

YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete *Abarenicola pacifica*

by W. Herbert Wilson, Jr.¹

ABSTRACT

Experimental data were collected to assess the effect of a bioturbating species on associated tube-building species in an infaunal community. The deposit-feeding polychaete *Abarenicola pacifica* feeds below the sediment surface and deposits sediment on the surface in the form of castings. In a field experiment, this sediment movement is associated with a decline in the abundances of the spionid polychaete *Pygospio elegans* and the cumacean crustacean *Cumella vulgaris*. A larger spionid, *Pseudopolydora kemp*i, was not affected nor was the amphipod *Corophium spinicornis* or total oligochaete abundance. A laboratory experiment demonstrated that mortality rather than emigration from areas of high *Abarenicola* activity is responsible for the decreased *Pygospio* abundance in the presence of *Abarenicola*. Both spionids move their tube locations when subject to *Abarenicola*-induced sediment movement. At intermediate levels of sediment deposition, this increased motility permits the spionids to maintain high survivorship. At higher levels of sediment deposition, even frequent migration by *Pygospio* cannot prevent sediment-induced mortality. Both *Pygospio* and *Pseudopolydora* significantly reduce the survivorship of *Abarenicola* juveniles, presumably by ingestion of juveniles. Spionids apparently can influence *Abarenicola* only when *Abarenicola* are juveniles. It is suggested that consideration of three factors: the relative and absolute sizes of the interacting species, the motility of the interacting species, and the frequency and magnitude of the effect on the sediment may allow us to refine a functional group model of soft-bottom community dynamics, ultimately leading to a species-level theory for the organization of densely populated infaunal communities.

1. Introduction

Soft-sediment communities differ fundamentally from rocky shore communities in that most resident species live within their substratum rather than on it. In rocky shore communities, competitive interactions may be either direct organism-organism interactions such as overgrowth or crushing (Connell, 1961; Paine, 1974; Lubchenco and Menge, 1978; Buss and Jackson, 1981) or indirect interactions such as competition for food (Buss, 1979; Buss and Jackson, 1981). In either

1. Department of Earth and Planetary Sciences, The Johns Hopkins University, Baltimore, Maryland, 21218, U.S.A.

case, very little change in the substratum occurs on an ecological time scale as a function of organism interactions. In contrast, the nature of the substratum in soft-bottom communities is constantly being changed by both physical and biological processes. The three-dimensionality of the substratum may alter the importance of direct organism-organism interactions (Peterson, 1979). Many biological interactions in infaunal communities may be mediated through organisms' effects on the substratum.

Rhoads and Young (1970) presented the first demonstration of indirect interactions mediated by sediment change in an infaunal community. They showed that deposit-feeders tend to facilitate the resuspension of sediments and correlated a decrease in growth of suspension-feeding bivalves with the resuspension of sediment in areas of high deposit-feeder activity. Rhoads and Young (1971), Aller and Dodge (1974), Woodin (1974), Ronan (1975), Myers (1977), Brenchley (1978) and Thistle (1980) among others have presented data on the effects of sediment binding or bioturbation on other organisms. From these studies, a conceptual framework for understanding how infaunal organisms interact is emerging. Data and arguments have been advanced to suggest that there should be a negative relationship between organisms which bind the sediment as tubes and organisms which tend to move and destabilize sediments. I shall refer to this relationship as the functional group model for soft-bottom dynamics, noting that other functional group models, based on different criteria, have been advanced (e.g., Jumars and Fauchald, 1977).

In this study, I investigated the effect of the arenicolid polychaete, *Abarenicola pacifica*, on its associated deposit-feeding community. In a field experiment, I found that sediment movement by *Abarenicola* defecation led to a decline in abundance of some species while other species showed no change. For one affected species, the decline in abundance was due to mortality, presumably by suffocation, rather than emigration from areas of high *Abarenicola* density. These results are discussed with respect to the functional group model above for soft-bottom dynamics.

2. Study site and organisms

The area chosen for study was False Bay in the Straits of Juan de Fuca, Washington state, USA (see Hylleberg (1975) for map of area and Pamatmat (1968) for physical features). The experimental site is high in the intertidal zone (+4-5 feet) and can be characterized as a well-sorted fine sand.

