ON THE FERTILITY OF MARINE CLADOCERA WITH A NOTE ON THE FORMATION OF THE RESTING EGG IN *EVADNE NORDMANNI* LOVÉN AND *PODON INTERMEDIUS* LILLJEBORG

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(Text-figs. 1–5)

CONTENTS

Introduction

The present paper is the second in a series dealing with the reproductive capacity of marine Crustacea, the first being concerned with the fecundity of some gammarids (Cheng, 1942).

Relatively little is known of the reproductive capacity of marine Cladocera. Lilljeborg (1900) in a taxonomic study on the Cladocera of Sweden recorded the size of broods in various marine species. Rammer (1933) made a comparison of the fertility of *Evadne nordmanni* Lovén in different regions, showing that it is, on the whole, highest in the warmer water. Jorgensen (1933), who carried out an investigation into the life cycle of *E. nordmanni* off the Northumbrian coast of England, made a few remarks on its reproductive capacity. In the present investigation a statistical study was made of the fertility of various species of marine Cladocera together with a note on the formation of the resting egg[1] in *E. nordmanni* and *Podon intermedius* Lilljeborg.

It is a great pleasure to express my gratitude to the late Director of the Marine Biological Laboratory at Plymouth, Dr S. Kemp, F.R.S., for providing

[1] It is also called 'winter' egg, which is rather misleading, as it can be produced in the summer as well. The word 'resting' is more appropriate, because the egg is incapable of developing immediately after fertilization; it requires a certain period of 'rest'.

me with facilities and to members of the staff for their kind help in various ways. I wish to thank Prof. A. C. Hardy, F.R.S., for putting his Clyde samples at my disposal.

Material and Method

The material was collected partly off Plymouth during the summer of 1938, but largely from the Clyde Sea-Area by Prof. Hardy in the summers of 1941 and 1942 in an investigation on the yield of zooplankton. The Clyde samples were taken by the Plankton Indicator[1] at a depth of 10 m. in 1941 and by a 50 cm. diameter tow-net with 200 meshes to the inch at a depth of 18 m. in the following year.

The method of studying fertility was as follows. A number of adult parthenogenetic females were picked out at random. After measuring the total length of each (from the anterior margin of the head to the posterior end of the caudal furca) by means of an ocular micrometer, all the embryos in the brood-pouch were taken out and counted. The total number of parthenogenetic females of various species thus examined for the two areas is shown in Table 1.

When working at Plymouth in the summer of 1938, the writer was able to make some observations upon the formation of the resting egg in living specimens of *Evadne nordmanni* and *Podon intermedius*. The different stages of the formation were drawn with the aid of a camera lucida.

Notes on the Species

Four species[2] occurred in the Clyde Sea-Area material: *Evadne nordmanni*, *Podon intermedius*, *P. polyphemoides* (Leuckart) and *P. leuckarti* G. O. Sars, all of which have been recorded for this region by Scott (1905). Only two species were present in the Plymouth samples: *Evadne nordmanni* and *Podon intermedius*. According to the Plymouth Marine Fauna list published in 1931, *P. leuckarti* occurs also in this region, but *P. polyphemoides* does not. The three species of *Podon*, though very much alike in appearance, can easily be distinguished from each other not only by the number of setae on the exopodite of the first trunk-limb (*P. leuckarti* 1, *P. intermedius* 2, *P. polyphemoides* 3), but also by the mean length of the body (Table 1).

Evadne nordmanni is, by far, the commonest species of Cladocera in the Clyde Sea-Area, attaining its maximum in August. Of the three species of *Podon*, *Podon intermedius* and *P. polyphemoides* are more common in our samples than *P. leuckarti*, but this is most likely due to the fact that the last-named is a typical surface form (Apstein, 1910) and our samples were collected at a depth of either 10 or 18 m. As a rule, these species of *Podon* reach their maximum abundance later than *Evadne nordmanni*, i.e. in September.

[1] For its construction and method of use, see Hardy (1936).

[2] For the geographical distribution of the four species, see Cleve (1900), Gibitz (1922), Rammer (1931) and Stephensen (1938).

TABLE I. MEAN BODY LENGTH (IN MM.) AND FERTILITY (IN NO. OF EMBRYOS PER BROOD) OF VARIOUS SPECIES FOUND IN THE CLYDE SEA-AREA AND MEAN FERTILITY OF *EVADNE NORDMANNI* AND *PODON INTERMEDIUS* OFF PLYMOUTH (IN BRACKETS).

