

Microalgal-meiofaunal trophic relationships in muddy intertidal estuarine sediments

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ABSTRACT: The determination of the primary factors controlling carbon (C) transfer rates *in situ* are a basic requirement for developing a mechanistic view of the processes that regulate benthic microbial community structure and function. In many estuarine ecosystems, the base of the food web is dominated by microalgal production; however, information on the quantitative relationships and process rates of meiofaunal grazers and benthic microalgal (BMA) producers is limited to a few habitats and short temporal scales. The primary objective of this study was to examine the trophic interactions between meiofaunal grazers and BMA producers to determine if grazing is a primary limiting factor for BMA biomass and productivity in Terrebonne Bay, Louisiana. Sediment cores were collected from 24 intertidal locations in June 1999 and January 2000 to quantify meiofaunal abundance and grazing rates as well as BMA biomass, community composition and productivity. In June, the benthic community was characterized by high meiofaunal abundances, while BMA showed lower biomass and a shift in community composition towards increased cyanobacteria relative abundance. Measurements in January showed lower meiofaunal abundances, but high BMA biomass dominated by diatoms. However, BMA primary productivity was the same for both sampling dates. Statistical tests revealed a significant interaction between sampling date and meiofauna grazing responses and suggests that the trophic relationships were different in January and June. Meiofaunal grazing, as a percentage of BMA biomass, was high in June (116.7 %) and exceeded the available BMA standing stock. However, in both June and January, grazing was less than 16 % of the rate of BMA net primary production. During periods of high grazing pressure, BMA community production was more than sufficient to supply food resources for meiofaunal consumers. Our results highlight the tight coupling between microalgae and meiofauna in the upper few millimeters of estuarine sediments. The trophic relationships are complex, with linked feedback mechanisms that operate over small spatio-temporal scales. The coupling of measurements of rate and biomass responses for both producers and grazers provides useful insights into the mechanisms underlying meiofaunal-microbial trophodynamics.

KEY WORDS: Microphytobenthos · Herbivore · Benthic · Photopigment · Estuary · Louisiana

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INTRODUCTION

The precise and simultaneous quantification of carbon (C) exchange rates is a prerequisite for understanding the processes regulating the trophic structure of benthic communities. Although biomass and abundance measures provide a useful snapshot of quantitative relationships at a single point in time, they offer little information about the rates of change, turnover and

cycling. The common currency for measuring exchange between food-web compartments is C, and C flow between trophic levels is a fundamental structuring feature for food webs. Therefore, the determination of the primary factors controlling C transfer rates *in situ* are a basic requirement for developing a mechanistic view of community structure and function.

In many estuarine ecosystems, the base of the food web is dominated by microalgal production (Pinckney

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& Zingmark 1993a, Cahoon 1999, Sullivan & Currin 2000). Benthic microalgae (hereafter BMA; also referred to as 'microphytobenthos') describes the group of photoautotrophic microorganisms inhabiting surficial sediments of shallow aquatic ecosystems. Diatoms, cyanobacteria and chlorophytes are usually the primary BMA photoautotrophs in estuarine and salt-marsh sediments (Admiraal 1984, Pinckney & Zingmark 1993b, Underwood & Kromkamp 1999, Sullivan & Currin 2000). Several stable isotope studies have demonstrated that BMA are a major source of nutrition fueling secondary production, even in salt-marsh food webs where production by vascular plants is high (Peterson & Howarth 1987, Herman et al. 2000, Sullivan & Currin 2000). Although these studies provide important evidence of the source of primary production supporting higher trophic levels, they reveal little about specific interactions between microbial autotrophs (BMA) and primary consumers (grazers). For example, information on the quantitative relationships and process rates of meiofaunal grazers and BMA producers is limited to a few habitats and short temporal scales.

BMA biomass, like most microbial communities, is regulated by both top-down and bottom-up controls (Carpenter et al. 1985, Worm et al. 2002). Grazers can potentially limit BMA standing stock via high consumption rates (Hargrave 1970, Connor et al. 1982, Carman et al. 1997), while nutrients and light may regulate BMA biomass and productivity (Ludden et al. 1985, MacIntyre et al. 1996, Barranguet et al. 1998). In addition, grazers may indirectly stimulate BMA production by enhancing nutrient availability while simultaneously 'thinning' the microalgal overstory and allowing deeper penetration of light into the sediments (Fenchel & Straarup 1971, Jørgensen & Des Marais 1986, Kuhl et al. 1994). The ecological processes mediating the interactions between BMA, grazers, nutrients and light are, however, poorly understood for intertidal estuarine ecosystems.

