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The Effect of Freshwater Inflow on Meiofaunal Consumption of Sediment Bacteria and Microphytobenthos in San Antonio Bay, Texas, U.S.A.

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If meiofauna are food-limited then they should respond with increased feeding rates when microbial production is stimulated. River inflow into estuaries is a source of organic matter that can be limiting to bacterial production, and nutrients that might limit primary production. Therefore, inflow should stimulate microbial primary and secondary production, and eventually meiofauna grazing rates should increase as a functional response to increased food availability and quality. To determine if meiofauna grazing rates were affected by inflow, two replicate stations were sampled in the upper, river-dominated end, of San Antonio Bay and contrasted with two replicate stations at the lower end of the estuary. The experiments were performed three times. Water column nutrients and sediment organic matter were higher in the upper end of the estuary than in the lower end. Benthic primary production was 2·5 times higher in the upper end than in the lower end. Benthic metabolism (measured by oxygen consumption) was also higher in the upper end, but bacterial production (measured by thymidine uptake) was not significantly different between the two ends. Grazing rates were 3·5 times higher on bacteria, and 2·5 times higher on microalgae in the upper end of the estuary than in the lower end, confirming our hypothesis that inflow would stimulate grazing rates. Grazing rates were dominated by juvenile molluscs (temporary meiofauna) which accounted for 39% of the microalgae and 68% of the bacteria ingested by the community. Juvenile molluscs were most prevalent in the upper, freshwater zone. Harpacticoid copepods and nematodes had higher grazing rates in the lower end of the estuary. Grazing rates were higher on microalgae than on bacteria: 4% of the microalgae were removed per hour, compared to only 1% of the bacteria. Grazing rates on microalgae were 2·6 times higher than productivity, indicating meiofauna might be food-limited. Grazing on bacteria was low, and production (based on oxygen metabolism) exceeded grazing; thus bacterial food is not apparently limiting. Freshwater inflow can affect meiobenthic community structure, stimulate microbial production, and stimulate feeding rates by small invertebrates that can benefit by the increase in microbial production.

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Introduction

Food limitation is difficult to prove since we can never be sure we have measured all factors that might be limiting to a population. However, it is possible to measure a functional response to changes or variability of resources in the environment. A change in feeding rate is one functional response that can be measured. Current feeding models predict that feeding rates will change as a function of food quality, and it has been demonstrated that a deposit-feeding worm varies its sediment-processing rate as sediment protein content changes (Taghon & Greene, 1990). There is a relatively rich literature of theoretical and empirical studies on feeding and sediment processing of deposit-feeding macrofauna. In contrast, relatively little is known about meiofauna feeding. This is unfortunate considering that meiofauna, because of their small size and rapid turnover times, are probably as (or more) productive than macrofauna in benthic systems (Gerlach, 1971). One feeding study, in a South Carolina high salt marsh, suggested that meiofauna were not food-limited because their grazing rates on microbes were equal to microbial production rates (Montagna, 1984*b*). But we do not know if meiofauna feeding rates respond to gradients of food quality in the environment. If meiofauna are food-limited then they should respond to higher food availability or quality with higher grazing rates.

Riverine nutrient input to bays and estuaries is thought to maintain or enhance productivity (Deegan *et al.*, 1986). High nutrient concentrations in the head (i.e. the upper end) of an estuary should result in higher primary production than in the more marine-influenced (i.e. the lower) end (Nixon *et al.*, 1986). There is a strong positive empirical relationship in fresh and marine waters between bacterial abundance and chlorophyll concentration (Bird & Kalff, 1984), and bacterial production and net primary production (Cole *et al.*, 1988). Therefore, high primary production should stimulate or correlate with higher secondary production by benthic bacteria (Graf *et al.*, 1982). Enhanced productivity by microbial producers such as microalgae (via autotrophy) or bacteria (via heterotrophy) should be readily available to benthic consumers. Benthic respiration (Hargrave, 1973) and biomass (Grebmeier & McRoy, 1989) are positively correlated with primary production. Therefore, meiofauna should respond to river inflow (and the concomitant increase in the quantity and quality of food available) with increased feeding rates.

To test this hypothesis, meiofaunal grazing rates were measured in upper (strongly influenced by freshwater inflow) and lower (weaker inflow-influenced) ends of San Antonio Bay, Texas. This study was part of a multidisciplinary effort to investigate the effect of freshwater inflow on nitrogen processes in Texas estuaries (Whitledge *et al.*, 1989). We also measured benthic bacterial responses to inflow, and McIntyre and Cullen (1988) measured benthic microalgal responses to inflow. This allows us to compare meiofaunal grazing activities with microbial dynamics.

Materials and methods

Study design

Four stations in San Antonio Bay, Texas, were chosen for study (Figure 1). Two replicate stations (A and B) were at the head of the bay where freshwater influence is greatest. Two other replicate stations (C and D) were near the intracoastal waterway where marine influences are greatest (Figure 1). Marine water enters San Antonio Bay from the north, nearest to station D. By using two stations in the freshwater-influenced zone and two

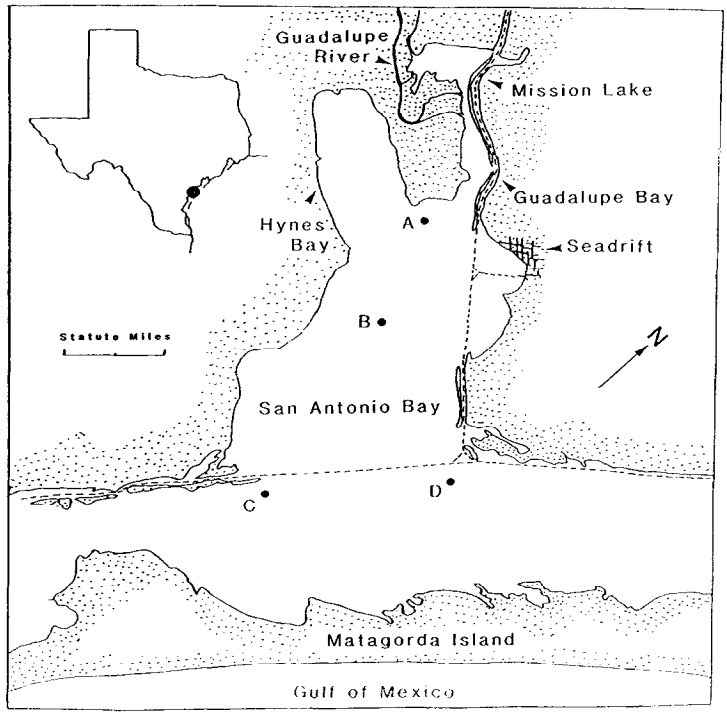

Figure 1. San Antonio Bay, Texas. The locations of the four sampling stations (A, B, C and D) are shown. The intracoastal waterway is shown by a dashed line.

stations in the marine-influenced zone we are replicating effects at the treatment level and avoiding pseudoreplication (Hurlbert, 1984). The four stations were sampled three times, in January, April and July 1987. This is a completely random two-way factorial design, with stations and time as the main effects. Since the treatments were replicated within the main station effect, linear contrasts were performed to test for differences between the mean grazing rate at the upper (i.e. stations A and B) and lower (i.e. stations C and D) ends of the estuary. Tukey multiple comparison tests were used to determine if there were differences among all station means.

