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Spatial niches and long-term performance in meiobenthic Plathelminthes of an intertidal lugworm flat

Karsten Reise

Biologische Anstalt Helgoland, Litoralstation, D-2282 List, Federal Republic of Germany

ABSTRACT: A spatio-temporal study over 7 yr and 26 microsites revealed a significant correlation between interannual variability and the location, size and shape of spatial niches for 56 plathelminth (turbellarian) populations in a sandy, marine sediment. Each June, microsites of the surface layer, of the sulfide layer, of vertical shafts, and of coarse sand at feeding pockets of lugworm burrows were investigated on a sand flat in the lower tidal zone near the island of Sylt (North Sea). Microsite preferences were consistent over time. Populations distributed over a wide range of microsites tended to persist longer than populations confined to narrow spatial niches. The latter fluctuated more in population density than those scattered over several sites. Surface-dwelling species were more variable over time than species characteristic of the sulfide layer. Two species deviated from this pattern. They were restricted to pocket sand and yet their population size remained almost constant over the years. They may be microsite specialists. Apparently, meiobenthic plathelminths perceive the sediment as a dinstinctly structured habitat, and species of the sediment surface differ in their adaptive traits from species living in the sulfide layer.

INTRODUCTION

In marine benthic ecology, long-term population cycles and trends have been viewed in the perspective of environmental causation. Various proximate causes such as temperature (Ziegelmeier 1978), salinity (Heip & Herman 1985), oxygen (Rachor 1980), and food supply (Buchanan & Moore 1986) have been singled out, and ultimate causes such as human impact (Blegvad 1928, 1951) or astronomical periodicities (Gray & Christie 1983), and a switching from atmospheric 'white noise' to oceanic 'red noise' (Steele & Henderson 1984, Steele 1985) have been discussed.

This study makes and attempt to relate long-term performance in a multi-species plathelminth assembly to the differential use of habitat structures. I explore to what extent the size, shape and location of spatial niches affect local persistence and interannual variation of population size. The term 'spatial niche' describes within-habitat distribution, and corresponds to the range over which the organism gathers its food (trivial range in the sense of Southwood 1977), where it hides and reproduces. Following Connell & Sousa (1983), persistence is used as a qualitative term, indicating the time span a population has been present in the area. Variation in population size is described by the ratio of the standard deviation to the long-term mean.

It is shown in this investigation that spatial niches have implications on the persistence and the amplitude of population fluctuations. Spatial niches mirror to some extent the adaptive attributes of a species, and may serve to predict temporal perfomance within the limits set by the external forcing functions which cause the actual changes in population size.

Free-living Plathelminthes (Turbellaria) constitute from 7 to 25 % of total meiofauna in marine sand, and in species richness they rival the diverse nematodes (Martens & Schockaert 1986). Body sizes are in the upper range of meiofauna. Development is direct and holobenthic. Most species have a univoltine life cycle, i.e. one generation per year (Ax 1977). On a sandy tidal flat near the island of Sylt in the North Sea, I analyzed on a 10 × 10 m plot species composition, size spectra, abundance, diversity and spatial partitioning in a plathelminth assembly (Reise 1984). Microsites alongside burrows of the lugworm *Arenicola marina* (L.) play a prominent role in most patterns. Seasonal variation of

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plathelminths associated with lugworm burrows is described by Scherer (1985). During summer abundance is high, in winter it is very low.

The present paper reports on the interannual performance of populations on this sand flat. Over a period of 7 yr, each summer (June) 26 microsites were sampled. It is asked whether spatial patterns are consistent over time, and whether attributes of spatial niches are correlated with local persistence and variability of population size.

METHODS

Study site. The sand flat is located in the Wadden Sea near the island of Sylt. Exposure is about 2 h per semi-lunar tidal cycle. The sediment remains water-saturated throughout, and patches of residual waters cover the surface until the tide returns. Temperatures range from −1 °C (1 to 2 mo with ice cover) to +32 °C in low tide puddles. Average water temperature in June is 15.5 °C. Average salinity is 29 ‰, with a range from 26 to 31.

Sand particles have a median of 0.5 mm (phi = 1.14). Weight loss (organic matter) of sediment on combustion at 600 °C is 0.44 %. In June, the surface of this sheltered flat is rarely rippled. Surface morphology is dominated by funnels and fecal mounds of the lugworm *Arenicola marina* (30 to 60 burrows m^{-2}). Burrows are U-shaped and irrigated through tail shafts (Fig. 1). The feeding pocket at the base of the head shaft is enveloped by coarse-grained sediment. This is not recycled by the lugworms and therefore accumulates at this depth. For more details of burrows see Baumfalk (1979), Rijken (1979) and Reise (1984).

Sampling. During low tide, sediment cores were obtained with a transparent tube of 2 cm^2 cross-sectional area. Cores were taken from normal sediment and from lugworm burrows as shown in Fig. 1. Pocket sand and galleries were sampled by digging up burrows with a spade. Altogether, 26 microsites were sampled 10 times each June from 1980 to 1986 (in 1985 only 5 replicates of vertical cores were taken). This amounts to 2 $cm^3 \times 26 \times 10 = 520$ cm^3 of sediment each June, searched for free-living Plathelminthes directly without applying sieves or narcotics. Collection of living specimens is essential for identification. Therefore, sampling was spread over 3 wk each June to keep storage time < 3 d. All vertical cores were taken from a 10 × 10 m plot, and the digging for pocket sand and galleries was done in the immediate surroundings.

Data analysis. Microsites generated by lugworms are over-represented in the sampling design. No factor of burrow abundance is used to recalculate this distortion, because there are many other biogenic structures with similar effects on meiofauna (Reise 1981a, b, 1983). These were not sampled in this survey, and they would have considerably strengthened the effects of lugworms.

