Diatom burst-driven silica depletion under the Antarctic sea ice: evidence from sponge spicules

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Earlier studies have documented the role of diatoms in reducing the diversity and abundance of other silica-dependent organisms, such as radiolaria. Here we hypothesize that diatom burst-driven depletion of dissolved silica (DSi) in the Antarctic under sea-ice waters affects other silica-biomineralizing organisms. We found intense diatom-dominated, ice-edge phytoplankton bloom in the Enderby basin resulting in severe depletion of DSi (<5 μM) under the sea ice. We also found siliceous sponge spicules within the surface sediment collected from under the Antarctic sea ice. Dominance of small style spicules (170 spicules/g sediment) under the sea ice along with dissolution seen on them, suggests DSi deficiency in the Antarctic waters. We, therefore, conclude that there is a rapid depletion of DSi due to seasonal diatom blooms under sea ice in the Antarctic waters.

Keywords: Diatoms, dissolved silica, sea ice, sponge spicules.

SILICON (Si), the seventh most abundant element in the universe, is a key nutrient in the ocean, required for the growth of diatoms and some sponges and utilized by radiolarians, silicoflagellates, several species of choanoflagellates, and potentially some picocyanobacteria[1]. The silica cycle is strongly intertwined with other major biogeochemical cycles, like those of carbon and nitrogen, and as such is intimately related to marine primary production, the efficiency of carbon export to the deep sea, and the inventory of carbon dioxide in the atmosphere[1]. In the modern oceans, the silica cycle is strongly influenced by the activities of skeleton-forming organisms[2]. The precipitation of silica by diatoms, and to a lesser extent by radiolarians, silicoflagellates, ebridians and sponges depresses dissolved silica concentrations in shallow marine waters[3]. Diatoms are responsible for the depletion of silica in the photic zone and largely control the marine biogeochemical cycles of silica in recent oceans[4]. In the geological past, during Cambro-Ordovician time, there was a transition from the inorganic silica deposition of the Precambrian to the biologically dominated silica deposition of the Phanerozoic[3]. With the evolution of demosponges near the beginning of the Cambrian, subtidal biogenic cherts became increasingly common, and with the Ordovician rise of radiolaria to ecological and biogeochemical prominence, sedimented skeletons became a principal sink for oceanic silica[5]. Since the mid Cretaceous, radiating diatoms dominated the silica cycle[5]. The ecological success of the diatoms over the Mesozoic and Cenozoic is associated with biogeographic shifts in siliceous sponges, decreasing silicification in the radiolarians, and a global decrease in oceanic silicic acid concentrations[6]. More recently, Lazarus *et al.*[7] studied the effect of diminution of silica in seawater and demonstrated that the radiolarian skeletons became much lighter.

Siliceous sponges are far more refractory to dissolution in seawater and sediments than diatom skeletons. This makes these deep-sea sponge populations function as benthic Si traps, retarding recycling of Si into silicate[8]; thus the standing stock of silica in sponges surpasses that in diatoms[9]. The fossil record suggests siliceous sponges were established by the Late Proterozoic, thrived during the middle Cambrian, diversified during the Jurassic when they formed vast reefs in the Tethys Sea and reached their maximum radiation and diversity during the Late Cretaceous[10]. Siliceous sponges are emerging as an important group of animals which, because of their ancient heritage, can shed light on fundamental questions such as the origin of multicellular animals, molecular evolution and the evolution of conduction systems[10]. Siliceous sponges are characterized by fine spicules with their characteristic terminal hypersilicification features[4,11]. Recent experiments have demonstrated the influence of environmental factors in modulating spicule size, shape and the presence or absence of one or more spicule types[12]. The concentration of dissolved silica in seawater regulates the phenotypic expression of the various spicule types in a sponge species[13]. Maldonado *et al.*[13] concluded that different sponge spicule types may be secreted by a specific sclerocyte type, which is activated by a particular threshold of silica concentration. Here we hypothesize that diatom burst-driven depletion of dissolved silica in the Antarctic under sea-ice waters affects other silica-biomineralizing organisms.

