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Differences in silica content between marine and freshwater diatoms

Abstract—Marine diatoms are shown to have on average one order of magnitude less silica per unit of biovolume than freshwater species. Silica content (pmol cell^{-1}) increases linearly with biovolume (μm^3) in both marine ($\log_{10}$[silica content] = 0.91 $\log_{10}$[biovolume] − 3.16; $r = 0.92$; $P < 0.0001$; $N = 44$) and freshwater diatoms ($\log_{10}$[silica content] = 1.03 $\log_{10}$[biovolume] − 2.45; $r = 0.91$; $P < 0.0001$; $N = 62$). Therefore, a first-order estimate of the amount of silica utilized by diatom production can be made from diatom biovolumes. Si : C molar ratios for marine diatoms and for freshwater diatoms also are different and demonstrate that appropriate molar ratios must be used for marine and freshwaters in estimating biogenic silica production from primary production. Among possible reasons for the disparity are differences in sinking strategy, the adaptation of marine diatom species to a low dissolved silica environment, and differences in salinity between the two environments.

Variation in silica content of diatom cell walls among species has attracted attention in a wide variety of scientific fields including taxonomy, physiology, ecology, and geochemistry. Einsele and Grim (1938) recognized that part of the variation in silica content among diatom species is related to cell size. They also recognized that silica content varies greatly within a given species—up to an order of magnitude (Taylor 1985). Variation in silica content within a species occurs during cell division and with growth rate, light, nutrient limitation, salinity, and temperature (e.g. Brzezinski 1985; Taylor 1985; Davis 1976; Paasche 1973*a*, 1980*a*; Tuchman et al. 1984; and many others).

A large component of variation in silicification is reflected in differences between freshwater and marine diatoms. Paasche (1980*b*) observed that Si : surface area ratios are somewhat less for marine species than for freshwater species. However, Werner (1977) suggested that reported values of diatom silica content for freshwater species, primarily those of Einsele and Grim (1938), were overestimates. Sicko-Goad et al. (1984) argued that reported values of diatom silica content are confounded by the use of laboratory cultures in the marine studies. They felt that there has been an unintentional but systematic bias, by using laboratory cultures, toward diatom species that have relatively thin frustules and thus low silica contents.

Physiological differences in dissolved silica utilization also have been observed between marine and freshwater diatoms. Paasche (1980*b*) reported that Monod half-saturation constants of marine planktonic

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diatoms for dissolved silica were, in general, an order of magnitude lower than for freshwater species. Tilman et al. (1982) summarized available Monod constants for dissolved silica of freshwater diatoms and showed that centric diatoms generally had lower Monod constants than pennate species. Most marine species studied to date have been centric diatoms, so it is possible that apparent differences between marine and freshwater diatoms are simply a result of taxonomic characteristics.

To test the hypothesis that the silica content of marine diatoms is different from that of freshwater diatoms, we collected literature values on silica content and biovolume. Most literature values for silica content were from direct analysis on cultured diatoms. Some values were determined indirectly from the change in dissolved silica concentration in natural waters in which a known number of diatoms were produced (e.g. Sommer and Stabel 1983) or from the volume of the frustule (e.g. Sicko-Goad et al. 1984). Only data that included direct measurements of cell size or biovolume were used. Additional data on freshwater silica content and biovolume for seven clones of centric diatoms and five clones of pennate diatoms were obtained from laboratory cultures (Conley et al. unpubl. data).

Silica contents of diatom species varied over five orders of magnitude (Tables 1–4). A significant log-log linear relationship (Fig. 1) was obtained between freshwater diatom silica content and biovolume ($r = 0.91$; $P < 0.0001$; $N = 62$):

$$\log_{10}[\text{silica content (pmol cell}^{-1})] = (1.03 \pm 0.06)\log_{10}[\text{biovolume } (\mu\text{m}^3)] - (2.45 \pm 0.19). \quad (1)$$

A significant log-log linear relationship between marine diatom silica content and biovolumc also was obtained ($r = 0.92$; $P < 0.0001$; $N = 44$):

$$\log_{10}[\text{silica content (pmol cell}^{-1})] = (0.91 \pm 0.064)\log_{10}[\text{biovolume } (\mu\text{m}^3)] - (3.16 \pm 0.22). \quad (2)$$

