Meiobenthic interactions with macrobenthic larvae and juveniles: an experimental assessment of the meiofaunal bottleneck*

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ABSTRACT: The meiofaunal bottleneck hypothesis states that permanent meiofauna (e.g. nematodes, copepods, foraminifera) negatively affect macrofaunal larval settlement and juvenile survivorship. Field studies suggest enhanced meiofaunal densities decrease recruitment of some macrofauna but do not identify whether this is a settlement or post-settlement process. Our experiments specifically examined the settlement response of the spionid polychaete *Streblospio benedicti* Webster and the venerid bivalve *Mercenaria mercenaria* (L.) to functionally different meiofaunal taxa (burrower, epibenthic, sediment sweeper). ANOVA revealed no significant effect of any meiofaunal taxon on macrofaunal settlement. Further experiments on emigration of recently-settled (<24 h old) juvenile *S. benedicti* and *M. mercenaria* showed no difference in burial times (time from initial juvenile contact with the sediment surface until complete burial below the sediment surface) between meiofaunal treatments and control sediments. Our data suggest that if the meiofaunal bottleneck exists, it is not a settlement phenomenon nor does it cause emigration of these recently-settled macrofauna.

INTRODUCTION

Competition has presumably exerted considerable influence in the evolutionary history of natural communities, but has been generally difficult to document in nature (Miller 1967), especially in soft-bottom benthic communities (Peterson 1979, 1991, Wilson 1991). Neill (1975) described a competitive bottleneck for microcrustaceans where age- or size-specific competition at one stage of an organism's life history ramified throughout subsequent stages. The possibility of a meiofaunal bottleneck (Bell & Coull 1980) has been proposed, whereby permanent meiofauna negatively affect settling macrofauna larvae and recently-settled juveniles.

When macrofauna larvae settle into the benthos, they can be described as meiofauna-sized macrofauna or 'temporary meiofauna' (sensu McIntyre 1964). This term simply defines the stage during which they are physically the same size (< 500 µm; Shroeder & Her-

mans 1975, Sastry 1979) as the permanent meiofauna that is frequently dominated by nematodes, copepods and foraminifera (Hicks & Coull 1983). Warwick (1984) found that body size-frequency curves of recently-settled polychaetes and echinoderms overlapped with those of the meiofauna. Long-term field data from North Inlet, South Carolina, USA, on polychaete and bivalve abundances show distinct time lags in peak abundance between meiobenthic and macrobenthic stages, with apparent large losses in between (Stancyk & Feller 1986, Feller et al. 1992), suggesting important mortality events between these life-history stages.

Several observations suggest that juvenile macrofauna-meiofauna interactions may be important: (1) juvenile macrofauna appear in the meiofaunal community during periods of seasonal increases in permanent meiofauna (Yingst & Rhoads 1978, Bell 1979), (2) the majority of juvenile macrofauna utilize the upper 1 cm of sediment where meiofauna are also most abundant (Bell 1979, Coull & Bell 1979, Yingst 1978) and (3) juvenile macrofauna and meiofauna both feed on diatoms and bacteria (Fauchald & Jumars 1979, Montagna 1984).

Recruitment success of some macrofauna is reduced in treatments with enhanced meiofaunal densities in field manipulations of 1 to 4 wk duration (Bell & Coull 1980, Watzin 1983, 1986). One aspect of this reduction may be predation; predaceous turbellarians ingest polychaete and bivalve juveniles (Thorson 1966, Watzin 1985) in the laboratory. What is less clear is the effect of other, more numerically dominant, meiobenthic taxa (i.e. nematodes and copepods) on larval recruitment, especially in muddy substrates where predaceous turbellarians are not abundant. None of these field experiments could identify the exact nature of the interaction or distinguish between settlement and post-settlement processes that exert significant effects on subsequent population structure of macrofauna (Luckenbach 1984, Connell 1985, Peterson 1986, Woodin 1986, 1991).

