

Rhizosolenia mats: An overlooked source of silica production in the open sea

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Abstract

The contribution of *Rhizosolenia* mats to silica cycling in the central North Pacific and the coupling of mat silicon metabolism and their vertical migration was examined in areas to the west of the Hawaiian Islands (23–28°N and 159–175°W) in 1995 and to the east of Hawaii along 31°N (160–127°W) in 1996. The biogenic silica content of *Rhizosolenia* mats sampled in 1995 averaged 1.82 ± 1.87 (SD) $\mu\text{mol Si mat}^{-1}$. Larger mats that averaged 4.56 ± 3.54 (SD) $\mu\text{mol Si mat}^{-1}$ were observed in 1996. Kinetic experiments indicated that substrate limitation of mat silica production was widespread across the study region, with ambient $[\text{Si}(\text{OH})_4]$ restricting silica production to 33% of maximum potential rates. Three lines of evidence indicate that silicon metabolism is not tightly coupled to the migration of mats to and from the nutricline. In 1996, mats in surface waters could double their Si content in 0.55 d on average without migrating to the nutricline to obtain Si. However, average doubling times (9.8 d) in 1996 were of the same order as a migration cycle, necessitating significant Si uptake at depth. Si uptake rates did not differ significantly between ascending and descending mats, suggesting that mats ascending from the nutricline had not fulfilled their Si uptake requirements. Finally, small internal pools of Si in ascending mats indicated that if significant amounts of Si were taken up at depth, they were not stored for use in the surface waters. The biomass and silica production rates of mats collected using SCUBA in the upper 20 m were extrapolated to 150 m by using abundances determined using a video plankton recorder (VPR). The results suggest that mats account for about 3% of the standing stock of biogenic silica and 26% of silica production in the upper 150 m. The daily silica production by *Rhizosolenia* mats ($317 \mu\text{mol Si m}^{-2} \text{ d}^{-1}$) is 50–76% of the total silica production in the Sargasso Sea. This high rate of silica production combined with the wide geographic distribution of mats throughout several mid-ocean gyres suggests that mats may contribute significantly to global silica production.

Macroscopic aggregates of diatoms of the genus *Rhizosolenia* were first described in detail by Carpenter et al. (1977) in the Sargasso Sea. These “mats” range in size from 1–30 cm and have been reported in several oligotrophic warm seas, including the Indian Ocean (Wallich 1960), the California Current (Alldredge 1982), and in greatest abundance in the North Pacific Gyre (Villareal and Carpenter 1989). Regionally, these diatom mats contribute significantly to oceanic nutrient budgets. Episodic blooms of large diatoms such as *Rhizosolenia* have the potential to contribute significantly to oceanic new production (Goldman 1993), and several observations have supported this concept (Sanctetta et al. 1991; Blain et al. 1997). Observation of an extremely intense and extensive bloom of *Rhizosolenia* was documented in the equatorial Pacific in 1992 (Yoder et al. 1994). Large diatoms, including several *Rhizosolenia* sp., are

also responsible for a significant fraction of export production in the open sea (Scharek unpubl. data). An especially striking example was reported by Smith et al. (1996), where a layer of fresh phytoplankton, mainly diatoms, carpeted the seafloor beneath the equatorial Pacific.

Rhizosolenia mats are communities of intensely concentrated diatom biomass that are distinctively different from the rest of the phytoplankton assemblage. Mat primary production can be one–three orders of magnitude greater than that in an equal volume of the surrounding seawater (Carpenter et al. 1977; Alldredge 1982). Mats also contribute to new production, transporting $18\text{--}97 \mu\text{mol N m}^{-2} \text{ d}^{-1}$ of new nitrogen (N) into the euphotic zone, an amount equal to 9–48% of the turbulent diffusive flux into the surface mixed layer (Villareal et al. 1999). They may also dominate oceanic diatom biomass. Villareal and Carpenter (1989) estimated that *Rhizosolenia* mats accounted for 98% of all living diatom Si in the central North Pacific, potentially making mats major contributors to regional silica cycling.

The open-sea habitat of *Rhizosolenia* mats plays a significant role in the global marine Si cycle. Nelson et al. (1995) estimated that the mid-ocean gyres account for 9–13% of global silica production, based on limited data from the Sargasso Sea. More recently, Brzezinski et al. (1998) raised the upper limit of that estimate to 40%, based on new data from the central North Pacific. Neither Nelson et al.’s (1995) nor

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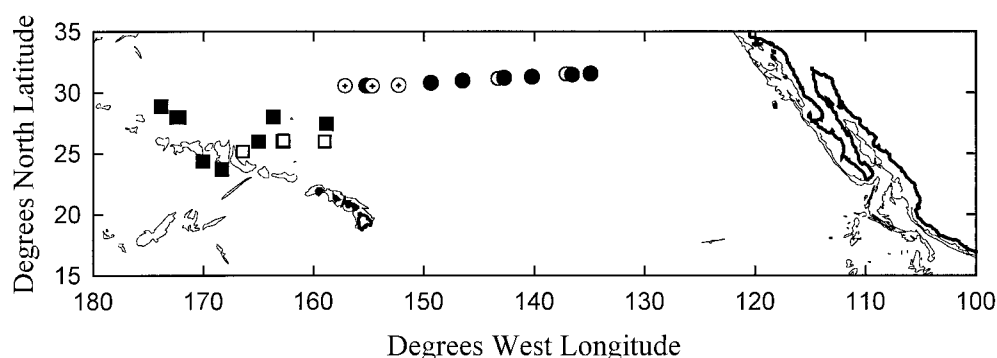


Fig. 1. Locations of stations at which *Rhizosolenia* mats were collected during August 1995 (squares) and July 1996 (circles). Si uptake kinetics were studied at stations denoted by unfilled symbols. Stations where mat abundance was determined using the VPR are shown with crosshairs.

Brzezinski et al.'s (1998) estimate includes the contribution of *Rhizosolenia* mats, as they are not sampled by traditional bottle samplers because of their relative rarity, i.e., 0.001 mats m^{-3} in the Sargasso (Carpenter et al. 1977) and up to 4.9 mats m^{-3} in the central North Pacific (Villareal and Carpenter 1989). However, mats may dominate diatom biomass in these regions (Villareal and Carpenter 1989), creating a unique situation where silica cycling in mid-ocean gyres that is significant in global terms may be dominated by large, rare cells that have been invisible to past investigations.

Rhizosolenia mats have a unique biology that makes the assessment of their contribution to elemental cycling particularly challenging. Large oceanic diatoms such as *Rhizosolenia debyana* H. Pergallo (Villareal 1988) and *Ethmodiscus* spp. (Villareal 1992) regulate their buoyancy and, like *Rhizosolenia* mats, contain large internal nitrate pools apparently derived from the nitracline (Villareal and Lipschultz 1995; Villareal et al. 1996). Mats have an isotopic composition similar to the deep nitrate pool (Villareal et al. 1993) and have active nitrate reductase activity that suggests a near total reliance on nitrate as their N source (Joseph et al. 1997). Such observations suggest that mats migrate several 10s of meters to the nitracline (Villareal et al. 1993). The migration to the nitracline and return to the euphotic zone is estimated to take 3.6–5.4 d, based on a model that considers photosynthetic rates, ascent/descent rates, and nitrate uptake kinetics (Villareal et al. 1996). A more complex model yields similar results (Richardson et al. 1998).

