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Enhanced degradation of algal lipids by benthic macrofaunal activity: Effect of *Yoldia limatula*

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ABSTRACT

We used the protobranch bivalve, *Yoldia limatula,* in a series of incubation experiments to test whether activities of deposit-feeding macrofauna cause differences in lipid degradation processes relative to controls lacking macrofauna. Uniformly ^{13}C-labeled algae (^{13}C > 98%) were used as a source of fresh planktonic lipids, easily distinguished from bulk sedimentary lipids by GC/MS. Variations in concentration of major lipid components ([16:1(ω7), 16:0 and 18:1(ω9)] fatty acids and phytol) were followed as a function of time in incubations with and without *Yoldia*. Results showed that *Yoldia* can significantly enhance the degradation of planktonic lipids in sediments. Net degradation rate constants of lipids such as fatty acids and phytol in surface sediments were linearly correlated with abundance of *Yoldia* (in the range 230–1160 animals/m^2). *Yoldia* altered the sediment and decomposition regime in several ways: (1) lipid-containing particles were ingested and then ejected into the oxic overlying water, with selective ingestion and digestion of different components; (2) particles were moved into subsurface regions by bioturbation; (3) sediment resuspension occurred, porosity increased, and dissolved oxygen and suboxic conditions penetrated deeper in the presence of *Yoldia;* (4) *Yoldia* grazed bacteria, influencing net degradation pathways of algal material, as indicated by higher accumulation of a bacteria-specific branched fatty acid and an intermediate C_{16} alcohol in the absence of *Yoldia* than in presence of *Yoldia* when plankton material was introduced as a pulse); (5) the activities of *Yoldia* enhanced solute exchange and altered the spatial and temporal patterns of redox reactions, as indicated by time-dependent depth distributions of Br (introduced tracer), ΣCO_2 and NH_4^+ in the microcosms.

1. Introduction

Decomposition of organic matter at the sea floor is a key process in the carbon and nutrient cycles of marine ecosystems. Degradation of sedimentary organic matter occurs through either aerobic or anaerobic pathways, depending on *in-situ* redox conditions. Oxygen plays a critical and complicated role in the degradation and preservation of organic matter (Emerson and Hedges, 1988; Pedersen and Calvert, 1990; Lee, 1992; Canfield, 1994). One key difference between marine environments having oxic and anoxic overlying water is the presence or abundance of benthic organisms. Abundance and diversity of

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benthic animals are generally higher in oxic than in anoxic sediments (Wishner *et al.,* 1990; Levin *et al.,* 1991).

A variety of studies have shown that benthic animals influence the decomposition of organic matter (Aller, 1982a; Andersen and Kristensen, 1992; Mayer *et al.,* 1996). For example, benthic animals can alter oxic/anoxic boundaries, control material transport processes, directly or indirectly affect microbial populations, and consume organic detritus. Animal grazing can stimulate continuous rapid growth of microbial organisms and also directly decompose significant amounts of organic matter by intra- or extracellular enzymes (Lopez and Levinton, 1987; Mayer *et al.,* 1997). Bioturbation can cause vertical transport of particles and can lead to movement of particles across oxic/anoxic boundaries; the frequency and duration of this movement may significantly influence degradation rates and net preservation of organic material (Sun *et al.,* 1993a; Aller, 1994). Although we know much about the influence of oxygen on total organic matter, there have been relatively few studies on the effects of benthic animals on degradation of specific compounds in sediments.

Phytoplankton are a major source of the organic detritus which fuels the benthic community in coastal sediments. Lipids are a major organic carbon pool in phytoplankton, making up ∼5–20% of the total carbon (Parsons *et al.,* 1961). Lipids are widely used as biomarkers in geochemical studies on the source, transformation and fate of organic matter (Gagosian *et al.,* 1983; Volkman *et al.,* 1987; Wakeham and Lee, 1993). Lipids deposited in sediments degrade at different rates depending on the redox conditions encountered (Farrington *et al.,* 1977; McCaffrey, 1990; Sun and Wakeham, 1994; Canuel and Martens, 1996). Laboratory simulations have shown clear differences between oxic and anoxic degradation rates of lipids (Harvey *et al.,* 1986; Harvey and Macko, 1997; Sun *et al.,* 1997). However, the significance of benthic organisms and their mechanisms of lipid degradation are not well understood, particularly with regard to the role of oxygen.

Following the fate of plankton-derived lipids in the sediment can be difficult since there are many potential sources of lipids, and distinguishing between these sources can be a complex task. The addition of isotope-labeled tracers to sediment, either as labeled algal material or specific compounds, allows one to distinguish between freshly-deposited material and material already present in the sediment or from other sources. Radiotracers have been used to track degradation of various lipids such as phytol (Brooks and Maxwell, 1974), cholesterol (Gaskell and Eglinton, 1975; Edmunds *et al.,* 1980; Taylor *et al.,* 1981), oleic acid and palmitic acid (Rhead *et al.,* 1971, 1972; Gaskell *et al.,* 1976; Sun *et al.,* 1997), and chlorophyll (Sun *et al.,* 1993b). Radiotracers have provided valuable insights into mechanisms and rates, but their use has been hampered both by the unavailability and expense of properly labeled compounds and the difficulties in using radioactive compounds in sophisticated instruments needed for structural elucidation. Recent work by Blair *et al.* (1996) showed the application of artificially-enriched ^{13}C algae as a tracer of labile carbon in marine sediments. As suggested by their study, the use of ^{13}C-tracers provides an opportunity to track organic matter and follow its transformation on a

molecular level using gas chromatography/mass spectrometry (GC/MS) and gas chromatography/isotope ratio mass spectrometry (GC/IRMS).

This study was designed to examine the overall influence of a single macrofaunal species, *Yoldia limatula,* on degradation of algal lipids within experimental sedimentary microcosms. *Yoldia limatula* is a protobranch bivalve common in shallow marine estuarine and shelf muds (Ockelmann, 1954; Sanders, 1960; Rhoads, 1963). It is a mobile, subsurface deposit feeder (Rhoads and Young, 1970) but occasionally feeds at the sediment surface (Bender and Davis, 1984). *Yoldia* intensively rework the upper $\sim$3–4 cm of sediment, transporting particles, grazing bacteria and irrigating sediments. *Yoldia's* feeding activities result in sediment resuspension through direct explusion of feces and pseudofeces into the overlying water, thus enhancing the erodibility of the interface by increasing sediment water content. In laboratory sediment incubations containing various abundances of *Yoldia,* we added uniformly ^{13}C-labeled algae to track degradation rates of lipids. Three major fatty acids [16:1(ω7), 16:0 and 18:1(ω9)] and phytol in the labeled algae were distinguished from natural sedimentary lipids by conventional GC/MS. Degradation rate constants were estimated based on decreases in lipid concentrations as a function of depth and incubation time; rate constants were related to varying abundance of *Yoldia.* Degradation pathways were assessed by tracking formation and appearance of ^{13}C-labeled degradation products in incubated sediments and ejected particles. The influence of macrofauna abundance on other measures of remineralization was also examined by following variations in porewater O_2 content, ΣCO_2, and NH_4^+, and sedimentary Fe oxidation states during the incubations. Effects on solute transport rates were quantified using bromide as a tracer (Dicke, 1986; Martin and Banta, 1992).

2. Experimental

a. Materials. Sediment samples used in this study were collected from a station in central Long Island Sound (LIS). This station has been the site of extensive biological and chemical studies in the past (e.g., Yingst and Rhoads, 1978; Gerino *et al.,* 1998). In the present study, the top cm of sediment was scraped from the surface of grab samples. Organic carbon content of this surface sediment varies seasonally from 1.4 to 2.5% (Sun *et al.,* 1994). The top cm of sediment was used since it is always partially oxygenated and closely simulates sediment that *Yoldia* would normally encounter. Shortly after collection, the sediments were passed through a 1-mm sieve (no water added) and homogenized for incubation experiments. Specimens of *Yoldia limatula* were obtained from the Marine Biology Laboratory (Woods Hole, MA); animals uniformly 1–1.4 cm in size were used. These protobranch bivalves are common in LIS sediments where their natural abundance is about 300–600/m^2, but were purchased to ensure enough specimens of a similar size at the precise time of the experiments. A ^{13}C-labeled alga (*Chlorella,* ^{13}C $> 98\%$) was obtained from Cambridge Isotope Laboratories. The major lipid composition of this alga consists of uniformly ^{13}C-labeled fatty acids [16:1(ω7), 16:0 and 18:1(ω9)] and phytol, hence they were the target compounds in this study.
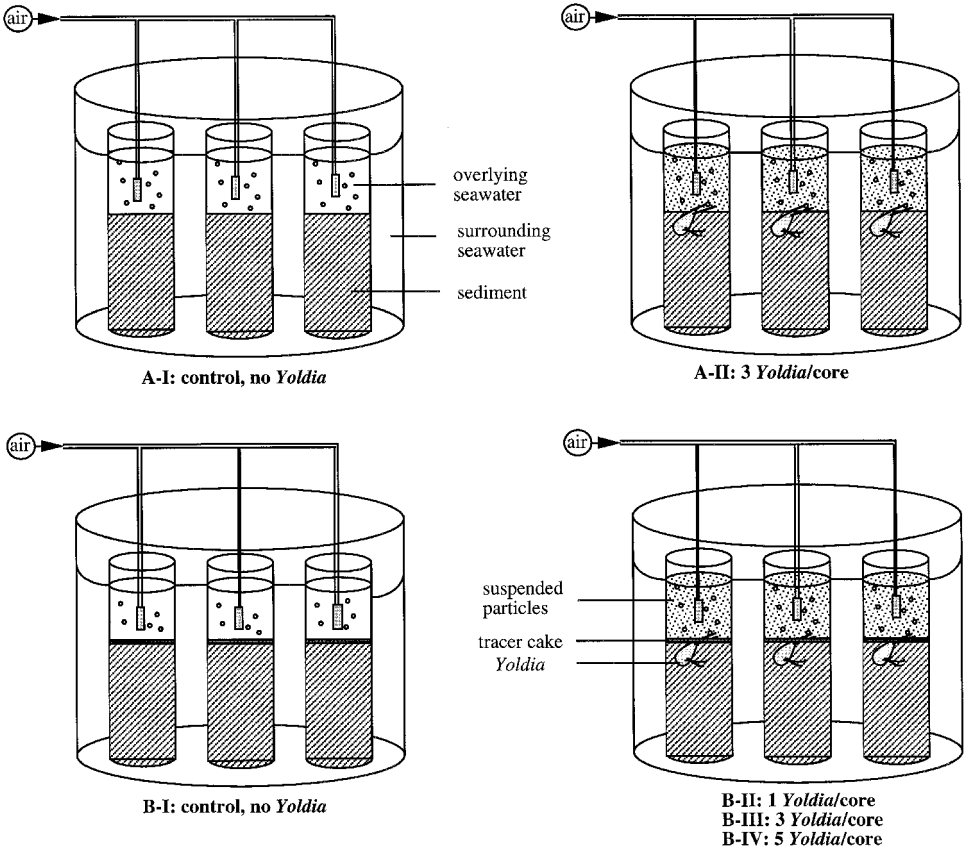
Figure 1. The schematic design of incubation experiments. Microcosms consist of a series of subcores (diameter = 7.4 cm) with 10 cm of bulk sediment (collected from central LIS surface sediments) and 0.8 L overlying seawater. Sets I (control, no *Yoldia* added) and II (*Yoldia* added) are natural homogenized cores. A pulse of tracer (^{13}C-labeled algae) mixed with sediment is added as a thin cake (5 mm) in all subcores of sets B-I (no *Yoldia,* as control), B-II (1 *Yoldia*/core), B-III (3 *Yoldia*/core), and B-IV (5 *Yoldia*/core). The overlying water is replaced once a week.