Our goal was to distinguish settlement from post-settlement events. Experiments specifically examined (1) larval settlement patterns and (2) recently-settled juvenile emigration of 2 common macrobenthic species in response to functionally different meiofauna.

METHODS

Meiofaunal treatments represented 3 functional groups: (1) burrowers – harpacticoid copepods *Nannopus palustris* Brady, *Stenhelia* (D.) *bifidia* Coull, and 'bulk' nematodes, (2) epibenthic flitters – the harpacticoid copepod *Microarthridion littorale* (Poppe) which actively moves across the sediment surface and (3) surface sediment sweepers – the foraminiferan *Ammonia beccarri* (L.) which extends its reticulopodia across the sediment surface to feed. Macrofaunal species included the planktotrophic morph of the spionid polychaete *Streblospio benedicti* Webster (Levin 1984) and the venerid bivalve *Mercenaria mercenaria* (L.) which also has planktotrophic development (Carriker 1961). All co-occur and are common meiobenthic (Coull 1985, Coull & Dudley 1985) and macrobenthic (Holland 1974, Service & Feller 1992) species in southeastern USA estuaries.

Meiofauna and *Streblospio benedicti* were collected from North Inlet (33° 19' N, 79° 10' W). Copepods and nematodes were collected fresh for each experiment, while cultures of *Ammonia beccarri* and *S. benedicti* were maintained in the laboratory. The 'bulk' nematode treatment was a composite of numerous species extracted from field sediments (Couch 1988). *Mercenaria mercenaria* pediveligers were hatchery reared (see 'Acknowledgements'). All cultures and macrofaunal larvae were fed the alga T-*Isochrysis galbana* (Chrysophyceae, Chrysophyta). Each meiofaunal and macrofaunal species was paired in single-species interaction experiments.

Settlement experiments were performed in glass chambers ($9 \times 9 \times 6$ cm) holding 500 ml synthetic seawater (28 ppt). The chamber base (Fig 1A) was a tissue culture plate cut into a 4×4 array of wells. These 16 wells (1.5 cm deep, surface area 2 cm^2) served as patch sites for controls (no meiofauna) and treatments arranged in a checkerboard pattern. Each well contained 1 ml of sterile mud (Chandler 1986), creating a sediment patch 0.5 cm deep; sediment patches occupied 40 % of the chamber bottom. Any stray sediment particles on the chamber bottom were aspirated away. Plastic tubes were inserted into each well, protruding above the water level. Meiofauna were pipetted into alternating tubes and allowed to establish themselves in well sediments for 24 h, after which the tubes were removed. Meiofaunal treatment densities per well reflected high intertidal field densities: *Nannopus palustris*, 25; *Stenhelia bifidia*, 20; *Microarthridion littorale*, 25; *Ammonia beccarri*, 70; nematodes, ca 250. Nematode treatments were established from a meiofaunal sample splitter (Elmgren 1973) to yield approximate densities of 250 well^{-1} ($\bar{x} = 263.3$, SD = 16.4, n = 10) while other taxa were allotted individually. *Streblospio benedicti* larvae (200 chamber^{-1}) in the terminal 11–12 setiger planktonic stage or *Mercenaria mercenaria* late pediveligers (500 chamber^{-1}) were added to the water contained within the chamber and allowed to settle for 24 h. At termination the plastic tubes were reinserted and the wells were inspected for meiofauna and metamorphosed juveniles. All experiments followed this procedure except for the *M. littorale* treatment. This epibenthic copepod is errant; to maintain the treatment densities, plastic tubes were left in each well (treatment and control) throughout the duration of the experiment. Larvae were placed into each tube (*S. benedicti*: 10 well^{-1}; *M. mercenaria*, 25 well^{-1}) and restricted by the tube to sediment patches rather than dispersed throughout the chamber. In all experiments, meta-
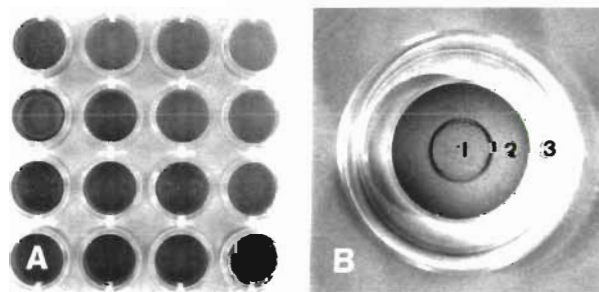