Although BMA production may be enhanced by intermediate levels of grazing by herbivores, overgrazing can reduce productivity (Hargrave 1970, Connor et al. 1982) and limit the standing crop (Gargas 1970, Pace et al. 1979, Davis & Lee 1983, Montagna 1984). Similarly, high grazing pressure by deposit-feeding macrofauna may also reduce BMA abundance (Miller et al. 1996). Significant positive spatial relationships between meiofauna and BMA have been detected at small spatial scales (1 to 2 cm²), suggesting that meiofauna are attracted to BMA patches (Decho & Castenholz 1986, Decho & Fleeger 1988, Pinckney & Sandulli 1990). Only a few studies have attempted to quantify BMA-meiofauna trophic relationships under natural conditions and the conclusions vary broadly. Admiraal

et al. (1983) extrapolated laboratory-based estimates of nematode grazing rates on diatoms and concluded that meiofauna had only a minor impact on BMA biomass. Montagna (1995) reviewed 7 studies of meiofaunal herbivory and reported that meiofaunal consumption of BMA standing stock ranged from 0.08 to 4.1% h⁻¹ with an average of ca. 1% h⁻¹. Sundbäck et al. (1996) concluded that grazing could control BMA biomass in subtidal sediments, but not in sandy coastal habitats. Blanchard (1991), working in an oyster pond along the west Atlantic coast of France, reported that meiofaunal grazing on BMA exceeded production and also concluded that meiofauna were food-limited. These few estimates of grazing come from a variety of habitats including beach sand, salt marshes and mud flats, and most were one-time measurements (Montagna 1984, Bauer et al. 1988, Blanchard 1991, Montagna et al. 1995a,b). Based on correlations of meiofaunal and microbial biomass (Montagna et al. 1983) and calculated meiofaunal grazing rates on microbes (Montagna 1984), Montagna and colleagues concluded that meiofauna were usually not food-limited.

Other evidence, however, suggests that meiofauna are limited by availability of BMA food. Carman et al. (1997) performed a microcosm experiment at the Louisiana site examined in the present study and concluded that meiofaunal copepods alone could consume 68 to 112% of the BMA biomass on a daily basis. In microcosms exposed to hydrocarbon contaminants, copepods were killed and BMA bloomed; in control (uncontaminated) microcosms, BMA biomass remained relatively constant, suggesting that BMA production was sufficient to balance the grazing rate. These findings led to the present study in which we sought to simultaneously measure grazing and production rates to better understand the trophic interactions in this habitat. The primary objective of this study was to examine the trophic interactions between meiofaunal grazers and BMA producers in an estuarine, intertidal habitat during winter and summer. Specifically, we tested the hypothesis that meiofaunal grazing is a primary limiting factor for BMA standing stock and productivity in this estuary.

MATERIALS AND METHODS

Study site. Terrebonne Bay estuary (29°13'N, 90°38'W) is located near the Louisiana Universities Marine Consortium (LUMCON) laboratory in Cocodrie, LA. Tidal range in the estuary is approximately 0.3 m and water movement is frequently wind-driven. Salinity varies from 4 to 26 psu. Salt marsh cord grass *Spartina alterniflora* is the predominant intertidal macrophyte in this estuary. Intertidal sediments have a

median grain size of 38 μm , are composed primarily of silts (41%) and clays (17%), and have an organic content of ca. 2.5% (Chandler & Fleeger 1983). The benthic fauna is dominated by meiofauna (J. W. Fleeger unpubl.). Large macrofauna and associated structures (e.g. tubes or burrows) are virtually absent (K. R. Carman pers. obs.). Nematodes comprise from 61 (Carman et al. 1995) to 89% (Phillips & Fleeger 1985) of total meiofauna. Copepods (and nauplii) constitute most of the remaining individuals, but ostracods, chironomid larvae, juvenile polychaetes and oligochaetes can occasionally be abundant as well.

Field collections. A 1 m wide strip of intertidal mud-flat, running parallel to the line of *Spartina* vegetation, was divided into twenty-four 1 \times 1 m plots (each separated by 0.5 m). Field collections were made at approximately 10:00 h on 27 June 1999 and 13 to 14 January 2000. Duplicate sediment cores (3.5 cm in diameter \times 15 cm length) were collected randomly within each of the 24 plots. An additional core was collected from 12 of the plots for use as dark controls in ^{14}C incubations (see below). Cores were obtained by hand from the study site and transported to the LUMCON laboratory for experimental incubations and rate determinations. One of the duplicate cores was used for measurement of meiofaunal grazing rates. For 8 (June) or 16 (January) of the 24 plots, the second duplicate core was used for measurements of BMA primary productivity. BMA biomass and community composition were determined by HPLC photopigment analysis for all 24 plots.

