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Population biology of Darwinula stevensoni (Crustacea, Ostracoda) in an oligotrophic lake

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The population dynamics of the parthenogenetic ostracod *Darwinula stevensoni* was studied from spring 1975 to autumn 1977 in the littoral of Pääjärvi, an oligotrophic lake in southern Finland. The distribution of the species is patchy; numbers reach a maximum at 1.5 m in the soft bottom in front of the macrophyte zone. Nine instars (the ninth being the adult stage) can easily be separated by length measurements. The first two instars were observed only between the carapace valves of the adults; the third instar is the first that lives freely in the sediment. Five to six instars (including adults) were always present. All the changes in the population structure took place in summer: Reproduction starts in early June, has its maximum in July-August and ceases in September. The maximum number of embryos observed within a single adult was 11; the highest mean number of embryos per adult during the reproductive season was 7.8 in 1975 and 6.3 in 1976. In summer 1975 the maximum reproductive rate (embryos produced per adult per day) was 0.20 and in 1976 0.16. No changes in the population structure were observed during the long, cold winter period. The life cycle of this species in Pääjärvi is at least 3—4 years.

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1. Introduction

Ostracods are common in waters of all kinds, even in bogs and in the interstitial water. In the main, however, research on the ecology of the group has concerned marine species and communities (see Neale 1969 and Löffler & Danielopol 1977). But interest in the role of the meiobenthos in lake ecosystems has led to studies on Ostracoda (see Holopainen & Paasivirta 1977 for references to the meiobenthic literature). Currently some work is being carried out on the population ecology of certain freshwater species (McLay 1978a, 1978b, 1978c).

The work of the benthos group in the Pääjärvi ecosystem study (see Ruuhijärvi 1974) showed the importance of ostracods (in terms of both numbers and biomass) in the littoral system of the lake (Holopainen & Paasivirta 1977). The most abundant of the five species present was *Darwinula stevensoni* (Brady & Robertson). *D. stevensoni* is a cosmopolitan, eurythermic, freshwater species, which is unable to swim (Pinto & Sanquinetti 1958, McGregor 1969); it is viviparous (Alm 1921) and obligatorily parthenogenetic (Pinto & Sanquinetti 1958).

In this report I give results of the study on the population biology of this species in the littoral of Pääjärvi.

2. Study area

Pääjärvi is an oligotrophic lake situated in the communes of Lammi and Koski in southern Finland (61°04′ N, 25°08′E). It has an area of 13.42 km², a mean depth of 14.4 m, and a maximum depth of 87 m. The water is transparent to a depth of 2 to 2.5 m. The water is thoroughly mixed twice a year, and no oxygen deficit develops in the hypolimnion. The ice cover lasts from late December to early May, and a stable thermal stratification exists during the summer (Ruuhijärvi 1974).

This study was made in the littoral areas of the bay of Pappilanlahti at the end of the western arm of the lake (Fig. 1). The seasonal cycle of temperature in the littoral areas of the lake is characterized by low temperatures in winter (near 0°C), a rapid increase in early June, a peak (20—25°C) in July-August, and a decrease towards winter temperatures in late summer and autumn.

For most of the year the temperature in the littoral of Pääjärvi is below 4°C.

In the spring of 1975 some abiotic parameters of the sediment surface were studied in different vertical transects (from depths of 0.5—3.0 m) of the littoral of Pappilanlahti: Samples from the uppermost 10 mm of the sediment were taken for determinations of ash-free dry weight, water content, and contents of total nitrogen, organic carbon, total phosphorus, sodium, manganese, potassium, calcium, magnesium and iron (Table 1).

3. Material and methods

Preliminary sampling. The vertical distribution of *D. stevensoni* in the sediment was determined in the spring of 1975 by taking vertical slices from five sediment cores (15 cm² each) from 2 m depth (transect *c*, Fig. 1). Each core was divided into 0— 1 cm, 1— 2 cm, 2— 3 cm and 3— 5 cm layers from the top of the sediment surface. The sediment was then sieved through a 0.2 mm mesh, and the number of *D. stevensoni* were counted. Of the animals 92 % lived at 0— 1 cm, 7 % at 1— 2 cm, about 1 % at 2— 3 cm, and none at 3— 5 cm (n = 205).

