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ON THE VARIABILITY OF REPLICATE PLANKTON SAMPLES AND SOME APPLICATIONS OF 'CONTAGIOUS' SERIES TO THE STATISTICAL DISTRIBUTION OF CATCHES OVER RESTRICTED PERIODS

By H. Barnes and S. M. Marshall

The Marine Station, Millport

(Text-figs. 1–4)

The variability to be expected in replicate plankton hauls, using several methods of hauling and a number of different nets, has been examined by Winsor & Clarke (1940). Some of the variability is due to true sampling variations, inevitable when discrete entities in suspension are sampled, and some is due to inadequacies of sampling technique. Winsor & Walford (1936) found that the variability of their vertical net hauls could be explained on the basis of a random distribution of the population, the variations being ascribed to variations in the volume of water filtered in successive hauls. They fully realized that the alternative, namely a non-random distribution of the population, was not disproved; but they considered that since widely different organisms showed little difference in variability the evidence was strongly in favour of a random distribution. They did note, however, that agreement between these different organisms was less marked when the numbers caught were large.

Analysis of net data by Barnes (1949*a*) was not at variance with the above hypothesis, agreement with Winsor & Walford's results being quite satisfactory. However, when the volume of water filtered was carefully controlled by the use of a plankton pump the variability was of a similar order and the distribution of χ^2 as well as its relation to sample size was similar (Barnes, 1949*b*). This cast doubt upon the validity of the assumption of a random distribution of population.

Ricker (1937) has examined the variability of catches of fresh-water plankton, and has pointed out that the variance is often greater than the mean and that this is evidence of aggregation of the organisms. This work has been extended by Langford (1938), who compared the mean and variance of a number of hauls taken at one station as well as over an area. He found evidence that some of the organisms were aggregated while others could be considered as randomly distributed. However, only a small number of hauls were examined. Similar work by Southern & Gardiner (1926), Ruttner (1930)

and Baldi, Cavalli & Pirocchi (1945) has been done on various fresh-water lakes. The problem is in many ways similar to that of the distribution of individual plants, and there has been considerable progress in this work (see reviews by Ashby, 1936, 1948).

The detailed form of the distribution[1] can be determined if a number of samples are available for the construction of frequency diagrams. In the present paper a modified method of collecting small samples in large numbers is described and this has, for the first time, enabled frequency distributions to be set up for plankton.

One of us (H. B.) would like to take this opportunity of thanking Dr R. A. Robb for many valuable and friendly discussions on statistical matters, and we both wish to thank him and Dr F. J. Anscombe for criticism of this paper.

We also wish to thank Captain Stewart and the crew of the *Calanus* for their assistance in the collection of the samples.

The Collection and Counting of the Samples

In order to obtain a large number of small samples, in which the volume was accurately controlled, the following procedure was adopted. A series of fourteen matched aspirators was set up in a rack, and underneath the stopcock of each a copper tube 1 in. diameter was fastened to a bar running across the front of the whole series. A piece of fine bolting silk (200 meshes/in.) was held over the base of the tube by means of a 'jubilee' clip. The use of aspirators with a narrow neck enabled an accurate volume to be rapidly taken. The mean volume of the aspirators was 5867 ml. with a standard deviation of 84 ml., and therefore a coefficient of variation of only 1·4 %. In all the experiments water was pumped continuously, one person filling up the aspirators until they overflowed. The tap was then opened and the water filtered through the silk on the copper tube. After rinsing the aspirator with filtered sea water and passing the washings through the copper tube the silk was carefully removed, the plankton washed off into a small bottle or specimen tube and a little formalin added. By employing ten people the whole process was kept more or less continuous during the sampling period. Welch (1948) has recently criticized pump-sampling technique, but his objection, namely that water is drawn from depths other than that nominally sampled, does not apply to these experiments, where only small volumes were taken (for example 720 l. *total* in series I) and where some relative movement of ship and water must have taken place.

At first it appeared probable that a reversed-microscope technique would be most suitable for the examination and counting of the plankton. In the

[1] 'Distribution' is used throughout in both the statistical and general sense; it is clear from the context which meaning is intended.

earlier samples, therefore, after allowing the plankton to sediment in the specimen tube and removing the excess water, it was transferred to a small Perspex vessel holding about 40 ml. and allowed to settle for at least 2 hr. before examining with a reversed microscope. When the sample was clean and the animals were undamaged this was satisfactory, but some of the samples had a great deal of detritus and this, concentrated on the restricted area of the bottom, hid the smaller animals. In addition, it was impossible to re-orientate one animal without disturbing a large area of the sample, and if many animals had to be thus moved the whole sample was disarranged.

With the later samples therefore this reversed microscope technique was abandoned. It was found best to let the plankton settle in the specimen tube and then draw off the overlying water by suction through a tube whose mouth was covered with fine silk, taking care not to disturb the settled plankton, and to wash this out into a small Bogorov-type tray made of Perspex and holding about 8 ml. The plankton was then examined with a dissecting microscope. A number of samples were counted by both methods; when the samples were clean the numbers were the same but when there was much detritus the reversed-microscope count gave a smaller number. Although passage through the pump, on the whole, did not damage the animals appreciably, some of the nauplii had lost their long tail spines (e.g. *Temora* and *Centropages*) and a good many of the *Oithona* copepodites had lost the abdomen. It was then sometimes impossible to assign them to the correct copepodite stage.

Three series of samples have been taken. In the first two series (10 and 11 February 1949) 120 and 300 samples respectively were taken from a single constant depth of 10 m. In the third (3 May 1949) four depths, 1, 5, 8 and 10 m. were sampled (see pp. 252–5). In all the experiments the boat was allowed to drift.

Series I and II were taken at a depth of 10 m. in 60 m. of water, in the channel between the Islands of Cumbrae and Bute (about 4° 55′ W., 55° 47′ N.), there being a distinct tendency during the experiment to drift to the south-east. For several days previous to this the wind speed had averaged 19 m.p.h. and during series I it varied from 10 to 14 m.p.h. from a direction of 300° backing to 290°. There was rather more wind on the following day, 20–25 m.p.h., from direction 290° to 270°. The weather was bright on the 10th, overcast on the 11th. Both these series were collected between 10.30 and 14.00 hr. High tide was 9.28 and 10.38 hr. at Greenock on the 2 days, so that the samples were collected on the ebb tide. During the first two series no observations were made of temperature or salinity. However, the sea-surface temperatures were in the neighbourhood of the winter minimum, between 7·0 and 7·5° C., while the salinity was about 31·5 $^{\circ}/_{\circ\circ}$, these figures being obtained in routine observations at Keppel Pier.

In series III, 400 samples were collected at four depths, 1, 5, 8 and 10 m., the depth at the station being 60 m. The position was somewhat different,

slightly to the east of south of Little Cumbrae Island, about 4° 57′ W., 55° 41′ N., the ship again being allowed to drift. The wind had been very light for the preceding days (mean 7 m.p.h.), but during the morning of the 3rd it rose and remained at 15–20 m.p.h. during the experiment, the direction being 200–215°. The sky was overcast throughout. During this series temperature and salinity observations were made, the observations being taken as nearly as possible to correspond with the middle of the period during which any part of the collection was being made. The observations are summarized below (Table I), further reference to them being made later.

TABLE I. TEMPERATURES AND SALINITIES OF POSITIONS SAMPLED IN SERIES III

	Period									
	i		ii		iii		iv		v	
Depth (m.)	Temp. (° C.)	Salinity (‰)	Temp. (° C.)	Salinity (‰)	Temp. (° C.)	Salinity (‰)	Temp. (° C.)	Salinity (‰)	Temp. (° C.)	Salinity (‰)
1	9·64	31·85	9·61	31·78	9·70	31·67	9·78	31·65	9·90	31·73
5	9·23	32·00	9·46	31·89	9·64	31·78	9·56	31·74	9·70	31·82
8	9·00	32·09	9·21	32·03	9·60	31·80	8·88	32·03	8·90	31·92
10	8·76	32·07	9·18	32·09	9·58	31·65	8·81	32·09	8·79	31·96
Time B.S.T.	10.15 to 11.03		11.09 to 11.49		11.59 to 13.05		13.13 to 14.01		14.09 to 15.03	

A PRELIMINARY COMPARISON WITH PREVIOUS INVESTIGATIONS

It will facilitate subsequent discussion if the results are considered using the methods of previous workers, and for this purpose only those from the simpler series (I and II) will be used. In previous work (Winsor & Walford, 1936; Barnes, 1949*a*, *b*) comparison has been almost entirely limited to paired hauls (see, however, Winsor & Clarke, 1940). χ^2 has been calculated from such paired catches, and the resultant distribution of χ^2 compared with that expected on a Poisson distribution. Using this method the results from two former sets of data (Barnes, 1949*a*, *b*) and from the present series are compared. For the present series counts of all organisms were used when $n_1+n_2>9$, paired samples being obtained by grouping sets of ten small samples in consecutive pairs.

The results are shown as the distribution of χ^2 and as the relationship of χ^2 to sample size (Tables II and III). In spite of the very great differences in volume of water filtered, several cubic metres with the nets and several hundred litres in the present samples, the results are very similar. The most noticeable feature, as was originally pointed out by Winsor & Walford for their own data, is the very large number of values showing a high χ^2 ($>3{\cdot}841$) (Table II), and the fact that the larger values of n_1+n_2 contribute largely to this value of χ^2; both features are clearly common to all the collections.

