

THE ROLE OF DENSITY DEPENDENCE IN A MARINE INFAUNAL COMMUNITY¹

W. HERBERT WILSON, JR.²

Department of Earth and Planetary Sciences, The Johns Hopkins University,
Baltimore, Maryland 21218 USA

Abstract. Abundance data from a marine sand flat in the Pacific Northwest reveal a strong negative correlation between abundances of the spionids *Pygospio elegans* and *Pseudopolydora kempi*, and hence suggest that competition is occurring between these two deposit-feeding polychaetes. The data also suggest that the specific winner of a competitive encounter is determined by the initial densities of the two species. A density-dependence experiment was performed in the field to test this hypothesis, in which the density of each species was independently varied over four densities in experimental containers. Immigration, emigration, and mortality combined to cause *Pygospio* densities in all experimental treatments to converge to ambient density after 8 wk. After 8 wk, *Pseudopolydora* densities were converging on the ambient density; the densities of some experimental treatments were significantly different from each other, but in no case did an experimental density differ significantly from ambient. The rate of convergence was strongly density dependent in both species. In four different experiments, conducted for 1, 2, 4, and 8 wk, *Pygospio* survivorship was strongly affected by its own density but was weakly affected, if at all, by *Pseudopolydora* density. *Pseudopolydora* survivorship was affected only by its own density except for the 1-wk experiment, in which *Pygospio* density also had a significant effect. The field results conflict with the results from a laboratory experiment where *Pygospio* rapidly migrated away from *Pseudopolydora* but not from conspecifics. I propose a spacing hypothesis which predicts that *Pygospio* relocates as often as necessary to minimize contact with *Pseudopolydora*. Static spatial data from the field provide some support for the hypothesis.

In the laboratory, *Pygospio* underwent asexual reproduction only at low densities and in the absence of *Pseudopolydora*. This response is interpreted as an adaptation for the rapid utilization of resources.

Key words: asexual reproduction; competition; density dependence; infauna; *Pseudopolydora*; *Pygospio*; Spionidae; Washington State.

INTRODUCTION

In a classic paper, Nicholson (1933) argued for the importance of animal interactions in the regulation of population numbers. This view of the natural world was supported by Smith (1935), who expanded the concept with a model of population growth based on logistic growth and formally defined density dependence. Nicholson perceived density-dependent processes, especially competition, to be of paramount importance in determining the distribution and abundance of animals, and by analogy, other organisms. The theory denies the ability of climate alone, or physical factors in current parlance, to regulate population numbers. Despite opposition to this view (Andrewartha and Birch 1954), a plethora of data and theory has been advanced to support the central importance of density-dependent processes in population regulation (e.g., Lack 1954, Mac Arthur 1958, Connell 1961, Smith 1961, Menge 1972, Sprules 1974, Hairston 1980).

Most field studies of competition have been concerned with the demonstration of the existence of the

process. Few workers have gone beyond this level of enquiry to ask how density affects a competitive outcome. This lack of data is perhaps explicable in that most models of competition assume that competitive abilities, measured as α_{ij} 's, are constant and hence independent of density. Laboratory evidence has cast serious doubt on this assumption (Neill 1974, Longstaff 1976, Smith-Gill and Gill 1978, but see Abrams 1980, Pomerantz 1981). However, few field data bear on the validity of this assumption.

The past 10 yr have seen a burgeoning of literature emphasizing the importance of density-dependent processes in marine infaunal communities. A considerable body of experimental work (Rhoads and Young 1970, Woodin 1974, Ronan 1975, Peterson 1977, Peterson and Andre 1980, Stiven and Kuenzler 1979, Brenchley 1981, Wilson 1981) and an equally large body of descriptive data best interpreted in terms of competition (Levinton and Bambach 1975, Levinton 1977, Weinberg 1979, Whitlatch 1980, 1981, Levin 1981) attest to the importance of density-dependent processes in some marine infaunal communities. In this contribution to that body of knowledge, I experimentally examine the interactions of two species of abundant polychaetes from a marine sand flat. The experiments are designed to allow me to detect how competitive effects vary as a function of density.

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² Present address: Harbor Branch Foundation, RR 1, Box 196, Fort Pierce, Florida 33450 USA.

STUDY SITE AND THE ASSOCIATED INFAUNAL COMMUNITY

The study site, False Bay, is a large intertidal embayment in the Straits of Juan de Fuca, Washington State, USA. The entire 1 by 2 km bay is drained on a -0.6-m tide. Hylleberg (1975) gives a map of the bay and Pamatmat (1968) describes physical and geological features.

The community that I investigated is located high in the embayment (1-2 m above MLLW). It is numerically dominated by two tube-building spionid polychaetes, *Pygospio elegans* Claparede and *Pseudopolydora kempfi* (Southern). *Pygospio* commonly attains densities of 60 000 individuals/m² and reaches lengths of 12 mm. It feeds predominantly as a deposit-feeder, using its two relatively short palps to gather detrital material. Often, *Pygospio* extends the anterior portion of its body from its tube and picks up sand grains directly with its mouth (Woodin 1982). The dominant mode of reproduction for *Pygospio* in False Bay is asexual. A worm will fragment transversely in its tube into four to eight fragments (Rasmussen 1953). Each fragment regenerates its missing segments and then crawls from the "parent" tube to assume a free-living existence in a tube of its own. Sexual reproduction is known for this species (Hannerz 1956, Rasmussen 1973) but I have never found females brooding in False Bay. Ripe males and females did, however, appear in mid-November and persisted through December in both 1980 and 1981.

Pseudopolydora commonly reaches densities of 20 000 individuals/m². It is a larger and more robust worm than *Pygospio*, often attaining lengths of 30 mm. *Pseudopolydora* feeds by extending its long, extensible palps onto the sediment surface; it rarely extends any other part of its body from its tube. Given water currents and suspended material in the water column, *Pseudopolydora* will feed by holding its palps up in the water column (Taghon et al. 1980). *Pseudopolydora* females brood encapsulated larvae in their tubes. The larvae are provided with nutrition in the form of nurse eggs and are not released until the 15-17 setiger stage (Blake and Woodwick 1975, Myohara 1979). Dispersal of larvae is therefore limited and larvae commonly settle in the vicinity of the parents. Brooding females have been found in False Bay from April through October.

A third polychaete, conspicuous by its effect on the sediment, is the sediment-destabilizing arenicolid, *Abarenicola pacifica* Healy and Wells. Although normally not exceeding densities of 1000 individuals/m², it is much larger than the spionids (60 mm long). Its destabilizing effect on the sediment significantly depresses the abundance of *Pygospio*. Wilson (1981) examined the interactions of *Abarenicola* and the spionids.