Coefficients from the regression equations are reported ±1 SD. There was no significant difference between slopes of the two regressions ($F_{1,102} = 2.515$, n.s. at $\alpha = 0.05$). Because the minimal and maximal biovolumes of freshwater and marine diatoms were of the same orders of magnitude, dividing silica content by biovolume should provide a fair correction for the effect of size on silica content. In fact, there was no correlation between log silica content per unit of biovolume and log biovolume over all diatoms ($r = 0.07$; n.s. at $P < 0.05$; $N = 106$) or within freshwater diatoms ($r = 0.10$; n.s. at $P < 0.05$; $N = 62$) and only a weak correlation within marine diatoms ($r = 0.46$; $P = 0.002$; $N = 44$). As can be seen from the significantly different intercepts of the two regressions, marine diatoms averaged one order of magnitude less silica per unit of biovolume (0.000502 ± 0.000466 pmol μm^{-3}) than did freshwater diatoms (0.00558 ± 0.00400 pmol μm^{-3}).

Potential biases in the data set seemingly cannot account for the differences in silica content between marine and freshwater diatoms. We have not tested for differences within the marine diatom data set because there were only limited data for silica content per unit of biovolume for natural populations of marine diatoms. There was no significant difference between cultured and natural freshwater diatoms in log silica content per unit of biovolume ($F_{48,12} = 1.91$, n.s. at $\alpha = 0.05$). Silica content per unit of biovolume for *Melosira granulata* Ehrenb. (Table 1), the species with the most data for cultured and natural populations combined, shows no consistent differences between cultured or natural specimens. There was a slight tendency for freshwater pennate diatoms to be more heavily silicified than freshwater centrics, but the difference was not significant ($F_{40,20} = 4.47$, n.s. at $\alpha = 0.05$) and very small compared to the difference between marine and freshwater diatoms. Also, some part of the correlation between biovolume and silica content within and among freshwater and marine diatoms may be caused by an allometric relationship between biovolume and surface area. Marine and freshwater diatom shapes (and so surface areas at a given biovolume) are probably sufficiently similar, however, that surface area differences cannot account for the differences in silica content.

Casual observation suggests that benthic

Table 1. Silica content (pmol cell^{-1}) and biovolume (μm^3) of freshwater centric diatoms. Where a clone name is known it is indicated, otherwise N is used for values obtained from natural waters.