Mat migration to the nutricline leads to an uncoupling of their C and N metabolism. Carbon (C) fixation is confined to the well-lit surface waters that can support photosynthesis, while the bulk of N acquisition occurs at depth. As diatoms, *Rhizosolenia* mats also have a large requirement for Si to construct their frustules, but it is not known how their silicon metabolism is integrated into their migration. Mats may exploit the higher silicic acid concentrations in the nutricline during their migration, analogous to their pattern of nitrate use. However, significant silicic acid uptake may occur in the surface layer, as silicic acid is not nearly as depleted as nitrate in the euphotic zone of the open sea. Silicic acid concentrations range from 0.6 to 0.9 μM in the Sargasso Sea (Brzezinski and Nelson 1995) and from 1 to 3 μM in the central North Pacific (Villareal and Carpenter 1989; Brze-

zinski et al. 1998), while nitrate concentrations are <10 nM in both locations (Brzezinski et al. 1998). We have conducted the first study to address how silicon metabolism is coupled to the vertical migration of *Rhizosolenia* mats in the central North Pacific and provide the first quantitative estimates of their contribution to regional silica production.

Methods

Rhizosolenia mats were studied at 13 stations to the west of Hawaii (between 23–28°N and 159–175°W) from 5–23 August 1995 and at 12 stations between Hawaii and North America (along 31°N between 160–127°W) from 17–31 July 1996 (Fig. 1). Mats were collected from the upper 25 m of the water column at each station using SCUBA twice a day, at approximately 0900 and 1500 h. Divers quantified mat abundance at six depths (0–18 m) by recording the number of mats passing through flowmeter-equipped 1-m² frames that traveled a known distance through the water. In addition, mats were observed using a VPR (Davis et al. 1992) at three stations occupied in 1996. The VPR was towed obliquely through the water between the surface and 150 m four times at each station. The VPR video camera recorded sequences of images from 0.08-liter volumes, defined by a collimated light beam (Villareal et al. 1999). Data from 3 of the 10 stations where VPR surveys were conducted (30.31°N, 157.12°W; 30.50°N, 154.33°W; and 30.38°N, 152.14°W) revealed the presence of *Rhizosolenia* mats (identified by their unique morphology) down to a depth of 150 m. Mat abundances are derived from counts in the total water volume of 4.0–5.3 m³ that was imaged at each of these three stations.

Divers collected random, undisturbed mats in 250- or 500-ml polycarbonate, wide-mouth bottles for physiological studies aboard ship. The samples were returned to the ship in a closed ice chest and allowed to sit undisturbed for 15–30 min so that mats could be identified as having positive, negative, or neutral buoyancy (Villareal et al. 1996). Mats were classified as positively or negatively buoyant if they were touching the top or bottom of the container, respectively, while neutrally buoyant mats did not show a strong tendency toward either end of the bottle. Mats were generally dominated by one large species, either *R. debyana* or *R. acumi-*

nata, in a matrix of the relatively smaller *R. fallax*, as described by Villareal and Carpenter (1989). During the 1995 cruise, a visual assessment of the texture of each mat was used to identify the largest cells present, and the identifications were confirmed on selected samples by light microscopy.

Internal pools of dissolved silicon were determined on 68 mats from the 1995 cruise. Each mat was placed in a 50-ml polypropylene centrifuge tube and disrupted in 25 ml of filtered seawater by sonication, using a Fisher Scientific 50 Sonic Dismembrator with a ¼–20 microprobe vibrating at a fixed frequency of 20 kHz. Sonication lasted 5 min at power setting 10. The disrupted cells were filtered through a 0.6- μM polycarbonate filter and processed for biogenic silica concentration analysis (Brzezinski et al. 1998) so that the total cellular Si content (dissolved and particulate) of the mat could be calculated and compared to the internal dissolved silicon pool of each mat. Pool sizes were determined by the difference in the $[\text{Si}(\text{OH})_4]$ between the filtrate collected following sonication and the same seawater without added cells. All silicic acid samples were measured at sea using the acid-molybdate method of Strickland and Parsons (1972), modified to include a reagent blank (Brzezinski and Nelson 1986) and resulting in a detection limit of 50 nM. Biogenic silica was measured ashore using an NaOH digestion technique (Brzezinski and Nelson 1989).

Silica production rates in mats were measured by using either the $^{30}\text{Si}(\text{OH})_4$ method of Nelson and Goering (1977) or the $^{32}\text{Si}(\text{OH})_4$ method of Brzezinski and Phillips (1997). The tracer stock solutions were passed through Chelex resin columns to remove trace metal contaminants (Fitzwater et al. 1982). Before incubation, each mat container was opened, and a 10-ml sample was removed with a plastic pipet for silicic acid concentration analysis. That water was replaced with seawater from the sample depth during the same dive, so that no air bubbles remained in the container that might disrupt the mat during incubation. Then, either 0.67 kBq of a ^{32}Si stock solution with a specific activity of 50 kBq ($\mu\text{g Si}$) $^{-1}$ or a quantity of 95.28 atom % $^{30}\text{Si}(\text{OH})_4$ solution sufficient to increase ambient $[\text{Si}(\text{OH})_4]$ by 0.25 μM was added to each incubation bottle. Mats were incubated in deck incubators with flowing seawater and enclosed in neutral-density screens to simulate the light intensity at the depth of sample collection. After a 3- to 4-h incubation, each mat was vacuum filtered onto a 5- μm polycarbonate membrane and rinsed with filtered seawater. Each filter was then folded in quarters and dried in a polystyrene petri dish for mass spectrometry or in an empty plastic 20-ml scintillation vial for liquid scintillation counting. Samples employing $^{30}\text{Si}(\text{OH})_4$ as tracer were analyzed according to Nelson et al. (1976), using an MAAS 6–60 magnetic sector mass spectrometer with a precision of 0.002 atom % ^{30}Si . Liquid scintillation counting was done on a Beckman LS 5000 TA counter, following the recommendations of Brzezinski and Phillips (1997) and using count durations that achieved an analytical precision of <0.1–3.2%.

For samples with $^{30}\text{Si}(\text{OH})_4$ tracer, the biogenic silica content of each mat from the production rate experiments was determined during the preparation of the mat Si for isotopic analysis. Each mat was dissolved in 0.2 ml of 2.5 N HF,

followed by the addition of 670 μl of 10 N HCl. A 10–50- μl aliquot of the resulting mixture was analyzed for dissolved Si concentration (Brzezinski 1986). Then, BaCl was added to produce BaSiF_6 for mass spectrometry. The biogenic silica content of each mat incubated with ^{32}Si on the 1996 cruise was determined by adding 2 ml of 2.5 M HF to each scintillation vial containing a mat from a ^{32}Si incubation on a dried filter. The vials were placed upright for 1 h. Subsequently, each vial was rotated on a rolling table for 1.5 h to dissolve any biogenic silica that adhered to the walls of the vial. Silicic acid content was determined on a 30- μl aliquot of the HF containing the dissolved mat using an acid-molybdate assay (Brzezinski 1986).