Populations were not randomly scattered over the 26 microsites but showed various degrees of site selectivity. If this selectivity was recurrent and was not shifted to other sites every year, then the pattern of the pooled

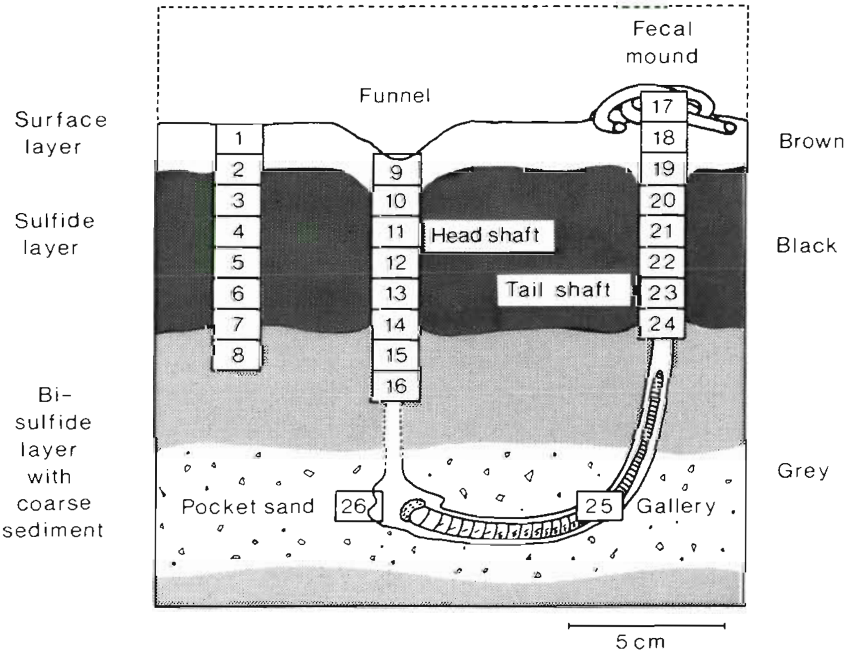

Fig. 1. *Arenicola marina* in its burrow in sandy sediment. Positions of samples (2 cm^3) are numbered: normal sediment, 1 to 8; head shaft, 9 to 16; tail shaft, 17 to 24; gallery, 25; pocket sand, 26

data (7 yr) will be aggregated. This may be measured with an index of patchiness (Lloyd 1967):

$$\frac{\dot{x}}{\bar{x}} = 1 + \frac{1}{\bar{x}}\left(\frac{s^2}{\bar{x}} - 1\right) \qquad (1)$$

Average density ($\bar{x}$) and variance (s^2) is calculated over all 26 microsites, where x_i = number of all individuals per site found in 7 yr. A ratio $\dot{x}/\bar{x} > 1$ suggests crowding. By introducing an appropriate chi-square (with $n = 26$ and $p = 0.05$, $\chi^2 = 37.65$) a ratio

$$\frac{\dot{x}}{\bar{x}} = 1 + \frac{1}{\bar{x}}\left(\frac{\chi^2}{n-1} - 1\right) \qquad (2)$$

is obtained which marks significant deviations from a random scatter of individuals. This procedure takes into account the numerical dependence of s on $\bar{x}$.

Recurrent preference in a species for the same sites can also be measured by comparing the locations of the top ranks of abundance over the 26 microsites and 7 yr. Only species with ≥ 3 individuals in at least 5 out of 7 yr are considered, and an index of constancy (C) of site selection is calculated for each species. First, microsites with the 3 highest densities are ranked from 3 to 1 in each year. Years with <3 individuals are excluded. Second, all possible rank differences (D) between years are calculated. With $n = 7$, 6 and 5 yr there are $\frac{n}{2}(n-1) = 21$, 15 and 10 rank differences, respectively. Third, ΣD is calculated for each species. With 3 ranks, max $\Sigma D = 12\,\frac{n}{2}(n-1)$. The predictability of microsite selection by a species may then be measured with an index of consistency written as

$$C = 1 - \frac{\Sigma D}{6\,n\,(n-1)} \;. \qquad (3)$$

In the case of identical rank locations between years, $C = 1$. If annual patterns are independent and the number of possible locations is infinite, then $C = 0$. With 26 locations, C remains <0.1 in random allocations.

Annual population size (x) is estimated by counting all individuals found at 10 × 26 microsites in June. Variation of population size over the 7 yr period is expressed as $CV = s/\bar{x}$. To emphasize small values of population size, the coefficient of variation is also calculated from $\log_{10}$ transformed data. Connell & Sousa (1983) simply used s of the $\log_{10}$ of population size to measure temporal variability. Although this parameter was highly correlated with CV, it was neither correlated with persistence nor with measures of spatial niches in the present data set. Presumably, s becomes unsuitable as an index when population sizes range over 3 orders of magnitude.

Three aspects of spatial niches are considered: size, shape and location. Size is expressed as the number of microsites occupied by a population in the course of 7 yr, ranging from 1 to 26. Shape is here characterized with Levin's measure of niche breadth, $B = (n\Sigma p_i^2)^{-1}$, where p_i gives the proportion of individuals at microsites $i = 1,2,3,\ldots,26 = n$. More elaborate descriptions of the distribution of individuals over resources by weighting techniques is pleasing in theory but the actual results remain the same (Reise 1984). Three comprehensive locations of spatial niches are differentiated: surface layer (0 to 1 cm), subsurface (1 to 8 cm), pocket sand and gallery (< 12 cm depth). A species is assigned to one of these categories when > 50 % of individuals were found within it. A case with < 50 % in all 3 categories did not occur.

Average properties of groups, such as CV and spatial niche size, are compared with Student $\hat{t}$-test. No assumption on the equality of variances is made, thus $\hat{t}$ and the degrees of freedom are calculated according to formulas given in Sachs (1984, p. 212). Correlation analysis is confined to conservative linear regressions. Throughout the paper, ns denotes not significant ($p>0.05$), $\cdot p<0.05$, $\cdot\cdot p<0.01$, and $\cdot\cdot\cdot p<0.001$.

