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POPULATION-DISPERSION IN *TELLINA TENUIS* DA COSTA

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(Text-figs. 1–8)

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Introduction

Although many investigations have been made of soil populations, both in terrestrial and aquatic environments, little is yet known of the distribution of individuals in relation to one another. A study of distribution in the horizontal plane lends itself either to a statistical treatment of samples from adjacent areas, or, where possible, to plotting of individuals *in situ*.

Salt & Hollick (1946) have studied the micro-distribution of wireworms by statistical treatment of eighty-one similar soil samples taken from a square yard of pasture. The wireworms were shown to be non-randomly distributed, there being a tendency for individuals to be aggregated.

In this paper an account is given of a population of the mollusc *Tellina tenuis* da Costa in which distribution is shown to be non-random, tending towards an even distribution. Investigations have been made both by statistical treatment of samples and by plotting of individuals.

Although there is some evidence that populations of this mollusc on other shores are not so distributed, the results from this area seem to be of sufficient general interest to be placed on record.

I am most indebted to Mr G. M. Spooner for assistance with the statistical calculations.

TELLINA TENUIS

Tellina is a small, thin-shelled, lamellibranch, which reaches a length of about 16 mm. in the Exe estuary. When excavated at low tide the animals are found at depths ranging from 2 to 4 in., smaller sizes usually being nearer the surface. Nearly all the animals are found lying on their sides, in a quiescent state, with neither siphons nor foot protruded.

At high tide, however, the animal probably assumes an upright position with siphons protruded, as shown in Fig. 1. The inhalent siphon is very extensile and ranges over the surface of the sand, drawing in material lying on

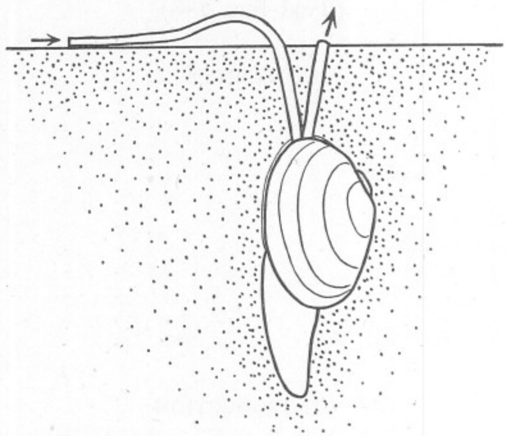

Fig. 1. Position of *Tellina tenuis* in the sand at high tide. After Yonge (1949).

or just above the surface. The shorter exhalent siphon does not project above the surface of the sand (see Yonge, 1949). Prof. C. M. Yonge, F.R.S., informs me that *Tellina* probably makes vertical migrations in the sand, coming nearer the surface at high tide.

DESCRIPTION OF THE HABITAT

The habitat, which has been described by the writer (Holme, 1949), is a sheltered sandy beach within the mouth of the Exe estuary. From about half tide downwards the soil consists of fine clean sand, which slopes down to a small stream known as Salthouse Lake. A bed of clay occurs at a depth of about 2 ft. below the surface, and the sand is consequently not very well drained.

In the lower half of the beach *T. tenuis* and *Arenicola marina* are dominant members of the fauna. *Cardium edule* and *Macoma balthica* occur in small numbers in this region.

The stations referred to are on a traverse from high- to low-water marks.

Stations were at 100 ft. intervals up the beach, heights above M.L.W.S.T. being: Station H, 2 ft.; Station G, 4 ft. (L.W.N.T.); Station F, 6 ft. (half-tide mark); Station E, $7\frac{1}{2}$ ft.

Other stations, indicated in Roman numerals, are at a little above half-tide mark, on a traverse ranging from sand to mud.

Population Counts

On a number of occasions counts have been made of populations of *Tellina* in adjacent areas on the beach. Each time a square metal frame was driven into the sand and the soil inside it excavated to a depth which appeared to include all the fauna. The soil was sieved through a 1 mm. mesh. In 1947, areas of $\frac{1}{4}$ m.^{2} were excavated, but later investigations have been on $\frac{1}{10}$ m.^{2} areas.

If individuals are distributed at random, the counts from separate samples should vary according to a Poisson distribution.

