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SPATIAL SEGREGATION IN COPEPOD SPECIES FROM A BRACKISH WATER HABITAT

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Abstract: The segregation along the horizontal space dimension of the niche has been investigated in six copepod species occurring together in a brackish water habitat. All but one species show an aggregated pattern which may be described by a negative binomial distribution. The aggregations are small with a radius of 5–15 cm and are distributed randomly in the habitat. Aggregations of different species do not overlap; niche-breadth and niche-overlap in this dimension show a somewhat wider utilization of space by the dominant species and insignificant overlap between species; there was no competition for space at the time of the investigation.

INTRODUCTION

One of the central themes in contemporary ecology, more specifically in the current theory of the niche, is the utilization of resources by different populations in the same community. Most of the research has centred on competition and was initiated by Hutchinson's (1957) definition of the niche, in which the population is characterized by its position along each of a set of k dimensions, ordering relevant environmental variables along axes in a k-dimensional space. Levins (1968) found that a set of four parameters is sufficient for the theory of the niche: niche-breadth and niche-overlap describe the utilization of the resource represented on the niche-dimension; the fourth parameter is community diversity.

The three dimensions which are almost always sufficient to separate species are habitat, food, and time. In this paper we investigate the ways in which benthic copepods partition space and whether or not competition is responsible for a possible spatial segregation; it has been shown previously that most species studied in this community are separated in time (Heip, 1973) and this dimension is, therefore, disregarded in this paper.

If populations have no influence on each other's resource utilization their niches will still differ, but competition should result in an over-dispersion of niches in niche-space (Schoener, 1974). On the other hand, non-random utilization of space by a population will result in a spatial pattern which is correspondingly non-random, regardless of whether this utilization depends on competition or not. There should be no relationship, however, between the spatial patterns of different populations when no common process is involved in their formation. The existence of such a relationship may, nevertheless, be due to other processes than competition, and pre-

dation will be important in many instances. It is clear that extreme caution is required as to the possible explanation of existing patterns.

The community of benthic copepods studied in this paper inhabits the sandy sediment of a very shallow polyhaline brackish water pond in northern Belgium. This habitat was chosen for two purposes: first, accurate sampling is possible; secondly, the number of species in brackish water is lower than in both the sea and fresh water, and community studies are therefore easier.

Material and Methods

Samples were taken on two occasions, namely, on 16th January 1971 and on 13th December 1971. Temperature of the water was low, 4.0 °C and 6.6 °C, respectively. Sampling was as follows (Heip, 1976). In order not to disturb the sediment a wooden frame 1.20 × 1.20 m was placed very carefully on the bottom of the pond where depth was about 10 cm. In this frame chords were stretched at intervals of 10 cm in both directions. In this way a grid was formed with square cells of 100 cm^2. A sample was taken in one of the corners of each cell to permit more accurate localization of the sample in the grid, with the aid of a glass tube covering a surface area of 6 cm^2. Samples were taken to a depth of 6 cm. Our previous studies have established that copepods do not occur in the anaerobic layers in this habitat; because the oxidized layer was only 1–2 cm deep, one could be sure that all animals were sampled in the vertical dimension.

The samples were fixed with 4 % formalin and elutriated in the laboratory using the method of Barnett (1968). This method has the disadvantage that the detritus is also removed from the sand and a careful extraction of the animals under the dissecting microscope becomes necessary. Even when done as carefully as possible separation probably accounts for the main source of errors.

After extraction, the number of males, females carrying eggs (c.e.) and females without eggs (w.e.) were counted. 100 samples were taken on both occasions. From the samples of 16th January 1971 only *Canuella perplexa* was treated; in this case samples No. 25 and 50 were lost. From the samples of 13th December 1971 all copepods were extracted, but only 64 samples were treated, representing a square of 80 cm side.

All calculations were programmed on a Hewlett–Packard 9810A desk-calculator; the negative binomial parameter k was calculated using the maximum likelihood method described by Bliss & Fisher (1953).

Results

Six species of copepods were found in the sample of 13th December 1971, namely, *Halicyclops magniceps* (Lilljeborg), *Canuella perplexa* T. & A. Scott, *Tachidius discipes* (Giesbrecht), *Nitocra typica* Boeck, *Mesochra lilljeborgi* Boeck, and *Parony-*

chocamptus nanus (Sars). The first is a cyclopoid copepod, all the others are harpacticoids.

TABLE I

Mean ($\bar{x}$), variance (s^2), and related parameters of the observed frequency distribution of the number of animals per sample: ad. tot., adult totals; c.e., carrying eggs; w.e. without eggs (and in subsequent tables): $n = 98$ for *C. perplexa* (1); $n = 64$ for all others.

	$\bar{x}$	s^2	$s^2/\bar{x}$	$(n-1)s^2/\bar{x}$
Paronychocamptus nanus				
♀♀ c.e.	11.78	43.73	3.63	228.69
♀♀ w.e.	54.56	338.63	6.21	391.23
♀♀ tot.	66.34	521.28	7.86	495.81
♂♂	42.97	148.76	3.46	217.98
ad. tot	109.32	1052.15	9.63	606.69
Canuella perplexa (1)				
ad. tot.	11.79	31.90	2.71	262.87
Canuella perplexa (2)				
ad. tot.	3.25	7.17	2.21	139.23
Tachidius discipes				
♀♀ c.e.	1.94	2.03	1.05	65.94
♀♀ w.e.	1.11	2.04	1.83	115.59
♀♀ tot.	3.05	4.33	1.42	89.46
♂♂	0.91	1.17	1.29	81.03
ad. tot.	3.95	6.81	1.73	108.99
Mesochra lilljeborgi				
ad. tot.	2.17	3.64	1.68	105.84
Nitocra typica				
ad. tot.	0.67	1.08	1.61	101.43
Halicyclops magniceps				
ad. tot.	0.19	0.25	1.32	83.16

In order to characterize the spatial pattern of these populations we investigated possible departures from the Poisson-distribution which describes random phenomena; in this distribution the variance equals the mean and the ratio $s^2/\bar{x}$ of these two parameters must equal one when the pattern is random. Mean, variance, and derived parameters of the number of individuals per sample are given in Table I. The $s^2/\bar{x}$-ratio is larger than one in all cases. The significance of this departure can be tested by the fact that $(n-1)s^2/\bar{x}$ is approximately distributed as χ^2 with $n-1$ degrees of freedom, at least for $\bar{x} > 5$ (Pielou, 1969). Using this parameter it is shown that the departure from the expected value of $s^2/\bar{x} = 1$ is significant in all cases, except for the total number of adults of *Halicyclops magniceps* and for the females carrying eggs and the males of *Tachidius discipes*. Since in these cases $\bar{x} < 5$ it is doubtful whether the test is valid. The density of *Halicyclops magniceps* was too small to allow almost any statistical tests and so this species was left out of consideration, the more because it

was found hibernating in the burrows of the polychaete *Nereis diversicolor* at depths considerably below 6 cm (Heip, 1975a).

