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Feeding ecology of *Leitoscoloplos fragilis*

II. Effects of worm density on benthic diatom production

T. S. Bianchi* and D. L. Rice

Chesapeake Biological Laboratory, University of Maryland, Solomons, Maryland 20688-0038, USA

Abstract

The present study examines the effects of density of *Leitoscoloplos fragilis* and of fine sediment on benthic microalgal abundance and production in laboratory microcosms, and the effects of fine sediment on diffusive transport of ammonia. Microcosms having different densities of *Leitoscoloplos fragilis* (Verrill, 1873) were determined in sediment collected from one of two field stations (each containing a different amount of fine particles <125 μm) from Cape Henlopen, Delaware, USA, in August 1986. The worms were acclimated in a recirculating seawater system for two months prior to experiments. Chlorophyll *a* concentrations were highest in sediments with less fine particles (<125 μm). Benthic diatom production, total microbenthic metabolic activity, and concentrations of pore-water ammonia were higher in sediment microcosms containing high densities of worms. *L. fragilis* grew more in microcosms containing less fine particles and higher worm densities. The upward flux of ammonia across the sediment-water interface was higher in sediments with less fine particles. A greater abundance of fine particles in these sediments impedes the upward flux of ammonia to surface and nearsurface diatoms. The coupling between population density and diatom production, which can be altered by fine-particle abundance could control the distribution and stability of populations of *L. fragilis*.

Introduction

In shallow marine environments, benthic microalgae are important food resources for deposit feeders and may limit their secondary production (Fenchel and Kofoed 1976, Wetzel 1977, Jensen and Siegismund 1980, Levinton and Bianchi 1981, Bianchi and Levinton 1984, Lopez and Levinton 1987). Patchiness and abundance of benthic microalgae on intertidal flats are affected by physical factors such as salinity (Admiraal 1977), temperature, light (Admiraal and Peletier 1980), nutrients (Admiraal and Peletier 1980, Hopner and Wonneberger 1985), sediment topography (Colijn and Dijekma 1981, Rasmussen et al. 1983), grain size (De Jonge 1985), and current speed (Grant et al. 1986). The feeding activity of macroinfaunal deposit feeders may significantly affect the abundance, distribution, and activity of microbes (Hargrave 1970, Hylleberg 1975, Lopez et al. 1977, Pace et al. 1979, Morrison and White 1980, Yingst and Rhoads 1980). Although the bioturbation, ingestion, egestion, and maceration associated with deposit-feeding activity all affect the microbial community, their relative importance, even in specific situations, is not known (Lopez and Levinton 1987).

In the intertidal sediments of Cape Henlopen, Delaware, USA, the subsurface deposit-feeder *Leitoscoloplos fragilis* (Orbiniidae: Polychaeta) appears to depend upon benthic diatoms for food (Bianchi 1988). The patchy distribution of *L. fragilis* in these sediments is associated with localized variations in benthic diatom production. Differences in light level and grazing pressure by other infauna cannot account for patchy diatom production. Diatom abundance is probably controlled by grazing associated with different densities of *L. fragilis* and by differences in the availability of ammonia, the principal inorganic nitrogen source (Bianchi 1988). A higher abundance of fine sediment particles (<125 μm), associated with lower population density of *L. fragilis*, may impede the upward transport of ammonia to benthic microalgae at the surface.

Materials and methods

Experimental worms and sediments

In August 1986, *Leitoscoloplos fragilis* (Verrill, 1873) were collected from the intertidal sediments of Cape Henlopen, Delaware, USA (75°06′ W; 38°47′ N) using a 500 μm sieve. Worms were acclimated in recirculating seawater maintained at 26 ± 2‰ (SD) and $17\,°C \pm 2\,C°$ (SD) in natural sediments for two months prior to experiments.

* Present address: Institute of Ecosystem Studies, New York Botanical Garden, Box AB, Millbrook, New York 12545, USA

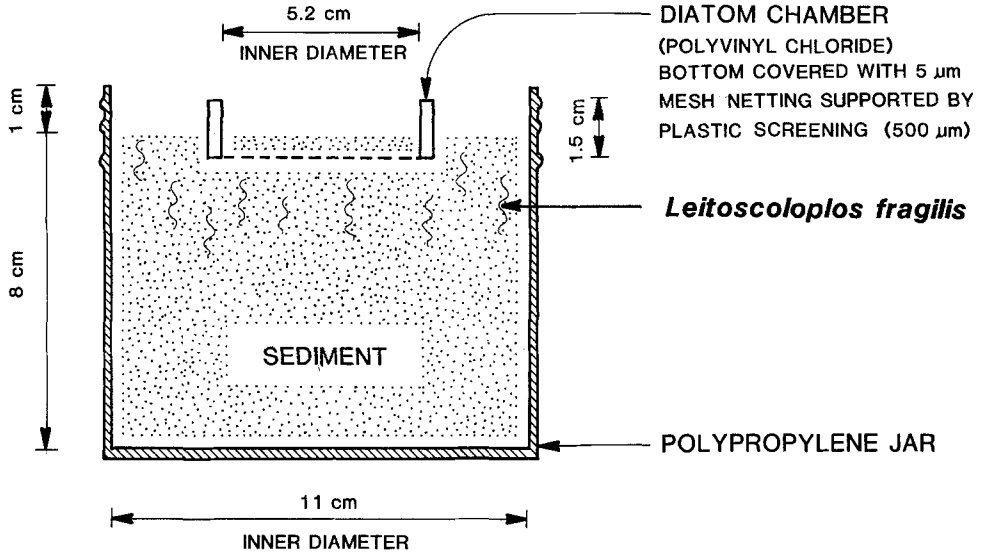

Fig. 1. Schematic drawing of longitudinal cross-section of microaquarium, with diatom chamber inserted into top 5 mm of sediment