Meiofaunal grazing rates. Grazing by copepods, ostracods, chironomids, polychaetes and oligochaetes on natural BMA assemblages (*in situ* grazing) was measured using intact sediment cores inoculated with $\text{NaH}^{14}\text{CO}_3$ (Montagna 1984, Carman et al. 1997). Water overlying the sediment in each core was adjusted to a height of 2 cm. Seventy μCi of $\text{NaH}^{14}\text{CO}_3$ was dispensed into water overlying the core and distributed with gentle agitation. This method does not disturb sediment and facilitates an even label distribution (Carman et al. 1989). Cores were placed on a shaker table to provide gentle mixing of overlying water, and illuminated with fluorescent light (ca. 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) for 3 h. Twelve dark incubated cores were used to determine biotic uptake of ^{14}C by mechanisms other than grazing microalgae (Montagna 1984). Average radioactivity in dark incubations was subtracted from light incubations before grazing rates were calculated. At the end of the incubation period, the top 5 mm of sediment was collected and weighed. The sediment was homogenized by stirring, and a subsample (ca. 0.5 g wet wt) was removed for measurement of ^{14}C uptake (using a Sample Oxidizer 307; Packard Bioscience) and chlorophyll *a* (chl *a*) content (described below) (Puckett & Carman 2002).

The sample was re-weighed and overlying water returned to the sample container. The remaining sediment was preserved in 4% (final concentration) buffered formaldehyde with Rose Bengal as a sorting aid, and refrigerated until meiofauna were sorted.

Meiofaunal grazing rates were determined using a synoptic-labeling model, $G = 2F/t$, where G = grazing rate, $F = M/A$, where F is the fraction of radioactivity taken up by the respective meiofaunal group (M) relative to algae (A), and t = duration (incubation time) of the experiment (Daro 1978, Montagna 1984). Grazing rates were expressed in units of $\text{mg chl a } 10 \text{ cm}^{-2} \text{ d}^{-1}$. Most of the major assumptions of the model have been tested and verified (Montagna 1984, Blanchard 1991).

BMA productivity. Benthic microalgal gross primary production was measured using Clarke-style oxygen microelectrodes (model 737GC, 20 m tip dia., Diamond General) (Revsbech & Jørgensen 1986). A motorized micromanipulator (Oriel Motor-Mike) was used to position the tip of the microelectrode in the sediment. The productivity measurement method consisted of illuminating the sample with a fiber-optic light (ca. 1250 to 1500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and measuring the initial slope of oxygen decrease at 100 m depth intervals immediately (within 1 to 2 s) after darkening the sediment surface (Revsbech & Jørgensen 1986, Pinckney & Zingmark 1993c). Incubation irradiances were representative of mid-morning light exposure at the intertidal site. The measured rate at each depth interval was then integrated over all depth intervals to give a depth-integrated areal estimate of gross primary production for BMA. Unlike ^{14}C methods, this technique is non-destructive and allows multiple measurements on the same core sample. All production measurements were made subaerially (i.e. not covered with water) at *in situ* temperatures. Because benthic microalgae exhibit microscale (cm) patchiness (Pinckney & Sandulli 1990), 5 vertical profiles of production were obtained at random locations within each core. Depth-integrated production was calculated for each profile and all 5 profiles averaged to provide an estimate of total community production for each core.

HPLC pigment analyses. High performance liquid chromatography (HPLC) was used to determine chemosystematic photosynthetic pigment concentrations. Each of the 5 cm diameter cores collected for the BMA productivity measurements were subsampled using a 1.75 cm diameter butyrate core tube and the upper 3 mm of the core was extruded, sectioned, frozen in 2.0 ml microfuge tubes. and stored at -80°C . For analyses, sediment samples were placed in 100% acetone (2 ml), sonicated and extracted at -20°C for 18 to 20 h. Filtered extracts (300 μl) were injected into a Shimadzu HPLC equipped with a monomeric (Rainin Microsorb-MV, $0.46 \times 10 \text{ cm}$, 3 mm) and a

Table 1. Group abundance means and SD for the June 1999 and January 2000 sampling dates. The p-values indicate the significance level for comparisons of the 2 dates using the non-parametric Mann-Whitney *U*-test. Higher values are indicated in **bold**

