On the Marine Cladocera from the Northumbrian Plankton.

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With 36 Figures in the Text and Diagrams A, B and C.

Contents.

PART I. DISTRIBUTION AND SEASONAL CHANGES OF POPULATION.

Introduction.

The material which forms the subject of this paper has been collected over a period of ten years. The samples are divisible into two groups, each including five years' catches. During the first half of the time, 1921–1925 inclusive, the stations varied from voyage to voyage but the hauls are comparable with one another as regards the nets used and the time of fishing in each case. An account of the method of sampling is given in the Dove Marine Laboratory Report for 1923, pp. 68–69 (**45**).

In 1926 a change was made in the number and kind of nets used and in the time of fishing, in order to bring the work into line with that of the Ministry of Agriculture and Fisheries. Since that year the new method

FIG. 1.

has continued, and the samples have been taken each time from the same series of stations (Fig. 1). Thus, during this period the results of different years' sampling can be correlated more satisfactorily. The new method of sampling is described in the Dove Marine Laboratory Report for 1926, p. 43 (**46**).

A preliminary statement as to the occurrence of the two genera of Cladocera which are found in the area sampled, during the period 1921–1923, is given in the above-mentioned Reports for 1923 and 1924 in "Plankton Investigations, No. 4 Crustacea" (**30** and **31**). In the analysis of these catches an attempt was made to indicate actual numbers of individuals, as is shown in the tables there presented. In the analyses of the subsequent years' samples only presence or absence and relative abundance is indicated, and for purposes of comparison the 1921–1923 records are here included in the same form.

Of the series of samples taken at every ten metres from surface to bottom at each station in the 1926 and subsequent catches, only three—surface, mid-water, and bottom—are here considered, in order to deal with the material on the same basis as in the earlier years when only three nets were used.

The data given in Figure 2 show the genera Evadne and Podon to be represented in the plankton. Of the former genus, only one species, *E. nordmanni*, is apparent in the samples. It is possible that a few *E. spinifera* may have been present on occasions amongst large quantities of *E. nordmanni*, but, if so, they were not distinguished. Norman and Brady include only *E. nordmanni* in their list of the Crustacea of Northumberland and Durham (**51**).

With regard to Podon, the two species, *P. polyphemoides* and *P. intermedius*, have been recorded for the district, the former being described as "not rare," and the latter as "taken occasionally." As the species are not easily identified in the course of general analyses of plankton samples, it is not proposed to discuss the distribution of the individual species of Podon in this paper. Only a general consideration of the occurrence of the two genera in the district will be undertaken. Problems of distribution and fluctuations in population will be discussed only in relation to our commonest Cladoceran, *E. nordmanni*.

Annual Records.

Reference to Fig. 2 and Diagrams A, B and C on pp. 186–188 will show the main facts relating to the individual years' samples as regards the occurrence of Evadne and Podon to be as indicated below.

1921.

During 1920 and 1921 abnormal conditions prevailed in the North Sea, due to a great influx of surface water from the Atlantic Ocean, as shown by the presence of *Salpa fusiformis*, *Limacina retroversa*, and other Atlantic forms in the plankton (**26**).

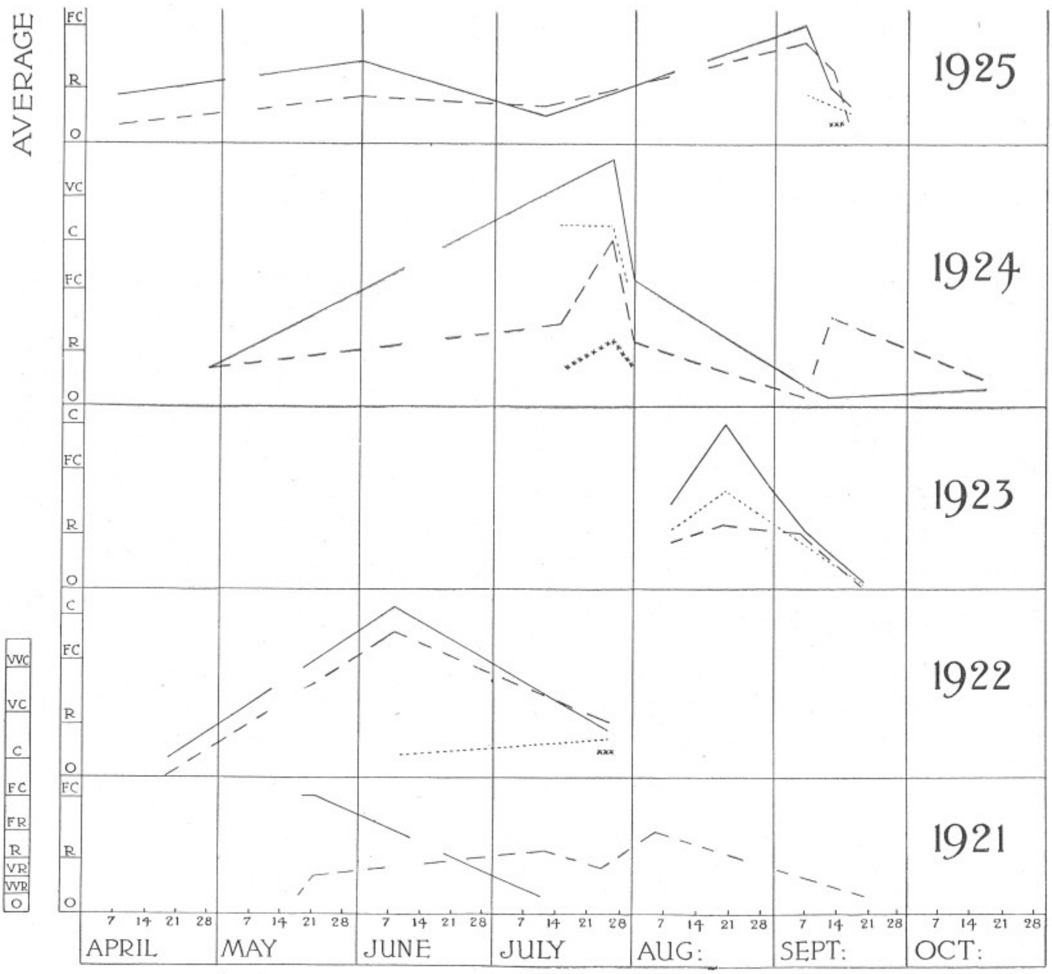

AVERAGE
1925
1924
1923
1922
1921
VVC
VC
C
FC
FR
R
VR
VVR
O
APRIL
MAY
JUNE
JULY
AUG:
SEPT:
OCT:
7 14 21 28

Fig. 2.

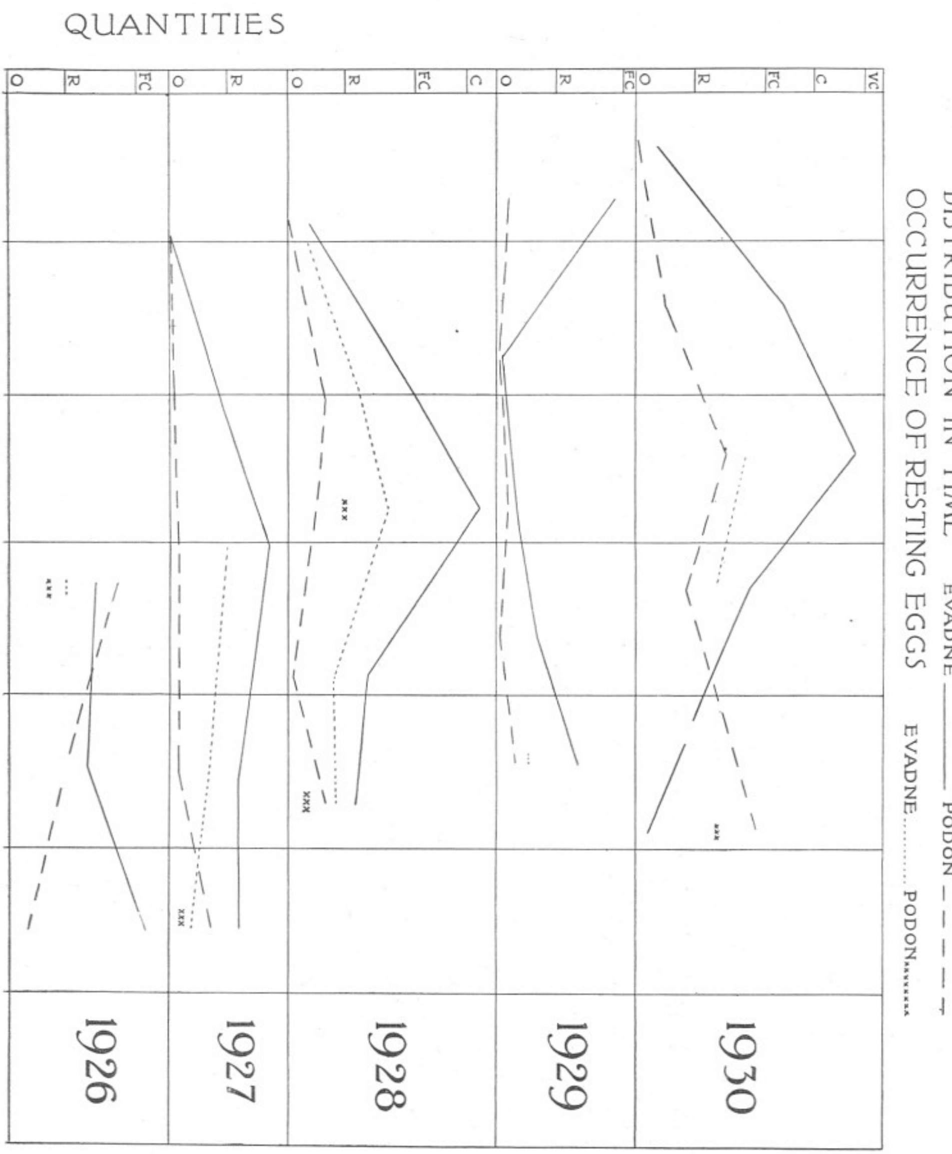

QUANTITIES
DISTRIBUTION IN TIME
OCCURRENCE OF RESTING EGGS
EVADNE —— PODON – – – –
EVADNE........ PODONxxxxxxx
O
R
FC
C
VC
1926
1927
1928
1929
1930

FIG. 2.

When the first of our series of plankton samples was taken, between May 4th and September 20th, 1921, Cladocera were present at all but two stations, namely, at 12 miles from the shore in July and inshore near Boulmer in September.

Evadne was very abundant in May at both ends of the district, after which time it was recorded only twice—in July. Podon, on the other hand, already present in May, attained a maximum early in August and persisted in decreasing numbers until the end of the sampling for that year.

No " winter eggs " or resting-eggs of either form were observed, although the catches were specially searched for them after they had been found to occur in subsequent years.

1922.

In 1922, when the Atlantic influence was abating, sampling began on April 20th when Evadne was found to be present already in the southern part of the district. Its numbers reached a maximum early in June, when it was specially abundant in the inshore region between Coquet Island and Newbiggin. On July 25th–27th, it was again taken fairly plentifully in the same region but was very sparsely represented to the north—no specimens were taken at Station 8, i.e. $7\frac{1}{2}$ miles east of the Longstone.

A few resting-eggs were noted in June and rather more in July, mainly from inshore stations.

Podon appeared first in the catches in June, its numbers increasing with distance from the shore. It was present throughout the district in July, but occurred then in greatest quantity at the inshore stations. Resting-eggs were taken only once, in July (Fig. 31, p. 208).

The analysis of a series of samples taken off the Tyne on July 13th and 14th by Savage (**61**), shows that *P. leuckarti* was fairly plentiful at 11 out of 20 stations and that *E. nordmanni* was nearly three times as abundant but rather more restricted in range. Both forms were decidedly more plentiful at Station 16, i.e. 10 miles from the coast, the farthest inshore of his stations which extended to 50 miles out (Station 30). Both forms were taken also in fair quantity, even at this last station.

We have no later records for the district in this year. A single haul was made off Spurn Head in September, but no Cladocera were present.

1923.

The more normal conditions of the previous year gave place in 1923 to an exceptional flow of Arctic water into the North Sea, bringing the large variety of *Sagitta elegans* to replace *S. setosa* which had been the predominant species since 1921 (**47**).

Unfortunately, no plankton samples were undertaken before August 7th, when Evadne was present in fair numbers over the whole district. In the third week of August it was found to have become very abundant, particularly in catches from the northerly stations. In September, the only records are of small numbers at the stations near Dunstanburgh.

Developing and fully formed resting-eggs were recorded in late August and early September in much greater quantity than in the previous year—again chiefly from inshore stations.

Podon was present throughout the period, but was taken only in small numbers except in the extreme north of the district towards the end of August when it was more plentiful, especially near the shore. No resting-eggs were recorded.

1924.

Except for three hauls in the middle region of the district at the end of April, when Evadne was taken in very small numbers, no catches were made until July 13th. From that time until August 1st this form was present in abundance at all stations. Developing and fully formed resting-eggs were obtained in considerable numbers during the whole period of maximum occurrence.