Sediment was collected from the two field stations described in Bianchi (1988), wet-sieved (<1 mm), and kept frozen (at –2 °C for 3 wk) until used. Sediment from both stations had a molar organic C:N ratio of 3 to 6 and a total particulate organic matter content of 0.4 to 0.8% (Bianchi 1988). The median grain size of both sediment types was 2.0 to 2.5 ø ; however, the fine particle content (<125 µm) at one station (Station HI associated with higher abundance of *Leitoscoloplos fragilis*) was about 0.05%, and the other was 1% (Station LO associated with lower worm abundance) (Bianchi 1988).

Experiment I

A two-factorial experiment was designed to determine the effects of worm density and abundance of fine particles <125 µm on benthic diatom production and worm growth. Cylindrical polypropylene microaquaria (9 cm high, 11 cm inner diam) were filled with 8 cm of processed sediment (wet-sieved, <500 µm, and dried at 80 °C for 48 h) from one of the two stations and then inoculated with about 2 g of sediment containing the field diatom assemblage which was collected in August 1986. Two weeks later, 0, 4, 11, or 34 worms (1.88 ± 0.22 SD mg^{-1} dry wt individual^{-1}, $N=20$), equivalent to control, 400, 1200, and 3600 worms m^{-2}, representative of the range of densities observed at Cape Henlopen, were added to each of three replicate microaquaria. There were 24 microaquaria, 12 for each of the two sediment types (i.e., from Stations HI or LO). Each was capped with plastic screening (500 µm mesh) to prevent worm escape and positioned randomly in aerated recirculating seawater maintained at 26 ± 2‰ SD and $17\,°C \pm 2\,C°$. The cultures were illuminated with fluorescent lights (sediment surface irradiance of ca. 60 to 70 µE m^{-2} s^{-1}) on a 12 h light:12 h dark cycle.

The experiment was run for 60 d. Afterwards, three syringe mini-cores (6.0 cm deep, 1.5 cm inner diam) were taken from each microaquarium and sectioned at 1 cm depth – intervals for determination of chlorophyll *a*, phaeopigments, and relative microbenthic metabolic activity (MMA). Relative MMA was determined using the tetrazolium salt 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyl-2H-tetrazolium chloride (INT), following a modification of the procedure used by Pamatmat and Skjoldal (1974). Because INT outcompetes oxygen as a terminal electron acceptor (Nachlas et al. 1960), it can be used to determine total metabolic activity in sediments. Worms were recovered and counted, kept for 24 h in seawater, rinsed in fresh water, lyophilized, and weighed.

Pigments were determined by reversed-phase high-performance liquid chromatograpy (HPLC) (Mantoura and Llewellyn 1983, Dawson et al. 1985). Sediment aliquots were extracted by sonication for 5 min at 5 °C with 90% acetone/water and centrifuged for 3 min. The extracts were kept frozen (at –5°C) until analysis.

Experiment II

This experiment examined the effects of density of *Leitoscoloplos fragilis* on benthic diatom production in the absence of grazing. Twelve chambers (1.5 cm high, 5.2 cm inner diam) were filled with the same sediment, inoculated in September 1986 with a mixed culture of surface diatoms from the field, and placed in the recirculating seawater system (Fig. 1). The bottom of each chamber was covered with 5 µm mesh nylon netting supported by plastic screening (500 µm mesh).

Two weeks later (determined from previous work to be a sufficient acclimation period for worms in the microaquaria), a chamber was implanted into each microaquarium so that the sediment surfaces in the chamber and the microaquarium were approximately coplanar (Fig. 1). The 5 µm mesh-lining at the bottom of each chamber was selected to prevent grazing of diatoms by *Leitoscoloplos fragilis* and yet allow vertical solute (specifically nutrient) movement. The experiment was run for 14 d. Two sediment cores (5 mm