		Body length		Fertility	
Species	No. of animals	Mean ± S.E.	Standard deviation	Mean ± S.E.	Standard deviation
P. leuckarti	32	0·67 ± 0·01	0·06 ± 0·01	2·6 ± 0·19	1·08 ± 0·13
P. intermedius	224 (198)	0·99 ± 0·005	0·08 ± 0·004	3·0 ± 0·08 (3·5 ± 0·11)	1·14 ± 0·05 (1·56 ± 0·08)
P. polyphemoides	199	0·39 ± 0·003	0·04 ± 0·002	4·7 ± 0·10	1·38 ± 0·07
E. nordmanni	753 (269)	0·45 ± 0·002	0·05 ± 0·001	4·4 ± 0·06 (3·2 ± 0·13)	1·77 ± 0·04 (2·11 ± 0·09)

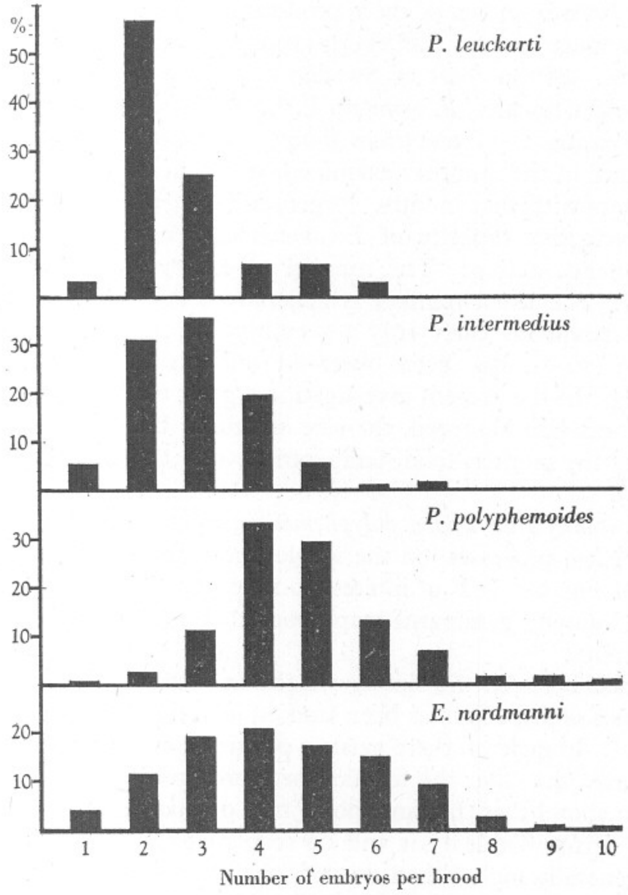

Fig. 1. Histograms showing the percentage frequency distribution of the fertility of various species found in the Clyde Sea-Area.

Fertility of Various Species

From Table 1 it will be seen that the mean fertility varies with different species: *Podon leuckarti* 2·6, *P. intermedius* 3·0, *P. polyphemoides* 4·7 and *Evadne nordmanni* 4·4; although the specific difference is by no means large. The mean value of *Podon leuckarti* is, however, less reliable than that of the others because of the small number of animals obtained. It is noteworthy that the mean fertility of *Evadne nordmanni* appears to be lower in the Plymouth region than in the Clyde Sea-Area (Table 1). Such discrepancy may be accounted for by the fact that the Plymouth samples were taken much earlier, i.e. in May. In Fig. 1 is shown the range and mode of the fertility of various species, the latter being as follows: *Podon leuckarti* 2, *P. intermedius* 3, *P. polyphemoides* 4 and *Evadne nordmanni* 4.

Relatively little is known of the reproductive capacity of marine Cladocera in other European waters. Lilljeborg (1900) recorded the size of broods of various species off the coast of Sweden as follows: *Evadne nordmanni* 7–8 embryos in older females, *E. spinifera* P. E. Müller 6–7, *Podon polyphemoides* 2–4, *P. intermedius* 2–5 (sometimes more), *P. leuckarti* mostly 2; but as he gives no record of the numbers examined, we cannot compare the fertility in Swedish waters with that in ours. Jorgensen (1933) made some observations on the reproductive capacity of *Evadne nordmanni* off the Northumbrian coast of England, stating: 'The number of embryos in a batch may vary considerably. The usual number is generally 6–8 or 9; while at times the majority of specimens carry only 2–5 embryos....The greatest number of embryos, i.e. 12–14 has been observed only in the very large form of *E. nordmanni*.' In the present investigation a great variation in the fertility of this species was also observed, the size of broods being probably controlled by the age of the mother, food, temperature, etc.; as suggested by Allen & Banta (1929).