All stations were located in shallow water. Depths of stations A, B, C and D were 1·3 m, 1·9 m, 2·0 m and 1·6 m, respectively. Sediment grain size composition was different among stations (Montagna, unpubl. data). This was primarily due to a higher average rubble content at stations A (11·5%) and B (7·6%) than at stations C and D (both 2·7%). Station B also had much less sand, average 4·0%, than the other stations, which averaged 30·7%. The differences in sediment composition indicate that bivalves are more common in the upper reaches of the bay, and deposition of fine material is more common in the centre of the bay.

Temperatures were similar in January and April but twice as warm in July (Table 1). Salinity throughout the bay was increasing through the winter, but a huge spring rain converted the entire system to a very fresh condition which persisted through July (Whitledge *et al.*, 1989; Table 1). Texas estuaries are subjected to a continuous cycle of floods and droughts. The sampling period was during a low-salinity year due to higher than average amounts of rain and river inflow. This indicates that we may not have good information about grazing in true marine conditions. The experimental design is still

TABLE 1. Conditions at San Antonio Bay stations during the experimental periods in 1987. Environmental conditions are salinity (ppt) and temperature (°C) at the bottom (about 1·5 m at all stations). Meiofaunal mean (± standard deviation) density (10 cm^{-2}) for nine replicates (all grazing samples)

Date	Station	Salinity	Temperature	Density
January 28	A	0·3	14·4	134 (28)
	B	0·4	14·8	368 (59)
January 30	C	6·5	15·5	2276 (385)
	D	4·1	15·8	1836 (105)
April 8	A	0·5	14·5	265 (96)
	B	6·3	15·2	277 (86)
April 10	C	9·2	14·5	1395 (383)
	D	13·2	14·9	615 (140)
July 15	A	0·4	30·5	325 (122)
	B	0·4	30·5	199 (11)
July 17	C	1·1	30·5	399 (110)
	D	0·9	30·5	301 (89)

valid, since stations are placed in the upper and lower ends of the estuary where influences of the inflow are still along a gradient. Hereafter, the upper end of the estuary will be referred to as the freshwater stations, and the lower end as the brackish stations.

Measurement of grazing rates

In situ meiofaunal grazing rates on bacteria and microalgae were measured by incubating sediment slurries with two radiolabelled substrates, tritiated thymidine (^{3}HTdR) and ^{14}C-bicarbonate ($H^{14}CO_3^-$) (Montagna & Bauer, 1988). The top 2 cm (12 cm^3) of 60-cm^3 sediment cores were placed in 60-cm^3 clear centrifuge tubes. Twelve ml of station water containing 5 μCi of ^{3}HTdR and 5 μCi of $H^{14}CO_3^-$ were added to the samples to make slurries and were incubated for 2 h at *in situ* temperature. Carman *et al.* (1989) determined that ' slurries ' were not good to use for feeding experiments, but they stirred the top 1 cm of a whole 9·6-cm^2 core diluted with only 50 μl of water added to the surface. We selected only the sediment surface (top 2 cm) and diluted with a 50:50 mix of sediment and seawater (Montagna & Bauer, 1988). Although both techniques have been referred to as ' slurries ', they represent different treatments.

Live controls were used to correct for non-grazing label uptake by meiofauna (Montagna, 1983). A saturated solution of nalidixic acid (200 μg ml^{-1}) plus 5'-deoxythymidine (2 μg ml^{-1}) (hereafter referred to as ND) was added to a sediment slurry sample to inhibit prokaryotic incorporation of ^{3}HTdR (Findlay *et al.*, 1984; Montagna & Bauer, 1988). These were incubated in the dark to inhibit photosynthetic fixation of $^{14}CO_2$. Although meiofauna were feeding during the control experiments, uptake of ^{3}H or ^{14}C is not due to feeding on microbes, because microbial uptake of label is inhibited in these treatments. Live controls consisted of three replicate slurries.

After 2 h, incubations were terminated by adding 2% formalin, and a 1-ml subsample was withdrawn from the slurries. The subsample was filtered onto a 0·2-μm Millipore filter and was rinsed three times with filtered seawater to estimate uptake of $H^{14}CO_3^-$ microalgae and ^{3}HTdR by bacteria. The subsample was dispersed and suspended in 5 ml distilled water and 15 ml Insta-Gel for dual-label liquid scintillation counting. Meiofauna

were separated from sediments by diluting samples with 2% formalin, swirling to suspend the animals, and decanting them and the supernate onto 63-μm Nitex screen filters. Meiofauna were then rinsed into jars and kept in refrigerated 2% formalin until sorting (1–2 days). Three replicate cores were taken for each treatment.

Sorting was performed under a dissecting microscope and meiofauna were sorted by taxa into scintillation vials containing 1 ml distilled water. Counts of meiofauna were recorded, and density is reported as the number of individuals per 10 cm^2 (which is equivalent to 1000 individuals m^{-2}). After sorting, meiofauna were dried at 60 °C and solubilized in 100 μl Soluene tissue solubilizer for 24 h. Samples were counted by dual-label liquid scintillation spectrophotometry in 15 ml Insta-Gel.