In order to test the hypothesis that there is depletion of silica under the Antarctic sea ice, we collected (i) surface water samples from 38°S to 66°S in the Indian sector of the Southern Ocean; (ii) a horizontal transect along the Antarctic coast from 12°E to 74°E, and (iii) drilled samples from under the ice cover. Sponge spicules were also collected from surface sediment from under the ice-covered region (Figure 1). Sponge samples were preserved at –20°C. In the laboratory, pre-weighed sediment sample was processed with H_2O_2 and sponge spicules were counted using a JEOL scanning electron microscopy (SEM). Elemental analysis was done using attached

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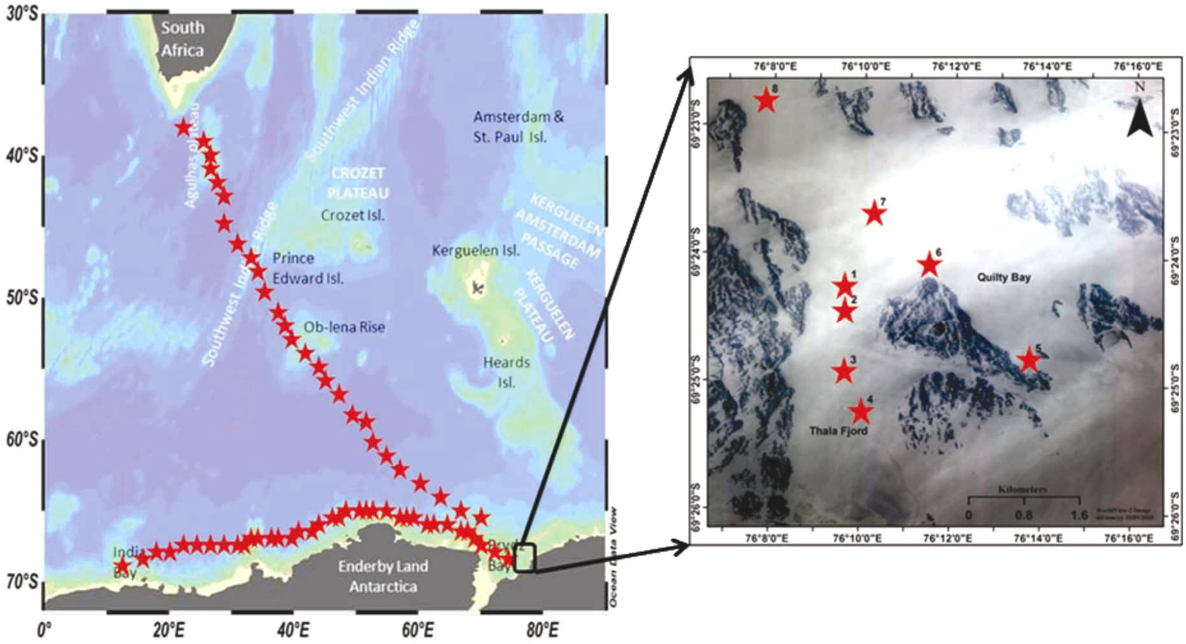


Figure 1. Map of study area showing the water sampling locations in Southern Ocean, coastal Antarctica and under the sea ice. Surface sediment was collected at station no. 6.

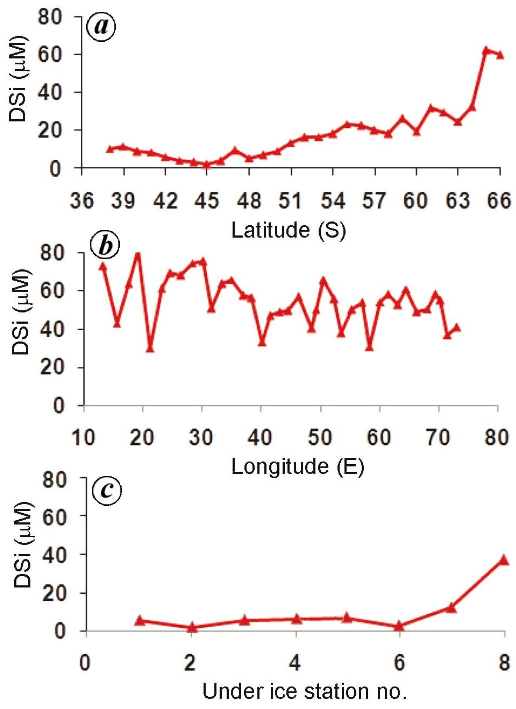


Figure 2. Variations in DSi concentration in (***a***) the Southern Ocean, (***b***) the Antarctic coast and (***c***) under sea ice.

