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Dispersion, feeding behavior and competition in two spionid polychaetes

by Lisa Ann Levin[1]

ABSTRACT

Spatial analysis, laboratory and field experiments, and feeding observations indicate contrasting patterns of aggression in the polychaetes *Pseudopolydora paucibranchiata* (Okuda) and *Streblospio benedicti* (Webster) and provide the first evidence of territoriality in a spionid polychaete (*Pseudopolydora*). On the intertidal mudflats of Mission Bay in San Diego, California, *Pseudopolydora* is spaced more evenly than expected from a random distribution, while the dispersion of *Streblospio* does not depart significantly from random. Recruitment patterns in *Pseudopolydora* indicate that uniform spacing is initiated during settlement and enhanced by subsequent interactions between individuals. Field manipulations provide evidence for adult interactions with settling larvae which may also play a role in generating non-random dispersion in *Pseudopolydora*. Differences between *Pseudopolydora* and *Streblospio* in aggressive behavior (palp fighting and biting) and feeding mechanisms are correlated with different space requirements for feeding and tube building. Laboratory observations of surface deposit and suspension feeding indicate that *Pseudopolydora* is more aggressive and frequently uses its mouth and palps to acquire food particles. These species also differ in their site of food particle selection. *Streblospio* relies primarily on lips and mouth to taste particles, while *Pseudopolydora* more frequently uses its palps. It is proposed that *Pseudopolydora* defends palp territories necessary for the acquisition of food and tube building materials. The spatial analysis, in conjunction with experimental results and behavioral observations suggest strong competition in *Pseudopolydora* but not in *Streblospio*.

1. Introduction

Spatial patterns created by individuals in a population or by populations in a community may be classified as aggregated, regular or random. Static patterns alone are of limited value, but can serve to alert biologists to dynamic physical and biological processes structuring communities. Aggregation may result from habitat heterogeneity, symbiosis, gregarious behavior and/or limited dispersal of progeny. Regularity may arise from such negative interactions as territoriality, avoidance behavior and/or allelopathy. Randomness may result either when specifically stochastic processes govern distributions or when no other processes come into play.

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Aggregated dispersion patterns are most common in nature, while both random and regular dispersions are rare (Pielou, 1977). This is particularly true of infaunal invertebrate populations inhabiting soft sediments, where heterogeneity of sediment organics, grain size and other structural features, as well as local disturbances, commonly create patchy distributions.

Quadrat sampling and multiple cell corers of various sizes have been used in conjunction with indices of dispersion and autocorrellation to examine fine-scale dispersion patterns in soft sediments. Alternatively, plotless sampling, which focuses on spacing of individuals, has been used in association with nearest-neighbor statistics to analyse dispersion patterns (see Pielou, 1977 for a discussion of methods). This technique has the advantage of being independent of sample size. Both approaches measure only intensity (the extent to which density varies from place to place) and not grain (size and spacing of aggregations).

Nearest-neighbor analysis involves measurements of distances between organisms. Because infaunal organisms are difficult to observe from the sediment surface (they are usually buried), their abundance and distribution are usually determined from sediment cores. Precise positions have occasionally been determined using X-radiography (Levinton, 1972) or core dissection techniques (Whitlatch, 1976). Under some circumstances infaunal organisms may be observed from the sediment surface and photographed or drawn, as was done in this investigation.

Only a few studies have demonstrated uniform dispersion in marine infaunal organisms. Holme (1950) demonstrated overdispersion in the lamellibranch *Tellina tenuis* and correlated it with foraging activities of the inhalent siphon. Johnson (1959) attributed the even spacing of the phoronid *Phoronopsis viridis* to space requirements for lophophore expansion. Connell (1963) observed that uniform dispersion of the tubes of the amphipod *Ericthonius braziliensis* and the burrow entrances of the fiddler crab *Uca pugilator* was maintained by aggressive interaction. Of the numerous species of infaunal polychaetes studied by spatial analysis (Ekman, 1979; Jumars *et al.*, 1977; Jumars, 1978; Reise, 1979; Roe, 1975; Rosenberg, 1974) only the following members of the family Nereidae exhibit uniform spacing: *Nereis diversicolor* (Reise, 1979), *Nereis vexillosa, Platynereis bicaniculata*, (Roe, 1975) and *Ceratocephale pacifica* (Jumars, 1978). Several of these species are known to defend territories around their burrows.

All of the infaunal invertebrates mentioned above build permanent tubes or burrows and feed at the sediment surface. Many of them deposit feed on sediment or detritus particles, though some exhibit predatory behavior as well. Infauna of other trophic modes tend to exhibit either clumped dispersion, as in the suspension feeding bivalves *Mya arenaria, Petricola pholadiformas* and *Modiolus demisus* (Connell, 1956) or random dispersion, as in the motile subsurface deposit feeder *Nucula proxima* (Levinton, 1972).

This paper presents studies of behavior and resulting spatial dispersion in related

(confamilial) infaunal species, *Pseudopolydora paucibranchiata* (Okuda) (hereafter referred to as *Pseudopolydora*) and *Streblospio benedicti* (Webster) (hereafter referred to as *Streblospio*). This investigation combines laboratory and field studies to look in depth at the mechanisms generating and maintaining the observed patterns. The results provide the first evidence for territoriality in spionid polychaetes, a ubiquitous and very abundant group in shallow soft sediment environments. Differences in the feeding biology and aggressive behavior of the two species are assessed and some implications of territoriality in *Pseudopolydora* are discussed.