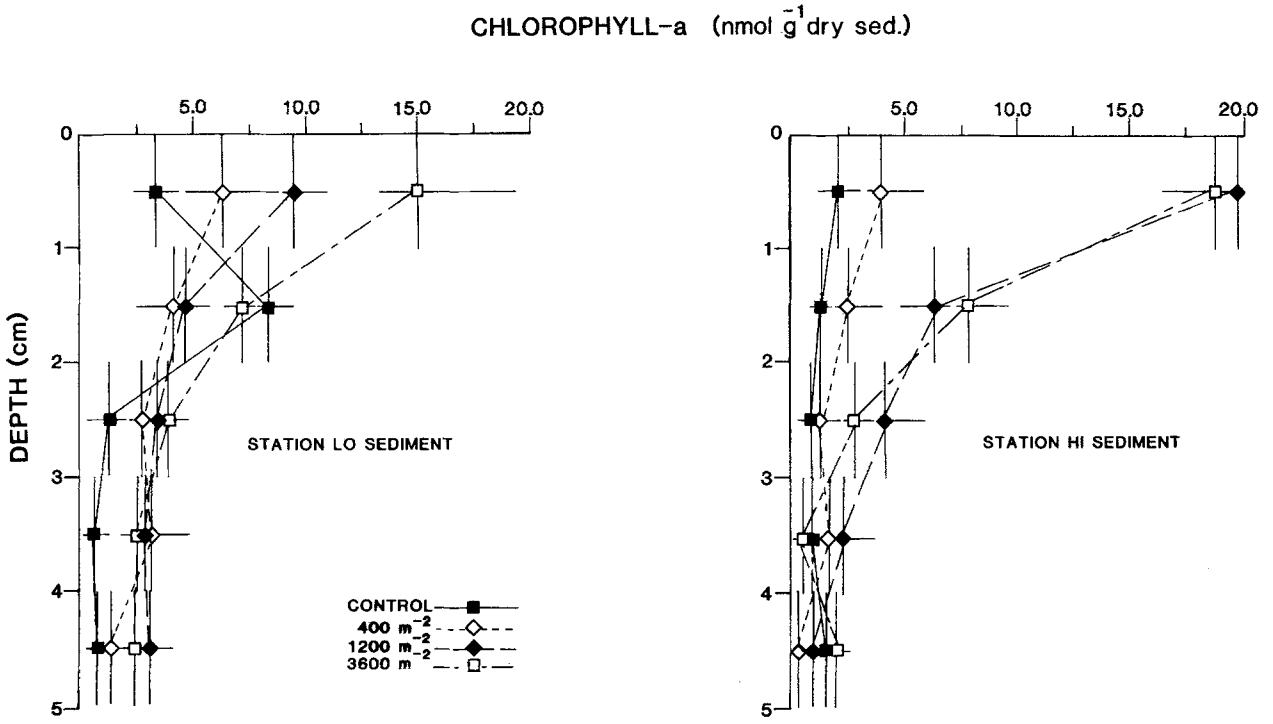

Fig. 2. Experiment I. Vertical distribution of chlorophyll *a* in microaquaria containing sediments from Stations HI and LO with different densities of *Leitoscoloplos fragilis*. Horizontal error bars denote 95% confidence limits

diam) were taken every two days from each chamber to enumerate benthic diatoms, using epifluorescence microscopy (Hobbie et al. 1977) modified for sandy sediments (Bianchi 1988). At the end of the experiment, pore water was extracted from the same depth (2 cm) in each microaquarium by acid-cleaned syringes, and ammonia concentration was determined using the phenol-hypochlorite method (Solórzano 1969). Although worm growth was not measured in this experiment, worms were counted at the end of the experiment to ascertain emigration and mortality.

Experiment III

This experiment was designed to test whether the abundance of fine particles <125 μm in the sediment could affect the transport of ammonia to diatoms. Three sediment cores (ca. 13 cm deep, 6 cm inner diam) were taken from each of the two field stations in August 1986, returned to the laboratory, and frozen for 3 d to kill the macrofauna. The cores were kept at room temperature until completely thawed, and flushed with boiling distilled water to insure that microbes were eliminated. A small hole was drilled in the side of each corer 2 cm below the sediment surface, the depth where a subsurface peak of fine particles <125 μm occurs at this time of year (Bianchi 1988). After sealing the bottom of each corer with a rubber stopper, a 200 m*M* NH_4Cl solution was added to each core through the side hole using a syringe, filling the core to 2 cm below the sediment surface. Then 200 ml of supernatant distilled water was added to each box corer without disturbing the pore-water solution. The water temperature in each box corer was 25 °C throughout the experiment. The overlying water in each box corer was stirred manually every 10 min and 2 ml samples were taken every half-hour for 5 h for determination of ammonia. After the experiment, each core was extruded and sectioned at 1 cm intervals for particle-size analysis.

Statistical analyses

An F_{max} test was used prior to ANOVA analyses to check for homogeneity of variances. When treatment differences were significant ($p<0.05$) by ANOVA, an *a posteriori* least-significance difference (LSD) test was performed on treatment means. Statistical analyses on percent growth were performed on arcsine-transformed data.

Results

Experiment I

Chlorophyll *a* was significantly higher (Two-way ANOVA, $p<0.001$) with increasing density of *Leitoscoloplos fragilis* in both sediment types (Fig. 2). Worm density and sediment type significantly (two-way ANOVA, $p<0.001$) affected chlorophyll *a* content, revealing the highest concentrations of chlorophyll *a* (ca. 18 to 20 nmol g^{-1} dry sediment: Fig. 2) at a depth of 0 to 1 cm in sediment with less fine particles (<125 μm). Total phaeopigments were also affected by den-