OXFORD energy dispersive spectrometer (EDS). For diatom analysis, samples were prepared following the method proposed by Schrader and Gersonde[14]. Qualitative and quantitative analyses were performed using a Nikon inverted microscope. Diatoms were identified to the lowest taxonomic level possible. Concentration of diatoms is expressed as valves per gram of dry sediment. Dissolved silica (DSi) was measured with a SKALAR autoanalyser by standard colorimetric methods[15]. Chlorophyll was measured on a fluorometer (Model 10-AU, Turner Designs). Organic carbon was estimated using Shimadzu TOC analyser.

The availability of silicic acid ($Si(OH)_4$), the major form of dissolved silica in the oceans is over 0.75 µM in a vast majority of the surface ocean. However, it has been known for several years that the surface water is seasonally or chronically depleted of silicic acid to submicromolar levels (<0.1–0.6 µM) over areas of the tropical, subtropical ocean[16]. The Southern Ocean is known to be a high nutrient low chlorophyll (HNLC) region, but the distribution of major nutrients differs greatly in the different subsystems of the region[17]. Surface DSi values show a gradual increase from the subtropical region towards the polar region; however, there is a rapid increase below 63°S and the values reach up to 65 µM (Figure 2*a*). Along the Antarctic coast the DSi values remain high; they are above 30 µM throughout the transect (Figure 2*b*). We found low DSi values (<5 µM) in waters under the sea-ice cover in Antarctica, which also had algal mats on the underflanks of the ice (Figure 2*c*). The most dominant diatoms in water under the 1.8 m thick sea-ice cover were: *Berkeleya adeliensis*, *Fragilariopsis curta* and *Navicula glaciei*. The diatom blooms made the under ice environment a highly productive area, as reflected by the chlorophyll values (6.01 mg/m^3). The organic matter generated by seasonal blooms of diatoms, serves as essential