Meiofaunal grazing rates on bacteria and microalgae were estimated by the model proposed by Daro (1978) and modified by Roman and Rublee (1981) and Montagna (1984*b*). The meiofaunal grazing rate (G) is the proportion of material flowing from the donor (or food) compartment to the recipient (or predator) compartment per hour. G is expressed in units of h^{-1} and is calculated as follows (Montagna, 1984*b*): $G = 2F/t$, and $F = M/B$, where F is the fraction of label uptake in meiofauna (M) relative to bacteria or microalgae (B) at time t. Log-transformed grazing rates were used in statistical analyses because the distribution of the residuals (i.e. the part of the measurement due to random error) was skewed to the left. Detransformed rates are reported throughout this manuscript. Detransformed 95% confidence intervals were calculated as follows: $10^{\{\bar{X} \pm t[0{\cdot}025, (n-1)]^{\times SE}\}}$, where SE is the standard error of the mean ($s/\sqrt{n}$).

Bacterial abundance and production

One-cm^3 subsamples for enumeration of bacteria were taken from larger cores. Bacterial samples were preserved in 4% buffered formalin that had been filtered through a 0·2-μm filter and were refrigerated until they were analysed. A surfactant, Tween 80 (final concentrations 0·001%), was used to facilitate dispersion of bacterial cells during homogenization of sediments (Yoon & Rosson, 1990). Bacterial cell counts were measured using the acridine orange direct count (AODC) technique (Daley & Hobbie, 1975). The sampling design employed by Montagna (1982) was used: 10 fields were counted from two subsamples of three sediment cores (which yielded 60 counts for each station).

Benthic bacterial production was measured by the incorporation of ^{3}HTdR into bacterial DNA (Fuhrman & Azam, 1980, 1982; Bauer & Capone, 1985). One final concentration of thymidine was used (50 nM), and time course experiments (with five points over 1 h) were performed. Since dilution experiments were not performed, productivity measurements may be underestimates of true production.

Results

The animals found in the sediment cores were sorted into six groups. Three groups included juvenile macrofauna (Amphipoda, Mollusca and Polychaeta) which are part of the temporary meiofauna. Amphipods occurred only during the January 1987 sampling period, but were present at all stations. The molluscs were composed of both bivalves and gastropods. Three groups were permanent meiofauna—Harpacticoida, Nematoda and other meiofauna. The category labelled 'other' meiofauna was usually represented by rare forms, or forms which occurred in very low densities. At stations A and B this was mostly ostracods with some kinorynchs. At stations C and D this was mostly turbellarians,

TABLE 2. Effect of treatment on average uptake of label for each taxonomic group. Meiofauna uptake is in units of DPM individual 2 h $^{-1}$, and for microbes it is in units of DPM core h $^{-1}$. Uptake is the average for replicates over all seasons and stations. The three treatments were (L) live feeding samples, (C) control microbial-inhibited (i.e. not feeding on label) samples, and (F) formalin-killed controls. Five μCi of ^{3}HTdR and 5 μCi of $H^{14}CO_3$ were added to the samples

	^{3}HTdR			$H^{14}CO_3$		
Taxa	L	C	F	L	C	F
Microbes	42 408	19 522	9395	10 755	3296	2605
Molluscs[a]	1580	1226	112	1037	386	117
Amphipods[a]	202	74	56	360	40	35
Polychaetes[a]	90	65	25	50	21	11
Others	17	9·1	13	25	2·6	1·6
Harpacticoids	14	9·5	3·5	14	3·8	1·2
Nematodes	12	3·6	3·3	3·4	1·3	0·5

[a]Juvenile macrofauna are part of the temporary meiofauna.

with some ostracods and kinorynchs. In July 1987 there were also a few halacarid mites in the C and D samples.

The average meiofauna abundances at stations A and B were relatively low (261 10 cm^{-2}) and did not change over time (Table 1). Nor were the abundances at A and B significantly different from each other (Tukey multiple comparison test). In contrast, average abundances decreased over time at stations C and D and were about four times that of the fresh stations (1137 10 cm^{-2}). The mean abundance at station C (1357 10 cm^{-2}) was always greater than the mean at station D (917 10 cm^{-2}) (Tukey multiple comparison test). Nematodes comprised about 62% of the meiofauna at stations C and D, but were depauperate, only 35%, at stations A and B. Meiofauna abundances co-varied with salinity; low at A and B when salinity was low, and decreasing at C and D as salinity decreased. Meiofauna abundances were originally four times greater in brackish stations than freshwater stations when salinity was high, but abundances at C and D decreased to the level at A and B when salinities became low and similar (Table 1).

The live control experiments were reasonably effective (Table 2). Formalin inhibited 76% of the uptake of ^{14}C by microalgae (compared to the live-lighted treatment), but the live–dark treatment inhibited 69% of the uptake. Formalin inhibited 88% of the total uptake of ^{3}H by bacteria, but the live ND treatment inhibited only 54% of the uptake. The difference of microbial label uptake between the poisoned and live control treatments is due to either ineffective inhibition or active uptake. Microbial uptake is estimated by filtering subsamples of sediment, so biotic and abiotic factors could be responsible for this response. The grazing live control values were used to correct feeding rates, so the grazing rates may represent underestimates of the true grazing rates. The underestimate may be twice as high for bacteria as it is for microalgae, because ND was half as effective as the dark treatment.

The labels used in this feeding experiment were also taken up by meiofauna in control experiments where label uptake by microbes was inhibited (Table 2). Formalin uptake averaged 12% of live uptake for ^{14}C, and 32% of live uptake for the ND treatment (Table 2). Formalin uptake averaged 32% of live uptake for tritium, and 56% of live uptake for the ND treatment (Table 2). About 70% of the tritiated label taken up was by

TABLE 3. Meiofaunal grazing rates (h^{-1}) on bacteria and microalgae. The rates are the overall averages for all stations and periods. Since some organisms were not found in all replicates the frequency of occurrence (n) is not always 36. Upper and lower 95% confidence intervals are uneven since the data is detransformed from logarithms

Taxa	n	Bacteria		Microalgae	
		Mean	(L95%CI, U95%CI)	Mean	(L95%CI, U95%CI)
Molluscs[a]	30	0·003297	(0·001018, 0·010629)	0·005968	(0·001681, 0·021118)
Others	36	0·000730	(0·000498, 0·001067)	0·005013	(0·003230, 0·007778)
Harpacticoids	35	0·000546	(0·000331, 0·000897)	0·002524	(0·001547, 0·004113)
Polychaetes[a]	33	0·000164	(0·000098, 0·000269)	0·000426	(0·000244, 0·000737)
Amphipods[a]	5	0·000059	(0·000014, 0·000188)	0·000643	(0·000173, 0·002318)
Nematodes	36	0·000028	(0·000009, 0·000068)	0·000816	(0·000476, 0·001394)

[a]Juvenile macrofauna are part of the temporary meiofauna.

non-feeding processes for molluscs, polychaetes and harpacticoids. About 40% of the ^{14}C label was taken up by non-feeding processes by molluscs, polychaetes and nematodes. The extensive uptake of label by non-feeding processes indicates the importance of using live controls in feeding experiments. Overall, twice as many tritium DPM were found as compared to ^{14}C DPM in the control experiments. This indicates that dissolved organic matter (thymidine) may also be incorporated (absorbed) by meiofauna. The other uptake process is adsorption (measured by the formalin-killed controls). Occasionally, label uptake was smaller in the feeding experiment than in the control experiments. This only occurred with nematodes and molluscs. The grazing rate was set to zero in all these cases.