Podon was present with Evadne in most of the July–August samples, but in much smaller numbers, and it was commonest inshore. During September and October it was observed in most of the catches and usually occurred in greater quantity than Evadne. Resting-eggs were recorded from three of the July–August stations, being most frequent at the end of the period.

1925.

In 1925 the first samples were taken between April 8th and 14th from ten stations covering the whole district from north to south, and extending nine miles eastward from the coast.

Evadne was present at every station and tended to be more abundant at some distance from the shore. Unfortunately, a period of six weeks elapsed before further catches were taken, when only two stations were sampled, on June 1st. Evadne was again recorded in fair numbers. In July the numbers showed a marked decline and specimens were obtained from only four of six stations. On September 7th a decided increase in abundance was noted at the more southerly stations, especially inshore, when, also, resting-eggs in an early stage of development were taken. A week later, numbers had again decreased and resting-eggs appeared only once, at Station 25.

The records for Podon show similar, but less strongly marked fluctuations, and a tendency for numbers to decrease with nearness to the coast. Podon was always the more scarce form except in July and late September. Resting-eggs were recorded only once, from Station 22.

1926.

In this year, the change in the method of sampling took place, and only three voyages were made. In July and August Evadne was taken in fair quantity throughout the district. Increased numbers reported for September were due chiefly to the catches from the most southerly stations. Resting-eggs were taken only in July, at Stations 1 and 3.

Podon was plentifully represented in July, becoming scarcer thereafter, as regards both range and numbers of individuals. Resting-eggs occurred in July at the northern station, No. 5.

1927.

Abnormal activity of the Gulf Stream, noticeable in north-eastern European waters as an increased mid-water current running through the Faroe–Shetland Channel in 1926, now produced its maximum effect, as is indicated, e.g. by the quantities of Ray's Bream taken in the North Sea from 1926 to 1928 (**77**).

Evadne, absent from all stations at the end of April, was present in small quantities throughout the district about a month later. It reached a maximum at the beginning of July, showed a slight decrease in August and was still fairly plentiful in September at the four stations fished. It is impossible, however, to give average quantities for September as the contents of three nets were lost, due to bad-weather conditions. Resting-eggs were taken in the July and subsequent samples, decreasing, in numbers and in proportion of developing to fully formed eggs, as time went on.

Podon was present from the May–June voyage onwards, but always occurred sporadically as to range, and was scarce. Resting-eggs were observed in September, at one station only.

1928.

In this year's catches Evadne appeared in April and increased in quantity up to the latter part of June, after which it decreased progressively until sampling ceased in the latter part of August. The records for resting-eggs are remarkable, in that they show these to have appeared as early as May 1st. They were taken in every month thereafter (i.e until August). The graphic representation of their distribution takes almost identically the same form as that of the average quantities of the species, over the entire period of their occurrence.

Podon made its appearance in June, touched a very low minimum in July, and increased in quantity in August. Resting-eggs were taken in both June and August.

1929.

Following upon the diminution in amount of Gulf Stream water in

1928, the North Sea again suffered an influx of surface Atlantic water in 1929, as evidenced by the occurrence of quantities of Pteropods in the plankton. The effect, however, on this occasion was less far-reaching than was the case in 1921 and 1922.

Our first samples, collected in April, showed Evadne to be already abundant in the district. After this, its numbers fell to practically nothing in May when it was present at a single offshore station only. This was followed by successive small increases in quantity from June to August. Except for a single record at Station 5 in the latter month, no resting-eggs were observed.

Podon was scarce throughout the period, with a feebly marked maximum in April. There were no resting-eggs in the samples.

1930.

Sampling began early in April of this year, and catches were made in each month until the end of August. Evadne, present sparingly in April, had reached a considerable maximum in June, after which the amounts recorded declined greatly until August when sampling ceased. Resting-eggs occurred plentifully in June, especially at offshore stations where early stages predominated, and more sparingly in July, nearer to the coast.

Podon appeared first in May, reached moderate numbers in June, decreased again in July, and finally rose to a marked maximum in August, when it was by far the commoner Cladoceran genus present. Stages in the development of resting-eggs were obtained from four stations on the last voyage.

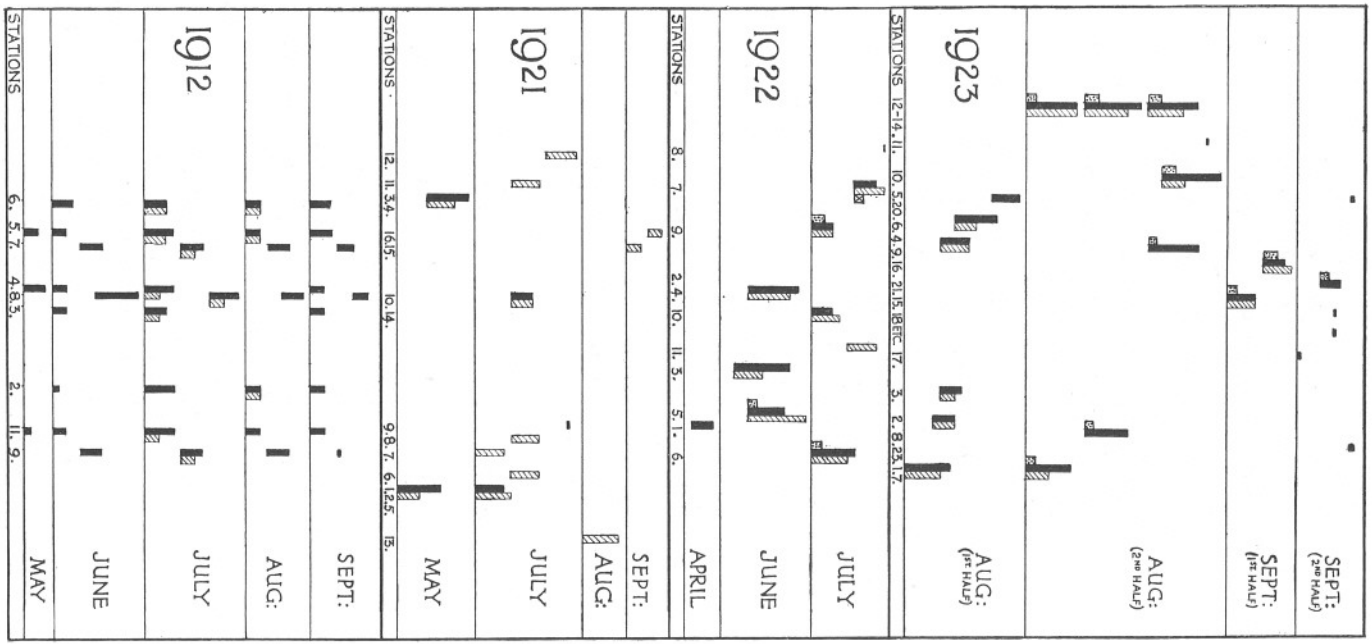
Summary of Records.

Figure 2 indicates graphically the average quantities of Evadne and Podon present in all nets at all stations sampled during each voyage.

During 1921 to 1925 inclusive, these averages represent numbers of stations—and therefore also of nets—which vary considerably from time to time; and there are, in some cases, long intervals of time between voyages. From 1926 onwards the quantities indicated are more uniform as regards the number of nets they represent, and the time intervals between voyages are more nearly equal.

As, however, series of samples taken over a fairly extensive area and generally at rather infrequent intervals can be used to acquire a general idea only as to the movements and phases of metabolic activity of planktonic forms, the two groups of data are regarded as being sufficiently comparable with one another to make it possible to use them to indicate the general trend of the fluctuations in numbers and distribution of the two genera of Cladocera under consideration, as they occur in our district.

DIAGRAM A.



AVERAGE QUANTITIES OF EVADNE, ▮
DO. DO. PODON, ▨
THE COLUMNS RESTING ON THE BASE LINE FOR EACH MONTHS RECORDS REPRESENT SAMPLES FROM INSHORE STATIONS. THE POSITION OF COLUMNS ABOVE THIS INDICATES RELATIVE DISTANCE OF OTHER STATIONS FROM THE COAST.

RESTING-EGGS OF EVADNE, ▤ RESTING-EGGS OF PODON, ⊠
THE SIZES OF THE COLUMNS REPRESENTING NUMBERS OF RESTING-EGGS ARE COMPARABLE WITH ONE ANOTHER BUT NOT WITH THOSE SHOWING AVERAGE QUANTITIES OF INDIVIDUALS. LEFT AND RIGHT SIDES OF THE DIAGRAMS REPRESENT RESPECTIVELY NORTHERN AND SOUTHERN ENDS OF THE REGION.

REFERENCE TO THE MAPS WILL SHOW THE ACTUAL POSITION OF THE STATIONS INDICATED HERE BY NUMBERS (EXCEPT FOR 1912).

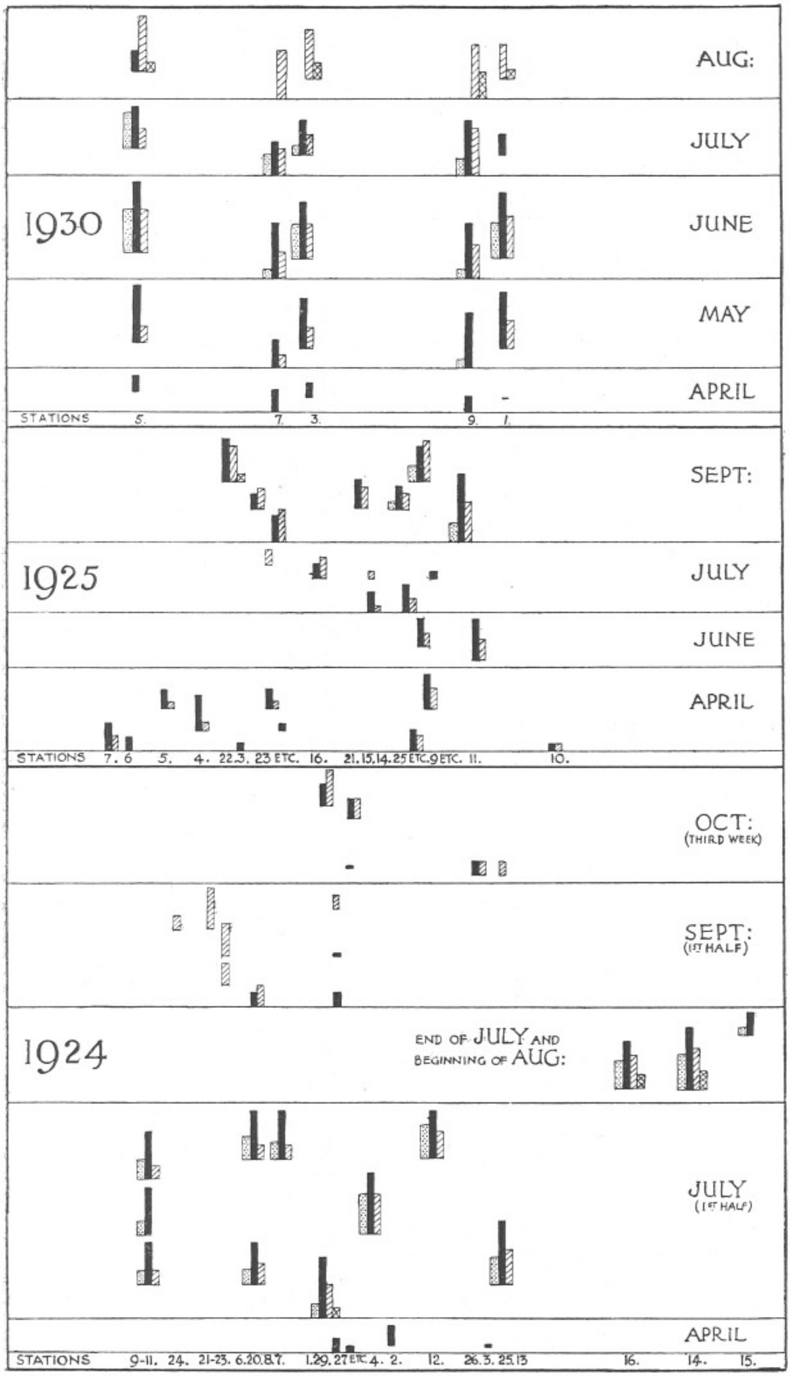

AUG:
JULY
1930
JUNE
MAY
APRIL
STATIONS 5. 7. 3. 9. 1.
SEPT:
1925
JULY
JUNE
APRIL
STATIONS 7. 6 5. 4. 22.3. 23 ETC. 16. 21.15.14.25 ETC. 9 ETC. 11. 10.
OCT:
(THIRD WEEK)
SEPT:
(1ST HALF)
1924
END OF JULY AND
BEGINNING OF AUG:
JULY
(1ST HALF)
APRIL
STATIONS 9-11. 24. 21-23. 6.20.8.7. 1.29.27 ETC. 4. 2. 12. 26.3. 25.13 16. 14. 15.

Diagram B.