Fig. 1 (a) Chamber for settlement experiments showing 4×4 array of alternating treatment and control sediment patches on the chamber bottom (9×9 cm). Note that there is no sediment between wells (well surface area 2 cm^2). (b) Nested dishes for emigration experiment. (1) Inner meiofaunal plug; (2) doughnut of control sediment; (3) outer dish. Outer dish diameter 6 cm

morphosed juveniles of *S. benedicti* were determined by tube building activity and lack of swimming setae. *M. mercenaria* were considered juveniles if they no longer possessed a velum. Two settlement chambers were run concurrently during each experiment. For each meiofaunal taxon (3 burrowers, 1 epibenthic flitter, 1 sediment sweeper), the experiments were temporally replicated 3 times for *S. benedicti* and twice for *M. mercenaria*. Since many meiofauna are positively phototactic, all experiments were conducted in a dark environmental chamber at 25 °C.

Emigration experiments were conducted within 3 nested plastic dishes (Fig. 1B). Sterile sediment was added to the inner 2 dishes. The innermost dish was slightly shallower than the middle dish, so there was a 3 to 4 mm continuous sediment layer across the 2 dishes. Synthetic seawater (28 ppt) was added to the taller outer dish (6 cm diameter) until the sediment of the inner rings was covered to a depth of about 0.5 cm. A plastic tube was inserted snugly into the innermost dish and meiofauna were added and allowed to establish themselves in the dark. The tube was removed after 12 h, yielding an innermost meiofaunal plug surrounded by a doughnut of control sediment. One recently-settled juvenile (< 24 h old) *Streblospio benedicti* or *Mercenaria mercenaria* was added to the surface of the meiofaunal plug or the control sediment and observed under a dissecting microscope. Time from initial juvenile contact with the sediment surface until complete burial below the sediment surface was recorded. In total, 6 juveniles were added to treatments or controls in each of 4 dishes, replicated twice in time for a total of 48 trials per meiofaunal treatment.

Raw *Mercenaria mercenaria* and log(x+1)-transformed *Streblospio benedicti* settlement densities were analyzed by 3-way ANOVA (treatment and chamber, fixed; time, random). A reduced ANOVA was performed on pooled data when factors and interactions were not significant. To maintain an experimentwise error rate of $\alpha = 0.05$, each ANOVA was evaluated at an $\alpha' = 0.025$ (Sokal & Rolf 1981). Raw emigration times were analyzed by 3-way ANOVA (treatment and dish, fixed; time, random; $\alpha = 0.05$). All ANOVAs were performed by SAS Institute (1985) statistical analysis programs. Sensitivity of settlement experiments was determined through post hoc power $(1 - \beta)$ analysis of pooled data following the methods outlined in Sokal & Rohlf (1981). When calculating power, the null

hypothesis is tested against a specific, alternative hypothesis. The null hypothesis (H_0) was no difference between treatment and control means. Two alternative hypotheses were a 35 % (H_a) and 50 % (H_b) reduction in treatment from control means.

To observe modification of sediment structure by meiofauna, small observation chambers were constructed out of clear, thin plastic slides ($6 \times 3 \times 1$ cm) with a 3×2 cm viewing trough cut from the long axis of the slide. Glass cover slips were mounted with silicone glue on both sides of the plastic slide, producing an observation chamber ca 2 cm thick. After 0.5 ml of sterile mud was gently placed into the chamber with artificial seawater, meiofauna were added at densities equal to settlement experiments. Meiofaunal effects on sediment structure could be assessed qualitatively after 12 h.