The arenicolid polychaete, *Abarenicola pacifica* Healy and Wells, is a conspicuous member of the upper intertidal community in False Bay. Attaining lengths of 10 cm, this worm maintains an L-shaped burrow. It feeds in a pocket at the blind end of the burrow (Hobson, 1967; Hylleberg, 1975). Periodically, the worm defecates ingested sediment on the surface in the form of castings. These castings occur in mounds which may measure 6-7 cm across. Adult densities of *Abarenicola* often

reach 1000/m². I have found that *Abarenicola* reproduces in the spring (March-May) and broods its totally benthic larvae in a cocoon near the sediment surface in the tail shaft of the burrow. The larvae move out of the cocoon no later than the 5-6 setiger stage and burrow in the top few millimeters of the sediment.

Two spionid polychaetes are the most numerous organisms in the assemblage. *Pygospio elegans* Claparède attains lengths of 10-12 mm. It is primarily a deposit-feeder, often extending the anterior portion of its body from its tube to forage. *Pygospio* in False Bay reproduces primarily by asexual reproduction (Rasmussen, 1953) and may attain densities of 60,000/m². The second spionid is *Pseudopolydora kemp*i (Southern). A more robust species, individuals may reach 30 mm in length. *Pseudopolydora* extends only its palps in feeding, capturing particles both on the sediment surface and in the water column (Taghon, Nowell and Jumars, 1980). Densities of 16,000/m² are commonly found. Other predictable but less abundant members of this community are a multi-specific group of small (<4 mm) subsurface deposit-feeding oligochaetes, the amphipod, *Corophium spinicornis* and the meroplanktonic cumacean, *Cumella vulgaris*.

3. Materials and methods

Field experiment. To assess the effect of sediment movement by *Abarenicola* (the movement of sediment onto the surface by defecation) on other infaunal organisms, I located a 4-m-by-4-m area where *Abarenicola* were present in low abundance (< 10/m²). Twelve 20-cm long sections of plastic pipe, 10 cm in diameter (0.008 m²) were pressed into the sediment until level to the sediment surface. I introduced eight *Abarenicola* onto the surface of each of six of these twelve cores. The *Abarenicola* readily burrowed into the sediment. These cores were designated *Abarenicola* inclusion treatments (1X). The density of *Abarenicola* in the 1X treatments was equivalent to 1000/m², a density commonly encountered in the field. The remaining six cores received no *Abarenicola* (0X treatments). The 1X and 0X cores were randomized in a 4 × 3 array with 30 cm between adjacent cores. At the beginning of the experiment, cores were taken adjacent to the experimental site to establish ambient densities of all macrofauna. At the conclusion of the experiment, six additional cores were taken within and adjacent to the experimental area as controls for possible container artifacts (Cont treatments). The experiment was conducted from December 1, 1980 until December 16, 1980. The length of the experiment ensured that all of the surface area of the 1X treatments was subjected to sediment deposition.

The *Abarenicola* introduced into the experimental cores were photographed with a cm rule for scale before introduction. The projected planar area of each worm was calculated by cutting out and weighing prints of the worms. Every one to three days, photographs were taken of the cores in the field as part of the monitor-

ing procedure. Prints of these photographs were used to assess the percent coverage of the 1X replicates by fecal castings again using the print weighing method. At termination, the top 10 cm of each core was sieved separately through a 500- μ m sieve. The lower 10 cm was sieved through a 4 mm screen. No macrofaunal organisms except *Abarenicola* and an occasional *Macoma balthica* (bivalve) occur below 10 cm. Both are easily collected on the larger screen. The samples were sorted live.

The abundance data for each species in the three experimental treatments were analyzed for significant differences by a one-way analysis of variance (Snedecor and Cochran, 1967). The data were $\ln(x+1)$ transformed to successfully eliminate heterogeneity of variance. If the ANOVA indicated significant differences, Student-Newman-Keuls (hereafter SNK) a posteriori multiple range tests were performed (Sokal and Rohlf, 1969). Also, an analysis of covariance was performed to control for differences in size, and thus possible effect, of the introduced *Abarenicola*. A second ANCOVA was performed to control for differences in average percent coverage of each of the 1X cores by defecated sediment. For all statistical tests, a significance level of $p < 0.05$ was used.