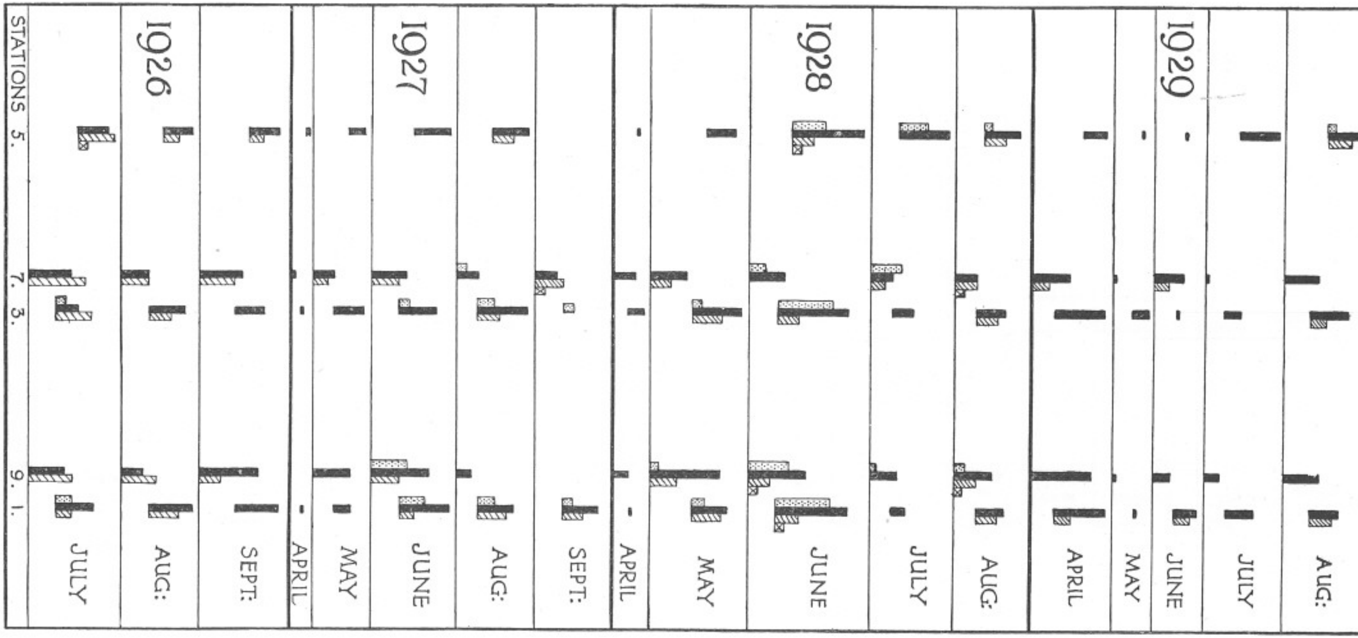


DIAGRAM C.

AVERAGE QUANTITIES OF EVADNE, ■
DO. DO. PODON, ▨

THE COLUMNS RESTING ON THE BASE LINE FOR EACH MONTHS RECORDS REPRESENT SAMPLES FROM INSHORE STATIONS. THE POSITION OF COLUMNS ABOVE THIS INDICATES RELATIVE DISTANCE OF OTHER STATIONS FROM THE COAST.

RESTING-EGGS OF EVADNE, ▩ RESTING-EGGS OF PODON, ⊠

THE SIZES OF THE COLUMNS REPRESENTING NUMBERS OF RESTING-EGGS ARE COMPARABLE WITH ONE ANOTHER BUT NOT WITH THOSE SHOWING AVERAGE QUANTITIES OF INDIVIDUALS.

LEFT AND RIGHT SIDES OF THE DIAGRAMS REPRESENT RESPECTIVELY NORTHERN AND SOUTHERN ENDS OF THE REGION.

REFERENCE TO THE MAPS WILL SHOW THE ACTUAL POSITION OF THE STATIONS INDICATED HERE BY NUMBERS (EXCEPT FOR 1912).

As the years 1921, 1923, 1927, and 1929 must be considered exceptional with regard to conditions in the North Sea, the other years' catches will be discussed first, as showing—in so far as the incompleteness of our sampling will permit—a more normal sequence of events in the life-cycles of these two genera generally, and of *Evadne nordmanni* in particular.

1. *E. nordmanni*—The "Normal" Years.

Evadne is the first Cladoceran to make its appearance in quantity near the Northumbrian coast, being present in fair numbers in April. It is by far the commoner genus on the whole, Podon, as a rule, being markedly more plentiful only from September onwards. Diagrams A—C show, as is to be expected, that Evadne is much more widely distributed throughout the area sampled under both sets of experimental conditions. The graphs indicate, furthermore, that there is a well-marked early summer maximum apparently in June (or earlier) and, for those years of which we have records, a second, but less extensive maximum in September or later is evident.

In 1924 the first maximum appears to be in July, but it must be noted that there are no records for May or June. Also, in 1925, the smallness of the first maximum, as here recorded, is probably due to the long intervals between successive samplings at this period.

It is noteworthy that the great increase in the numbers of individuals present in the samples at these times is due, not to the sudden appearance of large numbers of young, but is produced entirely, so far as our samples are concerned, by a temporary influx of adults. Although immense numbers of young forms are, no doubt, present at these times, no very small specimens are ever taken in our nets.

The population, at the times of maximal occurrence, consists principally of females with brood-pouches containing eggs and embryos in all stages of development. Males also are noted during these periods and the so-called "winter"-eggs are associated with the early maximum as well as with the later one. Indeed, our records go to show that the numbers of "winter"-eggs produced are roughly proportional to the numbers of individuals present, and that they are therefore more plentiful in summer than at the onset of winter when the physical conditions have been supposed to be most unfavourable for the continued production of parthenogenetic generations. It will be seen on reference to the graphs that the resting-eggs appear at or about the period of maximum development and continue to be observed during the subsequent decline in numbers. These findings require a consideration of the factors involved in the change from parthenogenetic to sexual reproduction. This will be dealt with later (Part II).

Occasional observations of resting-eggs as early as June have been recorded, e.g. by Hansen (**25**), and are looked upon as being unusual. Apstein, however, notes a marked occurrence of these in June on the Dutch coast and at Kiel (**2** and **3**). For our region the only record looked upon as being exceptionally early is that of both developing and fully formed resting-eggs at three stations on May 1st, 1928. Apstein gives a similar early record for Station 4 (100 miles E. of Hartlepool) in May, 1908 (**2**).

It would appear that the explanation of the frequency of resting-eggs in early summer, which is brought to light by these investigations, is to be sought in the comparative nearness of the stations to the coast, and the large number of samples taken in a restricted area, as compared with the stations used by the International Council and other investigators.

The appearance of resting-eggs in quantity at stations comparatively near the coast, such as ours are, is associated with movements of the population of *E. nordmanni* as a whole.

It is impossible to use the 1921–1925 samples to indicate movements within the district, as stations sampled on different voyages cannot be compared with one another satisfactorily ; but, from 1926 onwards, the three years 1926, 1928, and 1930 do give some suggestion of " trans-natant " movements.

In 1926 the population, represented over the whole area, was rather more abundant inshore in July, i.e. at the end of the first sexual period as indicated by the presence of a few resting-eggs. Diagram C shows a slight offshore movement in August, while in September there is evidence of a return to the inshore stations which was coincident with the onset of the decidedly early autumn maximum.

After April, 1928, in which month the small numbers present occurred mainly inshore, resting-eggs were being produced in all the months for which we have records, and the population was spread widely over the district.

The records for 1930 show a similar sequence of events up to the end of the summer sexual period, which ended in July, and the August records show the population to have disappeared from the district almost entirely.

It is suggested, therefore, that *E. nordmanni* seeks shallower coastal waters during the actively growing period when parthenogenetic broods are being produced ; that it remains in these regions until pairing has taken place and resting-eggs have been formed, and that it subsequently makes a migration or transnatation into deeper water. This is probably extensive after the autumn maximum and comparatively slight between the summer and autumn maxima—a difference associated with the length of time between these and with changes in physical conditions at different seasons of the year.

2. *E. nordmanni*—The "Exceptional" Years.

It is now necessary to consider the effect of the influence of surface Atlantic water in the North Sea in 1921 and again in 1929. In both years the changed conditions had the effect of speeding up the spring maximum, which occurred in April, 1929, and in May, if not earlier, in 1921. After this the numbers of Evadne decreased rapidly, the population evidently being swept away from our inshore waters.

The fact that no resting-eggs were associated with the first maximum in either year is regarded as significant, and will be discussed in relation to the general distribution of the species.

In 1921 there was no return of the population in autumn, but in 1929 numbers rose steadily from June onwards to produce an autumn maximum as is indicated by the taking of a few resting-eggs on the last voyage.

It is difficult to say what was the effect of the increased amount of Gulf Stream water in the North Sea in 1927, as the records show only one maximum, in early July, and this is capable of two interpretations. There is nothing to indicate whether it represents a much delayed early summer maximum or a greatly accelerated autumn one. The records are sufficient, nevertheless, to show that conditions were abnormal.

As the short sampling season in 1923—the year in which the influence of Arctic water was strongly marked—gives us records for August and September only, it is again impossible to do more than speculate as to its general effect on the species. From the fact that there was a distinct maximum in August, it would seem reasonable to assume that the autumn maximum had been produced unusually early. The phytoplankton of our samples has not yet been analysed, but when this is done it may be expected to throw some light on the problem.

One other point of interest, in this connection, remains to be mentioned, i.e. the occasional appearance of small numbers of individuals distinctly larger than the typical form. These were noticed first from the surface-net of Station 9 in 1925, and again on several occasions in the May–June records for 1927. A few occurred also at the beginning of July of that year. They were not noted again until 1930, when they appeared in both May and June. In the three years they were taken chiefly in the surface and mid-water nets.

These forms were remarkable also for the unusually large number of embryos contained in their brood pouches. The smallest number noted was 7, the majority had 9–11, and a few were observed with as many as 12 or 13. In May–June, and July, 1927, some were seen to be carrying resting-eggs.

Occurrence of Large Form of E. nordmanni.

Year.	Date.	Stat.	Net.	Record.
1925	April 14	9	S	9 or 10 embryos in brood pouch.
1926				
1927	May 30–	1	S	early stages ; some with resting-eggs.
	June 1	3	B	,, ,, ,, ,, ,,
		5	S	,, ,, ,, ,, ,,
		7	S	,, ,, ,, ,, ,,
		9	S	9–11 embryos in brood pouch.
		,,	M	10 embryos in brood pouch.
		,,	B	early stages.
	June 30–	1	S	,, ,,
	July 3	9	S	,, ,, some with resting-eggs.
1928				
1929				
1930	May 13	1	S	quite common.
		5	S	many ; one with 13 embryos.
		,,	M	11 and 12 embryos in brood pouch.
		9	M	scarce.
		,,	B	,,
	June 10	3	S	one specimen seen.
		,,	M	,, ,, ,,
		,,	B	,, ,, ,,
		5	S	several
		,,	M	one specimen seen, 7 embryos in brood pouch.

So far as 1927 and 1930 are concerned, the presence of the large form of *E. nordmanni* might possibly be considered to be associated with the influx of Atlantic water into the North Sea. The 1925 record, however, cannot be similarly explained and much remains to be discovered about the distribution of this form before it is possible to explain its presence in our coastal waters.

The only reference it has been possible to discover relating to marked variations in body-size of marine Cladocera, is that of Rammner who mentions de Lint's records for *P. polyphemoides* in the Zuider Zee where specimens taken from water of low salinity measured 500μ as against Lilljeborg's measurements of forms from more saline waters (600μ–660μ).

In relation to *E. nordmanni*, Rammner states only that individuals are bigger and have broader brood pouches at the beginning of the year than those produced towards the end of summer. If he means this as the rule rather than the exception he cannot have been referring to very large forms such as have been mentioned above. Also, if it is to be supposed that these larger, broader females are the direct products of the sexually formed resting-eggs, they ought to have been noticed in autumn also.

According to Lilljeborg, differences in shape correspond to local variations in populations, North Sea forms being ovoid or elliptical-oval and rounded posteriorly whilst the Baltic variety has a narrower body, due to the brood pouch being narrower and more pointed. He adds, furthermore, that the usual number of embryos produced by North Sea forms is 7 or 8, whereas the Baltic ones have only 3 to 5.

Our investigations show that it is necessary to have records covering a considerable period and to be sure that the forms compared occur in similar stages of the life-cycle before general statements such as the above can be made with safety.

The Northumberland population of *E. nordmanni* includes both of Lilljeborg's varieties (**35**), the proportions in which they are represented depending on the phase of activity of the species at the time. In so far as Rammner (**58**) may be understood to mean that rather larger, broader females occur at the beginning of the period of rapid increase in numbers by the production of successive parthenogenetic broods, his observations are in accord with ours. The proportion of these forms diminishes as the asexual stage of the life-cycle proceeds, until, at the time when developing resting-eggs first make their appearance in the samples, the population consists to a great extent of less bulky, more triangular forms.* These produce from 1 to 6 embryos, the majority having 2, 3, or 4. This change in body-bulk and shape, and the reduction in reproductive activity are regarded as indicating a depression in metabolic activity which is synchronous with the onset of the sexual phase. The relation of these observations to the life-cycle of marine Cladocera generally, will be considered separately below.

In this connection it may be mentioned also that the very few previous records of twin resting-eggs (Lilljeborg) have been considerably increased by these investigations. Whereas Lilljeborg observed them only in September, there are in our samples ten records for June and July as against a single one for September, indicating that not only as regards numbers of individuals present and of resting-eggs produced, but in reproductive power also, the early summer maximum is to be regarded as the chief period of activity in the annual cycle of *E. nordmanni*.

