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An Experimental Analysis of Spatial Competition in a Dense Infaunal Community: The Importance of Relative Effects

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A densely populated soft-sediment community was experimentally analysed for interspecific competition for space in laboratory experiments. No interspecific competitive interactions leading to a decrease in survivorship could be documented over a five-week period. The four most abundant species all coexisted in laboratory microcosms. The two tube-building species, the tanaid *Leptochelia dubia* and the polychaete *Rhynchospio arenicola*, could not exclude the mobile bivalve *Transennella tantilla* or the burrowing amphipod *Paraphoxus spinosus*. None of the species increases its emigration frequency when other species are present. *Paraphoxus* is found to be a browsing predator on *Rhynchospio* but inflicts no detectable mortality. The coexistence of these species is permitted by virtue of the fact that none of the species can alter the soft-sediment habitat sufficiently to make the habitat unsuitable for the other species.

Introduction

The application of experimental manipulation to densely populated infaunal communities has provided great insight into how such communities are structured (Rhoads & Young, 1970; Woodin, 1974; Ronan, 1975; Peterson, 1977; 1982; Peterson & Andre, 1980; Brenchley, 1981; 1982; Wilson, 1981; 1983; Levinton & Stewart, 1982; Race, 1982). (A dense infaunal community can be operationally defined as a community with macrofaunal densities in excess of 40 000 m⁻².) Much of this research has implicated competitive interactions as a primary determinant of distribution and abundance in such communities. Nonetheless, it is not presently clear if interspecific competition reigns as the dominant organizing force in all such communities. For instance, Ronan (1975) failed to document interspecific competition in the very dense sand flats of Bodega Bay, California.

Competitive interactions in soft-sediment environments may be classified on the basis of the limiting resource. In a general sense, food and space are regarded as potential limiting resources. Woodin (1974) was able to demonstrate interspecific competition for space. However, for organisms which feed in similar ways (e.g. surface deposit-feeders), it becomes difficult to separate food and space as separate resources (Buss, 1979; Peterson

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& Andre, 1980). Infaunal organisms require some minimum amount of space to acquire their minimum amount of food.

Competitive interactions in infaunal communities may alternatively be classified by mechanism. Direct interference mechanisms are sometimes documented among infaunal organisms (Reish & Alosi, 1968; Ockelmann & Vahl, 1970; Roe, 1975; Levin, 1981; Highsmith, 1982). Such aggressive interactions typically occur between organisms within the same family or genus (Woodin & Jackson, 1979). On the other hand, competitive mechanisms may involve indirect interactions mediated either through food or the sediment. Fenchel and Kofoed (1976), Peterson and Andre (1980) and Peterson (1982) provide evidence of exploitative competition for food. Sediment-mediated interactions represent perhaps a more important class of interactions because organism-induced changes in the sediment alter the nature of the habitat. Active burrowing increases the porosity of the sediment and increases the rate of resuspension of flocculent material. Such resuspension is inimical to non-burrowing species (Rhoads & Young, 1970; Brenchley, 1981; Wilson, 1981; Highsmith 1982). Conversely, some species may bind the sediment as tubes and thereby exclude burrowing species (Woodin, 1974; Brenchley, 1982). For interactions such as these which are mediated through effects on the sediment, the taxonomic relatedness of interacting species yields little insight into the intensity of the interactions; groupings of species according to their effects on the sediment transcend taxonomic barriers (Woodin & Jackson, 1979). Given the importance of sediment-mediated interactions (reviewed in Wilson, 1981), it is expected that interspecific interactions should be strong in densely populated soft-sediment communities. The effect of any species in altering the nature of the substratum may positively or negatively affect the abundance of any other species, regardless of taxonomic affinity.

In this paper, I describe a community from a densely populated sand flat in northwest Washington, U.S.A. Four species dominate the community (>90% of total numbers). These four species all feed in different manners on different resources, thus precluding direct competition for food. I experimentally analysed the community for spatial competition on a small scale (mm to cm) based on predictions from earlier work on dense infaunal assemblages. The results of my experiments are at variance with those predictions, preventing generalization to all dense infaunal assemblages.