b. Microcosm setup. Incubation microcosms consisted of a series of control (no *Yoldia*) and experimental (with added *Yoldia*) cylindrical cores (i.d. 7.4 cm). These cores were filled with sieved surface sediment to a depth of ~10 cm; the bottoms were sealed with caps, and ~ 500 ml filtered seawater (collected from the same LIS site) was gently added above the sediment. Three or four cores were placed into each of four large polycarbonate reservoirs (~19 L in volume), each containing enough seawater to equal the water height in the cores. The large reservoirs kept the temperature fairly constant during the incubation period and prevented leakage from the base of cores (Fig. 1).

Two series of experiments were conducted during October 96 (Exp. A) and March 97 (Exp. B). In experiment A, no ^{13}C-tracer was added to the homogenized cores. There were

no *Yoldia* present in reservoir A-I cores, which served as controls. In reservoir A-II, three *Yoldia* per core were added, corresponding to their approximate natural abundance in LIS sediments. In experiment B, ^{13}C-labeled algae were added to all cores in reservoirs I–IV. No *Yoldia* were added to B-I cores (controls), while 1, 3, or 5 *Yoldia* were added to B-II, B-III, and B-IV cores, corresponding to 230, 700, and 1160 animals/m^2, respectively. Labeled algae were added one day after the addition of *Yoldia,* after the *Yoldia* had buried themselves in the sediment. About 4 g of ^{13}C-algae (lyophilized cells) were ground finely and stirred for 30 minutes with $\sim$800 g wet sediment (sieved to $<$ 1 mm), thus increasing the organic content of the sediments by 0.5%. The mixed sediments were made into several thin ($\sim$5 mm) cakes with diameters the same as the cores. These cakes were frozen overnight and added to experimental cores by pushing the cake down along the core walls after the overlying seawater had been temporarily removed. The addition of ^{13}C-labeled algal cakes was designed to simulate the natural pulse of material that settles after a water column bloom. The overlying seawater in all cores was continuously purged with air to keep it oxygenated. Reservoirs were covered to minimize evaporative losses during the experiment. Incubations were carried out in the dark at room temperature (20 $\pm$ 2°C) for several weeks.

c. Sampling and inorganic analyses. During the incubations, overlying seawater in each core was replaced each week to avoid excessive accumulation of metabolites such as NH_4^+. Suspended particles present in the overlying water of cores with *Yoldia* were removed from the old seawater by centrifugation and added back into the new water to prevent physical removal of lipids from the system. Individual cores in each reservoir were removed at different sampling times ($t = 0, 6, 15$, and 27 days for A-I and A-II; $t = 0, 5, 10$, and 18 days for B-I, B-II, B-III and B-IV). Approximately 1 day prior to sediment sampling, NaBr was added to a concentration of $\sim$5–6 mM in the overlying seawater as a tracer of bioirrigation. At the sampling time, overlying seawater was removed and centrifuged to collect suspended particles. Sediment was extruded from the core and sliced into 0–0.5, 0.5–1, 1–2, 2–4, and 4–10 cm intervals. Part of the wet sediment was centrifuged at 2500 g to separate and remove pore water. In these pore waters and overlying seawater, ΣCO_2, NH_4^+, and Br^- concentrations were measured (ΣCO_2 by flow injection analysis with detection by conductivity (Hall and Aller, 1992); NH_4^+ by indophenol blue, (Solorzano, 1969); Br^- by phenol red oxidation (Presley, 1970)). Reactive solid phase Fe oxidation states were determined for centrifuged sediments using a 15-minute 6N HCl leach, and ferrozine with and without hydroxylamine (Stookey, 1970; Canfield, 1989; Aller *et al.,* 1996; reactive Fe, $Fe_R \sim$ ferrihydrite, lepidocrosite, mackinawite/greigite, siderite). The remaining wet sediment was immediately frozen for later lipid and pigment analyses. Pigment analyses and additional decomposition modeling are reported elsewhere (Ingalls *et al.,* 1999). At the final sampling time, dissolved oxygen contents in the sediments were measured with a Clark-style O_2 microelectrode (Revsbech, 1983).

d. Extraction and analysis of lipids. Procedures for extraction and analysis of sedimentary lipids have been described previously (Sun and Wakeham, 1994; Sun *et al.,* 1997). Briefly,

the incubated sediments were thawed, and ~0.5 g of the wet sediment was dried at 60 °C overnight to measure water content. The measured water content was used to estimate the porosity based on the average sediment density (2.5 g/cm³). About 1–2 g of thawed sediment was extracted with 10 ml methanol, followed by 3×10 ml methylene chloride-methanol (2:1 v/v); samples were sonicated for 10 min during each extraction. The four extracts were combined and partitioned into a methylene chloride phase formed by addition of 5% NaCl solution. The methylene chloride phase was dried, and lipids were saponified using 0.5 M KOH in MeOH/H_2O; neutral lipids were extracted out of the basic solution (pH > 13), while acidic lipids were extracted following addition of HCl (pH < 2).

Fatty acids in the acidic lipid extracts were converted to FAMEs (fatty acid methyl esters) by reaction with BF_3-MeOH at 100 °C for 2 h. Lipids in neutral extracts were further isolated into several fractions by silica gel chromatography using 7 g deactivated silica (Merck) and a sequence of solvents of increasing polarity. Phytol was eluted with 15% ethyl acetate in hexane and then treated with BSTFA [N,O-bis(trimethylsilyl)trifluoroacetamide] in acetonitrile to form its TMS(trimethylsilyl)-ether. FAMEs and phytol-TMS ethers were analyzed by capillary gas chromatography using a Hewlett-Packard 6890 GC with an on-column injector and flame ionization detector. Separations were achieved with a 30 m × 0.25 mm i.d. column coated with 5%-diphenyl-95%-dimethylsiloxane copolymer (HP-5) operated with a temperature program of 80–150 °C at 10 °C/min followed by 150–310 °C at 4 °C/min and a 5 min hold at 310 °C; H_2 was the carrier gas. Internal standards [5α(H)-cholestane for phytol-TMS-ethers and nonadecanoic acid methyl ester for FAMEs] were added to samples immediately prior to GC analysis to aid in quantification.

Triplicate measurements of various ^{13}C-labeled lipid tracers (fatty acids and phytol) were made on the initially mixed sediments. Relative standard deviations (RSD) were ±1–3% for various fatty acids and ±5.8% for phytol.

e. Identification of and distinction between ^{13}C-labeled lipids and natural lipids. Individual lipids were identified by GC/MS (Sun, 1999). Briefly, 1.4 g of wet LIS sediment or ~20 mg uniformly ^{13}C-labeled algae were extracted with methanol and saponified with KOH. After derivatization of neutral and acidic extracts, ^{13}C-labeled FAMEs and neutral lipid-TMS derivatives were analyzed by GC and GC/MS. Individual fatty acids and phytol in the acidic and neutral extracts were quantified by adding internal standards prior to GC. GC/MS was performed on a Hewlett-Packard 5890/Finnigan Incos 50 GC/MS system using a 30 m × 0.25 mm i.d. column (DB-5, J&W Scientific) with He as carrier gas. Operating conditions were: mass range 50–650 with a 1 s cycle time; 70 eV ionizing energy, temperature programming for FAMEs of 80–150 °C at 20 °C/min, 150–240 °C at 4 °C/min, and 240–300 °C at 20 °C/min with a 5 min hold at 300 °C. For neutral lipid-TMS derivatives, the temperature program was 80–150 °C at 20 °C/min and 150–320 °C at 4 °/min with a 10 min hold at 320 °C.

The discrimination between ^{13}C-labeled and unlabeled compounds was based on mass shift of major fragments in mass spectra (Sun, 1999). In brief, unlabeled fatty acid methyl

esters (FAMEs) have a characteristic fragment with $m/z = 74$ $(CH_2=C(OH)-O-CH_3)^+$ while the corresponding fragment of ^{13}C-labeled fatty acid methyl esters is $m/z = 76$ (that is, $^{13}CH_2=^{13}C(OH)-O-CH_3)^+$. Similarly, unlabeled phytol-TMS ether produces a fragment with $m/z = 143$ (that is, $CH_2-CH=CH-CH_2-O-Si-(CH_3)_3^+$) while ^{13}C-labeled phytol produces a fragment with $m/z = 147$ $(^{13}CH_2-^{13}CH=^{13}CH-^{13}CH_2-O-Si-(CH_3)_3)^+$. A series of mixtures of ^{13}C-labeled algal extracts and natural LIS sediment extracts were made at several mass ratios. Calibration curves were constructed for each individual compound according to its mass ratios (^{13}C to ^{12}C) and the characteristic fragment ratios in the mass spectra. The proportion of ^{13}C compounds in the incubated samples was calculated based on the calibration curve. The identification of newly-produced ^{13}C-labeled intermediates during incubation is based on a combination of relative increase in GC peaks and mass shift of characterized fragments in mass spectra.