It is noteworthy that *Podon polyphemoides*, though smaller than the other species of *Podon*, possesses, on the whole, the highest reproductive capacity (Table I and Fig. 1). It is of interest to note that Sexton (1928) and Cheng (1942) found among gammarid amphipods that the smaller species had the higher fecundity.

The relation between the size or weight and the reproductive capacity of the individuals of a species has been studied in various groups of animals (see Cheng, 1942). In general, there exists a positive correlation between the two. In other words, the older the female, the more productive it is. The present investigation shows that the same holds true of *Evadne nordmanni* and *Podon intermedius*. From Table II it will be seen that the mean fertility of large females is generally higher than that of smaller ones, although the difference between the two extreme size-groups is very small, i.e. less than two eggs per brood.

TABLE II. MEAN FERTILITY OF VARIOUS SIZE GROUPS (IN μ) OF *EVADNE NORDMANNI* AND *PODON INTERMEDIUS* TAKEN FROM THE CLYDE SEA-AREA.

E. nordmanni			*P. intermedius*		
Size groups	No. of animals	Mean fertility	Size groups	No. of animals	Mean fertility
300–400	42	2·7	800–900	34	2·7
400–500	489	3·4	900–1000	91	2·6
500–600	159	4·2	1000–1100	75	3·0
			1100–1200	22	4·4

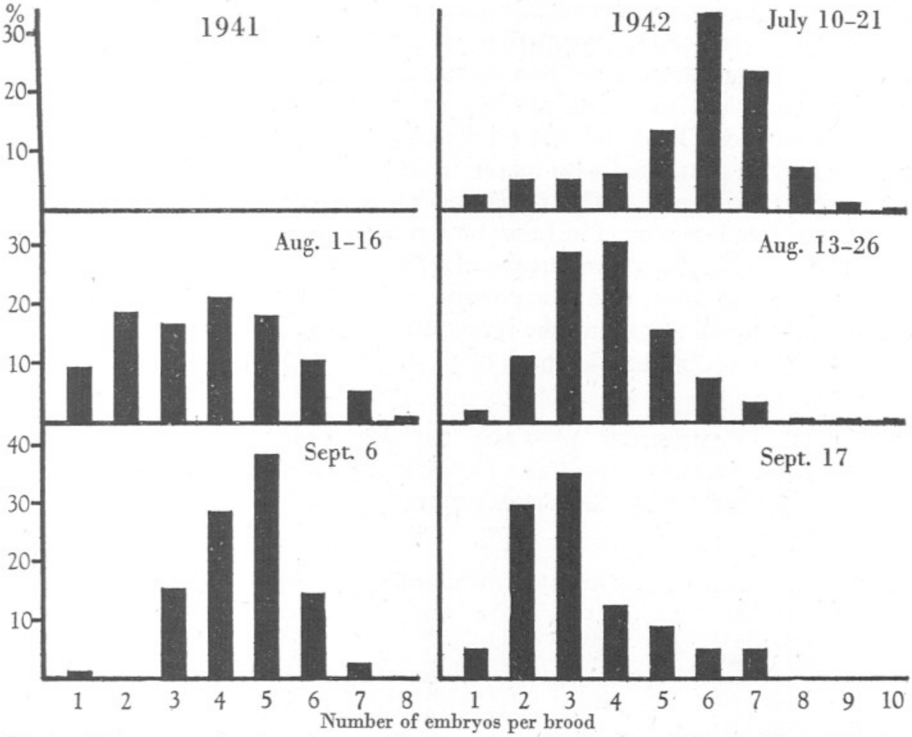

Fig. 2. Histograms showing the monthly frequency distribution of the fertility of *Evadne nordmanni* taken from the Clyde Sea-Area in the summers of 1941 and 1942.

TABLE III. MEAN FERTILITY AND PERCENTAGE OF SEXUAL INDIVIDUALS (♂, ♀) OF *EVADNE NORDMANNI* TAKEN FROM THE CLYDE SEA-AREA DURING THE SUMMER MONTHS OF 1941 AND 1942.