The amount of silica produced by each mat was calculated using the equations recommended by Brzezinski and Phillips (1997). The amount of new silica produced by a mat, BSi_{NEW} , when ^{30}Si was used as tracer was calculated as

$$\text{BSi}_{\text{NEW}} = \text{BSi}_0 ({}^{30}\text{A}_f - {}^{30}\text{A}_n) / ({}^{30}\text{A}_i - {}^{30}\text{A}_f) \quad (1)$$

where BSi_0 is the biogenic silica content of the mat at the beginning of the experiment, ${}^{30}\text{A}_n$ is the atom % ^{30}Si of natural Si, ${}^{30}\text{A}_f$ is the atom % ^{30}Si of the mat Si at the end of the experiment, and ${}^{30}\text{A}_i$ is the atom % ^{30}Si of the ambient silicic acid pool after the addition of tracer. Note that this equation differs from that originally formulated by Brzezinski and Phillips (1997) in that the lithogenic silica content of a mat was assumed to be zero.

For experiments employing ^{32}Si , BSi_{NEW} was calculated using

$$\text{BSi}_{\text{NEW}} = (\text{Bq } {}^{32}\text{Si}_{\text{Psi}} / \text{Bq } {}^{32}\text{Si}_{\text{tot}}) [\text{Si}(\text{OH})_4] \quad (2)$$

where $\text{Bq } {}^{32}\text{Si}_{\text{Psi}}$ is the amount of ^{32}Si in a mat, $\text{Bq } {}^{32}\text{Si}_{\text{tot}}$ is the total amount of ^{32}Si added to the incubation bottle, and $[\text{Si}(\text{OH})_4]$ is the ambient silicic acid concentration.

The uptake rate per mat (ρ) during an incubation period, t , was calculated as

$$\rho = \text{BSi}_{\text{NEW}} / t \quad (3)$$

Calculation of the specific production rate of biogenic silica (V_b) for mats is complicated by the fact that mats are not asynchronously growing assemblages of diatoms. Mats were generally dominated by two species of diatom, *R. fallax* and either *R. debyana* or *R. acuminata*, with each species displaying its own highly phased cell division, each with a diel pattern uniquely different from the other species in the mat (Shipe and Brzezinski unpubl. data). Phased division is known to induce a strong periodicity to silica production in diatom species that deposit most of their silica as new valves just prior to cell division (Lewin et al. 1966; Darley et al. 1976; Crawford and Schmid 1986). However, for highly elongated cells, such as *Rhizosolenia*, the vast majority of cellular silica is in the girdle, with only a tiny fraction present in the valves. In that case, Si uptake is more likely to be more continuous during the cell cycle. This decoupling of silicic acid uptake from the division cycle will cause an approximately linear increase in biogenic silica content with time for periods less than a generation time of the *Rhizosolenia* cells. V_b would then be calculated using the following equation:

$$V_b = \frac{BSi_{NEW}}{BSi_0 \cdot t} \quad (4)$$

If logarithmic growth is assumed (Brzezinski and Phillips 1997), V_b is then given by

$$V_b = \frac{\ln(BSi_{NEW}/BSi_0)}{t} \quad (5)$$

In a mat containing multiple species where each species displays its own unique diel phasing of cell division and generation time, Si uptake must proceed in a manner somewhere between the logarithmic and linear models. Differences in the values of V_b calculated from the two models were all <5% and typically <1%. The average of the rates given by the two models was used to represent V_b for each mat. Similarly, the time required for the mat population to double its silica content was calculated as the average of linearly and logarithmically derived doubling times. The following equation was used to calculate the doubling time (T_D), assuming a linear increase in cellular silica through time:

$$T_D(\text{lin}) = \frac{BSi_0}{\rho} \quad (6)$$

Doubling times under the assumption of logarithmic growth were calculated as

$$T_D(\text{log}) = \frac{\ln 2}{V_b} \quad (7)$$

The doubling times calculated using the two models differed by an average of 31%.

The kinetics of silicic acid use by mats was investigated four times in 1995 at three stations and once at each of two stations in 1996. For each experiment, several mats were pooled and gently disaggregated by mixing then divided among nine 80-ml polycarbonate bottles. The rest of the procedure was identical to that used in the production rate experiments, with the modification that chelexed sodium metasilicate was added to each series of experimental bottles to create a gradient in silicic acid concentration ranging from ambient to ambient + 20 μM . Mats were incubated at 50% of ambient light for 3–4 h. In 1995, biogenic silica concentrations were determined from a subsample of the disaggregated mats from each experiment. A more refined technique was used in 1996 where the biogenic silica concentration in each experimental bottle was determined after collection of the mat on a filter, using the HF/rolling technique described above.

Results

Mat abundance—Mats were present at all stations; however, they were sometimes below the detection limit of the divers. Average *Rhizosolenia* mat abundance in the upper 15.2 m (diver survey) in 1995 was 0.18 mats m^{-3} (range = 0–1.4 mats m^{-3}). Integrated mat abundance varied from 0 to 25.67 mats m^{-2} . In 1996, an average of only 0.06 mats m^{-3} (range = <0.01–0.41 mats m^{-3}) was observed from the surface down to 18.3 m. Integrated abundance to the

deepest sampling depth for each year averaged 3.07 ± 6.85 (SD) mats m^{-2} in 1995 and 1.13 ± 1.85 (SD) mats m^{-2} in 1996.

VPR-derived mat abundances are much higher than those estimated by divers. The VPR indicated average mat abundances in the upper 20 m that were 86-fold greater than those estimated by divers (Fig. 2a; Table 1) (Pilska 1998). A comparison of the average size of mats observed using the VPR (1.8 cm) and those collected by divers (1.5–10 cm) suggests that many smaller mats went unnoticed by divers. The VPR provided the first data on the distribution and abundance of mats at depths greater than those accessible by SCUBA. Mats were found below the nutricline (nutricline depth = ca. 100 m at all stations, Brzezinski et al. 1998) with significant abundances to 150 m (the deepest depth sampled, Fig. 2). Mat abundance was greatest at the surface and decreased with depth, but even between 100 and 150 m, the average VPR mat abundances were an order of magnitude greater than those observed by divers in the upper 20 m. The average depth-integrated mat abundance between 0 and 150 m was 300 ± 429 mats m^{-2} (range = 81–888 mats m^{-2}).

Mat biomass—The biogenic silica content of *Rhizosolenia* mats sampled in 1995 to the west of the Hawaiian Islands ranged from 0.22 to 11.99 $\mu\text{mol Si mat}^{-1}$, with a mean value of 1.82 ± 1.87 (SD) $\mu\text{mol Si mat}^{-1}$ (Fig. 3b). Although less abundant, larger mats with higher biogenic silica content were found to the east of the Hawaiian Islands in 1996 (Fig. 3b). Those mats contained from 0.87 to 20.23 $\mu\text{mol Si mat}^{-1}$, with a mean of 4.56 ± 3.54 (SD) $\mu\text{mol Si mat}^{-1}$.