RESULTS

Spatio-temporal patterns of populations

None of the plathelminth populations was evenly or randomly distributed over the 26 microsites. All tended to aggregate at certain locations, and thus to perceive the sediment as a heterogeneous habitat. Lloyd's index of patchiness indicates in every population significant ($p < 0.001$) deviation from random distribution (Table 1).

Three populations (*Gyratricella attemsi, Mariplanella frisia, Typhlopolycystis rubra*, Fig. 2) were almost confined to pocket sand and thus showed the highest degree of patchiness. Other populations gave a clear preference to pocket sand but were also widely distributed throughout the sulfide layer and alongside vertical shafts of lugworm burrows (i.e. *Polystyliphora filum* in Fig. 2). Thus, there was a large scatter around average patchiness in the group of pocket sand species (13.13 ± 9.57, n=9). There were no populations which occured both in pocket sand and in the surface layer.

Species with a clear preference for the surface also exhibited high ratios of patchiness (9.46 ± 2.78, n=15) since there were only 3 microsites positioned in the upper 1 cm of sediment (*Provortex tubiferus* and *Promesostoma rostratum* in Fig. 2). These species were significantly more patchy than populations living in the sulfide layer and alongside vertical burrow shafts (2.85 ± 1.60, n=6).

Table 1. Average density (D; ind 100 cm^{-3}), patchiness ($\dot{x}/\bar{x}$), and temporal consistency (C) in microsite preference for 31 populations found in at least 5 out of 7 yr with ≥ 3 individuals. The term 'boundary' refers to the transition zone between surface and sulfide layer

Species	D	$\dot{x}/\bar{x}$	C	Preferred microsites
Philomecynostomum lapillum	3.2	6.5	0.49	Surface layer
Promesostoma rostratum	12.0	9.7	0.68	Surface layer
Promesostoma marmoratum	6.5	10.6	0.68	Surface layer
Cicerina brevicirrus	3.0	7.0	0.66	Surface layer
Cheliplanilla caudata	2.8	7.0	0.49	Surface layer
Pseudaphanostoma pelophilum	2.6	8.3	0.61	Surface layer except funnel
Pseudograffilla arenicola	1.3	13.4	0.77	Surface layer except funnel
Zonorhynchus seminascatus	2.4	9.3	0.69	Surface layer except funnel
Postmecynostomum pictum	68.2	13.3	0.62	Surface layer except mound
Macrostomum pusillum	8.4	12.3	0.67	Surface layer except mound
Microstomum papillosum	5.9	9.0	0.79	Surface layer except mound
Provortex tubiferus	14.0	12.8	0.80	Surface layer except mound
Pogaina suecica	11.1	10.2	0.85	Surface layer except mound
Bresslauilla relicta	2.6	3.6	0.60	Surface layer except mound
Aphanostoma album	7.2	8.9	0.64	Funnel and mound
Monocelididae (4 spp.)	34.1	3.4	0.47	Upper head and tail shaft
Paedomecynostomum bruneum	3.5	2.7	0.50	Boundary and tail shaft
Neoschizorhynchus parvorostro	10.9	1.5	0.35	Boundary and tail shaft
Drepanilla sp. 1	2.0	3.1	0.47	Boundary and tail shaft
Carenscoilia sp. 1	4.0	2.0	0.45	Boundary and lower tail shaft
Convoluella brunea	7.2	1.9	0.29	Boundary and lower burrow
Retronectes sp. 1	1.4	5.9	0.52	Lower tail shaft
Haplopharynx rostratus	4.8	3.7	0.48	Pocket sand and gallery
Coelogynopora tenuis	3.2	3.0	0.29	Pocket sand
Carenscoilia biforamen	2.2	8.9	0.62	Pocket sand
Polystyliphora filum	7.8	8.6	0.67	Pocket sand
Mariplanella frisia	8.1	25.1	0.91	Pocket sand
Balgetia semicirculifera	2.6	12.0	0.61	Pocket sand
Schizorhynchoides spirostylus	2.2	6.0	0.61	Pocket sand
Typhlopolycystis rubra	12.6	24.2	0.98	Pocket sand
Gyratricella attemsi	2.1	26.7	1.00	Pocket sand

Some populations of the surface layer did not seem to differentiate between normal sediment, funnels and fecal mounds (i.e. genus *Promesostoma* with 6 spp.) when all years are taken together. However, at certain times, significant differences in abundance between these microsites did occur (Fig. 2). Some other populations consistently avoided fecal mounds (i.e. *Pogaina suecica*) or funnels (i.e. *Pseudograffilla arenicola*). Four species of the Monocelididae (*Archilopsis unipunctata, A. inopinata, Archiloa petiti, Promonotus schultzei*; it was not possible to tell the juvenile individuals apart) lived in the surface layer and were also spread over vertical burrow shafts. They were grouped neither into surface species nor into sulfide layer species.

The lowest ratio of patchiness was attained by *Neoschizorhynchus parvorostro* (Table 1, Fig. 2). In the course of 7 yr it was found at all sites, but was most common in the upper sulfide layer and alongside tail shafts of lugworm burrows. The vicinity of oxic tail shafts was attractive also to the other populations dwelling in the sulfide layer, while head shafts were less preferred.

There was a strong positive correlation between the degree of patchiness and the consistency of microsite selection throughout the period ($r=+0.875$•••). This is to be expected because of the way both parameters are calculated. The ratio of patchiness is derived from the combined pattern of all years. A population with a low consistency of microsite selection will be spread over several microsites which causes the ratio of patchiness to become low. Conversely, similar site selection in every year enhances the degree of patchiness.

Table 1 includes only those populations ($n=31$) which were present in at least 5 out of 7 yr with 3 or more individuals. The average degree of consistency is 0.62 ± 0.18. A respective number of random site allocations yields a much lower value (0.08 ± 0.04; $\neq 0$ because of rank overlap by chance). Corresponding to patchiness, consistency is significantly lower in species preferring the sulfide layer (0.43 ± 0.09) than in surface dwellers (0.67 ± 0.10), and also compared to species of pocket sand (0.69 ± 0.24). Neither the degree of patchiness nor the consistency is correlated with average population density.

