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ON THE SIGNIFICANCE OF AGGREGATION IN SOME BENTHIC MARINE INVERTEBRATES

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Abstract: Populations of most benthic marine invertebrates show an aggregated spatial pattern. This has been shown to be the case for Foraminifera, Gastropoda, Bivalvia, Polychaeta, Oligochaeta, Nematoda, Copepoda, Ostracoda, Amphipoda and Isopoda. Only among the Bivalvia does there seem to be important exceptions to this rule.

Evidence is presented that pattern formation is the result of two opposing forces: (1) the need for sufficient energy in which space is more evenly partitioned amongst individuals; and (2) the necessity for contact between individuals when copulation is part of the reproductive scheme. Since aggregation is the rule, the strategy in the majority of benthic marine invertebrates appears to be a reduction in the risk of failing to find a partner at the cost of an increase of the risk of not finding enough food.

It appears that aggregation in Ostracoda and Copepoda is not mechanical but an active process. The relationship $m = \sqrt{kV}$ between mean, variance, and the degree of aggregation for populations which are aggregated following the negative binomial distribution, and the constant variability $v = \sqrt{1/k}$ when density increases, shows that the degree of aggregation becomes constant at least at high densities. This degree of aggregation appears to be the same in different populations, indicating that the optimum strategy is the same for otherwise very different populations.

INTRODUCTION

Organisms, being physical objects, occupy space and space may, therefore, be considered as a resource. The utilization of this resource leads to a spatial pattern which may be a fundamental characteristic of the population. Spatial patterns in nature are of three possible kinds: in the uniform pattern individuals are arranged in a regular way, in the random pattern individuals are distributed at random, and in the aggregated pattern individuals are clumped together to form aggregations or clouds. When individuals are distributed at random in space, the frequency distribution obtained by sampling the number of individuals in each subunit of space may be approximated by the Poisson distribution, provided the number of subunits sampled is large and the number of individuals is also large. A property of the Poisson distribution is that its mean m is equal to its variance V. The V/m ratio, equal to one for the Poisson distribution, may, therefore, be used as a measure of aggregation: when it is significantly <1 the pattern is regular; when it is significantly >1 the pattern is aggregated. Aggregated patterns yield frequency distributions which are fitted by contagious distributions, one of the most frequently used of which is the negative binomial distribution.

In this study it is our purpose to compare aspects of the spatial pattern of two species of meiobenthic organisms, the ostracod *Cyprideis torosa* (Jones) and the harpacticoid copepod *Paronychocamptus nanus* (Sars). The ostracod is a comparatively long lived species with a long generation time and only one or two generations each year. The copepod is a short lived species with a short generation time and several generations each year.

Material and Methods

The investigated habitat is a very shallow (10 cm deep) brackish water pond in northern Belgium. This depth permitted accurate sampling which was carried out as follows. In a wooden frame of 1.20 × 1.20 m, chords were stretched in the two directions forming a grid with cells of 10 × 10 cm and covering a surface area of 1 m^2. One hundred samples were taken in one of the corners everywhere two chords met with the aid of a glass tube covering as urface area of 6 cm^2. The samples were immediately fixed in 4% formalin, and elutriated in the laboratory.

In each sample the number of males and females was counted, females carrying eggs being distinguished from egg-less females. From these raw data several parameters were calculated with the aid of a Hewlett-Packard 9810 A desk calculator; the value of the negative binomial exponent k was calculated by the maximum likelihood method as described by Bliss & Fisher (1953).