2. Natural History

Pseudopolydora paucibranchiata and *Streblospio benedicti* were studied on intertidal mudflats of Mission Bay in San Diego, California. Both are introduced species, *Streblospio* from the Atlantic Ocean and *Pseudopolydora* from Japan (Carleton, 1975). The following descriptions of these species are for Mission Bay populations and based on unpublished observations by the author. *Pseudopolydora* is the most abundant (up to 60,000 individuals/cm²) macroscopic species that surface feeds in the low intertidal (−2 to +2 ft) in spring and summer. *Streblospio* (4,000-16,000 individuals/m²) dominates the mid-intertidal sediments (+2 to +4 ft) in spring. Both species are annuals. Reproductive individuals can be found all year in both populations but peak larval availability occurs from February to May for *Pseudopolydora* and January to March for *Streblospio*.

The two species are similar in size, attaining live body lengths of 15 to 20 mm. *Pseudopolydora* constructs vertical tubes (1 mm diameter × 30 mm length) of cemented organic aggregates which protrude from the sediment surface. Contrary to a previous report of multiple tube openings (Blake and Woodwick, 1975) the individuals in Mission Bay each possess only one tube. *Streblospio* constructs a more fragile tube of fine silt, which also opens at the sediment surface. Under conditions of still water both species will build tubes which extend a centimeter or more above the mud surface.

Pseudopolydora and *Streblospio* feed primarily on organic aggregates and detritus at the sediment surface using cilliated palps for both suspension and deposit feeding. Their feeding behavior varies with water motion and three palp configurations have been observed during feeding in the laboratory. In still water the palps wander over the sediment surface deposit feeding, picking up sediment and detritus. In moving water palps suspension feed, are held upright and are often waving. At very high water velocities palps are spiraled and held perpendicular to the direction of water flow. These behaviors have also been observed in other spionid polychaetes (P. Jumars, personal communication) and may be a general feeding strategy among bitentaculate polychaetes feeding at the sediment surface. Both species deposit similar rodlike fecal pellets outside their tubes.

3. Methods

a. Study site

Spatial analyses were performed on *Streblospio* and *Pseudopolydora* from an intertidal mudflat located adjacent to the Kendall Frost Marsh Reserve in Mission Bay, California. In April and May, 1979, *Pseudopolydora* tubes were photographed and the worms were collected from the low intertidal (0 to +2 ft) and *Streblospio* were collected from +2 to +3 ft.

b. Spatial analysis

1. *Benthos*. To study the spatial dispersion of *Pseudopolydora* tubes protruding above the sediment surface, six 9 × 9 cm quadrats were marked on homogeneous portions of the mudflat surface, photographed and printed at life size for nearest-neighbor measurements (Fig. 1). *Streblospio* tube openings are inconspicuous and
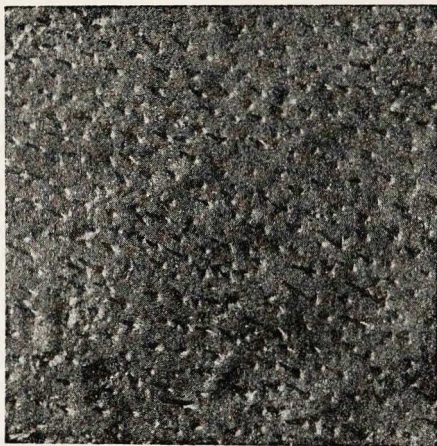

Figure 1. *Pseudopolydora paucibranchiata* tubes photographed May, 1979 at the Kendall Frost Reserve, Mission Bay, San Diego, California.

thus can not be reliably recorded by photography. Instead, 35 × 25 × 5 cm sections of the entire community were transported in plastic trays from the mudflat to the laboratory. Six 9 × 9 cm quadrats were marked in these sediments and a dissecting microscope (60× magnification) with a camera lucida was used to plot worm positions within each quadrat. Only those burrows with a worm present, or with fresh fecal pellets outside the burrow opening, were recorded. The spatial distribution studies were conducted only on quadrats in which either *Pseudopolydora* or *Streb-*

Iospio was the dominant species and there was little or no overlap in occurrence. The distance to nearest-neighbor was measured for every individual of these species in all quadrats to obtain six frequency distributions of nearest-neighbor distances for each species. When nearest neighbors occurred outside quadrat borders (as they sometimes did for worms on the edges of the quadrat), true nearest-neighbor distances were measured. The observed mean nearest-neighbor distance for each quadrat was compared to the expected mean nearest-neighbor distance using the Clark and Evans (1954) index:

$$R = \frac{r_{observed(mean)}}{r_{expected(mean)}}$$

The difference between the observed and expected means were tested for significance using the standard normal variate:

$$c = \frac{r_{observed(mean)} - r_{expected(mean)}}{\sigma_{r_{expected(mean)}}}$$

$\sigma_{r_{expected(mean)}}$ is the standard error of the mean nearest-neighbor distance. In addition each observed frequency distribution was compared to that expected in a random Poisson distribution using the Kolmogorov-Smirnov test (*K-S* test) (Sokal and Rohlf, 1969). Both Clark and Evans and Kolmogorov-Smirnov tests were employed because the mean, though a useful statistic, does not necessarily convey all the relevant information in a nearest-neighbor frequency distribution.

The ability of adult *Pseudopolydora* to regenerate uniform dispersion once disturbed was investigated by removing adults from mudflat sediments (by sieving) and reintroducing them to the sediment at various densities in 9 × 9 × 9 cm freezer cartons. The cartons were placed back on the mudflat or in the laboratory in standing or running seawater for one week.

2. *Laboratory recruitment studies.* The spatial patterns of new *Pseudopolydora* post-larvae were investigated both in the laboratory and in the field in March, 1980. Larvae were obtained for laboratory studies from net tows made over the mudflat at high water and from brooding adults which released larvae in the laboratory. Larvae fed *Monocrysis* and *Clamydomonas* were raised in still seawater at room temperature in cylindric 15 dram vials (6.15 cm² × 6 cm deep) containing 0.3 cm of fine sediment. Upon settlement *Pseudopolydora* recruits constructed small tubes at the sediment surface. Tube positions were plotted for 6 vials of larvae at several recruitment densities, using a dissecting microscope and camera lucida. Nearest-neighbor measurements were made and both Clark and Evans and Kolmogorov-Smirnov statistics were employed to assess spatial patterns.