Samples of the *Pygospio* from each treatment were measured to test for possible size-dependent mortality. The width of the peristomium was measured with an ocular micrometer at 50X. There is a strong correlation between peristomial width and projected worm area ($r = 0.97$, $p < 0.01$). Differences between treatments were tested for significance by χ^2 analysis (Siegel, 1956).

Laboratory mechanism experiment. An experiment was designed to determine if the reduced infaunal densities in the 1X treatments were due to mortality of the resident organisms or emigration of those organisms out of the experimental cores. Plastic flower planters, 158 mm in diameter, were filled with azoic sediment (placed in freshwater for seven days) until level with the sides. In the center of each planter, one of the plastic pipe sections used in the field experiment (104 mm in diameter) was pressed into the sediment until it was level with the surface. The inner area enclosed by the pipe was 0.80 times the area of the outer area enclosed by the inner walls of the planter and the outer walls of the plastic pipe. Both the inner and outer areas received equal densities of *Pygospio* (200 and 250 for the inner and outer areas, respectively) and *Pseudopolydora* (20 and 25, respectively). The 1X treatments each received eight *Abarenicola* in the inner area, as in the field experiment. Each treatment was replicated twice.

The experiment was terminated after ten days. The inner and outer areas were sieved separately and counted. The weight of the spionid tubes was also measured for the inner and outer area of each planter. The survivorship data, $\arcsin \sqrt{x}$ transformed, were analyzed by a one-way nested ANOVA. The data for the tube weights were $\ln(x+1)$ transformed and also analyzed by a one-way nested

Table 1. Results of the field *Abarenicola*-enclosure experiment. 1X- *Abarenicola* inclusion treatments, 0X- enclosures present but no *Abarenicola*, Cont- cores taken at termination of experiment from experimental area. Each value is the mean of six replicates. For species in which the ANOVA showed significant differences, Student-Newman-Keuls tests were performed. Underlined means are not statistically different ($p > 0.05$).

Species	1X	0X	Cont
<i>Pygospio elegans</i>	70.8	174.2	198.3
<i>Pseudopolydora kempfi</i>	8.5	20.5	18.0
<i>Cumella vulgaris</i>	25.8	40.1	62.8
Oligochaeta	11.0	15.9	10.0
<i>Corophum spinicornis</i>	3.0	5.4	4.9

ANOVA. In all cases, the transformations produced admissible data under the requirements of ANOVA (Snedecor and Cochran, 1967).

Adult spionid-juvenile Abarenicola interaction experiment. To test the effect of spionids on juvenile *Abarenicola* survivorship, I filled 20 plastic centrifuge tubes (26 mm in diameter) with sediment which had been covered with freshwater for seven days to kill all macrofaunal organisms and placed them in running seawater in a sea table at the Friday Harbor Laboratories. They were left undisturbed for five days to allow a bacterial and algal flora to become established. Then I introduced 100 5-6 setiger *Abarenicola* larvae into each tube. Five tubes received no additional organisms and served as controls. Five tubes received 25 *Pygospio*, five received 8 *Pseudopolydora* and the remaining five received both 25 *Pygospio* and 8 *Pseudopolydora*. The densities of *Pygospio* and *Pseudopolydora* used correspond to densities of 50,000/m² and 16,000/m², respectively. These densities are commonly encountered in the field. The water entering the sea table was filtered through 200- μ m Nitex screening to keep amphipods and other mobile animals out. After two months, the experiment was terminated. The top 5 mm of sediment was searched for *Abarenicola* juveniles under a dissecting microscope. The remainder of the sediment was sieved through a 500- μ m screen and the spionids counted. Differences in survivorship of *Abarenicola* juveniles among treatments were tested for significance by a one-way ANOVA and SNK multiple range tests, as discussed previously.