Several other taxa occur predictably in False Bay

in the upper intertidal zone, but in much lower densities than the two species above. The most abundant (10 000 individuals/m²) of these is a guild of deposit-feeding oligochaetes, all <4 mm long. They are subsurface deposit-feeders and there is little a priori evidence to suggest that they interact with the surface-feeding deposit-feeders. Other members of the community include the paraonid polychaete *Paraonella platybranchia*, the spionid *Boccardia proboscidea*, the cumacean *Cumella vulgaris*, the amphipod *Corophium spinicorne*, and the armed nemertean *Paranemertes peregrina*.

MATERIALS AND METHODS

To search for patterns of abundance suggestive of competition, a transect was established parallel to the shoreline at the 1.0 m tide level. The transect spanned an area which seemed homogeneous with respect to physical characteristics; there were no apparent gradients in sediment size or salinity along the transect. Nineteen stations were established, with consecutive stations separated by 4 m. At each station, I took four cores 26 mm in diameter (5 cm²) to a depth of 10 cm. Each sample was fixed in formalin and later sieved through a 500- μ m screen. All organisms retained were identified and heads and whole organisms were counted. Pearson product-moment statistics were calculated using the core abundances in pairwise species combinations to search for patterns reflective of possible interspecific competitive interactions.

As a test of the null hypothesis that *Pygospio* is distributed randomly on a small scale both with respect to conspecifics and to *Pseudopolydora*, I mapped the position of worms with the aid of a camera lucida in cores removed from the field site. The assumption is made that both *Pygospio* and *Pseudopolydora* are randomly distributed, irrespective of species. I compared the proportion of the number of *Pygospio* having another *Pygospio* as its nearest neighbor to the number having a *Pseudopolydora* as its nearest neighbor. This proportion is then compared to the proportion expected by chance under the null hypothesis, namely the proportion of the number of *Pygospio* in the core over the number of *Pseudopolydora*. After transforming the data with an arcsin \sqrt{x} transformation, a pairwise Student's *t* test was performed to test for significant differences in the two proportions.

To test the importance of competition in population regulation in this community, I performed a series of experiments in which I established different densities of organisms in experimental containers. For these experiments, it was necessary to use azoic sediment to avoid contamination of containers with nonexperimental animals. I prepared azoic sediment by sieving sediment from the study area through a 500- μ m screen and then immersing the sediment in freshwater for 7 d; this treatment removed or killed all macrofaunal animals. The sediment was then placed into experi-

mental containers and placed in running seawater for 2 d prior to the introduction of animals, so that a bacterial and algal flora could develop. Water entering the seawater table was filtered through 300- μm Nitex screening to avoid contamination of the experimental containers by macrofauna resident in the seawater system.

A number of experiments, described fully below, were conducted in which the densities of *Pygospio* and *Pseudopolydora* were systematically and independently varied over a range of densities, from absence ($0\times$) to triple normal density ($3\times$). Normal densities are taken to be 60 000 individuals/ m^2 for *Pygospio* and 20 000 individuals/ m^2 for *Pseudopolydora* (W. H. Wilson, Jr., *personal observation*). To conserve space, I will adopt the following convention to describe treatments. First, the symbolic density designation ($0\times$, $\frac{1}{3}\times$, $1\times$ or $3\times$) is given for *Pygospio*, followed by a hyphen, and then the symbolic density designation for *Pseudopolydora* is given. Thus, $1\times-3\times$ refers to the treatment with *Pygospio* present at normal densities and *Pseudopolydora* present at triple normal densities.

A laboratory experiment was designed to test for density-dependent emigration in *Pygospio* and *Pseudopolydora*. By introducing prescribed numbers of *Pygospio* and *Pseudopolydora* into the center of 470- cm^3 (one-pint) freezer containers ($10 \times 10 \text{ cm}$) filled with azoic sediment, I monitored the migration of each species outward into vacant sediment as a function of density. The animals were introduced into a circular area, 32 mm in diameter, in the center of each container, where they established tubes in the sediment in a matter of minutes. The experiment compared the rate of emigration of each species alone to the rate when heterospecifics were also present. The experiment required three treatments: *Pygospio* alone, *Pseudopolydora* alone, and both species present. The experiment was performed twice, once with both species present at $\frac{1}{3}$ normal densities and once at normal densities. All treatments were replicated three times. After 2 wk, the experiments were terminated. The central area into which the animals were originally placed was removed with a corer (8 cm^2) and sieved through a 500- μm sieve. Then three concentric cores around the central area were taken in order of increasing diameters and sieved separately. These cores measured 52, 67, and 84 mm in diameter, and subtracting the previously sampled inner cores, sample 13 cm^2 , 14 cm^2 , and 20 cm^2 , respectively. Lastly, the remaining sediment, $\approx 30 \text{ cm}^2$, exterior to the largest core was sieved. Although the areas are not equivalent, consistency of sampling method is all that is required for proper statistical analysis of the experimental data. For each species I could calculate the distribution of organisms. I compared emigration frequency and distance for replicates with only conspecifics present to that for replicates with heterospecifics present as well.

Differences in these distributions were tested for statistical significance by χ^2 analysis (Siegel 1956). These experiments were performed between 15 and 30 July 1980.

An experiment was designed to test for density-dependent asexual reproduction in *Pygospio*, predicting that fragmentation should be maximal at low densities. I established *Pygospio* in the laboratory in cylinders (32 mm in diameter) filled with azoic sediment at three densities ($\frac{1}{3}\times$, $1\times$, and $3\times$). I also established $\frac{1}{3}\times$ *Pygospio* treatments in the presence of *Pseudopolydora* at three different densities ($\frac{1}{3}\times$, $1\times$, $3\times$) to assess the effect of *Pseudopolydora* density on *Pygospio* fragmentation. Each treatment was replicated four times. After 8 wk, each core was sieved through a 500- μm screen and individuals counted. Survivorship was calculated as the number recovered/number introduced. Vales >1.0 indicate that asexual fragmentation occurred. Differences in survivorships between treatments were tested for significance by a one-way ANOVA and Scheffé post hoc comparisons on arcsin \sqrt{x} transformed data (Snedecor and Cochran 1967).

A series of field experiments was performed to test for the density dependence of competitive abilities of *Pygospio* and *Pseudopolydora*. The experimental design called for the density of each species to be varied independently over four different densities ($0\times$, $\frac{1}{3}\times$, $1\times$, $3\times$), yielding 16 experimental treatments. Experimental containers were constructed of plastic window screening (1-mm mesh) held together by HotGlue[®] (Master Mechanic Corporation, Chicago, Illinois). The containers were cylinders 32 mm in diameter and 50 mm long. The bottom was covered with a piece of plastic screening. The azoic sediment placed in the containers was cohesive enough to remain in the containers, although all grain sizes were considerably smaller than the 1-mm mesh openings. The experimental animals in appropriate densities were introduced onto the containers and allowed to establish tubes. I "planted" the containers in a 4×16 randomized block array in the field, level to the sediment surface. Adjacent rows and adjacent containers in rows were each 15 cm apart. In order to gauge the rate at which changes in abundance occurred, the entire experiment was repeated four times for 1, 2, 4, and 8 wk. All treatments were replicated four times in each experiment. Since the containers enclosed an area of 8 cm^2 , the $1\times$ treatments for *Pygospio* and *Pseudopolydora* required the addition of 48 and 16 worms, respectively. From these $1\times-1\times$ values, the number of animals introduced into the other 15 treatments can easily be calculated.