Results and Discussion

It has been shown that the spatial pattern of the species investigated is aggregated and may be described by the negative binomial distribution (Heip, 1973 and in prep.). Aggregation has been commonly observed in studies of marine benthic invertebrates and has been demonstrated for Foraminifera (Buzas, 1968), Polychaeta (Kosler, 1968; Gage & Geekie, 1973), Oligochaeta (Kosler, 1968), Gastropoda

(Kosler, 1968), Bivalvia (Lie, 1968; Franz, 1973; Gage & Geekie, 1973), Amphipoda (Kosler, 1968; Dexter, 1971; Gage & Geekie, 1973), Isopoda (Gage & Geekie, 1973) and, more specifically in the meiobenthos, in Nematoda (Vitiello, 1968; Gray & Rieger, 1971), Copepoda (Vitiello, 1968; Gray & Rieger, 1971; Heip, 1973 and in prep.) and Ostracoda (Heip, 1973 and in prep.).

A number of these authors have used the V/m ratio or some measure derived from it to study pattern. We must, however, point to a serious disadvantage in the use of this ratio. Pielou (1969) showed that the V/m ratio decreases linearly when density decreases due to random mortality and independent of the initial frequency distribution. There is another reason why this ratio is unable to tell us anything about aggregation when density is low. When the population has a spatial pattern corresponding to the negative binomial distribution, its variance is given by,

$$V = \frac{m^2}{k} + m \qquad (1)$$

The V/m ratio of this population is correspondingly,

$$V/m = \frac{m}{k} + 1 \qquad (2)$$

This equation shows that there is a linear relationship between V/m and m when the individuals are distributed according to the negative binomial. Apart from yielding an estimate of k which is easier to calculate than the one obtained by the maximum likelihood method, this equation shows that when density is low (m small), V/m must also be low; even when the population is aggregated, the V/m ratio will approach unity when density decreases. This relationship thus makes invalid some of the conclusions reached by Kosler (1968) and Gage & Geekie (1973) amongst others, according to whom the degree of aggregation increases with increasing density.

Another measure of the degree of aggregation is the negative binomial parameter k, which does not change with changing density due to random mortality (Pielou, 1969). From (2) we see that $1/k$ is the slope of the regression of V/m against m. Because this slope is constant, the degree of aggregation does not change with density, providing that this linear relationship holds.

Let us now examine the relationship between the negative binomial parameter k and density in a different way. The statistical variability of populations is given by $v = s/m = \sqrt{V}/m$, where s is the standard deviation of the mean m. Since $V = v^2m^2$, equation (2) becomes:

$$v^2 m = \frac{m}{k} + 1$$

$$v^2 = \frac{1}{k} + \frac{1}{m} \tag{3}$$

When density is large (m large), v^2 is approached by,

$$\lim_{m \to \infty} v^2 = \frac{1}{k} \tag{4}$$

Hence, when m becomes large,

$$v^2 k = 1 \tag{5}$$

And, since $v^2 = V/m^2$,

$$m = \sqrt{kV} \tag{6}$$

which gives a relationship between density, degree of aggregation, and variability of a population, valid for large values of m. This restriction

TABLE I

Observed values of the mean no. individuals/sample and calculated values from the equation $m = \sqrt{kV}$.

Cyprideis torosa	Obs.	Calc.	*Paronychocamptus nanus*	Obs.	Calc
Females with egg	12.2	14.0	Females with eggs	11.8	14.0
Females without eggs	4.7	5.9	Females without eggs	54.6	58.6
Females—total	16.9	18.4	Females—total	66.4	69.3
Males	9.5	11.9	Males	43.0	50.9
Adults	26.4	26.2	Adults	109.4	117.7

is not particularly severe because densities of common species in samples are normally high enough to use equation (6), as is shown in Table I where estimations of density as calculated from (6) are compared with the observed values. When the size of the sample increases equations (5) and (6) should hold better and better, indicating that the relationship $m = \sqrt{kV}$ may be considered as a true property of real populations.