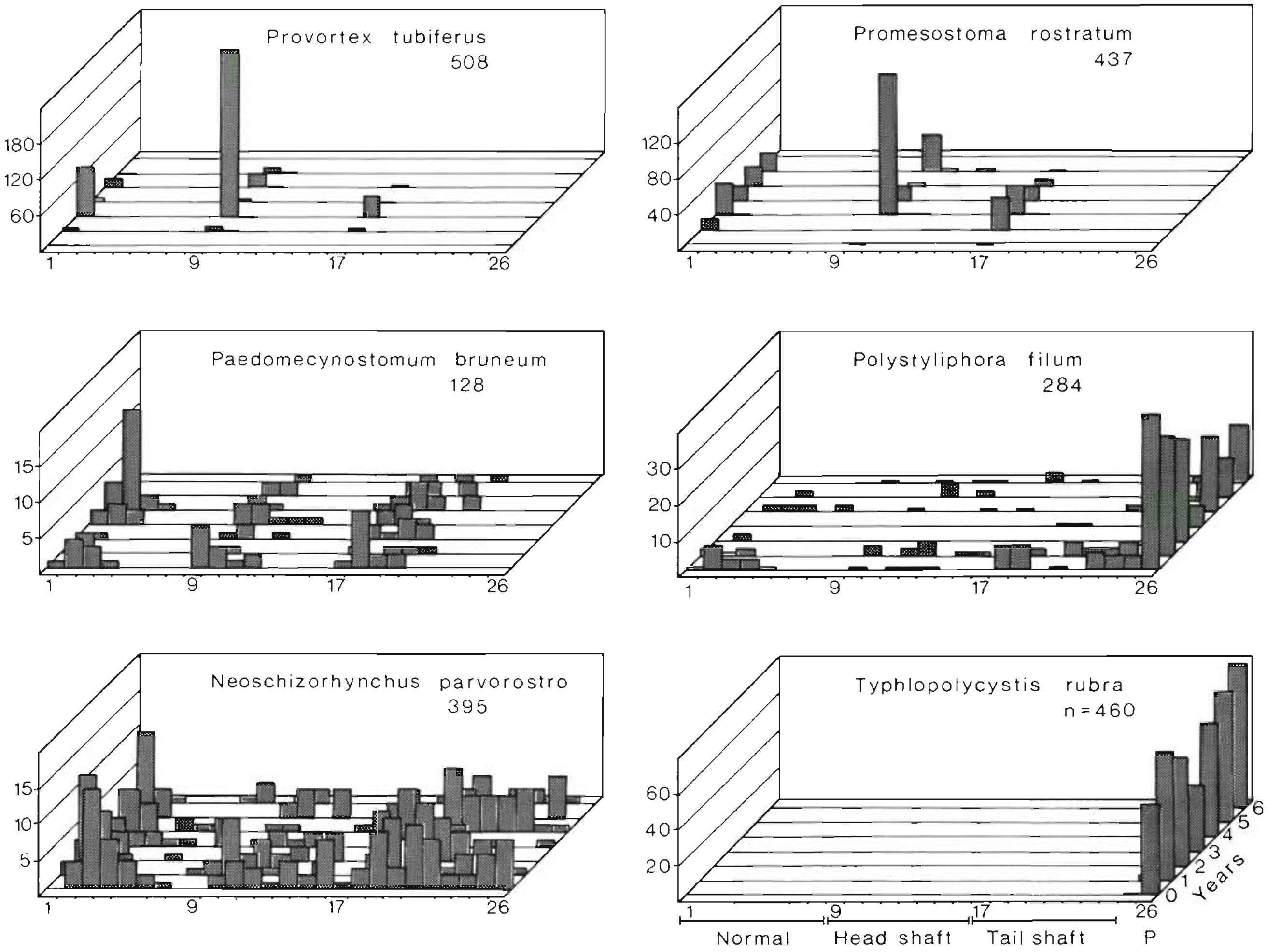

Fig. 2. Spatio-temporal patterns of plathelminth populations (ind $20cm^{-3}$) over 26 microsites (coding see Fig. 1) and 7 yr (June 1980 to June 1986). P: pocket sand; n: total number of individuals

Persistence of populations

The measure of persistence is based on the presence-absence record of species found per survey in June from 1980 to 1986. In spite of trivial correlations of persistence with population size and variability, it is shown that spatial niches have implications on the number of years a species was encountered in the area.

A total of 56 populations is considered (Table 2). These were found with ≥ 7 individuals in the entire survey. Present in all or all but one years were 33 populations. Large populations tended to persist longer than small populations ($r = +0.748$••• for log x in Table 2). None of the populations with ≤ 1.5 individuals $100\,cm^{-3}$ was able to persist over all 7 yr. Conversely, all populations with >2 individuals $100cm^{-3}$ were present in ≥ 5 yr. Populations with low interannual variability tended to persist longer than populations with strong fluctuations ($r = -0.950$••• for CV_{log}). This correlation is to be expected since persistence is a qualitative property of CV.