Mat biogenic silica concentrations were integrated to 15.2 m in 1995 and 18.3 m in 1996, using the diver-observed mat abundances (Table 2). The resulting values ranged from 0.3 to 60.1 $\mu\text{mol Si m}^{-2}$ and averaged 9.5 $\mu\text{mol Si m}^{-2}$ during the 1995 cruise. During 1996, integrated biogenic silica concentrations for mats ranged from 0.5 to 84.6 $\mu\text{mol Si m}^{-2}$ and averaged 10.7 ± 0.4 $\mu\text{mol Si m}^{-2}$. Diver-based mat abundance can be considered lower estimates for the upper 20 m, because the VPR results indicate that divers miss most mats (Villareal et al. 1999).

We estimated the integrated siliceous biomass and silica production of mats down to 150 m based on the mat abundance data acquired by VPR. That analysis required that we account for the difference in the average size of mats observed with the VPR (1.8 cm) and that collected by divers (ca. 3 cm). It was assumed that mat biomass scaled with mat volume. The best-fit relationship between mat length (longest dimension) and mat volume is a power function (Fig. 4). That relationship shows that the volume of the mats observed by the VPR is approximately 16% of that collected by divers. Because the mats were found to be 86-fold more abundant when enumerated using the VPR, we calculated that the integrated biomass for mats based on counts using SCUBA should be increased by $86 \times 0.16 = 14$ times. This adjustment results in an average integrated biogenic silica concentration for mats in the upper 20 m of 133 $\mu\text{mol Si m}^{-2}$ in 1995 and 150 $\mu\text{mol Si m}^{-2}$ in 1996. Therefore, mats comprised 16 and 18% of the total integrated silica biomass in the upper 20 m for 1995 and 1996, respectively. Extrapolated

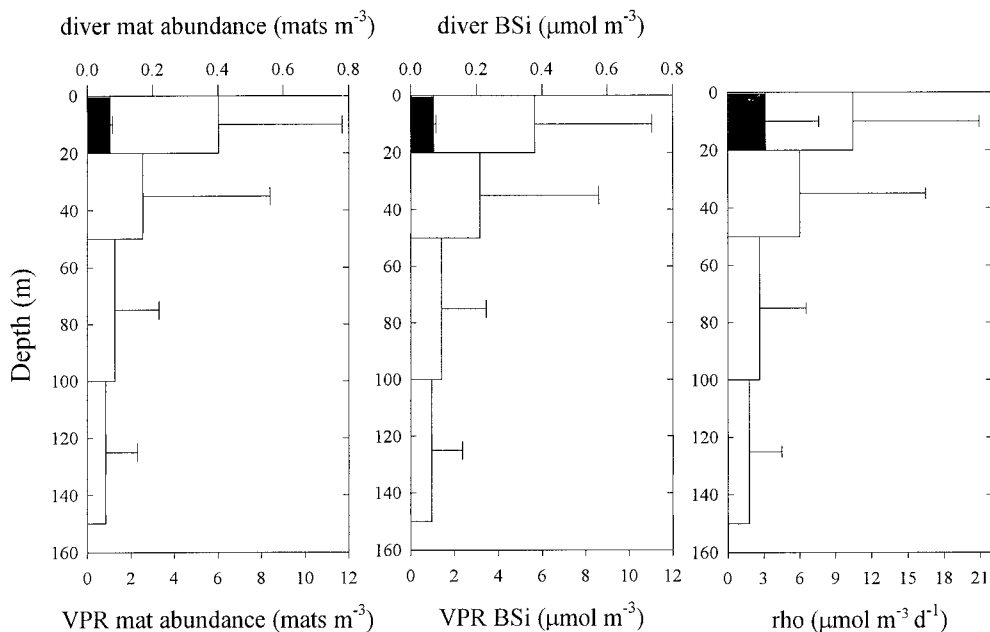


Fig. 2. Profiles of mat abundances, biogenic Si concentrations, and uptake rates derived from diver (solid bars) and VPR (open bars) mat counts. Values are averages from the three stations at which VPR data were obtained, with standard deviations. Mat biogenic silica content and production values were multiplied by 0.16 to compensate for the smaller size of mats observed by the VPR compared to those studies aboard ship (*see text*).

olation of those values to 150 m by multiplying the number of mats in the upper 150 m (400 mats m^{-2}) by scaled estimates of the average biogenic silica content of mats from each cruise yields $1.82 \times 0.16 \times 400 = 116$ and $4.56 \times 0.16 \times 400 = 292 \mu\text{mol Si m}^{-2}$ for 1995 and 1996, respectively, with an overall average of $204 \mu\text{mol Si m}^{-2}$.

Internal Si pools—The average amount of dissolved silicon stored internally by mats was 0.024 ± 0.028 (SD) $\mu\text{mol mat}^{-1}$ (range = 0.001 to $0.238 \mu\text{mol mat}^{-1}$) for mats with a mean biogenic silica content of 1.32 ± 1.66 (SD) $\mu\text{mol Si mat}^{-1}$. Internal pools represented 1.9% (mean percentage) of total cellular silicon (dissolved plus particulate). Comparison of internal Si pool size among positively, negatively, or neutrally buoyant mats showed no significant differences (ANOVA, $\alpha = 0.05$; Fig. 5). Interestingly, the mats whose largest cells were predominantly *R. debyana* had significantly

Table 1. Estimates of mat abundance, integrated biogenic silica concentrations, and integrated silicon uptake rates based on mat abundances determined by divers and the VPR at 30.31°N , 157.12°W ; 30.50°N , 154.33°W ; and 30.38°N , 152.14°W . VPR estimates of integrated properties were multiplied by 0.16 to account for the size difference in mats observed by divers and the VPR.

	Diver (0–18 m)	VPR (0–20 m)
Mat abundance (mats m^{-3})	0.070 ± 0.007	6.02 ± 5.68
Biogenic silica concentration ($\mu\text{mol m}^{-2}$)	8.5 ± 11.8	113 ± 108
Si uptake rate ($\mu\text{mol m}^{-2} \text{d}^{-1}$)	16.1 ± 22.8	210 ± 210

larger internal Si pools—i.e., a mean percentage of 2.7% of total silicon was stored in dissolved form—than mats whose largest cells were predominantly *R. acuminata*—i.e., 1.7% of total silicon was stored in dissolved form (*t*-test, $\alpha = 0.05$,

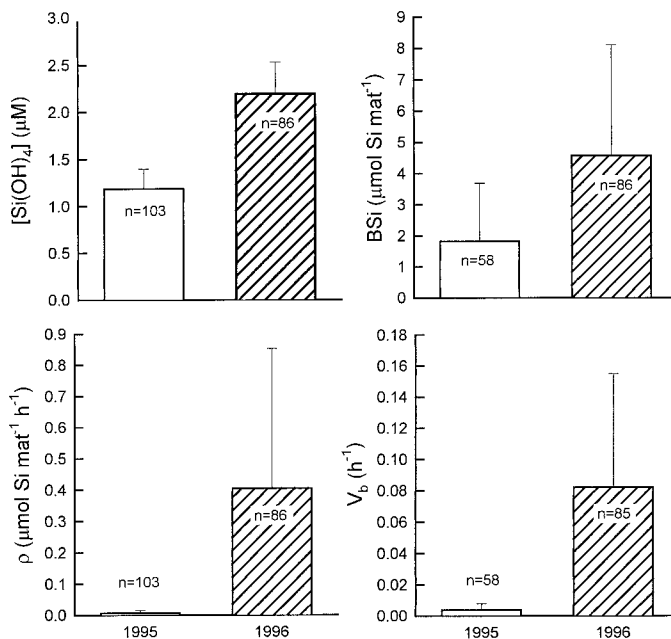


Fig. 3. A comparison of silicic acid concentrations, biogenic silica (BSi) content, uptake rates (ρ), and specific uptake rates (V_b) for mats studied in 1995 and 1996. Error bars denote standard deviations.