In the species we studied, the expected linear relationship between V/m and m is indeed observed (Fig. 1). As pointed out above, the slope of this regression line is $1/k$. The regression obtained in our study is:

$$V/m = 0.0734\, m + 0.28 \tag{7}$$

It follows that $k = 1/0.0734 = 13.6$, and introduction of this value in (6) yields,

$$m = 3.7\, s \tag{8}$$

The application of a constant value of k yields great departures from the observed values of m at low densities (Table II). The relationship between variability v and the degree of aggregation, as measured by the negative binomial exponent k, which is given by equation (5) shows that a constant degree of aggregation implies a constant variability. The value of this variability for the populations we investigated may be calculated from the slope of the regression of V/m against m, and is

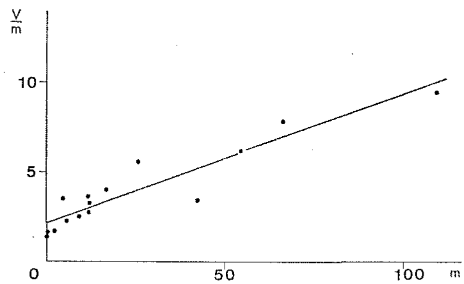

Fig. 1. Relation between V/m and m in different species of copepods and ostracods and for different groups within these species.

TABLE II

Observed values of the mean no. individuals/sample and calculated values according to $m = 3.7\,s$.

Cyprideis torosa	Obs.	Calc.	*Paronychocamptus nanus*	Obs.	Calc.
Females carrying eggs	12.2	23.3	Females carrying eggs	11.8	24.5
Females without eggs	4.7	14.9	Females without eggs	54.6	68.1
Females—total	16.9	30.6	Females—total	66.4	84.4
Males	9.5	17.9	Males	43.0	45.1
Adults	26.4	45.0	Adults	109.4	120.0

given by $\sqrt{0.0734} = 0.271$ or 27.1% (from equations (7) and (5)). The observed values of the variability of these populations as a function of the mean are given in Fig. 2, from which it is clear that variability indeed tends to a constant value when m increases and that this value is close to 27%. We may, therefore, conclude that with increasing density the populations we studied attain a constant degree of aggregation and a constant variability.

The regression of the hyperbola $v = f(m)$ observed is:

$$v = \frac{3.21 + 0.28\,m}{1.16 + m}$$

which is close to:

$$v = \frac{3.27 + 0.27\,m}{1 + m}$$

and this corresponds to a theoretical hyperbola,

$$(v - v_{\min})(m + 1) = 3$$

$$v = v_{\min} + \frac{3}{1 - m} \tag{9}$$

This hyperbola has an intersect with the ordinate at,

$$v_0 = v_{\min} + 3 \tag{10}$$

When density decreases, the values of k obtained with the maximum likelihood method are smaller, indicating that the degree of aggregation is larger. This is what is to be expected when energy is limiting. Indeed, consider a population with a mean density of 10 individuals/unit area surface. In a uniform pattern every individual has 0.1 surface unit

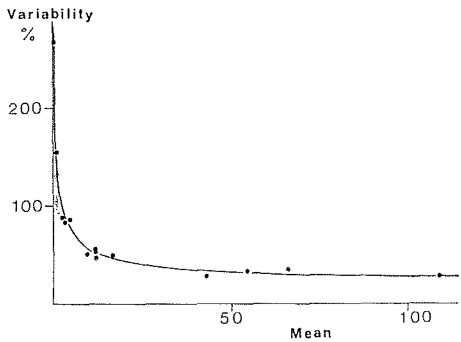

Fig. 2. Relation between variability and mean for different species of copepods and ostracods and for different groups within these species.

available. When the population is distributed at random, according to a Poisson series, the mean density is still equal to 10 individuals/unit area surface but only in 12.5% of all cases will a surface unit contain exactly 10 individuals. In 33.3% of all cases a surface unit will contain less than 10 individuals and in 54.2% of all cases it will contain more than 10 individuals. Suppose now that the energy supply to the population is 10 A units of energy/unit surface area/unit time. In the uniform population this supply will be exactly A units/individual, but in the random population 54.2% of all individuals will have $< A$ units of energy/unit time and 33.3% will have more than that. The extremes are 0.3% of surface units containing individuals which will obtain 3.3 A units of energy and 0.1% of surface units where individuals obtain only 0.45 A units of energy. When this energy supply of 0.45 A units is not sufficient to support an individual the random population has to decrease its density. When for instance the energy requirement is A units/individual, the uniform population can still maintain its original density but the random population has to decrease its density to 2.8 individuals/unit area surface to be certain that all individuals will obtain A units of energy. It is clear that the population with a uniform pattern has an advantage when energy becomes limiting even when we take in consideration that it requires energy to maintain a uniform pattern which is not required in random patterns.