TABLE II

Paronychocamptus nanus: a comparison between the observed frequency distribution and the negative binomial distribution.

	No. of individuals	Observed	Expected
♀♀ c.e.	0–4	4	6.83
$k = 4.49$	5–9	23	19.92
$\chi^2 = 2.17$	10–14	19	18.61
	15–19	10	10.85
	20–24	5	4.92
	25–29	2	1.91
	30–34	1	0.66
	35+	0	0.27
♀♀ w.e.	0–14	1	0.11
$k = 10.15$	15–29	3	4.23
	30–44	13	16.16
	45–59	26	20.55
$\chi^2 = 10.79$	60–74	14	13.85
	75–89	4	6.22
	90–104	2	2.11
	105–119	1	0.58
	120+	0	0.06
♀♀ tot.	0–19	1	0.24
$k = 9.22$	20–39	4	6.80
	40–59	23	20.09
$\chi^2 = 6.77$	60–79	21	20.20
	80–99	11	11.04
	100–119	3	4.11
	120–139	0	1.18
	140+	1	0.34
♂♂	0–9	0	0.01
$k = 5.99$	10–19	1	0.75
	20–29	6	7.40
	30–39	20	18.54
$\chi^2 = 2.29$	40–49	17	19.63
	50–59	15	11.58
	60–69	4	4.49
	70–79	1	1.27
	80+	0	0.34
Ad. tot.	0–19	0	0.00001
$k = 13.16$	20–39	1	0.16
	40–59	1	2.28
	60–79	8	8.74
	80–99	16	15.14
$\chi^2 = 8.13$	100–119	15	15.67
	120–139	12	11.30
	140–159	9	6.26
	160–179	1	2.83
	180–199	1	1.09
	200+	0	0.43

The test criterion $s^2/\bar{x}$ indicates an aggregated pattern and these patterns are described by contagious distributions, one of which is the negative binomial distribution which has been shown to be of general applicability by Bliss & Fisher (1953). The

TABLE III

A comparison between the observed frequency distribution and the negative binomial distribution for four species of copepods.

	No. of individuals	Observed	Expected
Tachidius discipes			
Adults total	0–1	13	11.11
$k = 5.07$	2–3	20	20.68
	4–5	12	16.65
$\chi^2 = 5.08$	6–7	11	9.17
	8–9	7	4.06
	10–11	1	1.55
	12+	0	0.75
Canuella perplexa			
Adults total (1)	0–4	8	6.81
$k = 6.99$	5–9	28	30.71
	10–14	37	33.03
	15–19	15	18.09
$\chi^2 = 7.11$	20–24	5	6.76
	25–29	5	1.98
	30+	0	0.59
Canuella perplexa			
Adults total (2)	0–1	20	19.75
$k = 2.32$	2–3	18	20.24
	4–5	13	12.46
	6–7	9	6.38
$\chi^2 = 5.79$	8–9	1	2.96
	10–11	3	1.30
	12+	0	0.92
Mesochra lilljeborgi			
Adults total	0	14	12.52
$k = 2.99$	1	12	15.74
	2	16	13.21
	3	10	9.24
$\chi^2 = 7.36$	4	3	5.82
	5	3	3.42
	6	4	1.92
	7	2	1.04
	8+	0	1.09
Nitocra typica			
Adults total	0	39	38.34
$k = 0.99$	1	14	15.35
	2	6	6.16
	3	3	2.47
$\chi^2 = 1.92$	4	2	1.00
	5+	0	0.67

observed frequency distribution of the number of individuals per sample was fitted with the negative binomial distribution (Tables II, III; Figs 1, 2). Using χ^2 as a