Salt & Hollick (1946) have made use of the 'coefficient of dispersion' when dealing with parallel samples of wireworm populations. It follows directly from the fact that the σ^2 of the Poisson distribution tends to equal the mean in value that the expression

$$\frac{\Sigma(x-\bar{x})^2}{\bar{x}(n-1)}$$

leads to unity when individuals are randomly distributed, to less than unity when they are evenly distributed, and to more than unity when they are aggregated. The significance of the divergence is tested by the formula

$$2\sqrt{\frac{2n}{(n-1)^2}}.$$

Where n, the number of samples, is less than 10, the latter expression is greater than unity, so that samples numbering less than 10 cannot be tested for an even distribution.

July and August 1947 (see Holme, 1949)

Pairs of samples, such as D+3 or D−3 were about 4 ft. $4\frac{1}{2}$ in. apart (6 ft. to their outside edges), and the collections around Station I were within 11 ft. of one another.

Numbers per $\frac{1}{4}$ m.^{2} were:

I−3B	5	E	II−3	19	D−3	3	G−3	47
I−3A	4		II+3	22	D+3	3	G+3	47
I+3	7							
I+8	7		III−3	1	F−3	45	H−3	42
			III+3	0	F+3	46	H+3	45
							H+15	48

The results show a general uniformity in density at any one station; also a very even population at Stations F, G and H, which range from low tide up to half-tide mark. The 'coefficient of dispersion' of the 7 samples from these three stations is 0·085. There are too few samples, however, to show a significant result.

20 *October* 1948

Twelve areas of $\frac{1}{10}$ m.^{2} were excavated within a radius of $4\frac{1}{2}$ ft. from Station G. Numbers of *Tellina* in each square were respectively: 27, 25, 24, 28, 26, 26, 32, 31, 32, 24, 29 and 29.

The 'coefficient of dispersion' is 0·307, but this lies within the limits of significance: $1 \pm 0{\cdot}89$.

18 *November* 1948

Four adjacent samples of $\frac{1}{10}$ m.^{2} were excavated at a position 30 ft. north-east of Station F.

Numbers of *Tellina* were 15, 15, 14 and 17 respectively. The 'coefficient of dispersion' is 0·13.

The above sets of readings taken together suggested that the distribution of *Tellina* is non-random, and this is confirmed by results shown below.

Plots of Individuals

Natural Populations

Further information has been obtained by plotting the position of each shell in $\frac{1}{10}$ m.^{2} squares. The frame was driven into the sand, and the soil outside it was then scraped away carefully, a little at a time. As each shell was uncovered its position was plotted, by measuring the perpendicular distance from the 'centre' of the shell to two adjacent edges of the square. It was nearly always possible to locate each shell without disturbing it. The length of each shell, and its approximate depth below the surface, was also noted. Excavation of a square usually took over an hour, and was only practicable in the better drained parts of the beach.

Although the shells occupy a depth range in the soil of about 2 in., their horizontal distribution only has been plotted. No clear correlation has been found between the horizontal spacing of individuals and the depths at which they occur. As it seems possible that the observed distribution is related to the activities of the siphons on the surface of the soil, the omission of any reference to depth seems permissible. In one square the orientation of each shell was noted, but here again there seemed to be little correlation with spacing of the animals. Plots of positions in this square are shown in Fig. 2, and in other squares in which the orientation was not noted in Figs. 4 and 6.

Although the spatial arrangement of individuals appears at first sight to be haphazard, there is, however, a suggestion of a general spacing out of the shells. A measure of this can be made by subdividing the large square into thirty-six