When we compare the random population to an aggregated population with the same mean, we see that the number of surface units containing more individuals than the mean decreases (40.4% for $k = 5$ and 39.0% for $k = 2.5$) but that the number of individuals on the most dense unit area surface increases (30 for $k = 5$ and 36 for $k = 2.5$). In summary, when energy is not limiting the uniform strategy is disadvantageous because a certain amount of energy needs to be expended to maintain it; when energy is limiting, the uniform strategy becomes the most advantageous, the aggregated strategy the less. Since we may suppose that some form of energy supply will be limiting in most cases and for most of the time, the question arises why aggregation is still the most commonly encountered form of spatial pattern in nature. In the first place there are certain passive mechanisms causing aggregation. Consider an asexual population with an initial low density and random distribution of the parents. When young animals appear they will be close to the parent individuals and we find an aggregated pattern. In the same way, when in a sexual population eggs are laid in clumps we will find aggregation of the young animals at least initially. The most important mechanism causing aggregation is, however, the active process of animals searching for each other and this is principally due to reproductive behaviour. Sexual reproduction involving copulation demands contact between individuals and we may assume, therefore, that the strategy developed in many populations involves the reduction of the risk of not finding a partner at the cost of an increase of the risk of not finding enough food. If this were true, this would point to group selection. A first confirmation of this hypothesis is the fact that the Bivalvia, where copulation does not occur, are often not aggregated (Connell, 1956; Kosler, 1968; Jackson, 1968; Levinton, 1972). Indeed, the very few cases of uniform distributions observed in nature are mostly in this group (Holme, 1950; Gilbert, cited from Levinton, 1972) and may be explained by competition for food. Exceptions have been found (Lie, 1968; Franz, 1973; Gage & Geekie, 1973), but when occurring it appears that special mechanisms are responsible. In the case of the *Mysella* sp. investigated by Lie (1968) and Franz (1973), aggregation may either be due to association with aggregated invertebrates or with partial brood protection.

To determine whether aggregation in the two species we studied is caused by a passive or an active mechanism, we compared the situation in space of samples yielding more than the mean number of individuals and samples yielding less than the mean. When we consider the number of samples which yield more individuals than the mean and which are