The spatial distribution was studied in regard to both water depth and horizontal areas of the littoral of Pappilanlahti. Seven transects were studied over a depth range of 0.5— 4.0 m at steps of 0.5 m (Fig. 1). At each step three replicate 15-cm² samples were taken with a modified Kajak-type corer (Hakala 1971). The uppermost 2 cm of each core was transferred to a plastic box. They were fractioned through 0.4 mm and 0.2 mm sieves with a water jet. The *D. stevensoni* individuals retained on the 0.2 mm sieve were counted (Fig. 1). From the results obtained, a 450 m² area (divided into 50 3 m × 3 m squares) around transect *g* was then selected as the routine sampling area for a survey of the population dynamics.

Routine sampling. An 8.0 cm² tube attached to a pole was used for sampling. The uppermost 2 cm of the sediment in each core was transferred to a plastic box. A sample consisted of ten cores, each taken in the middle of one randomly chosen constant square. The sediment was fractioned in the laboratory with 0.4 mm, 0.2 mm and 0.1 mm sieves. The ostracods were then removed from the 0.2 mm and 0.1 mm fractions on a grooved disc under a dissection microscope at a magnification of × 12 (Hakala 1971). The animals were killed with 94 % ethanol, placed on slides and counted, and their maximum length was measured to the nearest 0.006 mm. The strong ethanol makes the carapace valves of the animals clear and the number of embryos was easy to count. Routine sampling was started on 18 April 1975 and the last sample was taken on 30 September 1977. During the open-water season in 1975 the sampling interval was 10 days; in winter a sample was taken once a month. In the summer of 1976 the interval was about 15 days, and during winter two samples were taken. In the spring and summer of 1977 samples were taken about once a month. Thus, the material consists of 44 samples with 440 sub-samples in a period of 30 months; in all, 41 072 individuals were measured and counted.

4. Results and discussion

A. Spatial distribution

The abundance of the ostracod *D. stevensoni* in the bay of Pappilanlahti showed great spatial