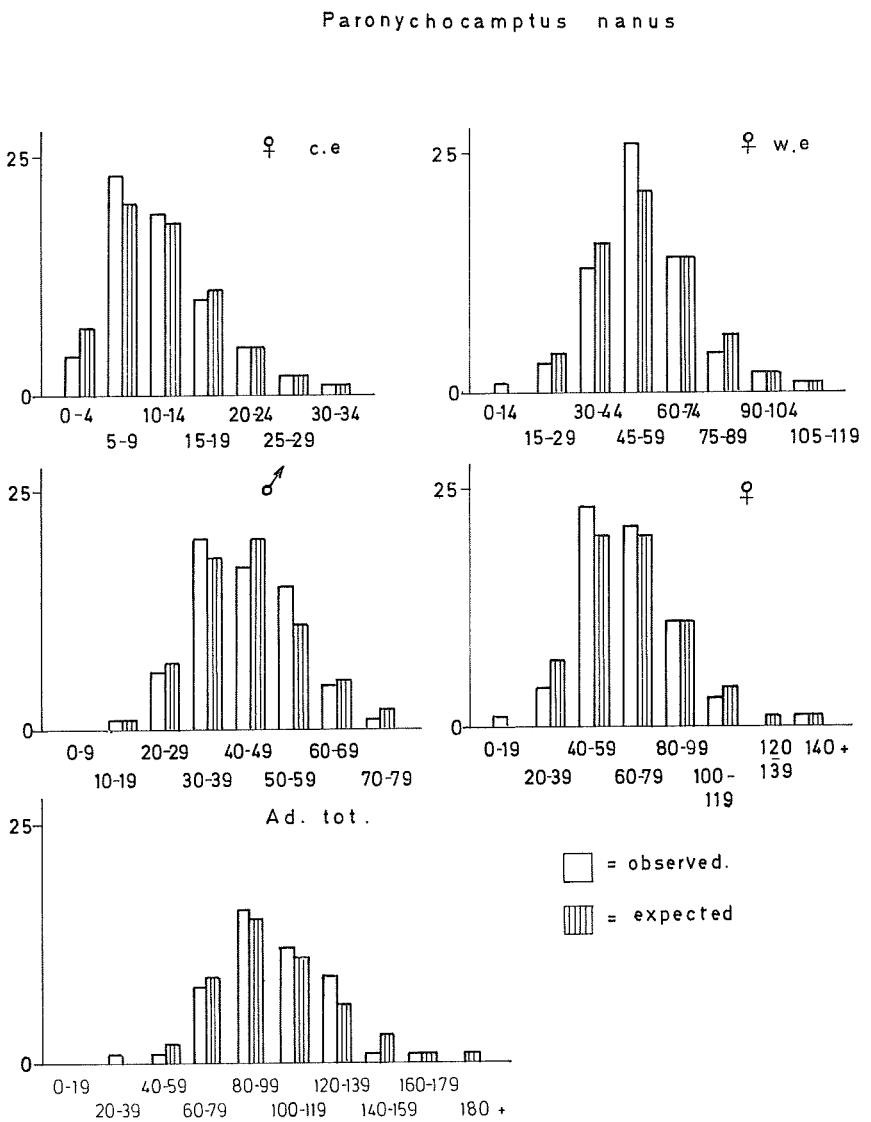

Fig. 1. *Paronychocamptus nanus*: comparison between the observed frequency distribution and negative binomial distribution: c.e., carrying eggs; w.e., without eggs (and in subsequent figs).

criterion with n–3 degrees of freedom (in which n is the number of classes) it is evident that the negative binomial distribution fits the data in all cases. When described by this distribution, the spatial pattern may be summarized by only two parameters, the

mean $\bar{x}$ and the negative binomial parameter k. Values of k as obtained by the maximum likelihood method are given in Tables II and III.

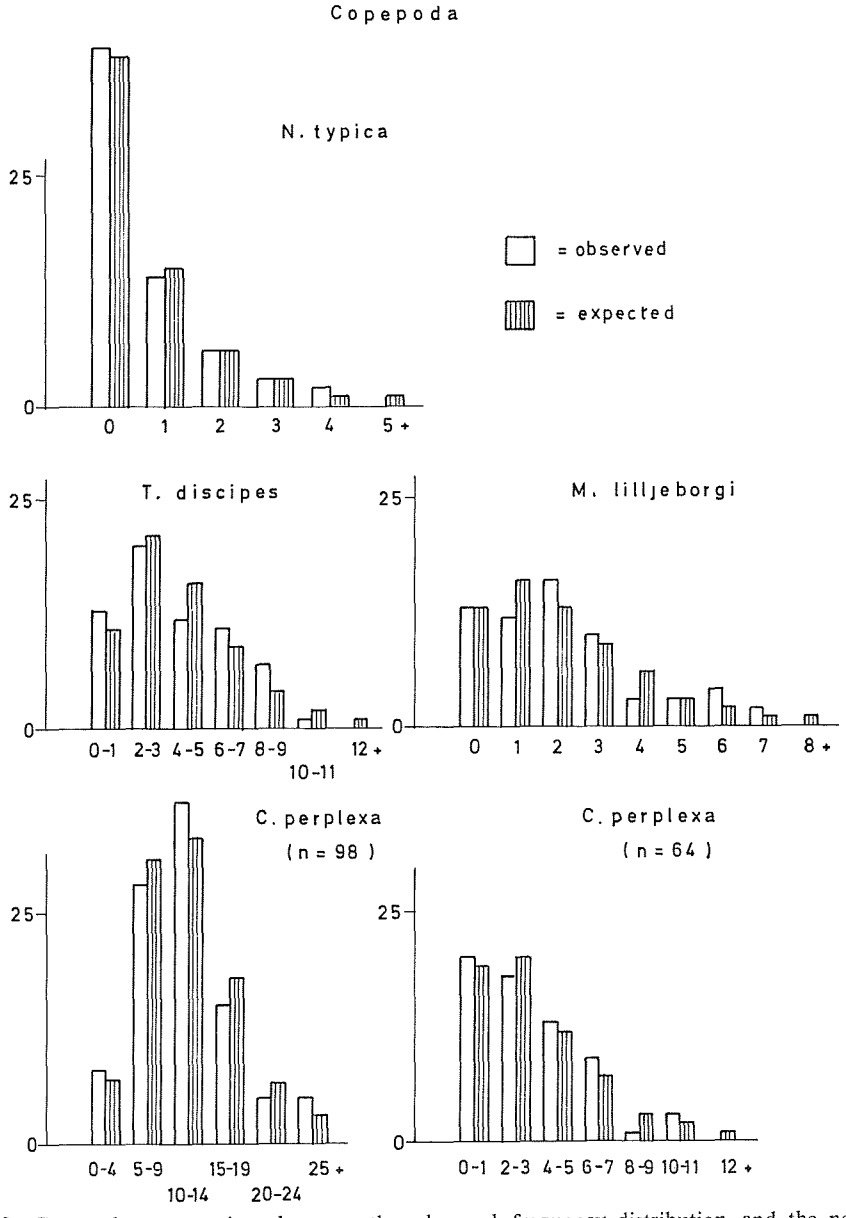

Fig. 2. Copepoda: comparison between the observed frequency distribution and the negative binomial distribution.