3. Results

a. Remineralization and transport indicators. Since the experimental cores (both control and *Yoldia*) were comprised of surface sediments homogenized through a 1-mm sieve, porosities of these cores were initially constant with depth (Fig. 2A). During the incubations, particle suspension was observed in all experimental cores with *Yoldia* while overlying water of the control cores remained clear. The direct resuspension rate of sediment particles is proportional to body size of *Yoldia* and positively correlated with water temperature (Bender and Davis, 1984). Based on animal size and temperature during our incubations, the resuspension rate may be estimated as roughly 50 mg/hr. Reworking by *Yoldia* resulted in an increase in porosity in surficial sediment compared with uninhabited controls (Fig. 2A and 2B). Below 3 cm depth, the porosity values in both control and *Yoldia* cores were similar and uniform ($\sim$0.75).

Overlying waters were oxygenated during the incubations, and dissolved oxygen typically penetrated 4–5 mm into the surface sediments. After about one month, dissolved oxygen penetrated deeper ($\sim$0.5–1 mm) in *Yoldia*-containing than control cores in experiment A (Fig. 2C). Bromide was added to the overlying water 1–2 days before sediment sampling. Br^- tracer was transported downcore about 3–4 cm; higher concentrations were observed relatively deeper in cores with *Yoldia* present (Fig. 2D), although this was less noticeable in experiment B. Profiles of total CO_2 and NH_4^+ concentrations (Fig. 3) were generally lower throughout A-series cores with *Yoldia* than in control cores, but NH_4^+ was distinctly elevated in surface regions of the B-series having algal layer addition and high *Yoldia* abundances (Fig. 3D). In addition, relative solid phase ratios of Fe^{++} to total reactive Fe were lower in the upper 2 cm of sediment in cores with *Yoldia* (A-II; top cm $\sim$70% oxidized) than in the controls (A-I; top cm $\sim$50% oxidized) within the first week (Fig. 4A). The extent of Fe oxidation in the upper 2 cm also increased with the number of *Yoldia* present (Fig. 4B).

b. Solute transport—reaction models. The Br^- penetration rates allow quantification of solute transport and thus remineralization rates at the time of sediment sampling. Because
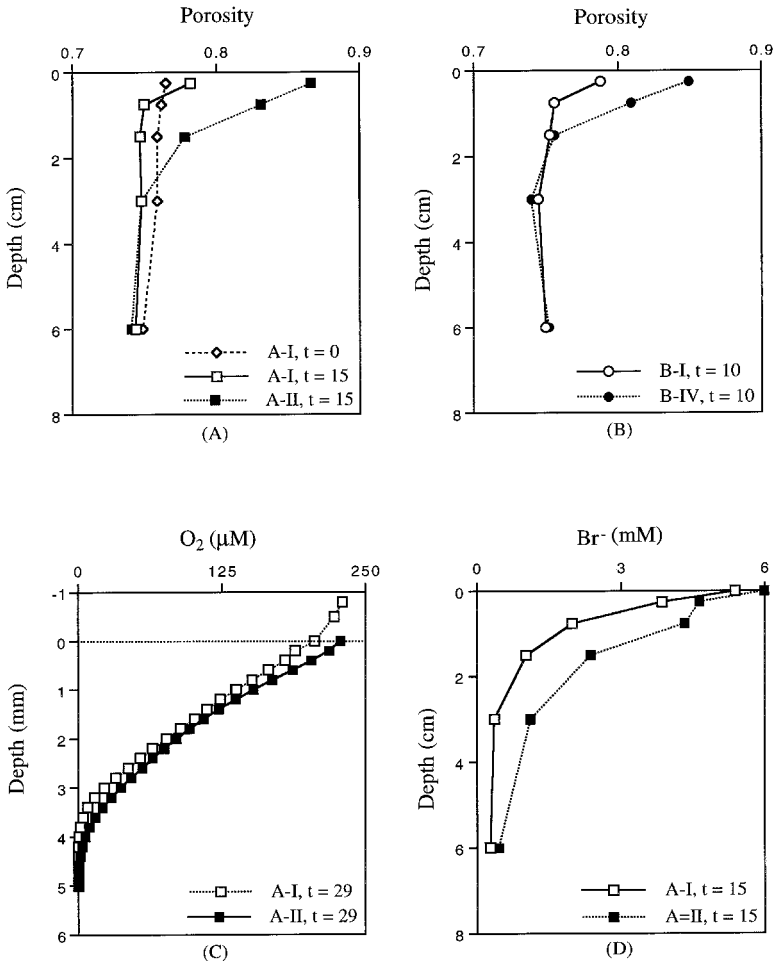
Figure 2. Profiles of porewater parameters in the experimental sediment subcores. (A) porosity in A-I and A-II subcores; (B) porosity in B-I and B-IV subcores; (C) dissolved oxygen in A-I and A-II subcores; and (D) bromide in A-I and A-II subcores.

Yoldia are highly mobile and their activities largely restricted to the upper ~2–4 cm, the solute transport regime in the presence of *Yoldia* can be modeled by assuming a composite two-layer system in which a biologically turbulent surface zone, $0 < z < L_1$, overlies a sediment zone, $L_1 < z < L_2$, dominated by molecular diffusion; where z is the depth coordinate below the sediment surface and L_1, L_2 are specific depths (Aller, 1978). L_1 varied between ~2–3 cm based on porosity variation and Br$^-$ penetration patterns. The distribution of Br$^-$ concentration, C_i, with time in a vertical zone, i, is then described by:

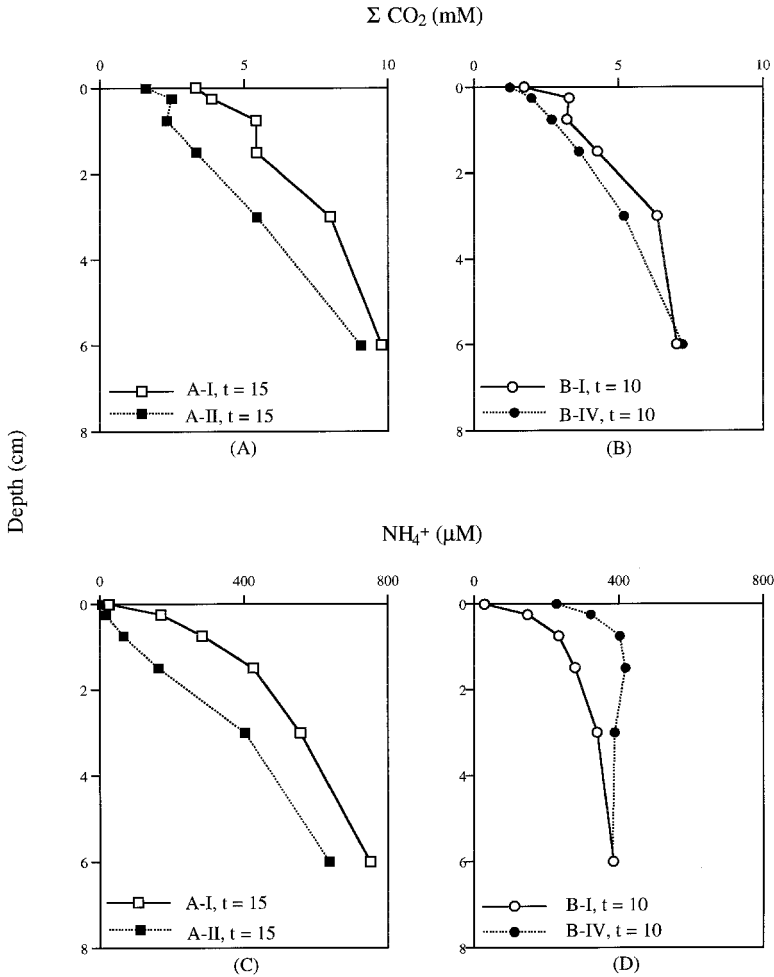$$\frac{\partial C_i}{\partial t} = D_i \frac{\partial^2 C_i}{\partial z^2} \tag{1}$$

Figure 3. Profiles of ΣCO_2 and NH_4^+ porewater of the experimental sediment subcores.

With initial and boundary conditions:

$$
\begin{aligned}
t = 0; \quad & 0 < z < L_2, \quad && C = C_0, \\
t > 0; \quad & z = 0, \quad && C = C_T, \\
& z = L_1, \quad && C_1 = C_2, \\
& z = L_1, \quad && \varphi_1 D_1(\partial C_1/\partial z) = \varphi_2 D_2(\partial C_2/\partial z), \\
& z = L_2, \quad && \partial C_2/\partial z = 0.
\end{aligned}
$$

The upper boundary condition in the present cases is an approximation because C_T is not exactly constant. An explicit, finite difference approximation was used to fit measured Br^- profiles and derive estimates of D_1 and/or D_2; the numerical routine was checked with the 2-layer analytical solution (Aller, 1978).

$$Fe^{++}/Fe_R$$

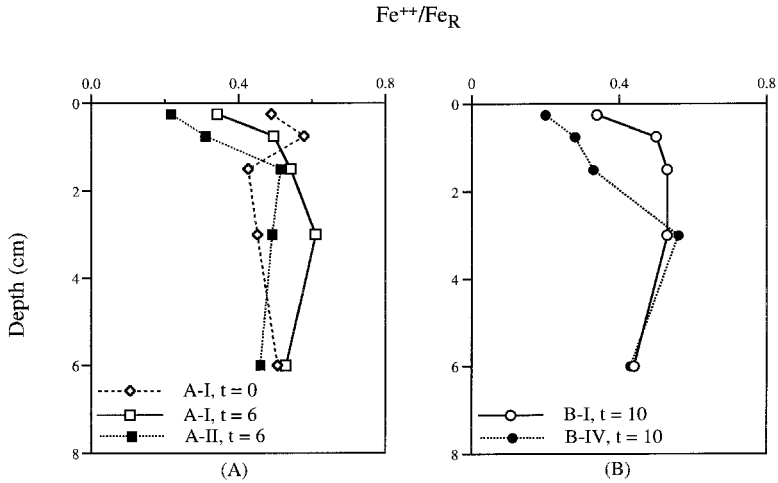Figure 4. Depth-dependent ratios of dissolved Fe^{++} to total reactive Fe_R. (A) A-I and A-II incubations at initial time ($t = 0$) and $t = 6$. (B) B-I and B-IV incubations at $t = 10$.