OCCURRENCE OF TWIN RESTING-EGGS.

Year.	Date.	Stat.	Net.	Record.
1924	July 13	5	S	One specimen seen.
		8	S	A few.
		9	S	,,
1925	Sept. 7	20	M	One specimen seen.
1926	July 8	1	S	A few.
1927				
1928	June 1	3	S	One specimen seen.
		9	B	,, ,, ,,
	June 24	1	S	,, ,, ,,
		1	M	A few.
		3	S	One specimen seen.
1929				
1930	June 9	1	B	,, ,, ,,

* Sharpe (**72**) states that the brood sac may contain from 3 to 8 embryos, this causing its outline to be quite variable.

3. Podon—Occurrence from 1921 to 1930.

Until the species (or varieties) of Podon present at various times in the samples have been identified, it is impossible to make definite statements as to the precise activities of members of the genus, but one or two general facts may be mentioned.

As already noted, Podon makes its appearance in our district later than Evadne and is comparatively rare during the early summer. Nevertheless, it shows a maximum, generally feebly marked and more or less coincident with that of Evadne. This is followed by a decrease in numbers which, however, soon gives way to a considerable increase in population producing an autumn maximum which may involve the presence of vastly greater numbers.

It has been noted from time to time that, while individuals of Podon are indistinguishable from one another in the earlier part of the year, there is evidence of the presence of two distinct species (or varieties) in the later months. Resting-eggs were never taken in quantity, but the graphs (Fig. 2) indicate that they may appear in association with both periods of greatest population. The two maxima appear to be little affected by abnormal conditions, except for a general speeding up of activity in relation to time in 1921.

The above-mentioned data indicate that, in addition to being generally a less abundant North Sea genus than Evadne, it is also less strongly attracted to shallow coastal waters as a breeding place.

Previous Records of Cladocera from Northern European Seas.

1. *Northumberland.*

The only previous records of Cladocera for the Northumbrian coast are from surface and, to a less extent, bottom tow-nettings taken at long intervals in various parts of the district, between 1889 (**44**) and 1912 (**76**). Only the last of these series of samples is sufficiently complete to be comparable with the present records, and these are included in Diagram A. The distribution of the two genera in time and space may be seen to take what is regarded as the normal course. Evadne arrived from the north of the district in May, spread along the coast in June and July—being more abundant inshore in the latter month, when maximum numbers were present. It was scarce, particularly inshore, in August, and in September showed a slight tendency to return to the coast, especially towards the north. There is a decided similarity between these and the 1924 records.

Podon (identified as *P. polyphemoides*) did not make its appearance so early as Evadne. It was recorded for July and August and showed a maximum coincident with that of Evadne.

In 1899 it is evident that large numbers of both forms were present in June. The remaining records are too vague to be of value in this connection.

2. *Firth of Forth.*

T. Scott's records (**65**) for this region give no details and show only that *E. nordmanni* is more abundant than *P.* (*?*) *polyphemoides* and has a wider distribution.

3. *Clyde Sea Area.*

Marshall's records (**42**) for *E. nordmanni*, "Common in May and June, fairly common till September and frequent in October," again indicate the occurrence of two periods of maximal occurrence near the coast.

4. *English Channel.*

A consideration of Bygrave's records (**9**) of Cladocera in 1905 and 1906 shows some interesting features. He, however, made no attempt at an analysis, merely noting occurrences and making a general statement to the effect that these forms are more frequent in the western than the eastern part of the Channel, that they always appear in spring and form an important part of the plankton in summer, disappearing again in autumn, "when they form their winter-eggs and thus are able to survive the winter." (This from a record of samples taken during a period of exceptional activity of the North Atlantic Drift: Salps were present in the North Sea in 1905 and Pteropods plentiful in 1906.)

The lightship records from the western and eastern ends of the Channel (Sevenstones and Varne) show Evadne to be the commoner form in the west in 1906, while only Podon occurred at the eastern end. In 1905 Evadne was scarce to the west also.

Quarterly records from other stations (E1 and E17—10 to 20 miles offshore on the northern side) in 1906 show Evadne to be present in February, fairly common in May and abundant in August. The Plymouth records for 1906 also indicate maxima in May–June and in August–September, the latter being the greater.

Bygrave connects the general scarcity of Evadne in 1905 with a patch of water of high salinity at the western end of the Channel (near Station E1).

It is evident from the summary of records given below, that the Cladoceran population enters the Channel with the Atlantic current and normally begins to breed as soon as it reaches coastal waters. In 1905 it was evidently swept away from its usual local centre of distribution, and the fact that in 1906 the early maximum was relatively small indicates that there had not then been a complete return to normal conditions. The taking of resting-eggs only in the late summer of 1906 further accentuates the similarity between these records and ours for later years in which similar conditions prevailed in the North Sea.

SUMMARY OF BYGRAVE'S RECORDS OF EVADNE.

Year.	Month.	Stations arranged in order from W. to E. Sevenstones.	E1–E17.	Plymouth.	Varne.
1905	Jan.–June	None	–	–	None.
	July	Rare	–	–	,,
	Aug.	,,	–	–	,,
	Sept.	Very rare	–	–	,,
	Oct.–Dec.	None	–	–	,,
1906	Jan.	,,	–	None	,,
	Feb.	,,	Very rare	,,	,,
	March	,,	–	Very rare	,,
	April	Rare	–	Rare	,,
	May	Rare to f. common	Common	F. rare	,,
	June	Rare to f. common	–	Rare to f. common	,,
	July	Common to rare	–	F. rare	,,
	Aug.	F. common to rare*	Common	Common	,,
	Sept.	Common	–	F. common to rare	,,
	Oct.	F. common	–	None	,,
	Nov.–Dec.	None	None	,,	,,

– indicates no samples taken. * indicates resting-eggs taken.

5. *The Irish Sea.*

The summaries of records of Cladocera given in the annual plankton reports of the Lancashire Sea-Fisheries Laboratory from 1907 to 1919 show them to refer to two species only, *Podon intermedius* and *Evadne nordmanni*. Considered together, they show the latter species to appear in the district in March or April, to increase in numbers to May or June and thereafter to fall off until September when a second maximum occurs. None are recorded later than October.

In the years 1908, 1913 and 1914, Evadne did not appear until April and, in the last two years, was always scarcer than usual. In 1912 it was not taken later than August.

Podon is shown to have a time range very similar to that of Evadne except that it generally appears rather later and persists longer.

The records are too scanty to show clearly variations in time of appearance and abundance of population from year to year, and indeed the reports frequently lay stress (perhaps rather more than would seem to be warranted) on the great constancy of occurrence of these forms.

A. Scott's records (**64**) of Cladocera from the spawning ponds at Port Erin in 1922 and 1923 indicate the presence of abnormal conditions in the earlier year, as also do our records for Northumberland. In 1923 Evadne first occurred at Port Erin in April and continued to be taken until September, while in the previous year it did not make its first appearance until June and disappeared again in August. Podon was present in 1923 from April till December excepting only August. In 1922 its range was restricted to May–July.

Gough's records (**21**) of samples taken at four lightships on the south and east coasts of Ireland in 1904 are insufficient to form a satisfactory picture of the general distribution of Cladocera in St. George's Channel and the Irish Sea although they serve to show that the population in these waters is distributed by the current entering from the south, and there is some indication of two periods of maximal abundance in inshore waters.

The fact that no Cladocera were taken at the South Arklow Lightship and their extreme scarcity at Skulmartin suggest that in this region there occurs a phenomenon similar to that noted by Bygrave and Apstein regarding the distribution of Cladocera at the eastern end of the English Channel and in the southern part of the North Sea. Apstein remarked that Cladocera were scarce in these regions, " although the physical conditions were suitable," and failed to account for this.

This matter will be discussed separately below.

6. *North Sea, Baltic Sea, etc.*

Plankton samples taken by several investigators and expeditions show *E. nordmanni* to be the commonest Cladoceran in the North Sea, on the western shores of Great Britain, in Danish waters, and in the Baltic. It is noted as being present in varying degrees of abundance at different stations, almost throughout the entire year, but always rare during the winter months. It has been mentioned as having been taken along the Norwegian coast up to 72 deg. N. lat., and, in the Atlantic, 13 deg. West of Scotland. Also, there are isolated records of its occurrence in the Barents Sea near the Murman coast and in the Irminger Current up to the south coast of Iceland.

Apstein regards the species as being abundant throughout the seas of North-West Europe during all the summer months. This conclusion is evidently based on the fact that the times of maximal abundance vary slightly from place to place and from year to year, and that the many different stations sampled were far from being equally distant from the shore. Although he quotes Hansen's records of resting-eggs taken in Dutch coastal waters in June, he does not appear to attach any significance to their production at so early a period.

Rammner, summing up records of the distribution of *E. nordmanni*, refers to its abundance in the North Sea and the Baltic and to its occurrence farther afield, but regards the Baltic as its real home. Apstein, on the other hand, considers the northern part of the North Sea to be its centre of distribution.

Rammner remarks also on its great variation in numbers from place to place, due to causes other than seasonal ones, and points out the necessity for more systematic sampling before it is possible to make a definite statement as to its distribution in a large area (such as the North Sea). He considers that currents are responsible for its distribution and notes its tendency to inhabit inshore waters.

With reference to his statement that *E. nordmanni* is not found within a distance of 100 or 200 metres from the shore, it may be noted incidentally that specimens were taken in August, 1922, in the Estuary of the River Coquet. Also, the species has been recorded by T. Scott (**67**) as being abundant at the head of Loch Fyne.

Lohmann's quantitative analyses of organisms taken in a measured volume of water, show the occurrence of two maxima in the numbers of *E. nordmanni* obtained, i.e. in June and August (1884) with a minimum between these, in July.

Investigators have remarked on apparent peculiarities in the distribution of the species, and, assuming it to be truly neritic, have had to account for its occurrence in certain places by its being carried by currents away from its normal area of distribution in coastal waters.

Rammner emphasises the effect of currents on its distribution and thinks that there may be some reason for considering the species to be a deep-sea form. Steuer goes farther and thinks that it is ridiculous not to regard *E. nordmanni* as an oceanic species since it has been shown to occur in the open ocean.

Ostenfeld explains the presence of occasional specimens along the Norwegian coast and in the Barents Sea as being due to the Gulf Stream carrying them away from the coast (of the western side of Scotland, presumably). He is unable, however, to explain the occurrence of *E. nordmanni* in the Irminger Current.

Apstein, referring to the distribution of this species, does not analyse his data, but his statements relating to that of *E. spinifera* are interesting. He regards isolated specimens taken near the Faroes as having been brought there through the influence of the Atlantic Drift. Also, while making no special reference to the exceptional conditions prevailing in 1905, he thinks that examples found in the English Channel in November, 1904, and in the south-west corner of the North Sea in the following May, might well have originated in the Atlantic Ocean. He mentions, furthermore, that the only specimens taken in any year near the Belgian Coast were obtained in May, 1905.

As 1905 is comparable with 1921, and to a less extent with 1929 as regards the cause of unusual conditions in the North Sea, the foregoing statements are of importance as emphasising the influence of an increased influx of Atlantic drift water into our coastal regions. The effect of such is evidently to interfere with the normal distribution and breeding times of the Cladoceran population, and to introduce other forms, e.g. *E. spinifera.* Its effect in 1921 and 1929 was to sweep away *E. nordmanni* from the Northumbrian coast after an early maximum in May, and to prevent the development of resting-eggs there at these times. Also, the records for 1929 show no indication of depression as regards body-shape and numbers of embryos formed, during the early part of the year. (The 1921 samples need re-examination for verification of this point.) It would thus appear that the increased amount of Atlantic drift water present produced a change in the physical conditions which are responsible, at least indirectly, for this effect. Bygrave's records for the English Channel show similar results to have been brought about there in 1905, as also do Lohmann's for the relative proportions of Podon and Evadne present at Kiel during the same period.*

From a consideration of the above data it is suggested that normally *E. nordmanni* is capable of migrating across current during the course of its denatant drift along the coast, so that it is brought into inshore waters where the environment is at first suitable for the rapid production of successive parthenogenetic broods, but which later has the effect of slowing down activity and bringing the asexual period to an end. An unusually strongly running body of water or one differently constituted from the normal coastal current may interfere very markedly with this series of events.

Geographical Distribution of *E. nordmanni*.

In addition to the distribution of the species in the regions already discussed, *E. nordmanni* is also known to inhabit the Labrador Current (Hansen) and to be common off the coasts of Nova Scotia (Wright, **89**) and Massachusetts (Sharpe, **72**).

The importance of the part played by current systems as indicated

* That similar conditions supervened in 1896 is shown by T. Scott's records for the Faroe-Shetland Channel in July and August of that year. Salps and Arachnactis larvæ were present, indicating an abnormal flow of Atlantic water. While *Podon intermedius* (or *polyphemoides*) was taken in 14 out of 19 catches, *E. nordmanni* was present in only 6 and was always rare.

above needs further consideration, and it is suggested that it is necessary to take a wider view of the geographical distribution of the species than has been done previously.

It is evident from the position of the stations from which *E. nordmanni* has been observed that one cannot regard it as a neritic species except in the sense that it " prefers " coastal waters as a breeding-place. That such regions are absolutely necessary for the purpose remains to be proved.