I decided a priori to run the longest experiments for 8 wk, predicting that such a duration should be sufficiently long to detect possible density-dependent reproductive effects. For *Pygospio*, significant asexual reproduction can occur in 8 wk (Rasmussen 1953). For *Pseudopolydora*, differences among treatments in the

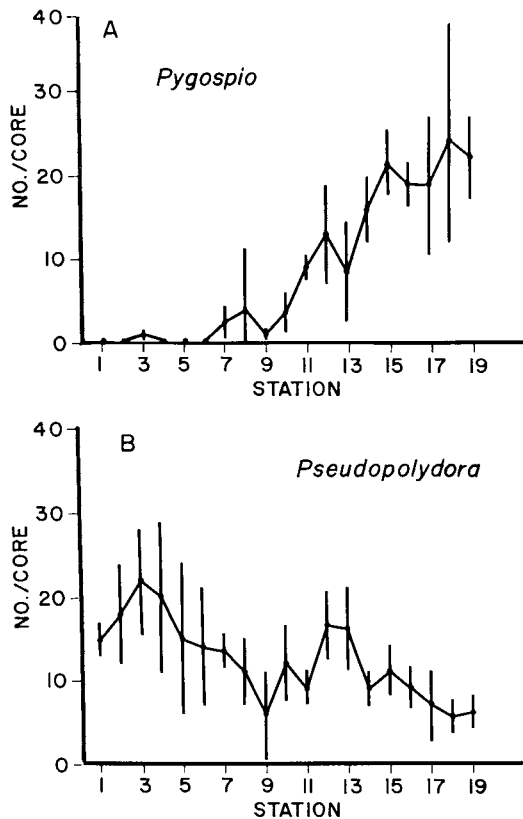


FIG. 1. Abundance data for *Pygospio elegans* and *Pseudopolydora kempfi* along a transect parallel to the shoreline. Consecutive stations are separated by 4 m. All abundances are the means of four cores (26 mm in diameter). Standard deviations are plotted.

number of females brooding and the number of juveniles recovered should reflect differences in reproductive effort. Myohara (1979) gives the generation time of *Pseudopolydora* as 50–60 d at 20°C, a temperature somewhat higher than the 11°–12° encountered in False Bay between September and December.

The relatively large mesh of the containers should minimize any container-induced artifacts on the physical and chemical milieu, such as changing the depth of the Redox Potential Discontinuity (RPD) layer. The presence of containers did not interrupt ripple marks on the sediment surface. The 1-mm mesh also provides minimal resistance to the immigration of subsurface organisms such as oligochaetes and *Paraonella*.

All of these experiments were conducted between 6 October and 1 December 1980 in an area slightly landward from the original transect, where both species were abundant (near stations 12 and 13 of Fig. 1A, B). Samples were taken at the initiation of the experiments on 6 October to define ambient densities. When an experiment was terminated, cores of the adjacent community were taken to assess any changes in ambient densities. The replicate experimental cores (four

for each treatment) were removed with a trowel, taken to the laboratory, and sieved separately on a 500- μ m mesh. All organisms were counted. During the course of the experimental period, some replicate cores were lost from the field, requiring the use of unbalanced ANOVA designs for the analyses below.

Two questions can be asked concerning the final abundances of *Pygospio* and *Pseudopolydora* in each of these experiments. First, do all treatments converge to an equilibrium density state? This is tested by searching for significant differences among final abundances ($\ln[x + 1]$ transformed to eliminate heteroscedasticity) by a two-way ANOVA, followed by Scheffé comparisons. Second, are there differences in survivorship among treatments as a function of *Pygospio* density or *Pseudopolydora* density? Survivorship is calculated as the number of animals recovered \div number introduced. However, survivorship here is actually a composite function of mortality, immigration, and emigration. Abundances are decreased by mortality and emigration, augmented by immigration and reproduction. Differences in survivorship among treatments were tested for significance by a two-way ANOVA and Scheffé comparisons. The data were $\arcsin \sqrt{x}$ transformed to satisfy the assumptions of ANOVA (Snedecor and Cochran 1967).

RESULTS

Distributional Data

The abundance of *Pygospio* along a 72-m transect parallel to the shoreline is given in Fig. 1A. There is a clear pattern of *Pygospio* increase from east to west (ascending station number). Fig. 1B provides the comparable data for *Pseudopolydora*. *Pseudopolydora* abundance decreases sharply from east to west. There is a strong negative correlation of *Pygospio* and *Pseudopolydora* abundances, utilizing individual core abundances (Pearson's $r = -.93$, $P < .001$, $n = 76$). The transect data therefore suggest that competition between these two spionids may be occurring. The nearest neighbor analysis (Table 1) gives additional support to this hypothesis. The analysis rejects the null hypothesis of random distribution of the two species. More *Pygospio* than would be expected by chance have a conspecific as a nearest neighbor rather than a *Pseudopolydora*. One possible interpretation of these data is that *Pygospio* experiences interspecific competition from *Pseudopolydora* and therefore seeks to minimize contacts with *Pseudopolydora* by avoidance on a small scale. An hypothesis of interspecific competition in these two species can be refined by consideration of the transect data (Fig. 1). There is only a narrow portion of the transect (stations 12 and 13) where both species maintain a relatively high abundance. This pattern suggests that the winner of competitive encounters is determined by a density-depen-

TABLE 1. Nearest neighbor analysis. The number of *Pygospio* in mapped field cores having a conspecific as its nearest neighbor vs. the number of *Pygospio* having *Pseudopolydora* as its nearest neighbor. This proportion is compared to that derived by random expectation based on the relative abundances of the two species in the core. The number of *Pygospio* for which nearest neighbor distances are measured is less than the number of *Pygospio* in the core because only *Pygospio* in the center of the core were used in the nearest neighbor analysis; peripheral *Pygospio* may have had nearest neighbors exterior to the core. The two proportions were inverted for the analysis to avoid zeroes in the denominators of some proportions.

Sample number	<i>Pygospio</i> in core/ <i>Pseudopolydora</i> in core	<i>Pygospio</i> closest to conspecific/ <i>Pygospio</i> closest to <i>Pseudopolydora</i>
1	15/4	10/0
2	10/6	6/1
3	10/3	5/1
4	14/2	8/1
5	10/3	6/1
6	12/3	5/1
7	15/4	7/1
8	9/7	5/0
9	16/5	5/3

$t = 1.96; P < .05$

dent process; high *Pygospio* densities suppress or exclude *Pseudopolydora*, and high *Pseudopolydora* densities suppress or exclude *Pygospio*.