		Fertility		
Month and year	No. of animals	Mean	Standard deviation	% of sexual individuals
1–16 Aug. 1941	167	3·7 ± 0·13	1·69 ± 0·09	13·3
6 Sept. 1941	84	4·5 ± 0·12	1·06 ± 0·08	6·9
10–21 July 1942	184	5·8 ± 0·13	1·80 ± 0·09	1·0
13–26 Aug. 1942	261	3·9 ± 0·09	1·40 ± 0·06	3·4
17 Sept. 1942	57	3·3 ± 0·20	1·49 ± 0·14	7·1

Owing to the limitation of material, it is impossible to undertake a detailed investigation on the seasonal variation in reproductive capacity. It is of interest, however, to compare the fertility of *Evadne nordmanni*[1] month by month during the periods 1 August–6 September, 1941 and 10 July–17 September, 1942. It will be seen from Table III and Fig. 2 that during the latter year the fertility appears to fall off towards the end of summer, the mean value of July being nearly twice as high as that of September. But the reverse holds true of 1941, the mean fertility of September being higher than that of August. In order to find out whether such seasonal variation in reproductive capacity is due to the corresponding fluctuations in the abundance of phytoplankton in the surrounding waters, a comparison was made between the mean fertility of *E. nordmanni* and the mean number of diatoms taken by the same net. It is evident from Table IV that no correlation exists between the two. This finding may be contrasted with that of Marshall (1937) who observed that the fecundity of a copepod, *Oithona helgolandica*, reaches its first maximum at the end of April and its second in June; both maxima appear to be correlated with the period of high diatom production. Unfortunately, owing to the lack of data on water temperature, it is not possible to study the relation between this important external factor and the reproductive capacity of *Evadne nordmanni*. The latter, according to Rammer (1933), is greatest in water of higher temperature.

TABLE IV. COMPARISON BETWEEN THE MEAN FERTILITY OF *EVADNE NORDMANNI* AND THE MEAN NUMBER OF DIATOMS TAKEN BY THE SAME NET IN THE CLYDE SEA-AREA DURING THE SUMMER MONTHS OF 1941 AND 1942

Date of collection	No. of animals	Mean fertility	No. of hauls	Mean number of diatoms
1 Aug. 1941	61	4·7	5	59,974
16 Aug. 1941	106	3·2	6	42,530
6 Sept. 1941	84	4·5	9	2,367
21 July 1942	156	6·4	7	5,550
13 Aug. 1942	147	4·1	3	9,867
26 Aug. 1942	114	3·7	7	19,552
17 Sept. 1942	57	3·3	6	16,450

During the summer months of 1942, a marked reduction in the fertility of *E. nordmanni* took place after July. This occurred at the time when the production of sexual individuals was steadily increasing, as shown in Table III. It is evident that there exists an inverse relationship between the reproductive capacity of parthenogenetic females and the intensity of sexual reproduction. The same holds true of 1941: the percentage of sexual individuals in August was nearly twice as high as that in September, whilst the mean fertility of the latter month was higher than that of the former. This finding is in accord with that of Berg (1931) and Uéno (1934) who observed in nature that the size of

[1] Owing to the small number of animals obtained, it is not possible to make a similar study on other species.

broods produced by the parthenogenetic females of fresh-water daphnids tends to decrease after the sexual reproduction has set in. According to the hypothesis put forward by Berg (1934), the diminution in the size of broods is regarded as a manifestation of a state of depression during the transition from parthenogenesis to sexual reproduction brought about by unfavourable external conditions such as poor nutrition and low temperature.

FORMATION OF THE RESTING EGG IN *EVADNE NORDMANNI* AND *PODON INTERMEDIUS*

Two kinds of eggs are produced by Cladocera, a thin-walled parthenogenetic egg and a thick-walled resting egg. The latter is larger, fewer in number, full of yolk spherules and incapable of developing without fertilization. The individual developed from a fertilized resting egg after a certain period of quiescence is invariably a parthenogenetic female. As a rule, the production of resting eggs is at its highest when parthenogenesis has reached its lowest ebb.

Sexual reproduction of *Evadne nordmanni* has already been studied by Jorgensen (1933) who gives a fairly complete account of the formation of the resting egg. The following notes give more details of this process and also describe that in *Podon intermedius*. All observations were made upon living specimens obtained off Plymouth in the summer of 1938.