Molluscs had the highest overall mean grazing rates on both bacteria and microalgae (Table 3). The dominant bivalves in macrofauna samples were *Mulinia lateralis* and *Macoma mitchelli*. *Mulinia* was four times more abundant than *Macoma* in the upper end of the estuary (Montagna & Kalke, unpubl.). There were significant differences in grazing rates among stations and dates for both bacteria and microalgae (Table 4). In general, molluscan grazing rates at the freshwater stations (A and B) were two orders of magnitude higher than in the brackish station (C and D) for both bacteria and microalgae (Table 4). Grazing rates were highest in summer (July) and lowest in winter (January) for both bacteria and microalgae (Table 4).

Amphipods occurred only in January and there were no differences in grazing rates among stations for bacteria ($P=0·3992$) or for microalgae ($P=0·1229$). Polychaetes also did not have significant differences in grazing rates among stations for bacteria ($P=0·5888$) and for microalgae (P0·9032). Polychaetes had no differences in grazing rates on microalgae between seasons ($P=0·1305$), but grazing rates on bacteria were an order of magnitude higher in April than in January.

The grazing rate trends for the permanent meiofauna (harpacticoids, nematodes and others) were much more complex. Each group had significant interactions between stations and seasons for grazing on both bacteria and microalgae. In general nematodes had very low grazing rates (Table 3, Figures 2 and 3). The grazing rates on bacteria were often zero (Figure 2). The only time that nematodes had a reasonably high grazing rate was in the brackish stations (C and D) during the winter (January) sampling period (Figure 3). Harpacticoid grazing rates were generally higher at the brackish stations (C and D) for both bacteria (Figure 2) and microalgae (Figure 3). The only exception was a very low

TABLE 4. Tukey multiple comparison tests on juvenile molluscs' grazing rates for main effects in the experimental design. Lines indicate that the means are not significantly different at the 0·05 level. Mean grazing rates are in units of h^{-1}, and detransformed from logarithm values

Grazing on bacteria	0·0201	0·0123	0·000668	0·000415
Station	B	A	C	D
Grazing on microalgae	0·0624	0·0172	0·000998	0·000862
Station	A	B	C	D
Grazing on bacteria	0·0131	0·00510	0·000437	
Month	July	April	January	
Grazing on microalgae	0·0226	0·0156	0·00551	
Month	July	April	January	

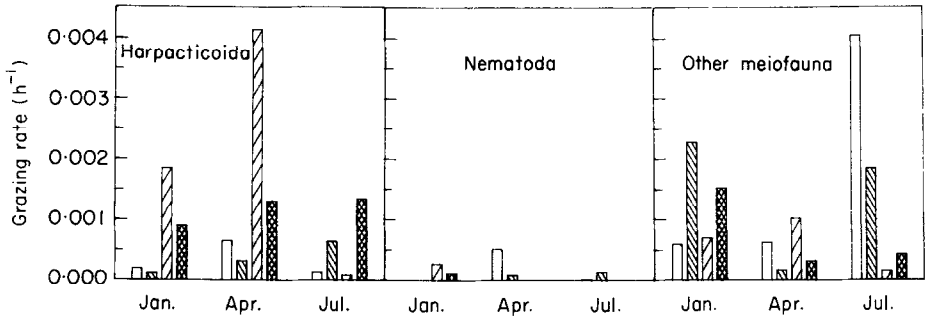

Figure 2. Mean meiofaunal grazing rates (h^{-1}) on bacteria in 1987. The interaction between stations and sampling periods was significant for all groups. Station: A, □; B, ▨; C, ▨; D, ▩.

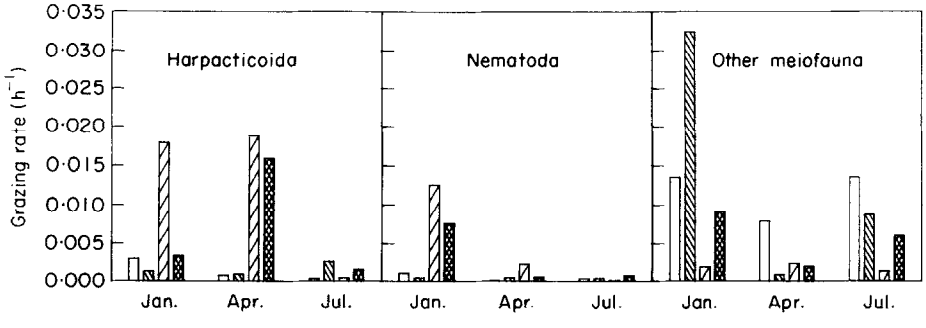

Figure 3. Mean meiofaunal grazing rates (h^{-1}) on microalgae i n 1987. The interaction between stations and sampling periods was significant for all groups. Station: A, □; B, ▨; C, ▨; D, ▩.

TABLE 5. Proportion and selection of microbes ingested. Proportion is the average per cent contribution of meiofaunal taxa to the total average meiofaunal grazing rate. Selection is the ratio of the average microalgae grazing rate (G_A) to the average bacterial grazing rate (G_B) for all samples

Taxa	Proportion ingested		Selection (G_A/G_B)
	Algae	Bacteria	
Molluscs[a]	38·8%	68·3%	1·8X
Others	32·6%	15·1%	6·9X
Harpacticoids	16·4%	11·3%	4·6X
Nematodes	5·3%	0·6%	28·4X
Amphipods[a]	4·2%	1·2%	10·8X
Polychaetes[a]	2·8%	3·4%	2·6X

[a]Juvenile macrofauna are part of the temporary meiofauna.

grazing rate on bacteria and microalgae at station C in July when salinity was 1·1 ppt. Grazing rates by other meiofauna were highest at Station B in January, and at A in April and July for bacterial and microalgae, indicating a general trend of higher rates in the fresher stations.