Ostenfeld, assuming that the species was indigenous to the coasts of North-Eastern Europe, was at a loss to explain its presence near Iceland, in the open Atlantic and in the Labrador Current.

If, however, these regions of occurrence are considered in relation to Wright's and Sharpe's records for the east coast of North America, its presence can be explained. *E. nordmanni* occurring in quantity off the coasts of Massachusetts and Nova Scotia must be picked up by the Gulf Stream and carried across the Atlantic to be distributed to the English Channel and the Bay of Biscay (**75**) on the one hand, and to the west coast of Scotland, northern North Sea, Danish waters, and Baltic Sea on the other hand. Furthermore, it may be carried likewise along the Norwegian coast even so far as the Barents Sea when conditions are favourable. Since the Irminger Current branches off from the Atlantic Drift farther to the west, this assumption provides the only explanation of the occurrence of *E. nordmanni* along its course. Since it is present in the Labrador Current also, it may be said to occur in every part of the North Atlantic circulation. Thus, the species may be regarded as having two main centres of distribution, the one on the west coast of North America, the other in the coastal waters of North-Eastern Europe. That it is a regular inhabitant of the North Atlantic Ocean is evident, though to what extent it breeds under other than coastal conditions is as yet unknown.

Records of the species from the Bay of Biscay, the Mediterranean, the coast of California, and various places along the west coast of Africa indicate that it has other centres of distribution, but the records are too scattered to make it possible to discuss this point.

Scarcity of *E. nordmanni* in Certain Coastal Areas.

A consideration of the horizontal distribution of Cladocera in the Irish Sea, North Sea, and English Channel in relation to the Admiralty chart (Fig. 3) showing the general drift of surface water in these regions, reveals the fact that the main spread of the population is along the course of the principal coastal surface currents in the regions concerned.

In the North Sea, Cladocera have been recorded as being generally scarce to the southward of a line drawn between the Tyne (55 deg. N. lat.) and Texel (53 deg. N. lat.), that is beyond the region in which the southerly flowing coastal current crosses over from the English to the Freisian coast. That a fraction of the population is retained in the offshoots of the current which continue south to about the region of Orford Ness is shown from the analysis of Savage's samples. In these the numbers of Cladocera decrease with distance southward as far as Lowestoft, the most southerly station fished.

Distribution in the Irish Sea is explainable along similar lines. The main population enters via the south coast of Ireland in the current which passes

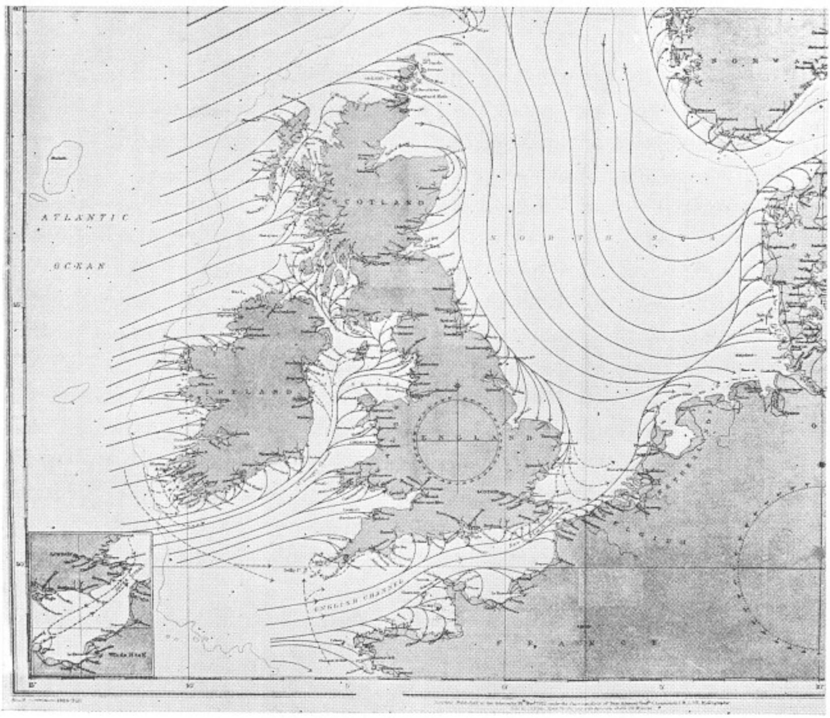


Fig. 3.—Admiralty Chart, showing direction of surface currents around the British Isles.

through St. George's Channel and, on reaching the Irish Sea, is deflected with it to the east, as seen from the Liverpool and Port Erin records. That it scarcely enters the region to the west of this, in which only temporary drifts approach the Irish coast, is indicated by the lightship records of that region (South Arklow and Skulmartin). Thus, in both the above cases, major movements of population depend on the circulation of the main surface currents, and only relatively small numbers are present in those parts not directly under the influence of these.

In the case of the English Channel, the scarcity of Cladocera in the eastern region is more difficult to account for. In consideration of the fact that the main current in which Cladocera are abundant at the western end of the Channel normally passes through the Dover Strait, would lead one to assume their presence in quantity both in the eastern part of the Channel and in the south-western region of the North Sea. Their general scarcity in these waters is probably to be accounted for in part by the effect on the current of the narrowing of the Channel eastwards, and partly to temporary conditions to be referred to shortly. On both sides of the main Channel current there are coastwise offshoots whose general tendency is to be deflected backwards. (Tidal movements here also tend in the same direction.)

If it is generally true that agamic reproduction is favoured by inshore conditions, the greater part of the Cladoceran population should be found in these parts—as it is, so far as our incomplete records including only the northern shore are able to show.

The Admiralty chart (Fig. 3) referred to includes an inset showing the temporary effect of northerly to easterly winds on the current of the Dover Strait. This illustrates that, in these circumstances, the direction of the current on the English side may be reversed and travel in the direction of C. Barfleur as far as about 1 deg. W. long. Also, the direction of the tidal streams on either side of the Dover Strait during the ebb will act in conjunction with this in its effect of further mitigating against the passage of quantities of Cladocera into this part of the Channel and through the Dover Strait into the southern North Sea. That an abnormally strong influx of surface Atlantic water into the North Sea may also accentuate this condition at times, is suggested by the entire absence of Cladocera from the Varne Lightship Station throughout the years 1905 and 1906.

Records of quantities of Cladocera in Dutch coastal waters on certain occasions—other than off the northern part of the Freisian coast—can however be accounted for only on the assumption that at times large numbers *are* able to pass through the Dover Strait, or that the temporary currents indicated as traversing the region between Lowestoft and the Hook, take part in their distribution, or that both may be contributory factors.

THE VERTICAL DISTRIBUTION OF *EVADNE NORDMANNI*.

The only material as yet available for the study of the vertical distribution of *E. nordmanni* in Northumbrian coastal waters is that taken in 1928, when all the samples were examined, i.e. the catches from the whole series of nets used at ten-fathom intervals at all stations.

The relative numbers of Evadne taken at the different depths are indicated in Fig. 4. F. S. Russell's (**59**) method of representation has been used. The narrow black lines indicate depth where no specimens were obtained.

Except in April and in a few of the later catches, when Evadne was scarce, it is shown to be present at all depths fished, i.e. down to 60 fathoms at the offshore stations with a decided tendency to be most abundant in the first 10 to 20 fathoms below the surface. If, as stated by Russell,

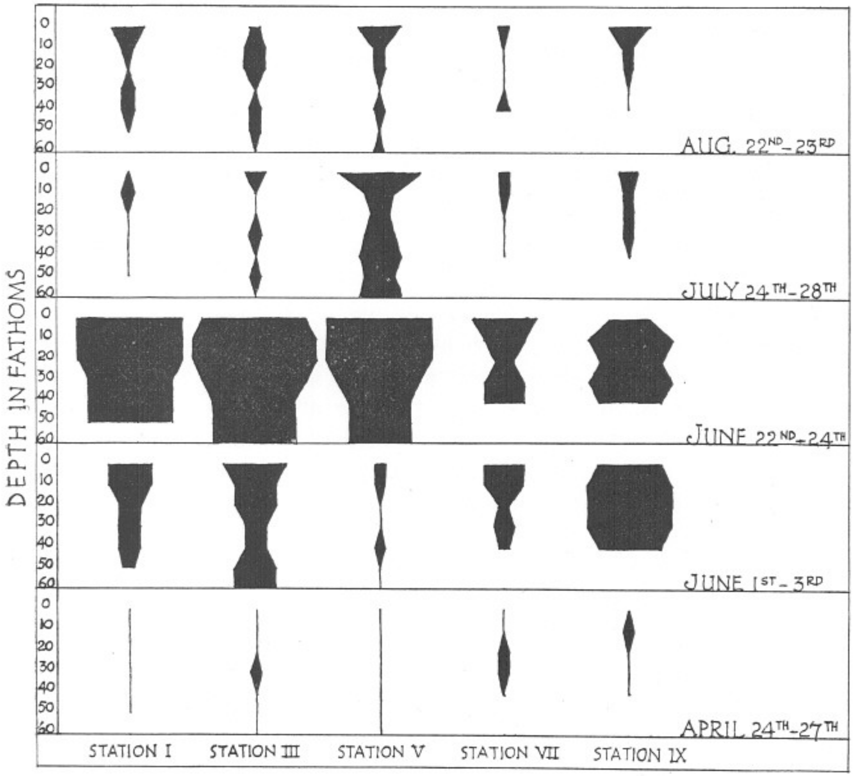


FIG. 4.—Vertical distribution of *E. nordmanni*, 1928.

light intensity is the main deciding factor of the depth at which a species normally lives, then the optimum intensity for *E. nordmanni* is evidently very high. Not only was it found abundantly near the surface during the summer months at times when visibility was comparatively poor, as in the early June and the August voyages, but its general distribution suffered no appreciable change when visibility was good in the later June cruise and exceptionally good in July. (A special note in the yacht's log has reference to the unusually clear conditions prevailing on July 24th to 27th.) See Table I, page 204.

Our records, therefore, bear out the general statements of other workers as to *E. nordmanni* being essentially an epiplanktonic form. Rammner however states that the species is not found actually at the surface except in dead calm weather, as it makes its way to deeper layers of water at the first sign of roughness of the sea. This does not hold good so far as our records are concerned, for the samples taken on the August voyage show a distinct aggregation of individuals at and near the surface on an occasion when the sea was moderating after a rough period. Sampling was to have begun on August 21st, but the sea was too rough for the work to be undertaken until the following day. The weather conditions prevailing during the several cruises, as recorded in the ship's log, are summarised in Table I.

The records of Stebbing and Fowler (**75**) of Cladocera in the Biscayan plankton further stress the fact of *E. nordmanni* being essentially a surface-water form. They record it from the surface on several occasions and give its lower limit as about 100 fathoms. Only a few isolated specimens were taken from greater depths (500 and 750 fathoms).

It is not expected that normal variations in temperature and salinity will be shown to have any appreciable effect on the vertical distribution of this species, as it has been observed to live under a wide range of conditions as regards both these factors (range of salinity 2–35°/$_{oo}$, limits 1·53–35·4°/$_{oo}$: range of temperature 6–18 deg. C., limits 1–22·6 deg. C), but until more data are available it is impossible to discuss this point or to consider differences between its diurnal and nocturnal distribution in relation to depth.

TABLE I

WEATHER CONDITIONS DURING 1928 PLANKTON CRUISES.

Date.	Wind.	Sea.	Visibility.	Remarks.
Aug. 20th	N.E.	E.; strong	Poor; rain	Too rough for work.
,, 21st	,,	,,	,,	,, ,,
,, 22nd	N.	N.E. moderating	Poor	
,, 23rd	S.S.E.; light	Moderate	,,	
,, 24th	Increased	"Hashy"	Poor; rain	
July 25th	W.; light	Smooth	Very good	Visibility exceptionally good throughout trip — coast seen from off-shore stations.
,, 26th	,,	,,	,,	
,, 27th	Light; variable	Light N. swell	Good	
,, 28th	Light; N.-N.W.	,,	Cloudy, rain	
June 22nd	Fresh, W.		Moderate.	
,, 23rd	Strong, W.		Better.	
,, 24th	Fresh-strong		Good.	
June 1st	Light, S.E.	E. swell.		
,, 2nd	Light, N.	Haze, clearing later.		
April 24th	Fresh, S.		Moderate.	
,, 25th	,,	S.E.	,,	
,, 26th	Light, N.E.	Calm	,,	

PART II. THE LIFE-CYCLE OF *EVADNE NORDMANNI*.

1. The Parthenogenetic Phase.

The paired ovaries of *E. nordmanni* are small, spindle-shaped structures lying at the sides of the intestine. The posteriorly directed end of the ovary is rounded while the opposite end may be drawn out to a fine point.

After the eggs have been shed into the brood pouch, the ovary is invisible in stained preparations (Figs. 5 and 11), but, as the embryos develop, the organ is again discernible, its contents developing meanwhile so that by the time the embryos are ready to be freed, a second generation of eggs has been formed and may be extruded even before the previous batch of embryos has been set free. (Figs. 6–9 and 14.)

