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SOME OBSERVATIONS ON *EVADNE NORDMANNI* LOVÉN

By V. BAINBRIDGE*
From the Marine Station, Millport

(Plate I and Text-figs. 1–6)

Apstein (1910) found *Evadne nordmanni* to be the most widely distributed and in general the commonest cladoceran in the plankton of the sea areas around the coasts of Europe investigated by the International Council. It is known to occur predominantly in coastal waters and has been regarded mainly as a neritic species in the past, but considering recent records Wiborg (1955) suggests that it may also be able to establish populations in the open ocean.

Despite its importance in the marine plankton our knowledge of the biology of this species is meagre compared with that of the common freshwater Cladocera. Rammner (1930) has reviewed the earlier investigations on *E. nordmanni* and other marine species. More recent studies include those of Jorgensen (1933) and Cheng (1947), while Baker (1938) gives a detailed account of the taxonomy of marine Polyphemidae.

In view of the often inadequate material available to previous workers for the study of seasonal changes in one locality, it was decided to follow the population of *Evadne* at a station in the Clyde Sea Area during 1951 with particular attention to fluctuations in abundance, size and the mode of reproduction.

Evadne reproduces mainly by parthenogenesis, in which case the eggs are laid into the brood pouch and develop there into free-swimming young. Often some of the females carry no developing embryos but show the formation of usually one resting egg. Males are normally present in the population on these occasions and it has been generally assumed that resting eggs develop as a result of sexual reproduction. This is known to be ordinarily the case in freshwater Cladocera, with the exception of some arctic populations of *Daphnia* which produce unfertilized resting eggs.

MATERIAL AND METHODS

Quantitative plankton samples were collected at a station near the Little Cumbrae lighthouse, where the depth is between 90 and 105 m. The samples were taken with a Clarke–Bumpus plankton sampler (Clarke & Bumpus, 1940) in a series of horizontal tows, each of 10 min duration, at average depths of 1, 10, 20, 30 and 50 m. An additional tow at 40 m was made on some

* Present address: Fisheries Laboratory, Lowestoft.

occasions. Unfortunately, it was not possible to tow at a constant depth, the angle of the towing wire varying between 30 and 45° to the vertical. The sampler was used fitted with a net of 200 meshes to the inch, until 7 May when it was replaced by one of 129 meshes to the inch. The volume of water filtered during a single haul varied between 2 and 4 m^3.

Additional tow-nettings were frequently taken off Keppel Pier at Millport using larger nets of the same mesh size, and data obtained from these samples have been used when *Evadne* were scarce towards the end of the year.

All samples were preserved in 5% formalin. When necessary samples were subsampled for examination and counts using the dilution method of Russell & Colman (1931).

All measurements were made with an eyepiece micrometer on which each division represented 9·7 μ. Embryo numbers were counted after dissecting the embryos out of each parthenogenetic female.

Baker (1938) has discussed the various points of reference which have been used for the measurement of marine Cladocera and has given diagrams to illustrate what she calls the morphological length. This dimension is useful to compare the size of different species, but demands some personal judgement to determine the anterior point on the margin of the head.

In this investigation lengths have been measured from the point of attachment of the antennal elevator muscles on the crown of the head to the tip of the claws on the caudal furca (see Pl. I). This measurement approximates to the greatest length of the body excluding the brood pouch. In a very small proportion of the preserved *Evadne* there was a slight depression at the point of attachment of the antennal muscles, and measurements were adjusted to correct for this by noting the body outline on each side of the depression. The short caudal furca is capable of a slight amount of movement, but is set at a nearly constant angle to the rest of the body in preserved specimens.

VERTICAL DISTRIBUTION

The investigations made by Wiborg (1940, 1944, 1954) on the plankton of Norwegian coastal waters have shown that *Evadne* is mainly to be found living near the surface.

This was also found to be true in the Clyde. All the samples were collected during the daytime and the numbers of *Evadne* at each depth are given in Table 1. Very few occurred in hauls taken at depths greater than 30 m and, with one exception, greatest numbers were found at either the 1 or 10 m levels.

SEASONAL DISTRIBUTION

In a survey of the Clyde plankton during 1923 and 1924 Marshall (1925) records that *E. nordmanni* was common in May and June, fairly common till September and frequent in October. From a study of tow-nettings taken in the North Sea off the Northumberland coast during the years from 1921 to 1930 inclusive, Jorgensen (1933) found that the numbers of *Evadne* usually showed an early summer maximum followed by a less extensive one during September or later. She also noted the presence of males during these periods and that the numbers of resting eggs produced were roughly proportional to the numbers of individuals present.

TABLE 1. NUMBER OF *EVADNE* PER CUBIC METRE

Date 1951	1 m	10 m	20 m	30 m	40 m	50 m
9. iii.	17	9	–	–	–	–
13. iii.	6	7	0	–	–	–
29. iii.	29	27	3	0	–	0
13. iv.	36	269	30	0	–	0
19. iv.	89	85	15	1	–	0
25. iv.	91	232	31	0	–	0
7. v.	1380	64	16	0	–	0
24. v.	375	1325	269	19	–	30
29. v.	428	465	168	51	60	64
7. vi.	211	1636	672	150	–	0
14. vi.	402	359	29	0	–	–
20. vi.	422	766	177	44	–	3
29. vi.	49	764	122	26	–	1
2. vii.	511	143	25	0	–	0
11. vii.	269	278	244	45	1	2
19. vii.	209	131	10	2	0	0
24. vii.	121	126	27	0	0	0
1. viii.	91	252	67	9	0	0
7. viii.	60	138	5	0	0	0
17. viii.	111	130	350	36	4	0
3. ix.	15	4	0	0	0	0
13. ix.	0	1	0	0	0	0
17. ix.	5	0	0	0	0	0
25. ix.	5	1	0	0	0	0
11. x.	16	2	1	0	0	0
24. x.	3	2	0	0	0	0
7. xi.	0	0	0	0	0	0

– No sample taken.

Text-fig. 1 shows the average numbers of *Evadne* per cubic metre in the upper 30 m at the station in the Clyde during 1951 and also the percentages of sexual individuals in the population (i.e. males, and females showing the formation of a resting egg).

Evadne was first observed in the plankton at the end of February; quantitative sampling was begun on 9 March and continued until 7 November. The population increased reaching a maximum from May to early June and declined during the following months to a very low density in September. There was a slight recovery during October, but the species was absent from all the samples taken in November and December. The first appearance of sexual individuals coincided with the marked increase in numbers during May and sexual reproduction became most intense in October.

There was, therefore, no clear development of a second maximum and the percentage of sexual individuals showed no relationship to the population density.