		Silica content		Biovolume		
	Clone	Min–max	Mean	Min–max	Mean	Reference
Cyclotella bodanica	N		533		40,000	Einsele and Grim 1938
Cyclotella comta	N		31.7		1,900	Einsele and Grim 1938
C. comta	LM85		39.8		4,170	Conley et al. unpubl.
Cyclotella glomerata	N		3.67		190	Einsele and Grim 1938
Cyclotella melosiroides	N		12.5		650	Einsele and Grim 1938
Cyclotella meneghiniana	N		2.43		1,270	Sicko-Goad et al. 1984
Cyclotella sp. No. 6	N		0.73		101	Sicko-Goad et al. 1984
Cyclotella pseudostelligera	N	0.52–0.70	0.63		200	Bailey-Watts 1976
Cyclotella socialis	N	14.2–19.2	16.7	1,600–1,900	1,750	Einsele and Grim 1938
Melosira granulata	N		2.17		420	Einsele and Grim 1938
M. granulata	N		10.1		1,030	Prowse and Talling 1958
M. granulata	N	3.22–4.00	3.57	410–590	500	Sommer and Stabel 1983
M. granulata	N		4.90		847	Reynolds 1984
M. granulata	N		9.68		5,127	Sicko-Goad et al. 1984
M. granulata	AUX5B		1.40		283	Conley et al. unpubl.
M. granulata	MEL2I		1.90		611	Conley et al. unpubl.
M. granulata	LM5MEL		8.60		1,172	Conley et al. unpubl.
Melosira islandica	N		17.7		3,633	Sicko-Goad et al. 1984
M. islandica var. *helvetica*	N	4.67–9.67	7.17	1,150–2,500	1,825	Einsele and Grim 1938
Melosira italica	N		5.33		800	Einsele and Grim 1938
M. italica	N		3.22		393	Gibson 1981
Stephanodiscus alpinus	N		13.2		5,192	Sicko-Goad et al. 1984
S. alpinus	LMI20		2.62		649	Conley et al. unpubl.
Stephanodiscus astraea	N		142		25,000	Einsele and Grim 1938
S. astraea	N		48.7		8,600	Gibson 1981
S. astraea	N	60.5–77.5	69.0		15,980	Reynolds 1984
S. astraea	N		34.8		8,300	Reynolds 1984
S. astraea	N		26.7	2,220–12,010	5,930	Reynolds 1984
Stephanodiscus binderanus	N		1.03		830	Sicko-Goad et al. 1984
S. binderanus	N	0.78–0.93	0.85	150–250	200	Sommer and Stabel 1983
Stephanodiscus hantzschii	N	0.73–0.80	0.77	694–961	828	Swale 1964
S. hantzschii	N		0.58		600	Reynolds 1984
S. hantzschii	N		0.18	30–70	50	Sommer and Stabel 1983
S. hantzschii	SaEVD		0.26		107	Conley et al. unpubl.
Stephanodiscus minutus	N		0.45		158	Sicko-Goad et al. 1984
S. minutus	LMSTEPH2		0.27		128	Conley et al. unpubl.
Stephanodiscus niagarae	N		51.0		21,360	Sicko-Goad et al. 1984
Stephanodiscus rotula	N	8.33–12.2	10.0		7,240	Happey 1970
S. rotula	N	2.12–5.75	3.93		1,150	Bailey-Watts 1976
Stephanodiscus subtilis	N		0.27		185	Sicko-Goad et al. 1984
Stephanodiscus tenuis	N		4.50		3,540	Sicko-Goad et al. 1984

Table 2. Silica content (pmol cell^{-1}) and biovolume (μm^3) of freshwater pennate diatoms. Where a clone name is known it is indicated, otherwise C is used to denote values obtained from cultured diatoms and N is used for values obtained from natural waters.

		Silica content		Biovolume		
	Clone	Min–max	Mean	Min–max	Mean	Reference
Asterionella formosa	N	1.58–2.83	2.28	320–440	400	Einsele and Grim 1938
A. formosa	N	2.53–2.87	2.70		754	Happey 1970
A. formosa	N		2.55		450	Bailey-Watts 1976
A. formosa	C	0.38–1.09	0.73		260	Holm and Armstrong 1981
A. formosa	N	1.85–2.48	2.17	443–589	516	Reynolds and Wiseman 1982
A. formosa	N	3.57–6.83	5.17	550–850	700	Sommer and Stabel 1983
Diatoma elongatum	N		4.17		1,000	Einsele and Grim 1938
Fragilaria capucina	N	1.48–1.77	1.63		400	Sicko-Goad et al. 1984
Fragilaria crotonensis	N	2.83–3.58	3.15	775–850	800	Einsele and Grim 1938
F. crotonensis	N	3.48–5.07	4.18	497–749	623	Reynolds and Wiseman 1982
F. crotonensis	N	3.50–5.00	4.33	770–1,230	1,000	Sommer and Stabel 1983
F. crotonensis	Frag3		2.20		544	Conley et al. unpubl.
Fragilaria intermedia var. *fallax*	N		1.63		300	Sicko-Goad et al. 1984
Synedra acus	N		25.7	1,520–2,480	2,000	Sommer and Stabel 1983
Synedra acus var. *angustissima*	N	18.3–20.8	20.0	3,000–3,400	3,200	Einsele and Grim 1938
Synedra delicatissima	DLKSYN5		26.2		4,787	Conley et al. unpubl.
Synedra ostenfeldii	SYNAX		12.2		2,985	Conley et al. unpubl.
Synedra ulna var. *danica*	N		35.0		8,500	Einsele and Grim 1938
Tabellaria fenestrata	N	6.17–7.00	6.58	1,150–1,400	1,275	Einsele and Grim 1938
Tabellaria flocculosa	TAB6		13.4		2,294	Conley et al. unpubl.
T. flocculosa	TAB2		29.3		2,419	Conley et al. unpubl.