Application of the negative binomial and similar distributions does not take the spatial origin of the samples into account. To avoid this important loss of information

we used a method described by Iyer (1949), which has recently been used in benthos studies by Jumars (1975) and Heip (1976). In this method, the cells of the grid are divided into two classes, those with a density higher than the mean and those with a density lower than the mean. The cells with a higher value are dotted, the cells with a lower value are left white. The dispersion of dotted and white cells can be examined by counting the number of joins between them and comparing this number with the number that should be generated when the dotted cells are distributed at random on the grid. The mean and variance of the number of joins have been calculated (Pielou, 1969) as,

$$m = A\frac{r_1^{(2)}}{b^{(2)}}$$

and,

$$V = 2B\frac{r_1^{(3)}}{b^{(3)}} + 2C\frac{r_1^{(4)}}{b^{(4)}} + m - m^2$$

in which r_1 = number of dotted cells, b = total number of cells, a = number of rows plus number of columns, $A = 2-3a+4b$, $B = 44-36a+28b$, $r_1^{(x)} = r_1(r_1-1)\ldots(r_1-x+1)$, $b^{(x)} = b(b-1)\ldots(b-x+1)$. In Table IV and Figs 3 and 4 the results obtained by application of this method are shown. The number of joins be-

TABLE IV

The number of dotted cells r_1, the expected number of joins between then *DD* exp., the observed number of joins between them (*DD* obs.), and the variance of the number of joins (s^2).

	r_1	*DD* exp.	*DD* obs.	s^2
Paronychocamptus nanus				
♀♀ c.e.	26	33.85	45	18.69
♀♀ w.e.	30	45.31	52	22.24
♀♀ tot.	31	48.43	61	23.55
♂♂	29	42.29	50	21.20
ad. tot.	33	55.00	66	24.34
Canuella perplexa				
ad. tot. (1)	45	68.40	78	32.38
ad. tot. (2)	26	33.85	55	18.69
Tachidius discipes				
ad. tot.	31	48.43	64	23.55
Mesochra lilljeborgi				
ad. tot.	21	21.87	30	13.70
Nitocra typica				
ad. tot.	25	31.25	28	17.45
Halicyclops magniceps				
ad. tot.	9	3.75	6	2.97

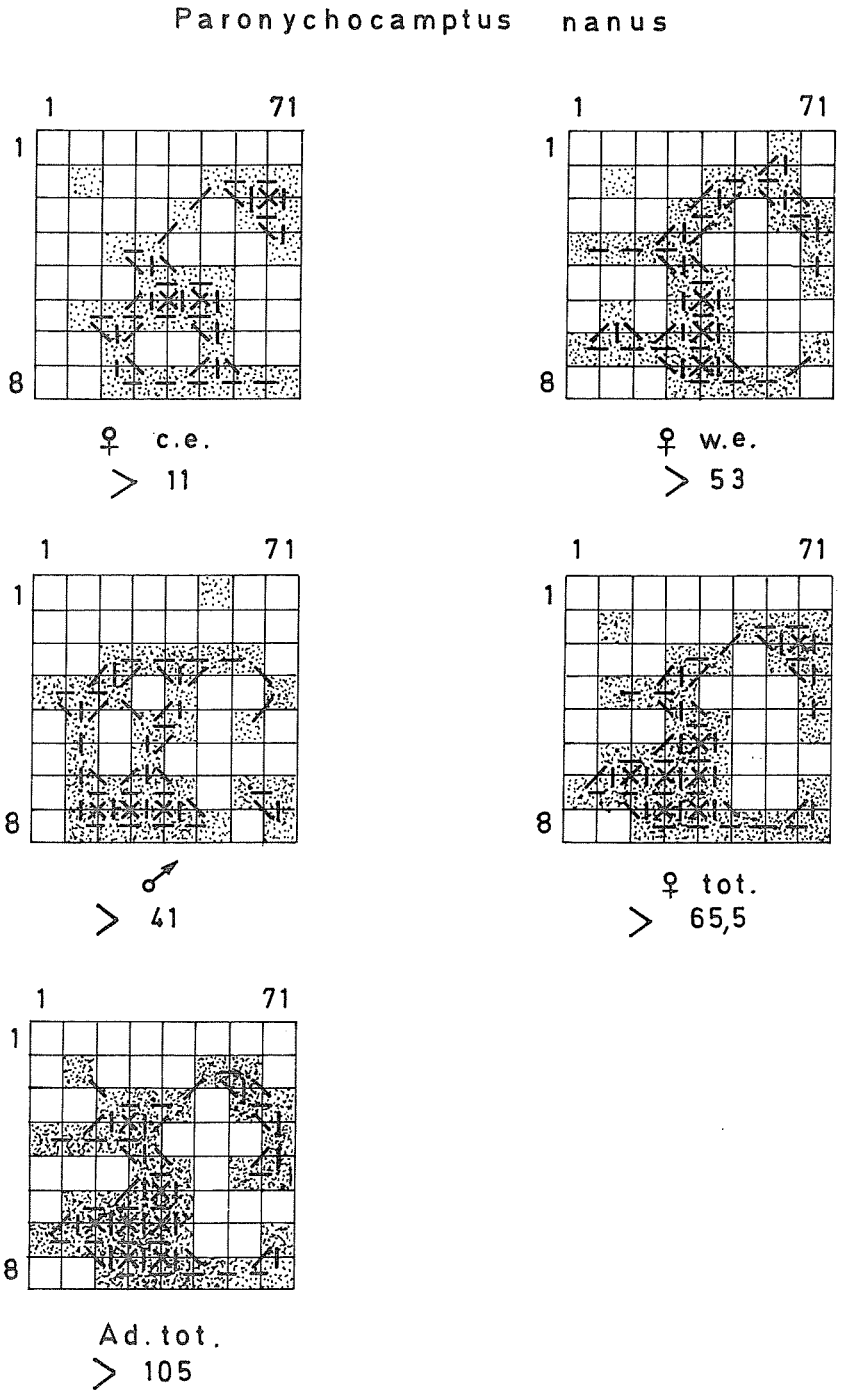

Fig. 3. *Paronychocamptus nanus*: position of cells yielding densities higher than the median (dotted) and the joins between them.