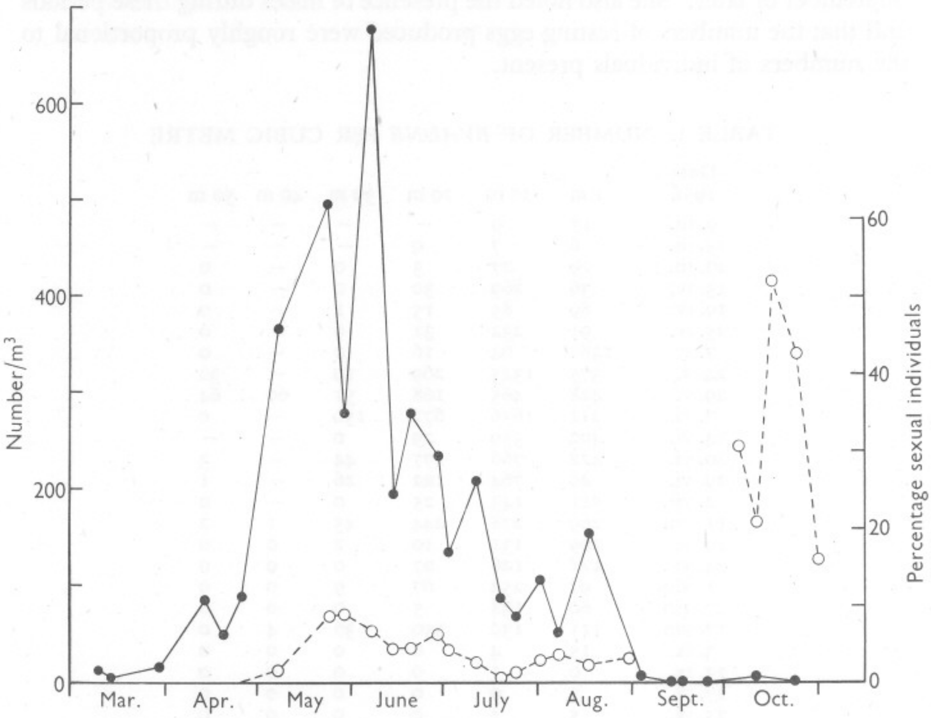

Fig. 1. Mean number of *Evadne* per cubic metre in the upper 30 m during 1951 (●——●), and the percentage of sexual individuals in the population (○- - -○).

GROWTH AND REPRODUCTION

Kuttner (1911) studied the development of the parthenogenetic eggs of *E. nordmanni* and found that when embryos reach an advanced stage of development and show the first traces of eye pigmentation, their own eggs mature and pass into the embryonic brood space. By the time the young are liberated from the brood pouch of the mother these eggs have segmented to a blastula stage with a large cleavage cavity. The young are in effect miniature adults.

Attempts were made to rear individual animals in order to determine the usual number of instars between birth and the liberation of the first brood of young, but proved unsuccessful. Two of the major problems are that *Evadne* tends to stick to any water-air surface film and since it is not a filter-feeder conditions suitable for feeding are difficult to produce.

In order to provide some information on the relation between size and reproductive state two large samples of *Evadne* were examined. The length of each individual was measured and the stage of embryonic development in the parthenogenetic females noted. Two easily recognizable stages have been selected and are arbitrarily classed as early and late stages. They are defined as follows:

Early. Embryos roughly spherical, though sometimes distorted owing to being pressed together in the brood pouch. They show no signs of elongation or the appearance of the second antennal rudiment.

Late. Embryos at an advanced stage of development and showing at least the first traces of eye pigmentation. All the limbs are present and the dorsal pouch is developing so that the embryo lies on its side when removed from the brood pouch.

The results obtained from the two samples are shown as percentage size-frequency distributions in Text-fig. 2 and the stages referred to are illustrated in Pl. I.

Text-fig. 2A shows the size distribution of all parthenogenetically reproducing females and Text-fig. 2B the size distribution of those with embryos at the stages of development described above. Primiparae carrying early embryos can be clearly distinguished from older females with a second or subsequent brood of early embryos on the basis of size, shape of the carapace and position of the embryos within the dorsal pouch formed by the carapace (Pl. I, figs. 1, 4). In view of the considerable overlap in sizes it proved impossible to separate females with late-stage embryos (Pl. I, fig. 2) into primiparae and older individuals. The striking change in the outline of the brood pouch of females following the emergence of young is illustrated in Pl. I, figs. 3, 4.

Text-fig. 2C shows the size distribution of males (Pl. I, fig. 5) and females producing a resting egg (Pl. I, fig. 6), presumably after fertilization. When present, these sexual females are among the largest individuals in a sample; they fall within a higher size range than the parthenogenetic females with late-stage embryos, and more closely correspond in size distribution to females with second or subsequent broods of early-stage embryos. This is shown only in the sample collected on 29 May since, when sexual reproduction is intense as on 5 October, older females with early embryos are very scarce. At their birth young females are carrying developing embryos and it would appear that at least one brood of young is first liberated before a resting egg can be produced.

Rammner (1930) noted the large size of the sexual females, but since they differ from the parthenogenetic females in the nature of the brood-pouch epithelium and have a carapace opening, he was of the opinion that they must be large at birth and do not first produce a parthenogenetic brood.

Because of the size range of sexual females and the fact that all embryos nearing the stage of liberation can be distinguished either as males or parthenogenetic females with blastulae, Rammner's suggestion is untenable. A new