4. Results and discussion

The results of the *Abarenicola* field inclusion experiments are given in Table 1. In all cases, there is no statistical difference between the cores with no *Abarenicola*

Table 2. Analyses of covariance controlling for differences in size of the experimental *Abarenicola* and differences in the area of experimental cores covered by defecated sediment. For each species, the two covariates were tested separately but are combined in the table.

A. *Pygospio*

Source	df	Sum of squares	F	p
Treatment	2	3.8272	18.76	0.0001
<i>Abarenicola</i> size	1	0.0684	0.67	0.4266
Area of defecation	1	0.0250	0.24	0.6333
Residual	14	1.4713		

B. *Cumella*

Source	df	Sum of squares	F	p
Treatment	2	2.3499	8.07	0.0051
<i>Abarenicola</i> size	1	0.1273	0.87	0.3657
Area of defecation	1	0.2255	1.63	0.2229
Residual	14	2.0394		

added (OX) and the unmanipulated controls (Cont) suggesting that there are no serious artifacts associated with the plastic pipe enclosures over the experimental period. Furthermore, there is no difference in species abundances between the Cont cores taken at the termination of the experiment and the cores taken at the initiation of the experiment (Student's t-test, $p > 0.05$ for all species). The data reveal that the presence of *Abarenicola* is associated with a dramatic decrease in *Pygospio* abundance. There is also a significant decrease in *Cumella* abundance in the 1X treatment compared to the Cont treatment. Since *Cumella* is highly motile and spends some of its time in the water column, it seems likely that the experimental effect is due to the avoidance of *Abarenicola* areas by *Cumella*. *Corophium spinicornis* numbers do not decline in the presence of *Abarenicola* nor as one would predict, do the subsurface oligochaetes. The rarity of *Corophium* perhaps makes detection of any *Abarenicola* effect difficult.

Table 2 presents analyses of covariance for species which showed significant differences in the experimental treatments, namely *Pygospio* and *Cumella*. For each species, the size of the *Abarenicola* in each replicate and the average percent cover by fecal matter were entered as covariates. For both species, *Abarenicola* size was not significant. This finding was expected since I tried to equalize *Abarenicola* sizes in the 1X replicates (range 67.3-100.5 cm³ for eight individuals). More surprising is the lack of significance of average percent cover of fecal matter. It may be that percent cover while the animals are submerged differs from that during emersion or that volume of fecal matter, not area covered, should be a good predictor of effect.

Figure 1 presents size-frequency distributions for *Pygospio* from the three experimental treatments. The prediction is that small *Pygospio* (operationally defined as

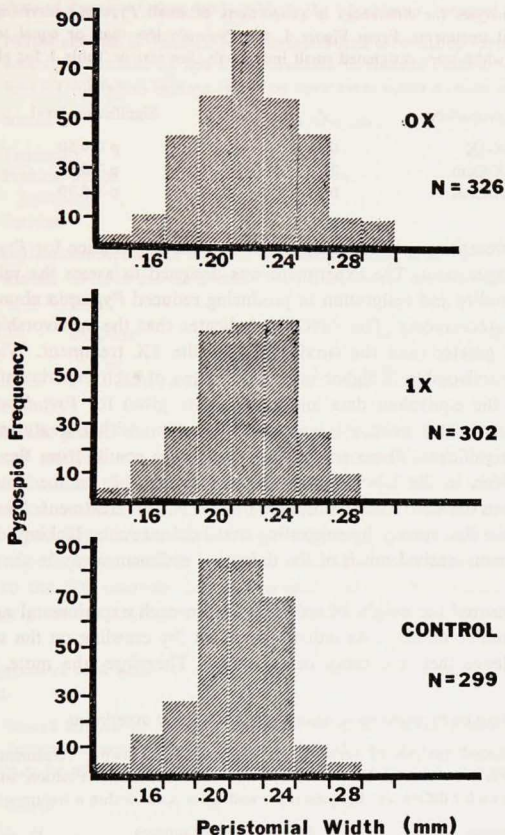


Figure 1. Size-frequency distributions for *Pygospio elegans* in the three experimental treatments in the field experiment. 0X- experimental container present but no *Abarenicola* added, 1X- experimental containers with normal *Abarenicola* density present, Cont- ambient samples adjacent to the experimental containers. N gives the number of animals measured in each treatment. Values for the abscissa range from 0.12 to 0.30.

the three smallest size classes measured) should be more susceptible to repeated burials by *Abarenicola* defecation than are larger conspecifics. The χ^2 analysis in Table 3 reveals the prediction to be wrong. There is not a disproportionate decline of small individuals in the 1X treatments.