Ecologically more interesting are the positive correlations of persistence with size (NS) and shape (NB) of spatial niches. NS and NB are strongly interrelated ($r = +0.715$•••). Populations distributed over a wide range of microsites tended to persist longer than populations confined to narrow spatial niches ($r = +0.577$•••). The same is true for populations distributed more evenly over the microsites compared to highly aggregated populations ($r = +0.343$•••). Since persistence is correlated with population size, and population size is correlated with NS ($r = +0.362$•••), the correlation between persistence and NS is partially explained by covarying population size. On the other hand, NB shows no correlation with population size ($r = +0.084$ ns) but has significant effects on persist-

Table 2. Population size ($\bar{x}$; ind $520\,cm^{-3}$ in 26 microsites averaged over 7 yr), number of yr (1 to 7) present, coefficient of interannual variation (CV), spatial niche size (NS) expressed as number of microsites (1 to 26) occupied, spatial niche shape (NB) expressed by Levin's measure of niche breadth, location (L) where $\geq 50\,\%$ of individuals were found (1 = surface layer of 0 to 1 cm; 2 = sulfide layer including vertical burrow shafts; 3 = pocket sand and gallery), and trophic group (TG with A = algivores, B = bacterivores, C = carnivores). Populations with < 7 individuals in the entire survey are not included. Species are arranged according to decreasing CV

Species	$\bar{x}$	Yr	CV	CV_{log}	NS	NB	L	TG
Pseudmecynostomum papillosum Faubel 1974	1.00	1	2.65	2.65	3	0.09	1	A
Achoerus pachycaudatus Dörjes 1968	1.00	1	2.65	2.65	2	0.05	1	A
Proxenetes ampullatus Ax 1971	1.71	1	2.65	2.65	4	0.07	1	C
Promesostoma meixneri Ax 1951	3.14	3	2.24	1.62	3	0.10	1	C
Provortex tubiferus Luther 1948	72.57	6	2.03	0.73	5	0.08	1	A
Promesostoma gracilis Ax 1951	5.29	6	1.98	0.92	3	0.08	1	C
Aphanostoma album Dörjes 1968	37.57	5	1.94	0.91	8	0.12	1	A
Promesostoma karlingi Ehlers 1974	1.86	2	1.88	1.74	3	0.12	1	C
Pogaina suecica (Luther 1948)	57.71	6	1.82	0.66	9	0.10	1	A
Proschizorhynchus helgolandicus L'Hardy 1965	1.00	2	1.73	1.71	1	0.04	3	C
Halammovortex macropharynx (Meixner 1938)	8.00	3	1.72	1.33	10	0.12	1	C
Oligophilomorpha interstitiophilum Faubel 1974	1.86	2	1.71	1.71	6	0.16	2	B
Postmecynostomum pictum Dörjes 1968	354.29	7	1.68	0.39	17	0.08	1	A
Philosyrtis cf. *fennica* Ax 1954	3.43	3	1.63	1.33	3	0.08	3	C
Nigerrhynchus opisthoporus Schilke 1970	1.14	3	1.63	1.40	2	0.05	3	C
Macrostomum pusillum Ax 1951	43.86	6	1.55	0.74	6	0.08	1	A
Promesostoma marmoratum (M. Schulze 1851)	22.86	6	1.53	0.52	7	0.10	1	C
Anaperus tvaerminnensis (Luther 1912)	2.00	4	1.44	1.10	4	0.13	1	C
Solenophilomorphidae sp. 1	1.71	3	1.42	1.30	6	0.17	2	B
Promesostoma caligulatum Ax 1952	2.71	4	1.42	1.13	3	0.07	1	C
Pogaina kinnei Ax 1970	3.43	3	1.39	1.29	4	0.09	1	A
Gyratricella attemsi (Graff 1913)	10.71	5	1.38	0.86	1	0.04	3	C
Proxenetes quinquespinosus Den Hartog 1966	3.71	4	1.37	1.04	7	0.12	1	C
Placorhynchus octaculeatus Karling 1947	3.57	6	1.36	0.76	5	0.14	1	C
Microstomum papillosum Graff 1882	30.57	7	1.36	0.61	5	0.11	1	A
Convoluella brunea Faubel 1974	34.43	6	1.31	0.60	20	0.50	2	B
Pseudaphanostoma pelophilum Dörjes 1978	13.29	6	1.31	0.65	7	0.12	1	A
Archimonotresis limophila Meixner 1938	7.00	6	1.20	0.65	7	0.11	1	A
Carenscoilia biforamen Sopott 1972	11.57	6	1.19	0.61	17	0.11	3	C
Proxenetes quadrispinosus Den Hartog 1966	1.29	4	1.16	1.02	4	0.09	1	C
Proschizorhynchus bivaginatus Schilke 1970	1.29	3	1.16	1.02	5	0.11	3	C
Pseudostomum quadrioculatum (Leuck. 1847)	2.14	4	1.16	1.01	6	0.11	1	A
Proxenetes segmentatus Den Hartog 1966	1.86	4	1.14	1.03	6	0.08	1	C
Promesostoma rostratum Ax 1951	42.57	6	1.11	0.59	9	0.11	1	C
Mariplanella frisia Ax & Heller 1970	42.00	7	1.02	0.26	2	0.04	3	C
Paromalostomum dubium (De Beauchamp 1927)	8.71	7	1.00	0.56	9	0.17	1	C
Zonorhynchus seminascatus Karling 1956	12.71	7	0.95	0.47	10	0.11	1	C
Pseudograffilla arenicola Meixner 1938	6.86	6	0.93	0.62	3	0.07	1	C
Balgetia semicirculifera Karling 1962	13.57	7	0.92	0.30	17	0.08	3	B
Acrorhynchides robustus Karling 1931	1.57	5	0.89	0.76	5	0.13	1	C
Retronectes sp. 1	8.57	7	0.88	0.47	11	0.16	2	B
Carenscoilia sp. 1	21.00	7	0.86	0.21	21	0.46	2	C
Cheliplana remanei (Meixner 1928)	2.29	6	0.86	0.61	3	0.10	1	C
Cheliplanilla caudata Meixner 1938	14.71	7	0.78	0.39	9	0.14	1	C
Drepanilla sp. 1	10.57	6	0.77	0.59	12	0.30	2	B
Paedomecynostomum bruneum Dörjes 1968	18.29	7	0.68	0.26	15	0.36	2	B
Philomecynostomum lapillum Dörjes 1968	16.71	7	0.66	0.27	9	0.15	1	B
Polystyliphora filum Ax 1958	40.57	7	0.66	0.20	22	0.12	3	C
Schizorhynchoides spirostylus Boaden 1963	11.43	7	0.65	0.28	19	0.16	3	C
Cicerina brevicirrus Meixner 1928	15.71	7	0.64	0.27	8	0.14	1	C
Coelogynopora tenuis Meixner 1938	16.71	7	0.62	0.19	23	0.32	2	C
Monocelididae (4 spp.)	177.14	7	0.53	0.08	23	0.30	2	C
Neoschizorhynchus parvorostro Ax & Heller 1970	56.43	7	0.46	0.12	26	0.68	2	B
Haplopharynx rostratus Meixner 1938	25.43	7	0.41	0.16	21	0.14	2	C
Bresslauilla relicta Reisinger 1929	13.29	7	0.37	0.14	15	0.27	2	B
Typhlopolycystis rubra Noldt & Reise 1987	65.71	7	0.24	0.06	3	0.04	3	C