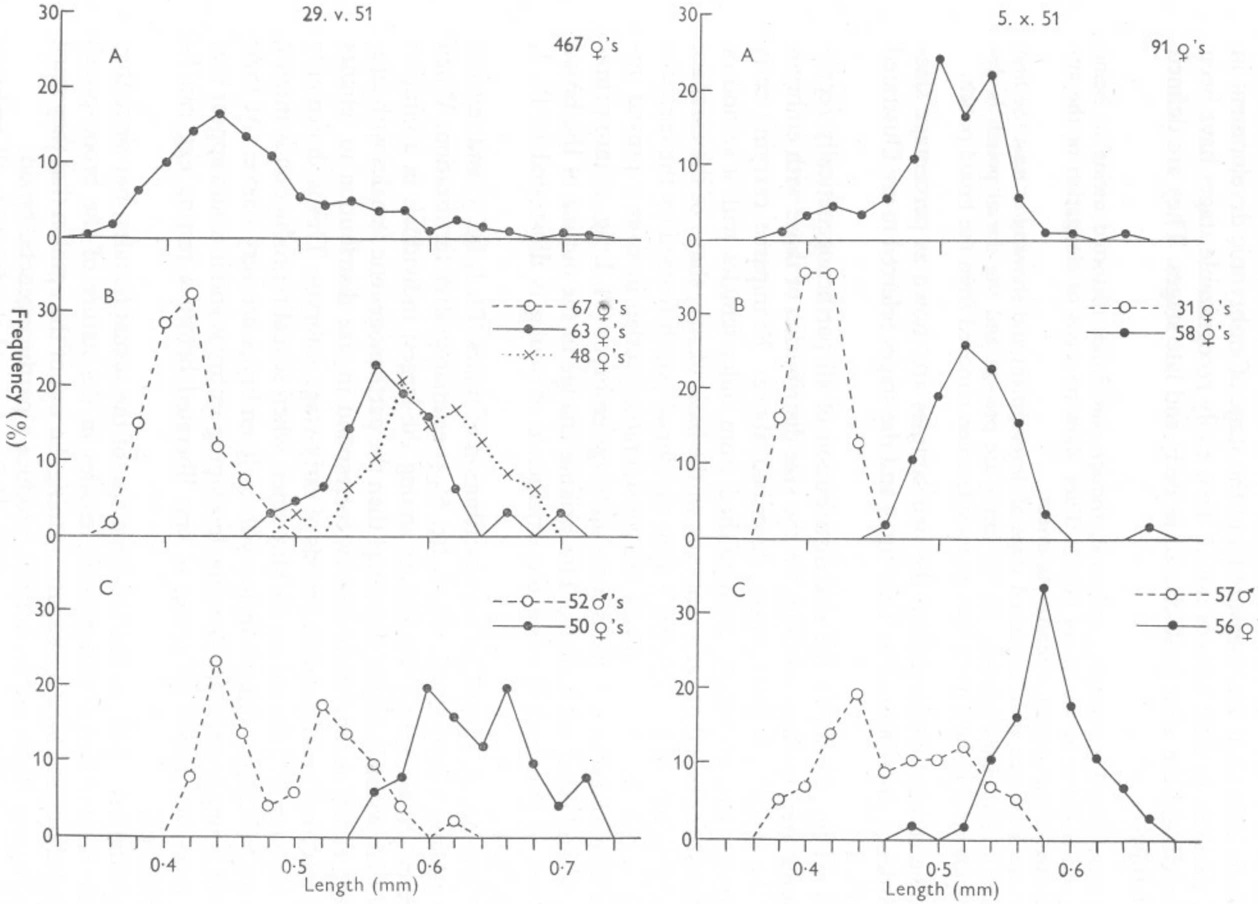

Fig. 2. Percentage size-frequency distribution of *Evadne*. A: parthenogenetic females. B: primiparae with early-stage embryos (○- - -○), females with late-stage embryos (●——●), and females with a second or later brood of early-stage embryos (× · · · · ×). C: males (○- - -○), and females showing the formation of a resting egg (●——●).

carapace is formed at the liberation of a brood of young as shown in Pl. I, fig. 3, and the carapace opening might possibly appear at this time. The shape of the carapace of females showing the first signs of resting-egg formation is also very similar to that of females with second or following broods of early embryos.

The fate of mature resting eggs can only be surmised. Jorgensen (1933) noted cast exoskeletons containing resting eggs in the plankton on several occasions, but these were never observed in the Clyde plankton. Nor, in fact, were any females with mature resting eggs ever found showing signs of an incipient moult. It therefore seems possible that the majority sink to the bottom after the death of the parent.

EMBRYO NUMBER AND SIZE

Cheng (1947) found that larger female *Evadne* generally have more embryos than smaller females. His results cannot, however, be accepted as conclusive, since he groups together individuals from several samples collected over a considerable period. Increased egg production with an increase in body size has been demonstrated in several species of *Daphnia* and other freshwater Cladocera by Green (1954, 1956).

In Text-fig. 3 the number of embryos is plotted against maternal length in two large samples. The means, standard deviations and ranges for both length and embryo number of females with embryos at the two stages defined are also shown.

The mean embryo numbers in the sample collected on 29 May are roughly constant in the lower size-groups, which represent only primiparae and increase in the higher size-groups, since these include older females with early-stage embryos.

In the sample taken on 9 March the embryo number shows a decrease with increase of size, individuals with late-stage embryos having fewer than the primiparae with early-stage embryos. This is at least partly due to a proportion of the embryos present at birth failing to develop, since disintegrating embryos and undifferentiated patches of tissue could be clearly seen in the brood pouches of some females. In preserved specimens these abnormal embryos are darker in colour, very fragile and occasionally recognizable as being at an earlier stage of development than normal embryos in the same brood pouch. As in other Polyphemidae the eggs of *Evadne* contain very little yolk, development depending on nourishment supplied by the mother through the fluid bathing the embryos in the closed brood pouch (Kuttner, 1911; Rammner, 1930). The loss of embryos could therefore be due to the effect of adverse conditions on the parents.

The apparent disintegration and resorption of embryos was observed in the samples collected 9 March, 13 April, 14 June and 30 October. Text-fig. 5B shows that in many of the samples collected during the year the brood number of females with late-stage embryos was smaller than that of the primiparae with early embryos, despite the fact that the former group will include a small and unknown proportion of individuals producing a second or even later brood.

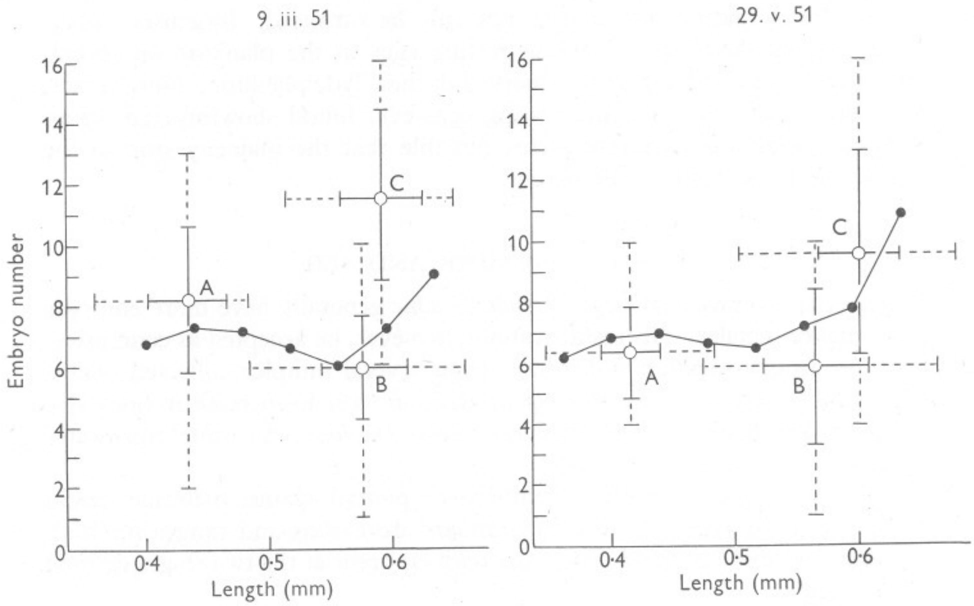

Fig. 3. Embryo number and size. Also shown are the means, standard deviations and ranges for embryo number and size of primiparae with early-stage embryos (A); females with late-stage embryos (B); females with a second or later brood of early-stage embryos (C).

Females with second and subsequent broods of early-stage embryos were very scarce in some of the samples and insufficient were obtained for the embryo numbers to be plotted on a seasonal basis. Their embryo numbers do, however, tend to fluctuate with those of females with late-stage embryos (Text-fig. 4).

It is clear that the best measure of the average production of young per brood can be obtained when only those individuals with late-stage embryos are considered.

Although the number of late-stage embryos is very variable and the range of sizes is rather small, larger individuals tend to produce larger broods of young. This is shown in Table 2 for several samples selected to cover a wide range of reproductive capacities.

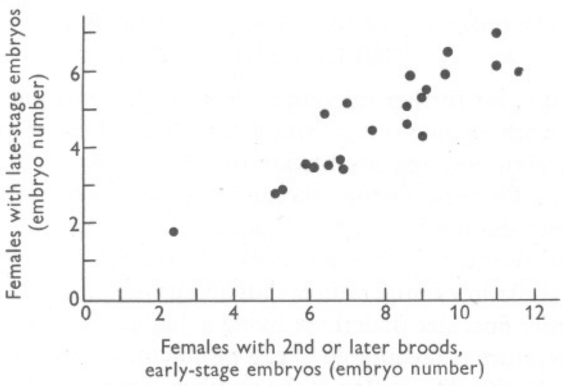

Fig. 4. Scatter diagram showing the relation of the mean embryo number of females with late-stage embryos and the mean embryo number of females with a second or later brood of early-stage embryos for each sample.