Table 3. χ^2 analyses for differences in proportions of small *Pygospio* surviving in the three experimental treatments. From Figure 1, the *Pygospio* less than or equal to 0.18 mm in peristomial width were designated small individuals. See text or Table 1 for abbreviations to treatments.

Comparison	χ^2	df	Significance level
0X-1X	0.33	1	$p > 0.50$
0X-Cont	2.73	1	$p > 0.09$
1X-Cont	0.85	1	$p > 0.30$

Table 4 presents survivorship data and analysis of variance for *Pygospio* in the laboratory experiment. The experiment was designed to assess the relative importance of mortality and emigration in producing reduced *Pygospio* abundance in the presence of *Abarenicola*. The ANOVA indicates that the survivorship in the 0X treatment is greater than the survivorship in the 1X treatment. Within the 1X treatments, survivorship is higher in the outer area of each experimental container. In Table 5, the equivalent data and analysis are given for *Pseudopolydora*. The analysis indicates that neither treatment nor position within treatment effects are statistically significant. These results corroborate the results from the field experiment. However, in the laboratory, *Pygospio* survivorship in the inner 1X areas was lower than the survivorship observed in the 1X field treatment. I would attempt to explain this discrepancy by suggesting that tidal currents, lacking in the laboratory experiment, washed much of the defecated sediment away in the field experiment.

I also measured the weight of spionid tubes in each experimental area as a surrogate for relative motility. As individuals move (by crawling on the sediment surface), they leave their old tubes behind them. Therefore, the more frequently a

Table 4. Analysis of *Pygospio* survivorship in the laboratory experiment.

A. Nested analysis of variance for *Pygospio* survivorship. Treatment tests for differences between 1X and 0X *Abarenicola* treatments. Position within treatment tests for differences between inner and outer areas within a treatment.

Source	df	Sum of squares	F	p
Treatment	1	243.10	8.78	0.0414
Position within treatment	1	1322.13	23.88	0.0060
Residual	4	110.74		

B. Student-Newman-Keuls tests for differences among treatments. 0X- no *Abarenicola*, 1X- *Abarenicola* present. Underlined means are not statistically different ($p > 0.05$).

1X-Outer	0X-Outer	0X-Inner	1X-Inner
<u>0.88</u>	0.80	0.79	0.31

Table 5. Analysis of *Pseudopolydora* survivorship in the laboratory experiment.

- A. Nested analysis of variance for *Pseudopolydora* survivorship. Treatment tests for differences between 1X and 0X *Abarenicola* treatments. Position within treatment tests for differences between inner and outer areas within a treatment.

Source	df	Sum of squares	F	p
Treatment	1	164.71	2.42	0.1948
Position within treatment	1	516.67	3.80	0.1191
Residual	4	272.24		

- B. Student-Newman-Keuls tests for differences among treatments. 0X- *Abarenicola* absent, 1X- *Abarenicola* present. Underlined means are not statistically different ($p > 0.05$).

1X-Outer	0X-Outer	1X-Inner	0X-Inner
<u>1.06</u>	0.86	0.80	<u>0.75</u>

worm moves, the greater the amount of sediment which will be bound up into tubes. The data and analysis are given in Table 6. The analysis shows that there are significant differences between treatments but not positions within treatments. Some defecation occurred in the outer areas of the 1X treatment as spillover from the central areas. This increase in sediment movement over the 0X treatment may explain the significant increase in weight of spionid tubes in the outer 1X treatment compared to the 0X controls. Since *Pygospio* and *Pseudopolydora* survivorships are the same in the outer 1X treatment as in the 0X treatments, it seems reasonable

Table 6. Analysis of total weight of spionid tubes in the various treatments of the laboratory experiment.

- A. Nested analysis of variance for weight of spionid tubes. Treatment tests for differences between 1X and 0X *Abarenicola* treatments. Position within treatment tests for differences between inner and outer areas within a treatment.