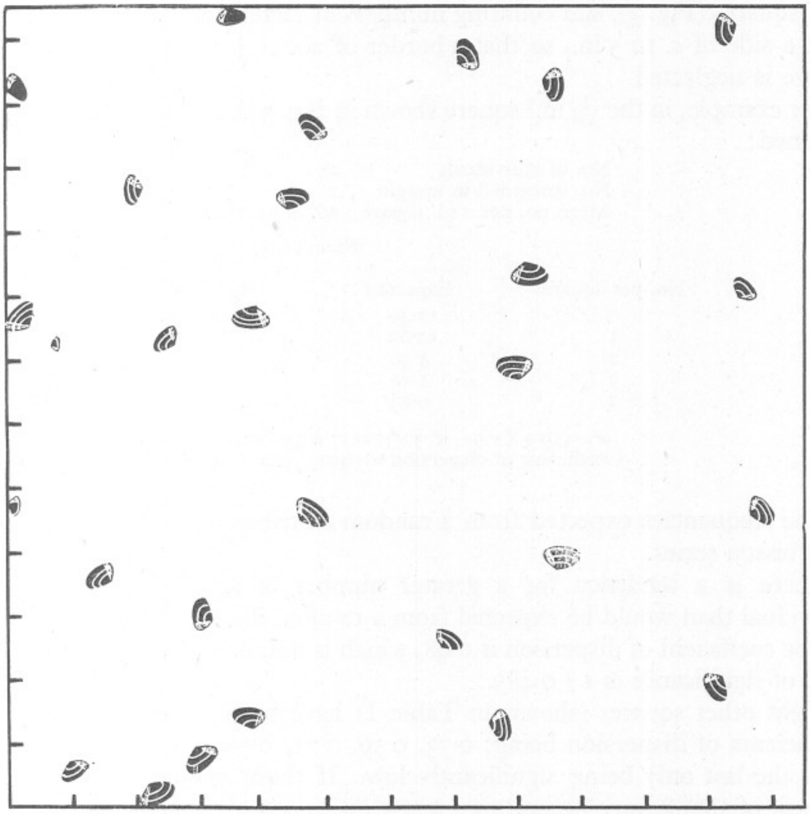

Fig. 2. Plot of positions of *Tellina* in a $\frac{1}{10}$ m.^{2} square (Station F, 11. vii. 49), density 280 per m.^{2} The sides of the square are divided into inches. The shells are drawn approximately to scale, and their orientation is shown by their shaded posterior end. The size and orientation of two shells (top right), shown without rings, is not known.

1	1	1	2	1	1	
3	1	0	2	0	0	
0	0	1	0	1	1	←2
1	1	0	1	0	1	
0	1	0	0	1	1	
1	0	1	0	1	0	

Fig. 3. Distribution of *Tellina* in the square shown in Fig. 2. This has been subdivided into thirty-six squares of side 2 in., the number of animals occurring in each square being indicated.

2 in. squares (Fig. 3), and counting numbers in each square. The $\frac{1}{10}$ m.^{2} areas have a side of *c.* 12·5 in., so that a border of about $\frac{1}{2}$ in. on two sides of the square is neglected.

For example, in the $\frac{1}{10}$ m.^{2} square shown in Fig. 3 the following results were obtained:

No. of individuals	28
No. discarded in margin	2
Mean no. per 2 in. square	26/36 = 0·722

No. per square	Frequency: Expected	Frequency: Observed (f)
0	17·49	14
1	12·63	19
2	4·56	2
3	1·10	1
>3	0·23	0

$$\sigma^2 = (19+8+9-18\cdot\dot{7})/35 = 17\cdot\dot{2}/35 = 0\cdot492$$

Coefficient of dispersion = 0·492/0·722 = 0·68

The frequencies expected from a random distribution are calculated from the Poisson series.

There is a tendency for a greater number of squares to contain one individual than would be expected from a random distribution.

The coefficient of dispersion is 0·68, which is not, however, significant. The level of significance is $1 \pm 0\cdot485$.

Eight other squares (shown in Table I) have been treated similarly, the coefficients of dispersion being: 0·73, 0·59, 0·78, 0·78, 0·82, 0·74, 0·87 and 0·51, the last only being significantly low. If these readings are combined the test of significance becomes $1 \pm 0\cdot485/\sqrt{9} = 1 \pm 0\cdot16$. The mean of the nine readings is 0·72, so taken together the results show a significant degree of uniform dispersion in the population.

