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Effects of nutrients on diatom skeletal silicification: Evidence from *Neodenticula seminae* culture experiments and morphometric analysis

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ABSTRACT

The diatom *Neodenticula seminae* (Simonsen and Kanaya) Akiba and Yanagisawa is important as one of the main primary producers in the subarctic North Pacific Ocean ecosystem. Its valve morphology showed a marked spatial difference between populations in the NW margin of the North Pacific Ocean and those of oceanic regions including the Bering Sea. There were also seasonal fluctuations in the degree of valve silicification found in the former region. Determining the origin of this intraspecific variability in morphology will improve our understanding of the detailed relationships between (paleo-) hydrography and the ecological and evolutional responses of microalgae.

We conducted time-series batch-culture experiments under different macronutrient conditions to evaluate the morphological responses of *N. seminae*. We used a cloned strain originally from the subarctic Oyashio Current off northeast Japan and made morphometric valve measurements. Under low ambient Si concentrations, we observed accelerated skeletal silicification, resulting in an increase of heavily silicified specimens when specific growth rates were high during logarithmic growth phases. In contrast, accelerated silicification continued throughout the entire incubation period (16 d) under high Si concentrations. These contrasting patterns of skeletal silicification under opposing Si conditions probably resulted from a balancing between Si availability and specific growth rates. There was an inconsistent relationship between the cell Si quota and skeletal silicification. This suggests that during logarithmic growth, Si was not always incorporated into the skeleton but was sometimes concentrated more in intracellular pools.

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1. Introduction

Neodenticula seminae (Simonsen and Kanaya) Akiba and Yanagisawa is a living, marine planktonic diatom. Since its first appearance (2.4 Ma), it has often been predominant in oceanic diatom communities preserved in bottom sediments as well as present day populations in the subarctic North Pacific Ocean and the Bering Sea (Karohji, 1959; Kanaya and Koizumi, 1966; Venrick, 1971; Hasle 1976; Sancetta, 1982; Sancetta and Silvestri, 1986; Takahashi, 1986; Yanagisawa and Akiba, 1998; Aizawa et al., 2005; Onodera et al., 2005). However, although it probably plays an important role in the Quaternary ocean-scale ecosystem and biogeochemical cycles, there is limited information about its ecology and physiology because of the difficulties in making observations and collecting samples in its oceanic habitat.

The intraspecific morphological variability of this species was first noticed in a comparison of specimens from North Pacific and North Atlantic waters (Semina, 1981). Kurihara and Takahashi (2002) reported a seasonal fluctuation in apical valve lengths with a maximum in spring, a minimum in autumn, and a bimodal distribution in autumn and winter. They attributed this variation to the annual life cycle of the species, with asexual reproduction dominant during the periods of higher production in spring and summer and sexual reproduction in autumn and winter when productivity drops. Shimada et al. (2003) and Shimada and Tanimura (2006) recognized spatial differences ("morphological provinces") in an internal valvar structure, the basal ridge, based on the examination of modern specimens from throughout the subarctic North Pacific Ocean. The basal ridge in most specimens from NW North Pacific populations was relatively thin, and those from the oceanic region in the subarctic North Pacific and Bering Sea were extremely robust. Shimada et al. (2006) also observed a seasonal variation in the robustness of the basal ridge, which they attributed to environmental factors, such as seasonal nutrient availability associated with the local hydrography, and to the survival strategy of the species. Thin morphotype dominated during spring phytoplankton blooms and

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during summer, periods of progressive nutrient limitation, whereas robust morphotype was abundant in autumn and winter, after the onset of vertical mixing.

A preliminary investigation using marine cores from the subarctic North Pacific demonstrated a geologic-scale variation in skeletal silicification of the species since its first appearance at 2.4 Ma (Shimada, unpublished data). The species morphology might reflect distinct changes in the Quaternary period. Therefore, it is important to understand in detail the physiology and ecology of this major species of the subarctic diatom community to realize its potential in paleoceanographic reconstruction. Furthermore, because fossil specimens hardly retain either nuclei or cytoplasm except for very unusual cases, it is important to derive as much information as possible from skeletal morphology.

For this study, we performed a series of culture experiments under controlled macronutrient conditions using a monoclonal strain of *N. seminae*. We further conducted morphometric analyses to examine the possible effects of nutrition on skeletal silicification.

2. Characteristics of *N. seminae*

2.1. Taxonomy and nomenclature

The original description of "*N. seminae*" (as *Denticula marina*) was based on a population from the western part of the Bering Sea (Semina, 1956). This publication did not provide the exact sampling location or a designation for the permanent slide containing the holotypic specimen. Simonsen and Kanaya (1961) amended the original description by Semina (1956) and re-identified the species as *Denticula seminae* as a nomen novum from observations of a Bering Sea bottom sediment (53°01′N, 176°15′W). Later, Simonsen (1979) transferred marine "*Denticula*" species with a different morphology from *Denticula* Kützing s.s. to his new genus *Denticulopsis*, and thus the species was became known *Denticulopsis seminae*.