3. *Field recruitment studies.* Recruitment patterns of *Pseudopolydora* in the field, and the effects of adult presence on recruitment, were studied by placing plastic cartons (9 × 9 × 9 cm) filled with 7 cm of sediment on the mudflat during peak larval

availability (April, 1980). Adult *Pseudopolydora* were added to some treatments at densities of 1.5-3.9 adults/cm². All cartons were enclosed in ½" galvanized wire mesh cages (30 × 40 × 12 cm) secured to the mudflat surface at +0.5 ft tide level. After two weeks on the mudflat the cartons were returned to the lab for immediate counts and for nearest-neighbor measurements of new recruits. A circle of area 0.001 m² was marked in the center of each carton using a plastic core of the same dimensions. In cartons without adults present positions of both tube openings and tube bases (site of tube contact with the sediment surface) were plotted for every individual within the marked area. In all other analyses in this paper *Pseudopolydora* tubes were oriented more or less vertically and positions were plotted for tube bases. Positions were plotted, nearest-neighbor distances were measured and their significance tested using the methods described above for the spatial analysis of recruitment in the laboratory. Counts of adult and recruit abundance were made visually with the aid of a dissecting microscope (60× magnification) for 0.001 m² areas marked in each treatment containing adults.

In the nearest-neighbor analysis used here, organisms are considered dimensionless (points). Although polychaete tubes are represented more accurately by circles than points, a recent assessment of spatial configurations of circles by Simberloff (1979) concludes that the classical nearest-neighbor analysis assuming points is accurate for circle diameters less than half the expected mean nearest-neighbor distance for points. The tube openings of adult *Streblospio* and *Pseudopolydora* have diameters of one milimeter and fall within the range stated above at all observed faunal densities. The tubes of new recruits are even smaller (0.2 mm) relative to nearest-neighbor distances. Thus using points instead of circles should not affect the outcome of the analysis. As an additional check $r_{observed(mean)}$ and $\sigma_{r_{observed(mean)}}$ were corrected for the benthic quadrats having the largest ratio of tube diameter to expected mean nearest-neighbor distance (based on the computer simulation in Simberloff, 1979). Probability levels were not affected in either *Streblospio* or *Pseudopolydora* quadrats.

c. Feeding studies

To evaluate aspects of spionid feeding biology which might affect dispersion patterns, sediment samples (9 × 9 × 9 cm) with live infauna were brought intact from the mudflat into the laboratory and maintained under running seawater. Intraspecific feeding interactions were observed for undisturbed worms in still water under 120× magnification. Small pieces of the alga *Enteromorpha* sp., commonly found on the mudflat in Mission Bay, were offered simultaneously to two individuals and the behavioral responses of the worms were recorded. This procedure was repeated for 52 pairs of *Pseudopolydora* individuals and for 25 pairs of *Streblospio* individuals. All pairs were randomly selected sets of nearest neighbors. In addition, individual worms of both species were observed in the lab to determine the site of

Table 1. Nearest-neighbor analysis of benthic dispersion in a 9×9 cm quadrat.

Pseudopolydora paucibranchiata

Quadrat	Density (#/cm²)	r_{mean} (cm)	R	Dispersion
1	2.36	0.48	1.49	Uniform*
2	2.95	0.40	1.36	Uniform*
3	3.39	0.39	1.42	Uniform*
4	3.72	0.40	1.54	Uniform*
5	4.15	0.37	1.50	Uniform*
6	5.78	0.30	1.46	Uniform*

$$\bar{X}_{r(mean)} = 0.39 \pm 0.10$$

Streblospio benedicti

Quadrat	Density (#/cm²)	r_{mean} (cm)	R	Dispersion
1	0.64	0.57	1.07	Random
2	0.71	0.57	1.03	Random
3	0.97	0.53	1.12	Random
4	1.32	0.42	1.03	Random
5	1.64	0.38	1.05	Random
6	1.64	0.45	1.24	Uniform*

$$\bar{X}_{r(mean)} = 0.49 \pm 0.15$$

r_{mean} = mean nearest-neighbor distance.

R = Clark and Evans (1954) index of dispersion = $\dfrac{r_{observed(mean)}}{r_{expected(mean)}}$

$R > 1$ indicates overdispersion
$R < 1$ indicates underdispersion
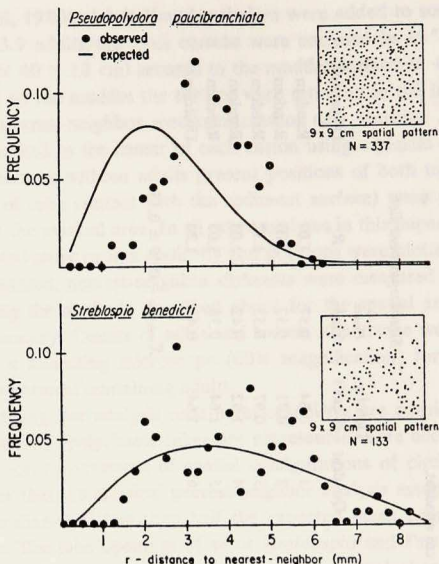*$p < 0.001$; Clark-Evans and Kolmogorov-Smirnov tests.

Figure 2. Sample nearest-neighbor frequency distributions for 9 × 9 cm quadrats of *Pseudopolydora paucibranchiata* and *Streblospio benedicti*.

particle selection. A slurry of suspended sediment was offered to suspension feeding individuals and the rejection site was recorded for any particles initially adhering to the palps.