Group	Jan		Jun		p-value
	Mean	±1 SD	Mean	±1 SD	
Copepods (10 cm ⁻²)	56.4	40.3	341.5	90.5	<0.001
Nematodes (10 cm ⁻²)	4767.8	3127.8	149.0	116.0	<0.001
Ostracods (10 cm ⁻²)	25.2	14.1	49.9	35.1	<0.05
Chironomids (10 cm ⁻²)	25.2	74.2	4.0	2.7	<0.01
Polychaetes (10 cm ⁻²)	2.6	2.3	5.8	3.7	<0.05
Oligochaetes (10 cm ⁻²)	29.2	32.2	1.3	1.9	<0.001
BMA chlorophyll <i>a</i> (µg 10 cm ⁻²)	61.41	26.34	3.21	1.92	<0.001
BMA zeaxanthin (µg 10 cm ⁻²)	1.65	0.54	0.42	0.23	<0.001
BMA fucoxanthin (µg 10 cm ⁻²)	18.71	8.07	2.35	0.87	<0.001
Fucoxanthin/zeaxanthin	11.34	8.15	3.78	6.23	<0.001
BMA biomass (mgC 10 cm ⁻²)	2.92	1.25	0.153	0.090	<0.001

polymeric (Vydac 201TP, 0.46 × 25 cm, 5 mm) reverse-phase C₁₈ column in series. A nonlinear binary gradient was used for pigment separations (for details, see Pinckney et al. 1996). Absorption spectra and chromatograms (440 nm) were acquired using a Shimadzu SPD-M10av photodiode array detector. Pigment peaks were identified by comparison of retention times and absorption spectra with pure crystalline standards, including chls *a* and *b*, β-carotene (Sigma Chemical), fucoxanthin, and zeaxanthin (Hoffman-LaRoche). Other pigments were identified by comparison to extracts from phytoplankton cultures and quantified using the appropriate extinction coefficients (Jeffrey et al. 1997).

Unit conversions. For direct comparisons of grazing rates, BMA biomass and primary productivity, the measured variables in this study were converted to common C units using the following relationships. Meiofaunal grazing rates, with measured units of mg chl *a* 10 cm⁻² d⁻¹, were converted to mgC 10 cm⁻² d⁻¹ assuming a C:chl *a* ratio of 47.6 (de Jonge 1980). BMA biomass, with measured units of mg chl *a* 10 cm⁻², was also converted to C units using the same C:chl *a* ratio. The measured unit for BMA primary productivity was mol O₂ 10 cm⁻² h⁻¹. Since the oxygen microelectrode technique measures gross photosynthesis (GPP), rates were converted to net photosynthetic rates (NPP) by assuming that NPP was 90% of GPP (i.e. NPP = 0.9 × GPP) (Pomeroy 1959). Oxygen units were converted to C units by assuming a conservative photosynthetic quotient (PQ) of 1.4

(Grant 1986). Hourly rates of NPP were converted to daily rates assuming constant photosynthetic rates for the time period when solar irradiance was greater than 500 µmol photons m⁻² s⁻¹ (7.0 h in January, 11.0 h in June). Daily BMA NPP was expressed in units of mgC 10 cm⁻² d⁻¹.

RESULTS

A comparison of meiofauna abundances on the 2 sampling dates indicated that nematodes, chironomids and oligochaetes were more abundant in January, while copepods, ostracods and polychaetes were more prevalent in June (Mann-Whitney *U*-test;

Table 1). Benthic microalgal biomass (as both chl *a* and C units) was higher in January. HPLC pigment analysis indicated that the major chemotaxonomic carotenoid photopigments in samples from both dates were zeaxanthin and fucoxanthin. Zeaxanthin was considered representative of cyanobacteria due to the absence of significant concentrations of chl *b*, ruling out the presence of other zeaxanthin-containing groups, such as chlorophytes and euglenophytes. Fucoxanthin was attributed to diatoms. Both zeaxanthin and fucoxanthin concentrations were significantly higher in January than in June (Table 1). The ratio of fucoxanthin to zeaxanthin, which may be used as a simple index of community composition, suggests a significant shift in the relative abundance of diatoms compared with cyanobacteria. The contribution of diatoms was much higher in January, while the relative abundance of cyanobacteria increased in June (Table 1).

Table 2. Rate measurement means and SD for the June 1999 and January 2000 sampling dates. The p-values indicate the significance level for comparisons of the 2 dates using the non-parametric Mann-Whitney *U*-test. The abbreviation ns denotes no significant difference. Statistical tests for grazing rates as a percentage of biomass and production are discussed in the 'Results'

Measure	Jan		Jun		p-value
	Mean	±1 SD	Mean	±1 SD	
Meiofauna grazing rate (mgC 10 cm ⁻² d ⁻¹)	0.202	0.357	0.097	0.056	=0.609 ns
BMA net primary production (mgC 10 cm ⁻² d ⁻¹)	1.31	0.54	1.07	0.44	=0.122 ns
Meiofauna grazing rate as a percentage of BMA biomass	7.6	13.1	116.7	148.0	
Meiofauna grazing rate as a percentage of BMA production	15.3	25.8	9.7	6.7	

