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Biodiversity and food web structure influence short-term accumulation of sediment organic matter in an experimental seagrass system

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Abstract

We tested the effects of grazer diversity and food chain length on the quantity and quality of accumulated sediment organic matter (SOM) in experimental eelgrass (*Zostera marina*) mesocosms. By use of a factorial manipulation of crustacean grazer species richness and predator presence, we examined the effects of epibenthic consumers on SOM composition by using stable carbon isotopes ($\delta^{13}C$) and lipid biomarker compounds. Grazer species composition strongly influenced nearly all measures of SOM quantity and quality. In particular, increased densities of the grazing amphipod, *Gammarus mucronatus*, decreased accumulation of benthic microalgae (chlorophyll *a*) and the relative abundance of polyunsaturated fatty acids (FA, a proxy for labile algal organic matter) and branched FA (a proxy for bacterial biomass). On average, increasing grazer species richness decreased SOM quantity (percentage of total organic carbon). Increasing food chain length by addition of predatory blue crabs (*Callinectes sapidus*) resulted in a trophic cascade, increasing algal biomass and accumulation of algal organic matter in sediments, and enhancing the quality of SOM. Concomitantly, the relative proportion of bacterial branched FA increased. The identity and number of epibenthic consumers strongly influence accumulation and composition of SOM and the pathways by which it is processed, and these responses are not easily predictable from bulk measurements ($\delta^{13}C$, percentage of total organic carbon) alone.

Benthic ecosystems play an important role in the storage and cycling of organic matter and nutrients. Key variables influencing these processes include animal activities (e.g., bioturbation, bioirrigation, grazing) and structures (e.g., burrows, tubes). Animals influence sediment environmental conditions by controlling the availability of oxygen and other electron acceptors, reworking the sediment, and removing metabolites (Aller 1982; Lee 1992; Aller and Aller 1998). These activities promote degradation of organic matter, thereby influencing global biogeochemical cycles and the preservation of organic carbon in marine sediments (Hedges and Keil 1995). Several experimental studies have demonstrated that marine benthic animal taxa can influence organic matter diagenesis and sediment geochemistry (Aller and Yingst 1985; Kristensen and Blackburn 1987; Sun et al. 1999). However, although these studies have provided many insights, it is important to recognize that in nature, animals do not live as single species but as members of a community. Thus, it is important to understand not only the effects of individual species on sediment biogeochemistry, but also how diverse communities of interacting species influence sediment geochemical processes.

Understanding the effects of diversity is critical because human activities are currently shifting local and global distributions of organisms, and contributing to the sixth major extinction event in the history of life (Chapin et al. 2000). Because of these drastic changes, a growing emphasis has been placed on understanding the interactions between biodiversity and ecosystem processes. For example, studies in terrestrial grasslands have shown that changes in species richness and the identity of plants affect ecosystem processes such as plant productivity and nitrogen cycling (Hector et al. 1999). In comparison, the potential impacts of species losses or changing functional diversity on biogeochemical processes in marine ecosystems are poorly known (Covich et al. 2004; Duffy and Stachowicz 2006). Marine benthic systems in particular are susceptible to human-induced stressors because species tend to be sedentary and unable to avoid disturbance. Previous studies have shown that individual taxa often have profound impacts on both the structure of ecosystems and the rates and pathways of carbon and other important bioelements (Chapin et al. 2000; Downing and Leibold 2002). Yet our understanding of relationships between biodiversity and ecosystem processes in marine systems is still preliminary (Covich et al. 2004; Duffy and Stachowicz 2006).

Recent studies have begun to address this gap. One approach to addressing relationships between diversity and ecosystem processes involves the use of simulation/modeling. Solan et al. (2004), by use of simulation models of benthic infauna, concluded that, on average, loss of marine benthic invertebrate species reduced bioturbation, an important process influencing sediment oxygen concentrations, organic matter diagenesis, and nutrient recycling. These results were driven largely, but not entirely, by the

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presence or absence of the large-bodied burrowing brittlestar, *Amphiura filiformis*, which had a disproportionately large effect. Similarly, a laboratory experiment (Waldbusser et al. 2004) demonstrated that the functional diversity of infaunal invertebrates influenced pore-water profiles of oxygen and pH, as well as sediment–water fluxes of oxygen and phosphate. These studies demonstrate that individual species often have unique impacts on ecosystem processes, that combinations of species can have complementary effects, and that biogeochemical processes often depend on the identity of benthic species as much as on their aggregate biomass. Equally importantly, responses to species extinctions depend on food web structure because biodiversity and trophic structure influence ecosystem properties interactively (Duffy et al. 2005).

Previous studies linking benthic species to sediment biogeochemistry have focused primarily on burrowing infauna. Yet much of the organic matter arriving at the water–sediment interface first passes through the epifaunal community, or is influenced by its activities, before it is deposited to sediments. Thus, it is reasonable to expect that epifaunal and infaunal animal communities influence both the fate of sediment organic matter (SOM), through activities such as bioturbation, as well as the abundance and quality of the SOM that accumulates. The quantity and quality of SOM are important ecosystem properties influencing water quality (e.g., bottom-water dissolved oxygen), distribution of contaminants, and nutrition of benthic organisms. At larger scales, degradation of SOM influences long-term carbon preservation and cycling (Hedges and Keil 1995). Despite the central importance of SOM abundance and quality to benthic ecosystems, and ongoing trends in changing benthic community structure (Thrush and Dayton 2002), to our knowledge, no study to date has specifically examined how marine biodiversity (which we define broadly to include species composition, richness, and relative abundance) influences SOM composition and abundance.

Here we report results of an experiment examining how benthic consumer diversity and food chain length influence the composition of newly deposited (~6 weeks) SOM. This article complements a previous publication reporting responses of the above-ground community in the same experiment (Duffy et al. 2005). Here, we first aimed to characterize the variance among grazer species in their influence on SOM composition and lability. We also predicted that predators would decrease grazer effects, thereby increasing the accumulation of algal organic matter through a trophic cascade, indirectly enhancing SOM quality. To test these hypotheses, we factorially manipulated grazer diversity (species composition and richness) and food chain length (presence/absence of a predator), and measured abundance and quality of accumulated SOM, including total organic carbon (TOC), stable isotopes of carbon ($\delta^{13}C$), and lipid biomarker compounds.

Methods

Experimental design—The experiment factorially crossed two food chain lengths with five grazer treatments (Duffy et al. 2005). We compared a two-level food chain (plants, grazers) with a three-level food chain (plants, grazers, predators). The five grazer treatments included each of four grazer species stocked alone, and all four species together, providing two levels of grazer richness (1 and 4 species) and four one-species treatments. All grazer treatments received the same initial abundance of grazers, following a replacement series design. Grazers included two amphipod taxa, ampithoids (a mixture of *Cymadusa compta* and *Ampithoe longimana*) and *Gammarus mucronatus*; and two isopods, *Erichsonella attenuata* and *Idotea baltica*. These grazers, hereafter referred to by genus or family name, are among the most abundant epifaunal species in local eelgrass beds (Parker et al. 2001; Duffy et al. 2001). The treatments with predators included three juveniles of the blue crab (*Callinectes sapidus*, carapace width 2.0–4.0 cm), an important generalist predator in Chesapeake Bay eelgrass beds (Hines et al. 1990). The control contained neither grazers nor predators. There were five replicate mesocosms of each of the 11 treatments.