A further point can be considered at this stage. It was emphasized by Winsor & Clarke that in their results the standard deviation of the catches was roughly proportional to the mean, and they therefore use logarithmic values to stabilize the variance in their analyses. In the present series, although not directly proportional, the standard deviation increases roughly linearly with the mean, and strictly a transformation of the type $1/\beta \sinh^{-1}\beta\sqrt{x}$ is more appropriate. However, in view of the arbitrary character of some of the

TABLE II. THE DISTRIBUTION OF χ^2 FOR POISSON (EXPECTED ON A RANDOM DISTRIBUTION) AND NET, PUMP AND PRESENT SAMPLES FOR ALL ORGANISMS

	Poisson	Nets	Pump	Series I and II, present observations
0–0·0039	5	4·5	5·5	5·7
–0·0158	5	1·5	3·6	1·6
–0·0642	10	3·7	3·6	6·6
–0·148	10	5·2	9·1	9·1
–0·455	20	10·4	9·1	10·1
–1·074	20	11·2	5·5	14·2
–1·642	10	9·0	12·7	11·3
–2·706	10	11·9	7·3	10·4
–3·841	5	11·2	3·6	7·6
>3·841	5	31·3	40·0	23·4

TABLE III. SUM OF χ^2 BY SAMPLE SIZE (POPULATION DENSITY)

(Numbers in brackets indicate number of samples in each group.)

n_1+n_2	Net	Pump	n_1+n_2	Series I and II, present observations
5–40	128·9 (50)	8·6 (12)	10–50	197·9 (133)
40–170	100·5 (44)	65·4 (19)	50–100	156·7 (72)
170–400	69·1 (19)	51·7 (7)	100–150	154·1 (35)
400–1000	161·5 (9)	128·7 (11)	150–200	99·5 (23)
>1000	1726·2 (12)	227·7 (6)	200–250	64·8 (12)
			250–350	64·4 (20)
			350–(3029)	343·2 (23)

divisions made in considering the results, the more complex transformation was not used, the logarithmic transformation being considered adequate. When both transformations were used on selected parts of the data there was no difference in the conclusions to be drawn.

THE STATISTICAL CONCEPTS USED

The study of variation leads naturally to the concept of frequency distributions in which the frequency of the variable quantity under consideration takes each of its possible values. In plankton sampling the number of organisms is discrete, and therefore the frequency distribution is essentially discontinuous. When there is a relatively small number of organisms compared with elemental

units of medium, then with the organisms randomly distributed the sampling distribution is described by Poisson's limit to the Binomial Expansion. The relative frequencies with which the samples will contain 0, 1, 2, ..., organisms is given by the series, $e^{-m}, me^{-m}, \frac{m^2}{2!}e^{-m}, \ldots, e^{-m}\frac{m^k}{k!}, \ldots$, where m is the mean number per sample.

Alternatively one may write, $P(x=k)=\frac{m^k e^{-m}}{k!}$, where $P(x=k)$ denotes the probability that a sample will contain k organisms. Agreement between a theoretical and an experimentally determined distribution may be tested by means of the χ^2 test, and $P(\chi^2)=0{\cdot}05$ will be considered the acceptable limit of significance (the classes are grouped when the expected value is less than 5; the degrees of freedom are $n-2$ for testing Poisson). A supplementary test is to calculate the variance and its ratio to the mean. With a Poisson distribution this ratio is unity and the departure from unity is a measure of dispersion. This ratio has been termed the relative variance by Clapham (1936), but Fisher's coefficient of dispersion (Blackman, 1942) appears a more suitable term. The coefficient of dispersion itself has a distribution, and in order to be significantly different from unity it must be greater (or less) by $2\sqrt{[2n/(n-1)^2]}$, where n is the number of samples. The coefficient of dispersion is sensitive as regards aggregation but it will not detect certain types of skew distribution.

It has been found, particularly by botanists studying the distribution of individual plants, that when a Poisson distribution does not fit their data, there are often too many samples containing no individuals and too few containing one individual when compared with the appropriate Poisson series, and as a result the observed frequency curves sometimes show bimodality. New series comparable with Poisson series have been developed which show this same tendency, such series being originally termed 'contagious' by Pólya (1931). Those developed by Neyman (1939) and Thomas (1949) seem to be particularly suitable for biological work (Archibald, 1948, 1950; Beall, 1940; Barnes & Stanbury, 1951).[1] Both are based on the same fundamental assumption, namely, a random distribution of the groups and a random number per group. The presence of a particular individual in a given region increases the probability of there being other individuals present (hence the term contagious series). Beall, working on insects, found that Neyman's Type A (which is the most easily calculated) is the most generally useful of the three Neyman series, and only Type A will be considered here. When the three types are different Beall showed that passing from Type A to B to C the expectation for the 0-frequency class falls, and for classes immediately after 0 tends to rise and then to fall for all subsequent classes. The Type A series, which was developed with

[1] For a further discussion of such series see Anscombe (1949, 1950).

particular reference to the emergence of insect larvae from egg masses, when put into the recurrent form of Beall is[1]:

$$P(x=0)=e^{-m_1(1-e^{-m_2})},$$

$$P(x=k+1)=\frac{m_1m_2e^{-m_2}}{k+1}\sum_{t=0}^{t=k}\frac{m_2^t}{t!}P(x=k-t).$$

The distribution is determined by two parameters m_1 and m_2 in contrast to the Poisson series which is completely determined by one parameter, the mean. These parameters can be taken to be proportional to the mean number of groups per sample (m_1) and to the mean number of individuals per group (m_2). They can be estimated from the first and second moments, since

$$m_2=(\mu_2-\mu_1')/\mu_1', \quad m_1=\mu_1'/m_2.$$

Since

$$\mu_2/\mu_1'=m_1m_2/m_1m_2(1+m_2),$$

it is clear that where m_2 becomes very small and m_1m_2 is finite the distribution approaches Poisson, where

$$\mu_2/\mu_1'=1.$$

Thomas's series, with similar fundamental assumptions, also expresses a contagious distribution. It is given by the following:

$$P(x=0)=e^{-m},$$

$$P(x=k)=\sum_{r=1}^{k}\frac{m^re^{-m}}{r!}\left[e^{-r\lambda}\frac{\lambda^{(k-r)}r^{(k-r)}}{(k-r)!}\right].$$

The parameter m is the mean number of groups per sample, whilst $1+\lambda$ is the mean number of individuals per group. As before, the parameters are obtained from the first and second moments:

$$\mu_1'=m(1+\lambda), \quad \mu_2=m(1+3\lambda+\lambda^2).$$

Clearly, as λ becomes very small the distribution approaches Poisson. Since this series is the sum of the products of two simple Poisson series

$$\frac{e^{-m}m^r}{r!} \quad \text{and} \quad e^{-r\lambda}\frac{\lambda^{(k-r)}r^{(k-r)}}{(k-r)!},$$

the terms can be obtained by interpolation from tables (Pearson, 1948).

The frequency distributions given by both Neyman's and Thomas's series are very similar, as might be expected, since they are based on similar fundamental assumptions regarding the population (Barnes & Stanbury, 1951).

[1] $P(x)$ denotes the probability that the number of individuals in any one sample is x. In applying the χ^2 test, 3 degrees of freedom should be subtracted from the total when dealing with the Neyman and Thomas distributions.

However, from the point of view of interpreting the aggregation mentioned, Thomas's parameters are more useful, since the mean number of groups per sample and the mean number of individuals per group are at once evident.

The Hauls of Series I

This was the first series using the new technique and 120 samples were collected in $2\frac{1}{2}$ hr.; improved organization enabled more samples to be taken in the same time in later series.

In this series the dominant organisms were: *Pseudocalanus minutus* (Krøyer), *Microcalanus pygmaeus* G. O. Sars, *Temora longicornis* (Müller), *Oithona similis* Claus (all as nauplii), lamellibranch larvae and small eggs (not identified). A small number of nauplii of *Acartia clausi* Giesbrecht were found.

Since the samples were taken over a considerable period of time it is first necessary to examine the results for possible changes in the population during the period of sampling. For this purpose the samples have been grouped in consecutive sets of fifteen, and the results are shown in Table IV and Fig. 1. It is clear from the figure that the organisms are behaving differently. The lamellibranch larvae and the egg population appear to be constant throughout, but *Pseudocalanus* and *Microcalanus* show a sharp, and *Temora* a less sharp, change at about sample 60, whilst *Oithona* nauplii show a tendency to change somewhat later in the series. The change in population is presumably a change either with time or with distance. There is little evidence to suggest that the change is dependent upon time *per se*, as for example in vertical migration. It is rather to be ascribed to a change in space consequent upon the relative changes between boat and water mass with time.

The above suggestion can be tested by considering the first four sets as replicates belonging to period 1 and the second four to period 2 (corresponding to the change indicated by Fig. 1 at sample 60) and an analysis for *Oithona* nauplii, lamellibranch larvae and eggs is given in Table V.

The mean squares for P and P × S are not significant[1] when tested against the appropriate residual, and one can assume that the same population was being sampled throughout. By contrast a similar analysis of *Pseudocalanus*, *Microcalanus* and *Temora* nauplii is given in Table VI.