Study site and associated community

This research was performed on a community in False Bay, San Juan Island, Washington near the Friday Harbor Laboratories of the University of Washington. False Bay is a large intertidal embayment ranging from well-sorted coarse sand at the mouth to a fine sand with a small silt-clay fraction in the upper reaches. Hylleberg (1975) provides a map of the bay. The particular community of interest is located at the 0·0 tidal level in well-sorted fine sand. This community is characterized by macrofaunal densities in excess of 100 000 m⁻².

The most abundant macrofaunal organism is the tanaid crustacean, *Leptochelia dubia*. This crustacean attains lengths of 6 mm and constructs sturdy sediment tubes. *Leptochelia* females feed on diatoms scraped from sand grains. The females are also raptorial, preying on metazoan larvae (Highsmith, 1982). This species is protogynous and males do not feed. Males usually comprise less than 5% of the population. *Leptochelia* may exceed densities of 50 000 m⁻².

The spionid polychaete, *Rhynchospio arenincola*, is a conspicuous member of the community. This deposit-feeding polychaete builds a flimsy, membranous tube consisting of little more than sand grains adhering to a mucus sheath around the body. *Rhynchospio* feeds by extending the anterior portion of its body from its mucus tube to gather detrital particles; this method of feeding has been documented in other spionids (Woodin, 1982; Wilson, 1983). *Rhynchospio* guts contained sand grains with a mean grain size of 200 μ (range 90–330) measured along the greatest diameter. *Rhynchospio* commonly exceeds densities of 30 000 m^{-2} .

Transennella tantilla is a venerid bivalve less than 7 mm long living just below the surface of the sediment. It is a filter-feeder and often reaches densities of 12 000 m^{-2} . Individuals are mobile, constantly ploughing through the top few mm of sediment. Nowell *et al.* (1981) show that the reworking of sediment by *Transennella* lowers the critical entrainment velocity of the sediment.

Paraphoxus spinosus, a phoxocephalid amphipod, is common in the community, burrowing in the top 5 cm of sediment. It attains lengths of 5 mm and densities of 18 000 m^{-2} . The faeces of *Paraphoxus* contained large numbers of capillary setae and hooded hooks of *Rhynchospio*; apparently *Paraphoxus* is a browsing subsurface predator. *Paraphoxus* maintained in the laboratory for five weeks with *Rhynchospio* had setae in their guts yet all the *Rhynchospio* survived. Oliver *et al.* (1982) provide evidence of phoxocephalids preying on larval and juvenile polychaetes.

Other species in the community which occur predictably but less abundantly than the four species above include the apodous holothurian, *Leptosynapta clarki*, and three polychaetes, the lumbrinerid *Lumbrineris zonata*, the oweniid *Owenia fusiformis* and the maldanid *Axiiothella rubrocincta*.

Based on the results of previous research (Woodin, 1974; Brenchley, 1981; 1982; Wilson, 1981), I generated the following predictions for this community:

- (1) High densities of the tube-builders, *Rhynchospio* and *Leptochelia*, should exclude the two burrowing species, *Transennella* and *Paraphoxus*, on very small scales (mm to cm).
- (2) The sediment movement induced by the ploughing of *Transennella* should
 - (a) increase the emigration frequency of the tube-builders
 - (b) reduce the survivorship of the tube builders.

Methods and results

Field Distributional Data

To seek patterns of abundance suggestive of interspecific competition, I took a series of 0.0015 m^{-2} cores from the field site within a homogeneous area of 9 m^{-2} . The cores were sieved through a 500 μ screen and the animals were sorted live. The abundance data were analysed in pair-wise species combinations by Pearson product-moment correlation analysis (Snedecor & Cochran, 1967). The results of these analyses are given in Table 1. Contrary to prediction, no negative correlations of abundance arose between species. The abundance of *Leptochelia* was positively correlated with the abundance of *Paraphoxus* ($p < 0.05$). The remaining five species pairs were not significantly correlated ($p > 0.05$) but in all cases the sign of the correlation coefficient was positive. The field data seem to fail to support an hypothesis of interspecific competition in this community. However, Woodin (1974) could document no evidence of interspecific competition from field data; competition was demonstrated only through experimentation (also see Istock, 1977). Thus,

TABLE 1. Pair-wise Pearson product-moment correlation statistics for the abundances of the four most abundant species in 0.0015 m² cores