The experiment was conducted in May–June 2002 in an array of 113-liter outdoor mesocosm tanks supplied with flowing water from the York River estuary (Duffy et al. 2003, 2005). The water was prefiltered through 150 μm mesh to minimize grazer introductions but allowed passage of microscopic propagules of algae and sessile invertebrates. Seventy-five defaunated eelgrass shoots were planted in clean sand (%TOC was below detection), and 80 individual grazers were added to each treatment. Although initial %TOC was low, seagrasses can grow in a wide range (coarse-grained, organic poor- to fine-grained, organic rich) of sediment types (Hemminga and Duarte 2000), and the initially uniform TOC levels reduced initial sediment heterogeneity among replicates. The initial grazer density was below that which is typical in the field to allow grazer assemblages to adjust through population growth and competition. Four-species treatments received 20 individuals of each grazer species such that all treatments (except grazer-free controls) began with equal total densities of grazers. Three juvenile blue crabs were added a few days later to each predator treatment mesocosm. The experiment ran for 6 weeks (one to three grazer generations), long enough for grazer relative abundances to adjust to natural levels and to approach carrying capacity, at least for the rapidly growing amphipods (Duffy and Harvilicz 2001). The experiment was terminated at 6 weeks to avoid contamination by nontarget grazers entering via the flow-through seawater system, and because plants were entirely consumed in some treatments by that time.

Densities of all the organisms used in our experiment began the experiment within the (admittedly wide) range of abundances found naturally in local eelgrass beds. Crabs were toward the high end of densities observed in local beds in recent years but are well below densities recorded regularly in recent decades. Grazers began the experiment at relatively low densities and increased greatly in the absence of crab predators, probably reflecting at least partial top-down control in nature. The communities that developed in treatments containing *Gammarus* alone or *Erichsonella* alone were most similar to those seen in the

field in supporting relatively healthy, unfouled and undamaged eelgrass.

Bulk SOM—At the termination of the experiment, small sediment cores (2.6-cm diameter) were collected from three approximately equally spaced positions within each mesocosm tank. The upper 1 cm from each core was removed and these upper sections from the three cores were combined into a single precombusted (450°C) jar. The sediment sample was homogenized and aliquots were removed to precombusted glass scintillation vials for benthic chlorophyll *a* and sediment total organic carbon (TOC) analyses. All samples were frozen immediately after collection. Benthic chlorophyll *a* (a measure of benthic microalgal biomass) was determined by the method of Neubauer et al. (2000). TOC and total nitrogen were analyzed by standard methods with a Fisons CHN analyzer (Model EA1108) after removing inorganic carbon (Hedges and Stern 1984). Acetanilide was used as the standard. $\delta^{13}C_{OC}$ was used to examine whether sources of organic carbon varied in response to the experimental treatments. The stable carbon isotope ratios of bulk organic carbon ($\delta^{13}C$) were determined at the stable isotope facility, University of California, Davis (Cloern et al. 2002). Values are reported in the "δ" notation as the per-mil (‰) difference between the sample ratio and the ratio of a standard (PeeDee Belemnite):

$$\delta(‰) = \left(R_{sample}/R_{standard} - 1\right) \times 1{,}000.$$

The analytical precision of these determinations was typically about 0.1 per mil for carbon (Cloern et al. 2002).

Lipid biomarker analysis—Sediment samples were extracted with methylene chloride : methanol (2 : 1, v : v) by using the Bligh and Dyer (1959) method modified for accelerated solvent extraction. After extraction, the samples were partitioned and the organic phase was removed. Hexane was added, the samples were partitioned a second time and the hexane layer added to the organic phase. The combined organic phases sat over anhydrous Na_2SO_4 overnight to remove traces of water and were concentrated to 1 mL by turboevaporation (Zymark Turbo Vap 500).

The total lipid extracts were saponified as described in Canuel and Martens (1993). After saponification, the residue was extracted under basic conditions to yield the neutral fraction (SAP-N). The pH of the saponified residue was subsequently reduced to 2 with HCl, and the acids were extracted (SAP-A). The SAP-A fractions were methylated with BF_3-CH_3OH and purified by silica gel chromatography. The SAP-N fractions were separated into lipid compound classes (Canuel and Martens 1993). The fraction containing the alkanols/sterols was collected and dried under nitrogen, BSTFA (bis(trimethylsilyl) trifluoroacetamide) and acetonitrile were added to each vial, and samples were heated in a heating block for 15 min. Just before gas chromatography (GC) injection, samples were dried and a small volume of hexane (50 μL) and the internal standard were added. Sterols (as trimethylsilyl ethers) were analyzed on a HP 5890 gas chromatograph using a DB-5 column (30 m × 0.20 mm inner diameter) and a flame ionization detector. Conditions for GC analysis followed previously published methods (Zimmerman and Canuel 2001; Arzayus and Canuel 2005). Peaks corresponding to sterols were quantified by an internal standard, 5α(H)-cholestane, added before GC analysis.

The fatty acids (FA; as methyl esters) were analyzed by gas chromatography following previously published procedures (Zimmerman and Canuel 2001 and references therein). Peaks were quantified relative to an internal standard, methyl nonadecanoate, added just before GC analysis. Peak identities of FA and sterols were verified by combined gas chromatography–mass spectrometry (GC-MS) with a Hewlett-Packard 6890 GC with a mass selective detector operated in the electron impact (EI) mode. FA are designated as A : BωC, where A is the total number of carbon atoms, B is the number of double bonds, and C is the position of the first double bond from the aliphatic (ω) end of the molecule. The prefixes "i" and "a" refer to iso and anteiso methyl branched FA (*see* Canuel et al. 1995 and references therein).

Statistical analyses—The experiment was analyzed as a fully factorial two-way ANOVA, with fixed factors food chain length (i.e., presence/absence of crabs, df = 1), grazer diversity (df = 4), and their interaction. The grazer-free control was excluded from statistical analyses because absence of a corresponding control including only crabs would render this analysis nonorthogonal, and because our primary interest was how grazer diversity, rather than mere presence of grazers, influenced ecosystem properties. ANOVAs were conducted on log-transformed data. From these ANOVAs we obtained both *F* tests of significance and estimates of effect strength (i.e., ω^2, percentage variance explained) for both factors and their interaction. To distinguish effects of grazer species richness versus grazer species composition, we partitioned the grazer diversity SS from the ANOVA into two orthogonal components (*see* Duffy et al. 2005 for details): (1) a planned contrast comparing the four-species treatment against all single-species treatments (richness effect), and (2) a planned contrast among the four single-grazer treatments (composition effect). When the effect of grazer species richness was significant, we also calculated Loreau's (1998) statistic D_{max}, a metric of "overyielding," which is positive when the diverse mixture has a larger value of the response variable than does any single component species. D_{max} is often considered a conservative estimate of whether a greater response in a mixture results from interactions among species (a "true" diversity effect), or simply from dominance by a particularly influential species (the "sampling effect").

To explore the influence on SOM of particular grazer species in more detail, we conducted multiple regressions of each SOM response variable against the log-transformed final abundances of each of the four grazer species. To aid in interpreting the biomarker data, we conducted multiple regressions of each SOM response variable against the final biomass of each primary producer group. In addition, factor analysis that used principal components analysis was used to reduce the dimensionality of the data set. The

analysis was conducted by the FA or sterol concentrations of individual compounds or groups of compounds normalized to the sum of all FA (percentage total FA or percentage total sterols). We included TOC, sediment chlorophyll *a* (Chl *a*), and macroalgal biomass in the analysis to aid in the interpretation. Data were transformed by the Orthtran/Varimax method (StatView version 5.0.1). Loadings and scores that use the oblique (i.e., nonorthogonal) solution are presented. The loadings are regression coefficients for predicting the relationship between variables and the defined principal components. The scores express relationships between each of the observations and the identified principal components.

