et al.*, 2002).

Nonetheless, average silicate concentrations in the surface layer in the oceanic provinces of the subarctic North Pacific and the Bering Sea during the summer indicate weaker seasonality than is the case in the Northwestern Pacific margin. This is illustrated by Ocean Data View (http://www.awi-bremerhaven.de/GEO/ODV/) and WOA01. Seasonal variations in nutrient (nitrate and silicate) concentrations in the Gulf of Alaska, for example, represent changes that are 2.6 and 2.8 times, respectively, the magnitudes of the corresponding changes for the Oyashio Region (Whitney and Freeland, 1999; Saito *et al.*, 2002). Furthermore, in the Gulf of Alaska, the observed silicate concentrations reach at least 12 to 13 μmol/L even in July and August; these levels are higher than those in the Oyashio Region during the summer (Figure 7; Whitney and Freeland, 1999). Therefore, we assume specimens collected from oceanic provinces outside the Oyashio Region were produced in ambient water richer in silicate than the waters in the Oyashio Region. This suggests a good agreement between the observed morphological provinces (*i.e.*, the degree of silicification of *Neodenticula seminae* valves) and silicate availability.

Furthermore, organisms in the Parmales, which possess small siliceous shells in cells that are several microns long, may compete with diatoms for silicate (Narita, personal communication). Recently, important aspects of the nutrient and plankton dynamics of that taxon have been identified and used to account for its predominant abundances in the phytoplankton associations in the subarctic Pacific. Some *in situ* observations have revealed more predominant standing stocks of Parmales than had been expected off the Kurile Arc in the northwestern Pacific (Jordan *et al.*, 2003), while the standing stocks of the taxon examined along a transoceanic traverse though the subarctic Pacific were distinctively higher in the northwestern part, at least in summer (Tanimoto *et al.*, 2003).

Based on all the above-mentioned data, the spatial distribution of properties that may affect silicate availability for diatoms seem to correspond with the observed degree of silicification of *N. seminae*. This empirical approach should be reasonable to account for silicate availability when considering the important factors that affect diatom morphology (silicification).

In high-nutrient, low-chlorophyll (HNLC) oceanic provinces, where iron limitations become more severe as the summer progresses, the uptake ratio $Si(OH)_4:NO_3$ is higher (between *ca.* 2:1 and 3:1) than in non-HNLC provinces, suggesting the possibility that thicker (more heavily silicified) diatom cells will be produced under such conditions (Takeda, 1998). The primary source of iron input into such oceanic provinces in the subarctic North Pacific and Bering Sea has been assumed to be terrigenous transport (Harrison *et al.*, 1999). In fact, mathematical simulations have suggested that the higher iron concentration available for use by phytoplankton in the western part of the subarctic North Pacific, the Okhotsk and Japan Seas, and the western Bering Sea resulted from inputs originating in the central Asian continental deserts (Duce and Tindale, 1991). Thus, a relatively good agreement between the spatial distribution of *N. seminae*'s morphological characteristics and nutrient (silicate) availability is apparent, and this strongly suggests that nutrient (silicate, iron, or both) availability is one of the potential factors that influences the degree of silicification of a species.

Note that a lower probability of a low-temperature dependence for silicification has also been suggested. Lower water temperatures increased silicification of the oceanic diatom *Thalassiosira tumida* in the Southern Ocean, based on the results of *in vitro* experiments (Fryxell, 1988). Our results agree with this finding to a limited extent.

Conclusions

Prior to this study, almost no information existed regarding spatial variability in the morphological characteristics of pelagic planktonic diatoms. We investigated the morphology of *Neodenticula seminae*, with a particular focus on internal microstructure that reflects skeletal silicification, using summer populations distributed widely throughout the subarctic North Pacific and the Bering Sea. We found that the Oyashio Region, which lies west of approximately 160°E in the northwestern Pacific margin, yielded more thinly silicified specimens with morphologically distinct characteristics compared with specimens from other provinces in the subarctic Pacific. The other oceanic provinces showed more morphologically homogeneous characteristics, and specimens tended to be more robust and heavily silicified. This suggests the existence of at least two distinct morphological provinces for *N. seminae*.

There is partly some evidence that spatial variation in nutrient (silicate and iron) availability may be responsible for this variation. However, additional investigations of other taxa at large spatial scales would be necessary to determine whether a species-specific effect exists. A description of the relationships between diatom morphology and various environmental factors using materials from time-series sediment trap experiments would also provide effective information (Shimada, unpublished data).

Because it is difficult to precisely determine the relationship between the morphology of most organisms and environmental factors, we should also consider the possibility of a synergistic effect between additional factors for *N. seminae*. At this time, unfortunately, little is so far known about the effect of salinity and other macronutrients, such as nitrate and phosphate. Therefore, it is also required to clarify the role of those factors in the species silicification.