Table 2. Integrated siliceous biomass and production values using diver-estimated mat abundances, showing variation in the percent of water-column biogenic silica and silica production of mats. Percent of mat contribution is shown in bold, as calculated by the ratio of the mean values of mat and ambient diatom Si biomass and Si production. Stations are listed in the order that they were occupied.

		1995						1996							
		Integrated BSi ($\mu\text{mol m}^{-2}$) (ca. 20 m)			Integrated ρ ($\mu\text{mol m}^{-2} \text{d}^{-1}$) (ca. 20 m)			Integrated BSi ($\mu\text{mol m}^{-2}$) (ca. 20 m)			Integrated ρ ($\mu\text{mol m}^{-2} \text{d}^{-1}$) (ca. 20 m)				
$^{\circ}\text{N}$	$^{\circ}\text{W}$	Profile	Mat	% mat	Profile	Mat	% mat	$^{\circ}\text{N}$	$^{\circ}\text{W}$	Profile	Mat	% mat	Profile	Mat	% mat
27.27	158.51	942	7.5	0.79		0.51		23.46	158.23	451					
28.00	160.30	503			44			29.02	158.31	279			104		
27.60	163.40	1,036			124			30.31	157.12	393	84.6	17.7	69	136	66.20
27.60	165.40	770			69			30.34	155.14	1,093	3.8	0.4			6.8
28.00	169.26	317			30			30.33	154.40	1,093	7.8	0.7			4.9
28.00	172.23	985			62			30.37	152.21	1,053	4.7	0.4			8.1
28.01	172.20	802	3.0	0.37		0.23		30.38	152.14	1,053	2.2	0.2			1.9
28.54	173.50	736	60.1	7.55	374	7.27	1.91	30.78	149.94	866			89		
28.01	172.11	509			84			30.48	149.22		2.7				5.0
28.01	169.48	596			93			30.59	146.30	460	11.1	2.3			28.6
24.23	170.02	445						31.11	143.17	654	1.1	0.2	583	2.7	0.46
23.42	168.19	518	0.3	0.06	38	0.01	0.02	31.12	142.46		0.9				2.1
25.14	166.22	362						31.18	140.13	407	8.4	2.0			14.3
25.60	164.50	308	0.6	0.20	50	0.01	0.02	31.21	140.10	407	0.5	0.1			0.6
26.00	162.45	517	2.0	0.39	77	0.45	0.59	31.44	140.84	1,152			111		
26.04	162.53	331	1.0	0.31	32	0.07	0.22	31.33	134.55	461	0.7	0.2			
25.60	158.59	1,399	1.1	0.08	14	0.16	1.15	31.53	132.85	1,166			95		
25.59	158.50	2,068						31.47	129.17	351					
								31.88	127.26	490			39		
Mean		690	9.5	1.4	84	1.09	1.3	Mean		663	10.7	2.4	145	19.1	12.0
SD		465	21		92	0.0025		SD		329	0.4		178	39.4	

$P = 0.007$). However, the dissolved internal Si pools for both species are not large enough to allow cells to deposit a significant fraction of their frustule using internal Si reserves.

Si uptake rates—The specific rates of silica production for mats averaged 0.004 ± 0.004 (SD) h^{-1} in 1995 and 0.082 ± 0.073 h^{-1} in 1996 (Fig. 3d), corresponding to doubling times of 237 and 13.2 h for the 2 yr, respectively. Values of ρ ranged from <0.001 to 0.018 $\mu\text{mol Si mat}^{-1} \text{h}^{-1}$, averaging 0.006 ± 0.008 (SD) $\mu\text{mol Si mat}^{-1} \text{h}^{-1}$ in 1995. Rates were higher in 1996, with an average ρ of 0.405 ± 0.448 (SD) $\mu\text{mol Si mat}^{-1} \text{h}^{-1}$ (range = <0.001 – 0.048 ; Fig. 3c).

Integrated biogenic Si production by mats ($\int \rho$) was estimated for the upper 20 m at each station by employing the estimates of mat abundance from both the divers and VPR and the average ρ for mats from each station. Diver-based estimates of $\int \rho$ showed that although mats were more abundant in 1995, lower mat biomass and lower uptake rates during that year led to an average integrated silica production rate of only 1.09 ± 0.003 (SD) $\mu\text{mol Si m}^{-2} \text{d}^{-1}$ (integration depth = 15.2 m) compared to a average value of 19.1 ± 39.4 (SD) $\mu\text{mol Si m}^{-2} \text{d}^{-1}$ for 1996 (integration depth = 18.3 m) when larger, more productive mats were observed (Table 2). The VPR abundance data were used to scale these values to account for the discrepancy between diver and VPR abundance estimates under the assumption that silica production scales directly with mat volume. The resulting average integrated silica production in the top 20

m was 15.3 ± 0.04 $\mu\text{mol Si m}^{-2} \text{d}^{-1}$ and 267 ± 552 $\mu\text{mol Si m}^{-2} \text{d}^{-1}$ for 1995 and 1996, respectively.

The VPR data allowed the first estimate of silica production by *Rhizosolenia* mats to depths comparable to those used in studies that employed water-bottle samplers. Scaling the average values of ρ for the two cruises by the difference in the size of mats collected by divers and seen by the VPR yields values of $0.006 \times 0.16 = 0.001$ $\mu\text{mol Si mat}^{-1} \text{h}^{-1}$ for 1995 and $0.405 \times 0.16 = 0.065$ $\mu\text{mol Si mat}^{-1} \text{h}^{-1}$ for 1996, with an overall mean of 0.033 $\mu\text{mol Si mat}^{-1} \text{h}^{-1}$. The average of 400 mats m^{-2} detected with the VPR yields an integrated silica production rate in the upper 150 m for the two cruises of $0.033 \times 400 \times 24 = 317$ $\mu\text{mol Si m}^{-2} \text{d}^{-1}$ (range = 10–624 $\mu\text{mol Si m}^{-2} \text{d}^{-1}$).

Comparisons of silica production among mats with different buoyancy characteristics (positive, negative, or neutral buoyancy) showed that silica production was not closely tied to a specific stage of mat migration. Silica production rates by mats with different buoyancy characteristics exhibited no significant differences during either year of the study (AN-OVA, $\alpha = 0.05$).