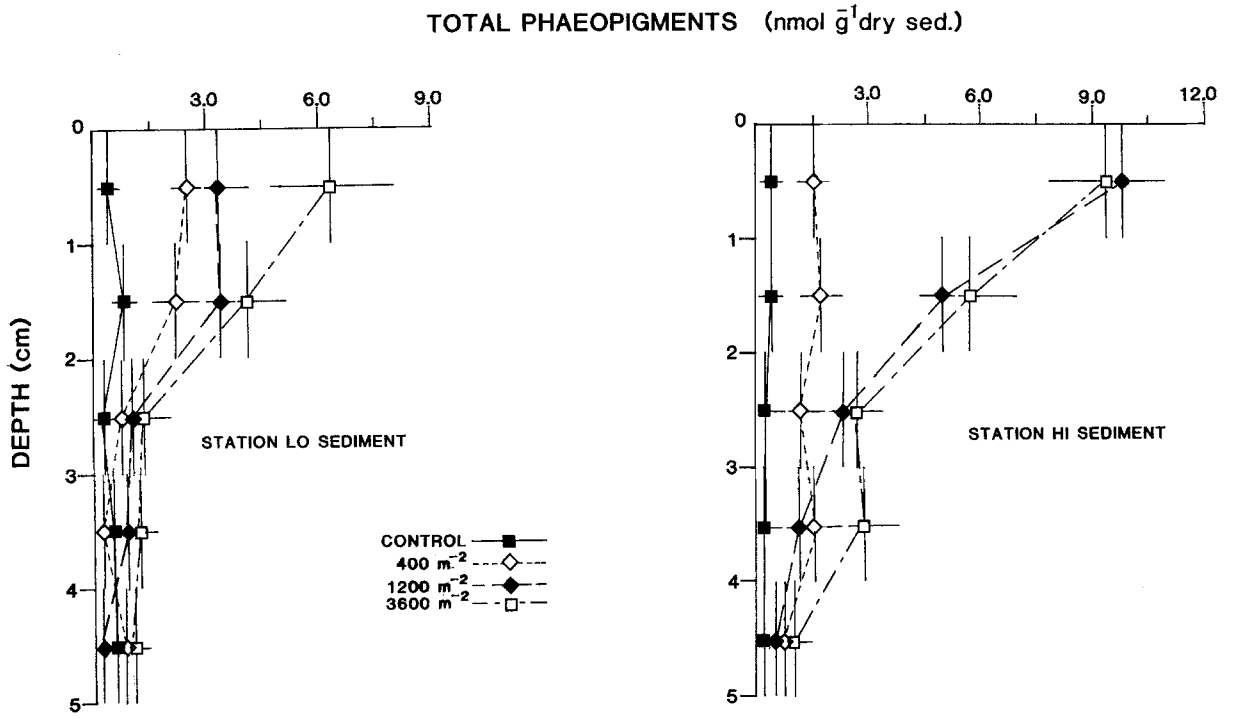

Fig. 3 Experiment I. Vertical distribution of total phaeopigments in microaquaria containing sediments from Station HI and LO with different densities of *Leitoscoloplos fragilis*. Horizontal error bars denote 95% confidence limits