Table 3. Silica content (pmol cell^{-1}) and biovolume (μm^3) of brackish and marine centric diatoms. Where a clone name or number is known it is indicated, otherwise C is used to denote values obtained from cultured diatoms.

	Clone	Silica content		Biovolume		Reference
		Min–max	Mean	Min–max	Mean	
Bacteriastrum furcatum	149a		0.91		2,000	Brzezinski 1985
Cerataulina pelagica	C	3.15–3.45	3.25		21,400	Paasche 1980a
Chaetoceros affinis var. *willei*	C	1.18–1.48	1.33		4,200	Paasche 1980a
Chaetoceros constrictus	CHS-1		1.00		3,350	Brzezinski 1985
Chaetoceros convolutus	548		7.30		15,100	Brzezinski 1985
Chaetoceros debilis	C	0.11–0.30	0.25	229–380	292	Harrison et al. 1977
Chaetoceros pelagicus	854		0.30		983	Brzezinski 1985
Chaetoceros sp. 1 cf. *vixvisibilis*	847		0.73		572	Brzezinski 1985
Chaetoceros sp. 2	AS1A		0.12		379	Brzezinski 1985
Chaetoceros sp. 3	140A		1.70		1,720	Brzezinski 1985
Corethron criophilum	35P		11.0		30,160	Brzezinski 1985
Coscinodiscus granii	357		100		97,600	Brzezinski 1985
Coscinodiscus sp.	C		5,630		3,420,000	Parsons et al. 1961
Cyclotella cryptica	C	0.28–0.43	0.35	482–1,190	814	Werner 1977
Ditylum brightwellii	C	6.07–7.85	7.25	20,100–27,680	23,900	Eppley et al. 1967
D. brightwellii	C		3.17		24,000	Strickland et al. 1969
D. brightwellii	C		24.0	6,000–175,000	90,500	Chisholm et al. 1978
Hemiaulus sinensis	125		3.40		7,550	Brzezinski 1985
Lauderia borealis	536		1.50		5,950	Brzezinski 1985
Leptocylindrus danicus	793a		0.19		1,660	Brzezinski 1985
Rhizosolenia alata	717		39.0		482,000	Brzezinski 1985
Rhizosolenia fragilissima	C	0.99–1.82	1.23		20,800	Paasche 1980a
Skeletonema costatum	C		3.40		1,390	Parsons et al. 1961
S. costatum	C	0.03–0.10	0.05	125–150	138	Harrison et al. 1976
S. costatum	C	0.02–0.05	0.03	99–199	129	Conway et al. 1976
S. costatum	C	0.04–0.08	0.07	131–181	154	Harrison et al. 1977
S. costatum	C	0.06–0.10	0.08		335	Paasche 1980a
S. costatum	312		0.04		202	Brzezinski 1985
S. costatum	S3		0.61		1,040	Brzezinski 1985
Stephanopyxis palmeriana	80a		28.0		332,000	Brzezinski 1985
Thalassiosira aestivalis	543		13.0		16,300	Brzezinski 1985
Thalassiosira gravida	C	1.08–2.00	1.47	3,710–6,030	5,080	Harrison et al. 1977
Thalassiosira oceanica	13-1		0.11		153	Brzezinski 1985
Thalassiosira nordenskioeldii	TN-2	1.05–2.67	1.93	1,384–24,680	10,700	Durbin 1977
Thalassiosira partheneia	47		0.31		893	Brzezinski 1985
Thalassiosira pseudonana	C	0.05–0.07	0.06		256	Paasche 1980a
T. pseudonana	3H		0.21		136	Brzezinski 1985
Thalassiosira rotula	411		5.30		10,400	Brzezinski 1985
Thalassiosira weissflogii	ACTIN		1.20		1,800	Brzezinski 1985

Table 4. Silica content (pmol cell^{-1}) and biovolume (μm^3) of brackish and marine pennate diatoms.