For planktonic microorganisms, long distances between populations could represent a barrier to gene exchange (Norris, 2000). If such conditions continued over evolutionarily significant (geological or much shorter) time intervals, some gene pools that vary in their control of frustule morphology might have emerged in the different oceanic provinces. Also, it is implied that the degree of silicification might be related to a certain ecological and/or evolutional strategy, such as competition against predators. Thus, the observed morphological variability in *N. seminae* could provide a key to understanding the interactions between the evolutionary strategies of phytoplankton and global environmental change.

Acknowledgments

We appreciate John A. Barron of the journal reviewer, Taro Kanaya, Fumio Akiba of Keiso Mini Lab, Ltd., and Yukio Yanagisawa at AIST, who provided helpful suggestions on the taxonomy of *Neodenticula* spp. Yuichiro Tanaka at AIST and Takeo Horiguchi at Hokkaido University offered us the use of their facilities for our research. Kazuhiko Uemura of the National Science Museum, Tokyo, and Andrei V. Grischenko of Hokkaido University assisted our translation of some of the Russian literature. We also thank the shipboard scientists and crews of the oceanographic cruises that recovered the samples that we analyzed. Our work was supported financially by the Sasakawa Scientific Research Grant from the Japan Science Society and the MEXT Grant-in Aid for the 21st Century COE Program "Neo-Science of Natural History" at Hokkaido University.

References

Akiba, F. and Yanagisawa, Y., 1986: Taxonomy, morphology and phylogeny of the Neogene diatom zonal marker species in the middle-to-high latitudes of the North Pacific. *In*, Kagami, H., Karig, D. E., Coulbourn, W. T., *et al.*, *Initial Reports of Deep Sea Drilling Project*, vol. 87, p. 483–554. U. S. Government Printing Office, Washington, D.C.

Banse, K. and English, D. C., 1999: Comparing phytoplankton seasonality in the eastern and western subarctic Pacific and the western Bering Sea. *Progress in Oceanography*, vol. 43, p. 235–288.

Brzezinski, M. A., 1985: The Si:C:N ratio of marine diatoms: interspedific variability and the effect of some environmental variables. *Journal of Phycology*, vol. 21, p. 347–357.

Darley, W. M., 1982: *Algal biology: a physiological approach*, 168 p. Blackwell Scientific Publications, Oxford, UK.

Duce, R. A. and Tindale, N. W., 1991: Atmospheric transport of iron and its deposition in the ocean. *Limnology and Oceanography*, vol. 36, p. 1715–1726.

Fryxell, G. A., 1988: Polymorphism in relation to environmental conditions as exemplified by clonal cultures of *Thalassiosira tumida* (Janish) Hasle. *In*, Round, F. E., *ed*., *Proceedings of the 9th International Diatom Symposium*, p. 61–73. Otto Koeltz, Koenigstein.

Harrison, P. J., Conway, H. L., Holmes, R. W. and Davis, C. O., 1977: Marine diatoms growth in chemostats under silicate or ammonium limitation. III. Cellular chemical composition and morphology of *Chaetoceros debilis*, *Skeletonema costatum*, and *Thalassiosira gravida. Marine Biology*, vol. 43, p. 19–31.

Harrison, P. J., Boyd, P. W., Varela, D. E., Takeda, S., Shiomoto, A. and Odate, T., 1999: Comparison of factors controlling phytoplankton productivity in the NE and NW subarctic Pacific gyres. *Progress in Oceanography*, vol. 43, p. 205–234.

Honda, M. C., 2002: Biological pump in the Northwestern Pacific. *Journal of Oceanography*, vol. 59, p. 671–684.

Honjo, S., 1997: The Northwestern Pacific Ocean, as crucial ocean region to understand global change: Rationale for new international collaborative investigations. *In*, Tsunogai, S., *Biogeochemical processes in the North Pacific*, p. 233–248. Japan Marine Science Foundation, Tokyo.

Jordan, R. W., Komuro, C. and Narita, H., 2003: Microplankton assemblages collected in the Station KNOT, the Northwestern Pacific Ocean—Evidence of observations in 1999 and 2000—. *Monthly Kaiyo*, vol. 35, p. 451–457. (*in Japanese*)

Kanaya, T. and Koizumi, I., 1966: Interpretation of diatom thanatocoenoses from the North Pacific applied to a study of core V20-130 (Studies of a deep-sea core V20-130. Part IV). *Science Reports of the Tohoku University, Second Series* (*Geology*), vol. 37, p. 89–130.

Karohji, K., 1959: Report from the "Oshoro maru" on oceanographic and biological investigations in the Bering Sea and northern North Pacific in the summer of 1955. IV. Diatom associations as observed by Underway Samplings. *Bulletin of Fisheries Science, Hokkaido University*, vol. 9, p. 259–267.