Br^- diffusion rates in the absence of *Yoldia* averaged 0.79 ± 0.13 cm²/d in experiment A-I, and 0.83 ± 0.08 in B-I. Biogenic diffusion coefficients were: 2.1 ($t = 6$ d; $L_1 = 2$ cm) and 2.0 ($t = 15$ d; $L_1 = 3$ cm) cm²/d for homogenized treatment A-II and average 1.01 ± 0.16 for B-II, 1.08 ± 0.19 for B-III, and 1.5 ± 0.12 for B-IV, over the 18 d period of experiment (Fig. 5).
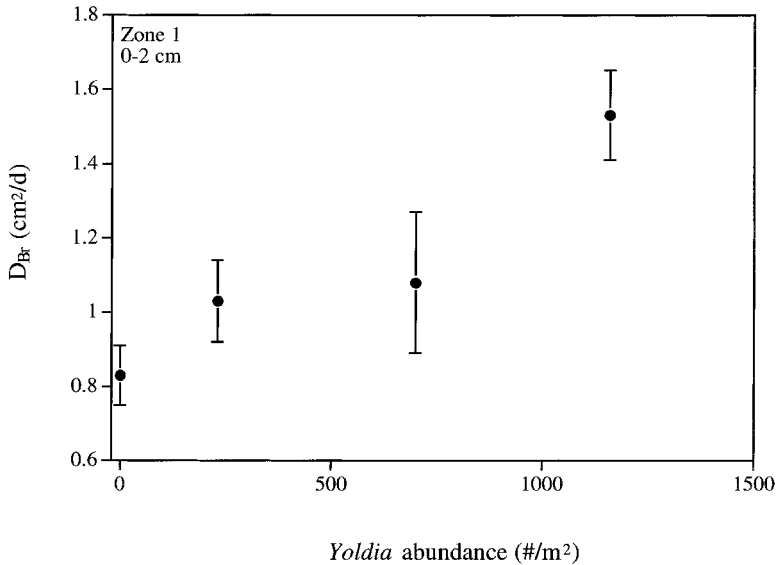

Figure 5. The time-average apparent diffusion coefficient of Br^- in zone 1 (0–2 cm) increases regularly as a function of *Yoldia* abundance in experiment B.

A similar transport model structure was used to estimate net ΣCO_2 and NH_4^+ production rates. Reaction rates were assumed to be independent of solute concentration (zeroth order). The profile shapes and concentration gradients over specific depth intervals indicated that net reaction rates varied as a function of depth, particularly near the sediment-water interface in the presence of *Yoldia*. Because of the relatively coarse depth resolution of solute profiles, average reaction rates, $R(z)$, were assumed to be constant within specific depth intervals and to have a simple step-wise depth distribution. Four separate depth intervals each having constant net reaction rates were generally assumed: $0 < z \leq 0.5$; $0.5 < z \leq 1$; $1 < z \leq L_1$; $L_1 < z \leq L_2$. These corresponded to the intervals sampled for pore water. In some cases, a fifth reaction interval was used, $L_1 \leq z \leq 4$. The transport—reaction model equation for solute concentration in the i-th specific depth interval is:

$$(1 + \text{K}) \frac{\partial C_i}{\partial t} = D_i \frac{\partial^2 C_l}{\partial z^2} + R_i \tag{2}$$

where K is a reversible, linear adsorption coefficient and D_i is either the molecular diffusion coefficient or the biogenic transport coefficient, depending on the depth interval and experimental treatment. For experiment A, boundary conditions were as in equation (1). In experiment B, the high resuspension rate and large numbers of *Yoldia,* required that the surface boundary values be allowed to vary with time (e.g., Fig. 3D). In these cases, a finite overlying water volume and no net water column reactions were assumed. Initial conditions for a given time-series sample at time t, were taken as the appropriate solute profile from the previous sampling time, $(t - \tau)$: $0 < z \leq L_2$; $C(z, 0) = C(z, t - \tau)$. The initial concentration profile in each case was estimated using a cubic spline and interpolation fit procedure to the measured distribution. An explicit, finite-difference approximation was then used to derive the best-fit estimates of R_i that were required to obtain the next time-series profile.

The biogenic transport coefficients obtained from Br^- profiles were used for zone 1 calculations when *Yoldia* were present (i.e. D_1 for $0 \leq z \leq L_1$), and molecular diffusion coefficients were used otherwise. Whole sediment molecular diffusion coefficients were estimated from penetration profiles as 0.79 ± 0.13 (A) and 0.83 ± 0.08 (B) cm^2/d for Br^- diffusion in the absence of *Yoldia,* and as 0.51 and 0.85 cm^2/d for ΣCO_2, and NH_4^+ respectively using the approximation $D_i \sim \phi^2 D_0$, (D_0 = free solution diffusion coefficient, Li and Gregory, 1974; Ullman and Aller, 1982). K was taken as 0.91 for NH_4^+ (based on 2N KCl displacement of NH_4^+ in surface sediment from the collection site) and 0 for ΣCO_2.

Model-derived estimates of net reaction rates demonstrated higher average net remineralization rates (2–6X) in the surface mixed zone, particularly for ΣCO_2 near the sediment-water interface, and much greater complexity of reaction rate depth distributions in the presence of *Yoldia* than in their absence (Fig. 6). Slight concavities in depth distributions required uptake of ΣCO_2 and NH_4^+ in specific intervals in the surface or subsurface zones (negative R_i). The activities of *Yoldia* clearly promoted both consumption and production
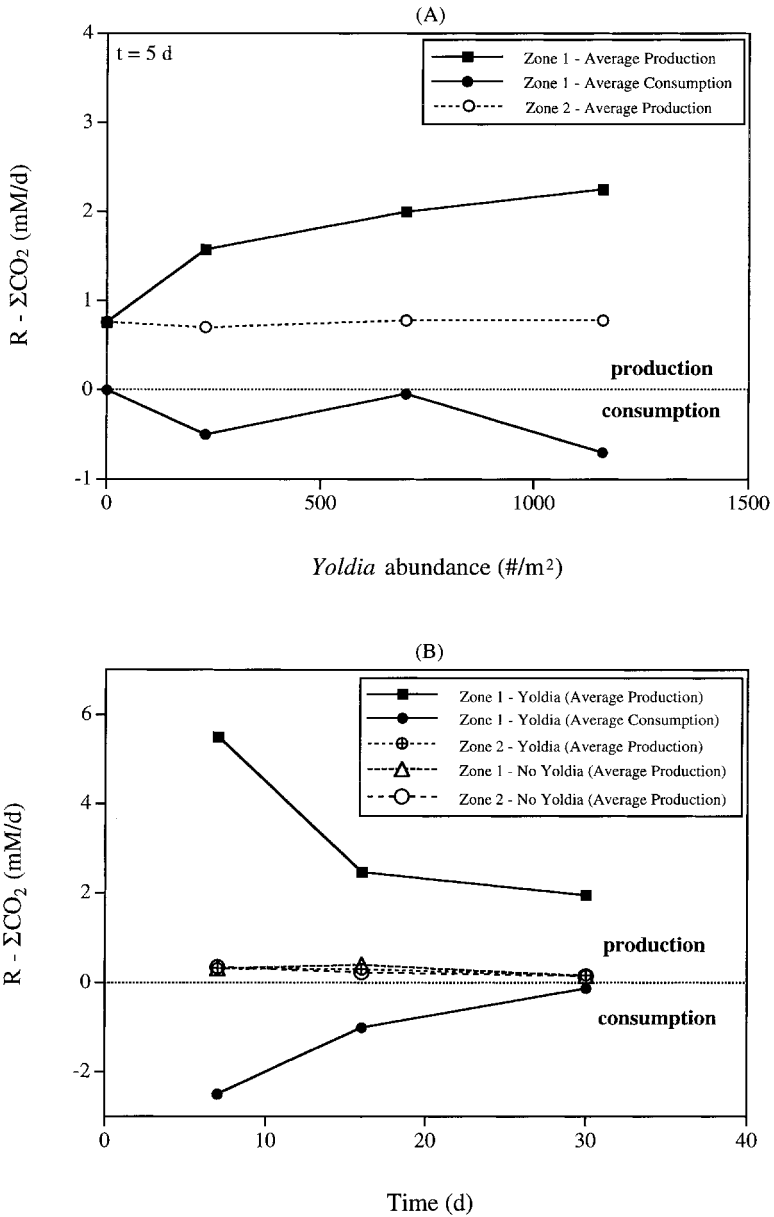
Figure 6. (A) The total production rate of ΣCO_2, estimated from pore water distributions and averaged over sediment zone 1 (0–2 cm), increases regularly with *Yoldia* abundance, as illustrated by samples at t = 5 d. Reactions that consume ΣCO_2 also increase in distinct surface or subsurface layers (shown as the rate averaged uniformly over zone 1) in the presence of *Yoldia*. The net rate of ΣCO_2 in zone 1 is the sum of the two average rates. Zone 2 (2–10 cm) rates show no analytically detectable change as a function of *Yoldia* abundance. (B) Average rates of ΣCO_2 production and consumption in zones 1 and 2 as a function of time and presence/absence of *Yoldia* in experiment A. *Yoldia* increase both the absolute rates and the complexity of ΣCO_2 cycling in zone 1.

reactions within specific sediment intervals. Only zonally averaged rates of production or consumption are illustrated here for simplicity (Fig. 6). Net loss of NH_4^+ (nitrification) near or just below the sediment-water interface is enhanced in the presence of *Yoldia* and increases in a given treatment with total time of incubation (Fig. 7), consistent with a dominance of suboxic conditions in the surface mixed layer (Fig. 4). Zones of net production and consumption of ΣCO_2 are also enhanced in the presence of *Yoldia,* the latter presumably due to a combination of nitrification, sulfide and metal oxidation, and shell deposition. In each treatment, average depth-integrated rates of ΣCO_2 production decrease ($\sim 2\times$) with time (e.g., Fig. 6B).

c. Variation in depth profiles of lipids. Experiments A-I and A-II compared cores with and without *Yoldia* in homogenized sediments without addition of ^{13}C-labeled algae. Differences in the concentrations of several fatty acids [*iso*-15:0, 16:1(ω7), 16:0, and 18:1(ω9)] were observed between control and *Yoldia* cores in this series of experiments (Fig. 8). After two weeks, differences in fatty acid concentration were noted in the top 2 cm of sediment in all cores. Surface concentrations decreased with time and were lower than those in deeper intervals; greater decreases were observed in the *Yoldia* cores. The fatty acid inventories in the upper 2 cm of *Yoldia* cores were 20–30% lower than control cores after two weeks of incubation relative to the original inventory at $t = 0$ (Fig. 8). Below 2 cm depth, there was little change in specific lipid concentrations during the 2–4 week incubations.