Akiba and Yanagisawa (1986) divided *Denticulopsis* into 3 genera—*Denticulopsis*, and their newly created genera *Crucidenticula* and *Neodenticula*—on the basis of differences in the size of punctation distributed over the valve surface, and the stratigraphic and geographic distributions. *Neodenticula* was characterized by (1) extremely small puncta on the valve face that were invisible under the light microscope, (2) marginal ribs asymmetrical on the raphe-bearing side of the valve, (3) pseudosepta diverging on the raphe-bearing side, and (4) a continuous raphe with no break at the center. Three species previously assigned to *Denticulopsis* were transferred to the new genus *Neodenticula*; *N. kamtschatica*, *N. koizumii*, and *N. seminae* (Akiba and Yanagisawa, 1986).

N. seminae is the only modern representative of this genus; it is distinguished from the other extinct species by having the largest and broadest valve shape and by possessing closed copulae and densely arranged pseudosepta. Note that this series of descriptions includes little mention of variability in the robustness of either the basal ridge or the pseudoseptum, both internal structures of the valve (Fig. 1).

On the basis of a closer examination of the fossil record, Yanagisawa and Akiba (1990) hypothesized that these 3 *Neodenticula* species shared a single evolutionary lineage with the common and extinct ancestor *Nitzschia rolandii*. Since then, Medlin and Sims (1993) have pointed out morphological similarities between *Fragilariopsis* in the Southern Ocean and the complex of taxa including *Denticulopsis*, *Neodenticula*, and *Crucidenticula*, along with some phylogenetic implications.

2.2. Ecology

Time-series sediment trap experiments have documented increased abundance of *N. seminae* during periods of high productivity in oceanic regions, suggesting that the species principally occurs in phytoplankton blooms (Takahashi, 1986; Onodera et al., 2005; Shimada et al., unpublished data). In contrast, it seems to be a relatively minor contributor to spring phytoplankton blooms around the coastal Oyashio Current, because *Thalassiosira nordenskioeldii* and *Chaetoceros* spp. (mainly subgenus *Hyalochaete*) are predominant in this region (Kuwata, unpublished data).

N. seminae is believed to be distributed throughout the Northern Hemisphere but is most abundant within the subarctic North Pacific and the adjacent marginal seas as a boreal or cold water species

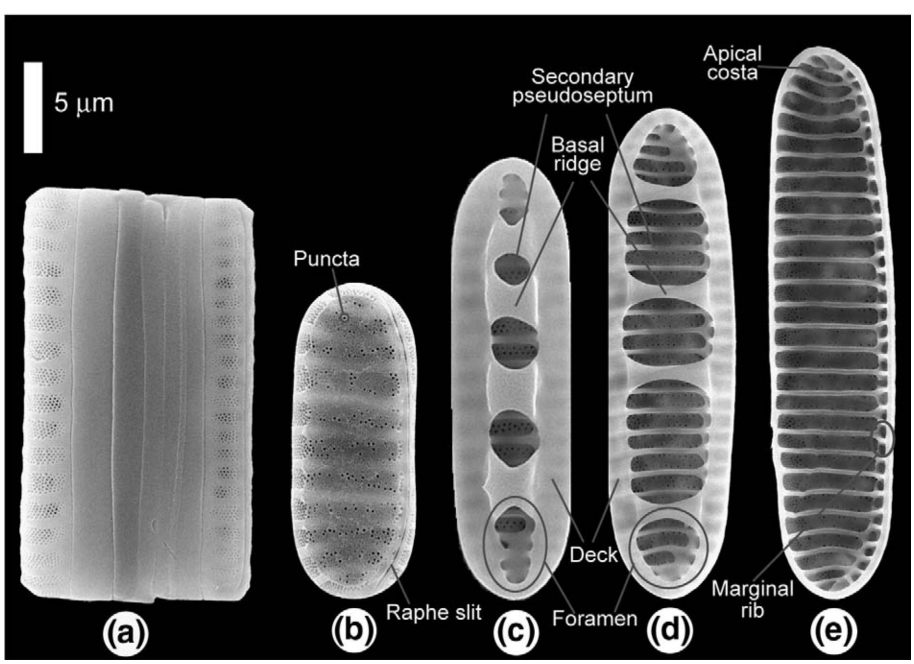

Fig. 1. Photographs of natural specimens taken by a scanning electron microscope; (a) girdle view of a frustule (=a cell), (b) valvar view, (c–e) internal valvar views. Photographs (c–e) indicate the morphological variation of the species. Note the difference in the development of basal ridge; types of (c) robust, (d) moderate and (e) thin, respectively. All specimens are from modern seawaters.

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