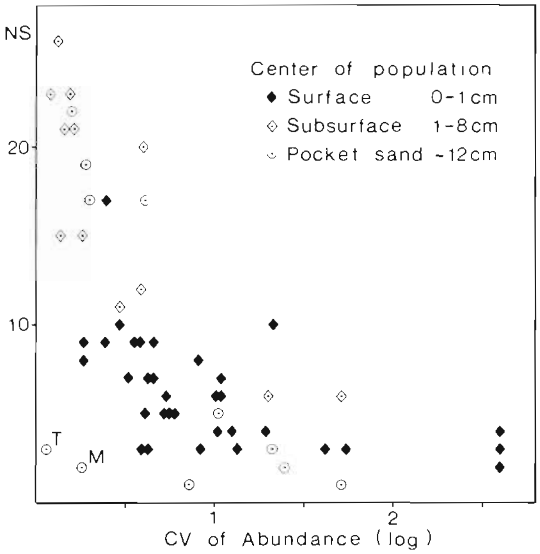

Fig. 3. Coefficient of interannual variation (CV of log abundance) versus spatial niche size (NS: number of microsites occupied) for 56 plathelminth populations on a lugworm flat. T: *Typhlopolycystis rubra*; M: *Mariplanella frisia*

Table 3. Correlations between interannual coefficients of variation (CV_{log}) and the size and shape of spatial niches in plathelminth populations living on a lugworm flat. For categories of location and trophic group see Table 2

Correlation coefficient r	Spatial niche	
	Size	Shape
All populations (n = 56)	-0.594^{***}	-0.377^{**}
Surface layer (33)	-0.530^{**}	-0.464^{**}
Sulfide layer (12)	-0.815^{**}	−0.424 ns
Pocket sand (11)	−0.562 ns	−0.303 ns
Carnivores (35)	-0.571^{***}	-0.431^{*}
Bacterivores (10)	-0.670^{*}	−0.346 ns
Algivores (11)	−0.554 ns	−0.137 ns

ence. This indicates that there is indeed a spatial component involved in the persistence of plathelminth populations. Significant location effects on persistence do not show up in the data.

Long-term variation of population size

Coefficients of variation (CV) for population size over 7 yr range from 0.24 in *Thyphlopolycystis rubra* to 2.65 in 3 species which showed up only once (Table 2). In the following some correlates with this range of variability are explored, and it is shown that size and location of spatial niches have strong implications on the temporal performance of populations (Fig. 3).

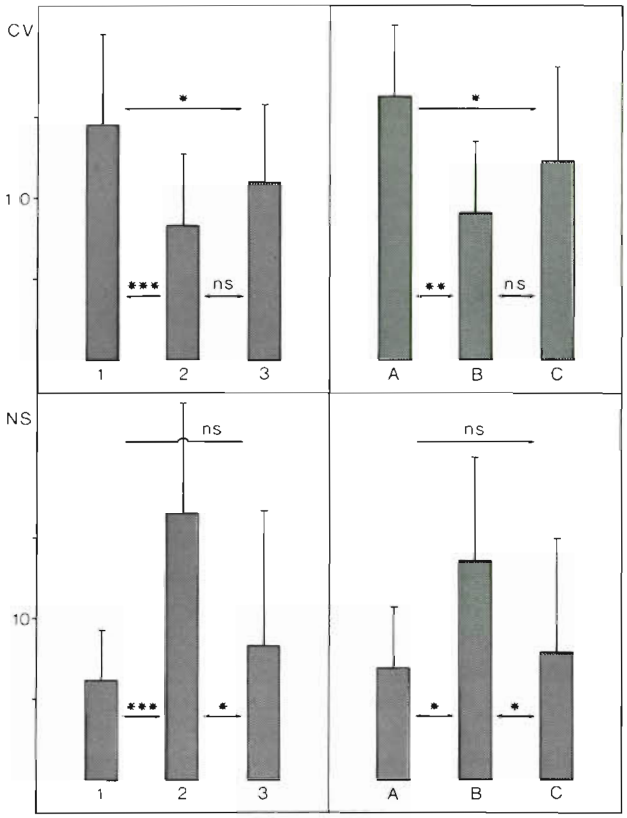

Fig. 4. Coefficient of interannual variation (CV of abundance) and spatial niche size (NS) for location groups (1,2,3) and trophic groups (A,B,C), both defined in Table 2. Vertical lines give upper range of standard deviation

There is also an effect of population size on CV_{log} ($r = -0.31^{*}$). Large populations tended to fluctuate less than small ones. This trend may be an artifact because sampling errors become aggravated at low population densities. Ecologically more relevant correlates of CV are summarized in Table 3 and Fig. 4. Generally, populations with wide spatial niches tended to fluctuate less than populations with narrow spatial niches (Fig. 3). There are no populations which combined a wide spatial niche with a high interannual variability. However, there are 2 populations (T and M in Fig. 3) with narrow spatial niches and a remarkably low variability. Both were restricted to pocket sand.