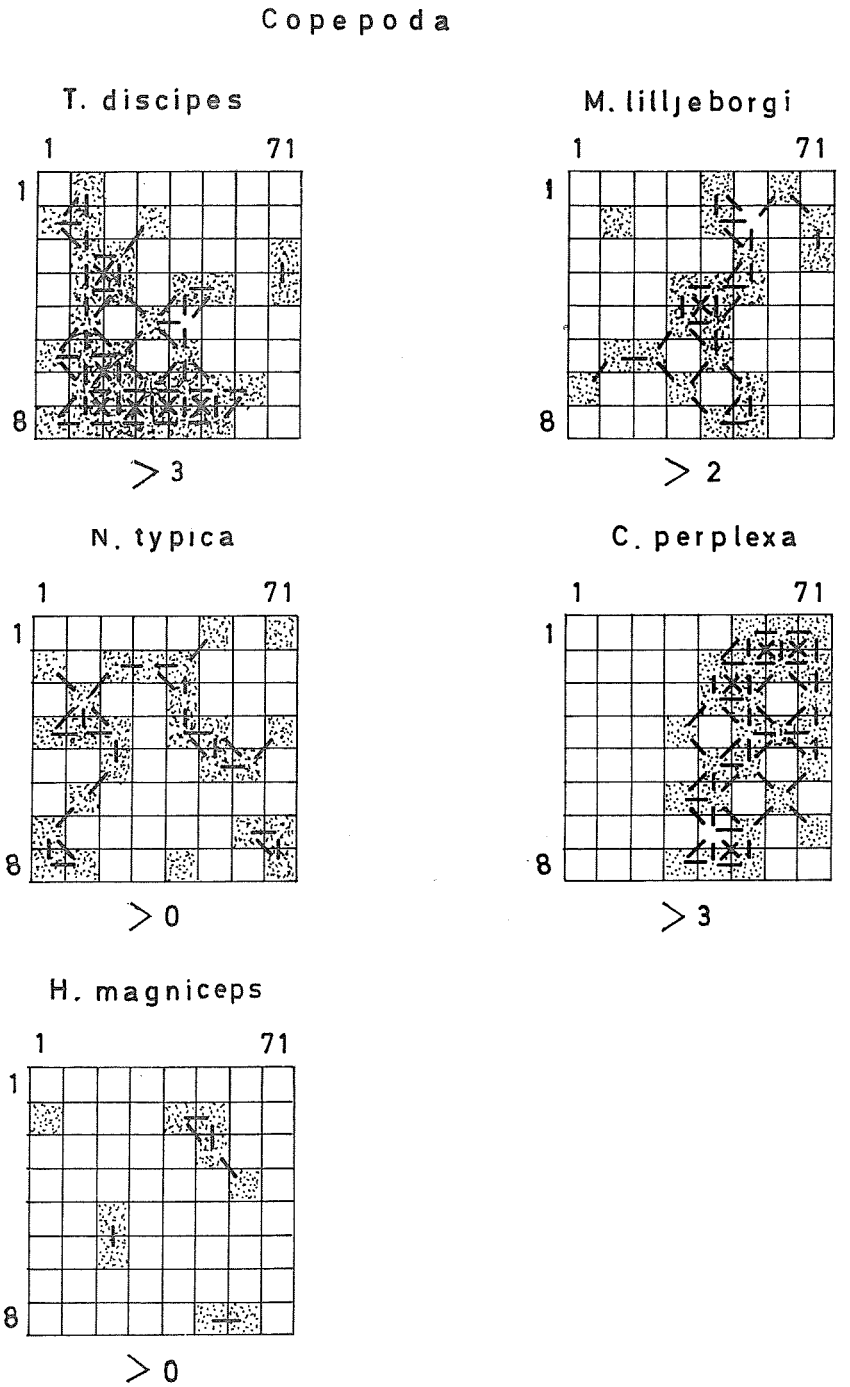

Fig. 4. Copepoda: position of cells yielding higher densities than the median (dotted) and the joins between them.

tween dotted cells is higher than expected from a random distribution of the cells, except for *Nitocra typica*, but the difference is not always significant.

Information on the size of the patches was at first obtained by a method described by Wiebe (1970). In this method samples are considered to have been taken from a patch when they show densities higher than the median. By counting the number of adjacent subsamples having an abundance higher than the median and surrounded by subsamples with abundances less than the median Wiebe (*loc. cit*) obtained an average distance towed through a patch and derived from this the mean patch radius. This method has been criticized by Fasham, Angel & Roe (1974) who demonstrated that estimates of the mean patch size obtained in this way are dependent on subsample size; they calculated patch size using a model developed by Skellam (1952). In this method a two-dimensional sample area is considered and the organisms are assumed to be distributed around centres of aggregation which are distributed at random throughout the area. When the organisms are distributed around the centre according to a bivariate circular normal distribution, an estimate of the standard deviation of this distribution permits evaluation of patch size and the number of patches per unit area.

TABLE V

Radius of patches (cm) as obtained by the method of Wiebe (1970) and that of Skellam (1952).

Organism	Wiebe	Skellam
Paronychocamptus nanus		
♀♀ w.e.	10.0	–
♀♀ c.e.	9.1	–
♀♀ tot.	9.5	8.5
♂♂	9.4	5.3
ad. tot.	10.3	7.4
Tachidius discipes		
ad. tot.	9.9	16.9
Nitocra typica		
ad. tot.	7.4	12.9
Canuella perplexa		
ad. tot. (1)	11.0	–
ad. tot. (2)	11.6	103.1
Mesochra lilljeborgi		
ad. tot.	10.0	14.9

A comparison between estimates of patch radius as obtained by both methods is given in Table V. These estimates depend on the assumption that density in the core is a good estimate of density in the cell. From this Table it appears that there is a good agreement between the values obtained by both methods. Due to the nature of the calculations involved in the application of Skellam's method it is not always possible to obtain estimates at all, a difficulty also encountered by Fasham *et al.* (*loc. cit.*),

but, with the exception of *Canuella perplexa*, the order of magnitude of the patch radius as obtained by both methods is the same and patches with a radius between 5 and 15 cm may be a robust result.

Even when estimates of patch size obtained by Wiebe's method are not reliable, this method can provide us with a pictural representation of the patches in a way described by Heip (1976). Sample values are plotted according to their position in the grid twice, once in each of the perpendicular directions where they occur. The median of the sample values is also plotted as a straight line parallel to the abscissa. By measuring the distances cut off on the median by connections between a sample value or a set of consecutive values above the median and the two adjacent values or sets of values below the median, and plotting these distances in their correct position in the grid (the solid lines in Figs 5, 6) we obtain a picture of the aggregations. In general this picture is rather similar for groups within *Paronychocamptus nanus* (Fig. 5) and rather different between species (Fig. 6).

A more rigorous approach to investigate differences in spatial location of the aggregations is made by counting the cells yielding samples with a density higher than the mean (the dotted cells from Figs 3, 4) which are common to both species or groups within species which are compared. The probability that this number is due to chance is given by the hypergeometric distribution as:

$$P_a = \frac{m!n!r!s!}{a!b!c!d!N!}$$

in which a = number of samples yielding more individuals than the mean in both species or groups, b = number of samples yielding more individuals than the mean in species or group 1 and less in species or group 2, c = number of samples yielding more individuals than the mean in species or group 2 and less in species or group 1 and d = number of samples yielding less individuals than the mean in both groups; $m = a+b$, $n = c+d$, $r = a+c$, $s = b+d$, and $N = a+b+c+d$ (Pielou, 1969).