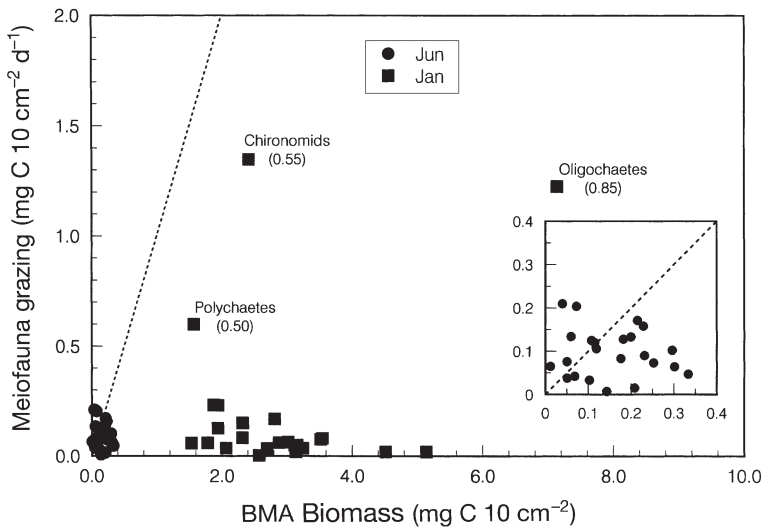


Fig. 1. Meiobenthic grazing rates versus benthic microalgal (BMA) biomass for June 1999 and January 2000. The inset graph shows a magnification of the points in the low BMA biomass region of the larger graph. The dashed line indicates a 1:1 relationship between the 2 variables (i.e. grazing rate equals BMA biomass). High grazing rates are annotated with the major meiobenthic grazing group and grazing rate

The overall mean (± 1 SD) meiobenthic grazing rates were 0.202 ± 0.357 and 0.097 ± 0.056 $\text{mg C } 10 \text{ cm}^{-2} \text{ d}^{-1}$ for January and June, respectively (Table 2). Although the means seem to suggest that grazing rates were higher in January, statistical testing (Mann-Whitney *U*-test) revealed that the rates were not significantly different ($p = 0.61$). Meiobenthic grazing rates were paired with the corresponding measures of benthic microalgal biomass for the 2 dates and graphed for comparisons (Fig. 1). For the January period, the daily grazing rate for meiobenthic (mgC d^{-1}) was less than the standing stock of benthic microalgae (mgC) for all 24 replicates and suggests that the meiobenthic were unable to consume the available food resources within a diel cycle. High grazing rates in 3 of the experimental blocks was attributed primarily to polychaetes ($0.50 \text{ mg C } 10 \text{ cm}^{-2} \text{ d}^{-1}$), chironomids (0.55) and oligochaetes (0.85). In contrast, grazing rates in June were similar to January, but BMA biomass was much lower. Meiobenthic grazing in 7 of the 24 experimental blocks exceeded the BMA standing stock and an additional 7 blocks were slightly below the threshold. In addition, high grazer densities and high grazing rates were not detected in any of the experimental blocks in June. There-

fore, meiobenthic grazers seem to be much more effective at grazing the available BMA biomass in June relative to January.

BMA production was measured directly on 8 of the 24 experimental blocks in June 1999 and on 16 of the 24 blocks in January 2000. NPP for the unmeasured cores was estimated using linear regression analysis to relate NPP to BMA biomass (as chl *a*) for the cores measured directly. Since BMA biomass was measured for all the experimental blocks, linear regression equations were used to approximate BMA NPP based on BMA biomass in the upper 3 mm of sediment. The mean (± 1 SD) BMA production estimates for the January and June sampling dates were 1.31 ± 0.54 and 1.07 ± 0.44 $\text{mg C } 10 \text{ cm}^{-2} \text{ d}^{-1}$, respectively (Table 2). BMA net primary production was not significantly different for the 2 time periods ($p = 0.122$) (Table 2). Meiobenthic grazing rates and BMA NPP for both sampling dates were compared to evaluate the relationship between grazing and production rates (Fig. 2). With the exception of a single case, daily BMA production rates were far in excess of grazing rates. In January, chironomid (midge) larvae were the major grazers in one of the blocks, and their grazing rate, in combination with the other meiobenthic groups, outpaced daily primary production.