4. Results

a. Adult dispersion. The results of the nearest-neighbor analysis for benthic quadrats are summarized in Table 1 and sample frequency distributions for each species are shown in Figure 2. The tubes in all six *Pseudopolydora* quadrats were more uniformly distributed than expected from the null hypothesis of Poisson randomness. The nearest-neighbor frequency distributions were right skewed ($p < 0.001$ by the *K-S* test) and the mean nearest-neighbor distances were consistently greater ($p < 0.001$ by the Clark and Evans test) than would be expected from a random distribution. In contrast, five out of six *Streblospio* quadrats did not depart significantly from a random distribution. However, for one quadrat the nearest-neighbor distribution was right skewed ($p < 0.001$, *K-S* test). Whitlatch (personal communication) has found that *Streblospio benedicti* on the east coast commonly displays aggregated
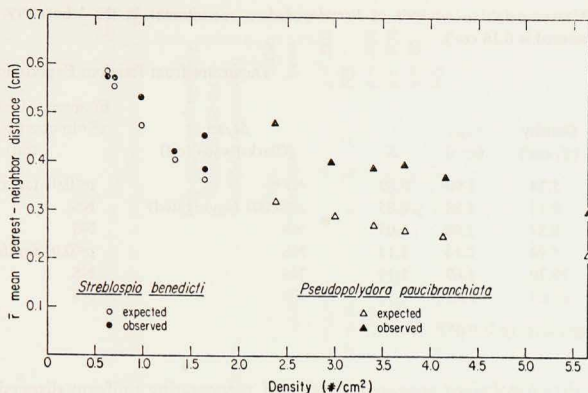
Figure 3. Nearest-neighbor distance as a function of density in *Pseudopolydora paucibranchiata* and *Streblospio benedicti*, based on analysis of 9 × 9 cm quadrats.

dispersion. The Clark and Evans (1954) index of dispersion consistently fell between $R = 1.36$ and $R = 1.54$ for *Pseudopolydora* quadrats, indicating that the tubes were approximately one and a half times farther apart than expected. R values for *Streblospio* ranged from 1.03 to 1.24 suggesting slight overdispersion. R values differed significantly between the two species ($p < 0.01$, Mann-Whitney U test) indicating contrasting patterns of adult dispersion over the range of densities tested.

Figure 3 presents the relationship between spionid density and nearest-neighbor distances for both species. In both *Pseudopolydora* and *Streblospio* the observed mean nearest-neighbor distances for each quadrat varied approximately inversely with density; however, in *Pseudopolydora* observed nearest-neighbor values remained consistently greater than expected indicating that *Pseudopolydora* individuals do not maintain fixed distances between one another. Instead this distance decreases with increasing density.

The overall mean nearest-neighbor distance in benthic quadrats was 0.39 cm for *Pseudopolydora* and 0.48 cm for *Streblospio*. In randomly distributed populations one would expect very small nearest-neighbor distances, < 2 mm, to be found more frequently in *Pseudopolydora*, which occurs at much greater densities, than in *Streblospio*. In fact only 2% of all *Pseudopolydora* ($n = 1605$) fell within this range compared to 7% of *Streblospio* ($n = 673$). Random expectations were 29% and 14% respectively. Though small nearest-neighbor distances were less frequent than expected in both species, they are far more common in *Streblospio* than in *Pseudopolydora*, indicating different patterns of dispersion.

Table 2. Nearest-neighbor analysis of *Pseudopolydora* recruitment in the laboratory. (Actual area measured is 6.16 cm².).

				Departure from Random Expectations	
Vial	Density (#/cm²)	r_{mean} (mm)	R	Mean (Clark-Evans test)	Frequency Distribution (Kolmogorov-Smirnov test)
1	5.24	1.90	0.89	NS*	$p<0.01$ (aggregated)
2	6.18	1.88	0.85	$p<0.001$ (aggregated)	NS
3	6.37	2.08	1.05	NS	NS
4	6.94	2.14	1.13	NS	$p<0.01$ (uniform)
5	10.20	1.69	1.10	NS	NS
6	10.90	1.55	1.02	NS	NS

* Not significant ($p > 0.05$)

Adult *Pseudopolydora* appeared capable of regenerating uniform dispersion following severe disturbance. Disrupted individuals (at densities above 0.60/cm²) which were returned to the field or left in the laboratory in still water had reassumed the appearance of even spacing within a week. *Pseudopolydora* maintained in the laboratory under unidirectional running seawater did not reconstruct tubes in a uniform arrangement, even at high densities (3.0/cm²). Spatial homogeneity of food supply and/or hydrodynamic factors may be necessary for spacing behavior to occur.

b. Post-larval dispersion. Nearest-neighbor analysis of *Pseudopolydora* recruitment patterns in the laboratory (Table 2) revealed mean nearest-neighbor distances ranging from 1.55 to 2.14 mm, only one of which differed significantly from random expectation toward overdispersion. In two out of six replicates the nearest-neighbor frequency distributions differed from expected significantly at $p < 0.01$ (*K-S* test). In one case this was due to a shortage of small nearest-neighbor distances, indicating overdispersion and in the other instance to a shortage of large nearest-neighbor distances, indicating clumping. At lower densities (5/cm²) the settlement patterns tended to be aggregated and at higher densities (11/cm²) they tended toward overdispersion.