RESULTS

Meiofauna treatments maintained fidelity throughout the experiment. Examination of all 16 sediment patches within a chamber revealed no significant movement from treatment to control patches. *Streblospio benedicti* settlement showed a consistent response across all 5 meiofaunal treatments (Fig. 2). ANOVA revealed no treatment or chamber effect on settlement for any of the 5 meiofaunal taxa, and all interactions were non-significant. Between 18 and 94 % of *S. benedicti* larvae settled per chamber. This variation in
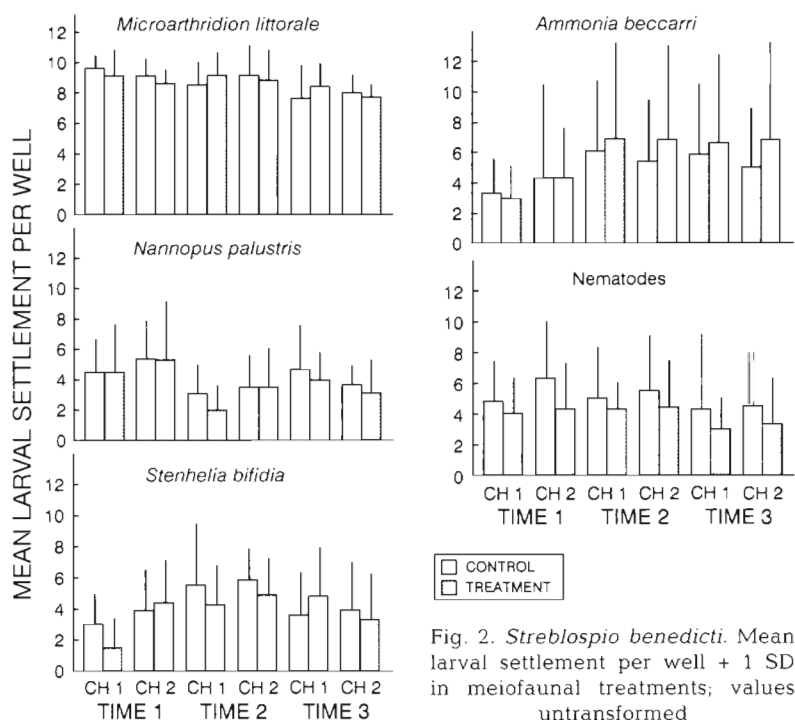

Fig. 2. *Streblospio benedicti*. Mean larval settlement per well + 1 SD in meiofaunal treatments; values untransformed
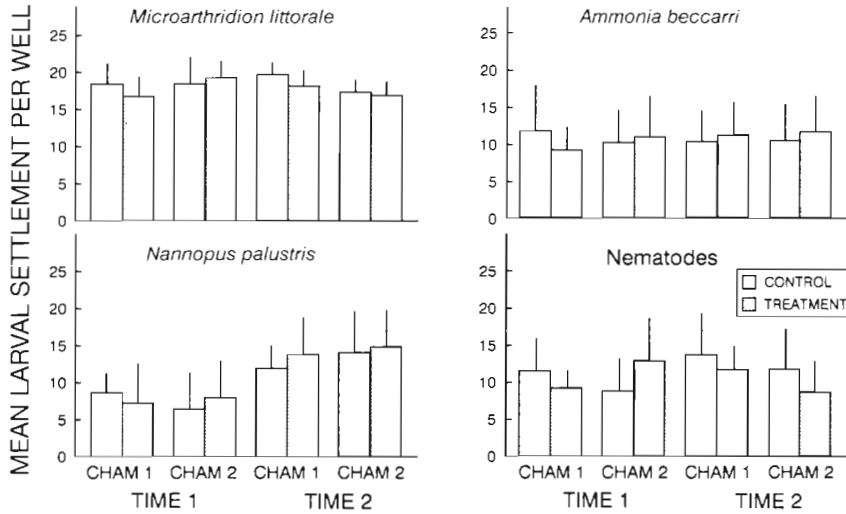
Fig. 3. *Mercenaria mercenaria*. Mean larval settlement per well + 1 SD in meio-
faunal treatments; values untransformed