The remaining abundant taxon along the transect is a multispecific group of oligochaetes. They show no trend of increase or decrease along the transect (W. H. Wilson, Jr., *personal observation*). Their core-by-core abundances are positively correlated with those of *Pygospio* ($r = .44, P < .05$) and negatively correlated with those of *Pseudopolydora* ($r = .56, P < .05$). However, as predicted, it is evident that oligochaete abundance explains only a small portion of the variance in either *Pygospio* or *Pseudopolydora* abundance. Explanations of the significant oligochaete-sponiid correlations should probably be sought in degrees of freedom ($n = 76$) rather than biological interactions.

Density-dependent asexual reproduction

To test the hypothesis that asexual fragmentation in *Pygospio* is maximal when densities are low, an 8-wk experiment was conducted in which *Pygospio* density was varied. The results (Table 2A) reveal that *Pygospio* survivorship at $\frac{1}{3} \times$ is > 1.0 , indicating reproduction in excess of mortality. *Pygospio* survivorship at $1 \times$ and $3 \times$ is significantly lower than the $\frac{1}{3} \times$ survivorship. I observed asexually produced fragments only in the $\frac{1}{3} \times$ treatments. Thus, these data provide evidence of density-dependent asexual reproduction. I also tested the effect of *Pseudopolydora* on the frequency

TABLE 2. Density dependence of asexual reproduction in *Pygospio*. $1 \times$ = normal density of the species in the field. Data are survivorship means derived from four replicate cores (8 cm²) after 8 wk. Values > 1.0 indicate that asexual reproduction has occurred. Results of Scheffé post hoc comparisons are indicated by letters to the right of each mean. Means sharing the same letter are not statistically different ($P > .05$).

A) Effect of <i>Pygospio</i> density on <i>Pygospio</i> survivorship				
	<i>Pygospio</i> density			
	$\frac{1}{3} \times$	$1 \times$	$3 \times$	
Survivorship	1.63 a	0.76 b	0.65 b	
B) Effect of <i>Pseudopolydora</i> density on $\frac{1}{3} \times$ <i>Pygospio</i> survivorship				
	<i>Pygospio</i> density- <i>Pseudopolydora</i> density			
	$\frac{1}{3} \times - 0 \times$	$\frac{1}{3} \times - \frac{1}{3} \times$	$\frac{1}{3} \times - 1 \times$	$\frac{1}{3} \times - 3 \times$
Survivorship	1.63 a	0.58 bc	0.78 b	0.30 c

of asexual reproduction in *Pygospio* at low densities (Table 2B). The analysis shows that *Pseudopolydora* depressed the survivorship of *Pygospio* and inhibited fragmentation; no fragments were found in any of the treatments where *Pseudopolydora* was present.

Laboratory emigration experiment

To determine how migration behavior of each species changes in response to the presence of the other species, I performed a laboratory experiment in which emigration could be monitored as a function of heterospecific density. The data and χ^2 analysis for this experiment are given in Table 3. For the low-density treatments, the presence of $\frac{1}{3}$ normal densities of *Pseudopolydora* does not affect the emigration rate of *Pygospio* at $\frac{1}{3}$ normal densities ($\chi^2 = 1.68, P > .10$). Similarly, the $\frac{1}{3} \times$ densities of *Pygospio* do not affect the emigration of *Pseudopolydora* at $\frac{1}{3}$ normal densities ($\chi^2 = 0.0, P > .10$).

Strong effects on *Pygospio* emigration are seen in the normal density treatments. The presence of normal *Pseudopolydora* densities causes dramatic increases in *Pygospio* emigration ($\chi^2 = 27.74, P < .001$). *Pygospio* at normal densities has no effect on *Pseudopolydora* emigration ($\chi^2 = 0.69, P > .10$). In fact, even at $1 \times$ densities with free space available, *Pseudopolydora* is reticent to move. *Pseudopolydora* under these conditions rarely relocates, regardless of conspecific or heterospecific density.

Field density-dependence experiments

In these experiments, the densities of *Pygospio* and *Pseudopolydora* were varied independently over four densities in experimental populations. The entire experiment was done for 1, 2, 4, and 8 wk to gauge the rates of change of experimental populations. Table 4 presents natural field densities of *Pygospio* and *Pseu-*

TABLE 3. Results of the laboratory emigration experiment. Known densities of *Pygospio* and *Pseudopolydora* were introduced into the center of 10 × 10 cm containers of azoic sediment. After 2 wk, the containers were sampled with a series of concentric cores. Data for each treatment are the totals of three replicates except the 1/3 × 0 × and 1 × 0 × treatments where one replicate was lost. Results of χ^2 analyses are also given. The number of animals introduced and the percent recovered are given in parentheses.

Treatment	Center	Concentric area			
		1	2	3	4
Number of animals recovered					
1/3 × 0 ×					
<i>Pygospio</i> (32, 100%)	32	0	0	0	0
1/3 × 1/3 ×					
<i>Pygospio</i> (48, 60%)	26	0	1	0	2
<i>Pseudopolydora</i> (15, 100%)	15	0	0	0	0
0 × 1/3 ×					
<i>Pseudopolydora</i> (15, 73%)	11	0	0	0	0
1 × 0 ×					
<i>Pygospio</i> (96, 83%)	65	4	2	5	3
1 × 1 ×					
<i>Pygospio</i> (144, 71%)	45	13	12	16	16
<i>Pseudopolydora</i> (48, 85%)	38	3	0	0	0
0 × 1 ×					
<i>Pseudopolydora</i> (48, 73%)	34	1	0	0	0
χ^2 analyses					
<i>Pygospio</i>					
1/3 × 0 × vs. 1/3 × 1/3 ×	$\chi^2 = 1.68, P < .10$				
1 × 0 × vs. 1 × 1 ×	$\chi^2 = 27.74, P < .001$				
<i>Pseudopolydora</i>					
0 × 1/3 × vs. 1/3 × 1/3 ×	$\chi^2 = 0.0, P > .10$				
0 × 1 × vs. 1 × 1 ×	$\chi^2 = 0.69, P > .10$				

dopolydora at the initiation of the experiments and at the termination of each of the four experiments. ANOVAs and Scheffé post hoc comparisons indicate that no significant change in the abundance of either *Pygospio* or *Pseudopolydora* occurred in the unmanipulated areas over the 8-wk experimental period (Table 4). Therefore, any changes among experimental treatments through time are attributable to my manipulations rather than ambient population changes. The four experiments can be regarded as a time series. Note that my estimate of normal field densities (48 *Pygospio* and 16 *Pseudopolydora* per 8-cm² core), taken from samples earlier in the year, is somewhat high. However, this error does not affect the experimental results: the experiment merely requires the systematic variation of density over a nine-fold range.