TABLE 2. SIZE AND EMBRYO NUMBER OF FEMALES WITH LATE-STAGE EMBRYOS

Date 1951	Length (mm.)*	No. examined	No. of embryos Max.	Min.	Mean
9. iii.	0·49	4	6	2	4·0
	0·54	25	8	1	5·2
	0·59	36	10	3	6·4
	0·64	9	9	5	7·2
13. iv.	0·54	4	4	2	3·0
	0·59	20	6	2	3·4
	0·64	18	6	2	3·5
	0·69	6	5	1	3·7
	0·74	2	5	1	3·0
29. v.	0·49	8	8	2	5·1
	0·54	24	9	1	5·2
	0·59	27	10	1	6·5
	0·64	2	10	5	7·5
	0·69	2	10	7	8·5
7. vi.	0·49	11	5	1	2·1
	0·54	28	8	1	3·2
	0·59	5	6	2	3·8
	0·64	1	—	—	5·0
5. x.	0·44	1	—	—	2·0
	0·49	22	7	1	3·7
	0·54	31	7	3	5·1
	0·59	3	8	6	7·0
	0·64	1	—	—	5·0
31. x.	0·49	14	4	1	2·7
	0·54	18	5	1	3·2
	0·59	6	6	1	4·1
	0·64	2	6	5	5·5

* Class mid-point.

FLUCTUATIONS IN LENGTH AND EMBRYO PRODUCTION DURING THE YEAR

Green (1956, q.v. for further references) has summarized the main results of experimental work carried out to study the effect of environmental factors influencing growth and egg production of several species of the freshwater genus *Daphnia*. Of these factors, temperature and food supply are likely to be the most important which affect Cladocera living near the surface of the sea. In general terms, experimental work on cultures of *Daphnia* has shown two features: (i) At low temperatures individuals increase in size more slowly, but reach a larger final size than those living at higher temperatures. A certain range of temperature is favourable to egg production, above and below which there is a considerable diminution of the number of eggs produced. (ii) Starvation both decreases growth and reduces egg production. Green (1956) gives evidence that it also reduces egg size, which in cladocerans that do not secrete a nutrient fluid is directly related to the size of young at birth.

The samples of *Evadne* from the Clyde Sea Area during 1951 show that there were considerable fluctuations in size and the production of young. Text-fig. 5 shows the changes in the mean length and embryo number of females with late-stage embryos and primiparae with early-stage embryos. The mean lengths of these two classes of females show similar fluctuations and there is a notable fall from the end of May to late July. During this same period the mean number of late-stage embryos showed initially a sharp decline followed by a more steady rise. In early August, shortly after the recovery of embryo production, there was an increase in mean lengths, though they never attained their former level.

The seasonal variation in length of the two classes of females indicates that the size at which females had embryos nearing the stage of liberation was mainly dependent on their own size at birth, and that there were not usually any pronounced changes in the growth increment. A possible explanation of the relationship between fluctuations in the length of females and numbers of late-stage embryos produced, is that both are to a certain extent influenced by the same environmental conditions, but that changes in the size of young at birth are more gradual and lag behind fluctuations in the number of young produced per brood.

The fluctuations described can be correlated with surface sea temperatures at Keppel Pier, Millport, shown in Text-fig. 5C. In March, April and May females were larger than at any other time during the year. This may possibly be related to the lower sea temperatures during the spring, though otherwise there are no clear connexions since a partial recovery of size occurred during August when the temperature was about at a maximum for the year.

Both length and embryo number were better correlated with the amount of microplankton caught by the net, suggesting that food supply may be the more important factor. The greatest quantities of microplankton occurred from 13 April to 24 May and again from 24 July to 17 October. Details of the relationship to food supply will be discussed in a following section.

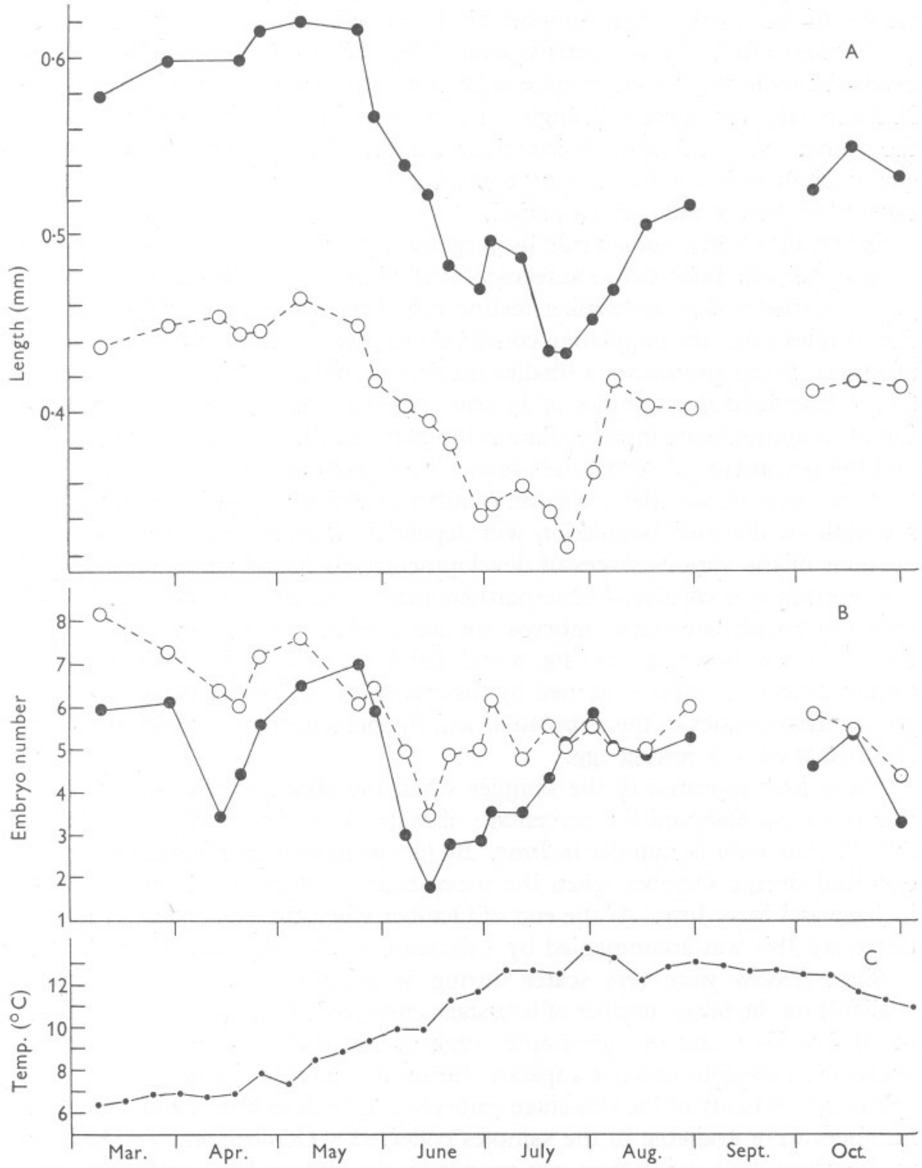

Fig. 5. Fluctuations in mean length (A), and mean embryo number (B), of primiparae with early-stage embryos (○- - -○), and females with late-stage embryos (●——●) (C). Surface sea temperatures at Keppel Pier, Millport, as 8-day means.