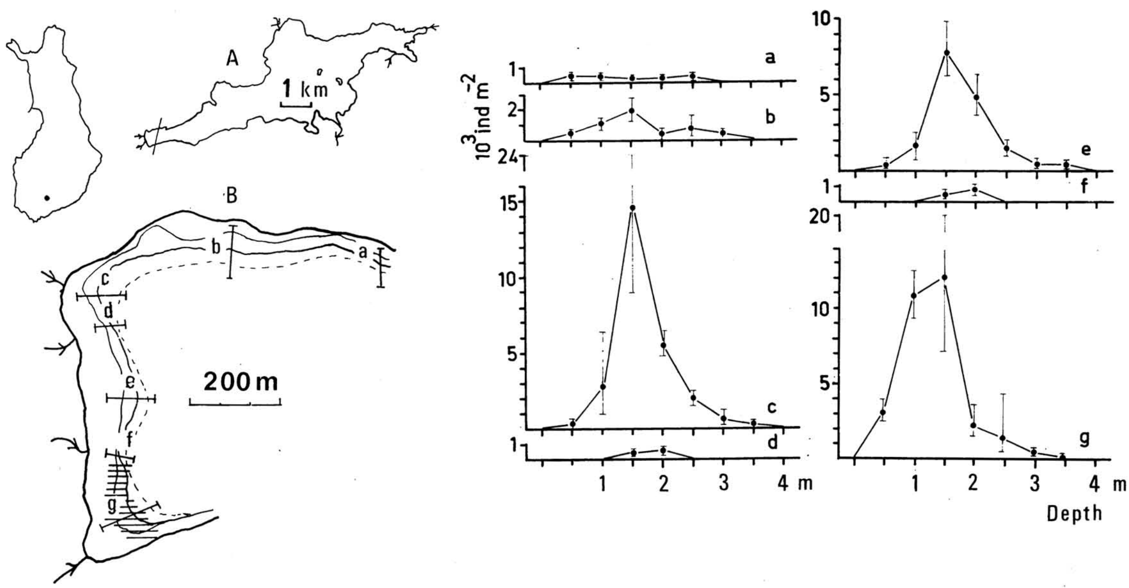

Fig. 1. Location of the study area, and the distribution of *D. stevensoni* in Pappilanlahti (B), a bay of Pääjärvi (A). The lower map shows the positions of the vertical transects (*a-g*); the right part of the figure shows the number of *D. stevensoni* (± 95 % conf. limits) as a function of depth in these transects. The routine sampling area (see above) around transect *g* is indicated by horizontal hatching.

Table 1. Abiotic parameters[1] of the uppermost centimetre of the sediment surface from different transects (see Fig. 1) in Pappilanlahti, a bay of Pääjärvi. Results are given as mg per ml (m is depth in metres, AFDW the ash-free dry weight of the sediment, H_2O % the water content, N_{tot} total nitrogen, C_{org} organic carbon, P_{tot} total phosphorus, Na sodium, Mn manganese, K potassium, Ca calcium, Mg magnesium, Fe iron^{++}, x mean of four determinations, C % coefficient of variation).

Transect	Depth	H_2O%		N_{tot}		C_{org}		P_{tot}			Na		Mn		K		Ca		Mg		Fe	
	m	$\bar{x}$	C%	$\bar{x}$	C%	$\bar{x}$	C%	$\bar{x}$	C%	C/N	$\bar{x}$	C%	$\bar{x}$	C%	$\bar{x}$	C%	$\bar{x}$	C%	$\bar{x}$	C%	$\bar{x}$	C%
b	2.0	16.8	14.4	80.6	3.5	0.65	15.5	8.6	23.5	13.1	–	–	0.13	6.1	0.19	6.9	1.5	0.0	2.5	1.2	9.7	1.2
c	1.0	22.7	14.5	57.8	11.2	0.50	49.7	–	–	–	0.49	0.8	0.24	3.3	0.30	20.8	2.8	5.2	4.7	14.0	16.8	6.8
c	1.5	23.2	1.6	70.2	2.2	0.67	9.3	–	–	–	0.31	0.8	0.17	9.6	0.12	6.4	2.5	4.8	3.1	3.9	12.6	1.7
c	2.0	20.4	4.6	78.6	1.4	0.67	3.0	14.9	54.5	22.0	–	–	0.15	5.9	0.26	3.4	1.5	22.1	3.0	1.3	13.0	1.0
c	2.5	20.4	3.1	79.6	0.7	0.63	5.4	–	–	–	–	–	0.13	14.0	0.27	1.6	1.5	4.2	2.3	4.8	10.4	1.5
d	2.0	29.4	3.7	67.3	1.6	0.91	6.2	13.83	6.2	15.1	0.42	11.8	0.19	3.6	0.19	3.4	2.9	7.2	4.2	6.9	16.1	4.6
e	2.0	33.4	4.9	67.7	1.6	0.92	3.2	17.3	18.8	18.8	0.41	0.0	0.20	1.3	0.18	2.1	2.9	3.9	4.3	1.3	17.0	0.2
f	2.0	31.6	4.0	79.6	1.5	0.77	8.7	17.1	28.9	22.1	–	–	0.09	0.2	0.12	11.8	1.4	3.5	1.9	6.6	15.2	3.0
g	2.0	28.1	6.2	83.1	0.7	0.79	6.9	13.3	13.3	16.7	0.27	4.0	0.09	2.5	0.11	11.4	1.2	2.2	2.0	3.4	12.0	1.5

[1] Field sampling was done in the spring of 1975 in collaboration with I. J. Holopainen; most of the analyses were done by the laboratory of the Finnish Water Board (Vesihallitus).

variation (Fig. 1). Numbers were maximal at depths between 1.0 and 2.5 m, the peak being at 1.5 m. The largest numbers were found on bottoms where the sediment consisted of soft ooze with some dead plant matter. This species seems to avoid running water (transects *d* and *f* in Fig. 1), and it was not abundant on a hard sandy bottom (transect *b*). Throughout the lake the abundance of *D. stevensoni* in the depth zone studied showed similar variation from site to site, although the numbers for Pappilanlahti were slightly larger than for the lake as a whole (own unpublished observations). For those physical and chemical properties of the sediment surface that were measured no correlation with the abundance of *D. stevensoni* was found in the vertical or horizontal direction (Table 1, Fig. 1). The explaining factors are probably the biotic components of the littoral habitats.