Results

Bulk SOM—Over the course of the 6-week experiment, measurable levels of sediment TOC accumulated in the mesocosms, ranging from 0.41 to 3.04 mg g^{-1} dry weight sediment (0.04 to 0.3 %TOC). Both grazer species composition ($p < 0.001$) and richness ($p < 0.035$) influenced accumulation of sediment TOC (Fig. 1, Table 1), together explaining 30% of the variation in TOC content ($\omega^2 = 0.30$), with the diverse grazer mixtures more strongly reducing TOC accumulation (Fig. 1). Indeed, the overyielding criterion D_{max} (Loreau 1998) was positive for sediment TOC in both absence ($D_{max} = 0.083$) and presence of crabs ($D_{max} = 0.084$), indicating that TOC content was more extreme (approximately 8% lower, in this case) in the diverse grazer treatment than for any single grazer species, a result usually interpreted as indicating a "true" diversity effect, i.e., an effect of interactions among species rather than simply dominance by a particular species. Of the single-species grazer treatments, the accumulation of TOC was lowest in the *Gammarus* (without crab) treatments and highest in the *Idotea* treatments (with or without crab). Because of the short duration of the experiment, total nitrogen content was low (often below detection) and unaffected by grazer species composition, richness, or predator presence. $\delta^{13}C_{OC}$ values ranged from −18.42 to −12.55 ‰, varying significantly among grazer species treatments ($p < 0.0001$), with the most depleted values occurring in the *Gammarus* treatments (±crab) (Fig. 1). Crab predators significantly enriched sediment $\delta^{13}C$ ($p < 0.001$) (Fig. 1).

Changes in epibenthic food web composition also influenced the quality of organic matter that accumulated, as evidenced by differences among treatments in accumulation of benthic Chl *a*, a proxy for sediment microalgae (Duffy et al. 2005). On average, increasing grazer species richness significantly reduced the accumulation of sediment Chl *a* in both the presence and absence of predators. With the exception of *Erichsonella*, individual grazer species each reduced sediment microalgae in the absence of crab predation, whereas crabs tended to reduce the impact of grazers on sediment microalgae (Fig. 1). Treatments containing *Gammarus* accumulated the least Chl *a* (Fig. 1).

FA and sterol biomarker composition—Changes in epibenthic food web composition influenced both the total abundance (ΣFA) and composition of FA biomarkers (Table 1, Fig. 2). Grazer species composition strongly affected accumulation of ΣFA ($\mu g\ g^{-1}$ dry sediment), explaining 29% of the variation in this variable, whereas grazer species richness, presence of predatory crab, and the grazer × crab interaction did not (Table 1). In the single-species grazer treatments with crabs, ΣFA ($\mu g\ g^{-1}$ dry weight sediment) ranged from 17.51 ± 3.52 (mean ± SE, $n = 5$) for ampithoids to 56.47 ± 15.38 (mean ± SE, $n = 5$) for *Erichsonella*. In treatments without crabs, ΣFA ranged

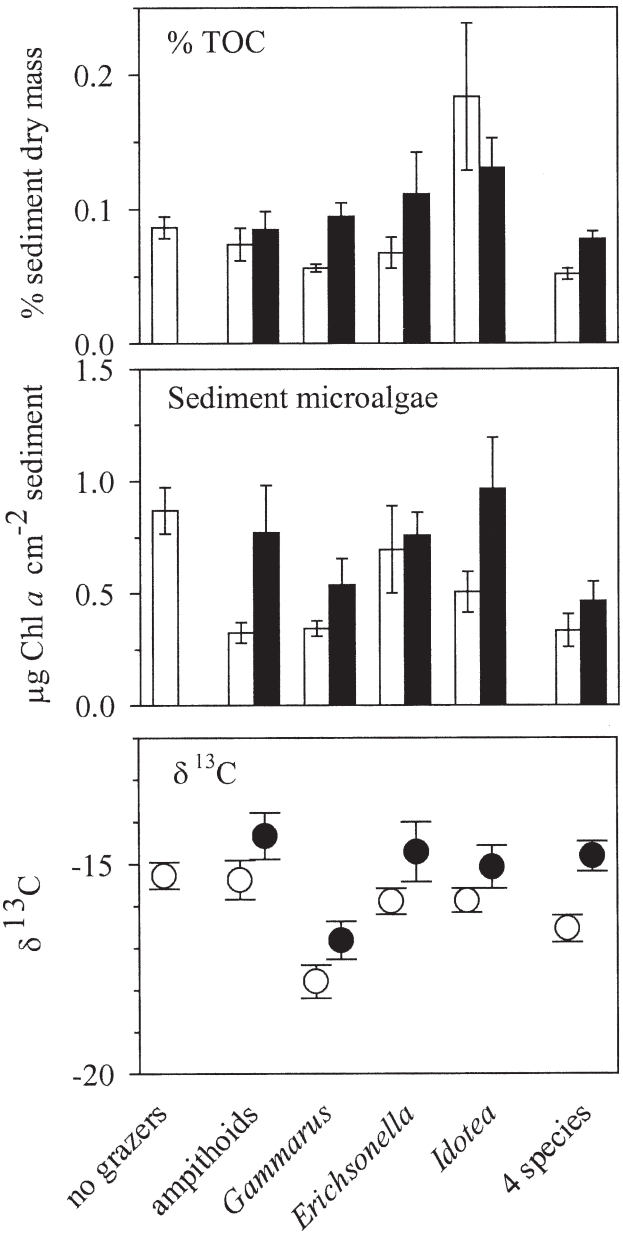

Fig. 1. Influence of grazer species diversity and presence/absence of crab predator on measures of surface SOM abundance (%TOC) and composition (sediment Chl *a* and $\delta^{13}C$ of the organic carbon). Mean ± standard error ($n = 5$) are presented in this and subsequent figures. Solid symbols represent treatments with crabs, and open symbols represent treatments without crabs in this and subsequent figures.

Table 1. Tests of significance and estimated magnitudes of effect (ω^2) of within-trophic level diversity (grazer), number of trophic levels (crab), and their interaction, on organic biomarker concentrations in sediments.