Streblospio benedicti and Mer-
cenaria mercenaria settlement was
consistently greater in the *Micro-
arthriodion littorale* treatment
(Figs. 2 & 3). We reasoned that
since larvae were tube-restricted to
100 % sediment patches in contrast
to the other treatments without
tubes where only 40 % of the
chamber bottom was sediment
patches (see 'Methods'), this mani-
pulation accounted for the higher
settlement. To test this idea we per-
formed additional settlement ex-
periments with tube-restricted *S.
benedicti* larvae and *Ammonia
beccarri* as the treatment. Settle-
ment rates of tube-restricted larvae
per chamber were higher (78 to
89 %) than in the non-tube *A. bec-
carri* treatment (25 to 52 %) and comparable to the *M.
littorale* treatments (88 to 94 %).

settlement produced a significant time effect within
the meiofaunal treatments *Nannopus palustris* ($F_{2,90}$ =
4.31, p < 0.05), *Stenhelia bifidia* ($F_{2,90}$ = 5.13, p < 0.01)
and *Ammonia beccarri* ($F_{2,90}$ = 4.83, p < 0.05). Settle-
ment response of *Mercenaria mercenaria* was also
consistent across the 4 meiofauna treatments tested
(Fig. 3). Treatment, chamber, time and all interactions
were non-significant. Larval settlement per experi-
ment varied from 25 to 76 % but only produced a
significant time effect within the *N. palustris* ($F_{1,60}$ =
25.70, p < 0.001) treatment. Nearly all *S. benedicti* and
M. mercenaria not found in chamber sediments were
unmetamorphosed larvae in the water column; fewer
than 5 % settled on the plastic bottom between wells.
Post hoc power analysis on all settlement data revealed
that a 35 % reduction in settlement (H_a) could be
detected with a power of at least 0.53 and a 50 %
reduction in settlement (H_b) could be detected with a
power of at least 0.79 for every treatment (Table 1).

Emigration experiments with recently-settled juve-
niles (< 24 h old) of *Streblospio benedicti* and *Merce-
naria mercenaria* indicated no differential response to
meiofauna. Although juvenile *M. mercenaria* required
more time to bury than *S. benedicti* juveniles (Table 2),
all main effects (treatment, dish, time) and interactions
were non-significant for burrowing times of both macro-
fauna species.

Meiofaunal activity generated dramatic and diverse
modifications of surficial sediments in our observation
chambers. The epibenthic copepod *Microarthridion
littorale* (Fig. 4A[1], A[2]) occasionally burrowed but
mostly fluffed surface sediments; *Nannopus palustris*
(Fig. 4B[1], B[2]) burrowed extensively into deeper sedi-
ments. Nematodes (Fig. 4C[1], C[2]) wove a fine network
of burrows that created a spongy surface of noticeably
reduced particle cohesion, whereas the foraminiferan

Table 1 Post hoc power analysis on transformed data [log(x+1)] of *Streblospio benedicti* and of untransformed *Mercenaria
mercenaria* settlement for each meiofaunal treatment. Alternative hypotheses tested were a 35 % (H_a) and 50 % (H_b) reduction
in mean settlement in treatments from controls. Data were pooled among time replicates not significantly different (Bonferroni
multiple comparisons, α = 0.05)