According to McGregor (1969), *D. stevensoni* was found in Gull Lake (Michigan) at depths between 3 and 12 m, with maximum abundance at 6 m. Hagerman (1965) gave the depth of occurrence of the species as 3 m in brackish water (Gulf of Finland, salinity 5 ‰). The differences probably reflect differences in the biotic-abiotic components of the substrate of these areas. However, they also show the plasticity of the species in regard to habitat selection.

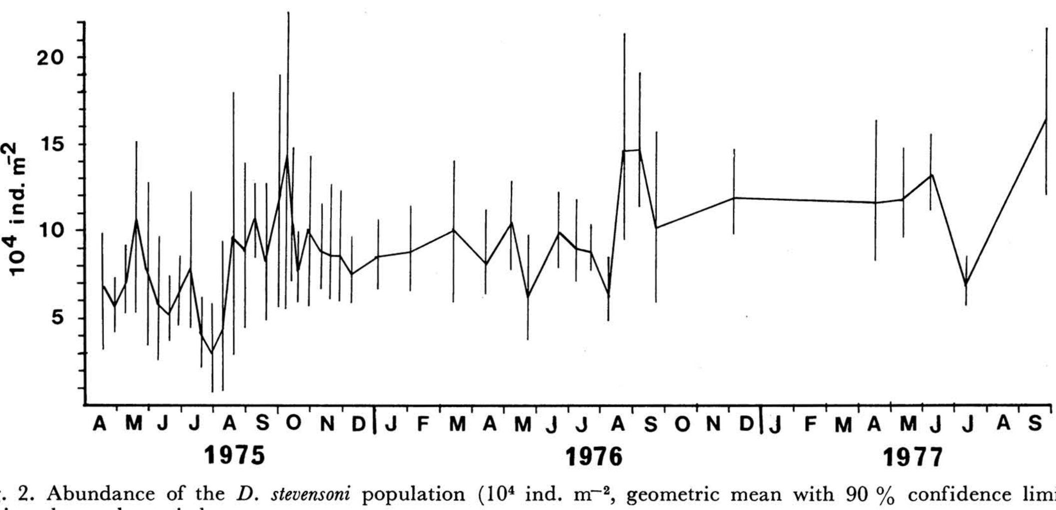

Fig. 2. Abundance of the *D. stevensoni* population (10^4 ind. m^{-2}, geometric mean with 90 % confidence limits) during the study period.

