Journal of Marine Research, 50, 745–779, 1992

Effects of polychaetes on silicate dynamics and fluxes in sediments: Importance of species, animal activity and polychaete effects on benthic diatoms

by Roberta L. Marinelli[1,2]

ABSTRACT

Laboratory experiments tested the effects of two polychaetes, a surface deposit feeder *Eupolymnia heterobranchia,* and a head-down deposit feeder *Abarenicola pacifica,* on silicate dynamics in sediment porewaters and overlying waters. Experimental chambers of sediment containing an individual deposit feeder, and controls with no macrofauna, were studied over a one month period during the summers of 1989 and 1990. Measurements included temporal changes in vertical depth profiles of pore water silicate concentrations, concurrent determinations of silicate accumulation in the water column, and the activities of experimental organisms. A diffusion-nonlocal exchange-reaction model was devised to determine, from the pore water profiles, both the magnitude of, and variability associated with, organism effects on pore water silicate. Model results within chambers containing worms indicate that the changes in silicate concentrations due to worm activity varied by as much as an order of magnitude at a given point in the sediment column, over time periods of several days. Biologically-driven fluxes calculated from the sediment model indicate that fluxes attributable to macrofauna were positively correlated with the frequency of new burrow or tube construction, and were strongly related to the activity of the organism. Variability in the rate of silicate transport due to worms likely was related to the mechanism of habitat construction, as well as the relative distances involved in tube/burrow relocation. Silicate fluxes calculated from the model were compared with direct measures of silicate flux via the accumulation of silicate in the water column. These comparisons show that benthic diatoms at times exerted a significant effect on silicate removal from sediments and the water column. The relative importance of this effect was dictated by differences in the activity of diatoms and surrounding macrofauna between experiments, and the type of macrofaunal organisms involved. Strong interactions between the surface deposit feeder and benthic diatoms significantly affected the magnitude and direction of silicate flux across the sediment-water interface. Such interactions were lacking in experiments with the head-down deposit feeder. In combination, the sediment model and water column measurements showed that net silicate fluxes to the water column may be masked by diatom activity, even when bioirrigation serves to actively transport silicate directly from depth across the sediment-water interface.

1. Marine Science Program, University of South Carolina, Columbia, South Carolina, 29208, U.S.A.
2. Present address: Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada.

1. Introduction

Infaunal organisms such as polychaetes, bivalves, and crustaceans are common in sedimentary environments, and have important effects on the exchange of sediment pore waters with overlying waters. Numerous studies suggest that macroinfauna enhance sediment-seawater exchange by as much as an order of magnitude relative to diffusive processes (e.g. Blackburn and Henriksen, 1983; Rutgers van der Loeff *et al.,* 1984). These exchange processes alter the chemistry of the surrounding sediments, pore waters and overlying water (e.g. Aller, 1978; Aller and Yingst, 1985; Kristensen, 1988; Doering, 1989; Huttel, 1990; and others). As a result, the cycling of important constituents such as carbon, nitrogen, sulfur, phosphate and silica may be increased, and productivity in the sedimentary environment and the water column may be stimulated (Grundmanis and Murray, 1977; McCaffrey *et al.,* 1980; Gust and Harrison, 1981; Waslenchuk *et al.,* 1983; Christensen *et al.,* 1984; Matisoff *et al.,* 1985).

Recent research has centered on identification of the properties of infauna and the characteristics of habitats which affect pore water composition and bioadvective pore water transport. The size, depth, and density of infaunal dwellings (Aller, 1980; Aller and Yingst, 1985); the sediment type (Kristensen *et al.,* 1985); the chemical composition of overlying water (Kristensen, 1984); the ventilation activity of infauna (Henriksen *et al.,* 1983); and the physico-chemical composition of the infaunal dwelling (Aller and Yingst, 1978; Aller, 1983; Aller *et al.,* 1983) all have been shown to influence the degree to which infauna alter the solute environment. Seasonal variation in biotic transport processes (due to temperature, organic matter input, and community-wide organism activities) also has been documented (e.g. Hines *et al.,* 1982). However, previous research has not examined the significance of the highly variable behaviors of individual animals, the spatial and temporal variability that exists among populations as well as among species, and the importance of interspecific interactions within an assemblage.

This study addressed these latter questions by examining how two species of polychaete affected silicate dynamics in sediment porewaters and overlying waters through bioturbation and their influence on surface microflora. Silicate is an important nutrient for many benthic and pelagic primary producers, and is useful as an indicator of pore water transport (e.g. Emerson *et al.,* 1984). The goal of this study was to determine 1) if different species of polychaetes exert similar effects on pore water transport and silicate dynamics, 2) if activities (e.g. feeding, tube building) of polychaetes are an important factor affecting silicate flux, 3) if interspecific differences in the magnitude and variability of infaunally-driven fluxes can be linked to the lifestyle of the organism, and 4) if organism-organism interactions can modify the extent to which silicate is transferred across the sediment-water interface.

2. Materials and methods

The study utilized laboratory chambers containing either 1) sediments and macrofauna, 2) sediments and macrofaunal dwellings or 3) sediments only (controls). With this experimental setup it was possible to obtain a time series of measurements of vertical profiles of porewater silicate and concurrent measurements of net fluxes of silicate to the water column, and to observe the activities of organisms. A model which accounts for diffusion, nonlocal exchange and reaction was devised to determine, from pore water silicate profiles, the extent and temporal variability of silicate removal from sediment pore waters due to organisms.

a. Benthic chambers

The chambers are constructed of clear, 0.63 cm-thick plexiglass and have inner dimensions of 18 × 12 × 21 cm (L × W × H). The sampling ports are made with Luer-design polypropylene fittings (Value Plastics, Inc). The portion protruding into the sediment is fitted with a 3 cm length of tygon tubing (0.237 cm I.D.) plugged with a rolled Whatman #1 filter. The tygon-filter extension is oriented parallel to the bottom of the chamber and allows filtered samples to be drawn from the chamber interior, thus avoiding edge effects. The portion on the exterior of the chamber accommodates a luer-tipped syringe which is used to withdraw sediment pore waters. Between sampling intervals, the exterior opening is blocked with a luer taper plug (Value Plastics, Inc.).

One face of each chamber contains fifteen staggered sediment sampling ports divided among two parallel columns. Each column is 5 cm from a chamber edge, and the ports within a column are spaced at 2 cm intervals, thus yielding two vertical pore water profiles. This arrangement was selected for two reasons. First, the analysis of two profiles per chamber gave more information regarding spatial variability in pore water characteristics over short (<10 cm) spatial scales. When averaged, the resulting profile provided a better estimate of the pore water characteristics of the chamber sediments than a single profile alone. Second, calculation revealed that the 2 cm sample interval was sufficient to avoid sampling pore water over adjoining strata.

b. Experiments and organisms

Two experiments were conducted, the first during August-September 1989 and the second during June-July, 1990, at the University of Washington's Friday Harbor Laboratories, San Juan Island, Washington. In both cases, dissolved silicate was chosen as an indicator of pore water transport because it does not undergo oxidation-reduction reactions. Also, silicate distributions in sediments are known to be affected by infaunal activities (Grundmanis and Murray, 1977; Gust and Harrison, 1981; Emerson *et al.,* 1984). The first experiment tested the effect of the polychaete

Table 1. A) Experimental design for chamber experiments. n = # replicates, Temp. = water temperature (degrees C). B) Sample dates for measuring vertical profiles of pore water silicate and conducting water column incubation studies. Under B, numbers in parentheses under dates indicate length of time (hours) of water column incubations. n.a. = not available.

A. Experimental design

Year	Treatment (n)	Trophic mode	Temp.	Controls (n)
1989				
	Eupolymnia (5)	surface deposit feeder	13	Light (3)
	Eupolymnia tubes (5)	surface deposit feeder	13	
1990				
	Eupolymnia (6)	surface deposit feeder	11	Light (3)
	Abarenicola (9)	head-down deposit feeder	11	Dark (3)

B. Sample schedule

1989					
Pore Waters	8/28	9/01	9/07	9/15	9/19
Water Column (hours)	n.a.	n.a.	n.a.	9/14 (8.8)	9/17–9/18 (16.25)
1990					
Pore Waters	6/13	6/18	6/22	6/26	7/04
Water Column (hours)	n.a.	n.a.	6/20–6/21 (17.25)	6/24–6/25 (19.33)	7/01–7/02 (20.0)

Eupolymnia heterobranchia (with its tubes), and abandoned *Eupolymnia* tubes, on pore water profiles and sediment-water column fluxes of dissolved silicate (Table 1). *Eupolymnia* is a terebellid polychaete, common in intertidal and subtidal sediments of the San Juan archipelago. It is generally a surface deposit-feeder, but has been observed to suspension-feed in the laboratory. Typically, it builds a fairly hardy, mucous-lined, U-shaped tube that extends 10 to 20 cm into the sediment. Irrigation is accomplished via peristalsis and the tube is irrigated in both directions (i.e. waves pass from posterior to anterior and vice-versa, Woodin and Marinelli, 1991).

The second experiment compared the effects of the polychaetes *Eupolymnia heterobranchia* and *Abarenicola pacifica* on pore water profiles and sediment-water column fluxes of dissolved silicate (Table 1). *Abarenicola* is an arenicolid polychaete commonly found in the high intertidal in muddy sand environments of the Pacific northwest. It constructs mucous-lined vertical burrows to a maximum depth of 20 cm

(Hylleberg, 1975). *Abarenicola* is a head-down deposit feeder which deposits consolidated fecal coils in hemispherical mounds on the sediment surface. As with *Eupolymnia, Abarenicola* irrigates its dwelling via peristalsis. For *Abarenicola,* body waves pass primarily from posterior to anterior (personal observations). *Abarenicola* and *Eupolymnia* thus represent two different lifestyles that are common among the polychaeta: burrowing, subsurface deposit feeders vs. tube-building, tentaculate surface deposit feeders.

To establish the arenicolids and terebellids in chamber sediments, two different methods were employed. These methods were chosen to accommodate the different tube-building and burrowing abilities of each species. *Eupolymnia* is an excellent tube builder but a poor burrower. It can easily "tunnel" through sediments from an established tube by loosening sediments with irrigation currents, followed by extension of the existing tube into the excavated portion. Pore waters and sediments are disturbed extensively during the excavation process. *Abarenicola* is an excellent burrower, and descends rapidly into an established sediment column without the use of irrigation. New burrows are evident within hours of introduction of individuals into sediments. Sediments and pore waters are displaced considerably smaller distances by *Abarenicola* burrowing, as compared to *Eupolymnia* tube building.