As the preparations examined were made from material not specially preserved for the purpose, it has not been possible to make out the details of the early development of the ovarian cells—the nuclei not being visible. In the earliest phase in which the ovary can be seen, it is filled with a mass of tissue not shown to be definitely marked off into cells. Later a number of irregularly shaped cells are closely pressed together in all but the narrow anterior end of the ovarian sac, and finally the same space is occupied by a string of large cells varying in number from four to six or rarely eight. The last of these is placed at the extreme posterior end of the organ, while the anterior part is now filled with a group of very small cells (Figs. 15 to 18). The anterior part of the ovary thus evidently constitutes the germarium described by W. F. R. Weldon (**84**) as occupying this position. The posterior end of the ovary is turned towards the dorsal side of the body and, at the time of egg extrusion, no doubt forms a short oviduct which becomes continuous with the wall of the brood sac as suggested, though not actually seen, by Claus (**12**).

In certain preparations only four large ovarian cells are present and there is no germarium. As this condition occurs in specimens bearing only very few embryos, indicating the condition of depression already mentioned as preceding the sexual phase, it would appear to be an early stage in the formation of the resting-egg (Fig. 34). This will be discussed below.

The process of development of the parthenogenetic eggs of Polyphemidæ was described originally by Claus who stated that the tetrad-formation of ovarian cells, which undoubtedly occurs in the production of the gamic egg, occurs also in the development of the agamic generations—one cell from each tetrad giving rise to an ovum, the others serving as "nurse-cells" or feeding cells for its nourishment.

Kuttner (**33**), on the other hand, states that never was the tetrad formation observed, that no "nurse-cells" are present and that each

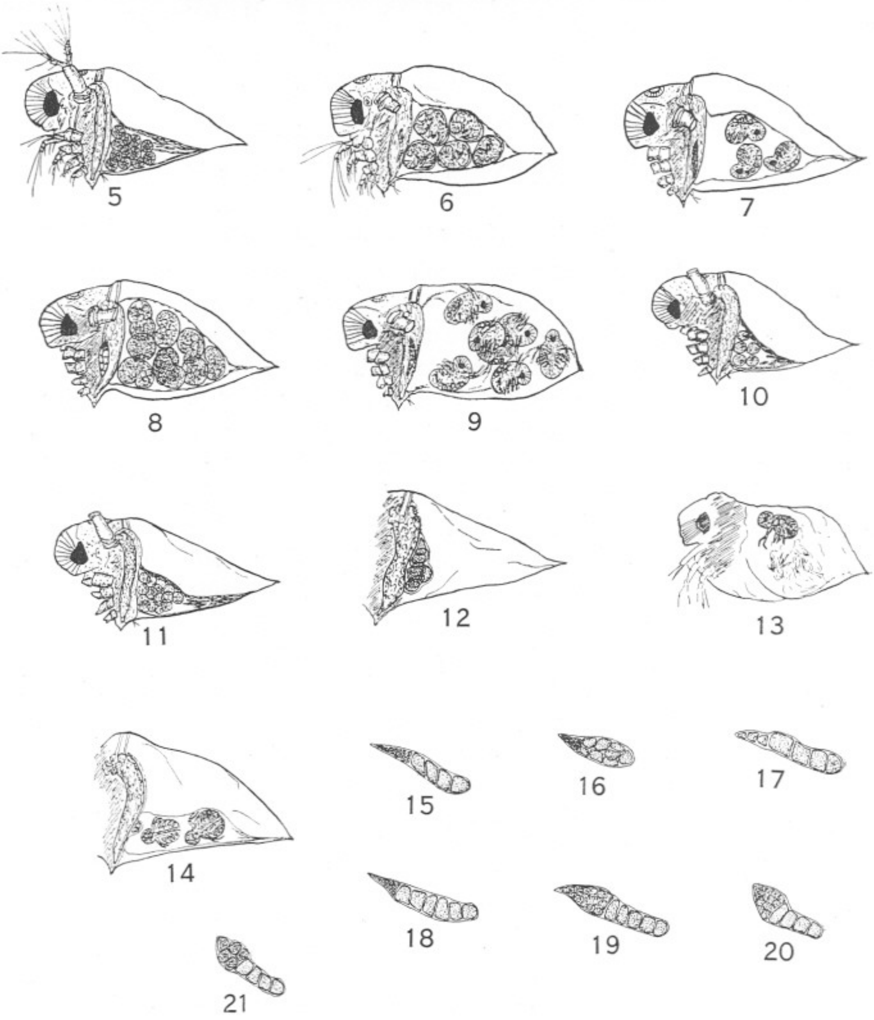


FIG. 5.—Parthenogenetic female of *E. nordmanni* with embryos in blastula stage. Shows thickening of anterior wall of brood pouch and cells suspended in cavity towards apical end.

FIG. 6.—Developing embryos in brood pouch; ovary again becoming visible.

FIG. 7.—Brood pouch containing well-advanced embryos bearing eggs. Maternal ovary further developed than in preceding figures.

FIG. 8.—Female showing conditions during height of parthenogenetic activity; nine embryos in brood pouch. Ovary with seven egg cells and germarium.

FIG. 9.—Fertile embryos in shell cavity ready for freeing. Shows torn walls of brood pouch.

FIGS. 10 and 11.—Brood pouch with eggs; shows its relatively small size at this stage and the glandular cells of its wall, as in Fig. 5.

FIG. 12.—Newly extruded eggs in very small brood pouch with glandular cells not yet visible.

FIG. 13.—Cast cuticle containing one embryo and what appear to be cuticles of two others in shell cavity.

FIG. 14.—Brood pouch containing two fully-formed embryos and enclosing second very small brood pouch with two newly extruded eggs. Here, as in Figures 9 and 13, the embryos are free from the egg membrane.

FIGS. 15, 16, and 18.—Ovaries with varying numbers of egg cells in posterior portion; anterior end occupied by germarium.

FIGS. 19 and 20.—Ovaries including egg cells and large germaria with cellular contents.

FIGS. 17 and 21.—Most advanced stage in development of ovaries, i.e. with two generations of germ cells. (Taken from preparations of specimens with several embryos in brood pouch.)

germ cell develops independently and produces an egg. This is evidently a fact in regard to the large cells which come to occupy the more posterior part of the ovary towards the end of the period of embryonic development of the previous batch of eggs, but it may well be that each of these is the product of one of a group of four small cells produced by the germarium as stated by Weldon. He described proliferation in the germarium as giving rise to quadri-nucleate masses which form four cells, one of which becomes an ovum and is nourished by the others, which then die. As already stated, the preparations do not show the details of these earlier stages at all clearly, but are good enough to indicate that the ovary contains more protoplasmic masses or cells at the earlier stages than there are large egg cells present when these are fully grown (Figs. 19 and 20). During the active period, when many embryos are produced, the germarium may occupy more space than the remainder of the ovary and its contents are definitely cellular. This is shown in Figure 21.

The failure of Kuttner to observe the germarium may be due to the examination of specimens nearing the end of the parthenogenetic period, or to mistaking it for the anterior end of one of the chain of egg cells from which it is sometimes difficult to distinguish it.

The presence of young germ cells and fully-formed eggs in the ovary, together with advanced embryos in the brood pouch, is interesting in that four generations of individuals may thus be seen together in different stages of development. This, taken along with the fact that the embryos also become fertile before leaving the brood sac, furnishes an adequate explanation of the rapid and enormous increase in numbers of individuals which takes place under conditions favourable to parthenogenetic reproduction.

Kuttner mentions the fact of the embryos being fertile as significant in regard to the recording of no females with empty brood sacs, but the two stages of cells in the ovary is equally important in this connection. Nevertheless, females with empty brood sacs have been observed. This occurs at the end of the agamic period and appears to be a necessary preliminary to the preparations for the nourishment of the sexually formed " winter-egg."

Claus has described the brood pouch as a closed feeding-chamber or " uterus " in which the embryos are nourished from the maternal circulation through the medium of the glandular cells of its wall and states that the feeding area is further increased by an infolding of the anterior wall by means of which glandular cells are suspended within the cavity of the brood chamber.

Kuttner's crudely figured " Blasenförmiges Organ " is shown as a band of large square-sided cells passing across the middle of the brood chamber. Nothing like this has been seen in the Northumberland material, which

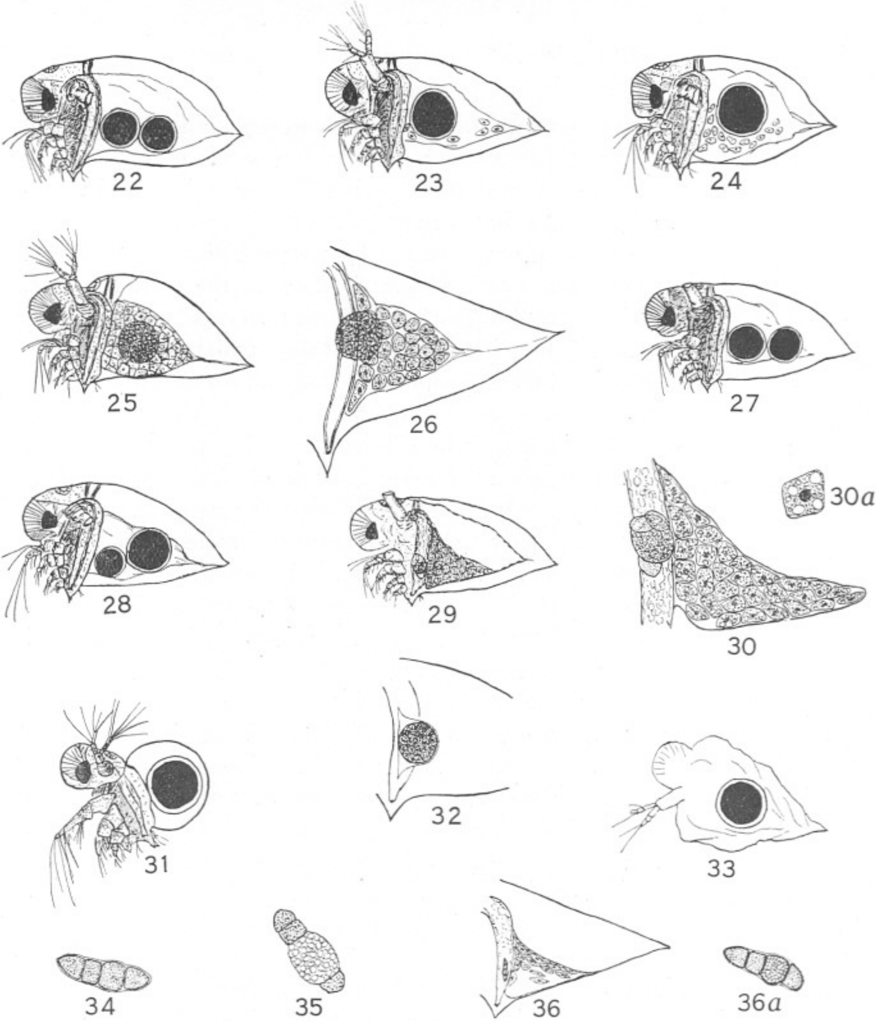


FIG. 22.—Female *E. nordmanni* with two fully-developed winter-eggs of equal size in brood pouch. Nurse-cells entirely disappeared.

FIGS. 23 and 24.—Winter-eggs almost or completely developed, with thick shell. Shrunken remains of some nurse-cells in brood sacs.

FIG. 25.—Developing winter-egg within closely packed mass of nurse cells. Protective shell not yet begun to be formed.

FIG. 26.—Rather later stage than last—nurse-cells less numerous and less closely packed.

FIG. 27.—Two fully-formed winter-eggs escaping through ruptured wall of brood pouch into shell space.

FIG. 28.—Specimen containing two winter-eggs of unequal size.

FIG. 29.—Young winter-egg surrounded by other three cells of the tetrad. Brood pouch already filled with nurse-cells.

FIG. 30.—Detail of Figure 29 more highly magnified.

FIG. 30a.—One of glandular nurse-cells enlarged to show nucleus, fat globules and granules.

FIG. 31.—Specimen of *Podon ? polyphemoides* with winter-egg in shell cavity.

FIG. 32.—Growing winter-egg of *E. nordmanni* showing formation of envelope. (Brood sac and nurse-cells not indicated.)

FIG. 33.—Cast shell of Evadne containing a winter-egg.

FIG. 34.—Earliest stage in winter-egg formation observed. Ovary contains only a tetrad with third cell slightly enlarged but not noticeably different from others in texture.

FIG. 35.—Rather later stage than last. Third cell now definitely larger and filled with fat globules.

FIG. 36.—Stage between those shown in Figures 34 and 35. Brood pouch formed and partially filled with nurse-cells which are situated chiefly along its anterior wall.

FIG. 36a.—Shows detail of ovary shown in Figure 36. Third cell of tetrad filled with fat globules.

shows, during certain stages of brood sac formation, a condition similar to that described by Claus.