The experimental design permits the testing of the effect of heterospecific density on the immigration of each species. For instance, for *Pygospio* there are four treatments into which no *Pygospio* were initially added (0 × 0 ×, 0 × 1/3 ×, 0 × 1 ×, 0 × 3 ×). For all of these treatments, all *Pygospio* recovered are indisputably

TABLE 4. Natural field densities of *Pygospio* and *Pseudopolydora* at initiation (week 0) and at the four sampling dates of the field density-dependence experiments. The data given are the means of four 8 cm² cores. Means which are not significantly different in Scheffé post hoc comparisons are indicated by underlining ($P > .05$).

Species	No. weeks since initiation				
	0	1	2	4	8
<i>Pygospio</i>	Number of individuals per core				
	21.8	24.8	36.2	24.0	26.8
<i>Pseudopolydora</i>	3.1	4.3	3.1	4.8	7.3

immigrants. Similarly, there are four treatments at different *Pygospio* densities in which *Pseudopolydora* was not added, and hence serve to test the effect of *Pygospio* density on *Pseudopolydora* immigration. I present only the 1- and 2-wk experiments, because in these experiments, initial differences in density have not been equalized by movement into and out of the containers; longer term experiments tend to converge to ambient densities (see below). The data for *Pygospio* immigration into various *Pseudopolydora* treatments is given in Table 5A. Scheffé post hoc comparisons show no significant differences among treatments: *Pseudopolydora* does not inhibit the immigration of *Pygospio*. The analogous data for *Pseudopolydora* immigration as a function of *Pygospio* density are presented in Table 5B. Scheffé post hoc comparisons show no effect of *Pygospio* on *Pseudopolydora* immigration.

In the laboratory, *Pseudopolydora* was found to move less frequently than *Pygospio* (Table 3). For the field data, I observed a *Pygospio* : *Pseudopolydora* immigration ratio of 14:1 (Table 5). Yet from field samples, *Pygospio* is only 6.3 times as abundant as *Pseudopolydora* (Table 4). These results corroborate the laboratory finding that *Pygospio* is the more mobile of the two species.

Given the original hypothesis of density-dependent determination of competitive outcomes, I predicted that after 8 wk there should be at least two different equilibria in the experimental treatments. Containers with abundances initially skewed toward *Pygospio* (e.g., 1 × 0 ×, 3 × 1/3 ×) should be dominated by *Pygospio*. Containers with abundances initially skewed toward *Pseudopolydora* (e.g., 0 × 1 ×, 1/3 × 3 ×) should be dominated by *Pseudopolydora*. The abundance data bearing on this prediction are given in Table 6. Analysis of the final abundances of *Pygospio* (Table 6A) in a two-way ANOVA shows that initial *Pygospio* density has a significant effect ($F_{3,20} = 5.89, P < .01$). The effect of *Pseudopolydora* is not significant ($F_{3,20} = 1.87, P > .15$), but the interaction term with the *Pygospio* effect is significant ($F_{9,20} = 3.40, P < .05$). However,

TABLE 5. Immigration of *Pygospio* and *Pseudopolydora* in the field into four different heterospecific densities. Each value is the mean of four experimental cores (each 8 cm² in area). Data are provided for total immigrants after 1 and 2 wk. Means that are not significantly different in Scheffé post hoc comparisons are underlined ($P < .05$).

A. <i>Pygospio</i> density- <i>Pseudopolydora</i> density				
Week	0×-0×	0×-1/3×	0×-1×	0×-3×
No. <i>Pygospio</i> immigrants				
1	14.0	19.2	19.5	17.7
2	17.2	20.5	18.7	17.8
B. <i>Pygospio</i> density- <i>Pseudopolydora</i> density				
Week	0×-0×	1/3×-0×	1×-0×	3×-0×
No. <i>Pseudopolydora</i> immigrants				
1	1.0	0.5	1.8	0.0
2	1.5	1.8	2.5	1.2

the three treatments means (0×-0×, 1/3×-1×, 3×-3×) which are significantly lower than the two highest means (3×-1/3×, 3×-1×) cannot be explained easily in terms of the known life history of these species. Rather, I would argue that these differences, especially the significantly low 1/3×-1× and 3×-3× treatments, are due to chance. In any case, none of the factor-level means is significantly different from the ambient abundance adjacent to the experimental containers (Student's *t* test, $P > .05$ in all cases). Contrary to the prediction, two equilibria, one dominated by *Pygospio* and one with *Pygospio* rare, are not evident; convergence on a single equilibrium density, the ambient density, is the rule.

The same general pattern holds true for *Pseudopolydora* (Table 6B). The two-way ANOVA indicates that the effect of *Pseudopolydora* density is significant ($F_{3,20} = 12.03$, $P < .01$). However, the effect of *Pygospio* density is not significant ($F_{3,20} = 1.60$, $P > .20$), nor is the interaction effect ($F_{9,20} = 0.47$, $P > .80$). Despite the significant ANOVA, Scheffé post hoc comparisons reveal no significant differences among treatments. There is a trend of treatments with higher original densities to remain denser, but convergence on the ambient density is apparent. The observation that *Pseudopolydora* moves less frequently than *Pygospio* (Tables 3, 5) may account for the less striking convergence toward ambient density of *Pseudopolydora*.

Oligochaete densities in the various treatments also converged to ambient densities after 8 wk. I could detect no effect of *Pygospio* density ($F_{3,23} = 0.16$, $P > .90$), *Pseudopolydora* density ($F_{3,23} = 0.13$, $P > .90$), or a second-order interaction ($F_{9,23} = 1.62$, $P >$

TABLE 6. Final abundances of *Pygospio* and *Pseudopolydora* in the 8-wk field density-dependence experiment. Results of Scheffé post hoc comparisons are denoted by letters to the right of each mean. Means sharing the same letter are not statistically different ($P > .05$). Abundance values are the means of four replicate cores (8 m²). The densities of the two species at the initiation of the experiment were 1× *Pygospio* = 48/8 cm², 1× *Pseudopolydora* = 16/8 cm². Final ambient densities were 1× *Pygospio* = 27/8 cm² and 1× *Pseudopolydora* = 5/8 cm².

A. Initial <i>Pseudopolydora</i> density		Initial <i>Pygospio</i> density			
		0×	1/3×	1×	3×
Final no. <i>Pygospio</i> per core					
0×		9.0 b	15.5 ab	21.2 ab	22.0 ab
1/3×		17.0 ab	16.2 ab	16.0 ab	35.5 a
1×		15.0 ab	7.0 b	22.0 ab	34.0 a
3×		18.2 ab	15.7 ab	17.0 ab	9.0 b
B. Initial <i>Pseudopolydora</i> density		Initial <i>Pygospio</i> density			
		0×	1/3×	1×	3×
Final no. <i>Pseudopolydora</i> per core					
0×		3.0 a	0.5 a	2.0 a	0.7 a
1/3×		4.3 a	4.0 a	6.0 a	5.5 a
1×		13.5 a	7.0 a	8.7 a	4.0 a
3×		10.5 a	11.3 a	16.0 a	20.0 a

.15) on oligochaete immigration. In fact, convergence to field densities had occurred after only 2 wk, and in none of the four experiments did I detect any effect of *Pygospio* or *Pseudopolydora* on oligochaete immigration.