In 1989 and 1990 experiments, *Eupolymnia* individuals were collected from the lower intertidal region of Griffin Bay, San Juan Island. Immediately upon return to the laboratory, one individual was placed in each of 10 chambers (1989) or 6 chambers (1990) with a small amount of sieved (0.5 mm) sediment taken from the surface sediment layer (0–10 cm) at False Bay. Chambers were immersed in running seawater tables to a depth of approximately 18 cm (3 cm below the chamber tops). This configuration was sufficient to maintain the sediment and water within each chamber at ambient temperature without allowing communication between individual chambers. Each chamber was supplied continuously with an individual line of running seawater. Circulation of seawater in chambers did not resuspend sediments. For several days subsequent to addition, worms used sediment in the chambers to build tubes along the bottoms and up the sides of the chambers. Subsequently, the remaining sediment was rinsed from each chamber. In the 1989 experiment, 5 chambers were designated as "Tubes only" treatments. In these chambers, worms were induced to evacuate their tubes and then removed. The remaining chambers in the 1989 experiment, and all chambers with *Eupolymnia* in the 1990 experiment, contained *Eupolymnia* with intact tubes and were designated "*Eupolymnia*" treatments. Over a two day period, freshly-sieved sediment (0.5 mm) was added to each chamber in 0.5–1.0 cm pulses every few hours, until the sediment depth reached 14–15 cm. Worms easily maintained their tubes flush with the sediment surface as sediment accumulated. In "tubes only" chambers, one or more tube entrances in each chamber extended above the sediment surface, and remained open for at least the early phase of the experiment.

In the 1990 experiment, chambers chosen to contain arenicolids were immersed in running seawater tables and also were maintained on the same sediment addition schedule as chambers with terebellids. When sediment addition was complete, arenicolids were collected from False Bay and were added to nine chambers, one individual per chamber. Worms burrowed quickly into chamber sediments and began to feed and defecate within 24 hours. These chambers also were equipped with individual seawater supply lines.

Control chambers consisting of sediment only were established to examine the role of other biotic and abiotic processes affecting the production and transport of silicate (e.g. silica dissolution, diffusive silicate transport, and silicate incorporation by diatoms). In 1989 and 1990 experiments, three control chambers were established in the same running seawater tables as experimental chambers. All of these chambers were maintained indoors and experienced fluctuations in light similar to a day/night cycle. In 1990, three additional control chambers were established in a nearby seawater table, but kept in complete darkness. Control chambers exposed to light are referred to as "light controls" (1989 and 1990). Control chambers kept in darkness are referred to as "dark" controls (1990 only). All controls were equipped with individual seawater lines.

In all chambers, final sediment depths ranged from 13–15 cm. The height of the water column above the sediments varied from 6 to 8 cm. All chambers were left undisturbed for one week prior to initial sampling.

c. Sampling schedule

i. Water column incubations. The accumulation of dissolved silicate in the water column of experimental chambers was analyzed twice in 1989, and three times in 1990 (Table 1), using the method of Strickland and Parsons (1972). In all cases, water column measurements were performed one day prior to sediment pore water sampling. This protocol permitted the comparison of the two methods of flux assessment. Pore water sampling and water column incubations could not be conducted simultaneously, because the disturbance to chambers during pore water sampling might have affected water column incubation results.

Prior to initiation of the water column incubation period, the seawater supply system was deactivated. To prevent the formation of silicate gradients in the water column during incubations, air was bubbled gently through the water column of each chamber, using an airstone. Pretests (analyses of silicate concentrations in water samples taken from different areas within chambers) indicated that circulation created by airstones was sufficient to homogenize silicate concentrations in the water column, but not so vigorous as to disturb the sediment surface. The difference between water column and sediment silicate concentrations (30 μM versus 80–300 μM, respectively) was sufficiently large that silicate diffusion from sediments was not affected negatively by water column silicate accumulation. Moreover, silicate re-

moval by diatoms at the sediment surface caused silicate values at the sediment-water interface to approach zero in many chambers (see results).

After thirty minutes of "mixing" by airstones, three initial water column samples were taken from each chamber. After an incubation period ranging from 8–20 hours (Table 1), three final samples were taken from each chamber. Incubation periods generally spanned light and dark periods. Silicate samples were fixed immediately after final sampling.

ii. Sediment pore water sampling. Pore water samples were taken from experimental and control chambers on five separate dates spanning 23 days in 1989 experiments, and 22 days in 1990 experiments (Table 1). To avoid sampling the water trapped in the tygon sample port extension, approximately 0.3 ml of water was withdrawn and discarded. Subsequently, 0.5 ml of pore water was drawn from each port and refrigerated. Analysis of all samples was completed within 24 hours. The error of analytical replicates from pretests typically was $< \pm 1\%$.

d. Other measurements and observations

The activities of worms and the condition of the sediment surface were recorded daily. The presence and location of feeding palps and traces (*Eupolymnia*), fecal material, or feeding depressions (*Abarenicola*) on the sediment surface were noted. The presence and extent of surface microflora (diatoms, filamentous bacteria, both evidenced by color), the construction and location of new tubes or burrows, and the infilling of old tubes or burrows, also were recorded.

e. Analyses

i. Water column incubations. Net fluxes of silicate across the sediment-water interface (hereafter referred to as NFWC, for net flux to the water column) were calculated as:

$$\text{NFWC} = \frac{(C_f - C_i) * V}{A * t} \tag{1}$$

where

NFWC = flux (μmoles/cm^2 day)

C_f = silicate concentration in water column at termination of incubation period (μmoles/cm^3)

C_i = silicate concentration in water column at initiation of incubation period (μmoles/cm^3)

V = volume of overlying water (cm^3)

A = area of sediment surface (cm^2)

t = time of incubation period (day)

ii. Statistical evaluation of water column fluxes. An average NFWC, based on the three replicate measures that varied typically by $< 2\%$, was calculated for each chamber on each incubation date. NFWC was evaluated statistically to determine whether water column fluxes varied as a function of the treatment or any of the observed characteristics of worms or worm tubes. For statistical evaluation, data from *Eupolymnia* 1989 and 1990 experiments were not combined, because they were run under different temperature conditions, and could not be considered experimental replicates in any sense. Thus, each experimental manipulation was considered as a separate treatment: *Eupolymnia* in 1989, *Eupolymnia* tubes in 1989, *Eupolymnia* in 1990 and *Abarenicola* in 1990.

A one way analysis of variance (ANOVA) was employed to determine whether NFWC varied among treatments for each incubation date. When appropriate, significant differences among treatments were further evaluated using Scheffe's multiple comparison method (Sokal and Rohlf, 1981). Multiple regression was used to evaluate relationships between NFWC (the dependent variable) and several characteristics of worms and their activities, including the number of new burrows (*Abarenicola*) or tubes (*Eupolymnia*), the dry weight of the individual, and the number of days fresh feces were observed on the sediment surface (an indicator of feeding activity, *Abarenicola* only). Multiple regressions analyzing NFWC vs. dry weight and the number of new dwellings were conducted by pooling all treatments containing animals, as well as separately within each treatment. For the regressions, the mean NFWC over all incubation dates was calculated for each chamber, and used as the dependent variable. The mean NFWC over all incubation dates provided the best estimate of silicate flux to the water column over the duration of the experiment.

iii. Sediment pore water profiles. For each experimental and control chamber, an average pore water profile was determined for each sample date. This was accomplished by 1) linear interpolation of silicate concentrations from the 2 cm depth intervals, to estimate silicate concentrations at the 1 cm depth interval between sample points within each pore water profile, and 2) averaging the measured and interpolated silicate concentrations for each depth from the two vertical profiles from each chamber. The processes affecting the distribution and transport of silicate in the experimental chambers included: 1) dissolution of biogenic opal, 2) molecular diffusive transport along concentration gradients, 3) exchange due to the activities of worms or physical irrigation of fluids in worm tubes (Vogel and Bretz, 1972; Aller, 1984; Ray and Aller, 1985), and 4) uptake of silicate by benthic diatoms near the sediment surface. These processes can be expressed in mass balance terms, following the formulation of the general diagenetic equation (Berner, 1980), with macrofaunally-driven exchange parameterized as a nonlocal exchange process (Boudreau, 1984;

Christensen, *et al.,* 1984; Emerson *et al.,* 1984):

$$\frac{\partial C}{\partial t} = D\frac{\partial^2 C}{\partial z^2} - \alpha(C - C_{ow}) + R \tag{2}$$

where

C = concentration of silicate at depth z and time t (μM)
C_{ow} = concentration of C in the overlying water (μM)
α = rate associated with nonlocal exchange (1/day)
t = time (day)
z = sediment depth (cm)
R = rate of chemical reactions affecting C (μM/day)
D = molecular diffusion coefficient of C, corrected for tortuosity (cm^2/day)

Eq. (2) assumes constant porosity. The nonlocal exchange term in (2) is here defined to include 1) irrigation and sediment disturbances associated with worm activities, and 2) physical irrigation of fluids in worm tubes. The reaction processes are chemical dissolution of biogenic silica, here assumed to follow first order kinetics (Berner, 1980), and incorporation of silicate by diatoms. The form of the reaction term is

$$R = k(C_a - C) + I \tag{3}$$

where

R = the dissolution + incorporation rate (μM/day)
k = rate constant (1/day)
C_a = asymptotic silicate concentration, (μM)
C = concentration of dissolved silicate at depth z (μM)
I = incorporation rate due to diatoms at depth z and time t (μM/day).

Over the short duration of the experiment, compaction was negligible and there was no measurable sedimentation in experimental chambers. Thus, the advection term of the general diagenetic equation was excluded from the model.

The time series of pore water silicate profiles provides a measure of changes in silicate concentrations over time and, therefore, permits the calculation of $\partial C/\partial t$ for each depth sampled. A forward-stepping finite difference numerical technique was employed to solve (2) and evaluate the nonlocal exchange, diffusion and reaction terms in experimental and control chambers.

The reaction rate constant k, and the concentration of dissolved silicate at saturation C_a, were determined from data in control chambers. A diffusion-reaction model (Eq. (2) without the nonlocal exchange term) was employed to predict pore water silicate profiles in control chambers over time, given 1) specified values of C_a and k and 2) the initial pore water profile (from the data). Model-generated profiles were compared to measured pore water profiles in controls (light controls in 1989, dark controls in 1990). The values of C_a and k for each experiment were chosen by

Table 2. Parameters (calculated [C] and assigned [A]) used in diffusion-reaction and diffusion-nonlocal exchange-reaction models.