This method has been used earlier to investigate differences between groups within *Paronychocamptus nanus*, but we will give these results again (Heip, 1975b). From Table VI it may be concluded that there is no relationship between the locations where densities higher than average occur when species are compared, except when the species occur in very low density. There appear to be significant correlations between *Tachidius discipes* and the low density species *Nitocra typica* and *Mesochra lilljeborgi*, but since in these species the numbers of empty cells is larger than half the total number of cells, the probability of overlap with an empty cell is larger than 0.5, independent of the real distribution. The highly significant avoidance (negative overlap) between *Mesochra lilljeborgi* and *Nitocra typica* is probably a consequence of this and has no biological meaning.

Comparisons between groups within species have been made in the two species with a sufficiently high density. In both *Paronychocamptus nanus* and *Tachidius discipes* males occur at densities higher than average together with females which are

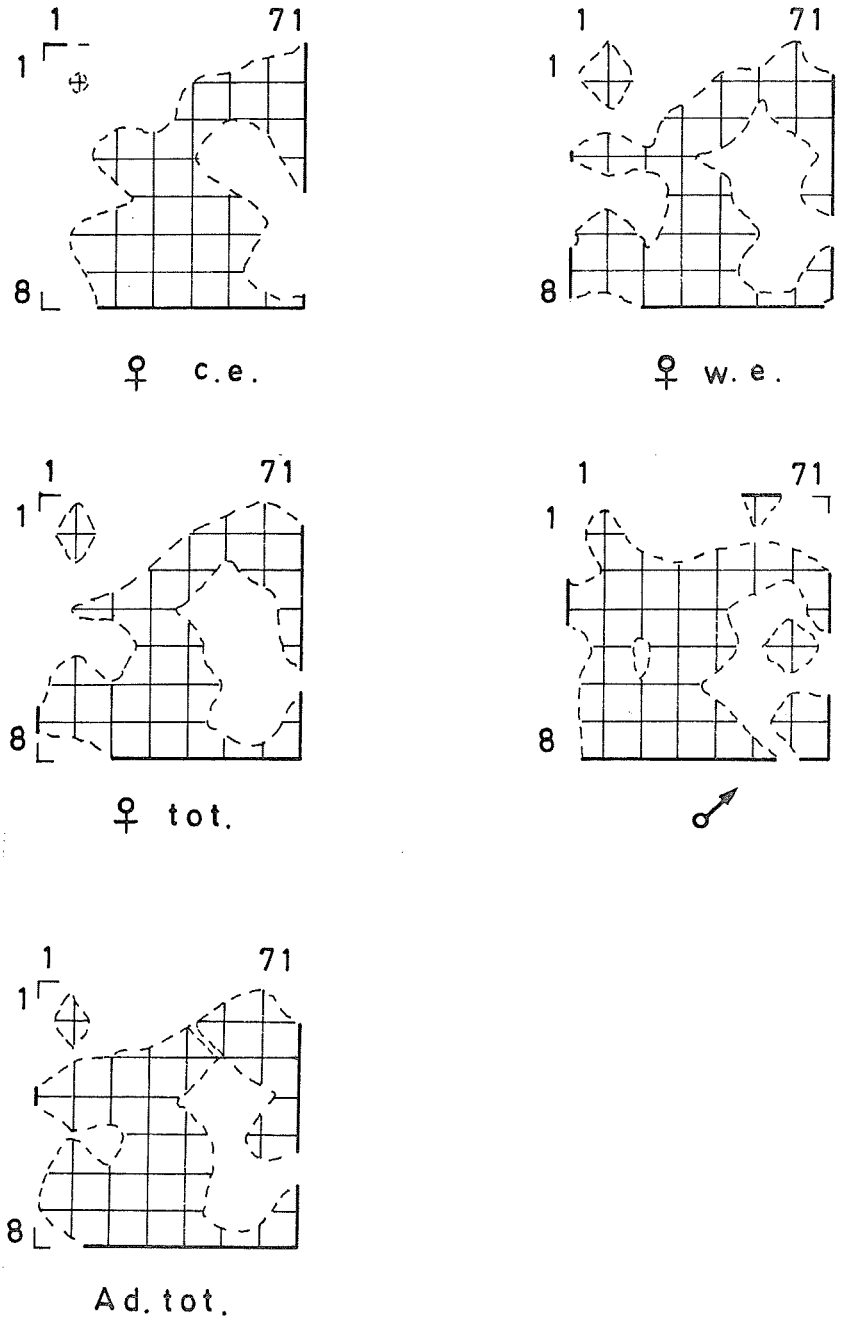

Fig. 5. *Paronychocamptus nanus*: form of the aggregations as defined by a modification of the method of Wiebe (1970).