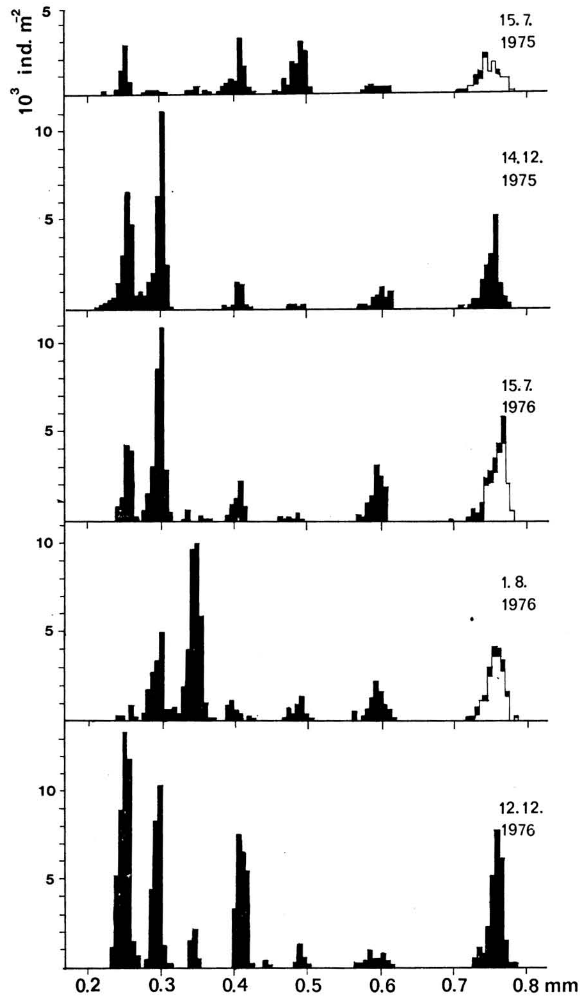

Fig. 3. Some examples of the frequency distribution (10^3 ind. m^{-2}) of the different size classes. The sampling dates are given, and the proportion of gravid adults is indicated by the white area in the last size class.

B. Abundance

Besides the small-scale fluctuation in the numbers of *D. stevensoni* a seasonal trend can be seen. During the early summer months (June-July) the numbers decrease but start to increase when the reproductive period ends (August-September) and the first juveniles (3rd instar, see below) are released into the sediment (Fig. 2). The minimum number observed was about 30 000 ind. m^{-2} (July 1975) before the release of the young, and the maximum was about 160 000 ind. m^{-2} (September 1977) just after the release of the young. During the winter the population size remains more or less constant. During the whole study period there was little variation in population density (Fig. 2). The abundance values and the annual fluctuation in numbers are in accordance with the observations of Holopainen & Paasivirta (1977).

C. Life cycle

A typical feature of the *D. stevensoni* population in Pääjärvi was the clear occurrence of distinct size classes throughout the study period (Fig. 3). Length measurements made during the entire study period were used to determine the modes and ranges of these size classes. Nine size classes were distinguished (Table 2). Seven of these were observed to live freely in the sediment but the two smallest were found only within the carapace of the largest size class. The size classes agree with the body lengths for each instar of this species given by Kesling (1951). Thus, henceforth the size classes are referred to as instars, from 1st to 9th, the last referring to the adults (Klie 1933). The rations between the body lengths of a larger instar and the next smaller instar (*i.e.* 9th/8th, 8th/7th,..., 2nd/1st) give values ranging from 1.15 to 1.33 (mean 1.24). This is also in accordance with Kesling's (1951) data (Table 2). According to Hutchinson (1959), a ratio of 1.3 (1.2—1.4) in length measurements is necessary for the coexistence of animal species utilizing the same food resource. Here the ratio 1.24 thus implies minimized intraspecific competition between the

Table 2. The sizes (in mm) of the different instars of the ostracod *D. stevensoni*. For each instar the length range and the modal class are given; ratio = the ratio between the $(i + 1)$th and ith instar. Kesling's (1951) results are included for comparison.

Instar	Size lower	Size mode	Size upper	ratio	Kesling 1951 size	Kesling 1951 ratio
1st	0.090	0.144	0.150	1.33		
2nd	0.156	0.192	0.210	1.22	0.168	1.33
3rd	0.216	0.234	0.252	1.25	0.223	1.15
4th	0.258	0.282	0.306	1.15	0.256	1.13
5th	0.312	0.324	0.348	1.20	0.290	1.21
6th	0.354	0.390	0.426	1.22	0.350	1.26
7th	0.432	0.474	0.516	1.23	0.440	1.18
8th	0.522	0.582	0.624	1.28	0.519	1.35
9th	0.654	0.744	0.780		0.700	