	<i>r</i>	<i>p</i>
<i>Rhynchospio</i> - <i>Leptochelia</i>	0.85	NS
<i>Rhynchospio</i> - <i>Transennella</i>	0.46	NS
<i>Rhynchospio</i> - <i>Paraphoxus</i>	0.48	NS
<i>Leptochelia</i> - <i>Transennella</i>	0.76	NS
<i>Leptochelia</i> - <i>Paraphoxus</i>	0.93	*
<i>Transennella</i> - <i>Paraphoxus</i>	0.48	NS

**p* < 0.05; NS—*p* > 0.05.

the lack of significant negative correlation is not sufficient to cease experimentation testing for interspecific competition.

Coexistence experiment

As a test of the null hypothesis that interspecific competition in this community does not occur, I performed a laboratory experiment in which I established experimental populations of all possible one, two, three and four species combinations of *Leptochelia*, *Rhynchospio*, *Transennella* and *Paraphoxus*. Based on samples from the field, I determined normal (mean) densities to be 32 000 m⁻², 12 000 m⁻², 9300 m⁻² and 15 000 m⁻² for each respective species above.

Embryological-grade glass jars, 43 mm in diameter (0.0015 m²) were used for experimental containers. The containers were filled with azoic sediment which had been prepared by sieving sediment from the field site through a 500 μ screen and then placing it in freshwater for three days. This procedure effectively removed or killed all macrofaunal organisms. To set up a replicate, I placed the prescribed number of organisms on the surface of the sediment. *Leptochelia* and *Rhynchospio* made tubes in the sediment within 5 min; *Transennella* and *Paraphoxus* burrowed immediately. The experimental populations were maintained in the laboratory in running seawater. The experiment required 15 treatments (all possible combinations of four species). The experiment with all four species present required the addition of 43 *Leptochelia*, 18 *Rhynchospio*, 22 *Paraphoxus* and 14 *Transennella*. All treatments were replicated four times. Each species is either present at normal density or absent in a given treatment and therefore the experimental data cannot be used to test for intraspecific competition. For each species, there were eight different treatments ranging from a given species alone to that species with the remaining three species present as well. As a shorthand convention, I will denote treatments by using the first letter of the genus to indicate the presence of a particular species; R-L, for instance, refers to the treatment with *Rhynchospio* and *Leptochelia* present.

The experiments were terminated after five weeks. At termination, each replicate was sieved and all surviving organisms were counted. The abundance data were ln(*x*) transformed and analysed by a balanced three-way ANOVA to test for significant interspecific effects. I first tested all the factors in the ANOVA for first and second order interactions. In no case was any interaction term significant. Therefore, I tested for interspecific effects by using a model with main effects only. Differences among treatments were tested for significance with Student-Newman-Keuls (hereafter, SNK) multiple comparisons (Sokal & Rohlf, 1969).

TABLE 2. Final abundances of organisms in the coexistence experiment. R denotes the presence of *Rhynchospio*, L—*Leptochelia*, T—*Transennella* and P—*Paraphoxus*. 19 *Rhynchospio*, 48 *Leptochelia*, 14 *Transennella* and 22 *Paraphoxus* represent the initial abundance for each species. Underlined means are not significantly different in SNK comparisons ($p > 0.05$)

<i>Rhynchospio</i>							
R-L-P	R-L-P-T	R-L-T	R	R-L	R-P-T	R-P	R-T
12.0	15.0	15.2	16.0	16.0	16.0	16.8	16.8
<i>Leptochelia</i>							
L	L-P-T	L-P	L-R	L-T	L-R-T	L-R-P	L-R-P-T
23.0	26.8	27.0	27.2	27.2	27.8	29.8	31.5
<i>Transennella</i>							
T-L-R	T-L-R-P	T-L	T-R-P	T	T-R	T-L-P	T-P
9.2	10.2	11.2	11.2	11.8	12.0	12.0	12.8
<i>Paraphoxus</i>							
P	P-R	P-R-T	R-T	P-L	P-L-R	P-L-T	P-L-R-T
13.2	16.0	17.0	17.0	19.0	19.2	20.0	20.0

The final abundance data for *Rhynchospio* are given in Table 2. The three-way ANOVA showed that the presence of none of the three species had an effect on *Rhynchospio* abundance (effect of *Leptochelia*: $F_{1,28} = 3.83$, $P > 0.06$; effect of *Paraphoxus*: $F_{1,28} = 1.72$, $P > 0.20$; effect of *Transennella*: $F_{1,28} = 0.77$, $P > 0.38$) although there is a nearly significant trend for *Leptochelia* affecting *Rhynchospio* in a negative fashion. The presence of the browsing predator, *Paraphoxus*, has no significant effect on *Rhynchospio* abundance.