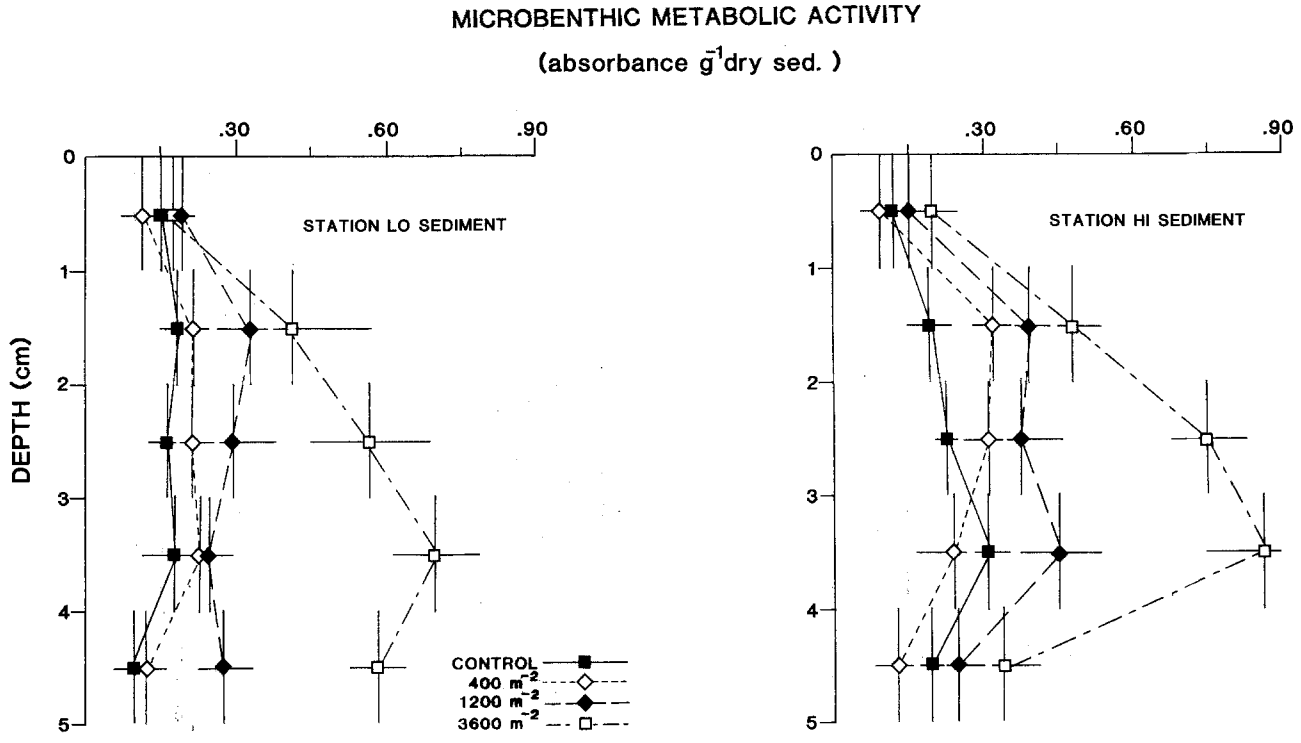

Fig. 4. Experiment I. Vertical distribution of microbenthic metabolic activity in microaquaria containing sediments from Stations HI and LO with different densities of *Leitoscoloplos fragilis*. Horizontal error bars denote 95% confidence limits

sity and sediment type, with significantly (two-way ANOVA, $p<0.001$) more phaeopigments (ca. 4 to 9 nmol g^{-1} dry sediment: Fig. 3) being produced at a depth of 0 to 2 cm in sediment with less fine particles. Because over 90% of the total phaeopigments were comprised of phaeophorbides, molar concentrations of total phaeopigments were based on phaeophorbide equivalents.

Relative MMA was significantly higher (two-way ANOVA, $p<0.001$) with increasing worm density (Fig. 4). The effects of density and sediment type on MMA were

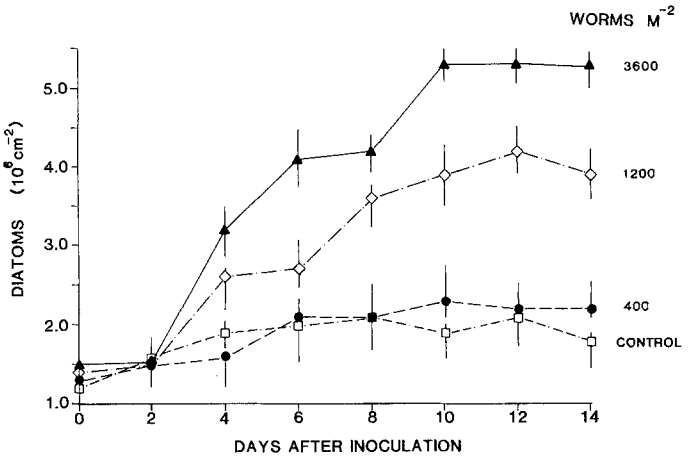

Fig. 5. Experiment II. Diatom standing stocks in Station HI sediment over time and at different densities of *Leitoscoloplos fragilis*. Error bars denote 95% confidence limits

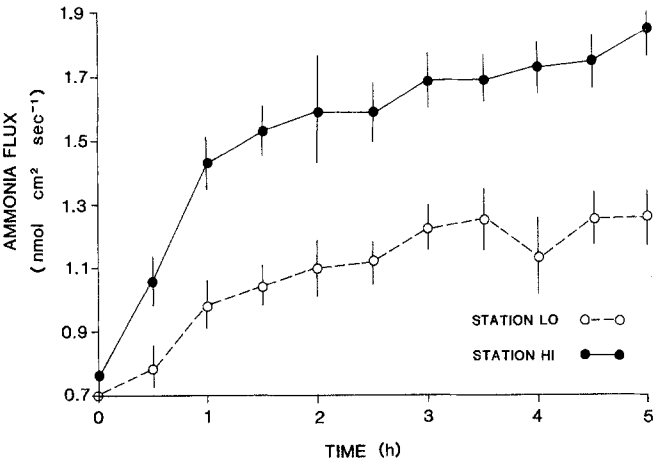

Fig. 7. Experiment III. Ammonia flux in sediments from Stations HI and LO over time. Error bars denote ± standard deviation

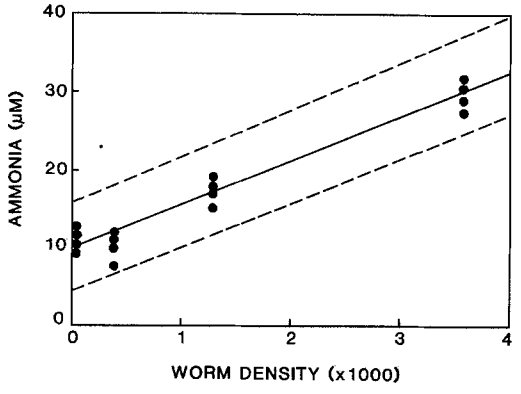

Fig. 6. Experiment II. Relationship between pore-water ammonia concentration and density of *Leitoscoloplos fragilis;* regression is significant ($r=0.93$). Dashed lines denote ± 1 standard deviation

Table 1. Experiment I. Percent growth and average individual weight gain over experimental period in treatments with varying worm densities and sediment type. Sediment was collected from Cape Henlopen, Delaware, USA, at two stations containing different percentages of fine particles < 125 μm: Station HI, 0.5 to 0.2%; Station LO, 0.2 to 0.4%. Values are means ± 1 SD

Worm abundance (worms m^{-2})	Sediment type	% worm growth	Av wt gain (mg)
400	HI	29±1	0.76±0.10
1200	HI	40±3	1.25±0.19
3600	HI	41±5	1.40±0.30
400	LO	13±6	0.30±0.14
1200	LO	27±1	0.64±0.12
3600	LO	32±2	0.86±0.11

significant (two-way ANOVA, $p<0.001$), showing the highest MMA (ca. 0.80 to 0.90) in sediments with less fine particles (< 125 μm: Fig. 4).