PARTHENOGENETIC AND SEXUAL REPRODUCTION

Berg (1931) carried out a detailed study of changes in the mode of reproduction of several species of *Daphnia* both in natural populations and cultures. The results of this work clearly support his hypothesis that the transition from parthenogenesis to gamogenesis is caused by the influence of unfavourable external conditions, the environmental factors producing a state of depression in the females and thereby changing the mode of reproduction and the sex of the young. One of the most obvious signs of depression shown by the parthenogenetic females is a reduction in the mean number of eggs produced and this takes place before each sexual period.

Observations on *Evadne* made by Jorgensen (1933) have been discussed by Berg (1936) who finds a close agreement with his own on freshwater daphnids. Jorgensen notes that developing resting eggs first made their appearance in the samples when the population consisted to a great extent of less bulky more triangular forms producing a smaller number of embryos than usual. Cheng (1947) examined five samples of *Evadne* collected during two summers and found an approximate inverse relationship between the mean embryo number and the percentage of sexual individuals in the population.

It has been shown that the mean number of embryos per female found in a sample of the total population will depend to a great extent on the proportions of the various stages of development, and that a better measure of the reproductive capacity of the parthenogenetic females can be obtained if only those with late-stage embryos are considered. The results obtained in the Clyde are shown in Text-fig. 6 and Table 3, in which fluctuations in the mean number of embryos carried by these females can be compared with the percentage of males in the population and the percentage of females showing the formation of a resting egg.

Males first appeared in the samples when the mean number of embryos was relatively high and the percentage of males decreased during the drastic fall of mean embryo number in June. By far the greatest percentage of males occurred during October when the mean embryo number was higher than in June and early July. At the end of October when the percentage of males decreased this was accompanied by a decrease in the mean embryo number.

Since *Evadne* were very scarce during September no adequate data are available on the mean number of late-stage embryos, but the embryo numbers of all females found in the samples suggest that there was no pronounced decrease in the reproductive capacity during this month (Table 3).

The sex of many of the late-stage embryos can be determined and sufficient numbers were available in the samples collected 5 October and 31 October to show that male production was greater on the former date, confirming the evidence of the different percentage of males in the two populations (Table 4).

These results do not admit a simple explanation on the basis of Berg's depression hypothesis. It is possible, however, that the first appearance of males in the samples is related to a period of depression indicated by the lower mean embryo numbers found in previous samples during April. Later fluctuations in the percentage of males might also be accounted for if it was considered that moderate depression favours greater male production than severe

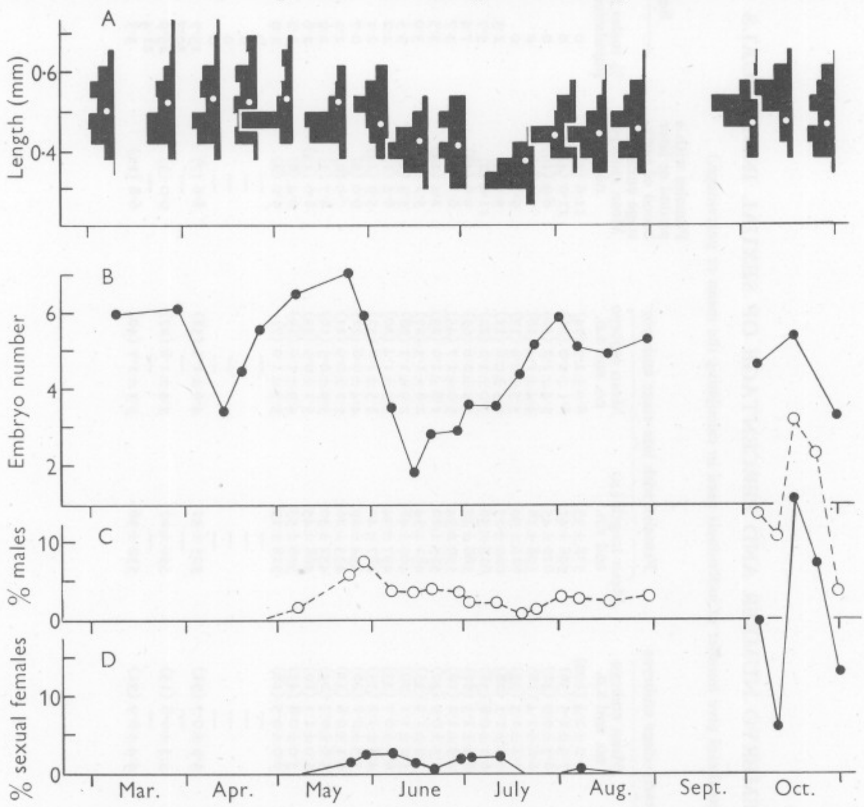

Fig. 6. A: percentage size-frequency distribution of females on some of the dates of sampling. The open circles within the histograms indicate the intermediate size between the means for primiparae with early-stage embryos and females with late-stage embryos. B: fluctuations in the mean number of late-stage embryos. C: percentage of males in the population. D: percentage of females showing the formation of a resting egg (sexual females).

depression. To explain the findings of Stuart, Cooper & Coady (1933) that under conditions of severe depression female *Moina* become what they term 'sex fast' and produce female young only, Berg (1936) suggests that severe depression might have a different effect from moderate depression. It is not, however, known whether sex-fast females occur in natural populations of freshwater Cladocera.

Fluctuations in the percentage of females showing the formation of a resting egg follow those of the males, but will give a distorted picture of

TABLE 3. LENGTH, EMBRYO NUMBER AND PERCENTAGE OF SEXUAL INDIVIDUALS

(Figures in parentheses give number of individuals used in calculating the mean or percentage.)