When the eggs first leave the ovary they lie at the posterior end of the shell cavity, just anterior to the caudal furca and closely surrounded by a fine membrane which forms the wall of the brood sac (Fig. 12). The eggs are thus pressed together and are not circular in outline as they become later. As the eggs develop, the wall of the brood pouch correspondingly expands and its cellular character becomes obvious. It is attached to the shell along its posterior border and becomes triangular in shape. The anterior wall appears thickened, and elongated spindle-shaped cells occupy the apex of the triangle (Figs. 5, 10, and 11). With further development of the embryos, the brood pouch lengthens until its attachment consists of a fine strand of tissue connecting its end with that of the shell (Fig. 6). When the brood sac contains only a small number of embryos its shape is not conspicuously altered, but when packed with many well-grown young its anterior side becomes rounded and it occupies a considerable portion of the shell space which is correspondingly altered in shape (Figs. 8 and 9).

As the development of the embryos nears completion the glandular cells of the brood sac wall are no longer visible (Fig. 7). When the young are fully formed and ready to be freed they are evidently capable of individual movement within the brood sac and the thin wall becomes ruptured, permitting their escape into the shell-space (Fig. 9).

From the torn appearance of the brood pouch after the embryos have passed out and from its very small size when the eggs first reach it, it appears to be used only once and renewed for the reception of each successive batch of eggs. Claus, quoting Lovén, mentions the immediate contraction of the walls of the brood pouch on the exit of the embryos, but that this does not occur invariably is evidenced by the torn remains of its walls visible in our preparations, and by the fact that a new batch of eggs may leave the ovary and be surrounded by a second tiny brood pouch while the embryos of the previous generation are still retained within theirs (Fig. 14).

That the complete freeing of the embryos takes place in two stages, as described by Lovén, is shown even from a study of fixed material. Following the first stage already described, the final freeing from the maternal shell space is brought about by ecdysis of the mother, when the embryos remain in the old shell, from which they can then make their escape.

Discarded shells containing one or more embryos have been observed as well as stages following the rupture of the brood pouch. One preparation, illustrated in Figure 13, shows a cast shell in which one embryo is retained together with what appear to be the cast cuticles of two other embryos, indicating that the young cast their skins at or about the beginning of their free existence. This is probably their first ecdysis, as the embryos are retained within the egg membrane during the greater part of their sojourn within the brood sac.

The number of embryos in a batch may vary considerably. That both ovaries shed their eggs simultaneously and that each of the large ovarian cells may, under favourable conditions, produce an embryo, is seen from the presence of as many as fifteen blastulæ and up to thirteen or fourteen advanced embryonic stages. (It is difficult to be sure of the exact number when so many embryos are packed together in the brood sac.) The usual number, however, is not nearly so large—generally six to eight or nine—while at times the majority of specimens carry only two to five embryos. An analysis of the samples taken at different periods shows this condition to be coincident with the several stages of the parthenogenetic phase. Ordinarily, during the period of more active metabolism, larger numbers of young are produced, while the depression mentioned as preceding the onset of the sexual phase is indicated by the presence of fewer embryos, as well as by the occurrence of males in the samples.

The number of embryos formed is, in the first place, dependent upon the number of ripe germ cells in the ovary, but it is apparent that it may be further regulated, especially towards the end of the agamic period, by some of these failing to develop. Although it has not been possible to demonstrate the fate of these cells, it is believed that they disintegrate before leaving the ovary, as batches of newly extruded eggs may consist of only two (Fig. 14).

The greatest number of embryos, i.e. twelve to fourteen, has been observed only in the large form of *E. nordmanni*, referred to as occurring occasionally among the ordinary population. As regards the others, carrying from two to nine or more young, there is no appreciable difference in body-size, although those containing large well-filled brood pouches have the shell distended into a more rounded contour instead of the typical triangular form of less heavily burdened specimens, thus making the body appear more bulky.

The progressive decline in activity during the parthenogenetic phase, here shown for *E. nordmanni*, as indicated by the decrease in the number of embryos produced, provides an explanation of the discrepancies between the accounts of various authors as to body shape and number of young borne by this species. In consequence, as noted above, it has been regarded as having a North Sea variety which produces seven or eight eggs and a Baltic variety with two to five. Also Claus, who examined Mediterranean specimens in September, gives the number of embryos as four to six. That he was dealing with material nearing the end of the parthenogenetic phase is evident, not only from the time of year when the specimens were taken, but also from his account of developing winter-eggs obtained at the same period.

The number of eggs in the first batch produced by a female while still in the maternal brood pouch apparently varies within only small limits. Claus gives the number as four to six. Kuttner figures an embryo bearing five blastulæ, and our material also gives examples varying from four to six eggs or blastulæ.

The presence of males was noted towards the end of the parthenogenetic period, but there are no special observations to record. They are readily distinguishable from the females by the absence of a brood pouch and by the rounded form of the paired testes which are easily discernible in stained preparations.

2. The Sexual Phase.

Claus' observations on the development of the winter-egg, which are incomplete due to lack of material, are here confirmed. There is no question as to the production of the gamic egg from one of a group of four ovarian cells as described by him, but our material includes quantities of females with such eggs in various stages of development, and a fuller account of the process is now possible.

The earliest stage seen shows the ovary to contain only four large cells arranged in a row, the third from the anterior end being already slightly broader than the others. No germarium is visible, the ovarian wall being closely apposed to the edges of the tetrad (Fig. 34). That this is an early stage in winter-egg production is indicated, as already stated, by the absence of the germarium, the size of the third cell and by the fact that the brood pouch contains only one embryo which appears to be a male as, although fully developed, it bears no eggs beneath the cuticle on its dorsal side.

There is at this stage no indication of the presence of the nurse-cells which later occupy the brood pouch prior to its reception of the growing winter-egg.

Claus noted the absence of any other cells in the ovary during the formation of the winter-egg and assumed therefrom that other oocytes formed at the same time as the one that gives rise to the tetrad must have passed out to become the glandular nurse-cells which nourish the growing egg in the brood sac. An examination of our material, however, shows the nurse-cells to have a different origin.

In the stage shown in Figure 34 the future winter-egg has the same granular appearance as the other three cells of the tetrad and is only distinguishable by its slightly larger size. There is no sign of the formation of the brood sac or of the presence of glandular cells. At a slightly later stage, that illustrated in Figures 36 and 36a, the winter-egg has assumed its characteristic appearance of being filled with globules of fat, and a brood pouch of moderate size has been formed. This contains a number of nurse-cells which partially fill it, and they, for the most part, are situated along its anterior border. That is to say that they arise in the same position as do the glandular cells present during the development of the parthenogenetic embryos. This would seem to indicate, in the absence of any other cells capable of nourishing the egg, that they are not derivatives of ovarian cells at all, but are actually the product of the wall of the brood pouch, arising, as in the former case, from an invagination of its anterior border. That they become markedly different from the cells which feed the parthenogenetic embryos in size, shape, number and contents will be seen by a comparison of Figures 5, 10 and 11 with Figures 25, 26, 29, and 30.

The slightly older stage shown in Figure 35 is drawn from a specimen in which the brood pouch is still only partially filled with nurse-cells; but when the stage represented in Figures 29 and 30 is reached and the egg, while retaining its original position, has increased in diameter to about the width of the intestine, the brood pouch has become packed with thirty to forty large glandular cells, polyhedral in shape through mutual pressure and having the appearance indicated in Figure 30a. A central nucleus is present, and a number of fat globules of various sizes are to be seen in the granular cytoplasm.

As the egg increases still more in diameter, a fine membraneous envelope appears, surrounding it closely on its dorsal side and drawn away from it ventrally, as shown in Figure 32, suggesting that it is the product of the ovarian wall. The three cells associated with the young winter-egg have now disappeared.

During the subsequent growth to its relatively enormous size the egg does not as a rule become far removed from the region of the ovary, but lies embedded, at the proximal end of the brood sac, in the mass of nurse-cells which now fill it. When, however, two eggs are developed simultaneously, one is placed more distally (Figs. 22, 27, and 28).

From the first appearance of fat globules in the egg, when it loses its ability to take up stains readily absorbed by the remainder of the body, and particularly the nurse-cells, it becomes difficult to distinguish, especially when it has come to be situated within the brood chamber. Due to this and the fact that the closely packed mass of nurse-cells may have the appearance of a large number of early embryos, it was not until a considerable quantity of material had been examined that the significance of these cells was appreciated and their presence in the brood pouch was found always to be coincident with the occurrence of a winter-egg in process of development.

As the winter-egg nears its limit of growth the nurse-cells decrease somewhat in size and number and become more sharply separated from one another (Fig. 26). The thick protective shell is then formed and when the development is completed a few shrunken remnants of the nurse-cells may still be present, as shown in Figure 23. When two eggs have been formed the brood sac is generally empty.

The fully-formed resting-egg breaks through the wall of the brood sac and lies in the maternal shell cavity. There is no production of an ephippium in Evadne, the winter-egg being simply left in the cast shell on the subsequent ecdysis of the mother. As cast shells containing winter-eggs have been taken in the plankton samples on several occasions (Fig. 33), it is possible that they do not immediately sink to the sea bottom as previously supposed and that, in the case of those formed in early summer, they may perhaps remain planktonic and develop comparatively rapidly without a marked resting period.

While the production of a single winter-egg is to be regarded as the normal condition, it is by no means rare to find two present—evidently one from each ovary—especially during the summer sexual period. When this occurs, the eggs may be sub-equal in size, both considerably smaller than the fully-grown single egg (Fig. 22), or they may be markedly different in size (Figs. 27 and 28).

A study of Geoffrey Smith's work (**73**) on the storage of glycogen and fat by Crustacea led to the making of preparations stained with neutral red and with osmic acid. As the material used was by no means ideal for the purpose, it was not expected to give particularly good results, but they were sufficiently convincing to be worthy of brief reference.

The osmic acid preparations showed the developing winter-egg to be more heavily loaded with fat than any other part ; also the nurse-cells and the gut took up the stain fairly strongly. Specimens carrying embryos showed a certain amount of fat to be present in these, but the neutral red preparations indicated that it is glycogen which is the predominating substance stored during the parthenogenetic phase. It is present at the bases of the limbs, in and about the intestine, and is particularly obvious in the ovaries (especially the germarium), and in the contents of the brood sac. Indeed, the neutral red served as a differential stain for the ovaries, showing up their contents as did none of the general stains previously used—such as borax carmine, alum cochineal, and methyl green.

Specimens in the sexual phase, treated with neutral red, showed glycogen to be present in the ovary during the tetrad formation, all four cells being deeply stained at first, but the young winter-egg ceases to take up the stain as soon as fat globules appear within it and thereafter remains unstainable. Some glycogen is present in the nurse-cells in addition to the fat, and also in the intestine.

These facts show that *E. nordmanni* behaves similarly to other Crustacea which have been investigated as regards alternating periods of fat and glycogen storage associated with the periods of sexual activity and of growth respectively.

The most interesting and striking feature of the analysis of the Northumberland material is the evidence of a definite double cycle in the annual history of marine Cladocera as shown for *E. nordmanni*. Except for Apstein, who touches briefly on the subject, no previous attempt has been made to work this out, to compare marine with freshwater forms in this respect or to correlate the phenomenon with environmental conditions.

General Conclusions.

The very considerable amount of work which has been done on the investigation of the life-cycle of Cladocera in relation to environmental conditions and to hereditary qualities, has been carried out almost entirely on freshwater forms. Observations on these under natural and experimental conditions have led to widely different theories as to the probable causes of the change from parthenogenetic to sexual activity.

Weismann was of the opinion that there is a definite inherent cycle which causes the production of a particular number of gamic generations —the number varying with the species—between every two gamic periods, regardless of external changes. On the other hand, the generally accepted idea has been that the life-cycle is intimately bound up with seasonal variations in the environment, and that the production of winter-eggs occurs at the onset of conditions unfavourable to continued activity of the organism, i.e. that in nature it precedes hot dry periods when small bodies of water are liable to become dried up, and cold spells when freezing may occur.

With regard to the effect on the organism of these conditions it is obvious that it is not the actual process of desiccation or freezing which brings about the development of the protected resting-egg, for to be of any value in preserving the species, its formation must be completed before the unfavourable conditions supervene, and the stimulus to sexual reproduction must be looked for in changes which take place some little time in advance.

If physical factors of the environment are regarded as being mainly responsible for changes in metabolic activity of the organism, it is necessary to consider what these are and to attempt to discover how they act. The more obvious changes are those of temperature and salinity*

* A detailed discussion of the effects of normal variations in the percentage of dissolved oxygen and carbon dioxide and in the amounts of different chemical compounds present in the water is regarded as unnecessary. Such variations will not ordinarily be of sufficient magnitude to act as direct limiting factors of the activities of epiplanktonic animal forms of open waters, with which the present discussion is primarily concerned. A knowledge of these and of their indirect effect is assumed in the following consideration of changes in abundance of the phytoplankton in its relation to the nutrition of Cladocera.

and, having regard to climatic conditions in various parts of the world, it is evident that species living in different climatic zones may react differently if these factors exert a direct influence. That is to say that the gamic phase may be associated in some cases with an increase in the amount of the factor or factors concerned and in other cases with a decrease in the amounts of the same factors.

Due to the occurrence of large swarms of Cladocera which have been observed to congregate in restricted areas (even in large lakes) during the agamic period, two other factors have been regarded as of importance, namely the accumulation of excretory products and the possible scarcity of food, or changes in the constitution of available food material. The question of nutrition is of vital importance both as a direct factor and in its relation to physical changes, notably temperature, as stimuli influencing both the amount of food material obtainable and the organism's ability to use it.