Porosity P	0.8 [A]
Formation factor f (based on the formula $f = P^{-M}$, with $M = 2.7$, after Ullman and Aller, 1982)	1.8267 [C]
Diffusion coefficient D_o (cm^2s^{-1}) (free solution)**	
1989 experiment	$7.17 * 10^{-6}$ [C]
1990 experiment	$6.78 * 10^{-6}$ [C]
Tortuousity-corrected Diffusion Coefficient D_s [cm^2s^{-1}, based on the formula $Ds = Do/(f * P)$, after Ullman and Aller, 1982]	
1989 experiment	$4.9065 * 10^{-6}$ [C]
1990 experiment	$4.6396 * 10^{-6}$ [C]
Timestep	10800 s (3 h) [A]

**Assuming the molecular diffusion coefficient for silicate is $10 * 10^{-6}$ cm^2s^{-1} at 25 degrees C (Wollast and Garrels, 1971) and a doubling of the diffusion coefficient for every 25 degrees C (Li and Gregory, 1974), i.e. $Do = 5e^{(0.0277259T)}$, where T = temperature; 13 degrees C in 1989 experiment, 11 degrees C in 1990 experiment.

selecting the best fit of the simulated profiles to the average pore water profiles in each set of controls. This approach assumes that k and C_a are the same both with and without polychaetes. The boundary conditions were:

$$C_{z=0} = 0$$
$$\partial C/\partial z_{max} = 0$$

where z_{max} is the lowest depth in each chamber (13–15 cm). The silicate concentration at the sediment surface ($z = 0$) is set to zero because benthic diatoms near the sediment surface removed nearly all available silicate in control chambers (see Results). Below the 6 cm depth interval, the influence of diatoms on pore water profiles was negligible (see Results and discussion). Thus, the pore water profiles below 6 cm were used to determine k and C_a. Because the amount or composition of diatom frustrules in False Bay sediments may exhibit seasonal variation, and because temperatures were different in 1989 and 1990 experiments, the data from the 1989 and 1990 controls were evaluated separately, and separate values of C_a and k were chosen for each year. Other model values are listed in Table 2.

A second model was devised using Eq. (2) which determines, by difference, the value of the nonlocal exchange term and the rate of silicate incorporation by diatoms in chambers with worms or worm tubes. The model calculates changes in concentration due to molecular diffusion and chemical reaction only, and subtracts these quantities from the total measured change in concentration for each depth to yield the rate of change in silicate concentration due to worm activity and diatom incorporation. This quantity represents the sum of biological processes affecting changes in silicate concentrations in sediments, and subsequently is referred to as

CSB (for changes in silicate due to biological processes). The model was used to calculate CSB for each chamber containing macrofauna or macrofauna tubes, using the previously calculated values for C_a and k for each experiment.

iv. Statistical evaluation of pore water data. Fluxes of silicate from sediments to the water column were calculated from the pore water data using the results of the diffusion-nonlocal exchange-reaction model (Eq. (2)). Model-generated profiles of CSB were integrated over depth and averaged over time to calculate a time-averaged biologically-driven flux (hereafter referred to as TBF, μmoles/cm^2*day) for each experimental chamber. As with the water column flux data (NFWC), TBF's were evaluated statistically to determine whether they varied as a function of the treatment, or with any observed or measured characteristics of the worms or worm tubes.

The pore water profiles from control chambers indicated that removal of silicate by diatoms near the sediment surface influenced pore water silicate to a depth of 6 cm (see Results). Thus, near the sediment surface, silicate fluxes in experimental chambers were influenced by the activities of diatoms, worms, and/or worm tubes. Time-averaged silicate removal by diatoms in control chambers was determined by taking the mean pore water profile for each sample date and calculating CSB (using Eq. (2)) and TBF. In this case, CSB reflects the incorporation rate I, as no macrofauna were present in controls. Light and dark controls for each year were evaluated separately. Replicate profiles were averaged and one estimate of TBF was obtained for each set of controls, as it provided the best estimate of the overall effect of diatoms on silicate removal in the upper sediment horizon.

Deeper in the sediment column, the effect of diatoms on pore water silicate was negligible, and biologically-driven fluxes in experimental chambers were due primarily to the activities of worms and/or effects of worm tubes. To evaluate these effects on pore water transport, biologically-driven fluxes for the lower sediment column (depth 7 cm to the bottom of each chamber, hereafter referred to as TBFL) were calculated and analyzed statistically in the same manner as TBF. It should be emphasized that biotic silicate transport in this region does not represent the total contribution of worms to silicate flux across the sediment-water interface. Rather, it provides a measure of the relative importance of the effects of the different worm treatments in the absence of diatom influences.

Three additional calculations were performed to further discern both the patterns and processes contributing to biological removal of silicate in chambers with worms or worm tubes. First, model estimates of CSB at each depth and time step were averaged for each treatment. This calculation reveals the average pattern of biological effects on pore water silicate for each treatment. Second, CSB values at each depth were averaged over time for each treatment, to determine the depth dependence of biotic effects on pore water silicate. Finally, the range of CSB over the course of the experiment was calculated for each depth in each chamber. The range

is here taken as an estimator of how variable the biological removal effects were in each treatment, perhaps due to cross-chamber movements of worms or changes in worm activity. Because CSB, and therefore the range of CSB, at adjoining depth strata may be correlated, a multivariate analysis of variance (MANOVA), with depth and CSB range as the dependent variates, was performed to determine whether the variability in animal effects on silicate concentrations is significantly different among treatments. The analysis was performed on data from the entire sediment column only. When the MANOVA indicated a significant difference due to treatment, Hotelling's T^2 statistic was used to analyze differences.

v. Comparison of fluxes calculated from sediment pore water profiles and water column incubations. Silicate fluxes measured using the incubation technique reflect the combined effects of biologically-driven and diffusive fluxes across the sediment-water interface, and the incorporation of silicate by diatoms. Silicate fluxes determined from pore water profiles were compared with those measured by the incubation technique by the following calculation. For each chamber containing a worm or tube, model-generated values of the rate of change in silicate concentration due to biologically driven processes and diffusion were calculated for the time periods over which water column incubations occurred. These values were integrated over depth and averaged over time, to calculate time-averaged diffusive and biologically-driven flux (hereafter referred to as TDBF, for time-averaged diffusive and biologically-driven fluxes, μmoles/cm^2*day). In addition to comparing model and incubation results, a one-way analysis of variance was used to determine whether TDBF was significantly different between treatments for each incubation date.

3. Results

a. General observations

i. 1989 experiment. Ambient water temperatures were approximately 13 degrees C. *Eupolymnia* actively fed and defecated onto the sediment surface, and frequently tunneled through the sediments to establish new tube openings (average of 5.4 tube entrances were established over the 23 d period, Table 3). At all times, at least two tube openings were present in chambers with worms. Abandoned tubes in chambers with *Eupolymnia* were obvious from the lack of feeding traces or defecation piles near tube entrances. In these cases, and in chambers containing *Eupolymnia* tubes only, tubes remained open for as little as one day and as long as several weeks subsequent to the worm's departure.

A rich cover of benthic diatoms was evident on the sediment surface in light control chambers at all times. However, the sediment surface in chambers containing *Eupolymnia* or *Eupolymnia* tubes varied considerably throughout the 1989 experiment. In chambers with worms, the diatom cover often was depleted by deposit

Table 3. Mean (±1 SE) values of 1) the number of dwellings constructed per worm, 2) worm dry weight (g) and 3) number of days fresh feces were observed on the sediment surface (*Abarenicola* only), for each treatment. n.a. = not available.

Treatment	Number of dwellings	Dry weight	Fecal mound
Abarenicola	5.67	0.2043	18.33
1990	(0.553)	(0.0153)	(1.00)
Eupolymnia	2.83	0.4847	n.a.
1990	(0.401)	(0.0717)	
Eupolymnia	5.40	0.6672	n.a.
1989	(0.510)	(0.0784)	
Eupolymnia	1.67	0.6025	n.a.
tubes 1989	(0.494)	(0.0853)	

feeding of the terebellids (e.g. Gremare *et al.,* 1989), exposing black, sulfidic sediment. Occasionally, a *Beggiatoa*-like bacterial mat was observed at the sediment-water interface. I observed similar conditions in terebellid beds in the field in the late summer. In the chambers, bacterial mats occupied as much as half the sediment surface but were transient, persisting only 1–2 days. Bacterial mats also were present on sediment surfaces in chambers containing *Eupolymnia* tubes only, but in smaller patches (1–2 cm diameter) than in chambers with worms. Bacterial mats were never visible in controls.

ii. 1990 Experiment. Water temperatures were cooler than in the 1989 experiment, averaging 11 degrees C. In chambers containing *Abarenicola,* worms usually showed some evidence of activity (e.g. appearance of fecal mounds or feeding funnels) daily (Table 3). The topography of the sediment surface was somewhat variable, due to shifts in the position of fecal mounds. Active burrow shafts were obvious from the presence of fresh fecal mounds and the appearance of burrow openings on the sediment surface. On average, arenicolds established 5.67 burrow shafts (determined by the presence of fecal casts) over the course of the 22 day experiment (Table 3). Old shafts collapsed less than one day after they were abandoned.

Eupolymnia were considerably less active in the 1990 experiment than in 1989. Worms built fewer new tubes (an average of 2.83 tubes per chamber over the 22 d period, Table 3). In addition, worms did not feed or defecate as frequently as in the 1989 experiment. Several individuals spawned during the experiment, suggesting that the population was in their reproductive phase. In control chambers, the benthic diatom cover was thinner and less prominent than in 1989 controls, and generally persisted throughout the course of the experiment. The sediment surface of light control chambers was slightly browner than in dark controls, indicating a more active benthic diatom population. Nevertheless, sediment surfaces of dark control chambers were somewhat golden, even after three weeks of darkness. In chambers with

worms, the diatom cover also was thin and somewhat brown, and never was depleted (as in 1989 experiments) by the feeding activity of worms or the deposition of fecal material by worms onto the sediment surface. In addition, bacterial mats were never noted in any of the experimental or control chambers.

b. Water column incubation results

Differences in net silicate fluxes (NFWC) among treatments were assessed for each incubation date using analysis of variance. On the first incubation date in 1989 (Sept 14), there were significant differences in NFWC among treatments (F = 12.83, $d.f.$ = 2, 10; p = 0.0017; Fig. 1). In all three treatments, absolute values of NFWC were high (Fig. 1). In *Eupolymnia* chambers, silicate moved from sediments to the water column. However, in *Eupolymnia* tube and light control chambers, net flux was from the water column to the sediments (Fig. 1). On the second incubation date in 1989, (Sept. 17), the magnitude of flux in all three treatments was lower, and silicate was transported from the water column to sediments (Fig. 1). No significant differences in NFWC among treatments were detected (F = 1.07, $d.f.$ = 2,10; p = 0.3807; Fig. 1).