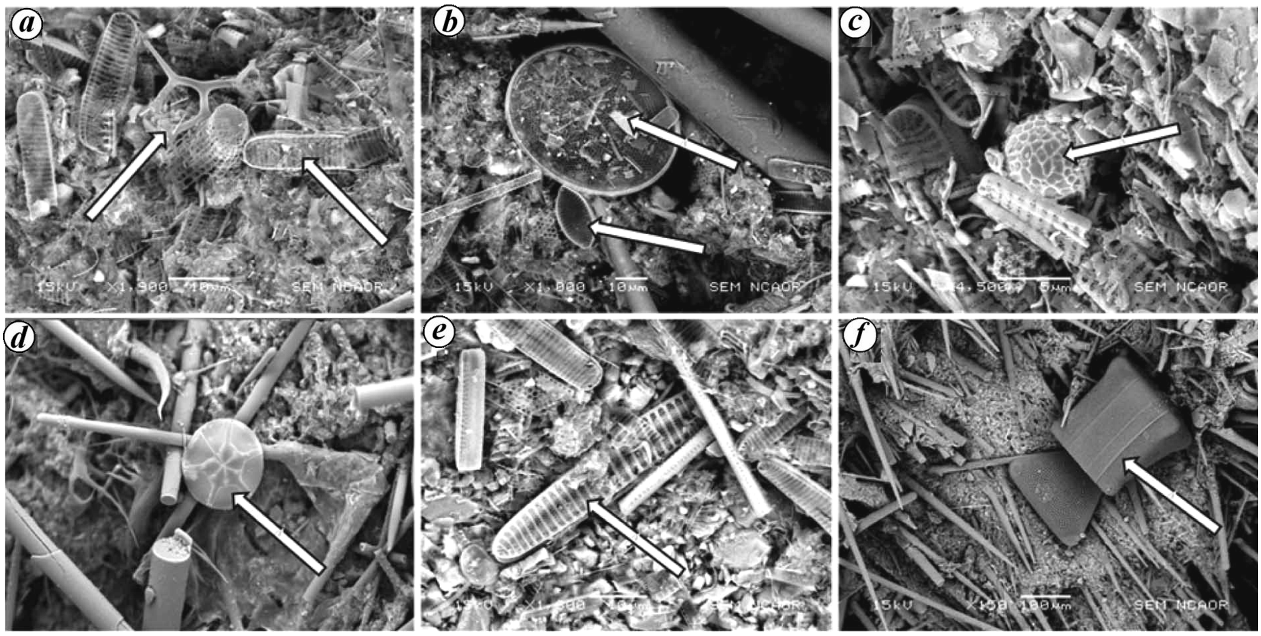
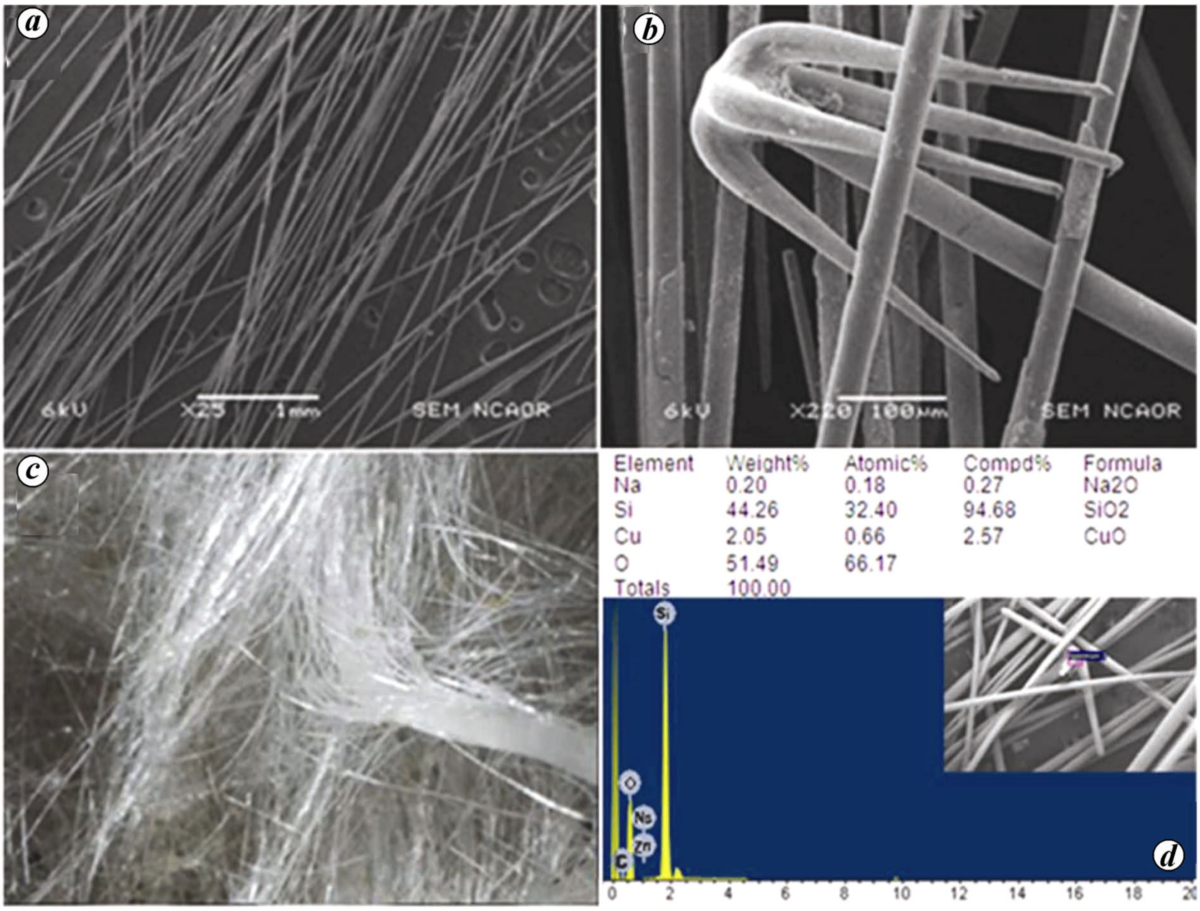