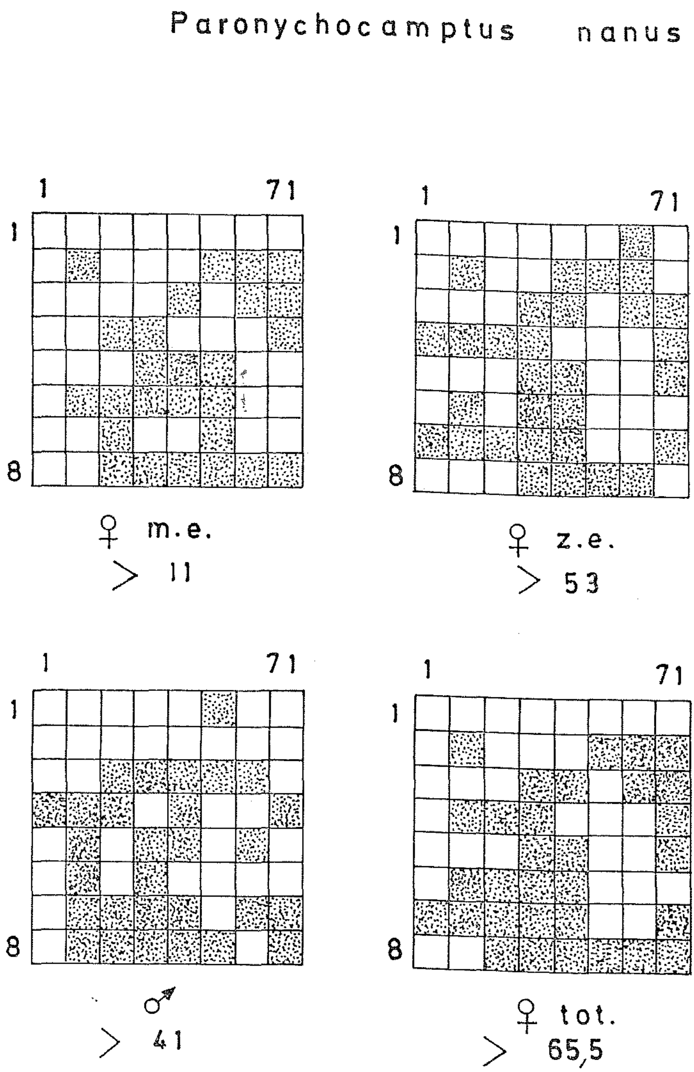

Fig. 3. Situation in space of samples yielding more or less individuals than the mean for the copepod *Paronychocamptus nanus*: cells yielding more individuals than the mean are shaded: m.e., carrying eggs; z.e., without eggs.

in common between two groups (or two sexes or species) then the probability that this number is due to chance is given by,

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

where a = number of samples yielding more than the mean for both groups; b = number of samples yielding more than the mean for group 1 but less than the mean for group 2; c = number of samples yielding less than the mean for group 1 and more than the mean for group 2; d = number of samples yielding less than the mean for both

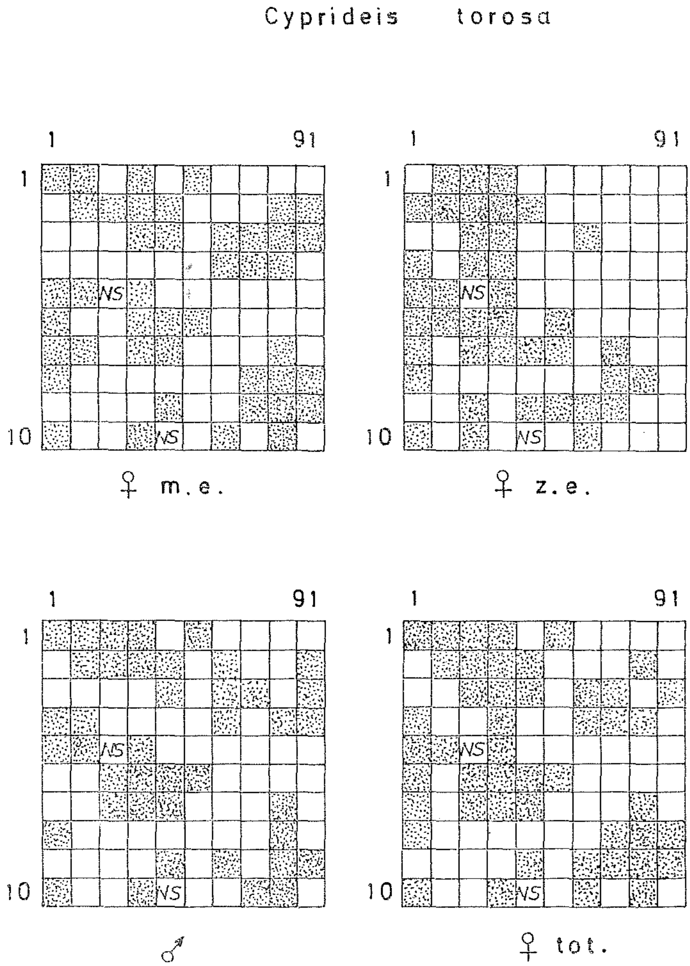

Fig. 4. Situation in space of samples yielding more or less individuals than the mean of the ostracod *Cyprideis torosa*: cells yielding more individuals than the mean are shaded m.e., carrying eggs; z.e., without eggs.