Recruitment of *Pseudopolydora* into sediment-filled cartons placed on the mudflat resulted in post-larval densities of 7.5 to 18.0 individuals/cm². Mean nearest-neighbor distances (Table 3; measured for tube openings) ranged from 1.39 to 2.85 mm. Four out of five replicates had means significantly greater than expected ($p < 0.002$) indicating overdispersion. Nearest-neighbor analysis of the same individuals based on distances between the base of their tubes (Table 3) revealed significantly smaller mean nearest-neighbor distances between tube bases than between tube openings (paired t test; $t_5 = 7.13$, $p < 0.01$). Three replicates were overdispersed ($p < 0.001$), two did not differ from random and one was underdispersed ($p < 0.025$). The over-

Table 3. Nearest-neighbor analysis of *Pseudopolydora* recruiting into sediment filled 9×9 cm cartons placed on the mudflat for 14 days. Positions of tube openings and tube bases (point of contact with the sediment surface) were analyzed for the same individuals. (Actual area measured is 0.001 m².)

Replicate	Density ($\#/cm^2$)	r_{mean} (mm)		R		Dispersion		Departure of frequency distributions from random expectation	
		Tube openings	Tube bases	Tube openings	Tube bases	Tube openings	Tube bases	Tube openings	Tube bases
1	7.47	2.85*	2.69*	1.56	1.48	Uniform	Uniform	$p < .001$	$p < .001$
2	8.61	2.07*	1.76	1.54	1.10	Uniform	Random	$p < .01$	NS
3	10.72	—[1]	1.87*	—[1]	1.22	—[1]	Uniform	—[1]	$p < .001$
4	13.00	1.47	1.15*	1.06	0.88	Random	Aggregated	$p < .05$	$p < .001$
5	15.75	1.74*	1.49*	1.39	1.21	Uniform	Uniform	$p < .001$	$p = .05$
6	18.03	1.39*	1.22	1.18	1.04	Uniform	Random	$p < .001$	NS

* Significant departure from Poisson expectation $p < 0.01$, Clark-Evans (1954) test.
[1] Accidental (irrecoverable) omission during data collection.

Table 4. Recruitment of *Pseudopolydora* into 9 × 9 × 9 cm sediment-filled cartons placed on the mudflat for 14 days. *Pseudopolydora* adults were added to 5 of 12 cartons. Recruitment differs significantly between treatments with and without adults (Students t test; $t_9 = 7.25$; $p < .001$).

Treatment (#/.001 m²)			Replicates				
	1	2	3	4	5	6[1]	$\bar{X} \pm 2$ S.D.
Adults present							
New recruits	76	93	68	85	79		80.2 ± 16.8
Adults	39	22	15	30	27		26.6 ± 16.0
Total	115	115	83	115	106		106.8 ± 24.8
Adults absent							
New recruits	126	105	117	120	134	137	123.2 ± 25.1

[1] Carton contents were accidentally spilled in transport from the field to the laboratory.

all mean nearest neighbor distance was 1.66 mm for tube bases and 1.90 mm for tube openings.

Recruitment of *Pseudopolydora* into settling cartons containing *Pseudopolydora* adults was significantly lower than recruitment into cartons without adults (Table 4; students t test, $t_9 = 7.25$, $p \ll 0.001$). Mean post-larval densities were 8.01 ± 1.7 individuals/cm² ($n = 5$) in treatments with adults and 12.3 ± 2.2 individuals/cm² ($n = 6$) in treatments without adults. Total *Pseudopolydora* densities (adults & larvae) are also lower in treatments with adults (10.78 ± 2.5 individuals/cm²) than in treatments without (12.3 ± 2.2) (students t test $t_9 = 2.35$, $p < 0.05$).

c. Feeding biology. The unusual occurrence of uniform dispersion and the differences in spatial pattern between *Streblospio* and *Pseudopolydora* suggests possible species-specific behavioral differences. In other investigations, uniform dispersion has been associated with surface deposit feeding.

Results of intraspecific feeding studies in which dried particles of *Entermorpha* sp. were offered simultaneously to two individuals revealed food fights accompanied by strongly aggressive behavior between *Pseudopolydora* individuals 98% of the time ($N = 52$ observations). Such struggles were much less frequent (24% of the time, $N = 21$ observations) and very weakly aggressive in *Streblospio*. A closer look at *Pseudopolydora* food struggles (Table 5) revealed a variety of behaviors which occur when their cilliated palps meet with resistance in transporting food or tube building materials toward the prostomium. Partial emergence from the tube and biting and pulling at algae with lips and mouth occurred frequently in these struggles. This behavior was also observed in *Streblospio* feeding alone, but never occurred when another worm was involved. Often direct palp contact and pulling on tubes took place between *Pseudopolydora* individuals involved in contests over large particles. In two instances *Pseudopolydora* individuals were observed to emerge from their tubes and bite off one palp of the opposing worm. The reach of

Table 5. Feeding interactions among *Pseudopolydora paucibranchiata*, based on 52 observations of food fights between pairs of worms.

Behavior	% Occurrence	
Use of mouth and lips, emergence from tube	59%	(30)
Bending of worm tubes due to resistance from opposing individuals	41%	(21)
Direct contact between palps of opposing individuals	39%	(20)
Withdrawal of one individual into its tube following the struggle	18%	(9)
One palp bitten off by the opposing individual	4%	(2)

one *Pseudopolydora* palp overlaps that of several other individuals and each palp is capable of carrying on separate struggles simultaneously. Occasionally *Pseudopolydora* palps are used as a grasping organ to pick up larger particles and carry them to the mouth. It is not uncommon for three, four, or even five worms to fight over a single food particle. Groups of *Pseudopolydora* have been observed struggling over algae, invertebrate larvae and other (dead) polychaetes. *Streblospio* palps, though slightly shorter, are long enough to reach neighboring worms easily, but are rarely used in an aggressive manner.