To analyze the effects of conspecific and heterospecific densities on the experimental populations, I analyzed survivorship data for both *Pygospio* and *Pseudopolydora*. It should be re-emphasized here that survivorship in the present sense is a composite function, decreased by mortality and emigration and increased by immigration (no reproduction was evident during the experimental period). Values may therefore exceed 1.0 and the values are not comparable to those of the laboratory experiments (Tables 2, 3) where immigration could not occur.

The survivorship data (in the composite sense) for *Pygospio* are given in Table 7. The 4-wk data are not given because loss of replicates left too few samples (11) for analysis. After 1 wk, *Pygospio* density has a very strong effect on *Pygospio* survivorship ($F_{2,36} = 67.27$, $P < .001$). However, neither the effect of *Pseudopolydora* density ($F_{3,36} = 1.74$, $P > .15$) nor the interaction term ($F_{6,36} = 0.87$, $P > .50$) is significant. The significant differences associated with *Pygospio* density result from immigration into the 1/3× *Pygospio* treatments and higher emigration or mortality in the 1× and 3× treatments (Table 7A).

In the 2-wk experiment, the effect of *Pygospio* density on *Pygospio* survivorship is significant ($F_{2,35} = 28.42$, $P < .001$). The effect of *Pseudopolydora* density ($F_{3,35} = 2.55$, $P > .07$) and the interaction of the

TABLE 7. *Pygospio* survivorship for the 1-, 2- and 8-wk density-dependence experiments from the field. The 4-wk data are missing because of loss of replicates. Survivorship is calculated as the final density of *Pygospio* divided by the initial density. Values are the means of four replicate cores (8 cm²). Results of Scheffé post hoc comparisons are shown by letters to the right of each mean. Means sharing the same letter are not statistically different ($P > .05$).

A. 1-wk data			
Initial <i>Pseudopolydora</i> density	Initial <i>Pygospio</i> density		
	1/3x	1x	3x
<i>Pygospio</i> survivorship			
0x	1.45 ab	0.52 cd	0.56 bcd
1/3x	1.56 a	0.70 bcd	0.56 bcd
1x	1.47 abc	0.63 bcd	0.51 cd
3x	1.09 abcd	0.38 d	0.44 d
B. 2-wk data			
Initial <i>Pseudopolydora</i> density	Initial <i>Pygospio</i> density		
	1/3x	1x	3x
<i>Pygospio</i> survivorship			
0x	1.91 a	0.94 abc	0.69 abc
1/3x	1.48 abc	0.88 abc	0.44 bc
1x	0.94 abc	0.87 abc	0.54 abc
3x	1.56 ab	0.68 abc	0.33 c
C. 8-wk data			
Initial <i>Pseudopolydora</i> density	Initial <i>Pygospio</i> density		
	1/3x	1x	3x
<i>Pygospio</i> survivorship			
0x	0.97 a	0.44 ab	0.15 b
1/3x	1.02 a	0.33 ab	0.25 b
1x	0.44 ab	0.46 ab	0.24 b
3x	0.98 a	0.35 ab	0.06 b

two main effects ($F_{6,35} = 1.51$, $P > .20$) are not significant. Net immigration into the 1/3x-3x treatment and net emigration/mortality from the 3x-3x treatment result in the significant differences among means (Table 7B).

The data from the 8-wk experiment corroborate the interactions seen in the 1- and 2-wk experiments. The effect of *Pygospio* density on *Pygospio* survivorship is significant ($F_{2,18} = 32.83$, $P < .001$). The effect of *Pseudopolydora* density is weakly significant ($F_{3,18} = 3.24$, $P < .05$), while the interaction term is not significant ($F_{6,18} = 2.16$, $P > .09$). From Scheffé post hoc comparisons, significant differences within a row or column are found between the 1/3x-0x and 3x-0x treatments, between the 1/3x-1/3x and 3x-1/3x treatments, and between the 1/3x-3x and 3x-3x treatments (Table 7C). Thus, the effect of *Pygospio* density is due to higher net immigration of *Pygospio* into the 1/3x *Pygospio* treatments and higher emigration/mortality from the 3x *Pygospio* treatments. 1x *Pygospio* treatments are intermediate between the 1/3x and 3x values. The results of the ANOVAs for the three different experiments are summarized in Table 9A.

TABLE 8. *Pseudopolydora* survivorship data for the 1-, 2-, 4- and 8-wk density-dependence experiments from the field. Survivorship is calculated as the final density of *Pseudopolydora* divided by the initial density. Values are means of four replicate cores (8 cm²). Results of Scheffé post hoc comparisons are shown by letters to the right of each mean. Means sharing the same letter are not statistically different ($P > .05$).

A. 1-wk data				
Initial <i>Pseudopolydora</i> density	Initial <i>Pygospio</i> density			
	0x	1/3x	1x	3x
<i>Pseudopolydora</i> survivorship				
1/3x	0.85 ab	0.95 a	0.95 a	0.85 ab
1x	0.75 b	0.83 ab	0.47 c	0.84 ab
3x	0.75 b	0.81 ab	0.38 c	0.78 b
B. 2-wk data				
Initial <i>Pseudopolydora</i> density	Initial <i>Pygospio</i> density			
	0x	1/3x	1x	3x
<i>Pseudopolydora</i> survivorship				
1/3x	1.05 b	0.70 bc	1.45 b	1.55 b
1x	0.48 bc	0.47 bc	0.64 bc	0.48 bc
3x	0.30 c	0.37 bc	0.52 bc	0.34 c
C. 4-wk data				
Initial <i>Pseudopolydora</i> density	Initial <i>Pygospio</i> density			
	0x	1/3x	1x	3x
<i>Pseudopolydora</i> survivorship				
1/3x	0.70 a	1.26 a	0.70 a	0.60 a
1x	0.12 a	0.39 a	0.52 a	1.00 a
3x	0.41 a	0.30 a	0.50 a	0.24 a
D. 8-wk data				
Initial <i>Pseudopolydora</i> density	Initial <i>Pygospio</i> density			
	0x	1/3x	1x	3x
<i>Pseudopolydora</i> survivorship				
1/3x	0.86 ab	0.80 ab	1.20 a	1.10 a
1x	0.84 ab	0.44 c	0.25 c	0.25 c
3x	0.22 c	0.24 c	0.33 c	0.42 c

The data for *Pseudopolydora* survivorship in the four field experiments are given in Table 8. In the 1-wk experiment, the effect of *Pseudopolydora* density on *Pseudopolydora* survivorship is highly significant ($F_{2,36} = 45.10$, $P < .001$). There is a significant effect of *Pygospio* density on *Pseudopolydora* survivorship ($F_{3,36} = 7.21$, $P < .001$). The interaction of the two main effects is also significant ($F_{6,36} = 3.04$, $P < .05$). Significant differences between factor-level means within a row or column are seen between the 1x-1/3x treatment and the significantly lower 1x-1x and 1x-3x treatments (Table 8A). The 1x-1x and 1x-3x treatments are also lower than the other 1x and 3x *Pygospio* treatments. The effect of *Pseudopolydora* density is a negative relationship; even for the instances where the factor-level means are not statistically different, there is always a trend of decreasing

survivorship with increasing *Pseudopolydora* density. For *Pygospio* density, the pattern is unclear. There is not always a pattern within a given *Pseudopolydora* density for *Pseudopolydora* survivorship to decline with increasing *Pygospio* density.