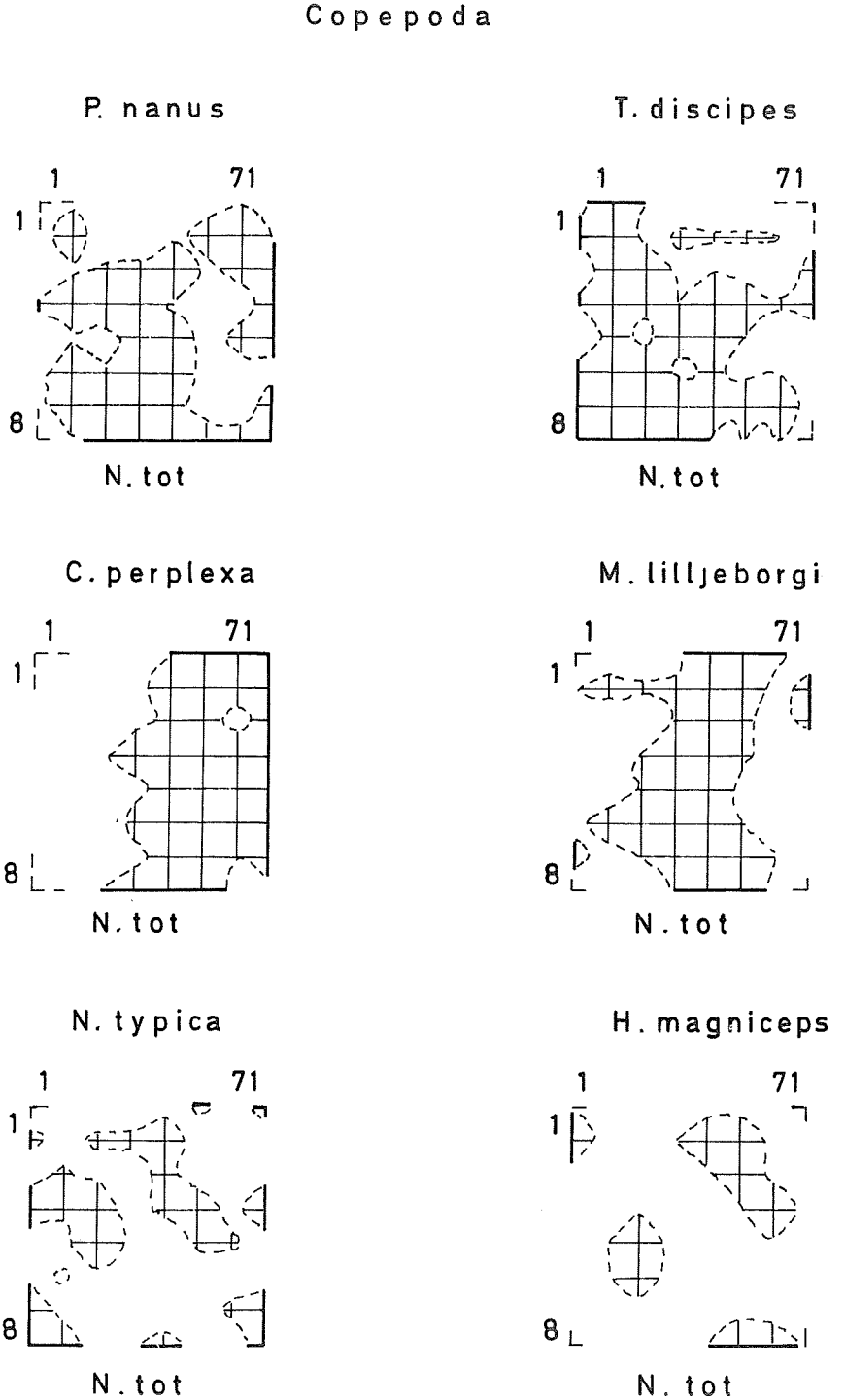

Fig. 6. Copepoda: form of the aggregations as defined by a modification of the method of Wiebe (1970).

not carrying eggs but not with females carrying eggs. When numbers are compared instead of locations the correlation between males and both groups of females is highly significant in *P. nanus*, whereas in *T. discipes* there is only a significant correlation between males and females without eggs. Here again a density effect must be assumed to operate.

TABLE VI

Probability $P(a)$ that the number of cells yielding more individuals than the mean in both groups which are compared is due to chance: see text (p. 000) for explanation.

	a	*b*	*c*	*d*	$P(a)$
Paronychrocamptus nanus					
♀♀ c.e.–♂♂	13	12	16	23	0.141
♀♀ c.e.–♀♀ w.e.	17	7	12	28	0.001
♀♀ w.e.–♂♂	19	10	11	24	0.005
Tachidius discipes					
♀♀ c.e.–♂♂	20	15	13	16	0.124
♀♀ c.e.–♀♀ w.e.	15	20	6	23	0.038
♀♀ w.e.–♂♂	15	7	18	24	0.034
Paronychocamptus nanus–Tachidius discipes					
Adults total	17	13	14	20	0.094
Paronychocamptus nanus–Mesochra lilljeborgi					
Adults total	12	18	9	25	0.110
Paronychocamptus nanus–Cannuella perplexa					
Adults total	15	15	11	23	0.074
Paronychocamptus nanus–Nitocra typica					
Adults total	10	20	14	20	0.167
Tachidius discipes–Canuella perplexa					
Adults total	10	21	16	17	0.086
Tachidius discipes–Mesochra lilljeborgi					
Adults total	14	17	8	25	0.046
Tachidius discipes–Nitocra typica					
Adults total	18	14	11	21	0.044
Mesochra lilljeborgi–Canuella perplexa					
Adults total	14	8	12	30	0.006
Mesochra lilljeborgi–Nitocra typica					
Adults total	6	16	19	23	0.002
Canuella perplexa–Nitocra typica					
Adults total	9	17	17	21	0.150

In order to characterize the niche along its horizontal habitat dimension we need measures of niche-breadth and niche-overlap in this dimension. The diversity of this community has been studied (Heip & Engels, 1974) but since this parameter is of no use in comparing communities from the same habitat at the same time it is disregarded.

The problem in using parameters describing niche-breadth and niche-overlap is one of scaling. This is because the discrimination of many important variables involved in displacement along a niche-dimension is on the basis of relative rather than on absolute magnitudes, and the variables are, therefore, scaled in terms of some power function (Cody, 1974). Scaling is necessary if resources are distinct and are treated as such by the species that use them; however, there is virtually no information on how copepods respond to environmental gradients and, indeed, no indication whether such gradients exist in the habitat studied. A sediment may look very homogeneous to an observer, which as we realize is not a very good argument but may be a good pretext to use simple measures in the absence of any idea on what kind of scaling should be used.