Meiofaunal grazing rates were dominated by molluscs and other meiofauna for microalgae and just molluscs for bacteria (Table 5). All taxa had higher grazing rates on microalgae than on bacteria indicating that microalgae were being selected for over bacteria (Table 5).

The total meiofaunal grazing rate is the sum of the grazing rates of each taxa for each replicate. Not all taxa were found in all replicates, so the total rate does not equal the sum of the average taxa rates found in Table 3. The mean total meiofaunal grazing rate on bacteria was 0·0099 h^{-1} (with a coefficient of variation of 21%). The overall mean meiofaunal grazing rate on microalgae was about four times higher at 0·0411 h^{-1} (with a coefficient of variation of 24%). There were no significant differences for meiofauna grazing on microalgae during the 3 months ($P = 0{\cdot}2477$). However, there were differences between months for grazing on bacteria (Table 6). Higher rates were measured during July and April (which were the same) than in January (Table 6). This might be due to the effect of higher temperatures or freshwater which occurred at the same time. Station differences in grazing rates on both bacteria and microalgae were very similar (Table 6). The hypothesis that there is no difference in mean total grazing rates between the freshwater (A and B) and brackish (C and D) stations was tested using linear contrast techniques and was significant for both bacteria and microalgae.

Microbial standing stocks and production are necessary to interpret the impact that meiofaunal grazing has on the microbial community. Microalgal dynamics were studied during these same cruises by McIntyre and Cullen (1988). Bacterial dynamics were measured in independent samples also (Table 7). Bacterial abundance and production were higher in the lower ends of the estuary. The average abundance at stations A and B was 1·51 10^9 cells cm^{-3} compared to 2·04 10^9 cells cm^{-3} at stations C and D. The average bacterial production as stations A and B was 2·01 10^6 cells $cm^{-3}\,h^{-1}$, compared to 2·32 10^6 cells $cm^{-3}\,h^{-1}$ at stations C and D. Bacterial abundance decreased and then increased through the study, but production decreased steadily (Table 7).

TABLE 6. Tukey multiple comparison tests on total meiofaunal grazing rates for main effects in the experimental design. Lines indicate that the means are not significantly different at the 0·05 level. Mean grazing rates are in units of h^{-1}, and detransformed from logarithm values. There were no significant differences in grazing on microalgae among months

Grazing on bacteria	0·0292	0·0112	0·0073	0·0040
Station	B	A	C	D
Grazing on microalgae	0·0681	0·0621	0·0296	0·0229
Station	B	A	C	D
Grazing on bacteria	0·0243	0·0105	0·0038	
Month	July	April	January	
Grazing on microalgae	0·0532	0·0419	0·0312	
Month	July	April	January	

TABLE 7. Bacterial abundance and productivity in San Antonio Bay sediments. Average abundance (10^9 cells cm^{-3}) and standard deviation, and average production (10^6 cells $cm^{-3}\,h^{-1}$) and R^2 for each month and station

Month	Station	Abundance	Production
January	A	1·31 (0·31)	2·06 (0·62)
	B	2·00 (0·26)	2·32 (0·87)
	C	2·02 (0·24)	2·65 (0·56)
	D	2·03 (0·17)	3·80 (0·89)
April	A	1·31 (0·21)	2·79 (0·65)
	B	0·77 (0·14)	1·53 (0·61)
	C	1·69 (0·21)	1·36 (0·82)
	D	2·03 (0·29)	2·35 (0·90)
July	A	1·86 (0·22)	2·13 (0·72)
	B	1·79 (0·24)	1·20 (0·78)
	C	2·15 (0·27)	2·53 (0·47)
	D	2·30 (0·27)	1·21 (0·85)

Discussion

San Antonio Bay

San Antonio Bay is part of the Guadalupe estuary. The estuary receives drainage from the Guadalupe and San Antonio River basins. Salinities are low in this estuary because it is a closed system, i.e. there is no direct exchange with the Gulf of Mexico. Exchange occurs via passes between the barrier islands with the adjacent estuaries to the north-east and

south-west. Therefore, freshwater has a long residence time in this estuary. During the present study the average salinities were 0·4 ppt at station A, 2·4 ppt at B, 5·6 ppt at C, and 6·1 ppt at D. This was an extremely fresh period. The long-term historic average salinity at a Texas Commission monitoring site near station D is 18·9 ppt (TDWR, 1980).

Freshwater flows into the bay from the Guadalupe River and along the south-western shoreline of the bay. Marine water enters from the north-east via a lagoon named Espiritu Santo Bay which is connected to the Gulf by Pass Cavallo. The upper end and south-western shoreline of San Antonio Bay (where stations A and B are located) is rich in nitrate (40–120 μM). In contrast, the lower end of the bay (where station C is) and the north-eastern entry of the lagoon (where station D is) has much less nitrate (1–10 μM) (Whitledge, 1989). Surface chlorophyll concentration is correlated with salinity and Secchi disc depth (i.e. water clarity) (Whitledge, 1989). Thus, the station pairs represent a contrast between zones with different freshwater influence due to circulation patterns.

The stations were originally chosen to represent two stations dominated by river influence and two brackish stations with marine influence. This design was successful in that the average salinity at A and B was 1·4 ppt which was much lower than the average of 5·8 ppt at C and D (Table 1). The salinities were rising to average conditions from January–April, but a large inflow event in June 1987 resulted in a total replacement of brackish water with very freshwater in July (Table 1). This caused a statistical interaction between stations and months in the design, because the brackish stations became freshwater stations in July. This is illustrated by salinity and meiofaunal density, where the values in July are similar at all stations (Table 1).

Bacteria produced and consumed

In San Antonio Bay, total grazing rates of meiofauna on bacteria are 3·5 times higher at the freshwater-influenced stations ($0{\cdot}0202\ h^{-1}$) than in the brackish stations ($0{\cdot}0057\ h^{-1}$) (Table 6). This difference was due almost entirely to the higher densities and concomitant higher grazing rates of juvenile molluscs in the upper end of the estuary (Tables 4 and 5). These were predominantly small bivalves and are probably suspension-feeders. Thus, uptake of label could be due to filtering of bacteria from the overlying water as well as deposit-feeding on edaphic bacteria. In contrast to the temporary meiofauna, permanent meiofauna taxa had higher grazing rates in the brackish stations (Figure 2). This was also due to abundance differences in the two zones. Densities of permanent meiofauna at the brackish stations were twice as high as those at the fresh stations (Table 1).