A further, and more revealing, method of showing the spreading tendency of the shells is obtained by plotting the distance of each individual from its nearest neighbour. Inevitably a number of shells are found closer to the edge than to their nearest neighbour within the square, and this tends to leave a fairly substantial residue of shells in which the minimum distance is unknown. Since it is intended to show that individuals do not occur close together, this procedure would leave an element of doubt in the results. This has been overcome by marking a marginal strip round the sample area, of width 1 in., in which the shells are to be neglected, except in their capacity as neighbours. That is, the shells lying in the margin do not contribute a 'minimum distance' reading: they are, however, available when 'minimum distances' for shells in the inner square are being measured (Fig. 4).

The only distances still in doubt are those of shells in the inner square which are nearer to the outer edge than to any other shell. These must, however, be at least 1 in. from their nearest neighbour.

The results of the minimum-distance measurements for the nine squares are shown in Table I. It will be seen that there is a tendency for individuals seldom to occur closer than 1 in. apart, and none was found closer than 0·6 in.

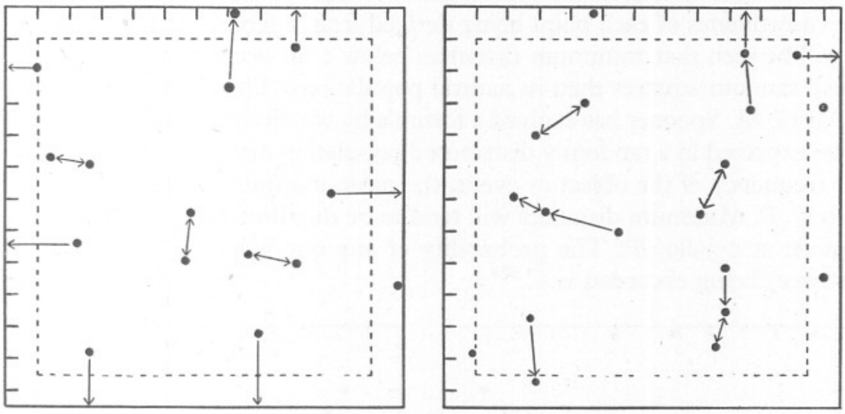

Fig. 4. Plot of positions in two $\frac{1}{10}$ m.^{2} squares, showing the method of measuring minimum distances. A, 30 ft. north-east of station F, 18. xi. 48, density 150 per m.^{2} B, Station F, 3. xi. 48, density 190 per m.^{2}.

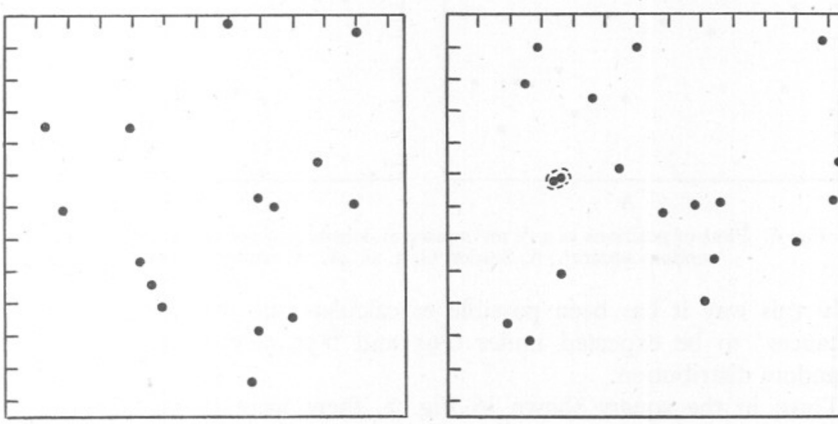

Fig. 5. Randomly distributed points in two $\frac{1}{10}$ m.^{2} squares, for comparison with Fig. 4. Points less than 0·6 in. apart are enclosed by dashes. A, density 150 per m.^{2} B, density 190 per m.^{2}

from its neighbour. That this lower minimum distance is not due to the space occupied by the shell itself is shown by subsequent results (p. 278) in which individuals occurred as close together as 0·1 in. Since the shells occupy a zone of 2 in. depth there seems to be no *a priori* reason why two should not occupy the same position in the horizontal plane, one above the other.

In interpreting the results it should be noted that where two shells are close to one another, the distance between them is often recorded twice, once in respect of each shell.