Studies of feeding mechanisms suggest reasons for the observed differences in aggressive behavior between the two species. The palps which have a similar role in acquiring and transporting food particles in the two species, play somewhat different roles in particle acceptance. In 25 observations of particle rejection for each species, particle rejection usually (84% of the time) occurred after tasting at the mouth in *Streblospio* whereas the palps generally (72% of the time) rejected particles in *Pseudopolydora*. This pattern was observed consistently for a variety of particle types including algae, polychaete fecal pellets and organic aggregates. All of these findings suggest that *Pseudopolydora* palps have a broader biological role than *Streblospio* palps.

5. Discussion

Differences in the dispersion of *Pseudopolydora* and *Streblospio* in Mission Bay may be associated with their respective feeding behaviors. The uniform spacing of *Pseudopolydora* is initiated during or soon after settlement and is maintained by aggressive behaviors in the form of palp fighting and biting. Because *Pseudopolydora* palps acquire, taste and transport food particles, it may be necessary for individuals to defend palp territories. Richardson *et al.* (1979) documents a similar case in which sweeper tentacles are used aggressively by the reef coral *Montastrea cavernosa* to maintain living space. In dense assemblages of sessile deposit and suspension feeders it is difficult to distinguish space and food as separate resources. The ability

of adult *Pseudopolydora* to regenerate uniform dispersion following disruption sug-
gests that territoriality and the resulting spacing enhances fitness.

Pseudopolydora palps are quite long (up to 15 mm) and territory overlap occurs
between individuals. The degree of dispersion (represented by the Clark and Evans
index R) remains fairly constant (approximately 1.5) with changing worm densities
across the mudflat (Table 1). Variability in territory size has been documented by
Roe (1975) for the territorial polychaete *Nereis vexillosa* and by Crisp (1961) for
the territorial barnacle *Eliminius modestus*. Reise (1979) notes that the dispersion
of territorial species responds to habitat heterogeneity in soft sediments. Weinberg
(1979) and Whitlatch (personal communication) found that spionids increase their
foraging radius (by extending further from their tube) in response to lowered levels
of surface organic matter. The variation observed in *Pseudopolydora* territory size
may reflect structural sediment heterogeneity and/or changes in food resource
availability.

Laboratory observations indicate that aggressive behavior in *Pseudopolydora* is
not limited solely to intraspecific interactions. *Pseudopolydora* individuals were
observed to fight with the spionid *Polydora ligni* over algal particles and with caprel-
lid amphipods over dead invertebrate larvae. *Pseudopolydora* exhibits aggression
toward smaller polychaetes (e.g. *Rhyncospio arenicola*, *Polydora ligni* juveniles)
using its palps to push these worms back into their tubes while stealing their food
and tube material. Whitlatch (personal communication) has observed similar inter-
specific interactions including palp intertwining and food stealing among several
spionid species on the east coast. *Pseudopolydora* usually dominates interactions
with other polychaete species present on the Mission Bay mudflat; however *Pseudo-
polydora* often loses encounters with gammarid and caprellid amphipods.

In a recent review of competition in soft sediments, Woodin and Jackson (1979)
note that direct competitive interactions vary in intensity as a function of the or-
ganisms' taxonomic relationships. For example, aggressive intrafamilial interactions
occur among herbivorous tube building nereid species, but these nereids ignore
herbivorous tube building representatives of other polychaete families. Similarly,
Reish and Alosi (1968) observed that among territorial nereids intra-specific ag-
gression was stronger than interspecific aggression and no aggression was exhibited
against other polychaete families tested. *Pseudopolydora* behavior follows this pat-
tern as well. Aggressive intraspecific interactions are common and result in uniform
spacing. Similar interactions take place with other tube building spionid polychaetes
but *Pseudopolydora* individuals do not appear to space themselves uniformly with
other tube dwelling species (personal observation). In sandy portions of the upper
intertidal region *Pseudopolydora* lives in a dense *Fabricia limnicola* bed (up to
200,000 individuals/m²) along with *Streblospio benedicti*, *Polydora ligni*, *Rhyn-
cospio arenicola*, *Capitita ambiseta* and *Phoronis* sp. The fact that *Pseudopolydora*

tubes are frequently found touching the tubes of other species (Levin, unpublished data) underscores the differences between intra- and inter-specific aggression.

Intraspecific aggression against established adult worms is probably the primary mechanism maintaining uniform dispersion in *Pseudopolydora* but does not necessarily generate the pattern. Both adult-larval and larval-larval interactions, before and shortly after larval recruitment, may initiate regular spacing. Field studies of *Pseudopolydora* recruitment (Table 4) indicate that adults interfere with recruitment success. This interference may take the form of predation on larvae or competition with newly settled individuals resulting in post-settlement mortality. *Pseudopolydora* individuals recruited early in the season may generate regular spacing by cannabilizing settling and newly settled forms. Ingestion of invertebrate larvae has been reported for several spionid species (Daro and Polk, 1973; Breese and Phibbs, 1972) and laboratory studies confirm that ingestion of conspecific larvae by adult *Pseudopolydora* does occur (Levin, unpublished data). The spatial pattern of new recruits among adults was not quantified, but appeared somewhat overdispersed. Large worms require more feeding space than new recruits. If competition is occurring between adults and new recruits, total densities (adults and post-larvae) are expected to be lower in treatments with adults than in treatments without them, and they were (p < 0.05, students *t* test). Unfortunately the available data do not permit separation of the effects of adult-larval competition from those of predation.