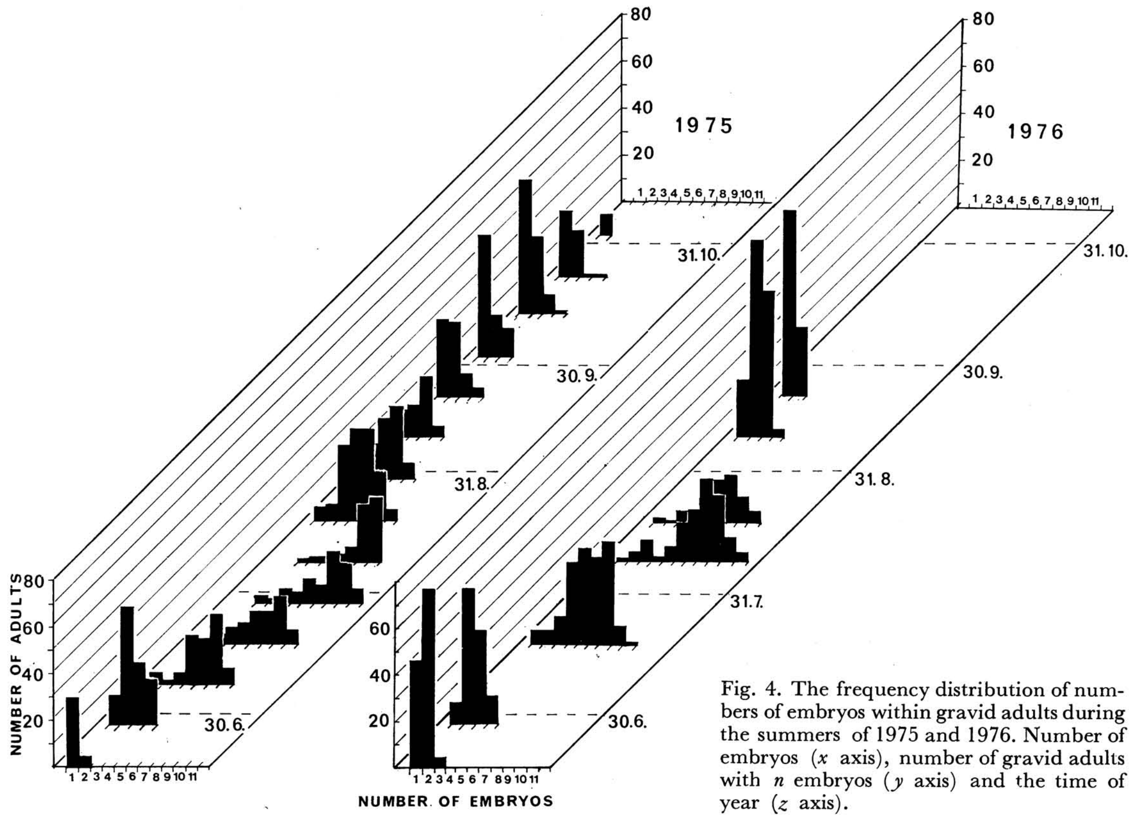

Fig. 4. The frequency distribution of numbers of embryos within gravid adults during the summers of 1975 and 1976. Number of embryos (*x* axis), number of gravid adults with *n* embryos (*y* axis) and the time of year (*z* axis).

instars; see, however, Wilson (1975) for a critical interpretation of Hutchinson's idea.

The first embryos within the carapace of adults can be observed in the second half of May, but the number of embryos within a single adult and the number of gravid adults starts to increase rapidly at the end of June. In July-August most adults are gravid and bearing more than five embryos (Figs 4 and 5). The mean number of embryos per adult in the population was calculated for successive samples; the increase was sigmoidal; in 1975 the maximum mean number of embryos was 7.8 and in 1976 it was 6.3 (Fig. 5). The proportions of adults that were gravid were similar in the two years analysed: within one month from the onset of reproduction the proportion was near 90 %, and it stayed at this value until the number of embryos began to decrease (Fig. 5).

The daily rate of increase in the mean number of embryos per adult was also calculated for both years: in 1975 it was maximally 0.20 embryos per day and in 1976 it was 0.16 (Fig. 5). These are underestimates, however, because, especially towards the end of the reproductive period, the rate is a dynamic balance between the rate of production of new embryos and the rate of release of juveniles into the sediment. The reproductive period lasted about 2 months. In mid-August the adults start to release their embryos into the sediment. This phase is rapid and is over in 1—1$^1/_2$ months. Some embryos, however, remain within the carapace over the winter and are released the following May-June, presumably because the reproduction of certain adults has been delayed. The death rate of embryos within the carapaces of adults was low: in summer 1975 I found only five dead embryos.