With these species, although the P × S interaction is not significant, that is the species were caught in the same proportion in the two periods, the value for P is highly significant.

It seems therefore that two distinct populations of *Pseudocalanus*, *Microcalanus* and *Temora* were sampled during the experiment, the boundary between these two populations being sharply defined. Furthermore, there co-existed constant populations of lamellibranch larvae, eggs and to a large

[1] It will be assumed throughout that the results and the tests of significance are to apply to these experiments only.

TABLE IV. COUNTS OF ORGANISMS IN SERIES I

Sample nos. ...	1–15	16–30	31–45	46–60	61–75	76–90	91–105	106–120
Pseudocalanus nauplii	7	8	13	17	38	41	33	26
Microcalanus nauplii	38	41	47	46	101	94	109	70
Temora nauplii	8	25	16	29	33	55	36	67
Oithona nauplii	29	23	20	26	30	28	33	43
Lamellibranch larvae	47	51	35	34	55	43	55	39
Eggs	9	7	11	1	8	9	6	12

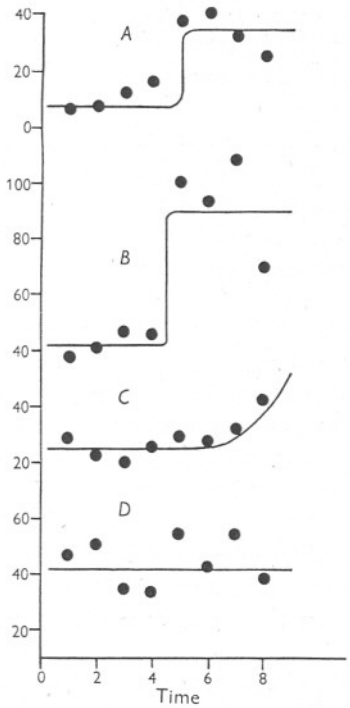

Fig. 1. Counts for repeated hauls, series I, for (A) *Pseudocalanus* nauplii, (B) *Microcalanus* nauplii, (C) *Oithona* nauplii, (D) lamellibranch larvae.

TABLE V

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	1	0·1149	0·1149
Residual 1	6	0·2812	0·0469
Species (S)	2	2·9845	1·4928
P × S	2	0·0244	0·0122
Residual 2	12	0·5329	0·0444

TABLE VI

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	1	1·0583	1·0583
Residual 1	6	0·1939	0·0323
Species (S)	2	1·1263	0·5632
P × S	2	0·0307	0·0154
Residual 2	12	0·2070	0·0173

extent *Oithona*. The biological relationship between these populations can be a matter for much speculation. If they have a common origin in a much denser concentration it may mean that one portion of the water mass in which this dense concentration was originally present has maintained its identity to a greater extent or for a longer time than the rest of the water mass. If this were so it is perhaps rather surprising to find extremely sharp boundaries. On the other hand, the two populations may have entirely different origins and may have come together as a result of water movements.

These possibilities might have been tested by a closer examination of the composition of the two populations, for example by size measurements or by finding the proportions of the different nauplius stages, but unfortunately the samples were thrown out before this was realized. The foregoing is based on the idea that the movement of copepod nauplii is dependent on the movement or mixing of water masses. Alternatively, such a mixing of populations may be due to the active movement of swarms of copepods away from denser centres of distribution.

The mean square for $P \times S$ is not significant in the analysis for *Pseudocalanus*, *Microcalanus* or *Temora* nauplii, although the value for P is highly significant, that is to say the proportions of the different species did not change significantly although the total numbers changed in the two halves of the experiment. This perhaps adds weight to the suggestion that the populations have a common origin and have become separated by a greater dilution of one portion.

In forming frequency distributions, the populations uniform throughout, namely *Oithona similis* nauplii, lamellibranch larvae and eggs, will be considered first. The frequency distributions and the various parameters are shown in Table VII.

Oithona similis nauplii. The coefficient of dispersion is not significantly different from unity and $P(\chi^2)$ for Poisson is 0·2–0·1, indicating an adequate fit to a random distribution. However, there is a clear indication of an excess of the 0-frequency class suggestive of aggregation or clumping, and it is clear from Table VII that both Neyman's and Thomas's series give a better fit to the observed results. From the Thomas parameters the estimated mean number of nauplii per clump $(1+\lambda)$ is 1·1.

Lamellibranch larvae. The results are very similar to those for *Oithona*. The coefficient of dispersion and the χ^2 test indicate an adequate fit to a Poisson series. Again the 0-frequency class is high, suggesting aggregation. The Neyman and Thomas series, again similar as would be expected, give a better fit and the mean number per clump as derived from $(1+\lambda)$ is 1·4. It should be noted that the mean is higher than with the previous species, and the increase in the mean is accompanied by an increase in the mean size of the aggregates.

Eggs. These small eggs were not identified and belonged to several different organisms and perhaps because of this none of the series gives an adequate fit.

There are an insufficient number of degrees of freedom to test the series but the 0-frequency class, although high, does not appear to be as high as required by contagion.

TABLE VII. SERIES I. ANALYSIS OF FREQUENCY DISTRIBUTIONS OF THE 'UNIFORMLY' DISPERSED FORMS. (120 SAMPLES)

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

	Oithona similis nauplii	Lamellibranch larvae	Eggs
Mean	1·933	2·992	0·517
Variance	2·349	4·849	0·975
C.D.	1·215	1·621	1·885
$2\sqrt{[2n/(n-1)^2]}$	0·260	0·260	0·260
Ny., m_1	9·000	4·819	0·583
Ny., m_2	0·215	0·621	0·886
Th., m	1·736	2·204	0·336
Th., λ	0·114	0·358	0·537
$P(\chi^2)$			
Pn.	0·2–0·1	0·1–0·05	<0·05
Ny.	0·5–0·3	0·7–0·5	<0·05
Th.	0·5–0·3	0·8–0·7	<0·05

Frequency class	Found	Expected Pn.	Ny.	Th.	Found	Expected Pn.	Ny.	Th.	Found	Expected Pn.	Ny.	Th.
0	**23**	17·4	21·1	21·1	**11**	6·0	12·9	13·3	**80**	71·6	85·2	85·8
1	**28**	33·6	33·0	32·8	**24**	18·0	20·8	20·4	**26**	37·0	18·2	16·8
2	**34**	32·5	29·3	29·1	**20**	27·0	23·2	23·0	**12**	9·6	9·9	10·6
3	**17**	20·9	19·2	19·1	**23**	26·9	20·7	19·9	**0**	1·7	4·2	4·3
4	**8**	10·1	10·2	9·9	**17**	20·1	15·9	15·9	**0**	0·1	1·6	1·6
5	**7**	3·9	4·7	4·2	**11**	12·0	11·0	11·4	**1**	—	0·5	0·6
6	**3**	1·6[1]	2·5[1]	3·8[1]	**5**	6·0	6·9	7·3	**0**	—	0·4	0·2
7	—	—	—	—	**4**	2·6	4·1	4·2	**1**	—	—	0·1
8	—	—	—	—	**3**	1·0	2·3	2·3	—	—	—	—
9	—	—	—	—	**1**		1·2	1·2	—	—	—	—
10	—	—	—	—	**0**	0·3[1]	0·6	0·6	—	—	—	—
11	—	—	—	—	**0**		0·3	0·3	—	—	—	—
12	—	—	—	—	**1**		0·1[1]	0·1[1]	—	—	—	—
13	—	—	—	—	—	—	—	—	—	—	—	—
14	—	—	—	—	—	—	—	—	—	—	—	—

[1] In this and all subsequent tables of this kind the last class shown of the expected values is obtained by subtraction and includes any higher frequency classes.

The two remaining species are dealt with in the two periods each with uniform population, the results of the analyses being given in Table VIII.

Pseudocalanus minutus nauplii (*samples* 1–60). An excellent fit to a random distribution is obtained and no further comments on this series are necessary.

Microcalanus pygmaeus nauplii (*samples* 1–60). The results for this copepod are in excellent agreement with a random distribution, $P(\chi^2)$ for Poisson being 0·9 and the coefficient of dispersion very little different from unity, although the population density is moderately high.

Pseudocalanus minutus nauplii (*samples* 61–120). $P(\chi^2)$ with Poisson is 0·1–0·05, but for Neyman and Thomas series it is much higher (0·9), showing a closer agreement and again indicating some aggregation.