In the 2-wk experiment, there is a significant effect of *Pseudopolydora* density on *Pseudopolydora* survivorship ($F_{2,35} = 13.44, P < .001$). Neither the effect of *Pygospio* density ($F_{3,35} = 1.99, P > .10$) nor the interaction effect ($F_{6,35} = 1.14, P > .30$) is significant. The two significant differences between treatments within a given *Pygospio* density are between the $0 \times \frac{1}{3} \times$ and $0 \times 3 \times$ treatments, and between the $3 \times \frac{1}{3} \times$ and $3 \times 3 \times$ treatments (Table 8B). Within a given *Pygospio* density, there is always a trend of decreasing *Pseudopolydora* survivorship with increasing *Pseudopolydora* density.

In the 4-wk experiment, the effect of *Pseudopolydora* density on *Pseudopolydora* survivorship is not significant ($F_{2,15} = 3.44, P < .06$). Neither the effect of *Pygospio* density ($F_{3,15} = 0.16, P > .90$) nor the interaction effect ($F_{6,15} = 0.88, P > .50$) is significant. None of the factor-level means is significantly different from the others in Scheffé post hoc comparisons (Table 8C). The lack of significance is due, at least in part, to a loss of replicates in the field, and hence a loss in degrees of freedom. The trend of decreasing survivorship values with increasing *Pseudopolydora* density (Table 8C), although not significant, is reassuring.

In the 8-wk experiment, there is a significant effect of *Pseudopolydora* density on *Pseudopolydora* survivorship ($F_{2,11} = 11.16, P < .001$). Neither the effect of *Pygospio* density ($F_{3,11} = 1.31, P > .30$) nor the interaction of the two main effects ($F_{6,11} = 0.69, P > .60$) is significant. In Scheffé post hoc comparisons within a given *Pygospio* density, the $0 \times 3 \times$ survivorship is less than that in the $0 \times \frac{1}{3} \times$ and $0 \times 1 \times$ treatments, the survivorships for the $\frac{1}{3} \times 1 \times$ and $\frac{1}{3} \times 3 \times$ treatments are less than that of the $\frac{1}{3} \times \frac{1}{3} \times$ treatment, the survivorships in the $1 \times 1 \times$ and $1 \times 3 \times$ treatments are lower than that in the $1 \times \frac{1}{3} \times$ treatment, and the $3 \times 1 \times$ and $3 \times 3 \times$ treatments are lower than that in the $3 \times \frac{1}{3} \times$ treatment. The significant difference indicated by the Scheffé procedure between the survivorship in the $0 \times 1 \times$ treatment and the survivorships in the $\frac{1}{3} \times 1 \times$, $1 \times 1 \times$, and $3 \times 1 \times$ treatments is inadmissible since the ANOVA showed that the effect of *Pygospio* density was nonsignificant. The results of the ANOVAs on the *Pseudopolydora* survivorship data from the four experiments are summarized in Table 9B.

DISCUSSION

The results of the field experiments (Tables 6, 7, 8, 9) fail to agree with the predictions from the hypothesis of density-dependent determination of competitive outcomes. I predicted that high *Pseudopolydora* densities should affect low densities of *Pygospio* more severely than high densities of *Pygospio*. This predic-

TABLE 9. Summary of ANOVAs for the field density-dependence experiments. The ANOVAs test the effect of *Pygospio* density and *Pseudopolydora* density on the survivorship of experimental *Pygospio* and *Pseudopolydora*. The 4-wk data are not given in part A because loss of replicates left too few samples for analysis.

Source of variation	Duration of experiment			
	1 wk	2 wk	4 wk	8 wk
A. <i>Pygospio</i> survivorship				
<i>Pygospio</i> density	***	***		***
<i>Pseudopolydora</i> density	NS	NS		*
Interaction	NS	NS		NS
B. <i>Pseudopolydora</i> survivorship				
<i>Pygospio</i> density	***	NS	NS	NS
<i>Pseudopolydora</i> density	***	***	NS	***
Interaction	*	NS	NS	NS

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant ($P > .05$).

tion is not supported, since *Pseudopolydora* density usually had no effect on *Pygospio* survivorship (Tables 7, 9). Within a given *Pygospio* density, there is not even a consistent trend of decreasing survivorship of *Pygospio* with increasing *Pseudopolydora* density. Furthermore, the interaction terms in the ANOVAs are not significant, meaning that competitive effects are additive and linear. This effect would not obtain if competitive abilities were a function of density.

The hypothesis of density-dependent competitive abilities must likewise be rejected for *Pseudopolydora*. The prediction that high densities of *Pygospio* should affect low densities of *Pseudopolydora* more than high densities of *Pseudopolydora* is not true. Only in one experiment (Table 8A) did *Pygospio* density have a significant effect on *Pseudopolydora* survivorship. In that instance, the effect was not in the predicted direction and is best explained by an appeal to chance events. Thus, I cannot explain the patterns of abundance along the transect (Fig. 1) with an hypothesis of density-dependent determination of competitive outcomes. The explanation of the pattern requires formulation and testing of new hypotheses drawn from a constellation of possibilities (e.g., accidents of history, differences along the transect of unmeasured physical/chemical characteristics).

In opposition to the field data, laboratory data indicate that *Pygospio* and *Pseudopolydora* do interact. From Table 3, *Pygospio* migrates rapidly away from normal densities of *Pseudopolydora*, but not from normal conspecific densities. This migration is probably accomplished by entering the water column. Many of the *Pygospio* in the $1 \times 1 \times$ treatment were found at the periphery of the containers (Table 3), much farther than would be required to escape any influence of *Pseudopolydora* by crawling. Also, the survivorship data from the 2-wk experiment of Table 3 (given in parentheses) are similar to the comparable values from the 8-wk density-dependent asexual reproduction ex-

periment (Table 2). It is not likely that the 2-wk and 8-wk survivorship means would be the same if mortality were the agent reducing abundance in the experimental containers. The diminished survivorship occurs in 2 wk, perhaps sooner, and is best explained by migration from the containers. By analogy, migration is probably also the primary competitive effect measured in the field, where I could not distinguish mortality from migration. Dauer et al. (1980) describe swimming behavior in a spionid polychaete in the Chesapeake Bay.