Treatment	*Streblospio benedicti*				*Mercenaria mercenaria*			
	35%	50%	n	Pooled replicates	35%	50%	n	Pooled replicates
Microarthridion littorale	ca 1.00	ca 1.00	48	1+2+3	ca 1.00	ca 1.00	32	1+2
Nematodes	0.79	0.99	48	1+2+3	0.97	0.99	32	1+2
Ammonia beccarri	0.65	0.93	32	2+3	0.94	0.99	32	1+2
Nannopus palustris	0.82	0.99	32	1+3	0.53	0.79	16	1
	0.80	0.99	32	2+3	0.90	0.99	16	2
Stenhelia bifidia	0.56	0.88	32	1+3	–	–	–	–
	0.67	0.94	32	2+3	–	–	–	–

Table 2. Burial times (s) of < 24 h old post-settlement juveniles of *Streblospio benedicti* and *Mercenaria mercenaria* to meiofaunal treatments. Data are pooled within each treatment (n = 24)

| Treatment | *Streblospio benedicti* | | *Mercenaria mercenaria* | |
	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range
Nannopus palustris	20.5 ± 8.0	10–38	93.8 ± 56.3	16–212
Control	15.8 ± 5.8	8–26	94.0 ± 48.7	8–223
Stenhelia bifidia	21.6 ± 6.9	11–37	–	–
Control	22.3 ± 6.7	14–35	–	–
Microarthridion littorale	20.5 ± 11.0	3–42	56.5 ± 38.4	14–167
Control	22.3 ± 7.5	9–36	75.7 ± 53.9	9–201
Ammonia beccarri	18.5 ± 8.5	7–41	82.7 ± 52.1	17–267
Control	23.8 ± 6.1	8–38	70.4 ± 48.9	12–243
Nematodes	27.8 ± 9.9	12–49	91.3 ± 62.2	8–296
Control	20.7 ± 8.8	6–37	73.1 ± 55.3	19–215

Ammonia beccarri (Fig. 4D[1], D[2]) granulated surface sediments and noticeably increased particle cohesion (also see Chandler 1989). The meiofaunal taxa in our experiments clearly modified sediment structure relative to control sediments (Fig. 4E[1], E[2]).

DISCUSSION

Competitive interactions are usually divided into 2 modes: interference and exploitation (Miller 1967). Considering the diverse nature of meiofauna in sedimentary habitats, it is puzzling that some form of interaction was not detected. Permanent meiofauna consist of at least 22 metazoan and several protoctistan phyla, possess many modes of existence (e.g. burrowing, epibenthic, tube building), reach very high densities (Higgins & Thiel 1988), and are known to alter surface sediment characteristics significantly (Cullen 1973, Yingst & Rhoads 1978, Chandler 1989). We chose meiofaunal treatments to represent functional groups that we thought would aid in identifying means of interactions. Perhaps burrowing meiofauna (nematodes and copepods *Nannopus palustris* and *Stenhelia bifidia*) do not affect macrofaunal settlement since they are not concentrated at the immediate sediment surface where larvae settle. Vertical distribution studies indicate *N. palustris* reaches highest densities at 2 to 4 mm below the surface and *S. bifidia* at 5 to 6 mm, while nematode numbers increase below 3 mm (Coull et al. 1989). Additionally, the 2 meiofaunal taxa active at the sediment surface did not affect larval settlement. The epibenthic copepod *Microarthridion littorale* flits actively across sediments (pers. obs.). The foraminiferan *Ammonia beccarri* dramatically increases median grain diameter (Chandler 1989) and consumes large amounts of sediment bacteria and microphytobenthos (Muller 1975, Lee et al. 1972)

through its feeding activities. Settling macrobenthic larvae and recently-settled juveniles are capable of distinguishing sediment patches over a scale of centimeters (Butman et al. 1988, Woodin & Marinelli 1991, Chandler & Scott 1991). Despite meiofaunal activities that seemingly might interfere with macrofaunal larval settlement or force juvenile emigration, neither settlement nor emigration of *Streblospio benedicti* or *Mercenaria mercenaria* was affected.