Microcalanus pygmaeus nauplii (*samples* 61–120). In the second part of this series the population density increased very considerably, and since there is

TABLE VIII. SERIES I. ANALYSIS OF FREQUENCY DISTRIBUTIONS OF *PSEUDOCALANUS* AND *MICROCALANUS*

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

	Samples 1–60		Samples 61–120	
	Pseudocalanus minutus nauplii	*Microcalanus pygmaeus* nauplii	*Pseudocalanus minutus* nauplii	*Microcalanus pygmaeus* nauplii
Mean	0·750	2·867	2·300	6·233
Variance	0·801	3·304	3·671	14·419
C.D.	1·068	1·152	1·596	2·314
$2\sqrt{[2n/(n-1)^2]}$	0·371	0·371	0·371	0·371
Ny., m_1	—	—	3·858	4·745
Ny., m_2	—	—	0·596	1·313
Th., m	—	—	1·715	3·364
Th., λ	—	—	0·341	0·853
$P(\chi^2)$	Pn., 0·7–0·5	Pn., 0·9	Pn., 0·1–0·05 Ny., 0·95–0·90 Th., 0·98–0·95	Pn., <0·05 Ny., 0·2–0·1 Th., 0·2–0·1

						Expected				Expected		
Frequency class	Found	Expected Pn.	Found	Expected Pn.	Found	Pn.	Ny.	Th.	Found	Pn.	Ny.	Th.
0	**28**	28·3	**2**	3·4	**11**	6·0	10·6	10·8	**2**	0·1	1·9	2·1
1	**23**	21·3	**12**	9·8	**13**	13·8	13·5	13·1	**3**	0·7	3·1	3·0
2	**6**	8·0	**14**	14·0	**13**	15·9	12·5	12·5	**6**	2·2	4·7	4·7
3	**2**	2·0	**15**	13·4	**8**	12·2	9·5	9·4	**5**	4·7	5·8	5·7
4	**1**	0·4	**9**	9·6	**7**	7·0	6·3	6·3	**6**	7·3	6·4	6·4
5	—	—	**3**	5·5	**4**	3·2	3·7	3·7	**7**	9·2	6·5	6·5
6	—	—	**2**	2·6	**2**	1·2	2·1	2·0	**5**	9·6	6·2	6·2
7	—	—	**1**	1·1	**1**	0·4	1·1	1·0	**8**	8·6	5·6	5·7
8	—	—	**1**	0·4	**1**	0·3	0·7	1·2	**1**	6·7	4·7	4·8
9	—	—	**1**	0·2	—	—	—	—	**2**	4·6	3·9	3·9
10	—	—	—	—	—	—	—	—	**6**	2·9	3·1	3·1
11	—	—	—	—	—	—	—	—	**4**	1·6	2·3	2·4
12	—	—	—	—	—	—	—	—	**0**	0·8	1·7	1·8
13	—	—	—	—	—	—	—	—	**3**	0·4	1·3	1·3
14	—	—	—	—	—	—	—	—	**0**	0·1	0·9	0·9
15	—	—	—	—	—	—	—	—	**2**	0·5	1·9	1·5

a large number of classes the number in any one class is small. Poisson is not an adequate fit, whilst Neyman and Thomas give $P(\chi^2) > 0{\cdot}05$. The high population density is accompanied by a higher degree of aggregation, the Thomas estimate of the mean number of nauplii per clump being 1·9.

THE HAULS OF SERIES II

This series was taken on the day following series I, at the same depth, and the abundant species were the same. The total time of sampling was $3\frac{1}{2}$ hr.,

somewhat longer than in series I, but a total of 300 samples was taken. The values for *Pseudocalanus*, *Temora* and *Oithona* are shown in Table IX, in which, since the numbers in any one sample were very small, they have been grouped into ten periods with paired sets of fifteen samples in each period. The analysis of Table IX is given in Table X.

TABLE IX. SERIES II. RESULTS FOR THREE ABUNDANT SPECIES

Period ...	1		2		3		4		5		6		7		8		9		10	
Pseudocalanus nauplii	17	25	14	22	32	40	28	27	24	28	29	23	14	17	21	22	8	13	21	14
Temora nauplii	22	41	28	32	51	49	44	62	63	45	62	48	45	60	72	56	40	65	95	72
Oithona nauplii	31	33	22	26	15	50	26	38	16	25	21	24	27	26	19	22	19	26	29	33

TABLE X

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	9	0·2877	0·0320
Residual 1	10	0·2081	0·0208
Species (S)	2	1·6100	0·8050
P × S	18	0·5670	0·0315
Residual 2	20	0·1755	0·0088

The P × S mean square is significant and one cannot assume that the whole population was constant throughout the sampling period. The population of *Oithona* nauplii appears, however, to be uniform and the analysis confirms this suggestion. Table IX suggests that the populations of both *Pseudocalanus* nauplii and *Temora* also are uniform between periods 3–8 inclusive, and this is confirmed by analysis.

The population with respect to the three species appears to be uniform between 1 and 2 as indicated by Table XI.

TABLE XI

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	1	0·0130	0·0130
Residual 1	2	0·0538	0·0269
Species (S)	2	0·0890	0·0445
P × S	2	0·0078	0·0039
Residual 2	4	0·0207	0·0052

The results for *Microcalanus* (Table XII) include nauplii and copepodite stages, and inspection suggests that three populations were sampled during the experiment. The numbers were moderately large, and for analysis they may be grouped in paired sets of ten for fifteen separate periods. When all the developmental stages of this species are considered the analysis of variance is shown in Table XIII.

The value for P × St is significant, indicating that the proportion of the stages changed during the experiment. Further, the highly significant value for periods indicates significant changes in the total *Microcalanus* population.

The indication that three populations were sampled has been tested by analysis of the three sections. Analysis of the first section of nauplii and copepodite stages I and II (periods i–v) is shown in Table XIV.

TABLE XII. SERIES II. RESULTS FOR *MICROCALANUS* NAUPLII, AND STAGES I AND II COPEPODITES

Initial section of hauls

	i		ii		iii		iv		v	
Nauplii	76	153	167	145	171	154	126	165	213	146
Stage I	27	18	19	23	30	16	11	14	29	25
Stage II	29	29	34	37	24	10	17	20	29	34

Central section of hauls

	vi		vii		viii		ix		x		xi		xii	
Nauplii	168	115	106	84	86	84	114	80	88	83	98	117	111	83
Stage I	9	5	5	1	2	4	4	2	11	5	2	2	1	11
Stage II	10	11	4	7	10	5	3	3	5	1	4	6	4	9

Late section of hauls

	xiii		xiv		xv	
Nauplii	85	112	141	169	130	99
Stage I	10	19	13	4	2	5
Stage II	18	36	24	23	5	7

TABLE XIII

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	14	6·5243	0·4660
Residual 1	15	0·8270	0·0551
Stages (St)	2	25·9737	12·9869
P × St	28	2·6901	0·0961
Residual 2	30	1·1141	0·0371

TABLE XIV

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	4	0·1802	0·0451
Residual 1	5	0·1031	0·0206
Stages (St)	2	4·5074	2·2537
P × St	8	0·1953	0·0244
Residual 2	10	0·1078	0·0108

The value for neither P × St nor the periods is significant, and it can therefore be assumed that the population as regards these stages was uniform in the first five periods.

The analysis for periods vi–xi, grouping into three sets since stages I and II are few in numbers, is shown in Table XV.

Again a uniform population can be assumed.

It will be remembered that P × St was significant for three developmental stages. However, if only copepodite stages I and II are considered this distinction disappears as seen in Table XVI, although the value for P still remains significant.

The proportions of stage I to stage II therefore remained the same although the totals changed.

The other organisms present in quantity were lamellibranch larvae, and inspection of the results suggests considerable variability at the beginning and towards the end of the experiment. However, analysis indicates the central section to be uniform (Table XVII).

TABLE XV

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	2	0·0971	0·0486
Residual 1	3	0·1450	0·0483
Stages (St)	2	7·3855	3·6928
P × St	4	0·0408	0·0102
Residual 2	6	0·2686	0·0448

TABLE XVI

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	14	7·9771	0·5698
Residual 1	15	1·2045	0·0803
Stages (St)	1	0·4527	0·4527
P × St	14	0·9044	0·0646
Residual 2	15	0·6082	0·0405

TABLE XVII

Source of variation	Degrees of freedom	Sum of squares	Mean square
Periods (P)	11	0·2203	0·0200
Residual	12	0·1663	0·0138

The situation is obviously more complex than in series I and the division by inspection in the first instance arbitrary. It will be as well therefore to recapitulate the results of the variance analyses in order to get a clear picture of the component populations.

(i) *Oithona* was uniform throughout. (ii) *Pseudocalanus* and *Temora* were uniform between 1 and 2 and between 3 and 8 at different population densities. (iii) *Microcalanus* nauplii and copepodite stages I and II were uniform from periods i to v and also from vi to xi but at a different population density. (iv) If only *Microcalanus* stages I and II are considered, they were caught in the same proportions throughout although the population density changed. (v) Lamellibranch larvae were uniform in the central section. (vi) There was considerable variation towards the end of the experiment.

The existence of a number of different populations sampled during the experiment is clear and confirms the situation evident in series I. However, there is a distinct tendency towards irregularity at some of the boundaries, which have to some extent been selected in an arbitrary manner. On the hypothesis, suggested in the discussion on series I, that populations may be associated with water masses, one might infer that this variability at the population boundaries was due to the breaking up and mixing of these water masses. Apart from these boundary variations, a tendency towards a division into three populations for all the species considered (except *Oithona*) is reasonable. This suggests that all three have some common origin and, in view of their different biological characters, further strengthens a physical interpretation. There is only limited information on the length of time taken by *Microcalanus* to develop from egg to stage II, but it is probably about a fortnight (see Marshall, 1949). The constancy in the proportions of three developmental stages at two different population densities and of copepodite stages I and II throughout suggests a common biological origin, unless egg production had taken place at the same time and environmental conditions had remained the same in the two different regions sampled.

Using only those populations shown to be uniform the frequency distributions can again be constructed (Tables XVIII, XIX, XX).

Oithona nauplii—all samples. The results are shown in Table XVIII. Poisson is a very good fit but even so the 0-frequency class is high and both the contagious series give a higher $P(\chi^2)$ indicating a tendency to aggregation.