Experimental work prosecuted with a view to determining the value of various physical and nutritional factors believed to be instrumental in bringing about the cessation of parthenogenesis, has resulted in many and conflicting conclusions. This experimental work has been summarised by Cutler (**14**) and more recently and completely by Schull (**63**), whose comprehensive and critical account makes it unnecessary to discuss it here.

As regards the theory of the inherent cycle in Cladocera, first formulated by Weismann and attributed to the effect of natural selection, there is again considerable difference of opinion resulting from more recent investigations. Papanicolau (on showing that early broods are strongly parthenogenetic in tendency, late broods gamic in tendency and intermediate broods easily influenced either way) assumed the existence of a graduated inherent cycle, but his results can also be interpreted in the light of changing environment, as shown by Agar (**1**) and others. Also Banta, having reared three hundred generations of Moina, found it no easier to induce the gamic phase then than in early generations.

Woltereck (**86**) takes the *via media*, being of the opinion that internal and external causes are equally contributory to the production of gamic forms. While retaining the idea of internal stimulus to periodicity and postulating the presence of " paralisators " and " activators " within the organism, acting in opposition to one another to produce alternating phases of its life-cycle, he permits these hypothetical substances to be set in operation by the action of physical factors of the environment.

That there is here an inherent cycle in the sense that periods of rapid somatic growth, of reproductive activity, and of comparative rest are characteristic of Cladocera as of living organisms generally, is obvious, but data relating to the behaviour of particular species in different types of natural habitat show plainly that nothing more need be claimed regarding the part played by heredity and natural selection. The work of Zschokke and of Ekman has demonstrated that a particular species of Cladocera may be dicyclic, polycyclic or even acyclic in varying fresh-water conditions presented on the European plains, but is strongly and definitely monocyclic in high Alpine lakes and in lakes and ponds of the far North.

Beyond the fact that gamic reproduction must occur at some period (except possibly in "acyclic" forms), it is evident that the stimulus which induces the gamic phase must be sought in those environmental factors which necessarily limit or accelerate, directly or otherwise, the rate of metabolism of the organism at any given time. This would appear to be the idea behind von Scharfenberg's attempt to reconcile the two opposed views regarding the relative importance of internal and external factors, by assuming that the influence of food on the cycle is an inherited quality acquired through natural selection.

With regard to the conclusions drawn by various workers from the results of their experiments, one or two points appear to be worthy of further mention. Much has been made of the effect of the accumulation of excretory products, resulting from overcrowding, in inducing gamic reproduction (or at least depression), but it seems to the writer that this must be of far less consequence in nature than under experimental conditions. That it is probably a contributory cause of depression in small or in very stagnant bodies of fresh water at times of maximal population is not denied, but that such an accumulation can occur to any marked extent in large water masses, whether of fresh water or the sea, where there is considerable movement, at least near the surface, the writer is unable to appreciate. Also, in so far as carbon dioxide is to be regarded as an important excretory product in this respect, it might with equal probability be assumed to have the reverse effect in that it would tend to increase the supply of phytoplanktonic food-material.

Geoffrey Smith's experiments on the effect of temperature also call for remark in the light of our observations on Evadne. He states that a lowering of the temperature, which induces gamic reproduction, acts as a stimulus to the storage of fat in the tissues as opposed to glycogen. That decreased temperature need not be operative, or is not the only stimulus regulating fat storage, is shown by the incidence of the gamic phase in Evadne at two different seasons—one when the temperature is rising prior to its August maximum value and the other usually when this is well past. Similar conditions obtain in regard to salinity in the case of Evadne, the first gamic phase occurring about or before the period of the annual maximum, the second considerably later.

The fact that the question of food-supply has generally been considered of vital importance is brought out, as noted by Schull, by the event of more experimental attempts having been made to connect the life-cycle with nutrition than with any other external factor—temperature being a close second. As decreased temperature is generally regarded as acting either through its effect on the amount of food-material available or in reducing the rate of the organism's metabolic activity and consequently lessening the nutritive process, it may be assumed to be an important contributory factor in nature at those times at which low temperature and depression or the occurrence of the sexual phase supervene simultaneously. This does not however take into account those times when gamic individuals occur also during periods of comparatively high temperature.

It was evidently this difficulty which led Keilhack, arguing from observations in nature, to reject the idea of low nutrition as an important factor in the production of sexual forms. He remarks that *Polyphemus pediculus*, a dicyclic form, has a gamic phase in June "when food is abundant." His contention is supported by Strohl who states that a gamic phase in June could not be due to lack of nutrition. As to the abundance of food suitable to continued asexual activity of dicyclic Cladocera at these times, there must be considerable doubt and, from a study of recent work on the periodicity of freshwater Cladocera together with our records for Evadne, this contention must definitely be rejected.

From observations in the field, the general conclusion of Dr. Robert Gurney, with whom the writer has been in correspondence, is that shortage of food is the main direct limiting cause of the cessation of parthenogenetic development of freshwater Cladocera, as it appears to be in the case of marine species also. Leaving aside the special problems relating to food-supply in temporary ponds and the like, and in lakes situated at high altitudes and high latitudes where, compared with permanent water-masses of temperate regions, the periods suitable to food production are of relatively short duration, the periodicity of abundance and scarcity of food is closely parallel in both marine and freshwater habitats.

It will be sufficient here to draw attention to the similarity in number, times of appearance and relative productivity of the periods of maximal abundance of the phytoplankton of fresh and sea-water, without entering upon a detailed discussion as to the causes of the same, and to show the close relationship between these and the life-cycles of characteristic Cladoceran inhabitants. It has generally been supposed that marine Cladocera were monocyclic and that their activities, therefore, bore no relation in respect to periodicity, to limnetic forms. Also, as it is only comparatively recently that the dicyclic character of the latter has been correlated with changes in abundance of phytoplankton, no comparison has been drawn between fresh water and marine Cladocera in this respect until now.

Taking into consideration regions in which temperate climatic conditions obtain, a similar periodicity of phytoplanktonic activity is found to occur in freshwater lakes and in the sea. In the former the two periods of upheaval caused by temporary full circulation of the water in spring and autumn due to the development of a thermocline (and in certain cases to other causes as in Lough Derg) (**74**), give rise not only to the provision of nutritive substances required for the rapid multiplication of diatoms, green algæ, etc., but also bring increased supplies of food-material directly within the reach of detritus feeders among the animal plankton such as are many of the freshwater Cladocera. Thus, two periods of reproductivity of the zooplankton are possible. While this may be associated in some species with the one, in others with the second period of optimal nutritive conditions, certain forms such as Cladocera and Rotifers may take advantage of both periods (**11**) : here the agamic phases are coincident in time with both the aforesaid periods and thereafter the population suffers a reduction in numbers followed by the sexual phase.

In the sea, a similar series of events takes place, the spring and autumn maximal periods of parthenogenetic development of Cladocera being associated in time, at least in a general way, with the corresponding periods of diatom abundance, after which numbers decline and the gamic phase supervenes. This has been shown for *E. nordmanni* to be more strongly marked after the spring maximum than it is in autumn, thus indicating an association between Cladocera and phytoplankton in regard to relative quantity as well as to time. Another aspect of the effect of varying quantities of food on Cladocera, while not having a direct bearing on the present problem, is nevertheless interesting. Wolterek (**88**), in his recently published book, shows the possibility of inducing modifications in the form of *Daphnia cucullata* in response to abundance or scarcity of food.

That there is a definite relationship between times of food scarcity and corresponding periods of depression in the metabolic processes of plankton organisms generally is now evident. It has been shown by Dieffenbach and Sachse, as quoted by Carpenter ; is suggested by the findings of Gurney (**24**), Zschokke, and Ekman referred to above ; is indicated in the analysis of samples taken by Scourfield (**70** and **71**) and is of common occurrence among marine planktonic forms. In addition to being demonstrated in the case of Evadne, the Northumberland plankton samples show the presence of spring and autumn periods of reproductivity in the common acorn barnacle (not yet worked out in detail), as is the case in many holoplanktonic forms and littoral animals with pelagic larvæ, e.g. Mysis spp., *Crangon vulgaris* (**6**), *Sagitta elegans* (**47**).

The emphasis laid on the influence of the vernal and autumnal maxima of phytoplankton on the zooplankton generally and on limnetic and marine Cladocera in particular, is meant to detract in no way from the importance of the physical factors of the environment but is meant to draw a comparison between the similarity of the more important features regulating the cyclic activities of both marine and freshwater pelagic animals, and to draw attention to the effect of physical changes being generally indirect rather than direct in their influence. There is, of course, no question of the direct effect of decreased temperature, for example in lowering the rate of nutrition; but so far as dicyclic Cladocera are concerned this is a secondary stimulus, brought to bear on the autumnal period of depression but not on the spring one.

As regards the results of experimental and other observations on the influence of increase or decrease in the intensity of physical and nutritional factors, it would appear that it is not necessarily or only the actual amount of any particular factor which affects the organism concerned, but rather "change as change." This is pointed out by Schull in reference to Whitney's work, and its importance in regard to the constitution of the available food-supply is shown by von Scharfenberg's experiments. That his conclusions are confirmed by the behaviour of plankton organisms in nature is indicated by the fact that while the spring increase of diatoms is followed by abundance of Peridiniæ in the summer, agamic reproduction in dicyclic Cladocera nevertheless comes to an end (or at least is greatly slowed down) and supervenes again at a rapid rate only when the diatom curve is once more on the up-grade in early autumn.

While the Northumbrian records of periodic abundance of Evadne show it to follow the trend of the general annual diatom curve, there is considerable variation in the times of maximal population from year to year, and it is not yet possible to show to what extent these variations are coincident with minor changes in the position of the cusps of the diatom curves in those years in which abnormal conditions have prevailed in the region under consideration.

SUMMARY.

Part I.

From an analysis of previous records of *E. nordmanni*, considered in conjunction with those furnished by the present investigation, the following points of interest emerge.

1. *E. nordmanni*, while being generally distributed in the North Sea and adjacent waters throughout the summer months, has been shown to breed freely in inshore waters in early summer and again in autumn when maximum numbers of individuals are obtained.

2. These two periods of maximal abundance are produced as the result

of successive parthenogenetic broods and alternate with periods of depression. This is indicated not only by the sexually-produced winter-egg, but also by a reduction in the number of embryos contained in the brood chamber and consequent change in body-shape. This serves to show that the supposedly distinct races, described as being characteristic of the North Sea and the Baltic, have no doubt been founded on material taken at different periods of the agamic phase.

3. The alternating periods of abundance and scarcity appear to be associated with transnatant movements of the population.

4. The earlier maximum is the more extensive one and the following period of scarcity of numbers in inshore waters is less marked and of shorter duration than that which follows the autumn maximum. Although the Northumberland records do not cover a sufficient number of months of any year to provide information as to the presence of *E. nordmanni* during the winter, it is evident from previous accounts that a certain proportion of the population is able to withstand both periods of depression and that these, together with new individuals produced from the resting-eggs and others entering the area from without, provide a stock from which the following early summer maximum is obtained.

5. The distribution of the species is affected by exceptional conditions wrought by changes in the current system of the area of distribution.

6. *E. nordmanni* is an inhabitant of both coastal and oceanic waters. It is present in great quantity on both sides of the North Atlantic, and it is suggested that its geographical distribution is intimately associated with the current system of that ocean. Its distribution beyond this region is merely indicated.

7. A comparison of the surface current systems of the southern North Sea, the Irish Sea, and the eastern English Channel is made in an attempt to explain the scarcity of Cladocera in these regions.

8. The material available for the study of the vertical distribution of Evadne is adequate to illustrate only diurnal conditions and shows the optimum light intensity to be very high for this form. There is no evidence that Evadne retires below the surface to any noticeable extent in rough weather.

Part II.

9. The account of the development of the parthenogenetic generations of *E. nordmanni* has reference to the formation of the oocytes; the development of the brood pouch and the production of the nutritive cells of its wall; the method of freeing of the embryos.

10. The presence of three generations of young within the mother and the fertility of the embryos are considered in relation to the rate of

increase of the population. The variation in number of embryos within the brood pouch is discussed in its association with the period of depression which is shown to precede sexual reproduction. The fact that the brood pouch may at times be empty is shown, and is correlated with the change from the agamic to the sexual mode of development.

11. A more detailed description of the formation and growth of the winter-egg than has been given heretofore is included, and has reference to the formation of a tetrad ; the disappearance of the germarium ; the production, derivation, constitution, and absorption of the nurse-cells and the freeing of the winter-egg. The significance of the production of two winter-eggs simultaneously is considered.

12. Evadne is shown to behave similarly to other Crustacea in the matter of fat- and glycogen-storage, being associated with alternating periods of active growth (parthenogenetic phase) and gamic reproduction.

13. The general conclusions arising out of the study of the life-cycle of Evadne which shows it to be definitely dicyclic, are concerned with the question of the relative value of internal and external factors as stimuli effecting the biannual series of changes which occur, and it is believed that food-supply is of primary importance and that other factors are of a secondary nature or are indirect in their influence.

14. A coincidence of the periods of maximal population of Cladocera with those of diatom abundance is shown to take place as regards both time of occurrence and relative productivity. A comparison is drawn between the behaviour, in relation to food-supply, of marine and limnetic species of Cladocera.

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