Date 1951	Parthenogenetic females. Mean embryo no.	Primiparae with early-stage embryos: Mean length (μ) and S.D.	Primiparae with early-stage embryos: Mean embryo no. and S.D.	Females with late-stage embryos: Mean length (μ) and S.D.	Females with late-stage embryos: Mean embryo no. and S.D.	Females with a second or later brood of early-stage embryos. Mean embryo no.	Sexual individuals: % males in population	Sexual individuals: % females with a resting egg
9. iii	7·1 (344)	436 ± 31	8·2 ± 2·4 (102)	578 ± 35	6·0 ± 1·7 (74)	11·6 (38)	0	0 (800)
29. iii	7·6 (97)	449 ± 22	7·3 ± 1·5 (36)	598 ± 41	6·1 ± 2·0 (16)	11·0 (4)	0	0 (510)
13. iv	5·5 (95)	454 ± 29	6·3 ± 0·9 (32)	622 ± 45	3·4 ± 1·2 (50)	6·9 (10)	0	0 (303)
19. iv	5·7 (97)	443 ± 26	6·0 ± 1·4 (18)	598 ± 18	4·4 ± 1·4 (16)	7·7 (4)	0	0 (202)
25. iv	6·7 (133)	445 ± 28	7·1 ± 1·3 (33)	616 ± 30	5·5 ± 0·9 (17)	9·1 (6)	0	0 (344)
7. v	7·0 (77)	464 ± 22	7·6 ± 1·1 (28)	620 ± 27	6·5 ± 0·8 (11)	9·7 (4)	1·5	0 (198)
24. v	6·4 (119)	448 ± 23	6·1 ± 0·8 (38)	616 ± 36	7·0 ± 1·2 (22)	11·0 (2)	5·7	1·4 (846)
29. v	7·0 (467)	417 ± 24	6·4 ± 1·5 (67)	566 ± 42	5·9 ± 2·6 (63)	9·6 (48)	7·4	2·3 (876)
7. vi	4·4 (130)	404 ± 36	4·9 ± 1·2 (16)	539 ± 34	3·0 ± 1·7 (45)	6·1 (9)	3·7	2·5 (539)
14. vi	2·7 (99)	395 ± 17	3·5 ± 0·9 (30)	525 ± 22	1·8 ± 1·0 (23)	2·4 (14)	3·5	1·4 (736)
20. vi	4·6 (127)	382 ± 32	4·9 ± 1·3 (35)	482 ± 34	2·8 ± 1·3 (27)	5·1 (10)	3·9	0·4 (908)
29. vi	5·4 (90)	341 ± 27	5·0 ± 1·1 (20)	469 ± 48	2·9 ± 1·1 (28)	5·3 (3)	3·5	1·9 (693)
2. vii	5·7 (107)	348 ± 33	6·1 ± 0·7 (23)	497 ± 34	3·5 ± 1·4 (20)	6·5 (12)	2·2	1·9 (495)
11. vii	4·6 (113)	359 ± 38	4·8 ± 1·2 (33)	487 ± 40	3·5 ± 1·8 (31)	5·9 (14)	2·1	0·7 (418)
19. vii	5·7 (99)	344 ± 37	5·5 ± 0·8 (28)	434 ± 29	4·4 ± 0·8 (21)	9·0 (5)	0·7	0 (137)
24. vii	5·2 (91)	324 ± 22	5·1 ± 0·8 (31)	433 ± 26	5·2 ± 0·9 (21)	7·0 (2)	1·2	0 (264)
1. viii	5·7 (106)	366 ± 37	5·6 ± 0·7 (23)	452 ± 30	5·9 ± 0·5 (16)	8·7 (3)	2·9	0 (204)
7. viii	5·5 (103)	417 ± 43	5·0 ± 1·1 (19)	468 ± 45	5·1 ± 0·9 (33)	8·6 (13)	2·6	0·5 (188)
17. viii	4·9 (107)	403 ± 32	5·0 ± 0·8 (43)	506 ± 55	4·9 ± 1·0 (19)	6·4 (8)	2·2	0 (368)
30. viii	6·1 (126)	401 ± 24	6·0 ± 0·5 (18)	518 ± 19	5·3 ± 1·0 (7)	9·0 (8)	2·9	0 (177)
3. ix	6·0 (45)	—	—	—	—	—	0	0 (45)
13. ix	5·0 (2)	—	—	—	—	—	0	0 (2)
17. ix	5·8 (8)	—	—	—	—	—	0	0 (8)
25. ix	5·7 (12)	—	—	—	—	—	0	0 (15)
5. x	5·4 (103)	411 ± 16	5·9 ± 0·7 (31)	525 ± 31	4·6 ± 1·1 (58)	8·6 (7)	13·7	19·6 (490)
11. x	7·3 (28)	—	—	—	—	—	10·7	6·0 (56)
17. x	5·8 (102)	418 ± 13	5·5 ± 0·8 (15)	550 ± 27	5·4 ± 1·8 (27)	9·0 (3)	25·9	35·6 (216)
24. x	5·8 (17)	—	—	—	—	—	21·4	27·2 (28)
31. x	4·3 (107)	414 ± 20	4·4 ± 0·9 (31)	532 ± 36	3·3 ± 1·7 (40)	6·8 (11)	3·5	12·9 (136)

changes in the intensity of sexual reproduction, since from the size distribution of whole populations it is clear that there is a considerable variation in the number of primiparae present on the different dates of sampling and these do not produce resting eggs.

Changes in the percentage size distribution of the parthenogenetic females during the year are illustrated in Fig. 6A. From March to August major increases and decreases in the mean number of late-stage embryos tend to be followed by similar changes in the proportions of small individuals in the population. The preponderance of the larger size groups of females during October may be partly accounted for by the high production of males and resting eggs, since this will reduce the number of young females entering the population.

TABLE 4. THE SEX OF VERY ADVANCED EMBRYOS

(A single brood may contain both male and female embryos.)

Date 1951	No. of females with advanced embryos examined	No. of females with male embryos	Total no. of embryos	% of male embryos
5. x.	50	16	229	27·4
31. x.	33	4	111	9·9

The results described are at variance with the observations of Jorgensen (1933). The samples used by Jorgensen appear to have been taken with nets which would tend to select the larger size groups. She has noted that during the two periods of maximum abundance usually found during a year, the great increase in numbers was produced, as far as the samples were concerned, by a temporary influx of adults and states that no doubt immense numbers of young forms were present though not taken by the nets. It is possible, therefore, that populations consisting entirely of small individuals, similar to those found in the Clyde during June and July 1951, would not be adequately represented in the samples she examined.

The data obtained by Cheng (1947) is insufficient to be accepted as conclusive (see page 360). In Table 3 the mean embryo number of all parthenogenetic females can be compared with the percentage of sexual individuals in the population for each date of sampling in the Clyde during 1951. The values show no inverse relationship and therefore do not support Cheng's results.

FOOD AND FEEDING HABITS

Rammner (1930) states that *Evadne* is a predator, feeding on small organisms which are captured by means of its powerful raptorial legs, but notes that no direct observation had been made of the taking up of food by the living animal. He suggests that they may also feed on organic detritus. Previously Lebour (1922) had recorded the cells and spores of *Phaeocystis* from the guts of two *Evadne*.

The gut contents of both living and preserved *Evadne* were examined on several occasions, and though soft reddish or brownish debris was often present at the posterior end of the gut, no recognizable remains were found of any organisms eaten.

Some of the individuals examined were, however, found to be holding a variety of small organisms, either grasped between the endites of the second and third legs or pressed between the labrum and the mouth. Of all those measured and dissected from the plankton-sampler catches during the year, 2·1 % were holding tintinnids, 1·4 % *Peridinium* and *Goniaulax* species and 0·1 % small copepod eggs. Tintinnids were most frequently present during the period from March to May and again during August and September, peridinians during June and July. Considerable quantities of *Skeletonema* and *Thalassiosira* were present in the plankton samples during the spring, but these diatoms were not found between the legs or mouth parts of the *Evadne*. During the investigation it became evident that the proportion of individuals holding microplankton organisms depended to a great extent on the treatment of the catch after hauling the net. On the whole, greater proportions were found in the non-quantitative samples which had been fixed immediately than in the quantitative samples which were not fixed for several minutes due to time spent in washing down the net. Living *Evadne* examined only a short time after collection were rarely observed holding any organisms.

A more detailed study of the feeding habits was made on two occasions towards the end of the year. *Evadne* were obtained from 10 min hauls with 50 cm medium-mesh tow-nets (48 meshes to the inch) taken at 4 h intervals through 24 h. Two nets were fished 25 fathoms apart on a trawl warp, to the end of which was attached a cable depressor. Rigged in this way, the upper net fished at 1–2 m and the lower at 33–38 m. These hauls were taken at a station just outside Tarbert, Loch Fyne. The catches were fixed in formalin as quickly as possible after hauling the nets. During the last series water samples were collected from a depth of 1 m and the number of organisms in the samples estimated by a method previously adopted by Marshall (1947).