Experiments B-I, B-II, B-III, and B-IV compared cores with no *Yoldia* (control, B-I) and with different numbers of *Yoldia* (B-II, B-III and B-IV); ^{13}C-labeled algae was added to the top of all cores. Since the ^{13}C-labeled algal cake was introduced into the microcosms as a thin layer at the sediment-water interface, ^{13}C-labeled algal lipids [16:1(ω7), 16:0 and 18:1(ω9) fatty acids and phytol] were detected only in the top 1 cm of sediment at the beginning of the incubation (Fig. 9). After 5 days, although depth profiles remained roughly exponential in shape in B-I (control), sub-surface maxima formed in B-II, B-III, and B-IV (with *Yoldia*). The sub-surface maxima formed earlier in B-IV (highest abundance of *Yoldia*) than in B-II and B-III (low and middle abundance of *Yoldia*). Surface concentrations of these compounds decreased fastest in B-IV (highest abundance of *Yoldia*) and slowest in B-I (control). ^{13}C-tracers were transported to a depth of 1–2 cm in B-II, B-III, and B-IV cores by bioturbation of *Yoldia,* while no ^{13}C-tracers were detected below 1 cm in B-I (control).

d. Formation of ^{13}C-degradation products during incubation. Two ^{13}C-labeled degradation products were identified in incubated sediments based on mass spectral analysis (Sun, submitted): *iso*-15:0 fatty acid and a C_{16} alcohol. Initially, these two ^{13}C-labeled compounds were not present in control (B-I) or *Yoldia*-containing cores (B-II, B-III, and B-IV) (Fig. 10). After 5 days, ^{13}C-labeled *iso*-15:0 fatty acid and C_{16} alcohol appeared in surface sediments. Higher net production of both compounds was seen in control cores compared to *Yoldia* cores. No ^{13}C-*iso*-15:0 fatty acid was found below 1 cm depth, while a small but
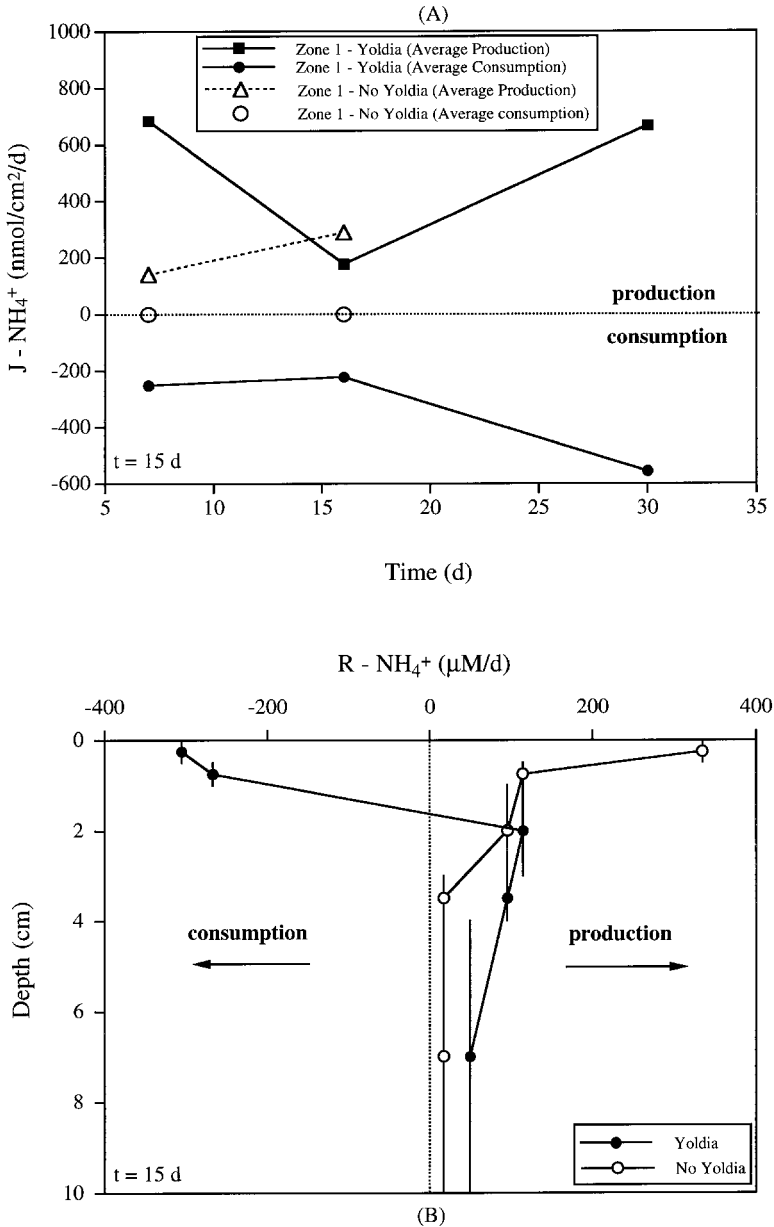
Figure 7. (A) The production and consumption fluxes of NH_4^+ as a function of time in zone 1 (0–2 cm) in the presence or absence of *Yoldia* in experiment A ($J = \phi RL_1$). Production and consumption tend to be higher in the presence of *Yoldia*. (B) Vertical profiles of reaction rates as function of depth in experiment A at t = 15 d ($L_1 = 3$ cm). Loss of NH_4^+, presumably through nitrification, is substantially elevated by *Yoldia*, consistent with greater dominance of suboxic conditions in the presence of *Yoldia*. Net NH_4^+ production is also relatively elevated in zone 2 in the presence of *Yoldia*.

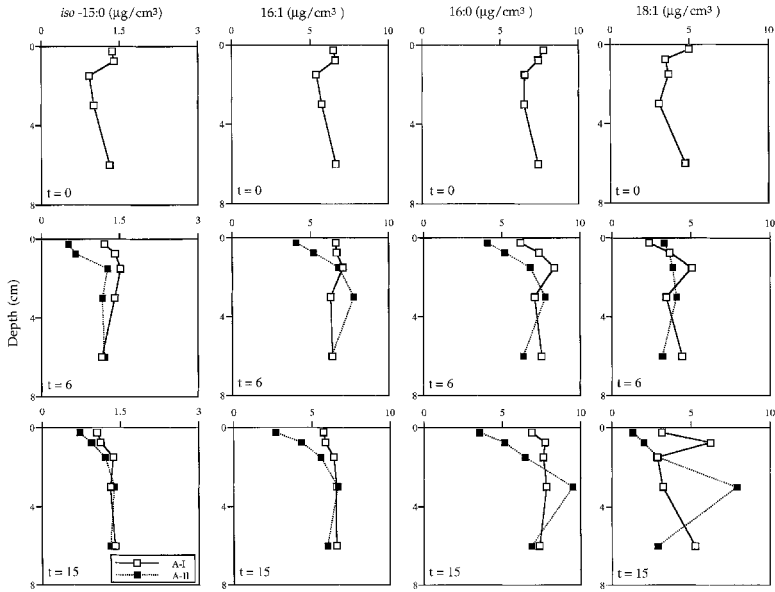Figure 8. Concentration profiles of natural sedimentary fatty acids (*iso*-15:0, 16:1(ω7), 16:0, and 18:1(ω9)) in A-I and A-II incubations.
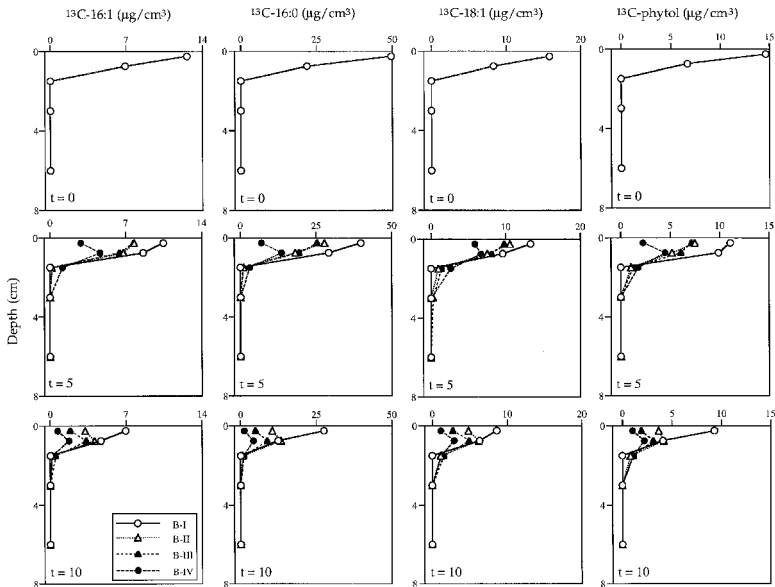
Figure 9. Concentration profiles of ^{13}C-labeled fatty acids and phytol in the control microcosm (A-I: no *Yoldia*) and the experimental microcosms with variable *Yoldia* abundance (B-II: 200/m^2, B-III: 600/m^2 and B-IV: 1000/m^2).
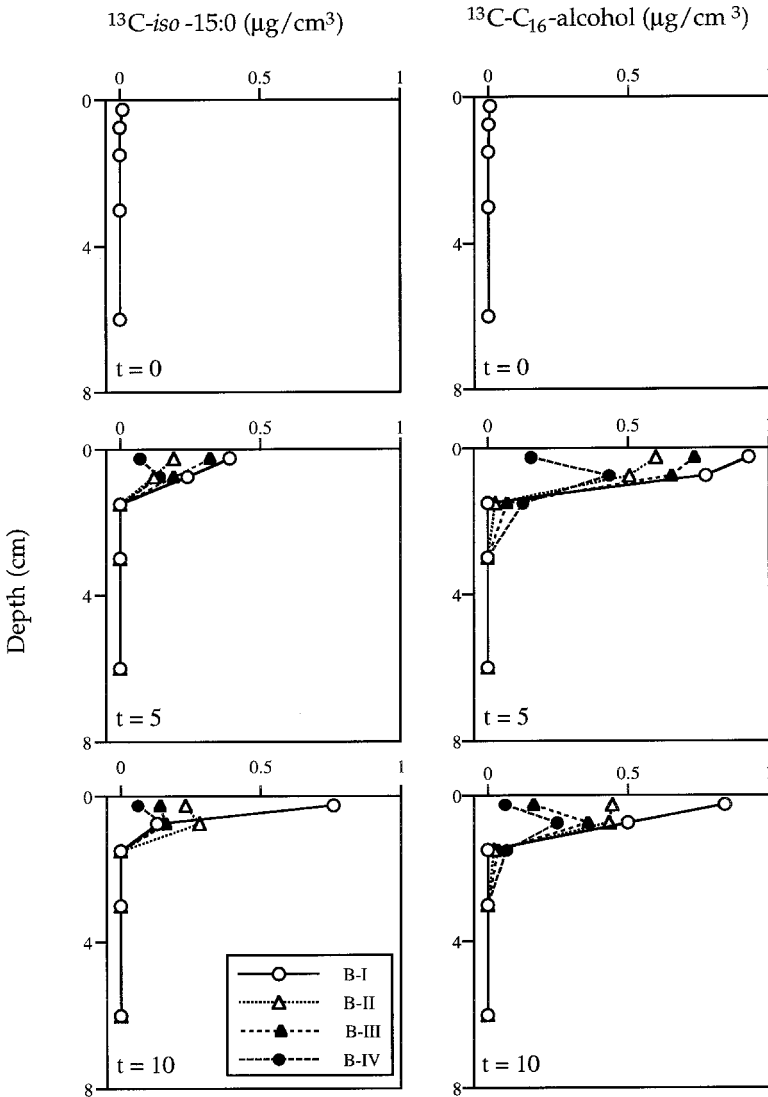
Figure 10. Concentration profiles of ^{13}C-labeled *iso*-15:0 fatty acid and C_{16} alcohol produced during incubations (B-I, B-II, B-III and B-IV).