Worm growth was significantly different (two-way ANOVA, $p<0.05$) among the different density treatments (Table 1). Over the experimental period, percent worm growth in the high-worm density (3600 m^{-2}) was significantly greater (LSD test, $p<0.05$) than in the low-density (400 m^{-2}) treatment for Station HI and LO sediments. Percent growth was significantly greater (two-way ANOVA, $p<0.05$) in sediment with less fine particles at the higher densities (41 ± 5 SD) than in sediments with more fine particles (32 ± 2 SD) (Table 1). No mortality of *Leitoscoloplos fragilis* was observed in any of the treatments.

Experiment II

Diatom standing stock increased significantly (two-way ANOVA, $p<0.001$) at higher densities of *Leitoscoloplos fragilis* (Fig. 5). There were no significant differences between control worms and those at a density of 400 m^{-2} (LSD test, $p<0.05$). The most rapid increase in diatom standing stock, in the higher worm densities occurred between Days 2 and 4 (increasing by ca. 1 to 3×10^6 diatoms cm^{-2}). Using the data in Fig. 5 for time = 2 to 4 d, gave estimated initial specific growth rates of 0.05, 0.12, 0.50, and 0.95 divisions d^{-1} for control, 400, 1200, and 3600 worms m^{-2}, respectively. After 10 d, the increase in diatom standing stock appeared to level off at maximum values that were significantly higher (LSD test, $p<0.05$) at a density of 3600 worms m^{-2}. Pore-water ammonia concentration increased linearly ($r=0.94$) with increasing density of *L. fragilis* (Fig. 6). Total mortality of *L. fragilis* from all treatments was 3%.

Experiment III

Ammonia flux was significantly higher (two-way ANOVA, $p<0.001$) in the sediment with less fine particles (< 125 μm) over time (Fig. 7). Flux was highest within the first hour for both sediment types, ranging between 0.8 and 1.4 nmol cm^{-2} s^{-1} for the sediment with less fine particles (< 125 μm) and 0.7–0.9 nmol cm^{-2} s^{-1} for sediment with a greater abundance of fine particles; it then leveled off after

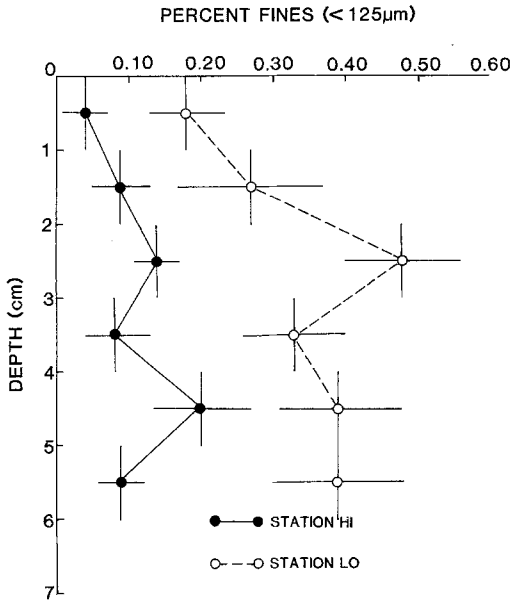

Fig. 8. Vertical distribution of particles < 125 μm in the ammonia flux cores containing sediments from Stations HI and LO. Horizontal error bars denote 95% confidence limits

2 h. The mean ($N = 3$) percentage of fine particles < 125 μm in cores from the lower density of *Leitoscoloplos fragilis* (0.2 to 0.4%) was significantly higher (Student's t-test, $p < 0.05$) than in sediment from the higher worm density (0.05 to 0.2%: Fig. 8).

Discussion

Accumulation of total phaeopigments in microaquaria sediments increased at higher densities of *Leitoscoloplos fragilis*. Because total phaeopigments represent cumulative "past" production of photosynthetic pigments over time, diatom production clearly increased at higher worm density. Although phaeopigment degradation can occur under intense light conditions (Welschmeyer and Lorenzen 1985), any effects from the lighting employed in this study would be negligible. The highest concentrations of total phaeopigments were found in the top 2 cm of sediment. Approximately 90% of the total phaeopigments in the top 2 cm were comprised of phaeophorbides *a* and *c*. Phaeophorbides are chlorophyll-degradation products formed during herbivorous digestion (Shuman and Lorenzen 1975, Billett et al. 1983). Phaeophorbides *a* and *c* are particularly abundant after gut passage in suspension-feeders (Jeffrey 1974, Bricelj 1984, Hawkins et al. 1986).