I will propose two different hypotheses to attempt to reconcile the lack of interaction of *Pygospio* with *Pseudopolydora* in the field but the strong emigration by *Pygospio* from *Pseudopolydora* in the laboratory. I shall term the first one the water-flow hypothesis. Taghon et al. (1980) showed that some spionids will switch from feeding on the sediment surface to feeding in the water column if water flow and suspended material exceed some threshold value. In the laboratory, water currents were slow and both species spent much of their time deposit-feeding on the sediment surface. In the field, however, where water currents are present, the spionids probably fed in the water column. I have found that *Pseudopolydora* is more predisposed to feed in the water column than *Pygospio*. Thus, the hypothesis predicts spatial partitioning of feeding in the field. In the laboratory, water currents never reached the threshold velocity and both species fed on the sediment surface and hence interacted. It should be noted that animals feeding in the water column are feeding primarily on suspended sediment, not planktonic organisms. Thus, an additional food supply is not being tapped by feeding in the water column; the mechanism of the competitive interaction under this hypothesis must be one of interference, not exploitation. Coexistence is permitted not by finding alternative foods but by spatial partitioning of food acquisition.

A second hypothesis, the spacing hypothesis, also serves to reconcile the laboratory and field data. Under this hypothesis, one predicts that *Pygospio* minimizes its contacts with *Pseudopolydora* in the field. This spacing may occur by movement toward conspecifics, independent of *Pseudopolydora* (gregarious behavior), or movement away from *Pseudopolydora* (avoidance behavior). Table 1 provides empirical support for the hypothesis. *Pygospio* is less frequently near *Pseudopolydora* than predicted by random expectation. These data cannot differentiate between movement toward conspecifics or avoidance of *Pseudopolydora*. The laboratory emigration experiment (Table 3) supports the avoidance mechanism. Regardless of mechanism, more of *Pygospio*'s encounters will be intraspecific than predicted on the basis of relative abundance of *Pygospio* and *Pseudopolydora*. If the spacing hypothesis is true, the strongest competitive effect will be an intraspecific effect.

Comparison of Tables 7 and 8 with Table 5 suggest

how this movement is effected. Assuming that migration rather than mortality is the chief influence on the composite survivorship function in the field experiments, emigration has a strong intraspecific density-dependent component. However, from Table 5, immigration into an occupied habitat is not dependent on the density of residents. Movement into and out of the experimental cores seems to be a trial-and-error process. An organism assesses its present habitat but not the habitat into which it will move. By such trial-and-error migration, *Pygospio* reaches locations where contact with *Pseudopolydora* is minimized. *Pygospio* should approach an ideal free distribution (Fretwell and Lucas 1970) where habitat suitability is a function not purely of resource level but also of *Pseudopolydora* proximity. *Pseudopolydora* serves only to occupy space, determined by some portion of its feeding area, and its effect on *Pygospio* effectively is to decrease preferred habitat. In the field, one measures *Pygospio* density as the strongest effect on survivorship (usually the only significant effect, Table 9), when, in fact, the density of *Pseudopolydora* is critical in determining how closely packed the *Pygospio* are. These arguments therefore support the spacing hypothesis as the primary mechanism of coexistence of these two species in the field, with the water flow hypothesis of secondary importance. The spacing hypothesis predicts lateral or horizontal partitioning of feeding, while the water flow hypothesis predicts vertical partitioning of feeding.

These arguments are not the first claim of avoidance behavior for adult infaunal organisms. For bivalves, Levinton (1977) showed that *Nucula proxima* avoids areas of *Yoldia limatula* abundance, and Peterson and Andre (1980) showed that *Sanguinolaria nuttallii* avoids areas of high *Tresus nuttallii* and *Saxidomus nuttallii* densities. For spionids, Dauer et al. (1981) showed that *Streblospio benedicti* moved its tube location to avoid interaction with *Paraprionospio pinnata*. I would expect measures of competition in the field to show analogous patterns to the False Bay community; the emigrating species should be influenced more by interactions with conspecifics.

If my interpretations of the mechanisms of coexistence of *Pseudopolydora* and *Pygospio* are correct, the ability of *Pygospio* to persist in False Bay depends on *Pseudopolydora* regulating its own density at or below 20 000 individuals/m², ambient field density. *Pseudopolydora* can maintain high survivorship at higher densities, at least for 8 wk, even though growth and reproduction may be seriously curtailed (W. H. Wilson, Jr., personal observation). Given high enough *Pseudopolydora* densities, *Pygospio* could not effectively avoid direct interactions with *Pseudopolydora*, and one would predict a sharp decline in *Pygospio* abundance. I propose the hypothesis that interactions of established infaunal organisms with settling larvae of *Pseudopolydora* prevent *Pseudopolydora* from achieving higher densities than are observed. I lack

data for the larvae and newly settled juveniles of *Pseudopolydora*, but I have demonstrated that both *Pygospio* and *Pseudopolydora* exert a strong negative influence on the benthic larvae of *Abarenicola pacifica*, probably by ingestion of larvae (Wilson 1981). Under this hypothesis, the continued existence of *Pygospio* is contingent on the continual difficult recruitment of *Pseudopolydora*. It is worth noting that the asexual reproduction of *Pygospio* bypasses the vulnerable larval stage; it is unlikely that the size-specific survivorship of a newly regenerated fragment (4–5 mm long) differs significantly from that of larger individuals in the population. The observation that *Pygospio* is contingent on the continual difficult *polydora* (Tables 3, 5) and the demonstration that asexual reproduction occurs at low densities (Table 2) would seem to confer an advantage on *Pygospio* for taking advantage of free space. Indeed, it is the most abundant macrofaunal organism in the community. Similar patterns of maximal asexual reproduction at low densities have been documented in dewberries (Abrahamson 1975) and wild strawberries (Holler and Abrahamson 1977). In *Pygospio*, this response seems to confer no interspecific competitive advantage, in the sense of competitive exclusion of adults, since invasibility is not density dependent (Table 5). The selective advantage of such density-dependent reproduction seems to lie in the capacity it confers for rapid proliferation in a favorable microhabitat.

The experimental results of the study establish that intraspecific competitive interactions play a major role in structuring this infaunal community. Concerning the original hypothesis investigated in this study, I could marshal little evidence to suggest that competitive ability varies as a function of density; competitive abilities over the experimental densities may be considered constant. However, emigration and asexual reproduction are strongly density dependent. The work also implicates physical regime (water flow) and behavior (avoidance/aggregation) as being critical to the understanding of community structure.

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