The less abundant species. An excellent fit [$P(\chi^2) = 0{\cdot}9$–$0{\cdot}8$] to Poisson is obtained, and although the population density is higher than in the other populations where Poisson was a less adequate fit, it should be remembered that this is the distribution of a grouped set of animals, each one of which is at a much lower population density.

Pseudocalanus nauplii (*central section*, 3–8). The numbers in the first section are small, and only the central section has been analysed. The results are shown in Table XVIII and Poisson is a very satisfactory fit.

Temora nauplii (*central section*). Again only the central section is analysed, and the results are shown in Table XVIII. As with *Pseudocalanus*, a satisfactory fit to Poisson is obtained even though the population density is double.

Lamellibranch larvae (*central section*). Again only the central section is used with similar results to those from the two preceding copepod nauplii. No account was taken of different species or size groups, but the larvae were mostly at an early stage of development and comparitively uniform in size.

Microcalanus nauplii (*initial and central sections*) The results are shown in Table XIX. The population density is high in both sections, but it is to be noted that the higher population density in the first section is due to a greater number of clumps per sample (8·8 against 5·1) rather than to an increase in the

mean number of nauplii per clump (1·852 and 1·889). The Neyman and Thomas series both give a $P(\chi^2) > 0{\cdot}05$.

Microcalanus copepodite stage I. This was the only copepod of which stages other than nauplii were taken in numbers sufficient for analysis in the small volume of water selected for these experiments. The results are shown in Table XX. Poisson is a very good fit for the initial section of stage I. For the

TABLE XVIII. SERIES II. ANALYSIS OF FREQUENCY DISTRIBUTIONS (1)

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

	Oithona nauplii (all samples)	Rare species (all together)	*Pseudocalanus* nauplii (central section)	*Temora* nauplii (central section)	Lamellibranch larvae (central section)
Mean	1·758	0·930	1·690	3·640	2·808
Variance	2·377	1·029	1·789	4·250	3·249
C.D.	1·352	1·106	1·059	1·168	1·157
$2\sqrt{[2n/(n-1)^2]}$	0·163	0·164	0·212	0·212	0·260
Ny., m_1	4·999	—	—	—	—
Ny., m_2	0·352	—	—	—	—
Th., m	1·474	—	—	—	—
Th., λ	0·192	—	—	—	—
$P(\chi^2)$					
Pn.	0·3–0·2	0·9–0·8	0·5–0·3	0·5–0·3	0·7–0·5
Ny.	0·5–0·3	—	—	—	—
Th.	0·5–0·3	—	—	—	—

Frequency class	Found	Expected Pn.	Expected Ny.	Expected Th.	Found	Ex-pected Pn.	Found	Ex-pected Pn.	Found	Ex-pected Pn.	Found	Ex-pected Pn.
0	**62**	52·0	68·5	69·2	**121**	118·4	**36**	33·2	**7**	4·7	**6**	7·2
1	**92**	91·4	84·7	84·1	**109**	110·1	**57**	56·1	**17**	17·1	**24**	20·3
2	**68**	80·5	67·3	67·3	**48**	51·2	**37**	47·4	**33**	31·2	**32**	28·5
3	**45**	47·2	41·7	41·9	**18**	15·9	**32**	26·7	**39**	37·9	**21**	26·7
4	**22**	20·8	22·0	22·1	**2**	3·7	**13**	11·3	**27**	34·6	**17**	18·8
5	**6**	7·3	10·3	10·3	**0**	0·7	**4**	3·8	**26**	25·3	**9**	10·5
6	**4**	2·1	4·4	4·4	**2**	—	**1**	1·5	**11**	15·4	**7**	4·9
7	**1**	0·5	1·7	1·7	—	—	—	—	**10**	8·0	**2**	2·0
8	**1**	0·1	0·6	0·6	—	—	—	—	**7**	3·6	**1**	0·7
9	**0**	0·1	0·2	0·2	—	—	—	—	**3**	2·2	**1**	0·4
10	**0**	—	0·1	0·1	—	—	—	—	—	—	—	—
11	**1**	—	0·5	0·1	—	—	—	—	—	—	—	—

central section the numbers of stage I and the frequency classes are small, and the χ^2 test is therefore very insensitive, but a tendency to aggregation is clear.

Microcalanus copepodite stage II (*central section only*). Here again the numbers and the frequency classes are small but the same tendency as seen in stage I is apparent.

Microcalanus copepodite stage III (*initial section only*). Again with the low population density the numbers and frequency classes are low. However, Poisson gives a fair fit.

TABLE XIX. SERIES II. ANALYSIS OF FREQUENCY DISTRIBUTIONS (2)

(Pn., Poisson; Ny., Neyman; Th., Thomas; C.D., coefficient of dispersion.)

Microcalanus pygmaeus nauplii

	Early section	Central section
Mean	16·330	9·600
Variance	37·759	22·664
C.D.	2·312	2·360
$2\sqrt{[2n/(n-1)^2]}$	0·286	0·233
Ny., m_1	12·450	7·060
Ny., m_2	1·312	1·360
Th., m	8·816	5·082
Th., λ	0·852	0·889
$P(\chi^2)$		
Pn.	<0·05	<0·05
Ny.	0·7–0·5	0·7–0·5
Th.*	0·5–0·3	0·8–0·7

Frequency class	Early section Found	Early section Expected Pn.	Early section Expected Ny.	Early section Expected Th.	Central section Found	Central section Expected Pn.	Central section Expected Ny.	Central section Expected Th.
0	**0**	0	0	0	**0**	0	0·8	0·9
1	**0**	0	0·1	0·1	**2**	0·1	1·9	2·0
2	**0**	0	0·1	0·2	**4**	0·5	3·7	3·7
3	**0**	0	0·3	0·3	**3**	1·5	5·8	5·8
4	**2**	0	0·6	0·6	**5**	3·6	8·0	8·0
5	**0**	0·1	1·0	1·0	**8**	6·9	10·0	9·9
6	**2**	0·2	1·6	1·6	**16**	11·1	11·6	11·5
7	**0**	0·5	2·2	2·2	**13**	15·2	12·5	12·5
8	**6**	1·0	3·0	3·0	**12**	18·2	12·9	12·9
9	**3**	1·8	3·8	3·8	**13**	19·4	12·7	12·7
10	**2**	3·0	4·5	4·5	**15**	18·6	11·9	12·0
11	**7**	4·5	5·2	5·2	**15**	16·3	10·9	10·9
12	**8**	6·1	5·8	5·8	**9**	13·0	9·6	9·6
13	**4**	7·6	6·2	6·3	**9**	9·6	8·2	8·2
14	**4**	8·9	6·4	6·5	**7**	6·6	6·8	6·9
15	**11**	9·7	6·4	6·5	**4**	4·2	5·5	5·6
16	**6**	9·9	6·3	6·5	**4**	2·5	4·4	4·4
17	**8**	9·5	6·0	6·2	**6**	1·4	3·4	3·4
18	**6**	8·6	5·6	5·8	**2**	0·8	2·6	2·6
19	**4**	7·4	5·1	5·4	**0**	0·4	1·9	2·0
20	**4**	6·1	4·6	4·8	**2**	0·1	1·4	1·4
21	**4**	4·7	4·0		**1**	—	3·5	3·1
22	**3**	3·5	3·5		—	—	—	—
23	**3**	2·5	2·9		—	—	—	—
24	**2**	1·7	2·5		—	—	—	—
25	**3**	1·0	2·0		—	—	—	—
26	**1**	0·7	1·6		—	—	—	—
27	**0**	0·4	1·3	23·7	—	—	—	—
28	**2**	0·2	1·0		—	—	—	—
29	**1**	0·1	0·8		—	—	—	—
30	**3**		0·6		—	—	—	—
31	**0**	0·3	0·5		—	—	—	—
32	**0**		0·4		—	—	—	—
33	**1**		4·1		—	—	—	—

* Calculated with later frequency classes grouped as shown.

Table XX. Series II. Analysis of Frequency Distributions

(Pn., Poisson; Ny., Neyman; Th., Thomas; c.d., coefficient of dispersion.)

Microcalanus pygmaeus copepodites

	Stage I (initial section)	Stage I (central section)	Stage II (central section)	Stage III (initial section)
Mean	2·217	0·353	0·529	0·560
Variance	2·783	0·468	0·675	0·675
c.d.	1·255	1·325	1·276	1·205
$2\sqrt{[2n/(n-1)^2]}$	0·371	0·261	0·261	0·274
Ny., m_1	8·686	1·087	1·925	2·727
Ny., m_2	0·255	0·325	0·275	0·205
Th., m	1·952	0·292	0·461	0·507
Th., λ	0·136	0·205	0·148	0·105
$P(\chi^2)$				
Pn.	0·7–0·5	<0·05	0·5–0·3	0·1–0·05
Ny.	0·8–0·7	—	—	—
Th.	0·9–0·8	—	—	—

Frequency class	Found	Expected Pn.	Expected Ny.	Expected Th.	Found	Expected Pn.	Expected Ny.	Expected Th.	Found	Expected Pn.	Expected Ny.	Expected Th.	Found	Expected Pn.	Expected Ny.	Expected Th.
0	**8**	6·5	8·5	8·5	**89**	83·6	88·0	88·9	**74**	70·1	74·8	75·1	**67**	62·3	65·7	65·7
1	**16**	14·5	14·6	14·4	**20**	29·5	22·4	21·2	**32**	37·1	30·1	30·0	**27**	34·9	30·0	30·0
2	**14**	16·1	14·4	14·3	**8**	5·2	6·5	6·9	**10**	9·8	10·1	10·3	**11**	9·8	9·9	10·0
3	**9**	11·9	10·5	10·5	**2**	0·7	2·3	2·0	**1**	1·7	2·8	2·9	**4**	2·0	3·4	3·3
4	**7**	6·6	6·3	6·1	—	—	—	—	**2**	0·3	1·2	0·7	—	—	—	—
5	**2**	2·9	3·3	2·8	—	—	—	—	—	—	—	—	—	—	—	—
6	**4**	1·5	2·4	3·4	—	—	—	—	—	—	—	—	—	—	—	—

The Hauls of Series III

In this series it was hoped to obtain further information both on the frequency distributions of populations and on their vertical relations. The set up was as follows.