Kasai, H., Saito, H., Kashiwai, M., Taneda, T., Kusaka, A., Kawasaki, Y., Kono, T., Taguchi, S. and Tsuda, A., 2001: Seasonal and interannual variations in nutrients and plankton in the Oyashio region: a summary of a 10-years observation along the A-line. *Bulletin of the Hokkaido National Fisheries Research Institute*, no. 65, p. 55–134.

Norris, R. D., 2000: Pelagic species diversity, biogeography, and evolution. *In*, Erwin, D. H. and Wing, S. L., *eds*., *Deep Time: Paleobiology's Perspective*, Supplement to vol. 26, no. 4, *Paleobiology*, p. 236–258.

Saito, H., Kasai, H., Kashiwai, M., Kawasaki, Y., Kono, T., Taguchi, S. and Tsuda, A., 1998: General description of seasonal variations in nutrients, chlorophyll a, and net plankton biomass along the A-line transect, western subarctic Pacific, from 1990–1994. *Bulletin of the Hokkaido National Fisheries Research Institute*, no. 62, p. 1–134.

Saito, H., Tsuda, A. and Kasai, H., 2002: Nutrient and plankton dynamics in the Oyashio region of the western subarctic Pacific Ocean. *Deep-sea Research II*, vol. 49, p. 5463–5486.

Sancetta, C., 1982: Distribution of diatom species in surface sediments of the Bering and Okhotsk seas. *Micropaleontology*, vol. 28, p. 221–257.

Sancetta, C. and Silvestri S.-M., 1986: Pliocene-Pleistocene evolution of the North Pacific ocean-atmospheric system, interpreted from fossil records. *Paleoceanography*, vol. 1, p. 163–180.

Semina, G. I., 1956: A new species of genus *Denticula* Ktz. *Botanical Contributions, Komarov Botanical Institute of the USSR Academy of Science, Division of Spore Plants*, vol. 11, p. 82–84. (*in Russian*)

Semina, G. I., 1981: Morphology and distribution of a tropical *Denticulopsis. In*, Ross, R., *ed*., *Proceedings of the Sixth Symposium on Recent and Fossil Diatoms*, p. 179–190. Otto Koeltz, Koenigstein, West Germany.

Shimada, C., Burckle, L. H. and Tanimura, Y., 2003: Morphological variability in *Neodenticula seminae*, a marine planktonic diatom in the North Pacific Ocean and Bering Sea. *Diatom Research*, vol. 18, p. 307–322.

Simonsen, R. and Kanaya, T., 1961: Notes on marine species of the diatom genus *Denticula* Kütz. *Internationale Revue der gesamten Hydrobiologie*, vol. 46, p. 498–513.

Takahashi, K., 1986: Seasonal flux of pelagic diatoms in the subarctic Pacific, 1982–1983. *Deep-Sea Research*, vol. 33, p. 1225–1251.

Takahashi, K., 1994: From modern flux to paleoflux: assessment. *In*, Zahn, R., Pedersen, T. F., Kaminski, M. A. and Labeyrie, L., *Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change NATO ASI Series*, vol. 17, p. 413–424. Springer-Verlag, Berlin.

Takahashi, K., Fujitani, N. and Yanada, M., 2002: Long term monitoring of particle fluxes in the Bering Sea and the central subarctic Pacific Ocean, 1990–2000. *Progress in Oceanography*, vol. 55, p. 95–112.

Takeda, S., 1998: Influence of iron availability on nutrient consumption ratio of diatoms in oceanic waters. *Nature*, vol. 393, p. 774–777.

Taniguchi, A., 1999: Differences in the structure of the lower trophic levels of pelagic ecosystems in the eastern and western subarctic Pacific. *Progress in Oceanography*, vol. 43, p. 289–315.

Tanimoto, M., Aizawa, C. and Jordan, R. W., 2003: Assemblages of living microplankton from the subarctic North Pacific and Bering Sea during July–August 1999. *Courier Forschungsinstitut Senckenberg*, no. 244, p. 83–103.

Whitney, F. A. and Freeland, H. J., 1999: Variability in upper water properties in the NE Pacific Ocean. *Deep-Sea Research II*, vol. 46, p. 2351–2370.

Yanagisawa, Y. and Akiba, F., 1990: Taxonomy and phylogeny of the three marine diatom genera, *Crucidenticula*, *Denticulopsis* and *Neodenticula. Bulletin of the Geological Survey of Japan*, vol. 41, p. 197–301.

Yanagisawa, Y. and Akiba, F., 1998: Refined Neogene diatom biostratigraphy for the northwest Pacific around Japan, with an introduction of code numbers for selected diatom biohorizons. *Journal of the Geological Society of Japan*, vol. 104, p. 395–414.