Due to sampling design, spatial niche size (NS) and location (L) are not independent variables. Only 3 microsites were located in the surface layer and 2 in pocket sand and gallery, while there were 21 in the sulfide layer. Thus, populations preferring the latter location had most microsites at their disposal. The fact that there are significant correlations between CV and NS within location groups (Table 3) suggests an independent effect of NS. However, in surface-layer populations a wide spatial niche is equivalent to its expansion into the subsurface region (Location 2). No such locational explanation can be offered for the correlation of CV with NS within the group of populations from the sulfide layer. At least here is an effect of NS independent from L. The significantly lower CV in sulfide-layer populations compared to surface-layer populations may be an effect of L or a corollary of NS (Fig. 4). Populations of pocket sand are a heterogeneous group. Seven lived almost exclusively in pocket sand and the gallery, while 4 were also scattered over various microsites in the sulfide layer (see *Typhlopolycystis rubra* and *Polystyliphora filum* in Fig. 2).

Feeding groups differ significantly in average CV (Fig. 4). Underlying this relation may be the effects of spatial niche size and location. Bacterivores have the lowest average CV, the largest average NS, and all but 2 populations prefered the sulfide layer. Algivores are the most variable, have narrow spatial niches, and all dwelled in the surface layer. Carnivores are intermediate in CV and NS. Among them there are 21 populations giving preference to the surface layer, 4 to the sulfide layer, and 10 to pocket sand. Within carnivores, surface dwellers fluctuated significantly more (CV = 1.41 ± 0.58) than those living deeper in the sediment (0.98 ± 0.49). Again, average NS is smaller in surface dwellers (5.57 ± 2.69) than in the others (11.64 ± 9.72). This is not significant because not all populations of pocket sand show effects of NS on CV (see T and M in Fig. 3).

The shape of spatial niches generally shows the same trends as their size, however, the level of significance is usually lower (Table 3).

DISCUSSION

Scale and distribution of observations

The results suggest that an understanding of spatial patterns sheds light on the temporal performance of populations. However, conclusions are necessarily biased by the chosen scale, and the distribution of observations in space and time. A survey which includes several independently fluctuating subpopulations is likely to reveal a higher degree of persistence and a lower variability of population size than a survey confined to a point in space, where even random movements of individuals appear to be immigrations and extinctions.

In the present survey a sampling area of 10 × 10 m was chosen, an arbitrary subunit of a lugworm flat of approximately 0.3 km^2. The choice of 100 m^2 represents a compromise. A larger area would have included gradients in tidal exposure, current regimes and sediment properties. A smaller area would have increased the problem of sampling effects on the phenomena under study.

Random distribution of plathelminth individuals is apparent when parallel samples are taken from a 1 m^2 area, while patchiness prevails at the scale of 100 m^2 (Reise 1984, Fig. 17). This patchiness increases the probability of sampling errors. As a consequence, temporal variation of population density will be overestimated, and persistence may be underestimated.

Relative to the organisms concerned, the plot of 100 m^2 seems to be sufficiently large to maintain populations. To cross the area, a plathelminth has to cover a distance of 10 000 times its own body length (1 mm on average). Plathelminthes on this sand flat have a direct, holobenthic development, and all life stages have been encountered. Thus, I assume that the area is potentially large enough to allow for recruitment, growth and survival of the resident populations.

Sampling occurred at annual intervals. This made sure that different generations were sampled each time. At the island of Sylt, Plathelminthes show pronounced seasonality in population size, and often a close correspondence to the annual temperature cycle has been noted (Ehlers 1973, Sopott 1973, Hoxhold 1974, Faubel 1976). Differences between years related to temperature may cause temporal shifts in population dynamics. Even if the population size remains the same between years, sampling at a fixed time interval will suggest apparent differences in abundance. Although 3 wk elapsed between the first and the last sample taken, this may overestimate interannual variability.

Thus, because of spatial patchiness and short-term shifts of annual dynamics in abundance, the given estimates of population persistence represent minimum values, and the variation in population size is probably exaggerated. Following these considerations, the 16 populations with a persistence of 7 yr and a coefficient of variation <1 consistute examples of remarkable constancy in a harsh, intertidal environment. Most noteworthy is *Typhlopolycystis rubra* with a CV of only 0.24.

Previous knowledge on the distribution of meiofauna on lugworm flats (Reise & Ax 1979, Reise 1981a, b) prompted me to sample specifically those habitat structures which are relevant to plathelminths. Such a sampling strategy emphasizes existing patterns and magnifies differences between populations. Since each of the 26 microsites is covered by 10 replicates, the approach can be regarded as a variant of stratified random sampling.

More samples are taken from lugworm burrows than is justified by their spatial share and frequency. This causes distortions in the obtained images of spatial niches. The analogy can be made of the distortions used in caricatures to reveal a person's outstanding characteristics. They shed light on phenomena which otherwise might have passed unnoticed. For instance, in a completely random sampling design, elite structures such as pocket sand or tail shafts would merely increase statistical 'noise' by contributing aberrant data points but would provide no particular information.

Consistency of site selection

None of the populations was indifferent to the spatial structure of the sand flat sediment. Over the years, they showed a high fidelity to certain preferred microsites. Species of the surface layer remained at the surface throughout or became locally extinct but did not take refuge in the subsurface region. Species of the sulfide layer varied in their vertical ranges and preferences, but always stayed below the surface. Vertical burrow shafts were usually attractive to sulfide-layer species but populations were never confined to these structures. A decline in population abundance did not result in a proportional increase at head or tail shafts. They are no refuges on an interannual time scale.

Species of pocket sand differed in their spatial behaviour. Restricted to pocket sand over the entire time span were *Gyratricella attemsi, Mariplanella frisia* and *Typhlopolycystis rubra*. Two other species, *Carenscoilia biforamen* and *Coelogynopora tenuis*, were initially abundant in pockets, moved to vertical burrow shafts in 1981, remained rare for some time, and eventually had a comeback to pocket sand. The same applies to *Convoluella brunea*; however there was no final comeback. *Polystyliphora filum* showed synchronous fluctuations in pocket sand and the sulfide layer.