detectable amount of labeled C_{16} alcohol was present below 1 cm, but only in cores with *Yoldia*. Concentration profiles of these newly-produced compounds were similar to those of other labeled algal lipids: an exponential decrease in control cores, but sub-surface maxima in *Yoldia* cores. After 10 days, concentrations of both products decreased slightly in *Yoldia* cores; in the control core, however, *iso*-15:0 increased and C_{16} alcohol remained at the same level as after 5 days.

Figure 11. Concentrations of ^{13}C-labeled fatty acids and phytol in suspended particles during incubations B-II (1 *Yoldia*/core) and B-IV (5 *Yoldia*/core).

e. Variation of ^{13}C-lipids in suspended particles. Over the course of incubations with *Yoldia,* particles (probably feces or pseudofeces) were ejected into the overlying water; suspended particle concentration was proportional to *Yoldia* abundance. In the control cases, the overlyin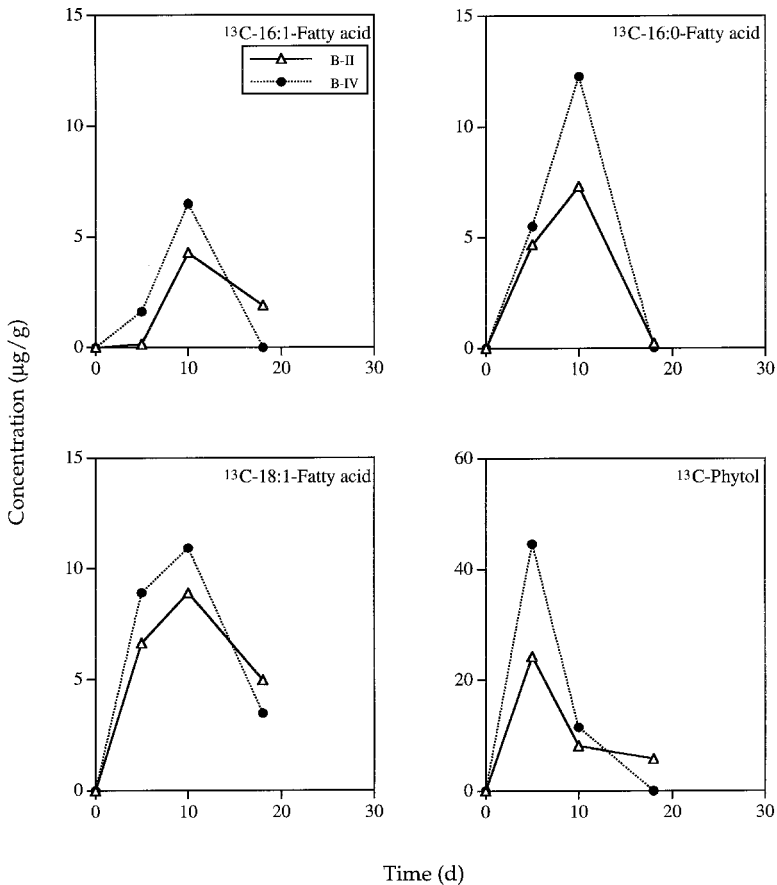g water remained clear, and no suspended particles were observed. Concentrations of suspended particle ^{13}C-labeled fatty acids and phytol were higher when more *Yoldia* were present (B-IV vs. B-II; Fig. 11). Concentrations of labeled compounds in suspended particles reached a maximum value and then decreased. Peak concentrations of ^{13}C-labeled phytol in suspended particles occurred after 5 days, while peak concentrations of labeled fatty acids [16:1(ω7), 16:0 and 18:1(ω9)] were observed on day 10. At times of peak concentrations in cores with the highest abundance of *Yoldia* (B-IV), ^{13}C-labeled phytol concentration reached a value approximately 30% higher than that in the algal cake added, while concentrations of ^{13}C-labeled fatty acids decreased to 10–30% of the original

Table 1. The ratios of various ^{13}C-labeled tracer concentrations in suspended particles to the concentrations in the original cakes.

	16:1 FA	16:0 FA	18:1 FA	Phytol
Incubation B-II ($t = 5$ d)	0.01	0.04	0.20	0.69
Incubation B-IV ($t = 5$ d)	0.08	0.05	0.26	1.27
Incubation B-II ($t = 10$ d)	0.22	0.06	0.26	0.23
Incubation B-IV ($t = 10$ d)	0.34	0.11	0.32	0.34
Original conc. In the cake (µg/g)*	25.4	104	31.8	29.5

*Tracer concentrations (µg/g dry sed) can be converted to (µg/cm^3) by using porosity and sediment density.

concentration present in the cakes (Table 1). ^{13}C-labeled *iso*-15:0 fatty acid but no ^{13}C-labeled C_{16} alcohol was found in suspended particles (Table 2). After 18 days, few ^{13}C lipids remained in suspended particles.

4. Discussion

a. Enhancement of lipid degradation. The presence of *Yoldia* in sediments significantly changed lipid vertical distributions and degradation rates in the experimental microcosms (Figs. 8–10), demonstrating that the biogenic reworking and feeding activities of *Yoldia* had major effects on planktonic lipid diagenesis. Overall enhanced lipid degradation can be demonstrated quantitatively using a first-order decomposition kinetic model that assumes a logarithmic decrease in lipid concentration or inventories with time ($dC_i/dt = -k_iC_i$, where C_i = concentration of lipid i). Decomposition rate constants were calculated from the slopes of log-transformed lipid inventories versus time in the surfacemost interval (0–0.5 cm) and the entire mixed zone ($\sim$0–2 cm).

The presence of *Yoldia* resulted in intensive biomixing, including both downcore transport and ejection of particles to the overlying water. Suspended particles in overlying water settled quickly, however; <0.3 g of particles existed in the overlying water at any time. Since this amount was <3% of sediment added with ^{13}C-labeled algae, it was not included in rate constant calculations. In cores with *Yoldia,* downcore transport was apparent, indicated by sub-surface maxima in ^{13}C tracer concentrations and deep penetra-

Table 2. The concentrations (µg/g dry sed) of ^{13}C-labeled iso-15:0 fatty acid in surface sediment (0–0.5 cm) and suspended particles during B-series incubations.

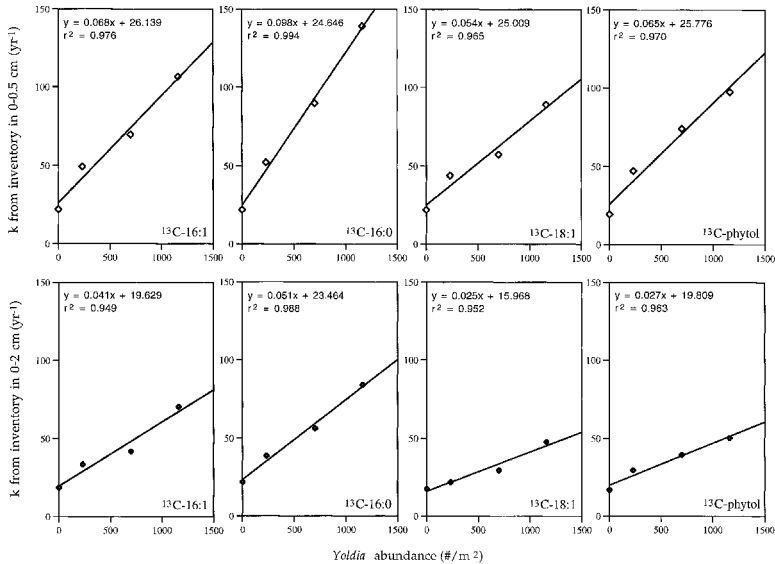|	Control cores I	*Yoldia* cores II	*Yoldia* cores IV
surface sediment ($t = 5$ d)	0.42	0.45	0.20
suspended particle ($t = 5$ d)	—	0.00	0.92
surface sediment ($t = 10$ d)	1.43	0.55	0.16
suspended particle ($t = 10$ d)	—	0.20	0.35

—: no suspended particles in control cores.