During the summer of 1975 a survey was made of the length distribution of the embryos within the carapaces of adults (a subsample of each successive sample). Two size classes were observed: in June-July the frequency distribution had a mode at about 0.15 mm, in August

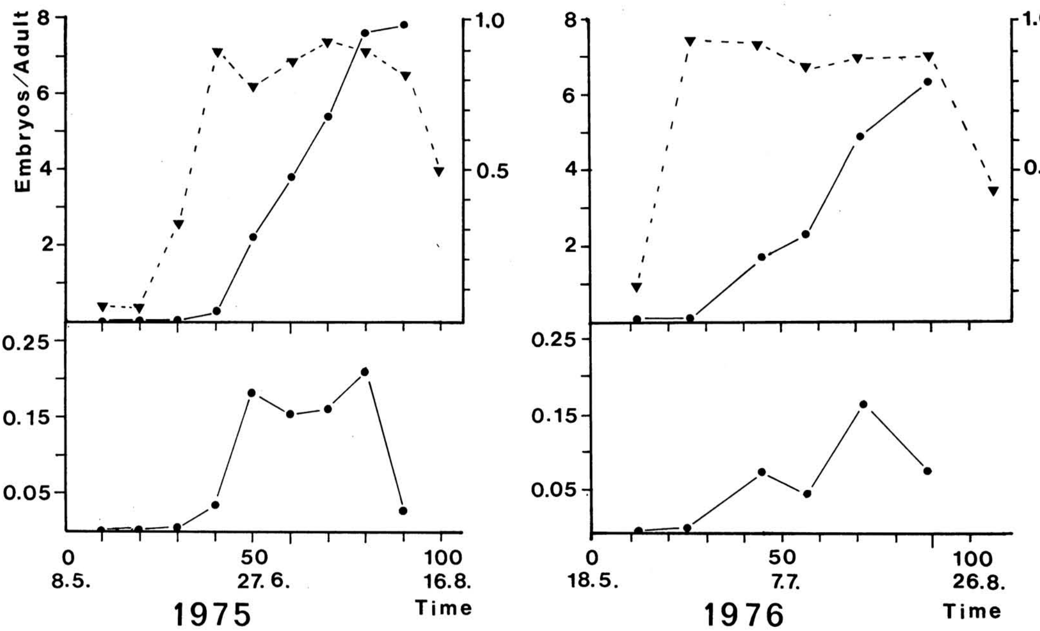

Fig. 5. Time course of the reproduction during the summers of 1975 and 1976. Upper part of the figure: mean number of embryos per adult, solid circles and lines; gravid adults as a proportion of all adults, triangles and broken lines. Lower part of the figure: Daily rate of increase (embryos/adult/day) of the population.

at about 0.19 mm (Fig. 6, Table 2). Thus, I conclude that the young shelter within the carapace during two instars, the 1st and 2nd. These are not found as free-living forms in the sediment.

Observations showed that the reproduction of *D. stevensoni* in Pääjärvi followed the same pattern as in Gull Lake (McGregor 1969).

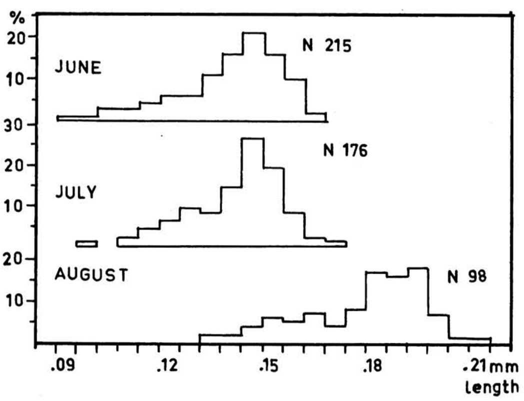

Fig. 6. Size distribution of embryos within the carapaces of adults during the summer of 1975.

According to McGregor, reproduction takes place from June to August. The maximum number of embryos within a single adult was in Pääjärvi 11, but in Gull Lake 15.