For comparison, plots have been made of points within 'random squares', the co-ordinates of each point being derived from a table of random numbers. It will be seen that minimum distances below 1 in. occur more frequently in these random squares than in natural populations (Figs. 5 and 6B; Table I).

Mr G. M. Spooner has evolved a formula by which the 'minimum distances' to be expected in a randomly distributed population may be derived. Given P, the frequency of the object or event, the mean minimum distance is shown to be $0{\cdot}5/\sqrt{P}$. Minimum distances will tend to be distributed asymmetrically with a mode at $0{\cdot}3989/\sqrt{P}$. The probability of any one value of x (the minimum distance) being exceeded is $\epsilon^{-x^2 \pi P}$.

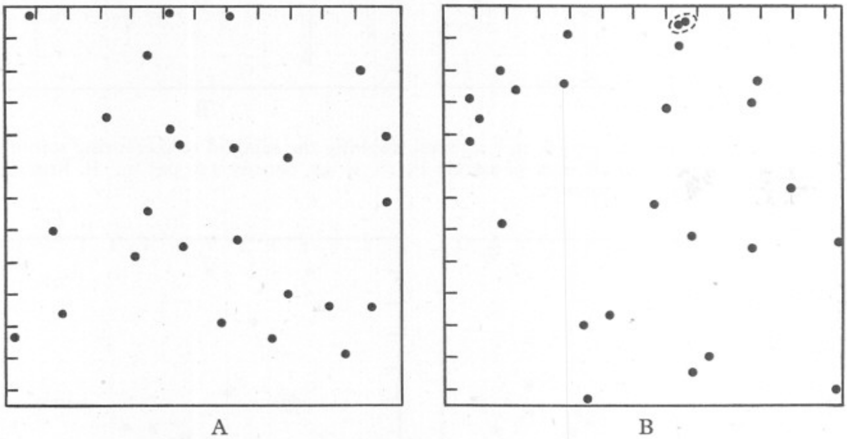

Fig. 6. Plots of positions in a $\frac{1}{10}$ m.² square of density 250 per m.², compared with a 'random square'. A, Station G, 3. xi. 48. B, random square.

In this way it has been possible to calculate the number of 'minimum distances' to be expected under 0·95 and 0·55 in. respectively, assuming a random distribution.

Thus, in the square shown in Fig. 2, there were twenty-eight animals ($P = 1/5{\cdot}54$ in.²), seventeen of which were within the 1 in. border. The probability of minimum distances exceeding 0·55 in. is calculated to be 0·8422, and $1 - 0{\cdot}8422 = 0{\cdot}1578$ are therefore expected below 0·55 in. Since seventeen animals occur, the number of minimum distances to be expected below 0·55 in. is $17 \times 0{\cdot}1578 = 2{\cdot}68$. In the same way a minimum distance of less than 0·95 in. has an expected frequency of 6·82.

Comparisons of expected and actual minimum distances are given in Table II. There is seen to be a tendency for minimum distances below about 1 in. to be eliminated by the spacing out of individuals.

Table I. Minimum Distances between Individuals in Natural Populations, Compared with those in the 'Random Squares' Shown in Figs. 5A, 5B and 6B.

The column marked 'others at least 1·0' refers to those shells in the inner square which are nearer the outside edge than to their nearest neighbour inside the square. The column marked 'Discarded, in border' refers to those in the outer border, whose minimum distances are not measured. Note that relatively more distances below 1·0 in. occur in the random squares.