The data for *Leptochelia* are given in Table 2. None of the remaining species has a significant effect on the final abundance of *Leptochelia* (effect of *Rhynchospio*: $F_{1,28} = 2.48$, $P > 0.12$; effect of *Paraphoxus*: $F_{1,28} = 1.63$, $P > 0.21$; effect of *Transennella*: $F_{1,28} = 1.20$, $P > 0.28$). In this experiment, the null hypothesis of no interspecific competition cannot be rejected for *Leptochelia*.

Table 2 gives the *Transennella* final abundances. The analyses shows that none of the remaining species has a significant effect on the final abundances of *Transennella* (effect of *Rhynchospio*: $F_{1,28} = 1.62$, $P > 0.21$; effect of *Leptochelia*: $F_{1,28} = 3.99$, $P > 0.05$; effect of *Paraphoxus*: $F_{1,28} = 0.07$; $P > 0.78$). However, the effect of *Leptochelia* is nearly significant and is associated with a trend of decreased *Transennella* abundance; better replication and further testing might demonstrate a significant but weak negative effect of *Leptochelia* on *Transennella*.

For the final abundances of *Paraphoxus* (Table 2), the analysis shows that the effect of *Rhynchospio* ($F_{1,28} = 0.67$, $P > 0.42$) and the effect of *Transennella* ($F_{1,28} = 3.49$, $P > 0.07$) are not significant but that the effect of *Leptochelia* is highly significant ($F_{1,28} = 18.44$, $P > 0.002$). However, the effect of *Leptochelia* is opposite that expected; the presence of *Leptochelia* is associated with higher *Paraphoxus* abundances. SNK tests show that the fewest *Paraphoxus* were recovered from the treatment with no other species present. Treatments with *Rhynchospio* and/or *Transennella* present had intermediate abundances. All of the treatments with *Leptochelia* present had the highest final abundances.

Following Wilson (1981), the total amount of sediment bound into tubes in different treatments can be used as a surrogate for relative mobility. The more frequently a tube-builder vacates a tube and constructs a new one, the greater the total amount of sediment

bound into tubes. I predicted that the surface burrowing of *Transennella* should cause both of the tube-builders to relocate more frequently. 0.592 g and 0.747 g are the mean weights of sediment bound into tubes in the R and R-T treatments. The means are not significantly different ($F_{1,6} = 1.84$, $P > 0.22$). The analogous data for *Leptochelia* mean tube weights are 5.906 g in the L treatment and 7.461 g in the L-T treatment. Again, there is not a significant difference between the two means ($F_{1,6} = 0.00$, $P > 0.90$). The presence of *Transennella* does not cause an increase in emigration frequency of either *Rhynchospio* or *Leptochelia*.

Immigration experiment

To test the effect of the tube mats of *Rhynchospio* and *Leptochelia* in impeding the immigration of the other species, I conducted the following laboratory experiment. Plastic beakers, 68 mm in diameter (0.0036 m²) were filled with azoic sediment, prepared as described earlier, and placed in running seawater. A plastic cylinder, 32 mm in diameter, was placed over the central area of the beaker. I populated the area inside the cylinder (0.0008 m²) with slightly elevated densities of the four species used in the previous experiment by introducing 40 *Leptochelia*, 16 *Rhynchospio*, 19 *Paraphoxus* and 10 *Transennella*. Augmented densities were used to attempt to force emigration into the outer area. In the outer area of the beaker, I established four treatments: *Rhynchospio* at normal density (35 in each outer area), *Leptochelia* at normal density (90 in each outer area), both species present at normal densities and neither species present. After the animals in the inner and outer areas had established themselves, I removed the plastic cylinder. All treatments were replicated four times. After two weeks, I terminated the experiment. For each replicate, I removed the inner area, sieved the sediment and counted the surviving organisms. Then I sieved the outer area and counted the organisms contained therein.