Source	df	Sum of squares	F	p
Treatment	1	2.2451	15.80	0.0165
Position within treatment	1	0.6667	2.35	0.2118
Residual	4	3.4804		

- B. Student-Newman-Keuls tests for differences in total weight of spionid tubes among treatments. 0X- *Abarenicola* absent, 1X- *Abarenicola* present. Underlined means are not statistically different ($p > 0.05$). Means are expressed in grams.

1X-Inner	1X-Outer	0X-Inner	0X-Outer
<u>2.349</u>	1.613	<u>0.745</u>	0.667

Table 7. Survivorship of juvenile *Abarenicola* in the presence of normal densities of *Pygospio* and *Pseudopolydora*. Each treatment is replicated five times. Each replicate received 100 *Abarenicola* juveniles. Cont denotes treatments with no spionids present, Pygo- normal densities of *Pygospio* present, Pseudo- normal densities of *Pseudopolydora* present, Pygo-Pseudo- both species present at normal densities. Results of Student-Newman-Keuls tests are given. Underlined means are not statistically different ($p > 0.05$).

Cont	Pygo	Pseudo	Pygo-Pseudo
24.8	5.6	<u>1.0</u>	<u>0.2</u>

to claim that little net emigration from the inner 1X area occurred. Therefore, the higher tube weight in the outer 1X area compared to the 0X areas (both inner and outer) can be reconciled by realizing that defecation activity in the outer 1X areas is intermediate between the 1X and control areas. At intermediate levels of defecation, spionids are required to move more frequently but are able to maintain their high survivorship (Tables 4,5). In the inner 1X areas, the spionids move frequently but cannot escape the intensive sediment reworking and *Pygospio* survivorship declines (Table 4). The simplest interpretation of these data then, is that sediment movement by *Abarenicola* forces the spionids to relocate their tubes on the order of mm or cm. At high levels of sediment reworking, mortality increases. At intermediate levels, the animals frequently relocate and in so doing, survivorship remains high. In the absence of sediment movement, less relocation occurs.

Table 7 presents the data for the adult spionid—juvenile *Abarenicola* interaction experiment. This experiment tested for the effect of *Pygospio* and *Pseudopolydora*, singly and together, on the survivorship of juvenile *Abarenicola*. The data reveal that *Pygospio* and especially *Pseudopolydora* have a strong negative effect on *Abarenicola* juveniles. Given the voracity of spionids (Breese and Phibbs, 1972; Fauchald and Jumars, 1979) and the frequent occurrence of setae in the guts of both of these species (unpublished observations), ingestion of the juveniles is a likely mechanism for this interaction. It is perhaps only at the juvenile stage that *Abarenicola* is susceptible to any influence by the spionids. The deeper vertical distribution and the ease with which *Abarenicola* burrows in spionid beds (personal observations) make it apparent that spionids can do little to exclude adult *Abarenicola*.

Based largely on the studies of Sanders (1958), Rhoads and Young (1970, 1971) and Woodin (1974), a functional group approach to competition-based (high density) soft-sediment communities has been developed (see review in Woodin and Jackson, 1979). This approach, based on how organisms modify the sediment, argues that burrowing animals should be excluded from areas of high tube-builder density by the binding of sediment into tubes and preemption of space. Tube-building species should be excluded from areas dominated by bioturbating species by constant sediment movements. Yet for many densely populated infaunal com-

munities, apparent exceptions to this model exist. The model can perhaps be refined by consideration of three inter-related factors: the sizes of the interacting species, the mobilities of the interacting species and the frequency and magnitude of the sediment effect. Each of these factors will be discussed separately below.