Invertebrate larvae, and polychaetes in particular, are known to be capable of complex settlement behavior and substrate selection (see Scheltema, 1974 for a general review of settlement behavior and Knight-Jones, 1951; D. P. Wilson, 1958; and Doyle, 1975 for examples of substrate selection in polychaetes). Settlement behavior may generate nonrandom spatial patterns. Aggregation often results from gregarious settlement. Microscale avoidance behavior during larval settlement has been reported for newly settled larvae of the barnacles *Eliminius modestus, Balanus balanoides* and *Balanus crenatus* (Crisp, 1961) and for the larvae of the polychaete *Spirorbis borealis* (Wisely, 1960). When these larvae settle they are initially attracted to conspecifics and subsequent physical contact is necessary to induce territorial behavior. This results in uniform dispersion that is attributable to avoidance behavior by the invading larva and not to any aggression by established individuals. Laboratory studies of larval recruitment in *Pseudopolydora* (Table 2) revealed a tendency (though not statistically significant) toward uniform spacing by new recruits in 4/6 experimental vials. *Pseudopolydora* larvae were attracted to initial recruits and settled a small distance away from them. This gave rise to somewhat even spacing within aggregations but resulted in either under or overdispersion in each experimental vial, depending upon the density of recruits.

Laboratory recruitment closely approximates settlement patterns in the field. Mean nearest-neighbor distances of new recruits were comparable in the laboratory ($r_{(mean)}$ = 1.88 mm ± 0.33 mm) and in settlement cartons on the mudflat ($r_{(mean)}$ =

1.90 mm ± 0.97 mm). Tube openings were more evenly spaced than tube bases for individuals recruited in the field over a 14 day period. The tubes were approximately 3 mm long and many of them were bent rather than vertical, suggesting that juveniles avoid their neighbors by bending or constructing their tubes away from one another. The nearest-neighbor distances of new recruits are too large for newly settled individuals to make contact with one another, so the initial tendency toward uniform spacing is probably generated by settlement behavior. However, nearest-neighbor distances at settlement are only one-half those observed among adults. Avoidance behavior and aggressive interaction among post-larvae, which widens spacing between tubes, must begin soon after settlement and continue through an individual's lifetime. The findings discussed above suggest that a combination of avoidance behavior during settlement, predation on larvae, and aggression in feeding and tube building, generate and maintain the characteristic dispersion of *Pseudopolydora*.

In contrast to *Pseudopolydora*, the dispersion of *Streblospio* does not depart from random, a result consistent with the apparently passive behavior of the species. *Streblospio* individuals are often found inhabiting burrows directly adjacent to conspecifics and contests between *Streblospio* individuals occur rarely. Interference with feeding activities and withdrawal into the tube is often caused by *Pseudopolydora* or other members of the community, never by other *Streblospio*. Passive behavior has also been observed in *Streblospio* from the Atlantic where the spionid *Spio setosa* has been observed to harass *Streblospio* by tearing its palps and pulling it from its tube (R. Whitlatch, personal communication). The shorter palps, the importance of the mouth in particle selection, and the absence of aggressive behavior in *Streblospio* suggest that feeding territories are not necessary to the population studied in Mission Bay.

Streblospio can occur at much higher densities than those reported for Mission Bay (e.g. 140,000/m² in Virginia; Virnstein, 1979). The spatial analysis in the present study suggests that both the behavior and dispersion of *Streblospio* may change as density increases. Only those *Streblospio* individuals in the highest density quadrat were significantly overdispersed (Table 1). Uniform spacing has been shown to become random at lowered densities in the fiddler crab *Uca* (Connell, 1963) and in the phoronid *Phoronopsis viridis* (Johnson, 1959), presumably due to a lack of intraspecific encounters. However, densities of *Streblospio* in Mission Bay are not so low that most individuals do not "see" each other. Thus observed dispersion patterns do not simply result from a low frequency of encounters.

In addition to feeding biology, other aspects of behavior contribute to differences in dispersion of the two spionid species. Both species are considered sessile tube dwellers, but *Streblospio* may be more mobile than *Pseudopolydora*. Adults of *Streblospio* have been collected in the estuarine water column over mud habitats at night (D. Dean, personal communication) and adult *Streblospio* will occasionally migrate into sediment trays placed on the intertidal mudflats in Mission Bay (Levin,

unpublished data). There is no evidence of such movement in *Pseudopolydora*. Thus the greater mobility of *Streblospio* may eliminate the need for maintaining feeding territories by allowing more flexibility in habitat selection.

Patterns of larval release and subsequent dispersal are known to influence dispersion (Reise, 1979). *Pseudopolydora* releases 3 setiger larvae which spend 7-10 days in the plankton before settling. *Streblospio* releases 9 setiger larvae which spend a few hours to a few days in the water column. Larvae of both species are initially photopositive and settle from the water column (Levin, unpublished data). This behavior acts to cancel any possible effects of different dispersal abilities on the small scale of dispersion (mm-cm) assessed in this study.

Territorial behavior reported here for *Pseudopolydora paucibranchiata* is the first report for any polychaete outside the family Nereidae. For space limited situations, territoriality, probably in combination with environmental heterogeneity, influences recruitment success and acts to regulate populations levels. *Pseudopolydora* belongs to a dense tube-building assemblage whose members probably experience severe space limitation. The important consequences of territoriality to the organization of *Pseudopolydora* populations suggest that interference competition may be of general importance in tubiculous infaunal communities.

6. Summary

1. Nearest-neighbor analysis of spionid polychaete spatial distribution on an intertidal mudflat revealed uniform dispersion in *Pseudopolydora paucibranchiata* and random dispersion in *Streblospio benedicti*.
2. Field and laboratory analysis of *Pseudopolydora* recruitment patterns indicate that uniform spacing is initiated during settlement and enhanced by subsequent interactions between post-larvae.
3. Adult competition or predation on settling or newly settled larvae may also contribute to the even dispersion of *Pseudopolydora*.
4. *Pseudopolydora* is more aggressive than *Streblospio* and will fight with neighboring conspecifics during feeding and tube building.
5. Both species are surface deposit and suspension feeders but differ in mechanisms of food particle selection. *Pseudopolydora* relies primarily on palps and *Streblospio* relies primarily on lips and mouth to select or reject particles.
6. Observations of feeding behavior and spatial patterns of adults and new recruits lead to the hypothesis that *Pseudopolydora* defends palp territories for the acquisition of food and tube building materials.
7. *Pseudopolydora* territories are maintained by strong intraspecific competition: such competition is not observed in *Streblospio*. Territoriality may serve to regulate population levels of *Pseudopolydora* within space-limited tube building assemblages.
8. This paper provides the first evidence for territoriality in a non-nereid polychaete.