On both occasions very few *Evadne* were caught by the lower net and there was no evidence of vertical movements to or from the surface throughout the 24 h. Results of observations are shown in Table 5, in which the number of *Evadne* per haul with the upper net and the percentage of these holding small organisms is given. From the marked difference between the percentages in the day and night hauls it is clear that small organisms were being captured almost exclusively during the hours of daylight. Since *Evadne* possesses a relatively large compound eye, this suggests that food organisms are normally taken by an act of capture depending on sight.

Table 6 shows the percentage composition of these organisms found held by *Evadne* and the percentage composition of the microplankton in the sea at 1 m on 17–18 October. In the series of samples taken on 15–16 August as many as five tintinnids and peridinians were sometimes held by a single individual, but no *Ceratium longipes* (Bailey) were so found, although large numbers were caught by the nets. *C. furca* (Ehrenberg) was the most commonly held prey on 17–18 October, but not the most abundant dinoflagellate

TABLE 5. PERCENTAGE OF PRESERVED *EVADNE* FOUND GRASPING SMALL ORGANISMS IN SAMPLES COLLECTED AT 4-HOUR INTERVALS

(Figures in parentheses give the numbers examined which in each case was the total number found in the sample.)

Time (h) ...	12.00	16.00	20.00	24.00	04.00	08.00	12.00
15 and 16. viii. 51	34·7 (121)	51·6 (250)	7·1 (294)	2·7 (150)	0 (152)	38·1 (134)	50·5 (198)
17 and 18. x. 51	19·6 (61)	25·9 (77)	0 (60)	0 (89)	0 (106)	27·3 (66)	20·4 (132)

Hauls taken in darkness (15 and 16. viii. 51: 24.00–04.00; 17 and 18. x. 51: 20.00–04.00)

TABLE 6. THE PERCENTAGE COMPOSITION OF ORGANISMS HELD BY PRESERVED *EVADNE*

(The percentages for 17 and 18. x. 51 are compared with the percentage composition of the microplankton at 1 m.)

	Organisms held by *Evadne*		Microplankton
	15 and 16. viii. 51	17 and 18. x. 51	17 and 18. x. 51
Phytoplankton			
Diatoms	0·2		0·03
Peridinium spp.	18·2	20·9	3·0
Peridinium spp. fragments	2·7	1·6	—
Ceratium furca	0·2	56·4	34·6
C. furca fragments	—	15·0	—
Ceratium spp. less *C. furca*	—	—	55·1
Other dinoflagellates	—	1·6	6·6
Zooplankton			
Tintinnopsis spp.	73·2	1·6	0·06
Tintinnopsis spp. fragments	1·3		
Small copepod eggs	1·3	3·2	0·5
Copepod egg membranes	0·7	—	—
Copepod nauplii	0·2	—	—
Larval lamellibranchs	0·9	—	—
Unidentified debris	0·9	—	—
Number of microplankton organisms examined	444	62	—
Mean number of organisms per litre	—	—	12,760

in the sea as estimated from the water samples. Peridinian plates and fragments of tintinnid cases were sometimes found near the mouth but never in the gut. The lack of any skeletons or hard parts of food organisms in the guts seems to indicate that only the cell contents are ingested and the hard remains later discarded.

The percentages of the various groups held by a sample of *Evadne* may not reflect the relative quantities of those eaten. Armoured organisms may be eaten more slowly than fragile or naked forms, while certain types may be rejected after capture. There is also the possibility that more active prey if undamaged may escape during the fixation of the catch. However, the results suggest that *Evadne* is a selective feeder, shape and size being two of the factors determining suitable food organisms. The majority are fairly compact bodies with average dimensions of between 30 and 120 μ. *Ceratium furca* is an exception, but it differs from the other ceratia of the Clyde plankton in that the two posterior spines are rather short and point straight backwards—a factor possibly influencing its selection by *Evadne*. It is also noteworthy that most of the food organisms are motile forms.

DISCUSSION

Information obtained on the food and feeding habits of *Evadne* helps towards an interpretation of several other aspects of the biology of the species.

During the two 24 h series of tow-nettings feeding was limited to the hours of daylight which indicates that light may be necessary for the capture of food organisms. This would also account for the species being an epiplanktonic form and mainly living in the illuminated surface layers of the sea. Another implication is that in temperate regions during the winter, when most groups of microplankton are poorly represented, the time available for feeding and the depth at which prey can be seen and captured will also be limited. When these adverse conditions are considered, the ability to produce resting eggs appears to be a great advantage in ensuring that the population is carried through to the following spring.

Observations indicate that *Evadne* is a selective feeder and that peridinians and tintinnids are the most important food organisms. The results of several comprehensive plankton investigations show that fluctuations in the population density of *Evadne* can often be correlated with variations in the abundance of *Peridinium* spp. and dinoflagellates of a shape and size similar to those eaten by *Evadne* in the Clyde Sea Area.

The tables given by Dakin & Colefax (1933) to illustrate the cycle of plankton in the coastal waters of New South Wales during 1931, indicate that the periods of maximum abundance of each of the three species of *Evadne* recorded were also the periods when highest concentrations of *Peridinium* spp. and *Ceratium furca* occurred. Greatest numbers of *Evadne nordmanni* were recorded on the same date as the maxima for these dinoflagellates. Accounts of the zooplankton (Deevey, 1956) and phytoplankton (Conover, 1956) of Long Island Sound during 1952, show that *E. nordmanni* was only recorded within the period when *Peridinium* spp. were present in other than trace quantities, and that it occurred in greatest numbers towards the end of a flowering of these species. Lohmann (1908) gives complete tables for the plankton in Kiel Bay during 1905–6. The two species of *Evadne* recorded were always very scarce, nevertheless, each small peak in numbers followed within 3 weeks of a maximum of *Peridinium* spp. excluding *P. triqueta* (Stein). This latter species was the dominant peridinian in Kiel Bay, but according to Lohmann's estimate of the average cell volume, smaller than any organism noted as captured by *Evadne* in this present investigation.

Although in all the reports of comprehensive plankton investigations examined significant increases in the population of *Evadne* could be correlated with flowerings of *Peridinium* spp., it is clear that factors other than food supply at times limit the population density. This is illustrated by the seasonal cycle of plankton at the Borkumriff Lightship station during 1910, described by Lücke (1912). Here the increase in numbers of *Evadne nordmanni* during April and May closely followed a flowering of *Peridinium* spp. After May numbers of *Evadne* declined and the species finally disappeared from the plankton in August, despite the fact that *Peridinium* spp. showed a second increase during July and remained fairly abundant until the end of October. A rather similar sequence of events occurred in the Clyde plankton during 1923, described by Marshall (1925). *Evadne nordmanni* was common during May and June and *Peridinium* spp. showed a maximum in May after the April diatom flowering. Fewer *Evadne* were recorded after June and there was no increase during or immediately after the second peak of *Peridinium* spp. in August.

All the investigations referred to reveal no clear relationship between the fluctuations in the numbers of *Evadne* and those of the Tintinnoinea when data on this group are available. Several recent studies, for example, that made by Digby (1953) on plankton production in Scoresby Sound, have, however, shown that tintinnids are often most abundant at about the same time as the peridinians, both groups being associated with the late phase of a phytoplankton outburst.