			Minimum distance, in inches																		
Position	Date	Density ($\frac{1}{10}$ m.^{2})	>2·0	2·0	1·9	1·8	1·7	1·6	1·5	1·4	1·3	1·2	1·1	1·0	Others at least 1·0	0·9	0·8	0·7	0·6	0·5	<0·5	Discarded, in border
G	3. xi. 48	25	1	—	—	1	4	2	4	2	—	—	—	—	3	—	—	—	2	—	—	6
F	3. xi. 48	19	2	—	2	4	—	1	—	—	—	2	2	—	1	—	—	—	—	—	—	5
30′ N.E. of F (i)	18. xi. 48	15	3	—	—	—	—	—	4	—	—	2	—	—	4	—	—	—	—	—	—	2
30′ N.E. of F (ii)	18. xi. 48	15	4	—	—	—	—	2	—	—	—	—	—	—	2	—	—	—	—	—	—	7
30′ N.E. of F (iii)	18. xi. 48	14	4	1	—	2	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	3
30′ N.E. of F (iv)	18. xi. 48	17	3	—	1	—	—	2	—	—	—	—	2	—	5	—	—	—	—	—	—	4
F	11. vii. 49	28	2	—	—	1	—	2	1	2	—	2	—	1	6	—	—	—	—	—	—	11
6′ S. of F	11. vii. 49	21	3	—	—	2	—	—	—	—	3	—	—	—	2	—	2	1	2	—	—	6
G+75	11. vii. 49	19	4	—	1	2	2	—	2	—	—	—	1	—	3	—	—	—	—	—	—	4
Total		173	26	1	4	12	6	9	11	4	3	6	5	1	30	—	2	1	4	—	—	48
Random (Fig. 5A)	—	15	1	—	—	1	—	—	—	—	—	2	—	—	4	—	3	—	2	—	—	2
Random (Fig. 5B)	—	19	2	—	—	1	—	—	—	—	2	1	1	—	3	2	2	—	—	—	2	3
Random (Fig. 6B)	—	25	—	1	1	—	—	—	3	—	—	—	—	—	2	2	2	6	—	—	—	8

Table II. Table of Expected and Observed Minimum Distances for the Squares Shown in Table I.

		1·00 in. or over		0·95–0·60 in.		0·55 in. or under	
Density	In border	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.
25	6	12·03	17	4·27	2	2·70	—
19	5	9·78	14	2·63	—	1·59	—
15	2	9·79	13	2·03	—	1·18	—
15	7	6·03	8	1·24	—	0·73	—
14	3	8·52	11	1·58	—	0·90	—
17	4	9·43	13	2·24	—	1·33	—
28	11	10·18	17	4·14	—	2·68	—
21	6	10·21	10	2·98	5	1·81	—
19	4	10·48	15	2·82	—	1·70	—
	Total	86·45	118	23·93	7	14.62	0

Artificial populations

If the population density is increased the chances of randomly distributed individuals coming to lie close together becomes greater. Two experiments have been made in which individuals were concentrated within a metal circle from which they could not escape. After a period of several weeks a $\frac{1}{10}$ m.^{2} area within the circle was excavated and positions of the shells plotted.

Experiment I

The metal circle was made from a strip of sheet steel 6 ft. long and 6 in. wide, which was bent into a circle of diameter *c.* 22 in., and the ends joined. The circle was pushed into the sand until its top was level with the surface.

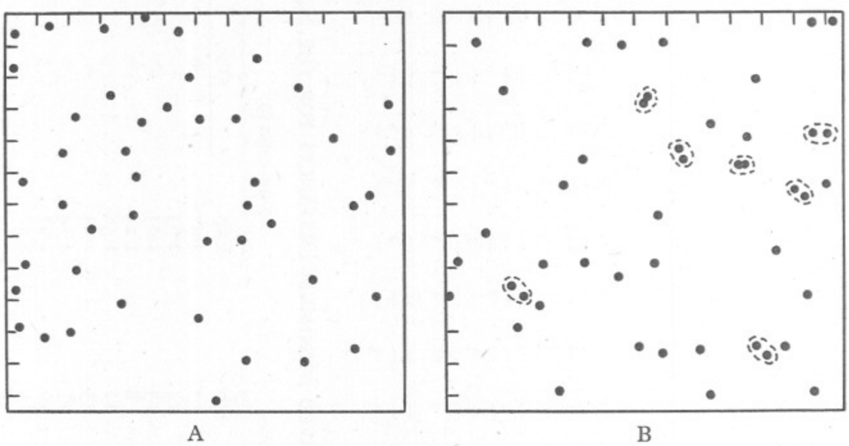

Fig. 7. A, plot of positions in a $\frac{1}{10}$ m.^{2} square of artificially high density (Exp. I), 30. iii. 49, density 460 per m.^{2} The animals have dispersed from a point just outside the top left-hand corner. B, random square of the same density.