Response	Grazer					Crab (df=1)			Grazer × crab (df=4)			Error (df=38–40)	
	Richness (df=1)		Composition (df=3)										
	MS*	p	MS	p	ω^2	MS	p	ω^2	MS	p	ω^2	MS	ω^2
Organic C (% sediment dry mass)	0.008	**0.035**	0.039	**<0.001**	0.30	0.004	0.139	0.02	0.002	0.272	0.02	0.002	0.66
Total N (% sediment dry mass)	0.000	0.792	0.000	>0.10	0.01	0.000	0.788	0.00	0.000	0.167	0.06	0.000	0.95
Total FAs (μg mg^{-1} dry sediment)	720.480	0.164	2,565.680	**<0.001**	0.29	38.560	0.745	0.00	217.856	0.660	0.00	359.060	0.75
% PUFA†	31.039	0.264	461.230	**<0.005**	0.21	229.151	**0.004**	0.11	46.911	0.122	0.05	24.155	0.64
% C20-C22 PUFA	7.132	0.578	191.400	**<0.001**	0.27	87.595	0.057	0.04	58.955	0.051	0.08	22.712	0.62
% branched FA	1.337	0.137	8.352	**<0.01**	0.19	4.375	**0.009**	0.10	0.122	0.931	0.00	0.580	0.76
% long-chain FA	0.064	0.922	32.900	**<0.005**	0.20	1.034	0.682	0.00	5.861	0.439	0.00	6.087	0.82
% short-chain FA	855.779	**0.042**	1,684.220	**<0.001**	0.37	14.279	0.788	0.00	7.894	0.997	0.00	194.513	0.70
Total sterols (ng mg^{-1} dry sediment)	21,018,252	**0.002**	45,506,954	**<0.001**	0.39	4,419,793	0.132	0.02	1,329,272	0.589	0.00	1,866,086	0.61
% brassicasterol	0.008	0.977	14.645	>0.10	0.01	11.543	0.290	0.00	7.471	0.566	0.00	10.004	1.00
% dinosterol	2.986	**0.034**	69.436	**<0.001**	0.71	0.431	0.408	0.00	0.242	0.812	0.00	0.616	0.31
% stigmasterol	5.974	0.392	2.532	>0.75	0.00	9.572	0.280	0.00	2.578	0.861	0.00	7.980	1.00
% cholesterol	1.277	0.811	77.500	**<0.025**	0.10	72.283	0.078	0.03	72.224	**0.021**	0.13	22.040	0.74
% 24-methylenecholesterol	7.337	0.165	27.105	**<0.001**	0.27	2.943	0.375	0.00	7.710	0.099	0.06	3.653	0.67
% 24-ethylcholesterol	47.930	0.221	484.900	**<0.001**	0.46	44.634	0.237	0.01	39.255	0.299	0.01	30.895	0.52
Mean					0.22			0.03			0.02		0.75

* MS = mean square.
† Response variables are percentage of total FA or percentage of total sterols, unless otherwise noted. Data were analyzed by two-factor Model I ANOVAs. p values <0.05 are in bold. Negative estimates of ω^2 are reported as zeros.

from 13.35 ± 3.01 (mean ± SE, $n = 5$) μg g^{-1} dry sediment for *Gammarus* to 25.95 ± 5.12 (mean ± SE, $n = 5$) μg g^{-1} dry sediment for *Erichsonella*.

Both species composition and richness of grazers strongly affected relative abundance (percentage total FA) of short-chain ($C_{12:0}$, $C_{14:0}$, $C_{16:0}$) FA, explaining 37% of the variation (Table 1, Fig. 2). The overyielding statistic for short-chained FA was negative in both absence ($D_{max} = -0.155$) and presence of crabs ($D_{max} = -0.154$), indicating that values in the diverse grazer assemblage did not exceed those of the most extreme single grazer species, i.e. that the significant richness effect in this case was probably attributable to dominance by a particular species rather than by interactions among them. Grazer species composition, but not richness, influenced the relative abundance of branched (iso and anteiso C_{13}, C_{15}, and C_{17}), polyunsaturated (PU) (C_{18}, C_{20}, and C_{22} PUFA), and long-chain saturated ($C_{22:0}$-$C_{30:0}$) FA, explaining about 20% of the variation in each case (Table 1, Fig. 2). Treatments with crabs had elevated levels of polyunsaturated and branched FA ($p < 0.01$; Table 1), explaining ~10% of the variance in each of these variables, and indicating that predation on the mesograzers influenced the quality of carbon accumulating in surface sediments. Sedimentary PUFA appeared to represent labile microalgal material as percentage PUFA was significantly and positively related to sediment microalgal biomass (Chl *a*, Table 2). In contrast, percentage of long-chain FA (LCFA) was positively related to macroalgal biomass (Table 2). Percentage of branched FA was positively related to benthic microalgal Chl *a* (Table 2), presumably reflecting bacterial response to labile organic matter produced by benthic microalgae.

Total sterol abundance and sterol composition were also influenced by grazer species composition (Table 1; Fig. 3). In the single-species grazer treatments, sterol abundances were lowest in the *Gammarus* (no crab) treatment and highest in the ampithoids (no crab) treatment. Overall, the accumulation of total sterols (μg g^{-1} dry sediment) was lowest in the "all species" treatment ($p = 0.0018$). Cholest-5-en-3β-ol (cholesterol) and 24-ethylcholest-5-en-3β-ol were generally the dominant sterols. 24-Ethylcholest-5-en-3β-ol often showed a pattern opposite to that of cholesterol. The presence of crab predators and grazer species richness had no effect on sterol composition (Table 1).

Principal components 1 and 2 (PC1 and PC2) explained 21.5% and 16.5% of the variance, respectively (Fig. 4). Loadings on PC1 were most positive for dinosterol and 24-methylenecholesterol, whereas loadings for all other biomarkers were either near the origin or somewhat negative (e.g., 24-ethylcholesterol, cholesterol, Fig. 4a). PC1 distinguished between sterols representing a subgroup of microalgae (represented by dinosterol and 24-methylenecholesterol) versus other biomarkers. Loadings on PC2 were highly positive for PUFA and sedimentary Chl *a* and slightly negative for LCFA, dinosterol and cholesterol (Fig. 4a). BrFA (bacteria) had intermediate positive loadings on PC2.