Bacterial food will be limiting to meiofauna if production does not replace meiofaunal grazing. For example, in high marsh sediments of South Carolina, *in situ* bacterial production is in equilibrium with meiofaunal grazing rates (Montagna, 1984*b*). If meiofauna grazing is in equilibrium with bacterial production throughout the Guadalupe estuary, then bacterial production should also be 3·5 times higher at the upper than at the lower end of the estuary (to follow the grazing rate pattern). The opposite was true. The average bacterial production was 15% higher in the brackish stations ($2{\cdot}32 \times 10^6$ cells $cm^{-3}\ h^{-1}$) than in the freshwater-influenced stations ($2{\cdot}01 \times 10^6$ cells $cm^{-3}\ h^{-1}$) (Table 7). This indicates that either river-influenced meiofauna are: (1) limited by bacterial food; (2) dependent upon bacteria advected by river inflow to make up the deficit of *in situ* production; (3) not solely dependent on bacterial food; or (4) passing most of the bacteria through the guts undigested and viable. These alternative explanations are needed only to explain high grazing rates by juvenile macrofauna (predominantly bivalves). The most likely explanation is that the juvenile bivalves (the temporary meiofauna) are also utilizing

water column bacteria at the freshwater-influenced stations. Grazing rates of permanent meiofauna are low, indicating that meiofauna at the brackish stations are either not eating bacteria or are not limited by bacterial food.

Another possible explanation for the apparent deficit of bacterial production in the upper bay is that production is underestimated. We suspect that the production rates measured using thymidine uptake rates were underestimates for several reasons: (1) we did not account for potential dilution of thymidine (Moriarty & Pollard, 1982); (2) thymidine uptake can underestimate DNA synthesis by six- to eightfold (Jeffrey & Paul, 1988); (3) oxygen flux measurements made in July 1987 (Montagna, unpubl. data) indicate benthic metabolism is more than twofold higher than bacterial production measurements made by the thymidine technique; (4) anaerobic sulphate-reducing bacteria may not take up thymidine as rapidly as aerobic heterotrophs (Gilmour *et al.*, 1990); and (5) the average bacterial turnover time (i.e. abundance/production) of 766 h is in the slow end of the range for sediment bacteria in 11 studies reviewed by Kemp (1987). It appears that the thymidine technique may have underestimated bacterial production in San Antonio Bay by at least twofold.

Using thymidine uptake may underestimate bacterial production rates, but measuring grazing rates is unaffected by these considerations. We do not extract DNA, so label in all bacterial macromolecules is counted. Only a lack of bacterial specificity of thymidine uptake would yield lowered grazing rate estimates. The grazing technique employed assumes that ^3H incorporated into DNA traces carbon flow through the food chain during the short time-span of the experiment.

The grazing rate in the freshwater zone is 7·5 times higher than the bacterial production rate measured by thymidine, but respiration studies indicate that grazing may be in equilibrium with production. Oxygen consumption by sediments in San Antonio Bay was measured during July 1987. The average respiration rate was 30% higher at station A (2·1 mmol $O_2\,m^{-2}\,h^{-1}$) than at station C (1·6 mmol $O_2\,m^{-2}\,h^{-1}$) (Montagna, unpubl. data). In contrast to findings based on thymidine uptake, this indicates bacterial production may actually be higher in the upper end than the lower end. Assuming a respiration quotient of 1 and that chemical oxidation is 11% of total oxygen consumption (Montagna, unpubl. data), the oxygen uptake by heterotrophs indicates secondary production is in the range of 20 mg C $m^{-2}\,h^{-1}$) (Montagna, unpubl. data). This is 15 times higher than the average bacterial production rate based on thymidine uptake (0·13 mg C $m^{-2}\,h^{-1}$). The latter estimate is derived by multiplying biomass estimates with thymidine production estimates. Average bacterial biomass is estimated to be 10·2 μg cm^{-3} by using average bacterial cell volumes from July 1988 (Montagna, unpubl. data) and conversion factors (Lee & Fuhrman, 1987). The production values estimated by oxygen consumption are consistent with the findings of higher grazing rates in the upper end of the estuary. Carbon turnover time (biomass/production) based on oxygen consumption is 4·6 h. The inverse of the average meiofaunal grazing rate (0·00990; Table 8) yields a turnover time of 101 h, which is much slower than the bacterial turnover time. Therefore, bacterial production rates measured using oxygen consumption indicate that bacterial food is not limiting.

One more caveat is necessary. Protozoans are also bactivorous (Kemp, 1988), but were not examined during the current study. We can only assume that additional grazing pressure by protozoans would further increase the demand for bacterial biomass. However, several studies indicate that protozoans may have a minor or no role in meiofaunal feeding experiments. In saltmarsh, saline pond, and mangrove sediments ciliated protozoans grazed only 4% of the bacteria abundance per day (Kemp, 1988). In tropical

TABLE 8. Summary of meiofaunal and microbial responses in San Antonio Bay. Abbreviations used in table: G, grazing; P, production; F, freshwater zone; and B, brackish zone

Process	Microalgae	Bacteria	
G>P	Yes	Yes[a]	No[b]
G[F]>G[B]	Yes	Yes	
P[F]>P[B]	Yes	No[a]	Yes[b]

[a]Production measured using thymidine uptake.
[b]Production measured using oxygen uptake.

mangrove sand flats (Alongi, 1988) and microcosms (Alongi & Hanson, 1985), changes in bacterial population abundances did not correlate with changes in protozoan abundance. However, in specialized environments, e.g. on *Capitella capitata* tube caps, there is a correlation with enhanced bacterial production and protozoan abundance (Alongi, 1985). These studies indicate that protozoans may not be important in controlling bacterial dynamics on broad scales within sediments, but small-scale, biogenic structure could be a controlling influence.

Microalgae produced and consumed

Grazing rates of meiofauna on microalgae are 2·5 times higher in freshwater-influenced stations (0·0651 h^{-1}) than in brackish stations (0·0263 h^{-1}) (Table 6). Grazing on microalgae was co-dominated by juvenile molluscs and other meiofauna taxa (mostly ostracods, kinorynchs and turbellarians) (Table 5). Both of these groups had higher grazing rates in the fresher stations, but harpacticoids had higher rates at the brackish stations. So, the response to freshwater inflow by meiofauna grazing on microalgae was consistent with the grazing response on bacteria.