The relative and absolute sizes of the interacting species may confound predictions based on functional groups. Woodin (1974) showed that tube-building species could effectively exclude the small opheliid polychaete, *Armandia brevis*. In the present study, even dense mats of spionid tubes could not exclude adult *Abarenicola*. Brenchley (1978) showed that juvenile *Rhynchospio arenicola* (spionid) and *Leptochelia dubia* (tanaid crustacean) were disproportionately affected by sediment deposition. It is thus possible that *Abarenicola* might have exerted a significant effect on *Pseudopolydora* in the field experiment (Table 1) if *Pseudopolydora* had been reproductive with newly settled juveniles present. Interestingly, the asexual reproduction of *Pygospio* bypasses the small sizes (< 2 mm long) that were so susceptible in Brenchley's study. This mode of reproduction may thus confer a strong selective advantage on *Pygospio*. In the present study, only juvenile *Abarenicola* can be excluded by spionids (Table 7). Woodin (1976) and Wilson (1980) have stressed the importance of size in determining successful recruitment into densely populated assemblages. In all of these examples, the relative and/or absolute sizes of the interacting species plays a crucial role in determining the outcome of interspecific or inter-functional group interactions.

The motility of the interacting species may determine the outcome of sediment-mediated interactions. Is a tube-builder mobile enough to burrow through or around sediment that has been dumped on it? Ronan (1975) showed that dumping up to 16 cm of sediment on *Phoronis viridis* beds induced no mortality: the phoronids readily burrowed up through the sediment and reestablished their tubes. Myers (1977) showed that *Prionospio heterobranchia* (spionid) and *Corophium insidiosum* (amphipod), both tube-builders, were mobile enough to persist in areas of intensive sediment reworking, principally by the holothurian *Leptosynapta tenuis*. Tables 4 and 6 reveal that *Pygospio* are more mobile in the presence of *Abarenicola* bioturbating activity. At intermediate levels of sediment movement, this motility allows them to maintain high survivorship; at high levels of sediment reworking, survivorship declines.

Lastly, the frequency and magnitude of biological effects of the sediment may affect the outcome of sediment-mediated interactions. Rhoads and Young (1970) describe the effects of the bioturbating holothurian, *Molpadia oolitica*, on the infaunal community. The fecal cone of this species supports, rather than excludes, a community of suspension-feeding organisms. Although feeding rates were not given, the sediment reworking is not sufficient to exclude tube-building species. Brenchley (1978) modeled a laboratory experiment after the *Molpadia* community and found some smaller species, particularly the smallest individuals within those

species, to be adversely affected. The amount of mortality depended on both the amount and rate of sediment deposition. Table 1 reveals that the sediment movement by *Abarenicola* was sufficient to affect *Pygospio* and *Cumella* but not other species. In considering exclusion of burrowers by tube-builders and sediment-stabilizing plants, Brenchley (1981) found that burrowers had more difficulty burrowing through a *Zostera marina* root mat and the associated tube mat than burrowing through the root mat alone. In all of these cases, the magnitude of organisms' effects on the sediment is critical in determining the outcomes of sediment-mediated interactions.

It is not the purpose of this discourse to impugn the functional group concept. Rather, it is to point out that the generality of the model has been useful in formulating interesting and insightful approaches to understanding pattern and process in infaunal communities. The model's generality does not allow it to incorporate many of the more subtle interactions as discussed above. (Vance's (1973) model of reproductive strategies of marine benthic invertebrates has played a similar role for larval ecology.) Many of these data emphasize the importance of sediment-mediated interactions. As data on this class of interactions accumulate, we should be able to fine-tune our understanding of how infaunal communities are structured. These data bring us closer to a predictive model at the species level for the dynamics of soft-sediment communities.

Acknowledgments. This work was generously supported by a grant from the Lerner Fund of the American Museum of Natural History, grants-in-aid of research from Sigma Xi, a National Science Foundation Dissertation Improvement grant and a National Science Foundation grant to Dr. S. A. Woodin. Dr. Eugene Kozloff, acting director of the Friday Harbor Laboratories, kindly made the facilities of the Labs available to me.

Terry Hughes, Pete Jumars, Scott Lidgard, Bob Steneck, Sally Woodin and an anonymous critic reviewed the manuscript. I am grateful for their criticisms, comments and suggestions.