The position chosen was 15 ft. north-east of Station F, where there is a fairly well drained sand supporting a small natural population of *Tellina*. About 100 specimens of *Tellina*, of various sizes, were sieved from sand near low-water mark and placed in a small pit near the edge of the enclosed area. They were then covered over with sand and left for 8 weeks, when a $\frac{1}{10}$ m.^{2} square was excavated. Forty-six shells were found, their positions being shown in Fig. 7A.

The pit in which the shells were originally placed is just outside the square, at the top left-hand corner in the figure, and it will be seen that the population density is higher towards this corner. Examination of the area where the shells had been introduced revealed quite a number which had not yet spread out.

Dividing the large square into thirty-six smaller squares, a coefficient of dispersion of 0·43 is obtained, which is significantly different from unity.

Plots of minimum distances gave the following results:

	Artificial population	Random square
Density	46	46
No. in outer margin	14	11
No. 1 in. or more from edge	2	2
Minimum distances (in.):		
<0·5	—	14
0·5	—	—
0·6	2	1
0·7	—	3
0·8	2	—
0·9	5	1
1·0	3	3
1·1	3	—
1·2	5	6
1·3	2	1
1·4	1	—
1·5	—	1
1·6	3	—
1·7	1	1
1·8	1	1
1·9	—	1
2·0	2	—
>2·0	—	—

These results may be summarized thus:

	Density	In border	1 in. or over	0·95–0·6 in.	<0·55 in.
Artifical population	46	14	23	9	0
Random square	46	11	16	5	14
Expected (from formula)	46	[14]	15·23	9·73	7·04

Spacing-out is shown by the absence of individuals below 0·55 in. rather than in reduced numbers between 0·95 and 0·6.

The results of this experiment show that individuals can spread out and take up their characteristic arrangement in the adult stage, and in a fairly short space of time.

After excavation, most of the shells were returned to the circle, and covered over. A $\frac{1}{10}$ m.^{2} square was again excavated $3\frac{1}{2}$ months later, only twenty-eight specimens being taken.

'Minimum distance' measurements were as follows:

Density		28	
No. in outer margin		7	
No. 1 in. or more from edge		1	
Minimum distances:			
in.		in.	
<0·5	2	1·3	2
0·5	—	1·4	—
0·6	—	1·5	1
0·7	2	1·6	1
0·8	—	1·7	6
0·9	2	1·8	—
1·0	1	1·9	—
1·1	2	2·0	—
1·2	1	>2·0	—

This square is the only one so far in which individuals have been found less than 0·5 in. apart. The general arrangement is otherwise as in natural populations.

Experiment II

About 200 specimens of *Tellina* were placed within a smaller circle, diameter 17 in., close to the previous position. The specimens were scattered over the surface of the sand and covered over. An attempt was made to excavate $4\frac{1}{2}$ weeks later, but this had to be abandoned owing to rain, which started to fill the hole. Only eleven specimens had been removed and these were replaced in the circle.

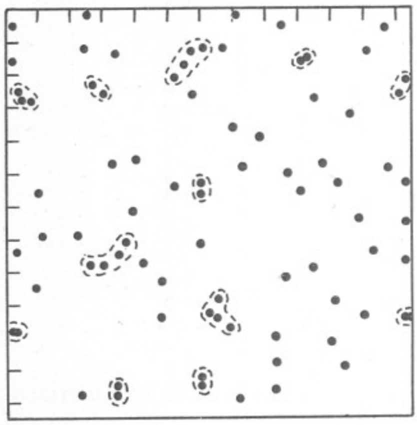

Fig. 8. Plot of positions in a $\frac{1}{10}$ m.^{2} square of artificially high density (Exp. II), 13. vi. 49, density 810 per m.^{2} Note that in thirty-one cases animals occur closer than 0·6 in. apart.

Eight weeks from the start of the experiment, a $\frac{1}{10}$ m.^{2} square was successfully plotted (Fig. 8). The density was eighty-one and when the square was subdivided into thirty-six 2 in. squares, seventy-four were contained within them. The coefficient of dispersion is 0·54, which is just within the limits of significance.