McIntyre and Cullen (1988) studied microalgae in the water column and benthos during January, April and July 1987 on the same cruises as this study. Microalgal production in the sediment is only a small percentage of that in the water column. Benthic production increased from 0·7% of total production in the freshwater zone to 2·3% of total production in the brackish zone. Since much of the productivity in the upper end of the bay is in the water column, it can be advected down the bay with current flow.

Average benthic microalgal midday production was 0·41 mg C m^{-2} h^{-1} at station A, 0·48 mg C m^{-2} h^{-1} at station B, 0·19 mg C m^{-2} h^{-1} at station C, and 0·07 mg C m^{-2} h^{-1} at station D (McIntyre & Cullen, 1988). Thus, production was about 3·4 times greater in the freshwater-influenced zone than in the brackish zone. This is in contrast to the pattern of bacterial grazing. The production ratio is correlated with, but higher than, the ratio for the meiofauna grazing rates. This indicates that meiofauna grazing is responding to microalgae production.

Microalgal biomass at the lower end was 33% higher than the upper end. The average chlorophyll *a* content of the sediments (to a depth of 3 mm) was 4·5 mg m^{-2} at A, 3·9 mg m^{-2} at B, 5·8 mg m^{-2} at C, and 5·4 mg m^{-2} at D (McIntyre & Cullen, 1988). This correlates with meiofauna densities 50% higher in the brackish zone (Table 1). Other studies have also shown meiofauna densities have a positive correlation with sediment chlorophyll content (Montagna *et al.*, 1983, 1987, 1989). The commonality of this finding in disparate environments suggests a very strong trophic link between meiofauna and microphytobenthos.

In January 1987, both chlorophyll and productivity were higher in the brackish than in the freshwater zone (McIntyre & Cullen, 1988). In April, a transition occurred and by July, biomass and production were much higher in the river-influenced portion of the bay. Similar patterns occurred in meiofaunal grazing. Harpacticoids had higher grazing rates in the brackish end during January and April, but similar values at all stations during July when salinity at all stations was near zero (Figure 3). A similar, but less pronounced transition occurred with nematodes, but other meiofauna taxa had the opposite trend (Figure 3). It is not possible to determine if this is the result of seasonal switching of preferred food or affected by freshwater inflow, since these events are confounded.

The overall average grazing rate on microalgae was 0·0411 h^{-1} (Table 8). This implies that microalgae would require turnover times of 24 h to be in equilibrium with the meiofaunal grazing rates. Assuming a carbon to chlorophyll ratio of 44·5 (de Jonge, 1980), the average microalgal biomass is 218 mg C m^{-2}. Since the overall average productivity is 0·288 mg C m^{-2} h^{-1}, the turnover time is about 758 h. This is much too slow for benthic microalgae to replace themselves due to losses by meiofaunal grazing. However, 38·8% of the grazing is due to filter-feeding juvenile molluscs (Table 5) which might be taking in mostly water column microalgae. The grazing rate on microalgae by non-filter-feeders is 0·00159 h^{-1}, which requires a turnover time of 63 h. Several factors might explain the discordance between the high grazing rates, and low production values: (1) advection, or the external supply of microalgae could make up the deficit due to *in situ* grazing; (2) ingested microalgae are not necessarily digested (Epp & Lewis, 1981), (3) grazing can enhance microalgal growth by breaking up protective gelatinous sheaths and providing nutrients (Porter, 1976). If one or some of these explanations is not true, then meiofauna are limited by microalgal food.

Microbial–meiofaunal trophic interactions in estuaries

Our primary hypothesis, that freshwater inflow would stimulate feeding rates, is confirmed by the higher grazing rates in the upper end of the estuary. This observation implies that water management practices should provide for adequate freshwater inflow to estuaries. However several caveats are necessary. There are slight differences among stations with regard to water depth and sediment texture, but these are all similar subtidal, shallow, muddy habitats. The largest differences among stations are in location (with respect to river influence) and community structure. The communities in the two zones were very different. The high grazing rates were found in the community by juvenile molluscs, which were probably filter-feeding and growing rapidly. Lower grazing rates were found in the brackish end of the estuary where the community was dominated by nematodes and harpacticoids. The final caveat relates to climatic variability. Texas estuaries are subject to cycles of floods and droughts. A flood did occur during this study (in June 1987) resulting in a completely fresh estuary in July 1987. After the flood in July molluscan grazing rates were high (Table 4), and nematode and harpacticoid densities (Table 1) and grazing rates (Figures 2 and 3) were low. Perhaps the meiofaunal functional response to freshwater inflow observed during this study is only characteristic of a wet year.

Meiofauna are probably responding to increased food availability and quality. Freshwater inflow, and the concomitant nutrient influx, can maintain productivity in estuaries (Deegan *et al.*, 1986; Nixon *et al.*, 1986). Apparently, nutrient input from the river stimulates microalgal growth, and riverine organic matter is deposited stimulating bacterial growth (based on oxygen consumption). Meiofauna, dominated by juvenile bivalves, at

the head of the bay respond by increasing their grazing rates. We hypothesize that this is an adaptation to obtain as much food as possible before it passes them by. Other studies have shown the importance of flowing water in determining food availability to suspension-feeders (Fréchette & Bourget, 1985), and benthic filter-feeders are known to be important in controlling phytoplankton biomass (Cloern, 1982). Other physical factors such as tides may also be important. For example, harpacticoid consumption rates respond to tidal cycles in Louisiana marshes (Decho, 1988). It appears that physical factors have some influence on meiobenthic feeding responses in a variety of habitats. For San Antonio Bay, we hypothesize that microbial biomass is advected down the bay with current flow, and this advected biomass complements low *in situ* production to maintain the high meiofaunal grazing rates in the freshwater stations. These hypotheses are put forward to explain how the grazing rates can be much greater than the turnover times or productivity rates of the food sources. The meiofaunal response in the head of the bay and the high grazing:production ratios, leads us to hypothesize that meiofauna would be severely food-limited in estuaries without significant freshwater inflow.