In the 1990 experiment, NFWC's in *Abarenicola* chambers were consistently high, with net fluxes always from the sediments to the water column (Fig. 1). On the first incubation date (June 20), *Abarenicola* chambers had significantly higher NFWC's than all other treatments (F = 33.60, $d.f.$ = 3,17; p = 0.0001; Fig. 1). Net silicate fluxes in dark control and *Eupolymnia* chambers were from sediments to the water column, but in light controls, fluxes were barely discernable from zero. On the second incubation date (June 24), silicate was transported from sediments to the water column in all treatments. NFWC's in *Abarenicola* chambers were significantly higher than in light control chambers only (F = 5.31, $d.f.$ = 3,17; p = 0.0091; Fig. 1). On the third incubation date (July 2), NFWC's in *Abarenicola* and dark control chambers were from sediments into the water column, but in *Eupolymnia* and light control treatments, a net flux was not evident. There were significant differences in NFWC's among treatments (F = 11.59, $d.f.$ = 3,17; p = 0.0002), with *Abarenicola* chambers having significantly higher fluxes than *Eupolymnia* and light control chambers (Fig. 1).

NFWC's were averaged over incubation date for each chamber, and regressed against worm dry weight and total number of dwellings constructed (all worm treatments), and the number of days fresh feces were observed on the sediment surface (*Abarenicola* chambers only) using multiple regression. A significant, positive relationship was detected between average NFWC and the number of dwellings constructed over the course of the experiment when all treatments were included in the regression, as well as when individuals from the *Eupolymnia* 1989 experiment only were considered (Table 4). No significant relationships were evident between

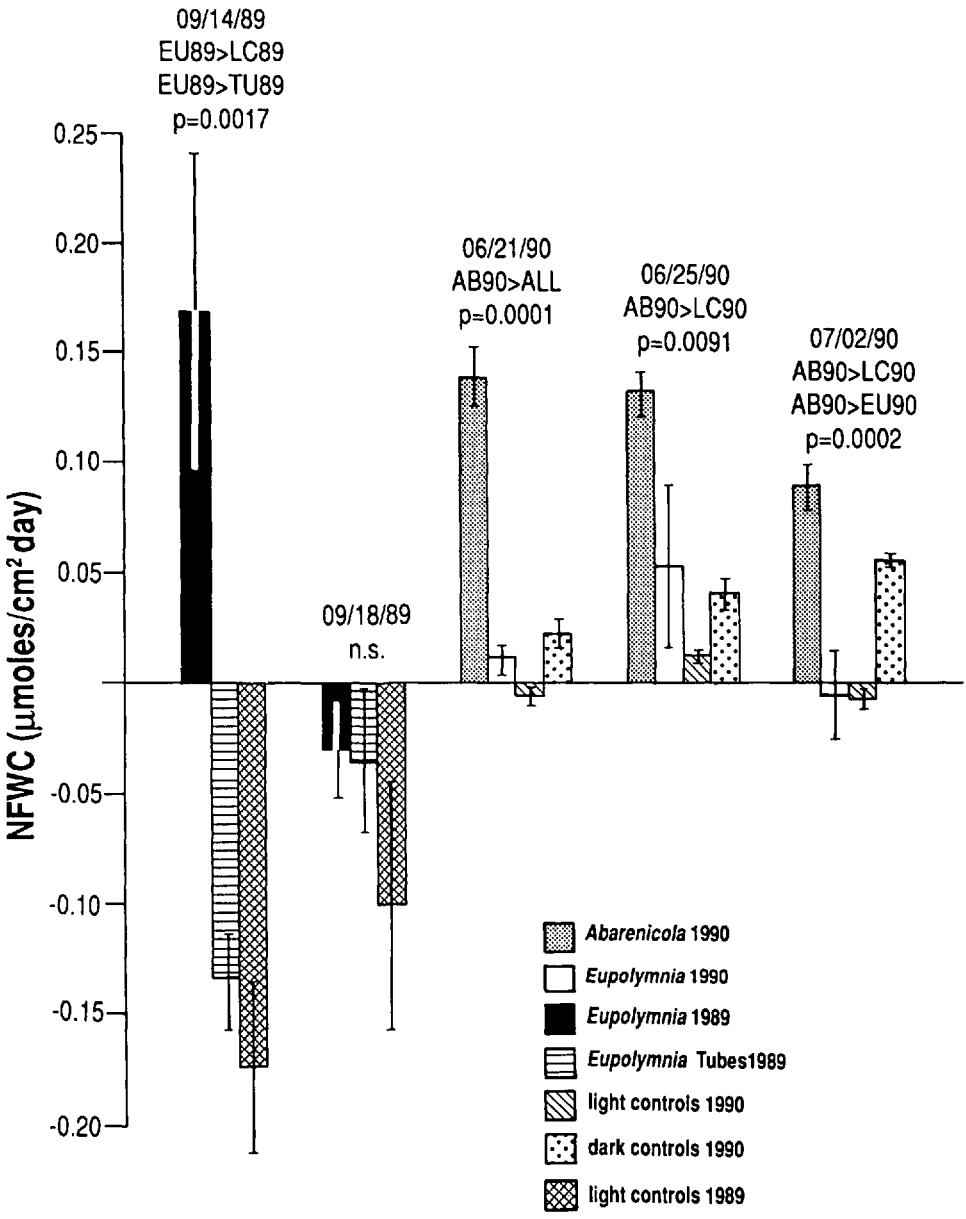

Figure 1. Mean (±1 SE) NFWC for all incubations conducted in 1989 and 1990 experiments. Incubation dates are listed over each set of bars. Positive values represent net transport of silicate from sediments to the water column. Symbols are AB90 = *Abarenicola* 1990; EU90 = *Eupolymnia* 1990; EU89 = *Eupolymnia* 1989; TU89 = *Eupolymnia* tubes 1989; LC90 = Light controls 1990; DC90 = Dark controls 1990; LC89 = Light controls 1989.

Table 4. Results of multiple regressions examining relationships between calculated (TBF, TBFL) and measured (average NFWC) fluxes and 1) worm dry weight (g), 2) total number of dwelling constructed (# dwellings), and 3) number of days fresh feces were observed on the sediment surface (fecal mound). Separate multiple regressions were conducted by combining all treatments with worms, where appropriate, and for individual worm treatments. Dep. term = dependent term; Indep. terms = independent terms; F = F ratio; *d.f.* = degrees of freedom; p = probability of significance, R^2 = partial coefficient of multiple determination; AB90 = *Abarenicola* 1990; EU90 = *Eupolymia* 1990; EU89 = *Eupolymnia* 1989. Underlined p-values indicate significant positive relationships at $\alpha = 0.05$. For $p > 0.15$, regression statistics are not reported (n.r.).

Dep. term	Indep. terms	F	*d.f.*	p	R^2
I. All treatments with worms					
TBF	worm dry wt	5.49	17	0.0315	0.1776
	# dwellings	10.24		0.0052	0.2726
TBFL	worm dry wt	3.20	17	0.0914	0.1075
	# dwellings	10.98		0.0041	0.3218
NFWC	worm dry wt	2.35	17	0.1440	0.0627
	# dwellings	15.98		0.0009	0.4829
II. Within worm treatments					
TBF					
AB90	fecal mound	n.r.	7	n.r.	n.r.
	worm dry wt	n.r.	7	n.r.	n.r.
	# dwellings	n.r.	7	n.r.	n.r.
EU90	worm dry wt	n.r.	4	n.r.	n.r.
	# dwellings	n.r.	4	n.r.	n.r.
EU89	worm dry wt	n.r.	3	n.r.	n.r.
	# dwellings	n.r.	3	n.r.	n.r.
TBFL					
AB90	fecal mound	n.r.	7	n.r.	n.r.
	worm dry wt	n.r.	7	n.r.	n.r.
	# dwellings	n.r.	7	n.r.	n.r.
EU90	worm dry wt	n.r.	4	n.r.	n.r.
	# dwellings	n.r.	4	n.r.	n.r.
EU89	worm dry wt	n.r.	3	n.r.	n.r.
	# dwellings	n.r.	3	n.r.	n.r.
NFWC					
AB90	fecal mound	n.r.	7	n.r.	n.r.
	worm dry wt	n.r.	7	n.r.	n.r.
	# dwellings	2.80	7	0.1381	0.2858
EU90	worm dry wt	n.r.	4	n.r.	n.r.
	# dwellings	n.r.	4	n.r.	n.r.
EU89	worm dry wt	n.r.	3	n.r.	n.r.
	# dwellings	10.59	3	0.0473	0.7793

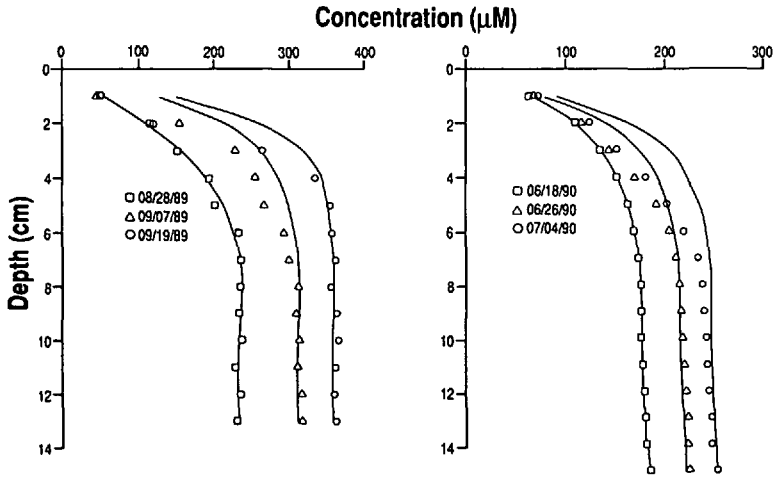

Figure 2. Vertical profiles of pore water silicate from light control chambers in 1989 (left) and dark control chambers in 1990 (right). Symbols represent the average profile for three chambers taken on the sample dates listed. Solid lines are predicted vertical profiles of pore water silicate from the diffusion-reaction model, and are the best fits to data in the deeper portions of the sediment. For clarity, only three of five data and model profiles are shown.