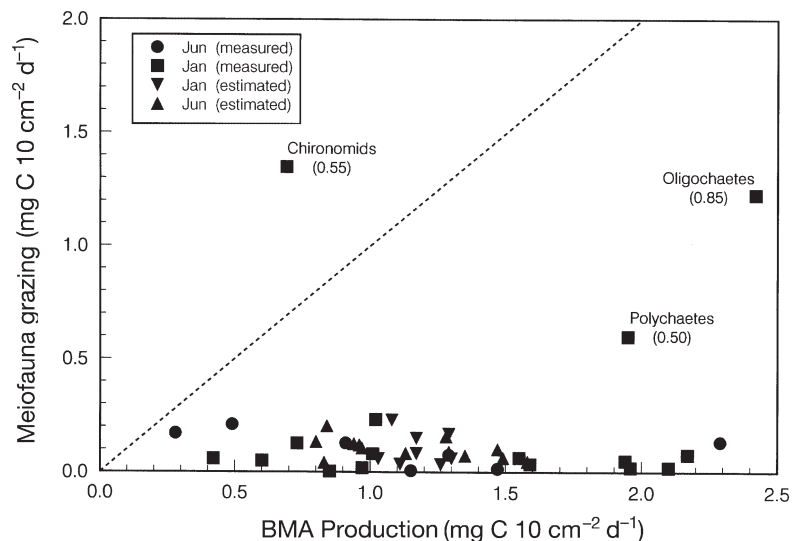


Fig. 2. Meiobenthic grazing rates versus BMA net primary production for June 1999 and January 2000. Triangles indicate values that were estimated using the regression relationship between BMA biomass and production. The dashed line indicates a 1:1 relationship between the 2 variables (i.e. grazing rate equals BMA production). High grazing rates are annotated with the major meiobenthic grazing group and grazing rate

The relationship between meiofauna grazing rates and BMA biomass was further evaluated by calculating the percentage of BMA biomass consumed by grazers (Table 2). In January, meiofauna grazed $7.6 \pm 13.1\%$ of the standing stock. In contrast, consumption was $116.7 \pm 148.0\%$ in June. Conversion of these rates to turnover times for BMA biomass yields values of 13.2 and 0.86 d for January and June, respectively. The grazing rates of individual meiofaunal groups were summarized in terms of the percentages of BMA biomass and daily production for both sampling dates (Fig. 3). In June, copepods consumed 85% of BMA standing stock but the grazing rate was only 7.5% of daily BMA production. Ostracods, chironomids and polychaetes were the other primary grazers in June. The other meiofaunal groups (ostracods, chironomids, oligochaetes and polychaetes) consumed smaller percentages of BMA biomass (<25%) and daily production (<10%).

Meiofaunal group responses for the 2 dates were compared using a 2-factor ANOVA (date, meiofauna groups, arcsine square-root-transformed percentages). For BMA biomass, there was a significant interaction between sampling date and the grazing rates of meiofauna groups ($p < 0.001$), indicating that meiofaunal group grazing responses expressed as a percentage of BMA biomass differed on the 2 sampling dates. Both main factors (date, meiofaunal group) were significantly different ($p < 0.001$). A similar comparison of grazer responses with BMA production also exhibited a significant interaction term (Groups \times Date) ($p < 0.01$). Tests of the main factors suggested that the

grazing rates of meiofauna groups (as a percentage of production) differed ($p < 0.001$), but there was no difference with respect to sampling date ($p = 0.220$). Overall, meiofauna consumed a higher proportion of available BMA biomass in June than in January. However, the grazing rates, as a proportion of BMA production, were not significantly different for the 2 sampling dates.

DISCUSSION

The results of this study provide a limited, but well-replicated contrast in seasonal changes in the trophic relationships between BMA and meiofaunal grazers. Unit conversions used to achieve a common unit for comparisons (i.e. C) are known to be highly variable, but were treated as constants in our analysis. Although these conversions undoubtedly increase the uncertainty of our conclusions, we chose conservative values for the constants and applied the same values to both sampling dates. Small changes in the conversion constants would not affect the overall conclusions of this study. In June, the benthic community was characterized by high meiofaunal abundances (particularly copepods), while BMA showed lower biomass and a shift in community composition towards increased relative abundance of cyanobacteria. Measurements in January showed lower meiofaunal abundances, but high BMA biomass dominated by diatoms. However, BMA primary productivity was not different between the 2 sampling dates. The high variation in meiofaunal

grazing rates made it impossible to demonstrate a statistically significant difference for the 2 sampling dates (Table 2). However, the mean values for grazing rates (0.202 vs 0.097 for January and June, respectively) suggest that rates may have been higher in January. A similar conclusion can be drawn regarding meiofauna grazing rates as a percentage of BMA production (Table 2). The statistical tests also revealed a significant interaction between sampling date and meiofauna grazing responses, and suggests that the trophic relationships were different in January and June.