Kinetics of Si uptake—The silicic acid concentration and specific Si uptake rates from the uptake kinetics experiments were fit to the Michaelis–Menten model of nutrient uptake kinetics:

$$V_b = \frac{V_m [\text{Si}(\text{OH})_4]}{K_s + [\text{Si}(\text{OH})_4]} \quad (8)$$

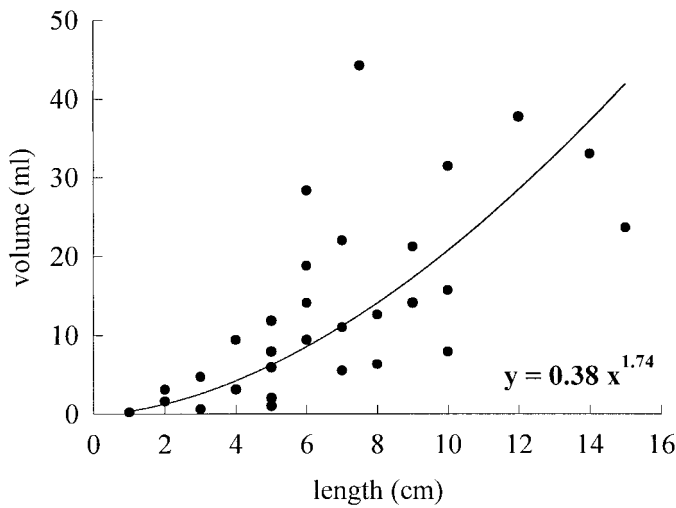


Fig. 4. Mat volume as a function of length (longest dimension) with best-fit regression ($r^2 = 0.64$). In situ measurements of the length, width, and height of cylindrically shaped mats collected in 1981 in the transition zone between the California Current and the North Pacific gyre were used to calculate mat volume as in Alldredge and Silver (1982).

where V_m is the maximum specific silica production rate at an infinite $[\text{Si}(\text{OH})_4]$, and the half-saturation constant, K_s , is the $[\text{Si}(\text{OH})_4]$ at which the specific production rate (V) is one-half the magnitude of V_m .

The kinetic curves for *Rhizosolenia* mats are plotted in Fig. 6, with the corresponding kinetic parameters presented in Table 3. The two uptake kinetic experiments conducted at a single station in 1995 did not fit the model of nutrient uptake discussed above. The first experiment showed very high, but extremely variable, uptake rates at all substrate

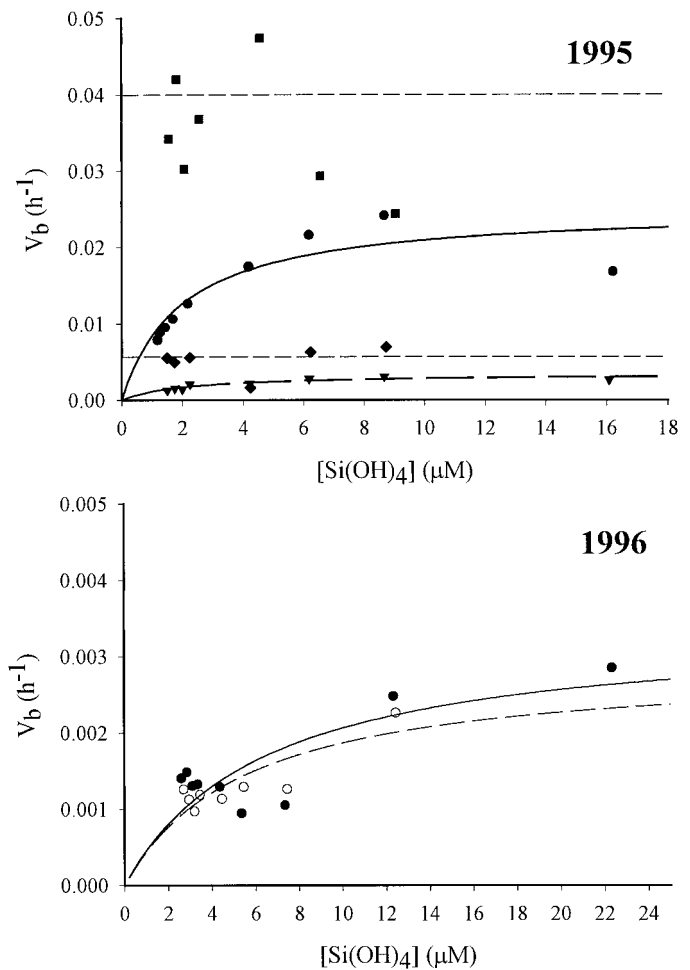


Fig. 6. Kinetic experiment results from four 1995 stations and two 1996 stations. Kinetic constants were found by fitting the data to the Michaelis–Menten model of uptake kinetics, using the Marquardt–Levenberg algorithm (Press 1992). At the two 1995 stations that did not fit this model, least-squares linear regression was used to approximate the V_m of the mats.

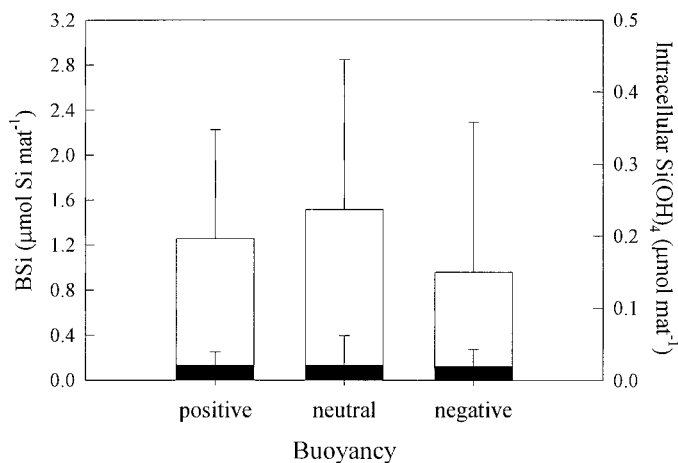


Fig. 5. A comparison of cellular biogenic silica concentrations (open bars) and internal silicon pools (darkened bars) within mats (both in micromoles per mat) with standard deviations showing a small proportion of total silicon stored internally. There was no significant difference among the size of the internal Si pools (ANOVA, $\alpha = 0.05$, $P = 0.13$) or biogenic silica content (ANOVA, $\alpha = 0.05$, $P = 0.50$) of *Rhizosolenia* mats with positive ($n = 46$), neutral ($n = 32$), or negative ($n = 19$) buoyancy.

concentrations. During the second experiment, silicic acid uptake was saturated in all treatments, indicating that K_s was less than the ambient silicic acid concentration, i.e., $<1.5 \mu\text{M}$. In 1996, the kinetics of Si uptake in all of the experiments conformed to the Michaelis–Menten model. In general, K_s values in 1995 were all $<2 \mu\text{M}$ with higher values, 5.51 and 6.47 μM , observed in 1996. Maximum specific silica production rates ranged from 0.003 to 0.041 h^{-1} at the stations occupied in 1995, while they tended to be lower, ca. 0.003 h^{-1} , in 1996. The kinetic parameters from four of five stations indicated substrate limitation of in situ Si uptake, with mats operating at between 27 and 38% of their maximum uptake rate at ambient $[\text{Si}(\text{OH})_4]$ (Table 2).