average NFWC and dry weight or the appearance of fecal mounds, either within a treatment or with all treatments combined (Table 4).

c. Pore water profiles and model results

i. Control chambers. Vertical profiles of dissolved silicate in sediment pore waters were similarly shaped in 1989 and 1990 control chambers (Fig. 2). Profiles from the light and dark controls in 1990 were strikingly similar, indicating that diatoms in dark controls remained viable for several weeks (Harper, 1977) and incorporated silicate during darkness (Werner, 1977). In 1990, results from dark control chambers only were used to evaluate k and C_a in the diffusion-reaction model. In all controls, profiles sloped toward 0 μM near the sediment surface, presumably due to uptake of silicate by benthic diatoms near the sediment surface. Deeper in the sediment column (below 6 cm), concentrations changed little with depth (Fig. 2). Model-generated profiles were fit to the raw data below 6 cm depth in control chambers (solid lines, Fig. 2). The best fit yielded values for the asymptotic silicate concentration and reaction rate constants for 1989 and 1990 experiments. For 1989 light controls, the estimated reaction rate (k) is $7.2 * 10^{-7}$/s, and the estimated asymptotic silicate concentration (C_a) is 400 μM. For 1990 dark controls, best fits are obtained when the reaction rate constant (k) is $2.7 * 10^{-7}$/s, and the asymptotic silicate concentration (C_a) is 400 μM. During experiments, silicate concentrations in the water column in controls ranged from 5 to 35 μM. To evaluate the effect of fluctuating water column silicate levels on pore water profiles in controls, model runs

were conducted with $C_z = 0$ set to 0, 30 and 50 μM. Results from these runs show that the top boundary condition had little effect (<1%) on pore water concentrations below the 3 cm depth interval.

In the 1989 experiment, final silicate concentrations in the lower sediment column at termination of the experiment were higher (>350 μM) than in the 1990 experiment (<260 μM). This may be due to higher temperatures (13 degrees C in 1989 vs. 11 degrees C in 1990) promoting faster dissolution, or to yearly differences in the amount or composition of biogenic opal in experimental sediments. The second explanation is considered less likely, for several reasons. First, the model predicts a similar asymptotic silicate concentration for both sets of controls, indicating that the composition of frustrules, and their tendency to dissolve, was not substantially different from year to year. Second, False Bay sediments are well-mixed by the activities of infauna and storms (Miller and Sternberg, 1987; Krager and Woodin, 1992). Experimental sediments were taken from 0–10 cm depth in a region containing *Abarenicola pacifica*. Sediment turnover in this area occurs to depth of 15 cm, twice per year (Hylleberg and Henriksen, 1980). Thus, although surface diatom abundances might have been different in August 1989 vs. June 1990, frustrule abundances at depth are probably more uniform, due to physical and biological sediment turnover.

Calculations of TBF in control chambers estimate the incorporation of silicate from sediment pore waters by diatoms in control chambers. The time- and chamber-averaged removal of silicate in light controls 1989, light controls 1990 and dark controls 1990 was 0.0621, 0.0172 and 0.0177 μmoles/cm^2*day, respectively. Thus, diatoms removed substantially more silicate from sediment pore waters in 1989 controls relative to 1990 controls. TBF was recalculated using model estimates of CSB for the upper 0–6 cm depth strata. This calculation revealed that 80–100% of the total silicate removed by diatoms occurred in the upper 0–6 cm of the sediment column. Calculations of TBF with the upper boundary condition set to 30 μM show slightly higher incorporation rates (.0736, .0218 and .0222 μmoles/cm^2*day, in light controls 1989, light controls 1990 and dark controls 1990, respectively) but similar trends.

ii. Experimental chambers. To examine trends in the biological modification of pore water silicate, CSB values for each depth and time were averaged over all chambers in each treatment (Fig. 3). In general, biological processes resulted in a net loss of silicate from sediments. For presentation purposes, model predictions of CSB were multiplied by (−1), such that silicate losses from pore waters are represented as positive values in all figures and in the discussion. CSB values for individual chambers are given in Marinelli 1991 (Appendix I).

CSB in *Eupolymnia* 1989 chambers were high (>16 μM/day), and varied by as much as an order of magnitude, both near the sediment surface and at depth.

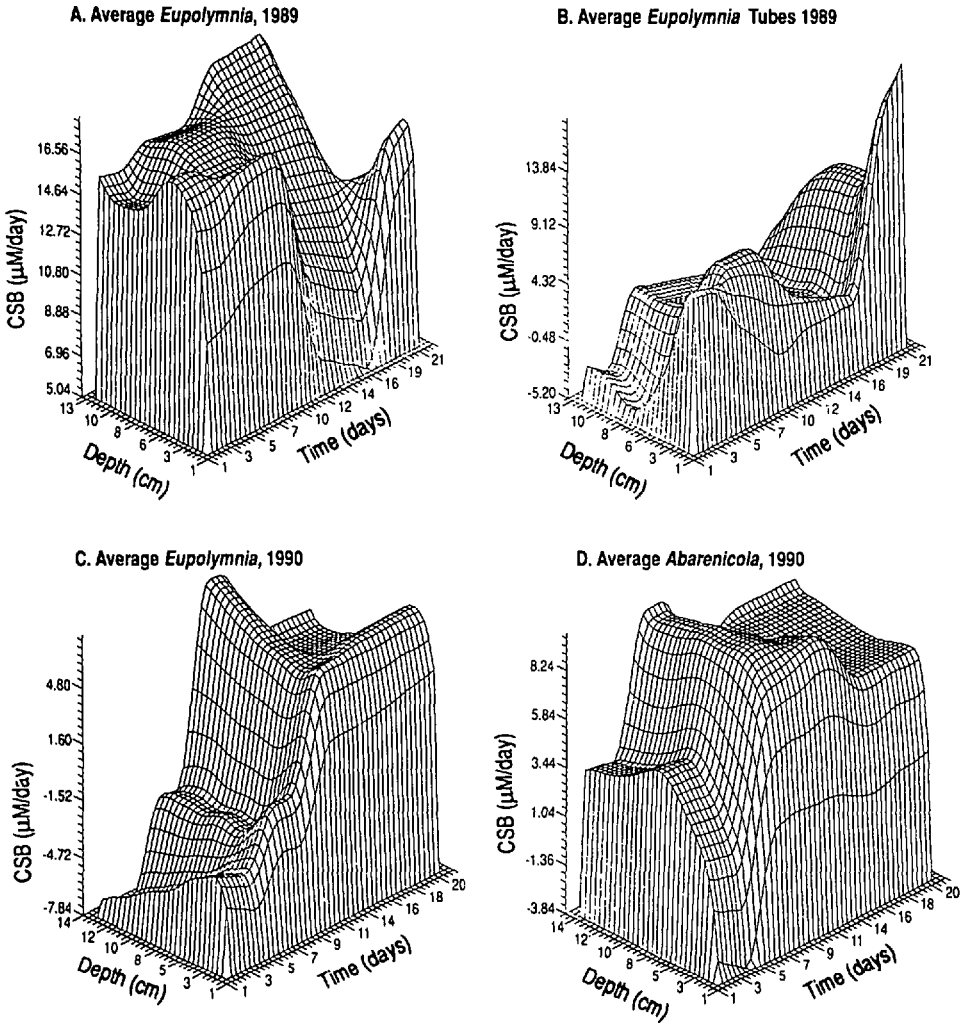

Figure 3. Rate of change in silicate transport out of sediment pore waters due to biological processes (CSB, µM/day), as a function of depth and time, averaged over all chambers in each treatment. Losses are represented as positive values on the vertical axis.

Highest rates of biogenic silicate removal occurred at depth, near day 16 (Fig. 3a). CSB in *Eupolymnia* tube 1989 chambers also were variable (Fig. 3b). Most of the biogenic removal of silicate occurred near the sediment surface, and was comparable in magnitude, direction and to a lesser extent, variability, to that in *Eupolymnia* 1989 chambers (Fig. 3a vs. 3b). However, at depth, CSB were nearly an order of magnitude lower and considerably less variable than in chambers containing intact worms (Fig. 3a vs. 3b). In chambers with tubes only, CSB values were negative at the sediment surface near the middle of the experiment, and at depth near the beginning

of the experiment (Fig. 3b). Thus, in the absence of worms but with worm tubes, biological processes sometimes resulted in a local increase in silicate concentrations within sediments.

The biological removal of silicate in *Eupolymnia* 1990 chambers was considerably lower than in 1989 chambers with worms (Fig. 3a vs. 3c). On average, CSB values for *Eupolymnia* 1990 chambers were most variable and reached their highest levels at lower depths in the sediment column. Near the sediment surface, CSB estimates were considerably lower and less variable than in *Eupolymnia* 1989 chambers. CSB was negative throughout the sediment column early in the experiment, indicating that silicate was imported by organisms. Subsequently, CSB values became increasingly positive, perhaps due to elevation in worm activity.

Patterns of silicate removal in chambers containing *Abarenicola* were considerably less variable over time than in other treatments (Fig. 3d). Highest levels of biotic silicate removal from sediments were > 8.24 μM/day, intermediate between those of *Eupolymnia* 1989 chambers and *Eupolymnia* 1990 chambers (Fig. 3a, 3c & 3d). As in *Eupolymnia* 1990 chambers, CSB values at the sediment surface were negative near the beginning of the experiment, indicating that biological processes caused a local increase of silicate in sediments.