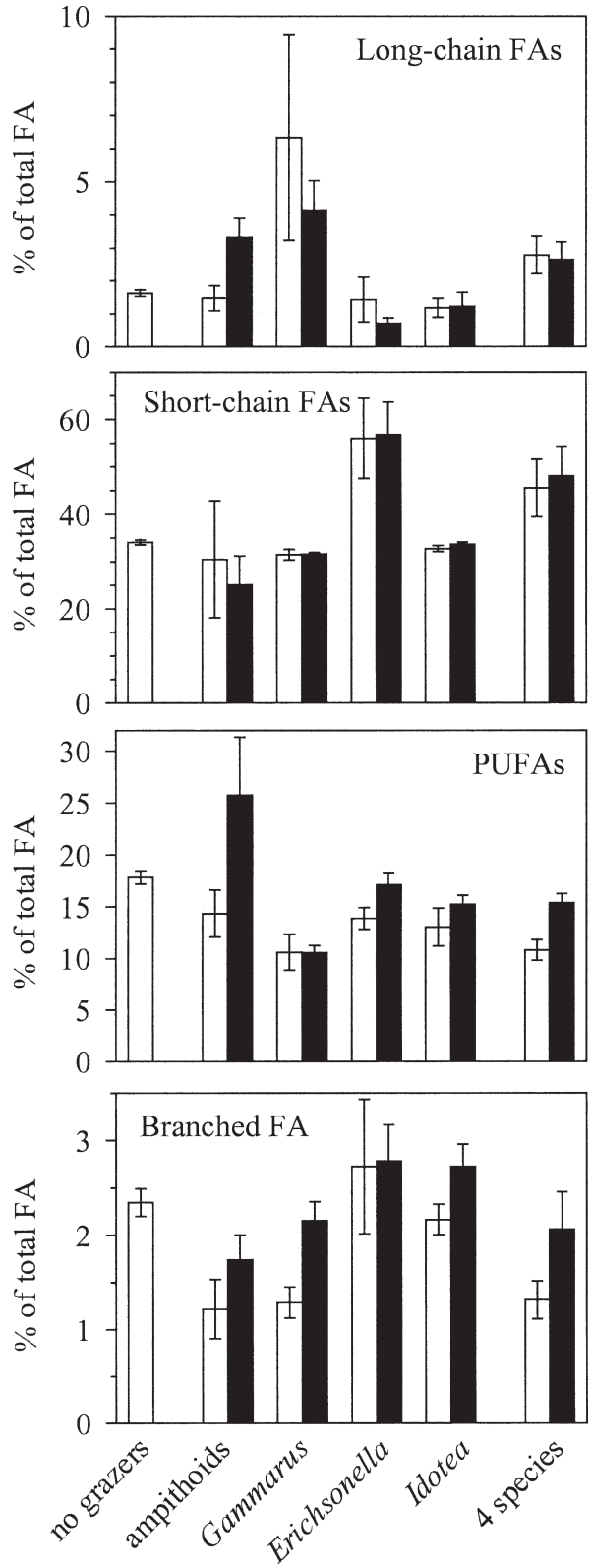

Fig. 2. Influence of grazer species diversity and presence/absence of crab predator on FA composition of surface sediments. FA groupings are expressed relative to total FA abundance. Long-chain FA ($C_{22:0}$-$C_{30:0}$) reflect contributions from higher plants/macroalgae, short-chain FA ($C_{12:0}$-$C_{16:0}$) derive primarily from aquatic (algal and microbial) sources, polyunsaturated FA (PUFA) represent labile, algal-derived sources, and branched (iso and anteiso) FA reflect contributions from heterotrophic bacteria (*see* text for additional details pertaining to source assignments).

Scores on PC1 were most positive for *Idotea* (with crabs) and *Gammarus* (with crabs), and most negative for the ampithoid treatments (±crabs) (Fig. 4b). PC2 provided resolution between samples with crabs versus those without; treatments without crabs generally plotted in the negative region of PC2. With the exception of *Ericsonella*, the treatments with crabs (Fig. 4b, solid symbols) had more positive values than the corresponding treatments without crabs (Fig. 4b, open symbols). The Control (no crab) treatment was positive for both PC1 and PC2, differing from all other grazer (no crab) treatments and indicating differences in the composition of SOM accumulating in treatments with grazers versus those without.

Multiple regressions suggested that grazing amphipods (ampithoids and, especially, *Gammarus mucronatus*) were indirectly responsible for most of the trends in SOM quantity and composition (Table 3). Across all treatments, final abundance of *Gammarus* was negatively correlated with sediment microalgal biomass (Chl *a*), %TOC, $\delta^{13}C$, total FA, total sterols, percentage PUFA, and percentage branched FA. *Gammarus* abundance correlated positively with percentage long-chain FA. Ampithoids influenced several of the SOM parameters but often in the opposite direction to *Gammarus*. Ampithoid abundance correlated positively with %TOC, $\delta^{13}C$, and %PUFA, but negatively with total FA and several sterols. In contrast, abundances of the isopods, *Idotea* and *Erichsonella*, were correlated with few of the SOM variables.

Discussion

SOM sources—Seagrass plants help internalize nutrient cycles within the seagrass ecosystem by producing and trapping detritus and dissolved organic matter (Phillips and Meñez 1988). Previous studies (e.g., Holmer and Nielsen 1997; McGlathery et al. 1998; Dudley et al. 2001) have shown that seagrasses can profoundly affect the chemical and microbiological characteristics of sediments through production and burial of detritus, altering fluxes of O_2, DOM release from roots and rhizomes, and nutrient consumption, and by supporting diverse biogeochemically active benthic invertebrates (Moriarty and Boon 1989). Seagrass influence on such processes can greatly alter the quality of organic matter available to benthic organisms and rates of organic matter degradation by detritus-based and herbivore food webs (Boschker et al. 2000).

In addition to the well-recognized influence of seagrasses on sediment biogeochemistry, there is a wealth of evidence that epibenthic grazers and predators can have strong and far-reaching effects on the biomass, composition, and productivity of seagrass communities (van Montfrans et al. 1984; Hughes et al. 2004). It therefore stands to reason that such consumer impacts may also cascade down to affect organic matter dynamics in seagrass ecosystems. In

Table 2. Results of multiple regression of sediment organic matter variables against final biomass of primary producer groups. Results are from stepwise regressions with threshold for entry and removal from model at $p = 0.05$. Regressions also included epiphytic microalgae, diatom mat biomass, and cyanobacterial biomass as independent variables but these were never significant. Response variables are percentage of total FA or percentage of total sterols, unless otherwise noted. Only statistically significant ($p<0.05$) results are reported.

	Sediment microalgae		Macroalgae		*Zostera*		Total
Grazer	Coefficient	Partial r^2	Coefficient	Partial r^2	Coefficient	Partial r^2	Model r^2
Total organic C (% sediment dry mass)					−0.003	0.075	0.075
δ^{13}C (per mil)	1.539	0.160	−0.057	0.105			0.265
Total FA (μg mg^{-1} TOC)							
% PUFA	5.871	0.115					0.115
% branched FA	1.002	0.166					0.166
% long-chain FA			0.181	0.259			0.259
% short-chain FA							
Total sterols (μg mg^{-1} TOC)	1.456	0.083			−0.112	0.106	0.188
% brassicasterol							
% dinosterol					0.127	0.155	0.155
% stigmasterol							
% cholesterol							
% 24-methylenecholesterol			0.110	0.129			0.129
% 24-ethylcholesterol							

this study, we showed experimentally that the structure of the epibenthic animal community strongly influenced the abundance and quality of organic matter accumulating in seagrass sediments, mirroring similarly strong impacts of the epibenthic community on above-ground variables in the same experiment (Duffy et al. 2005). Specifically, species composition of epibenthic grazers strongly affected nearly all response variables measured. Changes in food chain length (presence or absence of predators) had less pervasive effects on sediment geochemistry, but significantly influenced both lability of deposited organic matter (percentage PUFA) and contributions from heterotrophic bacteria (percentage branched FA). These latter results suggest that the enhanced biomass of macro- and epiphytic microalgae, shown previously to result from cascading impacts of crab predation in this same experiment (Duffy et al. 2005), are also reflected in short-term accumulation of labile organic matter in the sediments and enhanced response of bacteria.

Bulk SOM measurements (benthic Chl *a*, δ^{13}C) and lipid biomarker compounds indicate that the grazer community primarily influenced the accumulation of algal and bacterial sources of organic matter, as opposed to vascular plant sources, over the timeframe of the experiment. Accumulation of short-chain FA ($C_{12:0}$-$C_{16:0}$) dominated over long-chain FA ($C_{22:0}$-$C_{30:0}$), consistent with microalgal and/or bacterial sources of organic matter. To evaluate the relative contributions of higher plant (i.e., eelgrass) versus algal/microbial sources, we calculated ratios of long-chain FA (normally considered to be associated with vascular plants) to short-chain FA (bacteria, algae) by using the terrestrial to aquatic ratio (TAR_{FA}) developed by Meyers (1997). Across all treatments, the mean ± SD TAR_{FA} was 0.09 ± 0.12, supporting the dominance of microbial sources. However, unlike other vascular plants, long-chain FA are not abundant in *Z. marina*, the only vascular plant source in our study (Canuel et al. 1997) and accordingly were not correlated with the final biomass of *Z. marina*. Interestingly, long-chain FA were strongly positively correlated to total macroalgal biomass, and more specifically to biomass of the red alga *Polysiphonia* ($r^2 = 0.24$; $p < 0.0001$ and $r^2 = 0.27$; $p < 0.0001$, respectively), the dominant macroalga in this experiment (J.E. Duffy et al. unpubl. data). This suggests that the dominant macroalga may be the source of the long-chain FA accumulating in the surface sediments and that its FA composition should be further investigated. Trace levels of long-chain FA have been found previously in diatoms (Volkman et al. 1980). Additionally, long-chain FA may derive from incoming estuarine water. Although large detritus and grazers were removed by prefiltration through 150 μm mesh, microscopic propagules and small detritus from the adjacent estuary could enter the mesocosms.