Only qualitative observations were made on the net-caught microplankton in the Clyde Sea Area during 1951. It is, however, possible to state that both peridinians and tintinnids were present in greatest quantities from early April to the end of May and from late July to mid-October. The first period of abundance coincided with the spring diatom flowering and the second with the period when ceratia were predominant. Fluctuations in both length and the mean number of late-stage embryos of *Evadne*, as shown in Fig. 5 (p. 359), may therefore reflect changes in the density of food organisms. Variations in embryo production might be expected to affect in turn the population density of the species as shown in Fig. 1 (p. 352). The rapid growth of the population during May took place when embryo production was highest and numbers decreased shortly after embryo production had declined. However, the population density was very low in September, although embryo production had recovered the previous month. Such a situation might be accounted for if during the summer and autumn the population of *Evadne* was being greatly reduced by predation. This appears to be a reasonable hypothesis, since at

Borkumriff during 1910 (Lücke, 1912) and in the Clyde during 1923 (Marshall, 1925), two cases when the population of *Evadne* did not respond to an increase of food supply during the summer, known zooplankton feeders: coelenterates, chaetognaths and larger crustacean larvae, were more abundant at this time than during the spring. In this connexion it may be relevant that *Evadne* is a slow and rather weak swimmer compared with the copepods, and consequently may perhaps be more easily caught by the larger predatory animals.

In the Clyde during 1951 there was no such clear relationship between the number of young produced per brood by the parthenogenetic females, and the occurrence of gamogenesis as that described in natural populations of *Daphnia* by Berg (1931) and Green (1955). It has been suggested that in the case of *Evadne*, moderate rather than severe depression, to judge by size and production of young, promotes gamogenesis. Comparing the development of the parthenogenetic and resting eggs in *Daphnia* and *Evadne* it does not seem unlikely that gamogenesis will be influenced by different degrees of depression in each case. The resting eggs of *Evadne* are large in relation to the size of the female producing them, and also *Evadne* does not have the capacity for fat storage in the ovary and surrounding tissues possessed by *Daphnia* species. Most of the nourishment necessary for the formation of the large and heavily yolked resting egg will, therefore, depend on the immediate food supply available to the parent during the period it is being produced. In view of the lack of food reserves it would seem advantageous to the species if resting egg formation took place before any drastic decrease in the level of nutrition, causing severe depression and possibly leading to the extinction of the population.

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SUMMARY

During 1951 *Evadne nordmanni* was present in the Clyde plankton from late February to the end of October and was most abundant during May and early June. The bulk of the population was always found in the top 30 m. Reproduction is mainly parthenogenetic; sexual individuals first appeared in May and sexual reproduction was most intense during October.

The relation between maternal size and stage of embryonic development is described. Sexual females showing the formation of a resting egg are large and have previously produced at least one brood by parthenogenesis.

Of the females with embryos at an early stage of development the primiparae have smaller broods than larger and older individuals. During the development of embryos some may be resorbed and in the primiparae this results in a decrease of embryo number with increase of size. Larger individuals tend to produce larger broods of young.

There was a considerable decrease of size from June to July and a partial recovery in August. These fluctuations follow similar fluctuations in embryo production.

The reproductive capacity of the parthenogenetic females and the intensity of sexual reproduction did not show any clear relationship, though there are indications that the latter is favoured by moderate rather than severe depression.

Food organisms are captured only during the hours of daylight. *Evadne* appears to be a selective feeder the diet of which consists mainly of tintinnids and peridinians.

Several aspects of the biology of the species are discussed with reference to the findings on the food and feeding habits.

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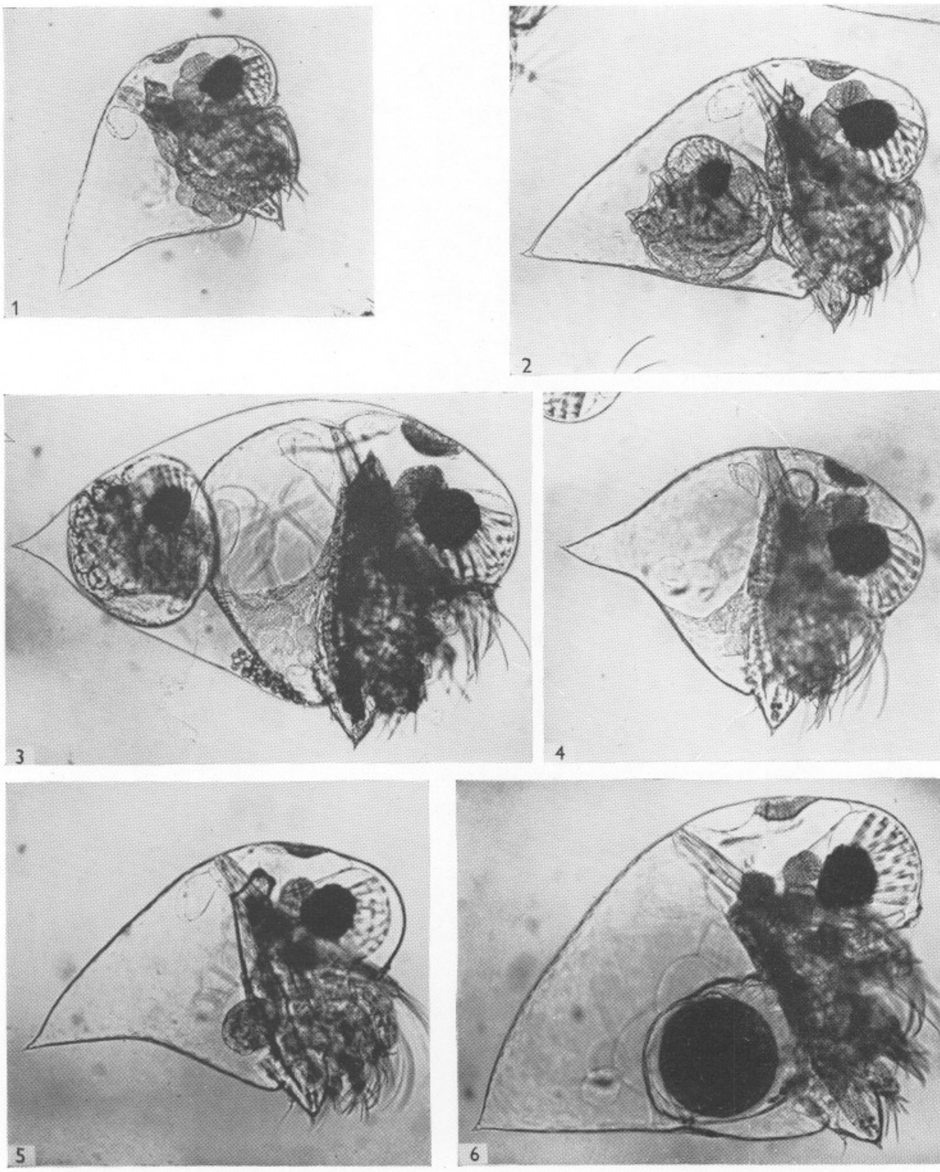
EXPLANATION OF PLATE I

(Magnification, ×66.)

Evadne nordmanni.

Fig. 1. Primiparous female with early-stage embryos.
Fig. 2. Female with a single late-stage embryo.
Fig. 3. Female about to moult and liberate a single late-stage embryo. Early-stage embryos are present in the newly formed brood pouch.
Fig. 4. Female with a second or subsequent brood of early-stage embryos.
Fig. 5. Male.
Fig. 6. Female with an almost fully developed resting egg.



(*Facing p.* 370)