A significant time effect was detected (ANOVA) in 3 meiofaunal treatments in experiments with *Streblospio benedicti* and one with *Mercenaria mercenaria*. Several spawns of both *S. benedicti* and *Mercenaria mercenaria* provided larvae for experiments. Even though all larvae were reared in an identical manner (e.g. temperature, light, food), variation in time to reaching larval competency could be observed (Hadfield 1984). Despite such a 'larval cohort' difference, *S. benedicti* and *M. mercenaria* settlement response was consistent across all meiofaunal treatments.

In light of such non-significant treatment effects, post hoc power analysis is appropriate to evaluate the sensitivity of tests of the null hypothesis (Andrew & Mapstone 1987). When calculating power $(1 - \beta)$ the null hypothesis must be tested against a specific alternative hypothesis. Our 35 % (H_a) and 50 % (H_b) reductions in mean larval settlement in treatments from controls were calculated from raw data. Power analyses for *Mercenaria mercenaria* were calculated on raw data; power analyses for *Streblospio benedicti* were calculated on log(x+1)-transformed data resulting in detectable differences far smaller than 35 and 50 % (ca 20 and 31 % respectively). Power was routinely above 0.80 (Table 1), the commonly accepted power level in ecological research (Underwood 1981). Our experimental design was strong enough to detect a 35 % reduction in settlement, and thus the non-
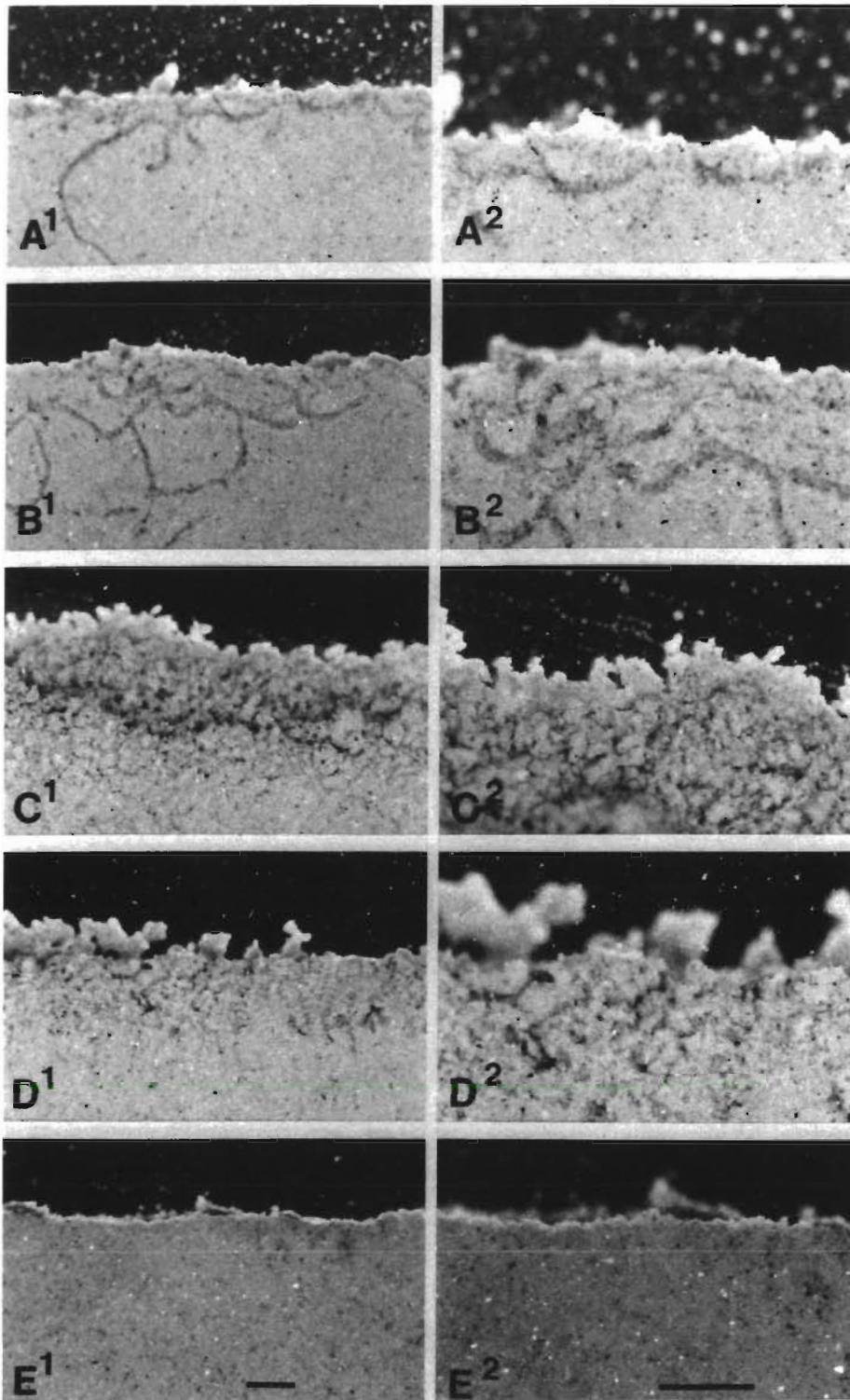
Fig. 4 Cross-sectional view [(^{1}) × 6.5; (^{2}) × 13] of sediment modification by meiofauna: (A) *Microarthridion littorale;* (B) *Nannopus palustris;* (C) Nematodes; (D) *Ammonia beccarri;* (E) Control. Scale bars = 1 mm