Samples were pumped continuously for a period of about 5 hr., during which time the boat was allowed to drift. With the hose at a depth of 1 m., twenty samples were taken as in the previous series. The hose was then lowered to 5 m., and, after washing out with water from that depth, a further twenty samples were collected. This was repeated at 8 and 10 m. The hose was then brought back to 1 m. and the sequence of samples and depths repeated five times. There are therefore four series of depths, twenty samples at each depth, and what may be termed five periods, each period corresponding to a complete vertical set of four depths, giving a total of 400 samples. Each set of twenty samples took about 10–15 min., each period, therefore, 40–60 min. and five periods 200–300 min.; in point of fact the whole series took 5 hr. (less 12 min.). Salinities and temperatures were determined for each depth corresponding to the sets of twenty samples from that depth, (see p. 236). Such a division into periods has, of course, an arbitrary character since changes *may* have been taking place at different depths at different rates. However, it is the most natural grouping that can be adopted.

On this occasion the more numerous species were: *Calanus finmarchicus* (Gunnerus), *Centropages hamatus* (Lilljeborg), *Temora longicornis* (Müller), *Acartia clausi* Giesbrecht, *Oithona similis* Claus, all as nauplii, *Calanus* eggs and lamellibranch larvae. Attention will first be confined to copepod nauplii and eggs.

For the analysis of variance the twenty samples of any set have been grouped into four sets of five which are considered as replicates for the given depth and period. The analysis is shown in Table XXI.

Table XXI

Source of variation	Degrees of freedom	Mean square
Periods (P)	4	0·4866
Depths (D)	3	0·5532
P × D	12	0·1768
Residual 1	60	0·0312
Species (S)	5	27·1112
P × S	20	0·1889
D × S	15	0·5616
P × D × S	60	0·0890
Residual 2	300	0·0147

The values for the mean squares indicate a complex situation. If the results are again to be interpreted as applicable to this experiment only, then, when the mean squares are tested against the appropriate residual, they are found to be significant. It is perhaps simpler, under these circumstances, to

consider the organisms separately. The mean squares are given in Table XXII, the degrees of freedom of each source of variation being the same throughout. Again for this particular experiment all the mean squares, with few exceptions, are significant. Thus had the catches for, say, *Calanus* nauplii been obtained by drawing a net vertically through the water column from 10 to 0 m. at each period, then a significant difference would have been found between the catches, equivalent to a significant value of P, the summing over depths being done by the technique. Similarly, the significance of D would have been found had horizontal hauls been taken at the appropriate levels over the given periods, the summation again being done by the sampling technique. The

TABLE XXII. SERIES III. THE MEAN SQUARES

Source of variation	Degrees of freedom	*Calanus* nauplii	*Calanus* eggs	*Centropages*	*Temora*	*Acartia*	*Oithona*
Period (P)	4	0·3183	0·0466	0·2978	0·4128	0·2333	0·0975
Depth (D)	3	0·3211	0·0499	0·2880	1·7440	0·6520	0·3060
P × D	12	0·1129	0·0372	0·0829	0·2525	0·0627	0·0741
Residual	60	0·0134	0·0053	0·0155	0·0225	0·0199	0·0286

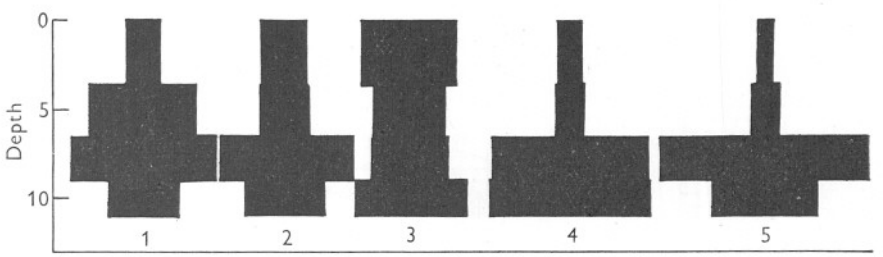

Fig. 2. Data for series III, for *Temora longicornis* nauplii, showing percentage occurrence of total at various depths.

significance of the P × D interaction can be illustrated by using the results for *Temora* in a more conventional way. In Fig. 2 the proportions at the various depths are shown as a percentage of the total, the value at each depth being taken to represent a column reaching half-way between that depth and the depth sampled above and below. The change in that proportion as one passes from period to period is clearly evident. In view of the time of day and the shortness of the interval between two consecutive periods it is hardly possible that these changes represent regular vertical migrations of the *Temora* population between 1 and 10 m. throughout the area of which these catches are samples. However, it must be pointed out that similar changes, based on catches expressed as percentages, and taken at intervals not longer than the beginning and the end of this series, have been held to imply vertical migration, although in such work the regularity of the change over longer periods and its correlation with factors such as light intensity strengthen the argument.

Fig. 3 represents the populations sampled in series III, and salinities are shown in the same type of figure. The salinity samples were taken as far as possible at the mid-point in time of the equivalent set of plankton samples, and the large range of values emphasizes that conditions in this area are not necessarily typical of the open sea.

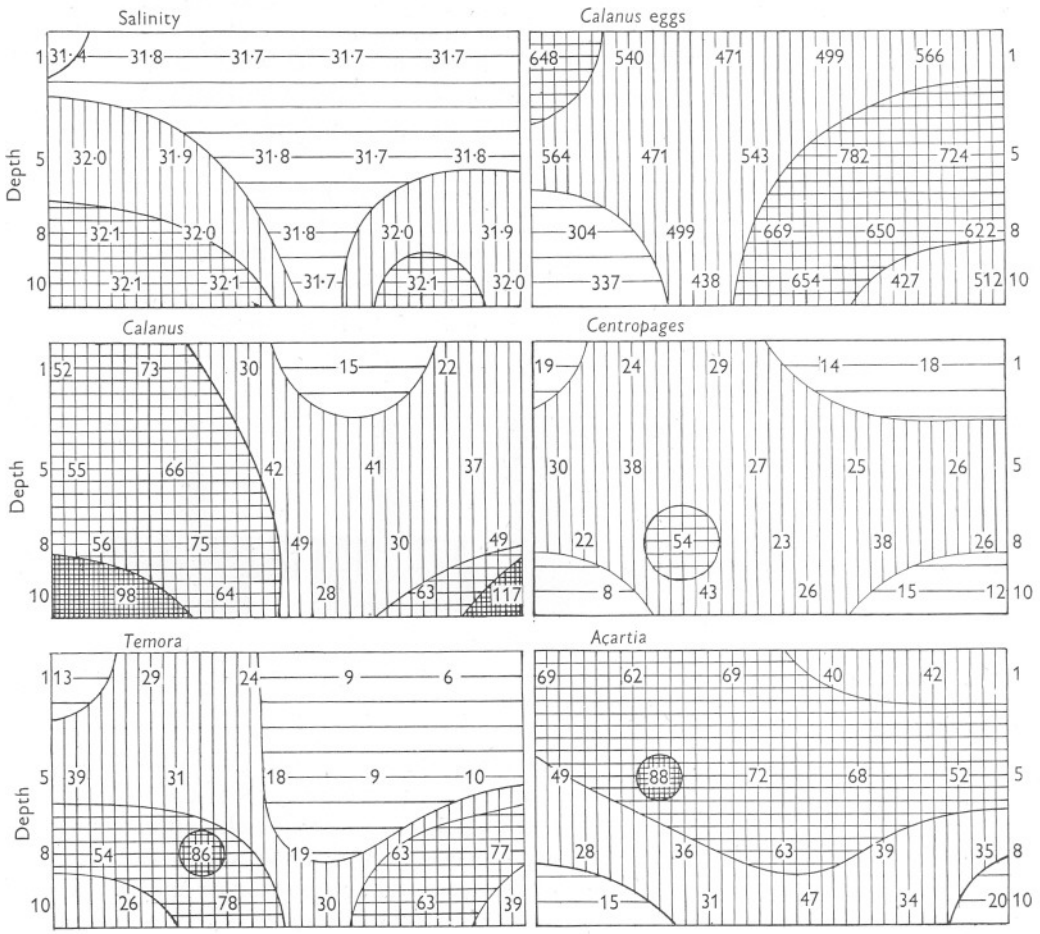

Fig. 3. Population density distributions compared with salinity (top left), for all hauls of series III. Vertical, depth in metres. Horizontal, time (assumed to represent some sort of spatial scale owing to drift). Each diagram shows up to four grades of shading indicating numerically: salinity (‰), <31·6, 31·6–31·8, 31·8–32·0, >32·0; *Calanus* eggs, <400, 400–600, >600; all nauplii, <20, 20–50, 50–80, >80.