Most of the time, microsites seemed to maintain their essential properties and were utilized by the plathelminth populations in a fairly predictable way. Lugworm burrows constitute a permanent biogenic feature on this sand flat. Populations of *Arenicola marina* are known to remain at relatively constant density in the Wadden Sea (Beukema & de Vlas 1979, Reise 1981c). All this suggests that the intertidal sand flat is perceived by the plathelminths as a diverse habitat with recurrent attractions, and not as an amorphous and hazardous place. Most populations are spread over several microsites. Switching between preferred regions is rather uncommon.

Persistence

Wide spatial niches with individuals scattered over several microsites tended to prolong persistence in plathelminth populations. Superficially, this observation bears some resemblance to Den Boer's (1968) concept of the spreading of the risk of extinction. However, this requires asynchronous fluctuations of subpopulations, with the consequence that the variance of total populations is less than the mean variance of the subunits (Andrewartha & Birch 1984). This phenomenon was not encountered. Instead, I assume that wide spatial niches are an expression of a wide tolerance range to environmental conditions. It is this adaptation which enables populations to show prolonged persistence.

The term 'persistence' should not be taken literally. It is not known how often species left and came back between 2 consecutive sampling intervals. Thus, annual sampling tends to overestimate persistence, while sampling errors cause an underestimate. It is virtually impossible to detect high persistence in sparse populations. This methodological limitation casts doubts on the ecological significance of correlations of persistence with population size and variation. On the other hand, both may very well result from real interdependences. Large populations are likely to persist longer than small ones, and the risk of extinction increases with the amplitude of population variations.

Interannual variability

Populations spread over several microsites fluctuated less in individual numbers than populations aggregated at few microsites. Inseparable from this relation were location effects: populations confined to the sediment surface were subject to stronger fluctuations than populations spread over the subsurface region. In addition, spatial niche size and location effects seem to underly relations between feeding type and interannual variability.

In nematodes, Bouwman (1983) observed higher seasonal fluctuations in diatom-feeders than in bacterivores. He also regarded the deep-living component of the Nematoda in an estuarine sediment as the more conservative one. These species are distributed over a vertical range of 2 to 30 cm, while the surface component occupies only the upper 2 cm. This is in obvious similarity with the plathelminth populations in the present study.

Plathelminthes of a mud flat were seasonally more variable than those of a sand flat (Dittmann & Reise 1985). In mud, all species were confined to the sediment surface, and diatoms were their main food source. Coull (1985) studied the meiofauna of a sand and a mud site over a period of 11 yr. Variability in mud was higher than in sand. In mud the upper 1 to 2 cm were sampled, in sand the upper 4 to 10 cm. Again, spatial niche size and location effects appear to be proximate determinants of temporal variability. In sand, Coull (1985) postulated hydrodynamic factors to maintain meiofaunal abundance at a relatively constant level within and between years. For the plathelminth populations on the sandy lugworm flat, I speculate that habitat complexity and intricate biotic interactions engender the high constancy of subsurface populations.

Microsite specialists

Typhlopolycystis rubra and *Mariplanella frisia* are exceptional in that they are restricted to pocket sand, a narrow spatial niche, and yet do not show wide fluctuations in populations size over time. Either both species are preadapted to maintain populations in small, insular sites, or they have specialized in micro-oxic conditions of biogenic origin. *T. rubra* is – up to now – not known from any other habitat. It is capable of encystment which may help to escape the vagaries of individual lugworm behaviour. *M. frisia*, on the other hand, though restricted to pocket sand at the study site, has also been found in other habitats with coarse-grained sediment (Ax & Heller 1970). On an exposed sandy flat, Ehlers (1973) found *M. frisia* in the upper sulfide layer and particularly high densities at various polychaete burrows.

These 2 exceptions to the overall relation between spatial niche size and temporal variability bring to attention that microsite specializations are not a general characteristic in this plathelminth assembly. On a geographical scale, Glazier (1986) found that species of rodents and moths with restricted ranges fluctuate less in their local populations than wide-ranging species. He offered the explanation that species confined to a small area and fluctuating strongly are unlikely to persist in nature because of a high risk of extinction. This explanation may apply to the 2 exceptions mentioned above. However, at the scale of my sand flat study, more species particularly adapted to narrow spatial niches do not show up.

Species of sediment surface and sulfide layer

Interannual variation of population size in surface-dwelling species is higher than in those which live below in the sulfide layer. Populations at the surface not only 'boom and bust', they are also subject to passive dispersal by currents, while the deep-living species are not. Surface-dwellers also tend to move faster, and some have >1 generation yr^{-1} while the majority of species have just 1.

The dominant Acoela of the sediment surface, *Postmecynostomum pictum* and *Aphanostoma album*, have 6 to 8 generations yr^{-1}, while *Paedomecynostomum bruneum*, an acoel of the sulfide layer (see Fig. 2), has at most 3 generations yr^{-1} (Faubel 1976). The surface-dwelling *Microstomum papillosum* (Macrostomida) is capable of rapid asexual reproduction. The large-sized Proseriata constitute a major component of the subsurface Plathelminthes. They have only 1 generation yr^{-1} (Sopott 1973). In the Rhabdocoela, surface-dwellers live shorter and are often bi- or polyvoltine, while in deeper sediment layers development lasts 1 yr and there is only one reproductive period (Ehlers 1973). The dominant species of the sulfide layer, the kalyptorhynch *Neoschizorhynchus parvorostro*, also seems to have no more than 1 generation yr^{-1}.

In general, there is a certain resemblance with the adaptive traits found in the macrofauna of marine sediments along pollution gradients (Pearson & Rosenberg 1976, Gray 1981) and to the succession following major disturbances (Rhoads et al. 1978). Phenomena which are exhibited by macrofauna on wide horizontal or temporal scales may be evident in meiofauna within small vertical gradients.

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