Even-numbered polyunsaturated FA (percentage C_{16}-C_{22} PUFA) are considered proxies for "fresh" algal material (Canuel and Martens 1993 and references therein). Supporting this generalization, the relative abundance of PUFA (percentage PUFA) was positively correlated with sediment microalgal biomass (Chl *a*) ($r^2 = 0.10$; $p = 0.011$) (Table 2). These variables also had strong loadings on PC2 and plotted in the same region of the PC2 versus PC1 biplot, indicating that they were influenced similarly by the grazer treatments (Fig. 4a). Because these proxies (percentage PUFA and sediment Chl *a*) derive from the labile fraction of SOM, we interpret factor 2 as an index for separating the most labile sources of organic matter from other SOM sources. Iso and anteiso branched FA are considered biomarkers for some groups of bacteria (Gillan and Johns 1986; Kaneda 1991; Boschker et al. 2000). Branched FA were positively correlated with sediment algal biomass ($r^2 = 0.15$; $p = 0.002$), suggesting that these compounds represent bacteria associated with the sediment microalgal community or that the sediment bacterial community is responding to the availability of labile (algal)

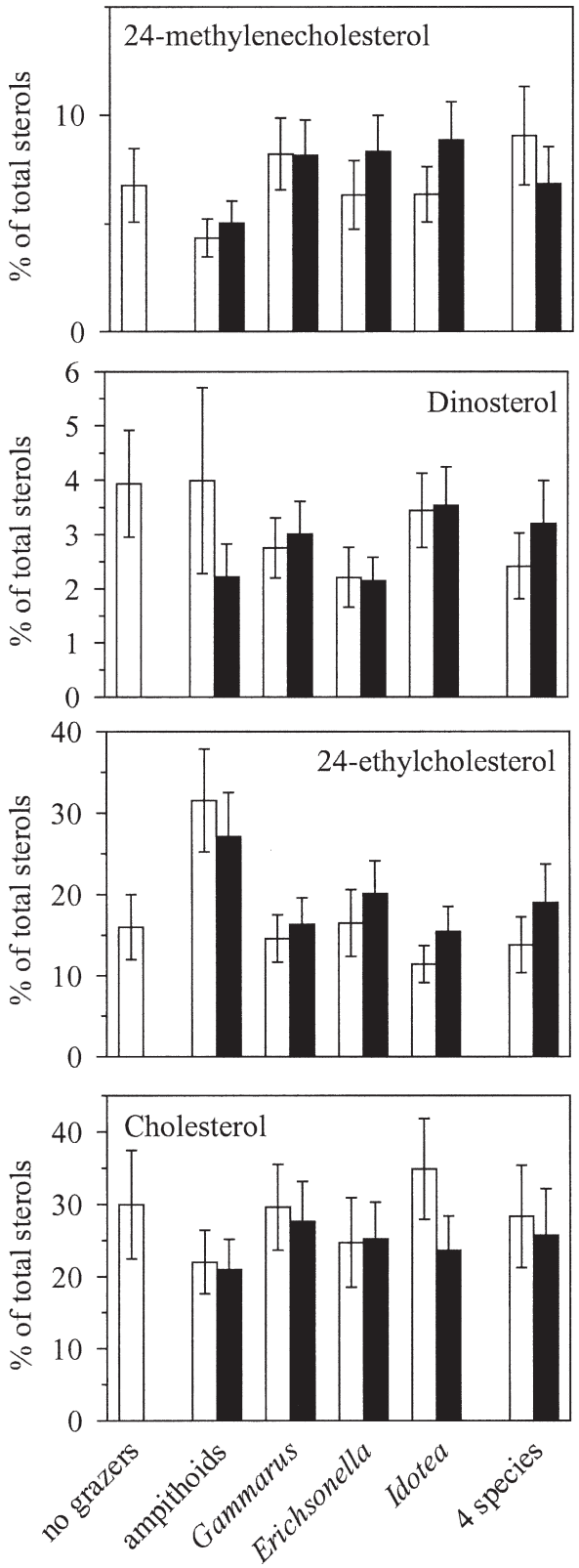

Fig. 3. Influence of grazer species diversity and presence/absence of crab predator on sterol composition of surface sediments. Sterol biomarkers are expressed relative to total sterol abundance. 24-Methylenecholesterol is derived primarily from diatoms, dinosterol represents contributions from dinoflagellates, and cholesterol is the dominant sterol found in crustaceans. 24-Ethylcholesterol is the dominant sterol in *Z. marina* but is also present in algae and cyanobacteria at trace levels. *See* text for additional details pertaining to source assignments.

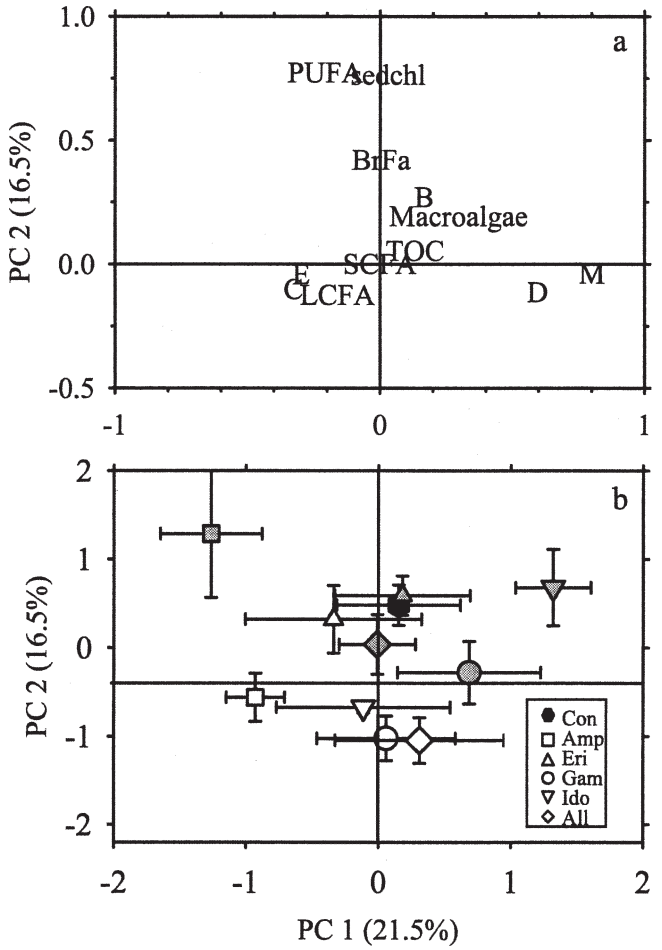

Fig. 4. Results from principal components analysis (PCA) showing loadings and scores for the two dominant principal components (PC) that together explain 38% of the variance. (a) Loadings for fatty acid and sterol biomarkers. Sterols are presented as letters: C = cholesterol; B = brassicasterol; E = 24-ethylcholesterol; D = dinosterol; M = 24-methylenecholesterol. Fatty acid abbreviations are given in the text. (b) Mean ± SE of PCA scores for grazer treatments. Con = control; Amp = ampithoids; Eri = *Ericsonella*; Gam = *Gammarus*; Ido = *Idotea*; All = all grazers. Open symbols represent grazer treatments without crabs, gray symbols represent treatments with crabs, and black hexagon represents control. Generally, the treatments with crabs (gray symbols) have more positive scores on PC2 than the corresponding treatments without crabs (open symbols).

organic matter. Like PUFA and sediment Chl *a*, Branched FA had positive loadings on PC2, consistent with their association with labile SOM (Fig. 4a). Interestingly, contributions of both the sediment microalgal biomarkers (PUFA) and bacterial biomarkers (branched FA) were significantly enhanced by adding predatory crabs (Table 1),

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Table 3. Results of multiple regression of sediment organic matter variables against log abundance of grazer species. Results are from stepwise regressions with threshold for entry and removal from model at $p = 0.05$. Response variables are percentage of total FA or percentage of total sterols, unless otherwise noted. Only statistically significant relationships ($p < 0.05$) are reported.