The feeding activity of *Leitoscoloplos fragilis* may be responsible for the observed increase in MMA at depth. The MMA subsurface peaks occurred just below the visual redoxocline (3 cm). Conveyor-belt species commonly feed at the redoxocline and can affect microbial abundance and activity (Rhoads 1974, Hylleberg 1975, Yingst and Rhoads 1980, Dobbs and Whitlatch 1982). At Cape Henlopen, the principal feeding depth of *L. fragilis* changed in accordance with the seasonal movement of the redoxocline (Bianchi 1988).

These experiments demonstrate that higher densities of *Leitoscoloplos fragilis* stimulate diatom production by mechanisms other than macrofaunal cropping. Specific growth rates of diatoms in the chambers increased in the absence of worm-cropping. The relative importance of micro-meiobenthic grazing activities in these sediments is not known.

In microaquarium sediments, higher pore-water ammonia concentrations at the high densities of *Leitoscoloplos fragilis* may be responsible for the observed increases in diatom production. Significantly higher net ammonia production occurs in sediments from the station with a high density of *L. fragilis* than at the station with a low density (Bianchi 1988). Ammonia is used in preference to other forms of nitrogen (NO_3^-, NO_2^-, urea) by most phytoplankton species (MacIsaac and Dugdale 1972, McCarthy and Eppley 1972, McCarthy et al. 1977, Glibert et al. 1982). Benthic diatoms may also assimilate ammonia in preference to other inorganic forms of nitrogen (Henriksen et al. 1980). Ammonia is the most abundant inorganic nitrogen source in nearshore sediments (Balzer 1984, Yamada et al. 1987). Because ammonia is formed early in the remineralization of particulate nitrogen, it is generally regarded as an index for the amount of organic nitrogen decomposition in nearshore sediments. Ammonia is perhaps the best measure of the breakdown of organic nitrogen.

To estimate the highest diatom production that could be supported by observed ammonia production, we will assume that 100% of the ammonia was utilized by diatoms. Using an estimated diatom nitrogen content of 2.3×10^{-4} μg N diatom^{-1} and the ammonia production for each station (Bianchi 1988), the maximum diatom production rates for Stations HI and LO were 1.1×10^3 and 5.0×10^2 diatoms cm^{-2} d^{-1}, respectively. Based on a seasonally averaged diatom standing stock of 0.8×10^7 diatoms cm^{-2} for both stations (from a depth of 0 to 15 cm: Bianchi 1988), the estimated specific growth rates at Stations HI and LO were 1×10^{-4} and 5×10^{-5} divisions d^{-1}, respectively. These estimated growth rates could not maintain the standing stocks observed in the field. However, these growth-rate estimates were based on the entire standing stock of diatoms from 0 to 15 cm depth. It is not probable that the entire population of diatoms would have the same photosynthetic activity throughout a depth range of 0 to 15 cm (Admiraal and Peletier 1980). The lower depth distribution of diatoms in Cape Henlopen sediments appears to be related to the amount of physical disturbance on the sandflat (Bianchi 1988). Therefore, only a fraction of the total diatom population can be supported by ammonia; these diatoms are likely to be localized within the upper few centimeters of sediments.

The abundance of fine particles < 125 μm may affect the availability of ammonia to surface and nearsurface diatoms. Laboratory experiments showed that ammonia adsorption coefficients for sediments from both Stations HI and LO

(using methods described by Mackin and Aller 1984) were not significantly different and well below 1. Because the percent of fine particles (<125 μm) in these sediments was low (ca. 0.05 to 1.0%), particle surfaces probably remained saturated with ammonia. On the other hand, a greater abundance of fine particles can fill pore spaces between the large sand particles, increasing the tortuosity of the sediment. Slower diffusion of ammonia in sediments with more fine particles from the low worm-density station, was probably due in part to the effects of tortuosity. The ammonia diffusion rates in both sediments leveled off at approximately 1 h. Assuming that porosity, molecular diffusion of ammonia at 21 °C, and sediment depth were the same in the laboratory and field (same diffusion geometry for each), an *in-situ* flux can be estimated based on the field : laboratory ratio of concentration gradients for each station at 21 °C. When the pore-water temperature reached 21 °C in the field, the typical pore-water concentrations for Stations HI and LO were 20 and 15 μ*M*, respectively (Bianchi 1988). Using the particular concentration gradient for each station, the estimated *in-situ* ammonia flux at Station HI was 130±23 (SD) μmol m^{-2} d^{-1}, and at Station LO was 71±14 (SD) μmol m^{-2} d^{-1}.

The ammonia fluxes reported here are in the same range as those repored for other intertidal sandflats (Asmus 1986). However, they may be high, because our laboratory flux measurements were made with no diatoms in the sediments. Benthic diatoms may influence ammonia exchange at the sediment-water interface largely through assimilation of this nutrient (Henriksen et al. 1980). If we subtract the estimated *in-situ* ammonia fluxes from the production rates for each station, the hypothetical excess ammonia at Stations HI and LO would be 57±49 SD and 13±18 SD μmol m^{-2} d^{-1}, respectively. These values, which are not statistically different from zero (Student's *t*-test), suggest that production and effusion of ammonia in these sediments is close to steady-state and support the hypothesis that ammonia may limit benthic diatom production in these sediments.