REFERENCES

Blake, J. A. and K. H. Woodwick. 1975. Reproduction and larval development of *Pseudo-polydora paucibranchiata* (Okuda) and *Pseudopolydora kempi* (Southern) (Polychaeta: Spionidae). Biol. Bull., *148*, 109–127.

Breese, W. P. and F. D. Phibbs. 1972. Ingestion of bivalve molluscan larvae by the polychaete annelid *Polydora ligni*. Veliger, *14*, 274.

Carlton, J. T. 1975. Introduced intertidal invertebrates, *in* Light's Manual, R. I. Smith and J. T. Carlton, eds. Berkeley, U. of Calif. Press, 716 pp.

Clark, P. H. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial rela-tionships in populations. Ecology, *35*, 445–453.

Connell, J. H. 1956. Spatial distribution of two species of clams, *Mya arenaria* L. and *Petricola Pholadiformis* Lamarck, in an intertidal area. 8th Rep. Mass. Shellfish Invest. (Contribution 876. Woods Hole Oceanographic Inst.).

—— 1963. Territorial behavior and dispersion in some marine invertebrates. Res. Popul. Ecol., *V*, 87–101.

Crisp, D. J. 1961. Territorial behavior in barnacle settlement, J. Exp. Biol., *38*, 429–446.

Daro, M. H. and P. Polk. 1973. The autecology of *Polydora cilliata* along the Belgian coast. Neth. J. Sea Res., *6*, 130–140.

Doyle, R. W. 1975. Settlement of planktonic larvae: A theory of habitat selection in varying environments. American Naturalist, *109*, 113–126.

Ekman, J. E. 1979. Small-scale patterns and processes in a soft substratum, intertidal com-munity. J. Mar. Res., *37*, 437–457.

Holme, N. A. 1950. Population dispersion in *Tellina tenuis* da Costa. J. Mar. Biol. Assoc. U.K., *29*, 267–280.

Johnson, R. G. 1959. Spatial distribution of *Phoronopsis viridis* Hilton. Science, *129*, 1221.

Jumars, P. A. 1978. Spatial autocorrelation with RUM (Remote Underwater Manipulator): vertical and horizontal structure of a bathyal benthic community. Deep Sea Res., *25*, 589–604.

Jumars, P. A., D. Thistle, and M. L. Jones. 1977. Detecting 2-D spatial structure in biological data. Oecologia, *28*, 109–123.

Knight-Jones, W. E. 1951. Gregariousness and some other aspects of the settling behavior of *Spirorbis*. J. Mar. Biol. Assoc. U.K., *30*, 201–222.

Levinton, J. 1972. Spatial distribution of *Nucula proxima* Say (Protobranchia): an experimental approach. Biol. Bull., *143*, 175–183.

Pielou, E. 1977. Mathematical Ecology. New York, John Wiley and Sons, 385 pp.

Reise, K. 1979. Spatial configurations generated by mobile benthic polychaetes. Helgolander wiss. Meeresunters, *32*, 55–72.

Reish, D. J. and M. C. Alosi. 1968. Aggressive behavior in the polychaetous annelid family Nereidae. Bull. So. Calif. Acad. Sci., *6*, 21–28.

Richardson, C. A., P. Dustan and J. C. Lang. 1979. Maintenance of living space by sweeper tentacles of *Montastrea cavernosa*, a Caribbean Reef Coral. Mar. Bio., *55*, 181–186.

Roe, P. 1975. Aspects of life history and of territorial behavior in young individuals of *Platynereis bicaniculata* and *Nereis vexillosa* (Annelida, Polychaeta). Pac. Sci., *29*, 341–348.

Rosenberg, R. 1974. Spatial dispersion of an estuarine benthic faunal community. J. Exp. Mar. Biol. Ecol., *15*, 69–80.

Scheltema, R. S. 1974. Biological interactions determining larval settlement of marine invertebrates. Thallassia Jugoslavica, *10-1/2*, 263–296.

Simberloff, D. 1979. Nearest neighbor assessments of spatial configurations of circles rather than points. Ecology, *60*, 679–685.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. San Francisco, W. H. Freeman & Co., 776 pp.

Virnstein, R. W. 1979. Predation on estuarine infauna: response patterns of component species. Estuaries, *2*, 69–86.

Weinberg, J. R. 1979. Ecological determinants of spionid distributions within dense patches of deposit feeding polychaete *Axiothella rubroicincta*. Mar. Ecol. Progr. Ser., *1*, 301–314.

Whitlatch, R. B. 1976. Seasonality, species diversity and patterns of resource utilization in a deposit feeding community. Ph.D. thesis, University of Chicago.

Wilson, D. P. 1958. Some problems in larval ecology related to the localized distribution of bottom animals, *in* Perspectives in Marine Biology, A. A. Buzzati-Traverso, ed., Berkeley, U. of Calif. Press, 621 pp.

Wisely, H. B. 1960. Observations on the settling behavior of larvae of the tubeworm *Spirorbis borealis* Daudin (Polychaeta). Aust. J. Mar. Freshw. Res., *2*, 55–72.

Woodin, S. A. and J. B. C. Jackson. 1979. Interphyletic competition among marine benthos. Amer. Zool., *19*, 1029–1043.