Figure 12. Correlation between *Yoldia* abundance and ^{13}C-labeled lipid degradation rate constants (derived from 0–0.5 cm inventory and from 0–2 cm inventory).

tion of the tracer. As particle mixing in the surfacemost interval (0–0.5 cm) influences a simple logarithmic concentration decrease, a first-order model likely underestimates decomposition rate in core A-II (upward mixing of lipid-rich sediment) and overestimates in cores B-II, B-III, and B-IV (downward mixing of lipid-rich sediment). Net degradation rate constants of both bulk sedimentary lipids and fresh ^{13}C algal lipids were enhanced by factors of ~2–4X, for example, based on the upper 2 cm inventory comparison between the control and a core with 3 animals/core (the natural abundance) (Table 3). Chloropigments also showed substantially increased rates of degradation in the presence of *Yoldia* in the same experiments and had exponentially decreasing rate constants with depth below the sediment-water interface (Ingalls *et al.,* 1999).

In the range of *Yoldia* abundance we used (230–1160/m^2), degradation rate constants (from either the 2 cm mixed-zone or from the surfacemost inventories) of various ^{13}C fatty acids and phytol were linearly correlated with *Yoldia* abundance, clearly showing the enhancement of algal lipid degradation by *Yoldia* (Fig. 12). Correlation coefficients (r^2) were greater than 0.9 in all cases. Rate constants were similar for all tracers, implying that the difference in molecular structure (e.g., saturated vs. unsaturated and fatty acid vs. phytol) did not significantly affect their degradation rate constants in this aerobic/suboxic regime with macrofauna present (Table 3).

Several field observations (Farrington *et al.,* 1977; Haddad *et al.,* 1992; Meyers and Eadie, 1993) have suggested that unsaturated fatty acids degrade faster than saturated fatty acids. Our previous laboratory experiments (Sun *et al.,* 1997) also showed differences between anoxic degradation rate constants for these compounds, although oxic degrada-

Table 3. Degradation rate constants (day^{-1}) derived from inventories in upper 0–0.5 cm and 0–2 cm sediment cores during incubation A and B. An independent incubation using 3 *Yoldia* per core (690 *Yoldia*/m^2) was conducted during October 96 (Exp. A), and the relative standard deviations of k estimates ($n = 2$, with experiment B-III) were ±30–40% for all tracers.

Incubation	16:1	16:0	18:1	Phytol
k derived from unlabeled inventory (0–0.5 cm):				
A-I: control	0.014 (0.92)	0.016 (0.75)	0.028 (0.61)	
A-II: 3 *Yoldia*/core	0.058 (0.98)	0.051 (0.8)	0.09 (0.99)	
A-II/A-I:	4.14	3.19	3.21	
k derived from unlabeled inventory (0–2 cm):				
A-I: control	0.005 (0.39)	0.005 (0.5)	0.018 (0.79)	
A-II: 3 *Yoldia*/core	0.018 (0.94)	0.016 (0.83)	0.037 (0.93)	
A-II/A-I:	3.6	3.2	2.06	
k derived from ^{13}C-labeled inventory (0–0.5 cm):				
B-I: control	0.06 (0.98)	0.06 (0.89)	0.06 (0.88)	0.053 (0.86)
B-II: 1 *Yoldia*/core	0.135 (0.97)	0.143 (0.98)	0.12 (0.97)	0.129 (0.99)
B-III: 3 *Yoldia*/core	0.191 (0.93)	0.246 (0.92)	0.157 (0.97)	0.203 (0.97)
B-IV: 5 *Yoldia*/core	0.292 (1.0)	0.381 (0.99)	0.244 (0.99)	0.267 (0.95)
B-III/B-I:	3.18	8.02	4.07	5.04
k derived from ^{13}C-labeled inventory (0–2 cm):				
B-I: control	0.051 (0.78)	0.06 (0.82)	0.048 (0.83)	0.046 (0.78)
B-II: 1 *Yoldia*/core	0.092 (0.94)	0.106 (0.99)	0.06 (0.95)	0.081 (0.99)
B-III: 3 *Yoldia*/core	0.115 (0.93)	0.154 (0.95)	0.081 (0.88)	0.108 (0.94)
B-IV: 5 *Yoldia*/core	0.193 (0.97)	0.230 (0.99)	0.131 (0.91)	0.138 (0.99)
B-III/B-I:	2.25	2.57	1.69	2.35

Number in parenthesis is correlation coefficient (r^2).

tion rate constants for saturated and unsaturated fatty acids were similar. Other than molecular structure, additional influences on degradation rate could include the source of the compound in the sediment matrix (molecular association) and redox conditions during decomposition. For example, saturated 16:0 fatty acid in sediments originates from multiple sources, including plankton, benthic fauna and bacteria (Parker and Taylor, 1983; Harvey *et al.,* 1987; Volkman *et al.,* 1989), while unsaturated 16:1 fatty acid is primarily from plankton (Volkman *et al.,* 1989; Dunstan *et al.,* 1994; Sun and Wakeham, 1999). Lipid compounds from various sources exist as different complexes or associate with different components. It was demonstrated that various lipid-protein complexes have different reactivities to degrading enzymes due to differences in size, solubility, association and molecular arrangement (Larkum and Barrett, 1983). It was also observed that physicochemical sorption of membrane lipids to the organic matrix may protect lipids from microbial attack and degradation (Harvey *et al.,* 1986). Initially (at $t = 0$), ^{13}C-labeled 16:0 and 16:1 fatty acids in our experiments were exclusively from algae, and oxic/suboxic

conditions dominated degradation processes. Thus, structural effects on degradation may have been minimized. In sediments that are anoxic below a few mm, fatty acid degradation may be dominated by anaerobic processes, which would result in different degradation rates between unsaturated and saturated fatty acids.

b. Alteration of solute transport and remineralization in the presence of Yoldia. The effects of *Yoldia* on lipid degradation rates presumably result from a combination of biogenic modification of solute transport, redox conditions, and associated indirect influences on microbial metabolism, digestive enzyme reactions, and direct grazing of bacterial biomass, particularly in the upper 2–3 cm. Solute exchange is clearly enhanced, as indicated by Br^- penetration ($\sim$1.3–2.7$\times$) in the surface zone, and distributions of ΣCO_2 and NH_4^+ are altered throughout the sediment, as expected in the presence of a surface mixed layer (Figs. 5–7). Increased solute exchange in irrigated sediment is known to promote increased net remineralization and microbial activity, regardless of redox conditions (Aller and Aller, 1998).

The activities of *Yoldia* also clearly alter the depth pattern of reaction balances and types, as indicated by the comparatively complex distribution of ΣCO_2 and NH_4^+ net production patterns in sediments when *Yoldia* are present. These latter variations likely reflect reactions other than remineralization of organic matter. For example, carbonate dissolution is promoted by biogenic reworking (enhanced ΣCO_2 production), as is alkalinity consumption, CO_2 degassing, and chemoautotrophic activity during reduced inorganic compound oxidations (sulfide, NH_4^+; Aller, 1982b; McNichol *et al.,* 1988; Green *et al.,* 1993). The progressive changes in reactions with time of incubation are also affected by reworking, as illustrated by steady increases in consumption of NH_4^+ in surface sediment in the presence of *Yoldia,* presumably initially through a nitrification (oxidation) pathway (Figs. 6 and 7).

Another indication of differences in reaction balances and increased overall sedimentary oxidation in the presence of *Yoldia* comes from the solid phase Fe distributions. Although O_2 penetrates only a few millimeters in all cases and is only slightly increased by *Yoldia,* Fe^{++}/Fe_R ratios are decreased by $\sim$50% in the upper 0.5–1 cm relative to no *Yoldia* treatments (mean $Fe_R = 139 \pm 6$ µmol/g). Continual resuspension and mixing downward of Fe-oxide enriched sediment together with increased nitrification (NH_4^+ loss, Fig. 7) must promote suboxic decomposition pathways in the bioturbated zone. The availability of relatively high-order oxidants such as Fe^{+3} and NO_3^- and repetitive exposure to O_2 presumably enhance lipid decomposition rates beyond that of sulfate reduction or fermentation alone (Schink, 1988).

c. Role of grazing by Yoldia. Bender and Davis (1984) observed that a single *Yoldia* can process sediment at a rate up to eight times its body weight hourly. In our microcosms with higher abundances of *Yoldia,* more particles were ingested and then ejected into the overlying water, and they had higher ^{13}C-labeled lipid concentrations than when fewer *Yoldia* were present. *Yoldia* predominantly feed on subsurface sediments about 2–3 cm

beneath the sediment-water interface (Rhoads and Young, 1970). The occurrence of a maximum concentration of labeled lipids in suspended particles after a several day delay (Fig. 11), is consistent with progressive penetration of the added ^{13}C-labeled lipid to a subsurface feeding depth (Fig. 9). The fact that labeled phytol in suspended particles can exceed the initial tracer cake concentrations, suggests that *Yoldia* were efficiently selecting labeled algae that were subducted to the feeding depth. The presence of an abundant source of food may also have attracted the *Yoldia* to feed at the surface.

To feed efficiently, deposit-feeders such as *Yoldia* always use a selective ingestion strategy. One way to ingest sediment particles selectively is to sort them at the collector end (at the mouth, labial palps), selectively ingesting and retaining certain particles (Lopez and Levinton, 1987). *Yoldia* can reject 90% of the particles they process as pseudofeces (Tantichodok, 1989). Another way to select particles is by increasing the gut residence time for selected components and quickly egesting less preferred components (Self and Jumars, 1978; Bricelj *et al.,* 1984).