Maxima in CSB occurred at depth in the sediment column in all chambers containing worms, but followed no particular periodicity, and did not correspond with any particular activities of worms observed during the experiment. Fluctuations in CSB near the sediment surface most likely were due to variation in silicate incorporation by diatoms, and variation in worm activity (see below).

iii. Patterns of biologically-driven transport over depth. To better understand the depth dependence of biological effects on pore water silicate, CSB estimates at each depth were averaged over time for each treatment. In general, patterns varied among treatments, probably due to differences in organism activity and dwelling morphology (Fig. 4). In *Eupolymnia* 1989 and *Abarenicola* 1990 chambers, biotic silicate removal was comparatively high throughout the sediment column (Fig. 4). However, while average CSB was relatively constant with depth in *Abarenicola* 1990 chambers, it increased slightly with depth in *Eupolymnia* 1989 chambers. Because a greater percentage of the total surface area of *Eupolymnia* tubes occurs at depth (due to the U-shaped tube) relative to arenicolid burrows, higher rates of silicate transport might have been expected at depth for *Eupolymnia.* In contrast to *Eupolymnia* in 1989 and *Abarenicola* in 1990, there were sharp declines in average CSB values over depth in *Eupolymnia* 1990 and *Eupolymnia* tube 1989 treatments. Most likely, these declines are related to the absence of macrofauna in *Eupolymnia* tube treatments or to reduced activity by *Eupolymnia* in 1990. In all treatments, there were relatively high values of CSB near the surface (2 to 6 cm), probably due to incorporation of silicate by diatoms (Fig. 4). In the top 1 cm, rates of silicate removal were low, or

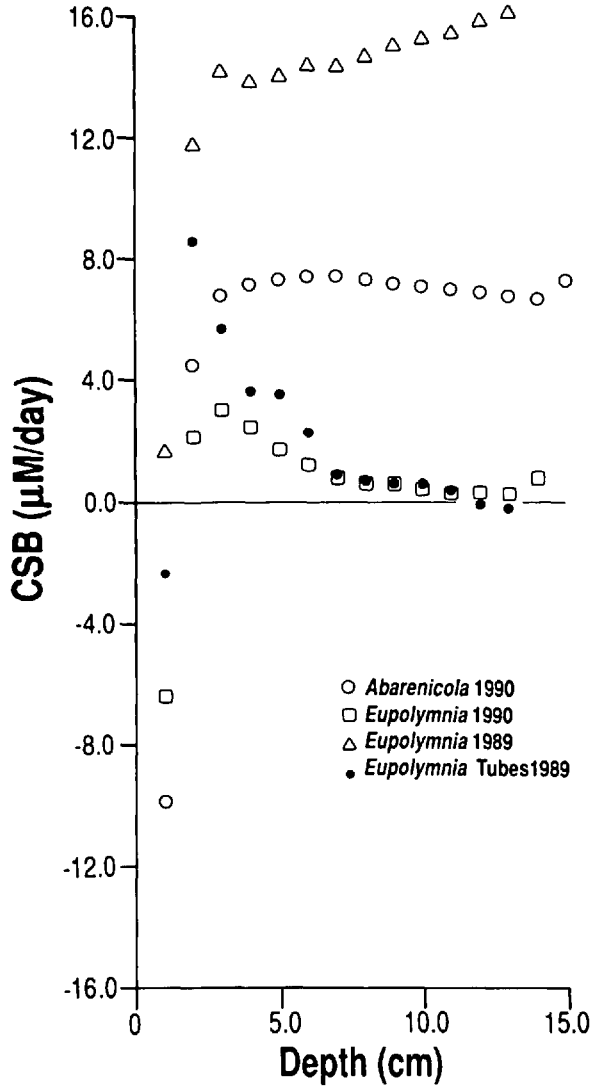

Figure 4. Time-averaged CSB as a function of depth for each treatment. Positive values of CSB indicate losses of silicate from sediment pore waters.

silicate was imported. This pattern was perhaps due to 1) demand for silicate by subsurface diatoms or 2) errors in the upper boundary condition of the model (see below).

iv. Statistical analyses of fluxes: Sediment data. A multivariate analysis of variance (MANOVA) assessed the effect of treatment on the range of CSB and depth for the entire sediment column. Significant differences occurred among treatments (Wilks'

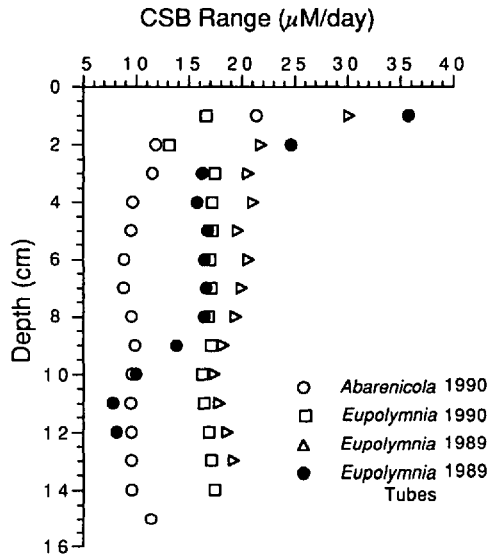

Figure 5. Range of CSB over the course of the experiment for each depth in each treatment. The range is taken as an estimator of how variable biotic removal of silicate was among treatments.

Lambda Statistic, $F = 11.19, d.f. = 6, 670, p = 0.0001$). Multiple comparison analysis revealed *Eupolymnia* 1989 chambers were greater than *Eupolymnia* tube 1989 chambers, and that all treatments containing *Eupolymnia* or *Eupolymnia* tubes were greater than *Abarenicola* 1990 chambers (Fig. 5).

A one way analysis of variance determined whether time-averaged biologically-driven fluxes (TBF and TBFL) of silicate from sediments to the water column varied among treatments. Where worms and diatoms affected silicate flux (TBF), there were significant differences among treatments ($F = 30.35$, $d.f. = 3,21$; $p = 0.0001$). TBF in *Eupolymnia* 1989 chambers was significantly higher than in *Abarenicola* 1990 chambers; both of these treatments had significantly higher TBF's than *Eupolymnia* tube 1989 and *Eupolymnia* 1990 treatments, which were indistinguishable from one another. At depths of 7–15 cm, where worms and tubes affected silicate flux, but diatoms did not (TBFL), similar patterns occurred (Fig. 6). The ANOVA for TBFL was highly significant ($F = 48.27$, $d.f. = 3,21$; $p = 0.0001$), and differences among treatments were identical to those for TBF. In *Abarenicola* 1990 and *Eupolymnia* 1989 chambers, the majority of biological silicate removal (>60%) occurred in the lower sediment column (Fig. 6). Conversely, in *Eupolymnia* 1990 and *Eupolymnia* tube 1989 chambers, the majority of the biological silicate removal from sediments (>55%) occurred in the upper 6 cm., presumably because diatoms accounted for most of the removal.

Multiple regression was used to examine the relationship between TBF or TBFL and the characteristics of worms. Within treatments containing worms, there were no

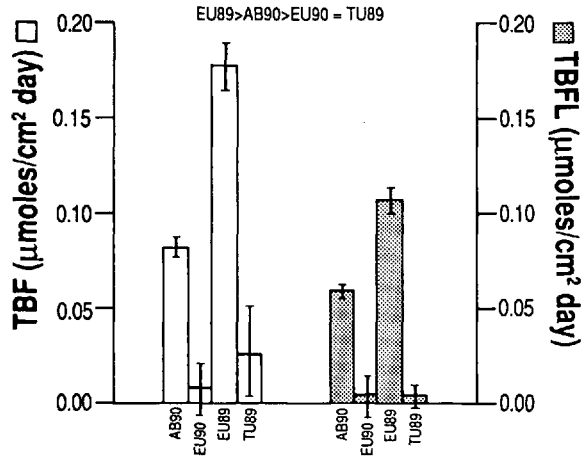

Figure 6. Mean (±1 SE) of TBF (left) and TBFL (7–15 cm depth, right) for each treatment. AB90 = *Abarenicola* 1990; EU90 = *Eupolymnia* 1990; TU89 = *Eupolymnia* tubes 1989; EU89 = *Eupolymnia* 1989. Results of Scheffe's multiple comparisons tests which were identical for each analysis, appear at top of figure.

significant relationships between TBF or TBFL and a) the dry weight of the worm, b) the total number of burrows or tubes constructed over the course of the experiment or c) the number of days fresh feces were observed on the sediment surface (*Abarenicola* 1990 only) (Table 4). However, when the 3 treatments with worms were combined, a significant positive relationship emerged between the total number of dwellings and both TBF and TBFL (Table 4 and Fig. 7), and worm dry weight and TBF (Table 4). On average, arenicolids in 1990 constructed new dwellings at the same rate as terebellids in the 1989 experiment (Fig. 7 and Table 3). However, for a given number of dwellings, fluxes were higher in *Eupolymnia* 1989 chambers.

d. Comparison of fluxes calculated from sediment pore water profiles and water column incubations

Model calculations of TDBF (time-averaged diffusive and biologically-driven fluxes) were made over the time period that coincided with water column incubations, and compared to corresponding measures of NFWC. Because only one estimate of TDBF was calculated for each set of controls, controls were excluded from this evaluation. On the first incubation date in 1989, TDBF's and NFWC's were consistent for *Eupolymnia* chambers, but not *Eupolymnia* tube chambers (Figs. 1 & 8). On the second incubation date, TDBF's and NFWC's did not agree well in either treatment. In the 1990 experiment, model-generated fluxes for *Abarenicola* chambers were consistent with measured fluxes both in magnitude and direction (Figs. 1 & 8). For *Eupolymnia* chambers, TDBF's and NFWC's were consistent on the second incubation date only (Figs. 1 & 8).

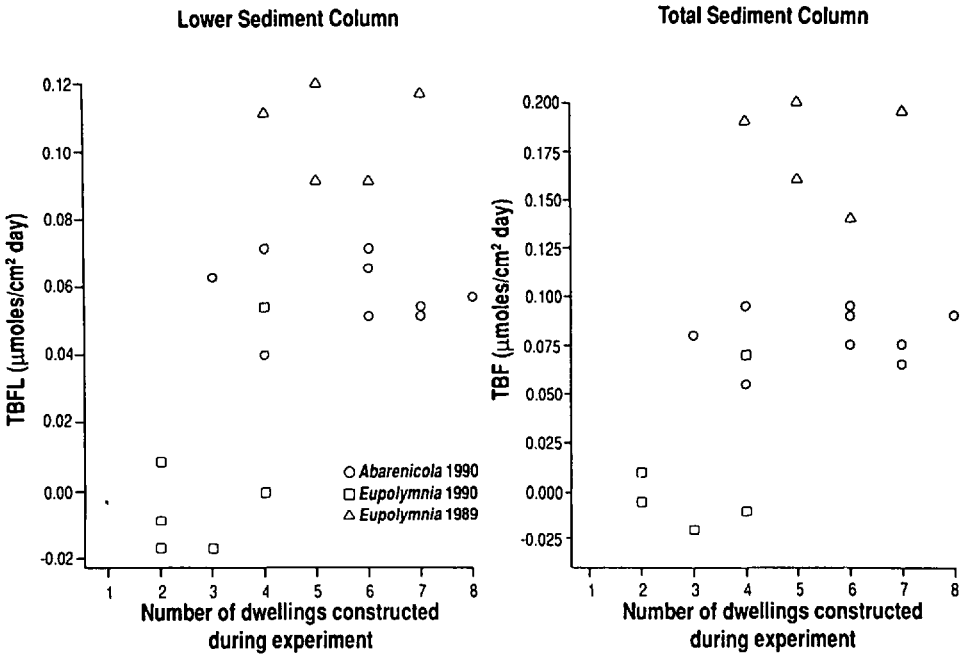

Figure 7. TBF and TBFL versus the number of dwellings constructed during 1989 and 1990 experiments.