	Gammarus		Ampithoids		*Idotea*		*Erichsonella*		Total
Grazer	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2	r^2
Sediment Chl *a*	−0.115	0.188							0.188
Total organic C (% sediment dry mass)	−0.013	0.078	0.014	0.087					0.165
Total N (% sediment dry mass)									
δ^{13}C (per mil)	−0.482	0.198	0.411	0.177					0.375
Total FA (μg mg^{-1} TOC)	−4.274	0.068	−4.483	0.090					0.158
% PUFA	−2.275	0.218	1.378	0.093					0.311
% branched FA	−0.230	0.142	−0.160	0.063					0.205
% long-chain FA	0.787	0.153							0.153
% short-chain FA									
Total sterols (μg mg^{-1} TOC)	−0.522	0.144					−0.485	0.069	0.213
% brassicasterol									
% dinosterol			−0.553	0.252					0.252
% stigmasterol									
% cholesterol			−1.207	0.084	2.035	0.169			0.253
% 24-methylenecholesterol			−0.477	0.078					0.078
% 24-ethylcholesterol			2.952	0.311	−2.504	0.121			0.432

mirroring the enhancement of sediment algal biomass via the trophic cascade described previously (Duffy et al. 2005). This is consistent with the hypothesis that crabs inhibit grazer activities, leading to accumulation of labile SOM and is illustrated by the results from the principal components analysis and our interpretation that PC2 resolves between SOM components on the basis of their lability (Fig. 4). With the exception of *Erichsonella*, the treatments with crabs (solid symbols) had more positive values than the corresponding treatments without crabs (open symbols), which generally plotted in negative region of PC2.

Compounds derived from microalgal, vascular plant, and crustacean sources dominated the sterol biomarkers. Dominating the sterol distribution was cholesterol (Fig. 3), the most abundant sterol in crustaceans, but which also occurs at low levels in many microalgae (Volkman 1986). Sterols, such as 24-methylenecholesterol and brassicasterol, are biomarkers for diatoms and other species of microalgae (Volkman 1986), and comprised 15–22% of the total sterol distribution (Fig. 3). Dinosterol, a sterol derived from dinoflagellates (Volkman 1986), made up a smaller portion of the sterol distribution (generally <5% total sterols). Interestingly, the diatom sterols were not correlated to sediment Chl *a*. This suggests that these sterols may derive from epiphytes or phytoplankton or that benthic microalgal communities contained substantial densities of non-diatom microalgae, such as dinoflagellates and/or cyanobacteria. Alternatively, the reactivity of Chl *a* may be greater than for sterol biomarkers; thus, Chl *a* may reflect ''fresher'' algal material, whereas the sterols may reflect a mixture of fresh and detrital algae. This is consistent with the results from the principal components analysis showing resolution between labile compounds such as PUFA and sediment Chl *a* versus most of the sterols (Fig. 4a).

Traditionally, 24-ethylcholest-5-en-3β-ol, 24-ethylcholest-5,22-dien-3β-ol (stigmasterol), and 24-methylcholest-5-en-3β-ol (campesterol) have been used as biomarkers for higher plants (Volkman 1986). Previous work identified 24-ethylcholest-5-en-3β-ol as the dominant sterol in *Z. marina* (Canuel et al. 1997). However, these so-called plant sterols can occur in algae as well (Volkman 1986; Volkman et al. 1998). In our study, 24-ethylcholest-5-en-3β-ol was abundant in surface sediments but varied considerably in its relative abundance (12–43% total sterols). This compound was not correlated with final biomass of total algae, *Z. marina*, or sediment Chl *a*, suggesting that it may be derived from a mixture of sources or by a source (e.g., cyanobacteria) not evaluated in our study.

Together, the biomarker results indicate that the SOM pool was dominated by contributions from microalgae and bacteria. This contrasts with field studies where seagrass detritus has been shown to accumulate in the sediments associated with seagrass beds (Hemminga and Duarte 2000). However, this aspect of our results may reflect the short timeframe of our experiment (6 weeks), under which it seems reasonable to expect a dominant influence of organisms with shorter response times (microbes). Recent work has shown that microalgae can be a major source of SOM in seagrass beds, often driving microbial degradation processes (Boschker et al. 2000; Kennedy et al. 2004). Despite the clear responses in the microbial biomarkers, we do not believe that the accumulation of SOM reflects only the benthic microbial community response. In subsequent mesocosm experiments and complementary field studies we have examined the abundance of both phospholipid-linked FA and total FA in both natural and experimental seagrass beds. Phospholipid-linked FA should reflect contributions from viable microbial biomass (microalgae and bacteria), while total FA should reflect contributions from both viable biomass and detritus. From this work, we find that phospholipid-linked FA comprise approximately 10% of total FA in the mesocosms and 3–27% in natural seagrass beds (Spivak, unpubl. data). These data suggest that our

experiments likely influence *both* the accumulation of microbial biomass as well as detritus. Future experiments should examine the influence of epibenthic food web structure on the accumulation of SOM and sediment biogeochemistry at longer timescales.

Influence of the epibenthic animal community on SOM—Previous studies have shown that responses of marine benthic ecosystems to species loss can vary considerably with species identity because different species often exert unequal effects on benthic processes (Emmerson et al. 2001; Duffy et al. 2001; Solan et al. 2004). Furthermore, ecosystem-level responses to species extinctions also depend on the trophic level from which species are lost (Duffy et al. 2005). A goal of our study was to elucidate how species identity and richness of epibenthic grazers, and of predators, influenced accumulation of SOM. We hypothesized that individual grazer species would influence the accumulation of SOM differentially as a result in known differences in feeding modes, mobility, and vulnerability to predators (Duffy and Hay 2000; Duffy and Harvilicz 2001; Duffy et al. 2005). *G. mucronatus* is highly mobile and feeds on a variety of algal sources, including epiphytes, benthic microalgae, and macroalgae (Duffy and Harvilicz 2001), as well as on detritus. In contrast, *C. compta* is a relatively sedentary, tube-building amphipod that lives on the seagrass blades and appears to feed primarily on epiphytes. The isopod *E. attenuata* also feeds primarily on epiphytic microalgae, whereas the isopod *I. balthica* feeds on microalgae, macroalgae, seagrasses, and even on juveniles of other grazers (Duffy et al. 2001; Bostrom and Mattila 2005). Both isopods are strongly depressed by crab predation, whereas the amphipods are much less affected (Duffy et al. 2005). Thus, grazer species composition is likely to influence biomass and species composition of primary producers and, by extension, quality, and quantity of organic matter delivery to sediments.