This experiment permitted me to test the effect of *Leptochelia* and *Rhynchospio* on the immigration of *Transennella* and *Paraphoxus*. Since I introduced *Transennella* and *Paraphoxus* only in the central area, all individuals of these two species recovered in the outer area had to be immigrants. I could therefore compare immigration of these species into all four treatments (R, L, R-L, control). The immigration data for *Transennella* are shown in Table 3. A one-way ANOVA shows that the presence of tube-builders had no effect on the immigration of *Transennella* ($F_{3,12} = 0.13$, $P > 0.90$). A similar pattern is seen for *Paraphoxus* (Table 3); there are no significant differences between treatments ($F_{3,12} = 2.43$, $P > 0.11$) in the number of *Paraphoxus* immigrants. The presence of the tube-builders does not prevent or decrease the immigration of *Transennella* or *Paraphoxus*.

TABLE 3. Results of the immigration experiment for *Transennella* and *Paraphoxus*. Results of SNK multiple comparisons are indicated by underlining. Underlined means are not significantly different ($p > 0.05$). See text for key to treatments

<i>Transennella</i> immigration			
Control	R	L	R-L
7.5	<u>7.8</u>	<u>8.0</u>	<u>8.0</u>
<i>Paraphoxus</i> immigration			
L	Control	R	R-L
12.0	<u>12.2</u>	<u>13.0</u>	<u>16.8</u>

TABLE 4. Results of immigration experiment for *Rhynchospio* and *Leptochelia*. The effect of *Rhynchospio* on *Leptochelia* immigration and the effect of *Leptochelia* on *Rhynchospio* immigration are tested. Underlined means are not significantly different ($p > 0.05$)

<i>Leptochelia</i> immigration	
Control	<i>Rhynchospio</i>
16.0	14.0
<i>Rhynchospio</i> immigration	
Control	<i>Leptochelia</i>
9.2	7.2

For *Rhynchospio* and *Leptochelia*, I can only compare the effect of *Leptochelia* on *Rhynchospio* immigration and the effect of *Rhynchospio* on *Leptochelia* immigration since it was not possible to distinguish animals introduced into the central area from conspecifics introduced into the outer area. The data for *Leptochelia* immigration are given in Table 4. The ANOVA shows that there is no significant difference between the control and the *Rhynchospio* treatment ($F_{1,6} = 0.0$, $P > 0.90$). Similarly, from Table 4, immigration of *Rhynchospio* is not hindered by the presence of *Leptochelia* ($F_{1,6} = 4.30$, $P > 0.08$). *Rhynchospio* cannot exclude *Leptochelia* nor can *Leptochelia* exclude *Rhynchospio*.

Emigration experiment

I performed an experiment to test for increased emigration of each species in the presence of the other species. The experiment was conducted by introducing normal densities of organisms in different combinations into the central 0.0008 m² of 10 cm by 10 cm plastic containers filled with azoic sediment. The experiment compared the frequency of emigration of organisms into the outer unpopulated sediment when only conspecifics were present to cases where heterospecifics were present as well. This comparison was accomplished by sampling at the termination of the experiment as follows: first, the central area where the animals were originally introduced was removed and sieved; then a series of cores of increasing diameter were used to remove concentric areas of sediment, each of which was sieved separately. I used cores of 54 mm, 70 mm and 99 mm diameters to sample the containers. These cores sample different sized areas but consistency of sampling is all that is required for proper statistical analysis. Lastly, the sediment exterior to the largest core was removed and sieved. I compared the radial distribution of organisms when only conspecifics were present to those cases where heterospecifics were present as well as by X² analysis (Siegel, 1956). I eschewed the heroic design of 15 treatments (all possible combinations of four species), choosing instead six treatments: each of the four species alone, all species present in one treatment and a final treatment with the two tube-builders, *Rhynchospio* and *Leptochelia*, present together. Each treatment was replicated twice and the data for each treatment were pooled for X² analyses. The experiment was terminated after two weeks.