Variations in ^{13}C-labeled tracer concentrations in suspended particles may provide insight into whether labeled algae were ejected by *Yoldia* as feces or pseudofeces in these experiments. Pseudofeces are usually made up of coarse organic and inorganic particles that are low in organic content and do not pass through extensive digestive processes. Thus, if labeled algae were being ejected as pseudofeces, relative ratios of the various tracers in ejected particles and the original sediment cakes should be similar. However, in the cores with the most *Yoldia* we observed a 30% enrichment in phytol concentration in suspended particles relative to the algal cakes initially added (particle selection), and a loss in fatty acid concentration relative to the original values in the cakes (digestion, decomposition; Table 1). Thus, our results suggest that the particles containing ^{13}C-labeled algae in our experiments were selected, ingested, and ejected into the overlying water primarily as feces rather than pseudofeces. In this way, *Yoldia* can more efficiently use fresh inputs of plankton detritus and play a significant role in degradation of organic compounds contained in these materials.

As mentioned above, labeled phytol was lost more slowly than fatty acids, and was for a short time, enriched in the suspended particles. Phytol is synthesized by photosynthetic plants as part of the chlorophyll molecule. Animals (zooplankton and benthic fauna) convert chlorophyll to phaeophorbide and other products (Welschmeyer and Lorenzen, 1985; Bianchi *et al.,* 1988), resulting in a release of phytol. In some cases, phytol is further converted to dihydrophytol during grazing (Prahl *et al.,* 1984). In LIS sediments, dihydrophytol is formed during spring blooms when recruitment of benthic macrofauna reach maximum levels (Sun *et al.,* 1998). However, no ^{13}C-dihydrophytol was found in sediments or suspended particles during the *Yoldia* experiments conducted. Passage of particles through the gut may be too rapid for significant phytol degradation to occur. In contrast, ^{13}C-labeled fatty acids were depleted in suspended particles relative to the original algal cake. Fatty acids exist mainly as membrane components in the algae we used (Si-gel chromatography results suggest as phospholipids). Dietary fatty acids, especially

polyunsaturated fatty acids, are easily assimilated by benthic animals (e.g., Tanoue *et al.,* 1982; Harvey *et al.,* 1987; Bradshaw *et al.,* 1990; 1991). Some animals preferentially assimilate unsaturated fatty acids while others (e.g., annelids) assimilate all fatty acids to a high degree. In our experiments, *Yoldia* apparently efficiently assimilated all three algal fatty acids we examined. Thus, the specific metabolic pathways involving fatty acids and phytol in the gut of *Yoldia* may be different even though the overall degradation rates in sediments are similar.

d. Bacterial biomass dynamics and microbial degradation. Bacterial degradation of organic matter results in remineralization of organic carbon to CO_2 as well as incorporation of C into biomass (Pomeroy, 1974; Lee, 1980; Kemp, 1990). In our experiments, spiked ^{13}C-labeled algae provided a traceable organic carbon supply for bacteria. Two newly-produced ^{13}C-labeled compounds that resulted from microbial processes, *iso*-15:0 fatty acid and C_{16} alcohol, were identified in incubated sediments (Sun, 1999). In the case of *iso*-15:0 fatty acid, this compound is a constituent of bacterial membranes (Volkman *et al.,* 1980; Parkers and Taylor, 1983), and production of a labeled version of this compound is direct evidence for bacterial biosynthesis. Following concentrations of these two compounds during incubations can provide insight into microbial degradation of algal lipids.

Two major influences on the synthesis of bacterial biomass and bacterial standing stock are substrate availability and grazing pressure. The influence of lability of organic matter present is seen in our experiments in the differences between *iso*-15:0 fatty acid concentrations in the initially homogenized set A (no addition of fresh algal material) and pulsed set B (with ^{13}C-labeled algae added). In treatments A-I (control) and A-II (*Yoldia*) with initially homogenized sediment, surface concentrations of natural *iso*-15:0 fatty acid decreased with time. In treatments B-I (control), and B-II to B-IV (*Yoldia*) with a superimposed pulsed input of relatively more labile ^{13}C-enriched algae, *iso*-15:0 fatty acid concentrations increased with time. Net synthesis of new bacterial biomass was apparent when more reactive organic matter was available.

The abundance of bacterial indicator compounds is also influenced by grazing. In cores with *Yoldia,* concentrations of *iso*-15:0 fatty acid were always lower than in corresponding control cores. In experiment A without a pulsed input of labeled substrate, surface concentrations of natural *iso*-15:0 fatty acid decreased more with time in sediment with *Yoldia* present (A-II) compared to the control (A-I) (Fig. 8). When a pulse of ^{13}C-labeled substrate was added (Exp. B), concentrations of ^{13}C-labeled *iso*-15:0 fatty acid increased markedly with time in cores without *Yoldia* (Fig. 10). Surface concentrations of this fatty acid increased less when *Yoldia* were present; the increase in concentration was least when animal abundance was highest (Fig. 10). These data imply that the concentration of ^{13}C-*iso*-15:0 fatty acid is controlled by the balance between production from bacterial synthesis and loss due to grazing by *Yoldia* and substrate depletion (series A). It is not clear how efficiently this compound is digested during grazing, and some loss also occurred in

the absence of *Yoldia* (A-I, Fig. 8), so microbial degradation may also cause significant losses. Animal grazing can stimulate rapid growth of microbial populations (Plante *et al.,* 1990), so algal lipid loss may have been more due to increased rates of microbial degradation rather than to direct digestion by *Yoldia.* Faster degradation of *iso*-15:0 fatty acid in the presence of *Yoldia* compared to controls is consistent with faster overall remineralization rates in the bioturbated cases as implied by net ΣCO_2 production patterns (Fig. 6) and increased chloropigment degradation rates (Ingalls *et al.,* 1999).

Significant amounts of ^{13}C-labeled *iso*-15:0 fatty acid (^{13}C-IFA) were present in suspended particles ejected by *Yoldia* (Table 2). In B-IV where animal concentrations were highest, the suspended particle concentration of this compound was higher than in surface sediments. Enrichment of ^{13}C-IFA in suspended particles can occur when *Yoldia* egest particles that are bacterially enriched either before or after ingestion of sediment. After ingestion of sediment, bacterial fatty acid concentrations could increase due to enteric microbial production of ingested labeled algae (Sochard *et al.,* 1979; Nagasawa and Nemoto, 1988; Bradshaw *et al.,* 1990, 1991). However, it is not clear that enteric bacteria could form quickly enough during passage of ^{13}C-labeled dietary material through the gut, so this pathway may not be important. Instead, bacteria can rapidly colonize freshly egested feces produced by grazers (Pomeroy and Deibel, 1980; Jacobsen and Azam, 1984), and in our experiments would produce ^{13}C-IFA from partially digested labeled algae excreted in feces. *Yoldia* may have been selectively feeding on bacteria, leaving behind ^{13}C-IFA depleted surface deposits and egesting particles enriched in ^{13}C-IFA. It is well known that deposit feeders ingest both organic detritus and bacteria attached on particles, including bacteria which have recolonized egested particles (Newell, 1965; Fenchel, 1970; Wetzel, 1976; Yingst, 1976; Lopez *et al.,* 1977; Cammen, 1980). However, it is impossible for us to distinguish between these two types of enrichment mechanisms since bacterially enriched particles in the surface sediment cannot be physically separated from newly-deposited egested feces.

Changes in concentration with time of [13]C-*iso*-15:0 fatty acid and ^{13}C-labeled C_{16} alcohol were similar in sediments (Fig. 10), but the formation pathways of these two compounds differ. As discussed above, [13]C-*iso*-15:0 is biosynthesized by bacteria as a structural component. In contrast, several lines of evidence show that the ^{13}C-C_{16} alcohol has a different mechanism of formation. First, mass spectral analysis (Sun, 1999) shows that [13]C-*iso*-15:0 fatty acid produced during Exp. B was partially labeled, implying that it had been biosynthesized using a mixture of unlabeled carbon from natural organic matter in the sediment and ^{13}C from the labeled algae we added. However, ^{13}C-C_{16} alcohol produced was uniformly labeled, implying that all its C directly originated from the labeled algae added. Second, even though more of both compounds were present in control cores (no *Yoldia*) over time than in *Yoldia* cores, [13]C-*iso*-15:0 fatty acid appeared in suspended particles while ^{13}C-alcohol did not. This suggests that *Yoldia* discriminate between sediment particles and bacteria containing these compounds during egestion and digestion. We have no direct evidence for a particular pathway of formation for the C_{16} alcohol, but

microbial transformation of compounds, e.g., phytol, in the labeled algae is a most likely source.

Apparent degradation rate constants of fatty acids and phytol were similar in sediments (Table 3). However, *Yoldia* significantly discriminated between fatty acids and phytol during digestion, enriching phytol and depleting fatty acids in ejected suspended particles. One possible explanation for this is that *Yoldia* make phytol more available for microbial degradation. Labeled phytol was present in experimental sediments in at least two forms: one as part of the chlorophyll molecule in initially-added algae, and another phytol "released" from chlorophyll by grazing. Phytol existing in a released form may be more efficiently degraded by bacteria, even if it is subsequently esterified or present in some other easily degraded association (Johns *et al.,* 1980; Volkman and Maxwell, 1984; Rontani *et al.,* 1996). Thus, *Yoldia* may enhance degradation of the phytol moiety by changing its availability to microbial decomposition rather than by direct digestion.

5. Conclusions

The deposit-feeder *Yoldia* significantly enhanced degradation of algal lipids in marine sediments. Degradation rate constants of various algal lipids were linearly correlated with abundance of *Yoldia.* This enhancement resulted from *Yoldia's* ability to efficiently mix solid particles containing algal lipids, and to significantly alter solute transport and redox boundaries. Selective grazing of algal detritus and bacteria by *Yoldia* appears to promote degradation by different pathways: regulating dynamics of bacteria growth, directly assimilating fatty acid components, and changing the bioavailability of phytol for further microbial degradation.

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