groups; $m = a + b$; $n = c + d$; $r = a + c$; $s = b + d$; $N = a + b + c + d$

This means that the probability of independent occurrence follows a hypergeometric distribution (Pielou, 1969). This probability has been calculated for the different groups between the two species; from Table III it is clear that the probability that the groups compared in this way are distributed independently is extremely small, except for one case, namely, *Paronychocamptus nanus* where the probability that females carrying eggs are distributed independently of males is about 14%. We may tentatively conclude that the aggregations are not formed passively; furthermore, from evidence not presented here and which shows that different species occupy different places (using the same test as above) we may conclude that is it is probably not the environment, which as far as we could see in our case was very homogeneous, but the animals themselves which are the principal determinants in the forming of aggregations. This is further supported by the fact that although the situation of patches of different species is different the form and size are roughly equal (Heip, 1973 and in prep.), again suggesting a common mechanism in the formation of aggregations.

TABLE III

The probability $P(a)$ that the number of cells yielding more individuals than the mean in both groups is due to chance.

	a	b	c	d	$P(a)$
Paronychocamptus nanus					
Females carrying eggs to males	13	12	16	23	0.141
Females carrying eggs to females without	17	7	12	28	0.001
Females without eggs to males	19	10	11	24	0.005
Cyprideis torosa					
Females carrying eggs to males	31	12	9	46	$<10^{-9}$
Females carrying eggs to females without	24	19	15	40	0.003
Females without eggs to males	24	16	17	41	0.002

A further test to investigate the probability of independent occurrence consists in the calculation of correlation coefficients between the numbers of the groups compared in the different samples. These correlation coefficients are all significant (Table IV), showing that high numbers in one of the groups are associated with high numbers of the other groups. There are however some interesting remarks to be made. The correlation coefficient is low between the two groups of females in *Cyprideis torosa* (significant at the 5% level only), as it also is between the numbers of egg-less females and males. Exactly the opposite phenomenon occurs in *Paronychocamptus nanus*, where high numbers of males tend to be correlated more with high numbers of egg-less females than with high numbers of females carrying eggs. It is possible that this is a chance phenomenon but the difference between the two species may be explained in terms of their generation time, which is about one year in *Cyprideis torosa* but only a few weeks in *Paronychocamptus nanus*. The presence of males is thus more essential for the latter species and males will be more frequently encountered in the vicinity of egg-less females which still need to be fertilized.

TABLE IV

Correlation coefficients (r) between numbers of different groups within species.

Cyprideis torosa		*Paronychocamptus nanus*	
Females carrying eggs to females without	0.254	Females carrying eggs to females without	0.571
Females carrying eggs to males	0.633	Females carrying eggs to males	0.331
Females without eggs to males	0.405	Females without eggs to males	0.457
Females total to males	0.677	Females total to males	0.464

In conclusion, we may formulate the hypothesis that aggregation in benthic marine invertebrates is the result of two opposing forces, one where the need for enough food results in a more even partitioning of space, and one where the need for contact between individuals results in aggregation. Evidence presented supports this hypothesis in four ways: (1) individuals belonging to different sexes or groups of the same species occur in the same places whereas individuals belonging to different species do not: (2) the bounds between the sexes are stronger when it appears to be more necessary for reproduction; this may explain the apparent independent occurrence of females carrying eggs and males in the copepod, a phenomenon which does not point to heterogeneity of the environment: (3) the fact that aggregations of different species are not in the same places but are about the same size, points to a similar mechanism causing aggregation which is not linked to environmental heterogeneity: and (4) aggregation does not readily occur when there is no need for contact between individuals in function of reproduction.

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