REFERENCES

- Aller, R. C. and R. E. Dodge. 1974. Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. *J. Mar. Res.*, 32, 209-231.
- Breese, W. P. and F. D. Phibbs. 1972. Ingestion of bivalve molluscan larvae by the polychaete annelid *Polydora ligni*. *The Veliger*, 14, 274.
- Brenchley, G. A. 1978. On the regulation of marine infaunal assemblages at the morphological level: a study of the interactions between sediment stabilizers, sediment destabilizers and their sedimentary environment. Ph.D. Dissertation, The Johns Hopkins University, Baltimore, Maryland.
- 1981. Mechanisms of competition for space in marine soft-bottom communities. *J. Exp. Mar. Biol. Ecol.*, (in press).
- Buss, L. W. 1979. Bryozoan overgrowth interactions—the interdependence of competition for food and space. *Nature*, 281, 475-476.
- Buss, L. W. and J. B. C. Jackson. 1979. Competitive networks: non-transitive competitive relationships in cryptic coral reef environments. *Amer. Natur.*, 113, 223-234.

- 1981. Planktonic food availability and suspension-feeder abundance: evidence of in situ depletion. *J. Exp. Mar. Biol. Ecol.*, *49*, 151–161.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecol.*, *42*, 710–723.
- Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Rev.*, *17*, 193–284.
- Hobson, K. D. 1967. The feeding and ecology of two North Pacific *Abarenicola* species (Arenicolidae, Polychaeta). *Biol. Bull.*, *133*, 343–354.
- Hylleberg, J. 1975. Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. *Ophelia*, *14*, 113–137.
- Jumars, P. A. and K. Fauchald. 1977. Between-community contrasts in successful polychaete feeding strategies, pp. 1–20, in *Ecology of Marine Benthos*, B.C. Coull, ed., University of South Carolina Press, Columbia, 467 pp.
- Lubchenco, J. and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.*, *48*, 67–94.
- Myers, A. C. 1977. Sediment processing in a marine subtidal sandy bottom community. II. Biological consequences. *J. Mar. Res.*, *35*, 633–647.
- Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, *15*, 93–120.
- Pamatmat, M. 1968. Ecology and metabolism of a benthic community on an intertidal sandflat. *Int. Revue ges. Hydrobiol.*, *53*, 211–298.
- Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons, pp. 233–264, in *Ecological Processes in Coastal and Marine Systems*, R. J. Livingston, ed., Plenum Publishing Co., New York, 489 pp.
- Rasmussen, E. 1953. Asexual reproduction in *Pygospio elegans* Clap. (Polychaeta, Sedentaria). *Nature*, *171*, 1161–1162.
- Rhoads, D. C. and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.*, *28*, 150–174.
- 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by *Molpadia oolitica* (Holothuroidea). *Mar. Biol.*, *11*, 255–261.
- Ronan, Jr., T. E. 1975. Structural and paleoecological aspects of a modern marine soft-sediment community: an experimental field study, Ph.D. Dissertation, University of California, Davis.
- Sanders, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.*, *3*, 245–253.
- Siegel, S. 1956. *Non-parametric Statistics for the Behavioral Sciences*. New York, McGraw-Hill, Inc., 227 pp.
- Snedecor, G. W. and W. G. Cochran. 1967. *Statistical Methods*. Iowa State University Press, Ames, 593 pp.
- Sokal, R. R. and F. J. Rohlf. 1969. *Biometry*. W.H. Freeman & Co., San Francisco, 776 pp.
- Taghon, G. L., A. R. M. Nowell and P. A. Jumars. 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science*, *210*, 562–564.
- Thistle, D. 1980. The response of a harpacticoid copepod community to a small-scale natural disturbance. *J. Mar. Res.*, *38*, 381–395.
- Vance, R. R. 1973. On reproductive strategies in marine benthic invertebrates. *Amer. Natur.*, *107*, 739–752.
- Wilson, Jr., W. H. 1980. A laboratory investigation of the effect of a terebellid polychaete on the survivorship of nereid polychaete larvae. *J. Exp. Mar. Biol. Ecol.*, *46*, 73–80.

- Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft-bottom environment: the importance of biological interactions. *Ecol. Monogr.*, **44**, 171-187.
- 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *J. Mar. Res.*, **34**, 25-41.
- Woodin, S. A. and J. B. C. Jackson. 1979. Interphyletic competition among marine benthos. *Amer. Zool.*, **19**, 1029-1043.