Niche-breadth was measured with a formula proposed by Levins (1968) as $\ln B = -\sum p_i \ln p_i$ in which $p_i = n_i/N$ is the proportion of the number n_i in cell i to the total number N. To measure niche-overlap we have used an idea developed by Cody (1974) in which the number of quadrats common to both species or groups within species is related to the number of quadrats occupied by only one of them. In our study it is impossible to compare with quadrats not containing individuals of a species, since with the exception of the rare species the species occur in all quadrats. When we assume that a density higher than average indicates a greater suitability of the habitat we may again compare the number of cells with higher densities common to both species or groups with the number of cells where only one of them occurs in densities higher than average and write in analogy with Cody's formulation:

$$\alpha_H = a/((b+a)\ (c+a))^{0.5}$$

TABLE VII

Niche-breadth of five copepod species and of groups within *Paronychocamptus nanus*: $\ln B = -\Sigma p_i \ln p_i$; E (ln B) and Var (ln B) are calculated from Hutcheson (1970).

	ln B	E (ln B)	Var (ln B)
Paronychocamptus nanus			
♀♀ c.e.	4.01	3.96	0.000413
♀♀ w.e.	4.10	4.09	0.000032
♀♀ tot.	4.10	4.09	0.000027
♂♂	4.12	4.11	0.000032
ad. tot.	4.12	4.11	0.000011
Tachidius discipes			
ad. tot.	3.93	3.80	0.001786
Canuella perplexa			
ad. tot.	3.79	3.65	0.001631
Mesochra lilljeborgi			
ad. tot.	3.74	3.54	0.003967
Nitocra typica			
ad. tot.	3.08	2.73	0.015456

in which a = number of cells with higher densities than average in both species or groups, b = number of cells with higher density than average in species or group 1 and lower than average in species or group 2, and c = number of cells with higher density than average in species or group 2 and lower than average in species or group 1. Values of niche-breadth and niche-overlap obtained in the ways explained are given in Tables VII and VIII. The significance of the observed differences can be evaluated

TABLE VIII

Niche-overlap between five species of copepods and between groups within *Paronychocamptus nanus*.

Paronychocamptus nanus	♀♀ c.e.	♀♀ w.e.	♂♂		
♀♀ c.e.	–	0.64	0.48		
♀♀ w.e.	0.64	–	0.64		
♂♂	0.48	0.64	–		
Adults total	*P.n.*	*C.p.*	*T.d.*	*M.l.*	*N.t.*
P. nanus	–	0.54	0.56	0.48	0.37
C. perplexa	0.54	–	0.35	0.59	0.35
T. discipes	0.56	0.35	–	0.54	0.59
M. lilljeborgi	0.48	0.59	0.54	–	0.26
N. typica	0.37	0.35	0.59	0.26	–

in the calculation of niche-breadth by observing that ln B is calculated as the Shannon–Wiener diversity index. The moments of this statistic have been studied by Hutcheson (1970) and from his formulae we calculated E (ln B) and var (ln B), which are also given in Table VII. By applying a t-test (Hutcheson, 1970) it can be shown that the differences between the species are highly significant, except for *Mesochra lilljeborgi* and *Canuella perplexa*; within *Paronychocamptus nanus* the differences between females carrying eggs and other groups are also highly significant; from Table VII it appears that niche-breadth is largest in the dominant species *Paronychocamptus nanus* somewhat smaller in *Tachidius discipes*, still smaller and equal in *Canuella perplexa* and *Mesochra lilljeborgi* and much smaller in the rare *Nitocra typica*. Within *Paronychocamptus nanus* niche-breadths of the different groups are very similar. As to niche-overlap, the values here are of the same magnitude whether one compares species or groups within species, except for *Nitorca typica* which shows very little overlap with other species; the significance of these differences is, however, not known.

DISCUSSION

The exploitation of the horizontal space dimension by the copepod populations studied here is not random. All species have an aggregated pattern which may be described by a negative binomial distribution. Although this result is somewhat dependent on sample size, and may be biased because the samples are not contiguous, the

bias introduced by this procedure will be of the same order for all species or groups and comparisons remain perfectly valid.

Aggregation of meiobenthic groups has been repeatedly demonstrated but the applicability of a contagious distribution to describe patterns of single populations has so far received little attention. The negative binomial has been used by Buzas (1968) and Olsson & Eriksson (1974) to describe foraminiferal patterns and by Heip (1976) to describe the pattern of the ostracod *Cyprideis torosa*. Although data are only slowly being accumulated it appears justified to postulate the ubiquity of aggregated patterns in meiobenthic populations; moreover, recent evidence (Heip, Smol & Delmotte, unpubl.) also demonstrates their general occurrence in nematode populations.

Aggregations form because individuals belonging to the same species tend to be distributed together. One hint on why this happens is obtained by the fact that males occur together with females without eggs but females carrying eggs are distributed independently of both females without eggs and males in the case of *Paronychocamptus nanus*, and of males only in the case of *Tachidus discipes*. Females carrying eggs are fertilized and do not need further copulation; because it is improbable that a female copepod would change its food drastically when fertilized it seems that food has nothing to do with differences in spatial occurrence and that these differences are the consequence of biologically active processes related to reproduction (Heip, 1975b). The most attractive hypothesis is that pheromones are involved and that this may be the case is indicated by the size of the aggregations, which are small with a radius of 5-15 cm, and this might well be the distance over which such substances act (Katona, 1973). It has been shown recently that the aesthetases on the antennules of calanoid copepods act as chemoreceptors which in the male probably respond to a pheromone produced by the adult female (Griffiths & Frost, 1976). In harpacticoid copepods the male very often has more aesthetases on the antennules than the female, and the same mechanism may be involved here.

When the size of the aggregations is indeed of the magnitude which has been calculated in our study, *i.e.*, the size of the cells, it follows that aggregations are distributed as the cells, *i.e.*, aggregations are mostly distributed randomly in the environment and do not overlap between species. Niche-overlap is only slightly higher within than between species, and this would indicate that these values are below the limit where competition begins, since otherwise intraspecific competition would be of the same magnitude as interspecific competition. MacArthur (1972) has shown that there is a limit to the closeness of species packing in fluctuating environments and that the greater the fluctuations the less close the packing can be. Competition in the very variable brackish water habitat is not expected to be important, and this is confirmed by our measures of niche-overlap.

Niche-breadth is largest in *Paronychocamptus nanus* which was to be expected on other grounds; this species is always dominant in the community and reproduces over a much longer period than the others. The smallest niche-breadth of *Nitocra typica*

is also reflected in its lesser abundance. It seems, therefore, that the width of utilization along the spatial dimension may be correlated with the width of utilization along other dimensions.

When aggregations are formed by the action of chemical messengers and when there is no influence of these messengers on individuals of other species, then the nuclei around which the aggregations are formed may be considered as being independent of each other as regards the different species; in this case segregation along the horizontal habitat dimension is attained by the production of pheromones, and avoidance of competition is the result, and not the cause, of this segregation. The selective advantage of producing pheromones will, however, be certainly enhanced when this leads to less competition.

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