The distributional data at termination are given in Table 5 and the results of the X² analyses are given in Table 6. For *Rhynchospio*, neither the presence of *Leptochelia*, nor the presence of all three heterospecifics cause *Rhynchospio* to emigrate more frequently. For *Leptochelia*, the presence of *Rhynchospio* alone has no effect on the frequency of emigration but the presence of all three heterospecific species does have a significant

TABLE 5. Results of the emigration experiment. This experiment measures the effect of heterospecifics on the emigration frequency of each species. Survivorships for each species in each treatment are given in parentheses. See text for key to abbreviations and experimental design

Treatment		Centre	Concentric area				
			1	2	3	4	
R							
	<i>Rhynchospio</i>	(0.80)	10	0	2	3	4
R-L							
	<i>Rhynchospio</i>	(0.75)	11	3	1	0	0
	<i>Leptochelia</i>	(0.80)	23	1	4	6	6
L							
	<i>Leptochelia</i>	(0.72)	14	7	4	4	7
R-L-P-T							
	<i>Rhynchospio</i>	(0.45)	7	1	1	0	0
	<i>Leptochelia</i>	(0.74)	28	2	1	4	2
	<i>Paraphoxus</i>	(0.71)	6	2	2	4	3
	<i>Transemnella</i>	(0.93)	3	0	2	0	8
P							
	<i>Paraphoxus</i>	(0.83)	1	1	2	3	13
T							
	<i>Transemnella</i>	(0.79)	2	0	2	2	5

TABLE 6. X^2 analyses for significant differences in distributions between treatments in the emigration experiment

Comparison	df	X^2	p
<i>Rhynchospio</i>			
R vs R-L	4	7.33	NS
R vs R-L-P-T	4	4.23	NS
<i>Leptochelia</i>			
L vs R-L	4	6.98	NS
L vs R-L-P-T	4	12.11	*
<i>Paraphoxus</i>			
P vs R-L-P-T	4	10.09	*
<i>Transemnella</i>			
T vs R-L-P-T	4	2.73	NS

$p < 0.05$; NS— $p > 0.05$.

effect. However, the effect is opposite that predicted; *Leptochelia* emigrates less frequently in the presence of the other three species. For *Paraphoxus*, the presence of the remaining species has a significant effect on its emigration frequency. Again, the effect is opposite that predicted but in accordance with the results of the coexistence experiment (Table 2); *Paraphoxus* abundance is greater in the presence of the three other species. This experiment substantiates the claim that the presence of heterospecifics does not increase

the frequency of emigration of any of the species and in two cases, the presence of heterospecifics decreases emigration frequency.

Discussion

Experimental research in the past decade has established the importance of competition as an organizing process in some densely populated soft-sediment communities (Rhoads & Young, 1970; Woodin, 1974; Peterson, 1977; Peterson & Andre, 1980; Brenchley, 1981; 1982; Wilson, 1981; 1983). Three levels of competition have been documented by this body of research: (a) interactions between functional groups; (b) interactions between species within functional groups and (c) intraspecific interactions. Each of these levels of competition will be discussed with the pertinent data from the present research.

Soft-sediment communities are unusual in that the activities of the resident organisms can radically alter the nature of the habitats in ecological time. For instance, the feeding of deposit-feeders can alter the vertical distribution of grain sizes, the median grain size and the porosity of the sediment (Rhoads & Stanley, 1965; Rhoads, 1974; Levinton & Lopez, 1977). The utilization of space by a given infaunal organism can thus alter the habitat and the suitability of that space for other infaunal organisms. Infaunal organisms can be classified by their effects on the sediment. The most useful classification involves identifying infaunal organisms as either sediment-binders (tube-builders) or sediment-destabilizers (bioturbators). Experimental work has shown that high densities of sediment-stabilizers can exclude sediment-destabilizers and that high densities of sediment-destabilizers can exclude sediment-stabilizers (Rhoads & Young, 1970; Woodin, 1974; Brenchley, 1981; 1982; Wilson, 1981). The present data do not fit this pattern. The tube-builders *Rhynchospio* and *Leptochelia*, singly and in concert, cannot exclude the sediment-destabilizing *Transennella* or the burrowing *Paraphoxus* (Table 3). Conversely, the bull-dozing of *Transennella* has no effect on the survivorship of *Leptochelia* and *Rhynchospio* (Table 2). None of the four species emigrates away from any of the other species; in fact, *Leptochelia* and *Paraphoxus* are less likely to emigrate when all the species are present (Tables 5, 6). The results of these experiments fail to support the predictions of the functional group model above.