Fig. 3 shows the various stages of formation of a resting egg in *Evadne nordmanni*. It will be seen that at the beginning the four oocytes are more or less alike in appearance (*A*). Later (*B* and *C*) the third cell (counted from the anterior end of the ovary) begins to outgrow the others. It continues to grow in size until becoming the large resting egg full of yolk spherules, whilst the other three remain somewhat unchanged and finally disappear, being probably absorbed by the egg; as shown by Allen & Banta (1929) in a fresh-water cladoceran, *Moina macrocopa*. They write: 'Only one sexual egg normally matures in each ovary at a clutch. During growth it absorbs three nurse cells.' The egg then migrates into the brood-pouch filled already with nurse cells which, according to Jorgensen (1933), are produced by the proliferation of cells lining the wall of the brood-pouch and not being, as supposed by Claus (1877), originally oocytes formed at the same time as the one giving rise to the resting egg. After reaching its maximum size, a thick chitinous wall is formed around it.

It is worthy of note that on one occasion a slender tubular structure containing cells of various size was observed in direct connexion with the posterior end of the tetrad (Fig. 3, I). It is very easily overlooked because of its minute size. Judging from its contents and position, it is most likely the germarium and the cells inside are oogonia. But Jorgensen (1933) failed to find it, stating: 'No germarium is visible, the ovarian wall being closely apposed to the edges of the tetrad.' This repays further investigation.

In the great majority of sexual females of *Evadne nordmanni* only one resting egg is present in the brood-pouch (Fig. 3, G). But, occasionally, two

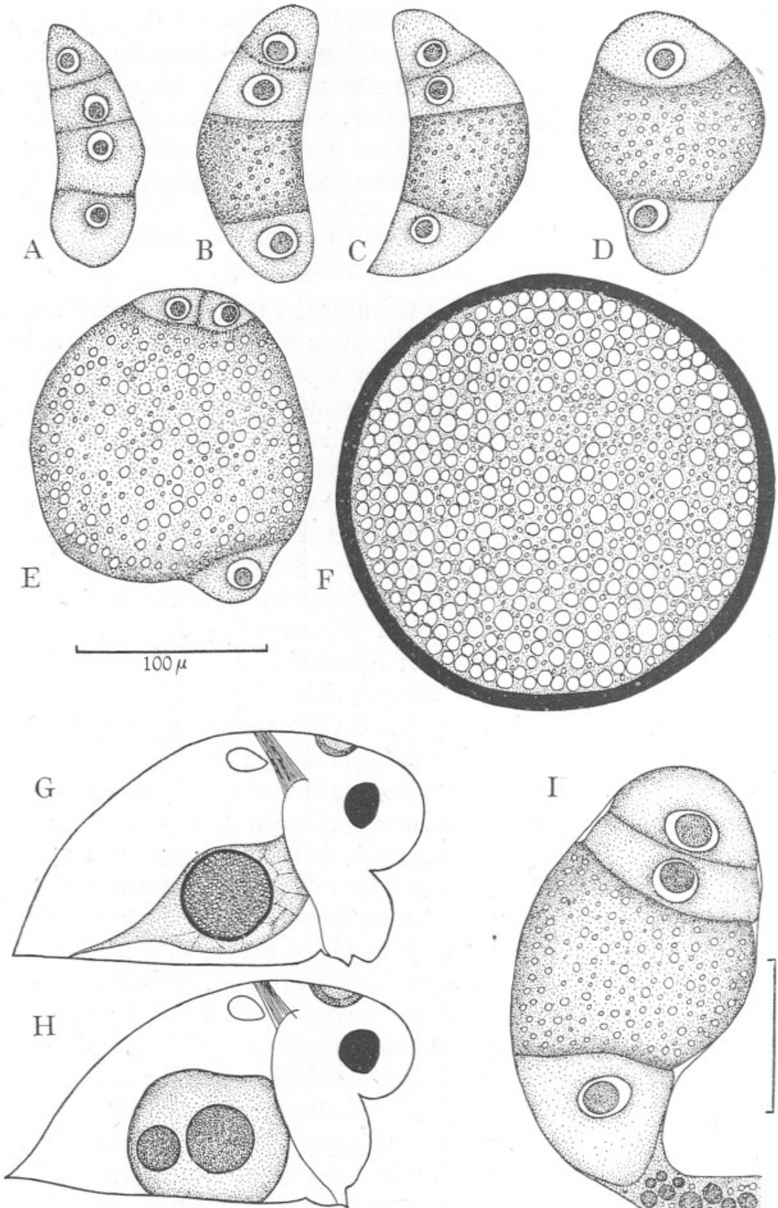

Fig. 3. Formation of a resting egg in *Evadne nordmanni*: A–E, a series of tetrad stages showing the gradual enlargement of the third oocyte to become the resting egg. F, a mature resting egg with a thick chitinous wall. G, a sexual female with a mature resting egg in the brood-pouch. H, a sexual female with two resting eggs of unequal size in the brood-pouch. I, a tetrad stage with a germarium attached to its posterior end.

were found, one being usually smaller than the other (Fig. 3, H). Such sexual females with two resting eggs were encountered more frequently in the Plymouth than in the Clyde samples. Their occurrence in this species has been recorded by Lilljeborg (1900) and Jorgensen (1933).