Figure 3. Diatom species and other elements found associated with spicules of sponge (Arrows: ***a***, *Fragillariopsis curta*, *Dictyocha speculum*; ***b***, *Actinocyclis* sp., *Fragillariopsis separanda*; ***c***, *Archaeomonad* cyst; ***d***, *Asteromphallus hyalinus*; ***e***, *Fragillariopsis obliquestata*, and ***f***, *Trigonium arcticum*).



Element	Weight%	Atomic%	Compd%	Formula
Na	0.20	0.18	0.27	Na2O
Si	44.26	32.40	94.68	SiO2
Cu	2.05	0.66	2.57	CuO
O	51.49	66.17		
Totals	100.00			

Figure 4. ***a***, ***b***, Scanning electron photomicrographs of sponge spicules. ***c***, Light microscopic image of spicule bearing sponge-mat. ***d***, EDS analysis of sponge spicules.

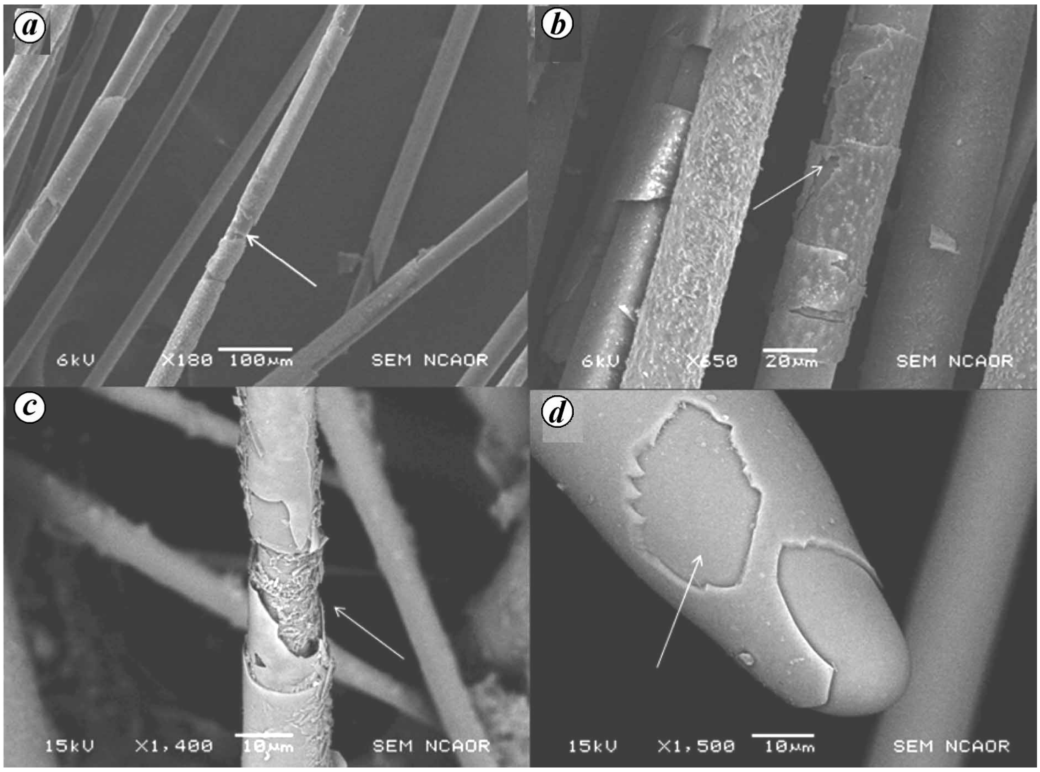


Figure 5 *a–d*. SEM images displaying sponge spicule dissolution caused by depleted silica.