	Clone	Silica content	Biovolume	Reference
Asterionella glacialis	428	1.10	1,100	Brzezinski 1985
Nitzschia sp. 1	117	0.39	1,680	Brzezinski 1985
Nitzschia sp. 2	130	0.06	215	Brzezinski 1985
Surirella sp.	421	2.20	1,660	Brzezinski 1985
Thalassiosionema nitzschioides	415	0.21	501	Brzezinski 1985

diatoms are generally more heavily silicified than planktonic diatoms. The majority of marine species for which silica content and biovolume data were available are probably true planktonic diatoms. Lowe (1974) classified 12 of the 32 freshwater species reported here as euplanktonic and only four species as tychoplanktonic or periphytic; the remainder were unclassified. Most of our reported species (centric and pennate) occur in abundance in the plankton of large, deep lakes such as the North American Great Lakes (e.g. Stoermer and Yang 1970). Occasional occurrence in the benthos does not qualify a diatom as benthic. Although some freshwater diatoms may spend part of their life cycle in the sediments during resting stages (e.g. *M. granulata*: Sicko-Goad et al. 1986), it is more significant that they spend the entire vegetatively active part of their life cycles in the plankton. If there is a tendency to being a true benthic species, in our experience it is among the pennates; we have already demonstrated no significant pennate vs. centric difference in silica content per unit of biovolume.

Differences in sinking strategies between diatoms from marine and freshwater environments might contribute to the variation in silica content between marine and freshwater diatoms. In freshwater, rapid sinking of diatoms occurs under nutrient limitation (Titman and Kilham 1976; Sommer and Stabel 1983) and in physically stable water columns (Reynolds 1973; Scavia and Fahnenstiel 1987). Sinking into the hypolimnion is not a terminal event for most diatoms in most lakes. In the oceans on the other hand, once a diatom is lost from the upper mixed zone, re-entry into the photic zone is difficult. Therefore, it may be an advantage to have a lower silica content, making it less likely for a diatom to sink out of the photic zone.

Relative dissolved silica availability might select for differences in silica content between marine and freshwater diatoms. In general, there is a connection between silicification and concentrations of ambient dissolved silica (Guillard et al. 1973; Paasche 1980*b*). In the laboratory, diatoms under continuous dissolved silica-limited culture often have low cell silica contents whether they are marine (Paasche 1973*a*) or freshwater species (Tilman and Kilham 1976). Although freshwaters may have low concentrations of dissolved silica (usually during summer), concentrations of dissolved silica are often well above limiting values during the seasons of optimal growth. By contrast, diatoms face low concentrations of ambient dissolved silica in most regions of the world ocean. Thus, there might be selective pressure for less silicification in most marine planktonic diatoms in order

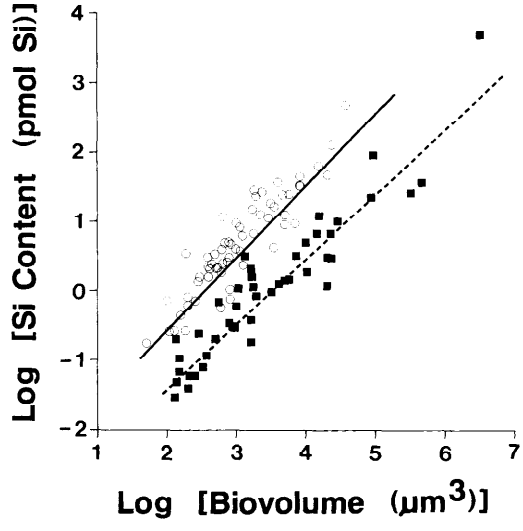

Fig. 1. Relationship of biovolume to silica content of freshwater diatoms (O and solid line) and of marine diatoms (■ and broken line).

to compete successfully in an environment that is low in dissolved silica.

Perhaps differences between marine and freshwater diatom silica contents are the result of salinity differences between the two habitats. Olsen and Paasche (1986) found that *Thalassiosira pseudonana* cells at a salinity of 24‰ had lower silica contents than cells grown in a freshwater medium. Tuchman et al. (1984) found that cells of *Cyclotella meneghiniana* Kutz. from cultures with higher NaCl concentrations (660–400 mg liter^{-1} Cl) had lower silica contents than cells grown at low concentrations of NaCl, even though initial concentrations of ambient dissolved silica were identical. It is not known, however, whether salinity effects on silicification are due directly to the effects of salt, osmotic pressure, or other factors (Olsen and Paasche 1986).