We used multiple linear regression analysis to examine relationships between the final grazer abundance and measures of SOM abundance and quality (Table 3). Overall, *Gammarus* and ampithoids had the largest number of statistically significant relationships with TOC and measures of SOM composition (Table 3). In particular, *Gammarus* abundance was negatively related to sediment Chl *a*, %PUFA (a measure of labile, algal-derived material), and %BrFA (a measure of biomass of heterotrophic bacteria). We suspect that this dominance of SOM effects by the two amphipods (Fig. 1, Table 3) reflects their high mobility and the habit, apparently unique to *Gammarus* among the grazer species we studied, of feeding at the sediment surface. The negative effect of *Gammarus* on benthic microalgae also appeared to influence other compartments of SOM, notably decreasing the abundance of labile organic matter, including PUFA, in surface sediments. Presumably in response to this decline in labile organic matter availability, contributions from heterotrophic bacteria (percentage branched FA) were also reduced by grazing amphipods. These findings are consistent with results from freshwater aquatic systems where litter decomposition and process rates were found to vary in stream microcosms with species identity and functional feeding groups (Jonsson and Malmqvist 2003). At the same time, *Gammarus* increased abundance of the macroalga *Polysiphonia* sp. in our experiment (Duffy et al. 2005), which appears to explain the positive relationship between *Gammarus* abundance and long-chain FA (Table 3).

In contrast to *Gammarus*, ampithoids increased TOC, %PUFA, and 24-ethylcholest-5-en-3β-ol, and negatively affected many of the sterol biomarkers (Table 3). The ampithoids are relatively sedentary, build tubes on the eelgrass blades, and graze on both epiphytes and macroalgae (although they also eat eelgrass when algal food is in short supply; Duffy et al. 2003). Thus, we expected them to have little impact on the accumulation of benthic microalgae, consistent with higher %PUFA and TOC found in the surface sediments. Interestingly, however, we found no significant relationship between ampithoids and benthic Chl *a*. Instead, the strongest positive relationship was between ampithoids and %24-ethylcholest-5-en-3β-ol, the dominant sterol in *Z. marina* (Canuel et al. 1997) but also present in some microalgae and cyanobacteria (Volkman 1986). Together, these results are congruent with previous studies (Duffy and Harvilicz 2001) showing that subtle differences in diet between grazer taxa can result in substantial differences in biomass and composition of algae and other components of the fouling assemblage on macrophytes. These, in turn, influence the abundance and quality of SOM.

Trophic level influences on SOM—Most previous studies exploring potential effects of diversity on ecosystem properties have been limited to a single trophic level, precluding examination of the full range of bottom-up and top-down effects (Duffy 2002; Covich et al. 2004). Yet the effects of declining biodiversity surely differ depending on the trophic level of the species lost and its influence on adjacent (horizontal) trophic levels. Moreover, the effects of changing diversity within a trophic level can be strongly influenced by food chain length and vice versa (Duffy et al. 2005). Further exploration of how diversity at different trophic levels affects ecosystem-level properties, including biogeochemistry, is needed to develop a predictive framework for understanding consequences of species loss and for effective environmental policies for managing coastal ecosystems (Duffy 2002; Solan et al. 2004).

A primary goal of our study was to elucidate how effects of individual grazer species on the accumulation of SOM were influenced by the presence/absence of predators. We found two parameters (percentage PUFA and percentage branched FA) for which both grazer composition and the presence/absence of crabs significantly influenced SOM composition (Table 1). The presence of predatory crabs generally enhanced accumulation of %PUFA, a measure of labile, algal organic matter. In these same treatments, there was a coincident increase in percentage of branched FA, a measure of sediment heterotrophic bacterial biomass. These data suggest the presence of a trophic cascade in which crabs reduce the effects of grazers either through predation or by inhibiting their activities (Duffy et al. 2005). As a result, algal material accumulates at the

sediment surface, leading to an increase in bacterial biomass (percentage branched FA). Previous studies have shown that bacteria respond to the availability of labile organic matter at the sediment surface (Canuel and Martens 1993). In this case, crabs promote algal biomass accumulation (Duffy et al. 2005), and presumably also accumulation of labile organic matter in sediments, by inhibiting the effects of grazers. These results imply that food web structure and diversity can influence not only the accumulation of bulk organic matter but also the pathways by which the SOM is processed. In the absence of crabs, algal material is processed by epibenthic grazers, reducing the amount deposited to the sediments; while in the presence of crabs, grazers are inhibited, algal material accumulates in the surface sediments, and there appears to be a response by sediment microbes.

Our findings present several intriguing contrasts with those of previous studies testing effects of grazer diversity and food chain length on the epibenthic community in this system. First, previous research suggested complementarity among grazers, i.e., that differences among species in feeding or other activities resulted in higher grazer biomass yield or more efficient feeding in diverse grazer mixtures than in any single monoculture (Duffy et al. 2003, 2005). Second, grazer diversity interacted with food chain length (predator presence) to influence several components of the above-ground community in the same experiment discussed in this paper (Duffy et al. 2005). In contrast, we found that grazer effects on SOM were dominated by one or both amphipod species (Table 3) and that there were few interactions between the ''horizontal'' (grazer species composition and richness) and ''vertical'' (food chain length) components of diversity (Table 1). We suspect that the apparent inconsistency between studies stems from the fact that only a subset of these grazers interact substantially with the sediment. Previous work (Duffy et al. 2001, 2003, 2005) showed that all of the crustacean grazers in this system strongly influence epiphytic algae, and most also have strong, but divergent, impacts on macroalgae and or eelgrass. These disparate impacts on above-ground primary producers and fouling invertebrates resulted in the complementary effects reported previously (Duffy et al. 2003). In contrast, sediment microalgal and SOM characteristics were affected almost exclusively by the ampithoid and *Gammarus* amphipods (Table 3). Interestingly, it is these same amphipods that were largely unaffected by predation in the previous experiment (Duffy et al. 2005), explaining why we found few significant interactions between predators and grazer diversity on SOM characteristics (Table 1). The strong effects of amphipods (especially *Gammarus*) on SOM characteristics highlight a previously unappreciated role of grazer diversity in this system, namely that a grazer with little impact on above-ground macrophytes nevertheless strongly influences sediment-associated algae and organic matter.

There is another inconsistency between this and previous studies that is more difficult to explain, however. Duffy et al. (2003) found that sediment organic carbon actually increased with increasing grazer species richness, a curious finding suggested to reflect greater microalgal biomass growing on the well-lit sediment surface where diverse grazer assemblages had denuded much of the macroalgae and eelgrass. In direct contrast, we found that sediment organic carbon was lowest in the diverse grazer treatment (Fig. 1, Table 1). Although we cannot definitively resolve the discrepancy between the experiments, we suspect that the lower sediment organic carbon at high grazer diversity is likely to be the more typical pattern in this system, reflecting intense grazing on sediment microalgae in the diverse grazer assemblages, in which most edible epiphytic and macroalgae had already been consumed by the end of the experiment.

In summary, our data indicate that benthic consumer species composition and food chain length strongly influenced the composition of newly deposited (~6 weeks) SOM. Invertebrate grazer species influenced SOM composition and lability differentially as a result of differences in feeding preferences, mobility, and microhabitat use. In particular, the generalist grazer-detritivore, *Gammarus mucronatus*, negatively affected accumulation of sediment microalgae, thereby influencing the accumulation and availability of sediment labile organic matter. Crab predators decreased grazer impact through a trophic cascade, thereby indirectly increasing the accumulation of algal organic matter, indirectly enhancing SOM quality and sediment bacterial response. Results from this study illustrate that not only bulk biomass but also species composition and trophic structure of the epibenthic community can strongly influence SOM accumulation, with implications for the accumulation of sediment carbon and the pathways by which carbon is processed.

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