significant ANOVAs result from genuinely small differences between controls and treatments. This reduction (35 %) may still appear large, but within the context of our experiments is very ecologically relevant. Larval settlement can be highly variable and can

differ by an order of magnitude over a scale of centimeters (Butman et al. 1988). Other processes exerting significant interactions at this spatial scale (cm) in soft-bottom habitats include interference among macrofauna (Holme 1950, Roe 1975, Levin

1982) and ammensalism and facilitation among meio-fauna (Chandler & Fleeger 1987, Chandler 1989).

Power analysis is a fundamental statistical tool in ecological research (Toft & Shea 1983) but only recently has been performed to gain inference on negative results (e.g. McCann & Levin 1989, Hall et al. 1990, Service et al. 1992). Negative results such as reported in this paper are just as insightful as positive results when subjected to power analysis. It is quite possible that understanding of certain ecological processes may be tainted as a result of 'unsuccessful' experiments going unpublished (Peterson 1979).

The meiofaunal bottleneck theory remains equivocal. Positive correlations of meiofauna and macrofauna in the field seemingly contradict negative interactions (Armonies & Hellig-Armonies 1987). In contrast, field experiments suggesting competition between oligo-chaetes and the ampharetid polychaete *Hobsonia florida* (Gallagher et al. 1990) add credence to a possible bottleneck; however, oligochaetes are usually not a major component of meiofaunal communities and many species are considered macrofaunal (Erséus 1988).

Data presented here indicate that the bottleneck is not a settlement phenomenon for the 2 macrofaunal species we tested when interacting with specific meio-faunal taxa. We chose *Streblospio benedicti* and *Mercenaria mercenaria* because they are common macro-benthic species. A significant reduction in settlement of a common species would suggest a greater univer-sality of the effect; however, they may be so common because they are not highly discriminating during settlement (but see Chandler & Scott 1991). The results reported here should be judged within the context of the experimental design. We recognize that macro-faunal settlement into a mixed meiofaunal assemblage may be affected differently via diffuse competition. Additionally, our results might differ under flowing water (Butman et al. 1988). Nevertheless, our experi-ments indicate that numerically dominant meiofauna such as nematodes and copepods do not significantly affect *S. benedicti* or *M. mercenaria* settlement or emi-gration. The question remains whether the bottleneck exists as a post-settlement process. What is needed are growth and survivorship data on macrofauna in the presence of major meiofauna taxa. They would answer whether the bottleneck occurs as a post-settlement interaction during the time macrofauna spend as temporary meiofauna.

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