The boundaries of the copepod nauplius populations are again selected somewhat arbitrarily, but they are in the main substantiated by variance analyses which need not be quoted. The arbitrary horizontal axis is a time-scale, but as

has already been noted (p. 236) it presumably corresponds with spatial changes in the water.

There is considerable resemblance between all these diagrams, including that for salinity. The regions of high salinity at 8 and 10 m., at the beginning and end of the series, are marked by distinct populations in most of the species, although the relative population density varies according to the species. Thus with *Calanus* nauplii these are regions of high, but with *Centropages* and *Acartia* of low, population density. The population density of these two areas is, however, similar for any one species and had greater depths been sampled in the central period this area might have extended across the figure.

In the third period the low salinity water extends to 10 m., and with *Calanus*, *Temora* and *Centropages* nauplii the populations at all depths during that period are fairly uniform. At the surface, or the surface and 5 m., there is in most species an area of low numbers within the low salinity area.

In general, although the population boundaries are not defined by salinity boundaries, they are most often contained within them; only occasionally does a uniform population spread over a wide range of salinities as it does, for example, for *Acartia* nauplii at 1 and 5 m. and for *Calanus* nauplii during the first two periods.

In several cases the population boundaries are sharp (e.g. *Temora*), but in others there is a suggestion that the nauplii have spread out from one or two centres of high population density. Thus for *Calanus* nauplii there are two apparent centres of distribution in deep water corresponding with high salinity water, and for *Acartia* nauplii one centre at 5 m. from which, although it is situated in low salinity water, the high numbers are spreading out across the boundaries into higher salinity water.

If in the early developmental stages regions of high population density exist, resulting from the production of a large number of eggs, then as time goes on there will be a tendency for these to become dispersed through physical forces, and such information would be essential for a complete interpretation of the figures.

The physical background has been emphasized in suggesting how these populations may be developed, maintained and eventually disseminated, but it must be remembered that the work has dealt mainly with nauplius stages. Clearly with later stages which perform vertical migrations a population could not in this way be restricted to a small water mass. We do not wish to maintain that a given population is always associated with a given mass of water as characterized by its salinity (see above) and it is possible too that a small body of water, apparently homogeneous, may contain separate plankton populations. A large body of water, homogeneous physically by the usually accepted standards, may certainly contain many populations (cf. Baldi *et al.* 1945; Rae & Rees, 1947). However, coincidence of physical conditions and nauplius populations have also been demonstrated above, and it is possible

that quite small physical differences which make up what might be termed the 'microclimate' would, on detailed investigation, be found to exist in the regions where those observations were made. It would be interesting to extend this work by trying to follow the history of some of these small zooplankton patches and to apply a similar technique to later developmental stages.

The Populations of Series III

Some of the uniform populations were sufficiently extensive to enable frequency distributions to be formed. Since, however, the results were of very

Table XXIII. Series III. Analysis of Frequency Distributions

(Pn., Poisson; Ny., Neyman; Th., Thomas; c.d., coefficient of dispersion.)

	Oithona	*Temora*	*Centropages* 1	*Centropages* 2
Mean	1·825	1·690	5·810	5·160
Variance	2·316	1·690	9·550	5·518
c.d.	1·269	1·000	1·644	1·069
$2\sqrt{[2n/(n-1)^2]}$	0·201	0·320	0·286	0·320
Ny., m_1	6·784	—	9·026	—
Ny., m_2	0·269	—	0·644	—
Th., m	1·597	—	4·232	—
Th., λ	0·143	—	0·373	—
$P(\chi^2)$				
Pn.	<0·05	0·5–0·3	0·1–0·05	0·3–0·2
Ny.	0·3–0·2	—	0·7–0·5	—
Th.	0·5–0·3	—	0·5–0·3	—

Frequency class	Found	Expected Pn.	Expected Ny.	Expected Th.	Found	Expected Pn.	Found	Expected Pn.	Expected Ny.	Expected Th.	Found	Expected Pn.
0	**42**	32·2	40·4	40·5	**17**	14·8	**3**	0·3	1·4	1·5	**0**	0·5
1	**59**	58·8	56·3	56·6	**20**	25·0	**3**	1·7	4·2	4·2	**5**	2·4
2	**36**	53·7	46·8	46·8	**22**	21·1	**6**	5·1	7·8	7·8	**6**	6·1
3	**34**	32·7	29·5	29·6	**16**	11·9	**13**	9·8	10·9	10·9	**15**	10·5
4	**18**	14·9	15·4	14·7	**5**	7·3	**10**	14·2	12·9	12·8	**10**	13·6
5	**6**	5·4	7·0	5·8	—	—	**14**	16·5	13·3	13·2	**10**	14·0
6	**5**	2·2	4·6	6·0	—	—	**16**	16·0	12·3	12·3	**8**	12·0
7	—	—	—	—	—	—	**6**	13·3	10·5	10·5	**9**	8·9
8	—	—	—	—	—	—	**10**	9·7	8·3	8·4	**9**	5·7
9	—	—	—	—	—	—	**9**	6·2	6·0	6·3	**8**	6·3
10	—	—	—	—	—	—	**4**	3·6	4·3	4·4	—	—
11	—	—	—	—	—	—	**2**	1·9	2·9	3·0	—	—
12	—	—	—	—	—	—	**0**	0·9	1·9	1·9	—	—
13	—	—	—	—	—	—	**1**	0·4	1·2	1·2	—	—
14	—	—	—	—	—	—	**2**	0·2	0·7	0·7	—	—
15	—	—	—	—	—	—	**1**	0·1	1·4	0·9	—	—

much the same type as those already given, it is not necessary to give them for each population. A selection is given as follows:

Oithona. Here Poisson is not an adequate fit but Neyman and Thomas are a good fit to the data.

Temora. Here Poisson is an adequate fit, indicated by a $P(\chi^2)$ value of 0·5–0·3, although again the 0-frequency class is in excess.

Centropages 1. The population density is high (5·81), yet Poisson gives an adequate fit. However, the agreement in earlier classes is to some extent the result of grouping.

Centropages 2. Here, as with the previous distribution, Poisson is an adequate fit, even though again the population density is high (see p. 261).

The Sampling Variations

The results from series I and II are shown in Tables VII, VIII, XVIII, XIX and XX, and the numerical data in the top halves of these tables should be compared. (The number per m.^{3}, if required, is readily obtained by multiplying

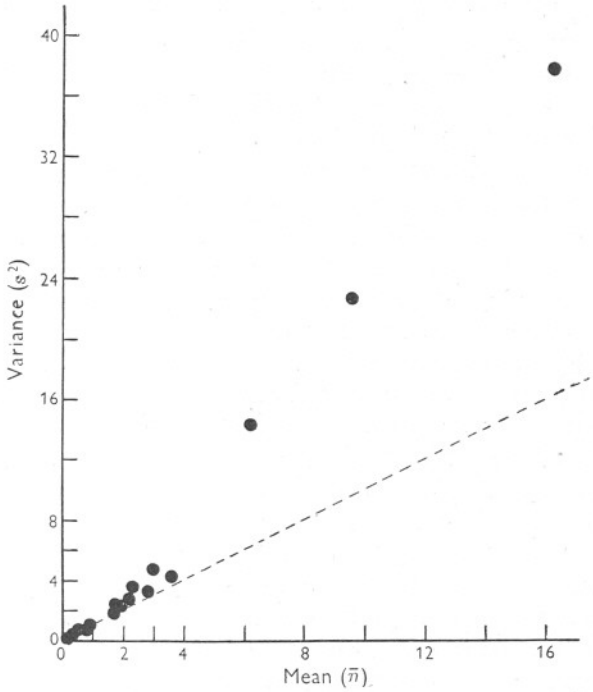

Fig. 4. The relation between the variance (s^2) and the mean ($\bar{n}$) of the populations from series I (Tables VII and VIII) and series II (Tables XVIII, XIX and XX).

the mean by 170.) In Fig. 4 the mean population density is plotted against the variance using the values from series I and II. It is clear that as the population density increases the sampling variance increases. If all the populations were randomly distributed then points would be scattered about a line corresponding to mean population density = variance (as indicated in Fig. 4). Only at low population densities is there a close approach to a random

distribution. As the population density increases there is clear evidence of aggregation, i.e. the chance of an organism being present is increased by the presence of an organism already there, so that the frequency distributions fit those of a contagious series.