food resource for grazers and most of the benthic organisms growing at greater depths, thereby facilitating carbon sequestration and its transfer to higher trophic levels[18]. Due to the high abundance of diatoms, the sediment organic carbon was high (3.5%). The surface sediment underneath sea ice was dominated by planktic diatom, *F. curta*. Relative abundance of *F. curta* was 91%, followed by *Fragilariopsis separanda*, *Fragilariopsis ritscheri*, *Thalassiosira gracilis*, *Porosira glacialis*, *Fragilariopsis cylindrus* and *Trigonium arcticum*. Diatom absolute abundance was 25.7×10^7 valves/g. Apart from diatoms, Archaeomonad cysts and silicoflagellate *Dictyocha speculum* were also recorded (Figure 3). Radiolaria were conspicuously absent, possibly due to silica limitation.

The second evidence for silica depletion under the ice comes from the Antarctic sponge, which had only small styles spicules (Figure 4). The abundance of small styles was 170/g. Elemental composition of spicules using EDS showed 44% Si, confirming that the sponges were siliceous. Spicule morphology showing the number of symmetry axes of their megascleres, which are monaxons and tetraxons, indicated that it belongs to demosponge (Figure 4). Also, the axial canal of spicules was sealed with silica, thus confirming it as a demosponge. The absence of isochelae and hypersilicification suggests silica-depleted conditions under the Antarctic sea ice. The third evidence for silica depletion comes from the penecontemporaneous dissolution features seen on small style spicules (Figure 5).

Harper and Knoll[19] provided correlative evidence that the blooms of diatoms reduced both diversity and abundance of other silica dependent organisms, such as radiolaria. In the past, the decrease in nutrient availability had resulted in an increasing number of small-sized[20] and lightly silicified, thin-walled diatoms[21], which is also seen in our results with smaller *F. curta* in water column (avg. length 20 µm) compared to that in surface sediment (avg. length 24 µm). Our results are also supported by those of Nelson and Smith[22], who found that intense diatom blooms in summer can suppress dissolved silica values to <l0 µM in the marginal ice zone of the Ross Sea.

In recent times, shallow-depth sponges occur either in microhabitat with enhanced silica supply or at high latitudes[23,24], where the concentration of silicate in surface water is higher. We, therefore, infer and attribute low silica concentration under the Antarctic sea ice to diatom blooms, which are severely affecting silicification in sponges. This pressure may be strong enough to restrict their distribution in ice-free areas in Antarctica. Our further studies would investigate how these remarkable benthic suspension feeders sustain themselves in silica-deficient marine ecosystem and their impact on other members of polar–marine food chain. Also, considering that the biological use of silica has relevant ecological effects, including control of marine primary productivity, indirect control of CO_2 production and linkage to the carbon cycle, we would study the rapidly occurring silica depletion in nature.

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Temperature-sensitive male-sterility system in pigeonpea

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The present communication reports successful breeding of the first temperature-sensitive male-sterility system in pigeonpea (*Cajanus cajan* (L.) Millsp.). This material was derived from a cross involving *Cajanus sericeus* (Benth. ex Bak.), a wild relative of pigeonpea, and a cultivar (ICPA 85010). The selections demonstrated marked changes in the fertility status of the plants under field conditions in different temperature regimes. At ≥25°C the plants were completely male-sterile, while at ≤24°C the same plants became fully male-fertile. These genotypes can be used to develop a two-line hybrid breeding system in pigeonpea.

Keywords: Fertility status, pigeonpea, temperature-sensitive male-sterility, seed production.

WHEN pedigree and population breeding programmes failed to break the decades-old low-yield plateau in pigeonpea (*Cajanus cajan* (L.) Millsp.), International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) breeders turned towards exploring hybrid technology. This vision was essentially based on the possibility of exploiting a small window of natural out-crossing for seed production. This endeavour began in 1974 with a massive germplasm search for a suitable male-sterility

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