Although nematodes were enumerated to provide abundance estimates, their grazing rates were not quantified in this study. Goldfinch & Carman (2000) found that grazing by nematodes accounted for only 1 to 5% of total meiofaunal grazing on BMA at

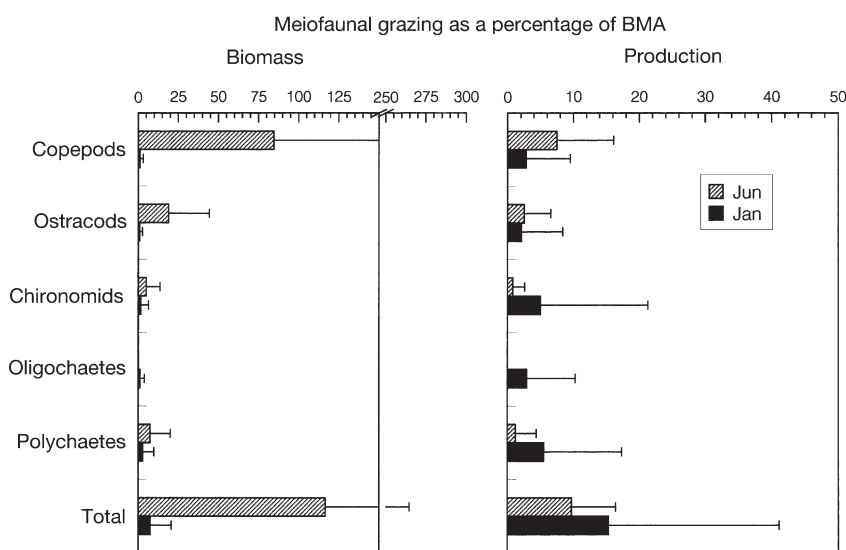


Fig. 3. Grazing rates of meiofaunal groups expressed as a percentage of BMA biomass and production (both in C units) for June 1999 and January 2000. Bars denote the mean \pm 1 SD

our study site and thus, the exclusion of nematodes in our estimates of grazing rates probably results in only a minor underestimate of total meiofaunal grazing.

Meiofaunal grazing, as a percentage of BMA biomass, was high in June (116.7%) and apparently exceeded the available BMA standing stock (Fig. 3). At the same study site, Goldfinch & Carman (2000) similarly found highest grazing relative to BMA standing stock in May (22 to 100%) and lowest rates in January (0.1 to 8%). Nonetheless, in both June and January grazing was less than 16% of the rate of BMA production (Table 2). Admiraal et al. (1983), working in the Eems-Dollard Estuary (The Netherlands), reported that a fraction of 10% of the daily BMA production was consumed by meiofauna. In contrast, Montagna (1984) found that meiofaunal grazing equaled BMA production in a South Carolina estuary. Furthermore, in San Antonio Bay, Texas, Montagna & Yoon (1991) determined that meiofaunal grazing outpaced BMA production in subtidal habitats. In a study along the west coast of Sweden, Sundbäck et al. (1996) concluded that grazing by meiofauna had a minor (<10%) impact on BMA production during summer, but grazing had a much greater impact (ca. 30 to 60%) on BMA production during other seasons. These findings highlight the importance of simultaneous rate measurements when examining trophic relationships. Our results show that, even during periods of high grazing pressure, BMA community production was more than sufficient to supply biomass for meiofaunal consumers. However, the trophic responses were different for the 2 sampling dates. This finding supports the speculation that there is seasonality in the rates associated with microalgal-meiofaunal trophic interactions. Differences in the meiofaunal community composition (species and abundances) in January and June make it difficult to separate truly seasonal effects from the effects of meiofaunal assemblages. In the statistical analyses, the main factor season is confounded by the covariate change in meiofaunal community structure. Thus, the measured seasonal effect may reflect the influence of both environmental and meiofaunal community differences for the 2 sampling dates.

The ratio of primary production (P) to BMA biomass (B) provides a useful measure of the turnover rate for the BMA community. Using the summary data in Tables 1 & 2, the P:B ratios were 0.45 and 6.99 d⁻¹ for January and June, respectively. Although a value of 6.99 seems unrealistic, P:B ratios as high as 24 have been reported for BMA in intertidal mudflats in the Bay of Fundy, Canada (Schwinghamer et al. 1986, Alongi 1998). In this study, the rapid P:B turnover rate corresponded with high copepod, ostracod and polychaete abundances in June. In January, higher nematode, chironomid and oligochaete abundances coin-

cided with the lower P:B ratio for BMA. Although BMA biomass was lower in June, the rapid turnover rate may reflect a compensatory response of BMA to grazing pressure.