It is now possible to explain the observed distribution of χ^2 in previous work both with nets and pumps. The variation, particularly noted at high population densities, is to be ascribed largely to the greatly increased true sampling variation with increasing population density. As will be discussed later, this change depends to some extent on the biological character and history of the population, but inspection of the above tables shows that in general the Poisson distribution begins to be an inadequate fit when the population density exceeds a value of 1000 organisms per m.^{3}. Now in the early work (Tables II and III) the great change in the mean value of χ^2 begins in the 170–400 n_1+n_2 group, increases considerably at the 400–1000 group, becoming very great at the >1000 group. The change can be taken at somewhere in the region of a population density of 200–300 organisms per sample. In the pump samples about 200 l. of water were taken, so this corresponds to a population density of 1000–1500 organisms per m.^{3}, agreeing with the above calculation. The change can therefore be ascribed largely to sampling variations dependent upon the population sampled, and not to inadequacies in sampling technique. With the net samples the increase in χ^2 began at catches of the same order, and nominally a much larger volume, about 11 m.^{3}, was filtered. The change is therefore taking place at a lower population density than expected. This may in part still be ascribed to errors of technique, such as variations in the volume filtered, but in contrast to a pump haul taken at a single depth it should also be remembered that in a net haul a whole series of populations even of any one organism can be sampled at different levels of the haul, so that the organisms may be concentrated in a relatively small proportion of the volume filtered. Under these circumstances minimal population densities are obtained by the use of 11 m.^{3} volume.

The preliminary examination of the data indicated that the standard deviation was roughly proportional to the mean. In Fig. 4 the estimated variance is plotted against the mean, and a shallow curve is obtained. The form of the curve and general consideration of heterogeneous distributions (see Anscombe, 1949) suggest that an equation of the following type expresses the relation between variance and mean

$$\sigma^2=\bar{n}+c\bar{n}^2, \tag{1}$$

or in a more convenient form as

$$\frac{\sigma^2}{\bar{n}}=1+\frac{1}{k}\bar{n}. \tag{2}$$

There are a number of sets of estimates of $1/k$ (one from each distribution) and

Anscombe has shown that an unbiased estimate of the value for any set, $1/\hat{k}_i$, is given by

$$\frac{1}{\hat{k}_i}=\frac{s_i^2-\bar{n}_i}{\bar{n}_i^2}\left(1+\frac{s_i^2}{N_i\bar{n}_i^2}\right), \tag{3}$$

where s_i^2, $\bar{n}_i$ are the estimated variance and mean for the ith set, and N_i is the number of samples in that set. The values of $1/\hat{k}_i$ are shown in Table XXIV. There is some variation but no apparent correlation of this value with the mean. (Four high values, one from Table VII and three from Table XX, stand out as somewhat different from the rest, and it is of interest to note that in contrast to the other data, which refer to nauplii, these values are derived from eggs and copepodite stages.)

TABLE XXIV

Table	Population	Estimated $1/\hat{k}_i$	Table	Population	Estimated $1/\hat{k}_i$
VII	*Oithona* nauplii	0·112	XIX	*Microcalanus* nauplii (initial)	0·080
VII	Lamellibranch larvae	0·208			
VII	Eggs	1·767	XIX	*Microcalanus* nauplii (central)	0·142
VIII	*Pseudocalanus* (1–60)	0·053			
VIII	*Microcalanus* (1–60)	0·093	XX	*Microcalanus* copepodites, stage I (initial)	0·116
VIII	*Pseudocalanus* (61–120)	0·262			
VIII	*Microcalanus* (61–120)	0·212	XX	*Microcalanus* copepodites, stage I (central)	0·949
XVIII	*Oithona* nauplii	0·201			
XVIII	Rare species	0·115	XX	*Microcalanus* copepodites, stage II (central)	0·532
XVIII	*Pseudocalanus* nauplii	0·035			
XVIII	*Temora* nauplii	0·046	XX	*Microcalanus* copepodites, stage III (initial)	0·373
XVIII	Lamellibranch larvae	0·056			

Now although an attempt has been made to fit distributions to these populations, an efficient estimate of a common value for the k's can, none the less, be obtained. The method used is equivalent to taking an appropriately weighted average of the separate estimates of $1/\hat{k}$, and $\hat{k}$ is chosen so that it satisfies the equation

$$\Sigma T_i(\hat{k})=0,$$

where

$$T_i(\hat{k})=\frac{(N_i-1)s_i^2-(N_i-1-\hat{k}^{-1})(\bar{n}_i+\bar{n}_i^2/\hat{k})}{(\bar{n}_i+\hat{k})^2}. \tag{4}$$

If the value for eggs (Table VII) is ignored, $1/\hat{k}=0{\cdot}121$; if the high values from Table XX (copepodites) are also ignored the values of $1/\hat{k}=0{\cdot}118$. It is sufficient to take a value of 0·12.

It will be remembered that the equation originally derived from paired observations on the assumption of a random distribution of organisms and variability due to variable volume of water filtered was

$$\chi^2=1+K^2n, \tag{5}$$

where K^2 lay between 0·04 and 0·05. For paired observations $\chi^2=s^2/\bar{n}$, and

clearly the equation is of the same form as that given above where $K^2 = 1/k$ with an estimated value of 0·12. Now K is not to be regarded as constant, as Winsor & Walford pointed out (they were, for example, not dealing with nauplius stages of copepods, but with a wide variety of organisms), and indeed Silliman (1946) in pilchard egg investigations obtained a value of $K^2 = 0{\cdot}12$, and here the agreement is striking. Now equation (1) was derived from experiment in which the volume of the samples was carefully controlled; the variability can therefore be ascribed to non-random distribution of the organisms (perhaps superimposed on some sampling variation), and it would seem an adequate explanation for Winsor & Walford's results.

Discussion

In the previous sections some of the features of the animal populations sampled by pump during periods of from 2 to 5 hr. have been considered. The results, however, have a bearing upon plankton work in general, which may now be considered.

Unlike most net catches the volume of water taken in a pump sample is accurately known, being unaffected by many of the factors causing errors in net hauls. Correct estimates of the population are therefore obtained, and these values are readily converted to organisms per m.^{3}, in the present instance, by multiplying by 170. The numbers obtained tend to be larger than those usually reported at this time of the year in this area (Marshall, 1949), which is to be expected since previous estimates have been based on net hauls.

In the present experiments there is no information on the relative movements of ship and water, but the rapid changes in population suggest very strongly the presence of numerous three-dimensional 'swarms' which may be quite small in volume, smaller than those which have been so clearly shown by Hardy & Gunther (1935) for Antarctic plankton, and by several workers for the North Sea, using the continuous plankton recorder (Rae & Rees, 1947). The evidence is in favour of their being restricted laterally and, since the samples of series III were taken at several depths, their vertical limits also are sometimes found to be quite small. If the patterns of Fig. 3 were extended into three dimensions they would give a picture of the situation.

Hitherto most of the work on 'swarms' has been confined to discontinuities in a horizontal direction. Variations in population density in a vertical direction for a given organism are well known, and a movement of these populations is implicit in results which indicate vertical migration. The evidence from the present work relates largely to nauplius stages and these are not known to show diurnal migration. Stress has been laid on the possibility that the 'swarms' are confined in a particular water mass, but if such small 'swarms' exist in the late developmental stages which do show diurnal migration then a similar relation to the water mass would be impossible. If such adult

swarms exist and if they preserve their identity during migration some other force must be responsible. This may be a 'positive' biological force such as causes swarming in other animal groups. Since, however, vertical migration is usually considered to be a response to a change in light intensity, and since this acts only in a vertical direction, the movement may occur much more freely in a vertical than a horizontal direction; with a consequent tendency to reduce horizontal dispersion. A repetition of this type of work extended vertically and horizontally and over a longer period is proving of considerable interest.

This evidence, derived largely from a consideration of nauplii, suggests that the distinct populations maintain their identity for some time, and are gradually broken down by physical forces and reduced by mortality as the organisms go through their development. It might be expected, therefore, that copepods which retain their eggs until the nauplii hatch (*Pseudocalanus* and *Oithona* of those here discussed) would, at a given time from hatching, be less widely distributed than those laid singly in the water (the other copepods concerned). There is no evidence about the age from hatching of the nauplii caught, and strict comparisons between the two types cannot therefore be made. It is interesting to observe, however, that in series I the *Pseudocalanus* at a mean population density of 2·300 has a coefficient of dispersion of 1·596, whereas *Microcalanus* with a higher mean population density (2·867) has a coefficient of dispersion of only 1·152. Further, *Temora* in series II with a mean population density of 3·640 and *Centropages* in series III (population density 5·160) have coefficients of dispersion of 1·168 and 1·069, respectively. The results from *Oithona* are in general agreement.

Summary

A brief review of previous work on the sampling variation encountered in the course of plankton work is given, and leads to the suggestion that the observed variability is not entirely accounted for by technical errors. A non-random distribution (statistical) of the population is suggested.

If the distribution is not random (Poisson) then the application of contagious distributions should be considered. A short account of two such distributions, Neyman's and Thomas's, is given; the parameters of the latter seem to be more readily interpreted in plankton sampling.

An account of the method of collection and counting of numerous small samples taken continuously over several hours is given. In the first two series the collections were made at a constant depth. The results suggest the existence of comparatively well-defined populations of a number of organisms, chiefly copepod nauplii. Series III, in which samples were taken at several depths, confirms this suggestion and indicates a similar state of affairs in a vertical direction. The population changes, it is suggested, might be

associated with different masses of water which have maintained their identity over a period during which the populations have been developed, and the association of a number of species maintained.

Frequency distributions are set up, and in general when the population density is low the distribution closely approaches that of Poisson. At higher population densities the Neyman and Thomas series give a better fit, indicating clumping of the organisms. An estimate of the mean number per clump is obtained.

The results are considered in relation to Winsor & Walford's work and it is shown that the sampling variation can be explained as dependent upon the non-random distribution of the organisms sampled. This explanation is adequate for earlier data.

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