Discussion

Environmental conditions—This investigation was conducted as part of a larger study that described the physics and biology across a substantial area of the central North

Table 3. Ambient silicic acid concentrations and kinetic parameters reported with standard errors for kinetic experiments. K_s values at the two stations exhibiting saturation kinetics are designated as being less than the lowest $[\text{Si}(\text{OH})_4]$ at which Si uptake was measured.

Year	Latitude (°N)	Longitude (°W)	V_m (h^{-1})	K_s (μM)	Ambient [Si(OH) ₄] ($\mu\text{mol liter}^{-1}$)	V/V_m
1995	26.04	162.53	0.025 ± 0.003	1.96 ± 0.81	1.18	0.38
	25.60	158.59	$0.003 \pm <0.001$	2.04 ± 0.61	1.25	0.38
	25.14	166.22	0.041 ± 0.008	<1.55	1.55	1.0
	25.14	166.22	0.006 ± 0.002	<1.24	1.24	1.0
1996	31.11	143.17	0.003 ± 0.001	5.51 ± 2.83	2.35	0.30
	31.44	140.84	0.003 ± 0.001	6.47 ± 3.50	2.45	0.27

Pacific gyre. The physical characteristics, nutrient fields, chlorophyll *a* (Chl *a*), and biogenic silica distributions along the transects sampled in this study are described in detail by Brzezinski et al. (1998). We will briefly introduce their results in order to provide an ecological context for the discussion of *Rhizosolenia* mat biology.

During both years of the study, the seasonal pycnocline was located between 30 and 60 m. The only notable exception was a longitudinal gradient in salinity between 137 and 130°W that marked the transition between the mid-ocean gyre and the California Current. At all of the stations, the 1% light depth was between 100 and 120 m. Surface silicic acid concentrations were lowest in 1995 (0.9–1.3 μM) and were 2–3 μM in surface waters during 1996. These concentrations rose to 4–8 μM below the 1% light depth. Nitrate concentrations in the surface waters were consistently low (<50 nM) but increased below the 1% light depth to values of 1–4 μM in 1995 and 2–9 μM in 1996. Distributions of Chl *a* and biogenic silica were patchy, with no clear longitudinal gradients. Chlorophyll values in the surface ranged from 50 to 200 ng liter^{-1} , and deep chlorophyll maxima at 100–125 m were as high as 480 ng liter^{-1} . Biogenic silica concentrations were generally <30 nmol liter^{-1} , with occasional subsurface maxima of 90–250 nmol liter^{-1} . In 1995, a diatom bloom occurred at the eastern extreme of the southern transect, as evidenced by Chl *a* concentrations of 410 ng liter^{-1} and biogenic silica concentrations up to 250 $\text{nmol Si liter}^{-1}$.

Mat biomass and silica production—Comparison of our data for *Rhizosolenia* mats with that of Brzezinski et al. (1998) for nonmat diatoms made during the same cruises reveals that the average mat contained as much biogenic silica as 119 liters (1995) and 140 liters (1996) of the surrounding seawater and produced silica at a rate equivalent to the nonmat diatoms in 29 liters (1995) and 920 liters (1996) of seawater. The average V_b for mats in 1995 was 51% of that for nonmat diatoms, as reported by Brzezinski et al. (1998). In contrast, the average V_b for the larger mats observed in 1996 was 5.9 times greater than that for the nonmat diatom assemblage in that region (Brzezinski et al. 1998). Mats are relatively rare, however, and our best estimate of the average integrated mat silica in the upper 150 m for both cruises, 204 $\mu\text{mol Si m}^{-2}$, is only 3.2% of the average biomass of nonmat diatoms in the upper 160 m mea-

sured by Brzezinski et al. (1998) on the same cruise, 6,330 $\mu\text{mol Si m}^{-2}$. The higher V_b for mats causes them to account for a greater fraction of silica production. Our best estimate of the daily silica production rate by mats in the upper 150 m, 317 $\mu\text{mol Si m}^{-2} \text{d}^{-1}$, is 26% of the average silica production rate for nonmat diatoms on these same cruises (1,240 $\mu\text{mol Si m}^{-2} \text{d}^{-1}$; Brzezinski et al. 1998).

Although the higher V_b in mats implies that they have higher specific growth rates than nonmat diatoms, they consistently accounted for a small proportion of the total siliceous biomass. This condition may be sustained by a higher mortality rate of mat diatoms, caused by more intense grazing pressure. The only documented grazing of mats is by euphausiids and copepods (Carpenter et al. 1977) and migrating myctophids (Robison 1984). However, other potential grazers, including hyperiid amphipods, ostracods, and pontellid copepods, as well as ciliates and other protozoan parasites, have been reported on mats (Alldredge 1982; Caron et al. 1982; Villareal and Carpenter 1989; Villareal et al. 1996). It is also possible that mats do not have higher growth rates than nonmat diatoms. Rather, the V_b in nonmat diatoms could be in part a consequence of a high fraction of detrital biogenic silica in the upper water column. This possibility finds support in the work of Villareal and Carpenter (1989), who found that *Rhizosolenia* mats comprised 98% of biogenic silica in the surface waters of the central North Pacific, based on the relative biovolume of living mat and nonmat diatoms, compared to a low fraction found here, based on biogenic silica measurement. Our biogenic silica determinations do not discriminate between living and dead cells. While >90% of the cells in a mat are alive (Shipe and Brzezinski unpubl. data), the fraction of detrital silica in the water column could be large.

The siliceous biomass and silica production of mat and nonmat diatoms in the upper 20 m are compared in Table 2. There is clearly a trend toward greater mat biomass and importance to total silica production during the 1996 cruise than during 1995. When these values are scaled to account for the difference in the size and number of mats observed using SCUBA and the VPR, the resulting values indicate that mats accounted for a mean of 17% (16–18% in 1995, 1996 respectively) of the biogenic silica and a mean of 40% (15–65% in 1995 and 1996, respectively) of silica production in the upper 20 m. The VPR data allowed us to estimate that *Rhizosolenia* mats produce 317 $\mu\text{mol Si m}^{-2} \text{d}^{-1}$, inte-

grated to a depth of 150 m. When this silica production is added to that by nonmat diatoms in the central North Pacific, the resulting value ($1,560 \mu\text{mol Si m}^{-2} \text{d}^{-1}$) is 2.4–3.7 times greater than that observed in the Sargasso Sea ($417\text{--}640 \mu\text{mol Si m}^{-2} \text{d}^{-1}$, Brzezinski and Kosman 1996; Nelson and Brzezinski 1997).

Diver-derived mat abundances much greater than observed during our study have been documented in past investigations, suggesting that our observations underestimate the contribution of mats to the regional silica cycle. Abundances of 6.0 mats m^{-3} in August 1992 and 11.5 mats m^{-3} in June 1993 were found in the same vicinity of the central North Pacific as occupied during the 1996 cruise. By comparison, during the 2 yr of this study, the highest measured abundances of mats at the surface were only 0.93 mats m^{-2} and 1.70 mats m^{-2} to the east and west of the Hawaiian Islands, respectively. On average, mat abundances of 0.18 and 0.06 mats m^{-2} over the depths sampled were found in 1995 and 1996, respectively. Much higher abundances of 0.7 mats m^{-3} in the upper 20 m were encountered in the North Pacific during a 600-km transect southwest of Monterey (Alldredge 1982). Mats are apparently quite variable in abundance in the North Pacific, both spatially and temporally, and could at times constitute a greater fraction of the water-column production and biomass than they did during the present study.