Measurements of minimum distance, however, show that the characteristic spacing found at lower densities had not been assumed:

Density	81
No. in outer margin	25
No. 1 in. or more from edge	1

Minimum distances:

in.		in.	
<0·5	20	1·0	6
0·5	1	1·1	3
0·6	2	1·2	0
0·7	2	1·3	2
0·8	9	1·4	0
0·9	9	1·5	1

The formula gives 21·93 individuals below 0·55 in., and 21·36 between 0·95 in. and 0·6 in., which is very close to that attained by the animals in this experiment.

Thus in this square the animals are spread rather evenly, judged by information obtained by subdividing the large square; but are distributed at random as shown by minimum-distance measurements. The even distribution is probably explained by the animals being spread out at the start of the experiment, and is of little consequence.

The absence of any tendency to spread out from one another is remarkable, and shows that the 'minimum distance' shown in previous results does not limit the density in an upward direction. Observations on dense natural populations are needed to confirm this break-down of the 'minimum distance' at higher densities, but in view of the constancy of results on previous occasions the results of the last experiment cannot be disregarded.

The occurrence of animals as close together as 0·1 in. shows that the minimum distance is not controlled by the size of the shell itself, but may be the result of some aspect of the animal's behaviour.

Discussion

Aggregation in a population can be quite easily shown by statistical treatment of a very few samples. If any two are widely divergent, aggregation can be shown to occur. On the other hand, an even distribution can only be shown by a much larger number of samples, and any small errors in technique will tend to make the figures approach random.

The results obtained with *Tellina* show that a significant degree of 'over-dispersion' or evenness of the population does occur. This over-dispersion applies to individuals occurring in any one small area, and also to populations extending from low tide up to half-tide mark on the beach in question.

One aspect of this distribution is shown by measuring the distance of each animal to its nearest neighbour. In natural populations it is shown that fewer than would be expected occur less than 1 in. apart, and none occur less than 0·6 in. apart. Where populations on the shore were artificially increased the same type of spacing was shown at a higher density (460 per $m.^2$), but not at a density of 810 per $m.^2$ As the density increases the chances of randomly distributed individuals lying close to one another is increased, so that at a density of 460 per $m.^2$ a result significantly different from random has been obtained.

It is possible that at moderate densities each individual occupies a territory delineated by the activities of the inhalent siphon on the soil surface, but that at higher densities the spacing breaks down owing to the confusion resulting from a number of siphons meeting one another on the surface. Thus the 'territory', if there be one, would seem not to limit density. This is supported by observations of Stephen (1928–30), who found populations as high as 7588 per $m.^2$ in Kames Bay. Examination of Stephen's data shows no evidence of uniform populations either at any one place or over a stretch of shore, as occurs in the Exe. In fact, Stephen (1930) has emphasized the variability in populations at any one place. He excavated four $\frac{1}{4}$ $m.^2$ areas within a few yards of each other at St Andrews and found the following numbers in each: 114, 136, 111 and 163 respectively. These show a coefficient of dispersion of 4·4, which indicates a significant degree of aggregation. It is possible, however, that there may have been drainage or other differences in conditions between the four areas.

Although the even distribution in the Exe might be due to an even spat settlement, the results with artificially increased populations indicate that the spacing can be taken up in the adult stage. It is not at all clear, however, how such an even spacing over a distance of 215 ft. up the shore has occurred.

Certain other lamellibranchs, notably *Macoma*, *Abra* and *Scrobicularia* have a similar mode of life to *Tellina*; and it would be of interest to examine their distribution where they occur in fairly dense beds.

Summary

A population of the lamellibranch *Tellina tenuis* in the Exe estuary is shown to be uniformly distributed, indicating a significant degree of 'over-dispersion'.

By plotting the position of each shell in squares of $\frac{1}{10}$ m.^{2} area it is shown that fewer individuals than would be expected occur less than 1 in. from their nearest neighbour, and none occurs closer than 0·6 in.

When the population density was artificially increased on the shore the same characteristic spacing was found at a moderate density, but not at a rather higher density.

It is suggested that spacing is correlated with the foraging activities of the inhalent siphon on the soil surface.

Very dense populations have been found by Stephen in other areas, indicating that the size of the 'territory' does not limit density. His results show no evidence of the same phenomena as observed in the Exe.

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