A second level of competitive interactions are those between species within a functional group. Such interactions have been shown for filter-feeding bivalves (Peterson, 1977), deposit-feeding snails (Fenchel & Kofoed, 1976) and deposit-feeding polychaetes (Whitlatch, 1980; Wilson, 1983). These authors have identified either food or space as the limiting resource. For the present community, predicted competitors at this level are *Leptochelia* and *Rhynchospio*; both species require space for tube-building and both obtain some of their food from the flora on sand grains. However, no interactions resulting in mortality between these two species were found. Both species coexist (Table 2), neither can prevent the other from immigrating (Table 4) and neither species avoids the other (Tables 5, 6).

For completeness, the final level of competitive interactions are intraspecific interactions which may occur through interference mechanisms (Reish & Alosi, 1968; Ockelmann & Vahl, 1970; Roe, 1975; Levin, 1981; Highsmith, 1982) or through exploitative mechanisms (Peterson & Andre, 1980; Wilson, 1983). The data from this study do not bear on this class of interactions.

Present research suggests that strong interspecific competition for space does not occur in this community. However, such possible competitive effects as growth and reproductive

effort were not measured. It is possible, for example, that the bull-dozing of *Transennella* could interfere with the normal feeding of *Rhynchospio* leading to a decrease in growth rate without affecting survivorship. Nonetheless, interspecific competition for space does not appear to be a mortality source in this community nor does it lead to exclusion on a small scale. I do not deny the possibility of intraspecific competition; in fact, it seems likely. The tendency for *Paraphoxus* abundance to be greater among tubes can conceivably be interpreted as a means of decreasing aggressive intraspecific interactions by reducing encounter probabilities although Eckman (1979) and Eckman *et al.* (1981) discuss other possible explanations for positive associations of burrowers with tube-builders.

It is becoming apparent that the emerging paradigm for spatial competition of dense infaunal assemblages ($> 40\ 000$ macrofaunal animals per m^2) is too simplistic to be of predictive value. This paradigm predicts that dense tube-builder assemblages should exclude burrowing, mobile species. Woodin's (1974) demonstration of exclusion of the polychaete *Armandia brevis* by three tube-building polychaetes remains the only example of exclusion of a burrower by tube-builders. Even there, Dayton & Oliver (1980) and Hulberg & Oliver (1980) have presented an alternative hypothesis to explain her results based on the larval behaviour of *Armandia*. Brenchley (1982) showed that *Zostera* roots and tube-builder mats slowed the burial times of several burrowing species but the difficulty of burrowing depended on the sizes and body types (hard- *vs.* soft-bodied) of the organisms involved. For most cases, exclusion of burrowers was not found. There is undoubtedly some energetic cost for a burrower to establish itself in a dense tube-builder/seagrass assemblage but it is not clear if that cost is sufficient to maintain exclusive distributions. Wilson (1981; 1983) showed that dense spionid tube-mats could not exclude the large burrowing polychaete *Abarenicola pacifica* or small oligochaetes. In the present study, *Transennella* and *Paraphoxus* (Table 3) are not excluded by the tube-builders.

On the other hand, the current paradigm predicts exclusion of tube-builders by dense assemblages of bioturbating/burrowing species. There have been several experimental demonstrations of this interaction (reviewed in Wilson, 1981). Mortality or exclusion is not always observed. Rhoads & Young (1970) documented only decreased growth of *Mercenaria mercenaria* in a regime of bioturbation. Wilson (1981) documented a potential energetic drain for two spionids which relocated more frequently in the presence of bioturbation induced by *Abarenicola pacifica*. Brenchley (1981) and Wilson (1981) show that the effects of bioturbation are strongly dependent on the rates of sediment reworking and the sizes of the interacting organisms. It is obvious that simply classifying infaunal organisms into general functional groups is of limited predictive power. It will be necessary to measure numerous parameters such as densities of organisms, rate of sediment reworking, sizes and burrowing abilities of organisms before a predictive model of spatial competition will arise. The primacy of interspecific spatial competition as an organizing force in dense infaunal assemblages has yet to be firmly established.

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