Paasche (1980*b*) observed that half-saturation constants for the uptake of dissolved silica for some marine species were an order of magnitude lower than those for many freshwater species. Olsen and Paasche (1986) found over an order of magnitude difference in the half-saturation constant for dissolved silica-limited growth of *T. pseudonana* Hasle and Heimdal at high and low salinities (0.04 mol liter^{-1} in a marine medium and 8.6 mol liter^{-1} in a freshwater medium). If uptake rates are expressed as a function of the calculated concentration of the monovalent conjugate base, $Si(OH)_3O^-$, rather than total silica (Riedel and Nelson 1985), differences in half-saturation constants may not be as great, because pH differences between marine and freshwaters influence silica speciation.

Given that marine diatoms contain one order of magnitude less silica per unit of biovolume than freshwater diatoms, the Si : C molar ratio also should be different. Brzezinski (1985) determined a Si : C molar ratio of 0.13±0.04 from 27 species of cultured marine diatoms. By contrast, Sicko-Goad et al. (1984) determined a Si : C molar ratio of 0.79±0.43 from 12 freshwater species collected from natural waters. Si : C molar ratios of particulate matter in dissolved silica-rich surface waters of the Antarctic Ocean, where many heavily silicified marine diatoms occur (E. Theriot pers. obs.), are intermediate between those of the two studies, with a Si : C molar ratio of 0.40 (Copin-Montegut and Copin-Montegut 1978).

Diatom Si : C molar ratios and estimates of primary production have been used to estimate biogenic silica production (Calvert 1968; Lisitzin et al. 1972; Heath 1974; Nelson and Gordon 1982; Jennings et al. 1984). Different and appropriate molar ratios must be used for marine and freshwaters in estimating biogenic silica production. An estimate of the amount of silica used by a diatom assemblage can be calculated from the regression equations (Eq. 1 and 2) if the abundances and biovolumes of the component species are known. This estimate is only first order, however, because silica content per unit of biovolume of a diatom may vary by an order of magnitude. It is clear that additional data are needed for Si : C at different salinities if accurate stoichiometric indices are to be useful for estimating diatom production.

In summary, the order-of-magnitude difference we report between silica contents of marine and freshwater diatoms cannot be accounted for by any reasonable adjustment for biovolume or unit surface area. The data show that marine diatoms average one order of magnitude less silica per unit of biovolume than freshwater species. Other potential correlations (i.e. cultured vs. natural populations and centric vs. pennate diatoms) contribute relatively little to the overall variation observed. Whether the differences in silica contents are genetic adaptations or merely the results of salinity or other factors is not known, but is a fruitful area for research.

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[Methyl-^{3}H]thymidine macromolecular incorporation and lipid labeling: Their significance to DNA labeling during measurements of aquatic bacterial growth rate

Abstract—It is essential during measurements of aquatic bacterial production with [methyl-^{3}H]thymidine (Tdr) that only labeled DNA is measured. We found in 12 freshwater and marine systems that DNA labeling represented a variable proportion of total macromolecular labeling. Up to 87% of label appearing in precipitated labeled macromolecules from acid–base hydrolysis treatments was soluble in ethanol. Reverse-phase, high-pressure liquid chromatography showed that the composition of labeled molecules in the ethanol was 78–88% [^{3}H]Tdr. The rate of labeling of the ethanol-soluble fraction was significantly correlated with the rate of total macromolecular labeling ($r = 0.88$, $n = 40$, $P < 0.001$) and less strongly with the DNA labeling rate ($r = 0.49$, $n = 28$, $P = 0.005$). Experiments in which bacterial cells were labeled with [^{3}H]Tdr or $^{32}PO_4^{3-}$ showed that above a total macromolecular labeling rate of ~1 pmol Tdr liter^{-1} h^{-1}, bacterial cells bind Tdr but do not incorporate it into phospholipids in the cell envelope.

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