Analysis of variance revealed that, in the 1989 experiment, there were significant differences in TDBF's between *Eupolymnia* and *Eupolymnia* tube treatments on the first incubation date only ($F = 14.58$, $d.f. = 1,8$; $p = 0.0051$; Fig. 8). In 1990 there was a significant difference in TDBF's between *Abarenicola* and *Eupolymnia* treatments on the first incubation date ($F = 146.1$, $d.f. = 1,13$; $p = 0.0001$), and a nearly significant difference on the third incubation date ($F = 4.41$, $d.f. = 1,13$; $p = 0.0558$; Fig. 8).

4. Sources of error in the sediment model

In several instances, CSB values near the sediment surface were negative, indicating that biological processes served to transport silicate into pore waters (Fig. 4). This trend may be related to the demand for silicate by subsurface diatoms, or may have been caused by errors in the model assumptions. Several potential sources of error which might lead to this condition are listed below:

1) Errors in the boundary condition at the sediment surface due to changes in the concentration of silicate at the sediment-water interface (e.g. Rowe and Howarth, 1985). The model assumed that silicate concentration at the sediment surface was zero in all chambers due to incorporation by diatoms. However, benthic diatom and bacterial activity appeared to vary throughout the experiment among treatments and

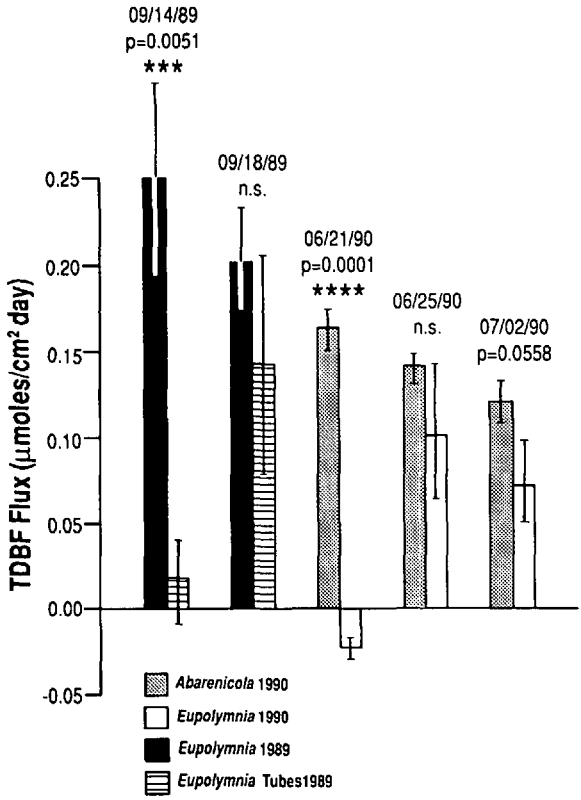

Figure 8. Mean (±1 SE) TDBF calculated over the time interval of water column incubations. Other interpretations as in Figure 1.

controls. If silicate concentrations at the sediment surface were greater than zero, the diffusive gradient would have been smaller than the model predicted. In this case, the model would overpredict diffusive silicate transport, and correspondingly underpredict biological silicate removal. For example, if the silicate concentration at the sediment-water interface was 30 μM (average overlying silicate concentrations during experiments), silicate flux due to biological processes in the upper (1–6 cm) sediment horizon would be underestimated by as much as 40 percent. In this instance, the majority of the underestimated flux would occur in the top 2 cm of the sediment column.

2) Errors in the estimation of the whole sediment diffusion coefficient near the sediment surface. The model also assumed that the diffusion coefficient was constant throughout the sediment column. However, near the sediment surface, diatoms and bacteria formed cohesive mats which may have hindered diffusive transport across the sediment surface. If this were true, the whole sediment diffusion coefficient should have been lower near the sediment surface than for the rest of the sediment

column. An artificially high diffusion coefficient would lead to an overprediction of diffusive transport, and therefore, an underprediction of biotic silicate removal near the sediment water interface. This may explain why the TBF estimate for the light control 1990 chambers was smaller than for the 1990 dark control chambers, despite the fact that the diatom cover (and associated diffusive impedance) was more extensive in light controls.

3) Errors in the boundary condition at the sediment surface due to changes in the height of the sediment surface relative to the sample ports. In chambers with worms, feeding and defecation by macrofauna altered the topography of the sediment surface. In addition, there was slight compaction of sediments in all chambers early in the experiment. Changes in the depth of sampling ports relative to the true sediment depth may have led to inaccuracies in the estimation of changes in concentration with depth and time, and correspondingly, inaccuracies in the calculation of biological removal of silicate from sediment pore water. These inconsistencies were most important in the top centimeter interval because a) worm-induced topographical changes were most dramatic at the sediment surface, rarely affecting the second and subsequent centimeter intervals, and b) compaction effects are diminished with depth in the sediment column (Berner, 1980).

An additional source of error in the model calculations lies in the estimation of the reaction rate, k. Previous calculations (see Results) showed that changes in the upper boundary condition had little effect on silicate profiles at depths below 3 cm in control chambers. Thus, changes in the activities of diatoms near the sediment surface would have a negligible impact on silicate profiles in the region where model fits to data were evaluated in controls (below 6 cm depth interval, see Fig. 2). Moreover, the estimated values of k are within the range of silica dissolution rates reported from other studies of marine sediments (e.g. Aller and Benninger, 1981; Table 2; Emerson *et al.*, 1984; Table 2). Given the excellent fit of model-generated profiles to the data from controls, and the slight effect of changes in the upper boundary condition on predicted silicate profiles below the 6 cm depth interval, estimated reaction rates are probably close to real values. However, if the reaction rate is in error, the effect of this error on estimates of biologically-driven removal of silicate is significant. For example, a doubling of the reaction rate leads to an increase in the biotic removal of silicate by nearly 50%.

5. Discussion

Benthic communities are dynamic assemblages, where the distributions and activities of organisms are spatially and temporally variable, due to physical, chemical and biological forcings. Because infauna have significant effects on solute transfer across the sediment-water interface, it is important to determine how the activities of different organisms, and interactions among organisms, affect solute exchange. Results suggest that there are identifiable differences in the effect of worms and

microflora on both the magnitude of, and variability associated with, silicate distributions and silicate transport in sediments. These differences can be related to species effects, and seasonal differences in the activities of worms, surface microflora, and worm-microflora interactions.

a. Effects of benthic macrofauna

The effect of worms and their dwellings on silicate transport is best examined by considering the pore water data from the lower sediment column. In this portion of the sediments, the effects of surface microflora were reduced (Fig. 2 and calculations in Results); therefore, worm activities most likely were the dominant forces affecting biologically-driven silicate exchange. Silicate flux in this realm is truly a transfer of material from sediments to the water column, and not a local removal of material from sediment pore waters by microflora.

i. Species differences. If species differences were important, one would expect differences in TBFL between *Eupolymnia* and *Abarenicola* in 1990. *Eupolymnia* and *Abarenicola* have different feeding behaviors and dwelling types, yet co-occur in many habitats in the San Juan archipelago. TBFL in sediments with arenicolids was an order of magnitude higher than in sediments with terebellids in 1990 (Fig. 6). This may have been due to higher irrigation rates (not measured in this experiment) or greater sediment disturbances by arenicolids. Rates of new dwelling construction were positively correlated with TBFL (Table 4, Fig. 7). Arenicolids built more dwellings (Table 3, Fig. 7), fed more frequently (personal observation), and translocated sediments over greater distances than did terebellids in 1990. Thus, in the spring of 1990, the head-down deposit feeder *Abarenicola pacifica* had a greater effect on pore water silicate exchange than did the surface deposit feeder *Eupolymnia heterobranchia.*

If variation in biologically-driven silicate transport was related to lifestyles of organisms, one would expect the range in CSB to parallel the variance in organism behaviors. In 1990, the range in CSB deep in sediments was higher in *Eupolymnia* chambers (1989 and 1990) than in *Abarenicola* chambers (Fig. 5). This pattern clearly was not caused by interspecific differences in the rate of new dwelling construction (Table 3). A likely explanation is the *mechanism* of tube construction, and the relative mobilities of these species. When *Eupolymnia* constructs a new tube, it creates a water jet via the irrigation current and hydraulically tunnels through the sediment column. New tube arms extend laterally, and usually are 5–18 cm from extant tubes. During tube construction, large amounts of surface water are channeled through relatively long distances deep in the sediment, and the location of the worm varies considerably relative to the fixed pore water sampling location. By comparison, *Abarenicola* burrows gently through the sediment column, without the use of hydraulic excavation. New burrow shafts are often only a few centimeters away

from previous locations (Krager and Woodin, 1992). For this species, the disturbance to pore waters associated with dwelling construction is likely to be much less, and the location of the silicate export source relative to the sampling area is comparatively more stable. The lack of a relationship between the number of dwellings and range in CSB is not surprising, because construction of only one burrow is sufficient to cause substantial variation in sediment silicate concentrations. Thus, the mechanisms by which worms relocate, and the extent of the relocation, may contribute to the observed variation in CSB deep in the sediment column.

ii. Activity differences. If activity rates of worms exerted significant effects on TBFL, one would expect TBFL to vary with indices of worm activity. In 1989, *Eupolymnia* individuals fed, defecated and constructed new tubes more frequently than in 1990 (Table 3), perhaps because: 1) Individuals in 1990 were reproductive, and may have allocated energy to gamete production and spawning at the expense of non-reproductive activities (Olive and Clark, 1978); 2) Water temperatures were 2 degrees C lower in 1990, perhaps resulting in lower metabolic activity (Mangum 1978); 3) In contrast to August 1989, in June of 1990, exposure of animals in the field at low tides was longer (> 6 hours), occurred near midday and could have been quite stressful. Organisms collected at this time may have responded by lowering their metabolic rates (Mangum 1978). TBFL was higher in the *Eupolymnia* 1989 than in all remaining treatments (Fig. 6). Moreover, TBFL in *Eupolymnia* tube 1989 and *Eupolymnia* 1990 chambers were similar to one another in magnitude (Fig. 6). Thus, active worms caused higher silicate exchange than inactive worms (1989 worms $\gg$ 1990 worms), and the presence of terebellids did not guarantee that nonlocal exchange occurred (1989 tubes = 1990 *Eupolymnia*). Episodes of silicate accumulation in the lower sediment column in *Eupolymnia* 1990 and *Eupolymnia* tube 1989 chambers (Fig. 3b vs. 3c) are probably due to the lack of an active irrigator within the tube. Without ventilation by worms, nonlocal exchange at depth would not have occurred. As a result, silicate accumulated in regions where inactive worms or tubes were present.