One feature that distinguishes the work presented here from other meiofaunal grazing studies is that we used the oxygen microelectrode light/dark shift technique (Revsbech & Jørgensen 1986) to measure BMA photosynthetic rates. Most previous studies have relied on ¹⁴C-based estimates of primary production in conjunction with radiolabel consumption by meiofauna. The ¹⁴C method for measuring BMA production is especially problematic because of the difficulty in measuring the ¹⁴C-specific activity of the porewater in the sediment photic zone (Vadeboncoeur & Lodge 1998). Due to the high concentrations of dissolved inorganic carbon (DIC), the ¹⁴C-specific activity is usually underestimated and results in a directly proportional underestimate of BMA photosynthetic rates. In contrast, the oxygen microelectrode technique provides accurate and reliable measurements of BMA gross photosynthesis that are integrated over the entire sediment photic zone (Revsbech & Jørgensen 1986). The relatively high rates of BMA productivity measured in this study are likely attributable to the measurement method.

Optimal rates of primary productivity at intermediate levels of herbivore grazing are well documented for many marine, freshwater and terrestrial ecosystems (Cooper 1973, Fenchel & Kofoed 1976, Connor et al. 1982, Worm et al. 2002). Our data suggest that this paradigm also applies to microalgal-meiofaunal interactions in an intertidal, estuarine habitat. Higher grazing rates may facilitate BMA production by a number of mechanisms. For example, the consumption and removal of BMA biomass in surficial sediments would be analogous to thinning the canopy in forests. The removal of the overstory would allow more light to penetrate below the canopy. The amount of light available for photosynthesis is probably the single most important limiting factor for BMA productivity (Whitney & Darley 1983, Sundbäck & Graneli 1988) and production has been highly correlated with incident irradiance (Pomeroy 1959, Leach 1970, Van Raalte et al. 1976, Hartwig 1978, Colijn 1982). The 1% light level, usually taken as the minimum requirement for photosynthesis, is limited to the upper few mm in muddy sediments (Fenchel & Straarup 1971, Jørgensen & Des Marais 1986, Barranguet et al. 1998). Therefore, the photic zone in sediments is highly compressed relative to most ecosystems. The removal of microalgal canopy biomass allows further light penetration into the sediments, thereby increasing the depth of the photic zone within the sediments. The reduction in BMA biomass associated with canopy removal would likely be balanced by

increased depth-integrated productivity in the sediment photic zone. This speculation is consistent with the observation that BMA production was similar for both sampling dates, but BMA biomass was significantly different. The lower BMA biomass in June would have allowed deeper light penetration into sediments, thereby increasing the depth of the photic zone and the integrated BMA production. Higher grazing rates will also likely result in a redistribution of nutrients (as waste products), enhanced rates of nutrient regeneration, and subsequent growth (McCormick 1994).

BMA biomass in the upper few millimeters of sediment seems to be limited primarily by the availability of resources (light, nutrients, DIC, etc.) (Admiraal 1984, Ludden et al. 1985, Kuhl et al. 1994, MacIntyre et al. 1996). This type of regulation is usually described as bottom-up (Carpenter et al. 1985). In intertidal sediments, the meiofaunal grazers seem to play a dual role. First, as herbivores, they function directly as top-down controls. However, our findings suggest that grazer demands are easily satisfied by enhanced BMA turnover rates. Thus, direct top-down control of BMA biomass and production does not seem to be a primary regulating mechanism. However, meiofaunal herbivores may play a secondary role by modifying the potential bottom-up controls on BMA biomass and productivity through alterations in the light environment and the enhancement of nutrient regeneration rates. Worm et al. (2002) examined the interactive effects of consumers and resources on ecosystem structure and function, and showed that when consumers are present, peak diversity occurs at higher levels of nutrient supply. Bioturbation and sediment reworking by meiofaunal activities may also increase porosity and solute transport rates, facilitating porewater exchange and nutrient supply to BMA (Aller & Aller 1992). Thus, diversity and primary productivity depend on the relative rates of nutrient supply and consumer pressure in many marine food webs. Our results are consistent with the general community structuring principles outlined by Worm et al. (2002) and highlight the tight coupling between microalgae and meiofauna in the upper few millimeters of sediments. The trophic relationships are complex, with linked feedback mechanisms that operate over small spatio-temporal scales (Buffan-Dubau & Carman 2000). The coupling of measurements of rate and biomass responses for both producers and grazers has provided some useful insights into possible mechanisms underlying meiofaunal-microalgal trophodynamics in muddy, intertidal sediments.

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