Rhizosolenia mats may also contribute significantly to export production. The fraction of C production that is exported from oligotrophic mid-ocean gyres tends to be low (Deuser 1980; Lorrenz et al. 1992). The same is true for biogenic silica; for example, in the Sargasso Sea, 64–82% of silica production is recycled within the euphotic zone (Brzezinski and Nelson 1995). The particles that are exported from surface waters are known to be dominated by large cells and aggregates (McCave 1975; Fellows 1981). Thus, while *Rhizosolenia* mats may be rare, they can contribute significantly to export from the euphotic zone and to sedimentation, especially if they are consumed by large vertically migrating predators, such as myctophids (Robison 1984). During the winter of 1992, seafloor accumulations of phytodetritus were photographed and recovered in cores in the central equatorial Pacific. These deposits were extensive and contained relatively intact diatoms, including *Rhizosolenia* (Smith et al. 1996).

Si limitation of Si uptake—Uptake kinetics experiments showed that silica production rates by the majority of mats that we examined were limited by ambient silicic acid concentrations (Table 3). Only two of six experiments showed that mats were taking up silicic acid at maximum rates at ambient silicic acid concentrations (Fig. 6). For the remaining four experiments conducted over 2 yr across a large fraction of the gyre, the mats were producing silica at an average of only 33% of V_m , suggesting that substrate limitation of silica production by mats is widespread in the central North Pacific.

Half-saturation constants of *Rhizosolenia* mats collected in 1995 ($<1.24\text{--}2.04 \mu\text{M}$) are similar to those that have been determined for diatoms in culture and in natural assemblages. Reported K_s values for tropical and temperate diatom

species in culture range from 0.02 to $2.3 \mu\text{M}$, including three isolates from the eastern tropical Pacific Ocean (Thomas and Dodson 1975; Nelson et al. 1976; Conway and Harrison 1977; Nelson and Tréguer 1992). Si kinetic uptake experiments of natural assemblages of diatoms in nutrient-depleted waters at the center of Gulf Stream warm-core rings yielded K_s values ranging from 0.53 to $0.90 \mu\text{M}$ (Nelson and Brzezinski 1990). Half-saturation constants for nonaggregated diatom assemblages on the same cruises where mats were examined were $0.55\text{--}2.33 \mu\text{M}$ in 1995, similar to that of the mats (Brzezinski et al. 1998). Although mats collected in 1996 had higher K_s values than those discussed above, the mats were more efficient at Si use than the ambient diatom assemblage, for which K_s values were as high as 25.9 and $56 \mu\text{M}$ (ibid). That difference in uptake kinetics may have led to the contribution by mats of a larger fraction of the total siliceous production in this area of the gyre.

Coupling of Si metabolism to mat migration—Doubling times, based on the major macronutrients needed by a *Rhizosolenia* mat, can be used to constrain the timing of its migration cycle. Villareal et al. (1996) outlined a simple model of the vertical migration of a mat through changing light and nutrient conditions. In the euphotic zone, cells use the available light to double cellular C through photosynthesis. The mat migrates vertically to the nitracline, where it spends enough time for the uptake of an amount of N sufficient for one doubling. The sum of the C and N doubling times, plus the time spent migrating to and from the nitracline, is the duration of one migration cycle. Balanced growth also requires the cellular silicon to double during each migration cycle because diatoms have an obligate requirement for Si (Lewin 1962).

Silicon metabolism is not tightly coupled to any one portion of the migration cycle. Doubling times for mats averaged 237 h (9.8 d) in 1995 and 13.2 h (0.55 d) in 1996. Thus, mats sampled in 1996 in the eastern sector of the central North Pacific could likely acquire the requisite Si to double their Si content in the euphotic zone without any Si uptake at depth, decoupling Si and N uptake. In the western sector of the central North Pacific, the doubling time of cellular silicon (9.8 d) is of the same order as the estimated migration time of mats (3.4–5.6 d, Villareal et al. 1996), suggesting that silicic acid uptake occurs both at depth and in the euphotic zone. In that case, silicic acid uptake may be enhanced in the high Si(OH)_4 water of the nutricline, consuming energy that could otherwise be used for nitrate uptake. On average, $[\text{Si(OH)}_4]$ at 100-m depth was $2.1 \mu\text{M}$ compared to $1.2 \mu\text{M}$ in surface waters. Based on average kinetic parameters of mats in the western central North Pacific, the increase in silicic acid concentration in the nutricline would increase V_b by 34%. Again, the bulk of Si taken up by *Rhizosolenia* cells is deposited into intercalary bands, such that enhanced Si uptake at depth does not necessarily imply that cells divide in the nutricline.

Two further pieces of evidence suggest that silicic acid uptake in mats is not restricted to one particular stage of their migration. We initially hypothesized that mats in different stages of the migration cycle may have different Si uptake rates because these states indicate that they are about

to descend to or have just ascended from more silicon-rich waters. However, there were no significant differences between the Si uptake rates between mats with different buoyancy characteristics (positively, negatively, or neutrally buoyant). Finally, internal Si pools are small in ascending mats, indicating that if $\text{Si}(\text{OH})_4$ is taken up at depth, it is not stored for prolonged periods as the mats ascend, as observed for nitrate (Villareal et al. 1993; Villareal and Lipschultz 1995).

Mat contribution to global silica budgets—Nelson et al. (1995) estimated that silica production in mid-ocean gyres accounts for 9–13% of global silica production. However, that estimate is derived from only two silica production studies in the Sargasso Sea (Brzezinski and Kosman 1996; Nelson and Brzezinski 1997). Since that time, Brzezinski et al. (1998) has reported production rates two–three times higher in the central North Pacific gyre, with an average daily production rate of $1,240 \mu\text{mol Si m}^{-2} \text{d}^{-1}$ in the upper 160 m, and has suggested that the central oceans may account for up to 40% of global silica production. Brzezinski et al.'s estimate did not include production by *Rhizosolenia* mats. Our best estimate of the daily production rates by mats in the upper 150 m, $317 \mu\text{mol Si m}^{-2} \text{d}^{-1}$, suggests that these large, rare cells produce biogenic silica at almost one-third the rate of the entire nonmat diatom assemblages in the central North Pacific and, at times, possibly much more (using previous cruise abundance estimates). Silica production by *Rhizosolenia* mats in the central North Pacific alone approaches that of the entire diatom assemblage in the Sargasso Sea ($417\text{--}640 \mu\text{mol Si m}^{-2} \text{d}^{-1}$, Brzezinski and Kosman 1996; Nelson and Brzezinski 1997). That level of silica production combined with the wide distribution of mats in several ocean basins (Villareal and Carpenter 1989) suggests that *Rhizosolenia* mats may constitute a significant but overlooked source of silica production in the sea.

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