b. The relative importance of worms and diatoms

As with worms, benthic diatoms seemed more active in 1989 than in 1990. This is supported by higher TBF in 1989 light controls (0.0621 μmoles/cm^2*day) than in 1990 controls (light controls = 0.0172 μmoles/cm^2*day; dark controls = 0.0177 μmoles/cm^2*day, respectively). The apparently higher diatom activity in 1989 may have been caused by higher temperatures (Admiraal 1977) or annual variation in activity or species composition. Model results imply that the influence of worms and diatoms on CSB in the upper sediment column fluctuated more in chambers with *Eupolymnia* and *Eupolymnia* tubes than in chambers with *Abarenicola* (Fig. 3). This probably was due to 1) more frequent relocation by *Eupolymnia,* 2) more intense

removal of diatoms by the surface deposit-feeding terebellids (which also were more active in 1989 than in 1990), 3) more frequent changes in the composition of surface microflora (e.g. development of bacterial mats) in *Eupolymnia* 1989 and *Eupolymnia* tube 1989 chambers, and 4) changes in the activity of diatoms (see water column incubation results below). Arenicolids affected the composition of the sediment surface primarily through fecal deposition and, to a small extent, subduction of sediment via feeding funnels. However, these activities probably displaced diatoms temporarily. These algae are motile and are capable of migrating several centimeters back to the sediment surface to resume their activity (Harper, 1977; McIntyre and Moore, 1977).

In *Eupolymnia* 1990 chambers, worms built fewer burrows, and model results indicate worms and diatoms had negligible effects on silicate flux throughout the sediment column (Table 3, Figs. 3c, 4 & 6). In *Eupolymnia* tube 1989 chambers, diatoms apparently were very active (Fig. 3b and TBF results for light controls), and worms were absent. As a result, most of the biologically-driven silicate flux occurred in the upper sediment column (Figs. 3b, 4 & 6). Thus, when worm activity was unimportant, any biologically-driven silicate removal from sediment pore waters occurred primarily near the sediment surface, and probably was due to incorporation by diatoms. By contrast, when worms were active (*Eupolymnia* 1989, *Abarenicola* 1990), silicate flux was dominated by nonlocal exchange processes occurring over most of the sediment column (Figs. 3a, 3d, 4 & 6).

i. Comparison of water column incubation and pore water model results during incubation periods. The water column method of measuring flux examines average silicate transport over the entire sediment surface, and provides a good estimate of transport processes over a relatively large area. However, it does not resolve the relative importance of worm versus diatom activities. The sediment model predicts flux over a rather small portion of the sediment column. While it does not provide the best average estimate of silicate transport processes in sedimentary systems, it gives valuable information regarding spatial and temporal variability in biogenic silicate transport, and highlights the importance of nonlocal exchange. Despite these relatively disparate approaches, the methods are complementary and can be used in tandem to confirm the importance of worm activity and worm-diatom interactions, and also evaluate the validity of the diffusion-nonlocal exchange-reaction model. A comparison of 1) model estimates of TDBF, (Fig. 8) and 2) incubation measurements of NFWC (Fig. 1), illustrates this point.

In cases where worm activity is important and diatom populations are relatively inactive, one would expect results from these two methods to be consistent. These conditions existed in *Abarenicola* 1990 chambers (all incubation dates, Fig. 3d) and *Eupolymnia* 1989 chambers (first incubation date only; Fig. 3a, day 18). In *Abarenicola* 1990 chambers, TDBF values were similar in magnitude and direction to NFWC

values on all three incubation dates (Figs. 1 & 8). In *Eupolymnia* 1989 chambers on the first incubation date, TDBF and NFWC estimates are comparatively farther apart, but still within 25% of one another. Thus, the sediment model effectively predicts biologically-driven silicate flux when worms dominate biological effects.

When silicate incorporation by diatoms is high, or when the effect of diatoms and worms on sediment silicate concentrations are of similar importance, one would expect that results from the sediment model and water column measurements would diverge. Diatoms may incorporate all available silicate from the water column, including that which is exported by nonlocal exchange. In *Eupolymnia* 1990 (all incubation dates) and *Eupolymnia* 1989 (second incubation date, day 21) chambers, benthic diatoms removed silicate from sediment pore waters on scales similar to worms (Figs. 1, 3a & 3c). Correspondingly, NFWC and TDBF values are consistent only on the second incubation date for the *Eupolymnia* 1990 chambers (Figs. 1 & 8). In *Eupolymnia* tube 1989 chambers, diatoms were extremely active, and worms were absent (Fig. 3b). As a result, the discrepancy between NFWC and TDBF values is greater than in all other cases (Figs. 1 & 8). These patterns suggest that, by themselves, the sediment model and water column technique can serve as poor predictors of effects of worms on pore water-overlying water silicate exchange. Only in combination can the two techniques appropriately evaluate the dynamics of sediment-seawater exchange in bioturbated systems when the biotic influences on a dissolved constituent vary both in nature and over time.

6. Summary and conclusions

This study examined effects of macrofaunal and microfloral organisms on silicate distributions and fluxes in sediment pore waters. Measurements of vertical depth profiles of pore water silicate and net fluxes of silicate to the water column, and a diffusion-nonlocal exchange-reaction model were combined to determine 1) how macrofaunal species and activity affect nonlocal silicate exchange, 2) how microfloral activity affects silicate distributions in sediments and the water column, and 3) how interactions between macrofauna and microflora affect silicate flux across the sediment-water interface. Results show that a surface deposit feeding terebellid polychaete and a head-down deposit feeding arenicolid polychaete had significantly different effects on biologically-driven silicate fluxes to the water column. Fluxes were positively associated with the frequency of new dwelling construction, arguing that mobile species may have greater effects on pore water flux than sedentary species. In addition, changes in silicate concentrations due to nonlocal exchange by macrofauna varied by as much as an order of magnitude over relatively short times (days to weeks) at a given point in the sediment column. This variation was highest for sediments containing the terebellid. It is most likely related to the higher sediment disturbance associated with tube construction in this species, and the relatively greater distances involved in habitat relocation in terebellids. Thus,

characteristics of organisms can substantially influence the magnitude of and variability associated with biologically-driven fluxes across the sediment-water interface.

The data suggest that interactions between macroinfauna and surface microflora may significantly alter the net nutrient transport from sediments to the water column. Previous studies have shown that diurnal fluctuations in microfloral activity can significantly affect nutrient flux across the sediment-water interface (Henriksen *et al.,* 1983; Hylleberg and Henriksen, 1980), and that grazing on microflora by macrofauna affects microalgal production (Hargrave, 1970). This study suggests that links among these components may be more complex than previously suggested. While surface deposit feeding serves to reduce standing stocks of microflora, irrigation may contribute to the supply of essential nutrients for recovery of microfloral populations. As microfloral populations recover, the food supply for deposit feeders is renewed. Thus, an important feedback loop may exist between worms and benthic microflora through the conduct of feeding and ventilation. Correspondingly, interactions between worms and surface microflora may alternately enhance or diminish the transport of dissolved nutrients from sediment pore waters to overlying waters. At first glance, such interactions may seem most important in shallow water systems, where constituents such as silicate, ammonium, and phosphorus are important to the growth and persistence of autotrophic organisms (Doering, 1989), and are transported to the water column by irrigation (Waslenchuk *et al.,* 1983; Rutgers van der Loeff *et al.,* 1984; Doering *et al.,* 1987; Davey *et al.,* 1990). Yet, in deeper environments where sediments are reduced (e.g. sediments surrounding hydrothermal vents; Grassle *et al.,* 1985), or organic-rich, similar interactions between macrofauna and bacteria also may affect solute fluxes.

Finally, the results emphasize the relative shortcomings of flux determinations by 1) calculation from pore water profiles or 2) direct measurement in overlying waters. Pore water profiles from cores give a "snapshot view" of solute distributions and do not capture the temporal variance in solute flux associated with organism activity. Moreover, steep gradients near the sediment surface may not indicate high diffusive or biologically-driven fluxes, but rather, an *in situ* sink for some soluble nutrients. Thus, fluxes calculated from pore water profiles may be erroneous, and the mechanism which drives the flux may be misidentified. Direct measures of flux in the overlying water reflect the net effect of all processes influencing a given constituent. Moreover, direct measures typically occur over longer time intervals (e.g. days) and provide more reliable estimates of average flux rates. However, they do not identify which mechanisms facilitate or inhibit flux, nor do they examine seasonal or annual variation in pore water-overlying water exchange, which these results suggest may be considerable. This study showed that, in shallow water environments, flux determinations by calculation or direct measurement may give misleading estimates of solute transfer across the sediment-water interface when tracers 1) are biologically active, and 2) are sensitive to influences of a suite of organisms and processes. These tenets

suggest that, to more accurately determine nutrient transfer between the benthic and pelagic domains, it is important to understand 1) what biological processes affect the measured constituent, 2) the abundance and distributions of organisms (Rabouille and Gaillard, 1990), and interactions among organisms which may affect the tracer, and 3) the attributes of organisms which significantly alter pore water composition and biologically-driven solute exchange.

Acknowledgments. I thank S. A. Woodin, J. E. Eckman, R. A. Jahnke and C. D. Krager for their contributions toward the development and execution of the experiments and interpretation of the results. This paper benefitted from critical comments by B. C. Coull, D. Lincoln, W. Moore, very thorough reviews by B. P. Boudreau, J. E. Eckman, R. A. Jahnke and S. A. Woodin, and the excellent suggestions of two anonymous reviewers. I thank the director of Friday Harbor Laboratories, A. O. D. Willows, for providing laboratory space, a stimulating work environment and access to field sites. I also thank the director of Skidaway Institute of Oceanography, D. W. Menzel, for providing office space, access to facilities and use of the graphics talents of Suzanne McIntosh and Anna Boyette. As always, my deepest gratitude to J. E. Eckman, for multifaceted support, and to N. A. C. Eckman, for "hanging in there." This research was supported by grants to R. Marinelli from Sigma Xi, Sigma Delta Epsilon, American Museum of Natural History (Lerner Grey Fund), and the International Women's Fishing Association; and by National Science Foundation grants OCE-8414673 and OCE-8900212 to S. A. Woodin.

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Received: *2 January, 1992;* revised: *13 August, 1992.*