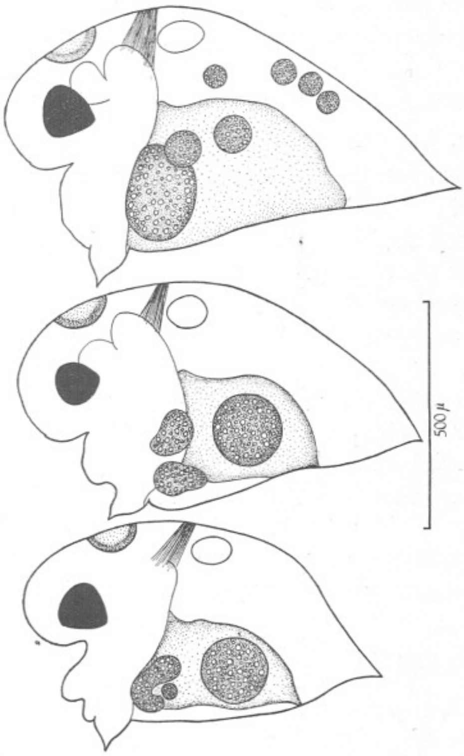

Fig. 4.

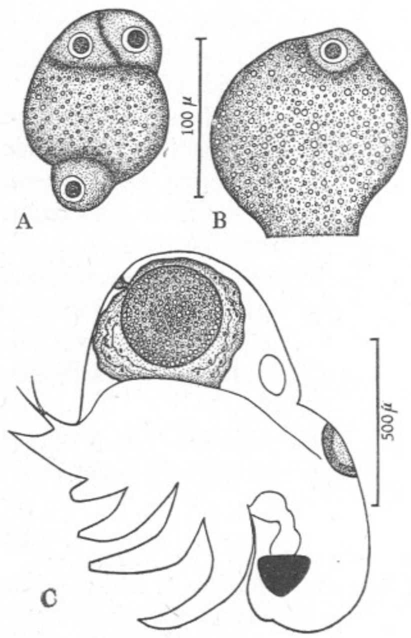

Fig. 5.

Fig. 4. Three sexual females of *Evadne nordmanni* with several irregular masses of yolk-laden protoplasm scattered in the shell-cavity. Note the large resting egg in the brood-pouch.

Fig. 5. Formation of a resting egg in *Podon intermedius*: A and B, two relatively late tetrad stages with the third oocyte enlarging to become the resting egg. C, a sexual female with a mature resting egg in the brood-pouch.

In the Plymouth samples there occurred some sexual females of *E. nordmanni* in the shell-cavity of which were found several irregular masses, usually rounded, of protoplasm full of yolk spherules (Fig. 4) which, in view of their contents, are probably formed by the disintegration of another resting egg. No such sexual females were, however, met with in the Clyde samples. So far as the writer is aware, this phenomenon has not, hitherto, been observed in either marine or fresh-water Cladocera.

Fig. 5 shows the formation of a resting egg in *Podon intermedius*. It will be seen that it commences too with the tetrad stage of which the third cell is destined to become the resting egg, whilst the other three serve as nurse cells and are finally absorbed by the growing egg. Unfortunately, owing to the lack of sufficient material, it is not possible to study it in such detail as in *Evadne nordmanni*. However, judging from the few stages available, the whole picture of the formation of the resting egg appears to be essentially similar to that of the latter species.

SUMMARY

A statistical study was made of the fertility of *Evadne nordmanni*, *Podon intermedius*, *P. leuckarti* and *P. polyphemoides* in the Clyde Sea-Area and of the former two species off Plymouth.

The mean fertility of parthenogenetic females varies with different species. This is not correlated with the size of the species.

Within the species, *Evadne nordmanni* and *Podon intermedius*, there exists, in general, a positive correlation between the size and the fertility of parthenogenetic females.

The fertility of *Evadne nordmanni* is subject to seasonal variation. This is not correlated with fluctuations in the abundance of diatoms.

An inverse relationship was observed in *Evadne nordmanni* between the reproductive capacity of parthenogenetic females and the intensity of sexual reproduction.

A brief account was given of the formation of the resting egg in *Evadne nordmanni* and *Podon intermedius*.

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