Particulate nitrogen from benthic diatoms can account for all the changes in nitrogen growth of *Leitoscoloplos fragilis*. *L. fragilis* grew more in sediments with higher benthic diatom production. Because deposit feeders are commonly nitrogen-limited (Tenore 1981, Tenore and Chesney 1985), Tenore (1981) argued that growth calculations should be made on the basis of nitrogen. Assuming that 8% of worm dry biomass is nitrogen (Rice et al. 1986), worm growth rates in Station HI sediment (over 60 d) were 1.03±0.13 SD, 1.74±0.25 SD, and 1.96±0.40 SD × 10^{-3} mg N $worm^{-1}$ d^{-1} for the 400, 1200, and 3600 worms m^{-2}, respectively. However, it is uncertain if worm growth was steady throughout the duration of the experiment. A gross growth efficiency (GGE) of 63% based on available nitrogen was reported for experimental populations of *L. robustus* in muddy sediments (Rice et al. 1986). When fed highly assimilable food, *Capitella capitata* (Type 1) had trophic transfer efficiencies as high as 88% (Tenore and Chesney 1985). If we assume a high GGE of 90% for *L. fragilis* in these sandy sediments, because benthic diatoms are highly assimilable (Kofoed 1975, Lopez and Levinton 1978), the ingestion rates for worms in Station HI sediment would be 1.1, 1.9, and 2.1 × 10^{-3} mg N $worm^{-1}$ d^{-1} for the 400, 1200, and 3600 worms m^{-2}, respectively. Assuming the nitrogen content of the benthic diatoms in these sediments to be 2.3 × 10^{-7} mg N $cell^{-1}$ (Bianchi 1988), the number of diatoms that would have to be ingested by worms at these densities would be as shown in Table 2. The diatom standing-stock curves in Fig. 5 were differentiated numerically, and, using the logistic equation, an estimated diatom production was calculated for each of the different worm densities over 60 d (Experiment I). Using these estimates of diatom production and the number of worms in each microaquaria, an estimate of the diatoms consumed $worm^{-1}$ d^{-1} can be calculated. All these estimates are significantly higher (Student's *t*-test, $p<0.001$) than the required ingestion rates of diatoms $worm^{-1}$ d^{-1}, based on nitrogen growth. Therefore, benthic diatoms could account for all the daily nitrogen requirements of *L. fragilis* in these experimental microaquaria. Even though there was an excess of benthic diatoms at all the worm densities compared to the estimated ingestion rates of worms, greater percent worm growth occurred at the higher densities. When fed the same daily ration of food, experimental populations of *L. robustus* grown in muddy sediments show more growth at higher densities (Rice et al. 1986). These density-dependent growth differences in *L. robustus* were probably due to increases in the subduction and availability of food from the surface down to the feeding depth because of faster sediment turnover rates at the higher densities (Rice et al. 1986). Although there is no evidence of enhanced sediment turnover rates at the higher population densities of *L. fragilis* at Cape Henlopen (Bianchi 1988), density-dependent differences in the subduction of surface diatoms to the feeding depth may have existed in the experimental microaquaria.

The coupling between worm density and benthic diatom production controls the distribution and stability of populations of *Leitoscoloplos fragilis* at Cape Henlopen. Regenerated ammonia can diffuse to the surface faster in sediment with a high density of *L. fragilis* because there are less fine particles (<125 μm), resulting in a higher production of benthic diatoms. If *L. fragilis* irrigates its burrow, the vertical movement of ammonia may have also been affected by

Table 2. Estimates of diatom production and *Leitoscoloplos fragilis* ingestion rates in sediments collected from Station HI at Cape Henlopen, Delaware. Ingestion rates were based on nitrogen growth of worms over 60 d and an estimated nitrogen content for diatoms of 2.3 × 10^{-7} mg N $cell^{-1}$. Values are means ± 1 SD

Worm abundance (worms m^{-2})	Diatom production (10^5 diatoms cm^{-2} d^{-1})	Ingestion rate (10^4 diatoms $worm^{-1}$ d^{-1})	Diatom production/worm density (10^5 diatoms $worm^{-1}$ d^{-1})
Control (no worms)	0.09±0.04		
400	0.13±0.05	0.48±0.15	3.35±1.25
1 200	1.51±0.06	0.83±0.12	12.51±2.51
3 600	2.31±0.05	0.91±0.20	6.42±1.39

differences in irrigation at high and low worm densities (Aller 1980a, b). Density-dependent feedback-processes are adaptations for the food-resource demands of a growing population. In Cape Henlopen sediments, the coupling between worm density and benthic diatoms results in an increase in diatom production. However, density-dependent control of resource availability can occur without affecting resource production. For example, population-level control of sediment turnover and rate of food subduction is probably important in maintaining stable populations of the conveyor-belt deposit-feeding polychaete *Scoloplos* (*Leitoscoloplos*) *robustus* (Rice 1986). On the other hand, opportunistic species have evolved life histories that enable them to respond to resource limitation without density-dependent feedback processes (Chesney and Tenore 1985, Zajac 1986).

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