Meiofauna obtain their food from a variety of sources other than bacteria and microalgae. Nematodes can be detritivores (Findlay, 1982), and harpacticoids can eat ciliates (Rieper, 1985). Microbial mucus exopolymers are utilized by harpacticoids (Decho & Moriarty, 1990), and are probably sources to other meiofauna as well. Harpacticoids (Decho & Fleeger, 1988) and nematodes (Lopez *et al.*, 1979) also can shift feeding preference from the juvenile to adult stages. Meiofauna also can shift feeding preferences seasonally (Lee *et al.*, 1976). Food production is not only production of bacterial, microalgal and protozoan biomass. Detritus supply can also be important to meiofaunal organisms (Alongi & Hanson, 1985). Finally, dissolved organic matter can be important in the nutrition of meiofauna (Lopez *et al.*, 1979; Montagna, 1984*a*). Dissolved organic matter may be important for juvenile molluscs in this study, since 76% of the label uptake was due to non-adsorption and non-grazing processes (i.e. the difference between the control and formalin treatment in Table 1). Since one can never measure the abundance, distribution, and feeding on all potential food sources, food limitation is impossible to prove. An assumption in this, and similar, studies is that bacteria and microalgae are the principal food sources for meiofauna.

How can the existing meiofaunal populations be sustained when they are depleting their food supply? Several hypotheses can explain this apparent paradox: (1) upstream production is advected downstream and makes up the deficit of *in situ* production; (2) all food ingested is not digested; (3) grazing rates will be slowed if food becomes depleted; (4) meiofaunal populations will decline and feeding pressure is reduced; (5) there will be switching to other less desirable food sources when microalgal food becomes depleted; or (6) bacteria and microalgae are not the principal food sources for meiofauna. If meiofauna are food-limited, then their populations should decline in 1988, and that did happen (Montagna & Kalke, unpubl.).

It is apparent that meiofaunal grazing rates on microalgae in San Antonio Bay are much greater than the *in situ* growth that microbial populations can support. When microalgae production is enhanced, as it is in the upper end of the estuary, meiofauna respond with higher feeding rates. These relationships are summarized in Table 8, and indicate that meiofauna may be limited by microalgal food in this system.

The link between meiofauna and bacteria is much less certain, since we have conflicting data on the absolute value for bacterial production. Thymidine uptake indicates grazing exceeds production by 7·5 times, but production based on oxygen uptake is only 5% of the

TABLE 9. Average total meiofaunal grazing rates (h^{-1}) for all stations and seasons in three estuaries

Area	Microalgae		Bacteria	
	Rate	CV	Rate	CV
San Antonio Bay, TX[a]	0·04110	24%	0·00990	21%
North Inlet, SC[b]	0·00648	32%	0·03372	89%
San Francisco Bay, CA[c]	0·00080	35%	0·00280	32%

[a]This study.
[b]Montagna (1984*b*).
[c]Montagna and Bauer (1988).

grazing rate. If the thymidine values are correct, then bacterial food is limiting, since grazing exceeds production. We don't believe this is the case, because: (1) there is too much evidence (reviewed above) that thymidine underestimates production; (2) the oxygen uptake rates are consistent with the organic content of the sediments in the two zones; and (3) feeding rates on bacteria are also consistent with oxygen uptake. Considering the low feeding rates on bacteria, and using the production estimates measured with oxygen uptake, we can not conclude that meiofauna are limited by bacterial food (Table 8).

The average total grazing rates on bacteria and microalgae range over one order of magnitude among three different North American estuaries (Table 9). The differences among the rates may be related to sediment texture. Sediments were intertidal sand in San Francisco Bay, subtidal mud in Texas, and intertidal saltmarsh mud in South Carolina, which represents a gradient of decreasing grain size and increasing organic and detrital content. Also, Texas was the only area with a large amount of freshwater inflow.

The grazing rates on bacteria ranged from 0·003 to 0·03 h^{-1} (Table 9). The bay-wide average grazing rates on bacteria measured in Texas are three times higher than those measured in San Francisco Bay, but only 30% of those measured in South Carolina (Table 9). The grazing rates increase along a gradient of decreasing sediment grain size, and increasing organic content. Within San Antonio Bay, sediment carbon content is twice as high in the freshwater end, where grazing is highest, than in the brackish end (Montagna, unpubl. data), consistent with this hypothesis. If this hypothesis is true, then meiofaunal grazing will be a valuable tool to measure benthic functional response to a variety of enrichment gradients in natural and polluted environments.

Average grazing rates on microphytobenthos range from 0·04 to 0·0008 h^{-1} (Table 9). The average grazing rate on microalgae measured in Texas is six times higher than that measured in South Carolina saltmarsh sediments, and 51 times greater than those measured from San Francisco Bay sediments. Therefore, grazing at sites with muddy sediments in South Carolina and Texas was higher than in the sandy sediments of California. This is in spite of the fact that subtidal sediments in Texas probably had less available light for autotrophs than intertidal sediments of South Carolina and California. Three factors unique to Texas help explain the larger grazing rates: high freshwater inflow (due to the flood) and the concomitant influx of nutrients that can stimulate primary production, a community composition (juvenile molluscs) that can take advantage of stimulated primary production, and higher average annual temperatures (that might regulate invertebrate physiology).

Microalgae are apparently being selectively grazed in Texas. The grazing rate on microalgae is 4·1 times higher than on bacteria in Texas, but bacterial grazing rates are five times higher in South Carolina and 3·5 times higher in California. In all three estuaries temporary meiofauna, i.e. juvenile macrofauna, dominate the grazing activity. Polychaetes were the dominant grazers in South Carolina, but relatively unimportant in Texas. Nematodes, harpacticoids and polychaetes can have overlapping food requirements, and may be competitors for food resources (Alongi & Tenore, 1985). The grazing studies indicate that juvenile macrofauna, i.e. temporary meiofauna, have a significant role as competitors to permanent meiofauna in benthic systems. Whereas microalgal production is in equilibrium with meiofaunal grazing in South Carolina (Montagna, 1984*b*), in Texas, grazing outstrips *in situ* production. Meiofauna in South Carolina and Texas are having a large impact on microphytobenthos production. In contrast, meiofauna consumed only 10% of the microphytobenthos production in the Eems–Dollard estuary (Admiraal *et al.*, 1983). Meiobenthos in Texas estuaries may be limited by microalgal production.

The relationship between meiofauna, macrofauna and their microbial food is obviously very complex and very different in different environments. Meiofaunal grazing response is a function of community structure, and environmental characteristics of the habitats studied. Deposit-feeding polychaetes are dominant grazers in intertidal depositional environments (like the South Carolina salt marsh) and bivalves are the dominant grazers in subtidal environments dominated by flowing river water (like San Antonio Bay). Meiofauna in the Guadalupe estuary are apparently responding to nutrient enrichment in the upper, freshwater-influenced zone, with higher grazing rates.

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