The cohort of 1975 consisted only of 1st instars until about the beginning of August (Figs 6 and 7) and then moulted to the 2nd instar. The 1st instar lasted about 40 days, the 2nd about 30—40 days. The first 3rd instar individuals were observed in mid-August, and the 4th instar began to appear at the end of that month (Fig. 7). Thus some individuals underwent the 3rd-4th instar moult within a few weeks after the appearance of the 3rd instar. In about one third of the cohort of 1975, however, the moult to the 4th instar was postponed until after the winter (Fig. 7); this was due to the low littoral water temperatures (near 0°C) in Pääjärvi during the winter. At the end of May 1976 the 1975 cohort was composed entirely of 3rd and 4th instars. Because of the winter the duration of the 3rd instar was from 1 to 10 months and that of the 4th instar about 10 months. The first 5th instar individuals were observed in June 1976, and this was a short-lasting instar: in September the 1975 cohort

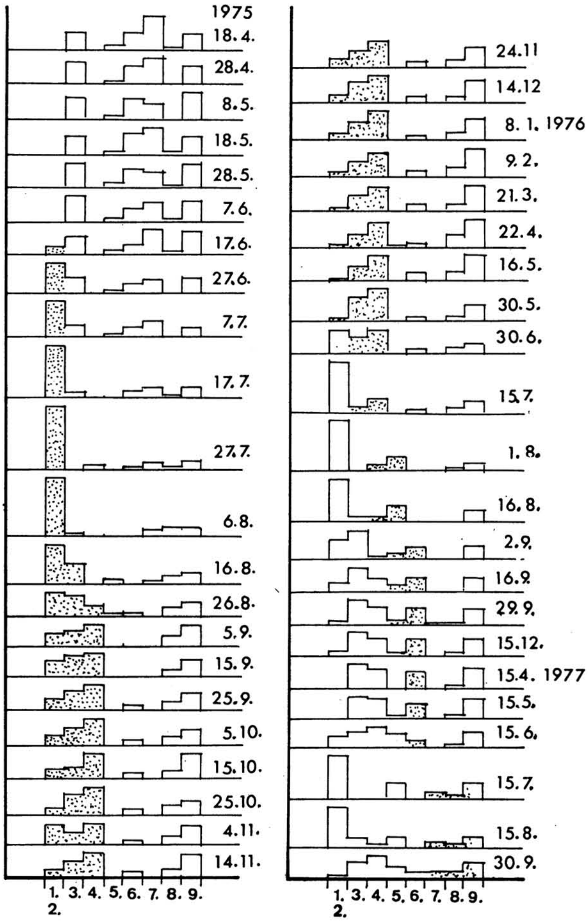

Fig. 7. Frequency distribution of different instars during the study period (the area of each histogram is 1.0). The 1975 cohort is denoted by stippling.

had moulted to the 6th instar, which lasted over the winter of 1976—1977. In the summer of 1977 this cohort reached the 7th and 8th instars, which together lasted about 3 months. The first individuals of the 1975 cohort became adults towards the end of the summer of 1977. Consequently, the life cycle of *D. stevensoni* in Pääjärvi has a duration of at least 3 to 4 years.

McGregor (1969) observed two age classes among the adults of the *D. stevensoni* population; they were separable by the number of epibionts on the carapaces. Adults in their second season carried more embryos than in their first season. In the *D. stevensoni* population of Pääjärvi no such separation could be made as there were no epibionts. However, the duration of the adult stage may be two years in Pääjärvi also. Support for this conclusion can be found from the varying annual structure of the overwintering population, and also from the strength of the cohort becoming adult (see Fig. 7). In all, the life history of this species is fairly complicated and the total life span very long for such a small animal, although it seems to be typical of some other menbers of the subclass Ostracoda: *e.g.* the life cycle of *Cyprinotus carolonensis* took 8 months, and of *Heterocypris reptans* 2 years and 2 months in a temporary pond (McLay 1978a, 1978b).

Although *D. stevensoni* is one of the most abundant meiofaunal species in the littoral of Pääjärvi, its importance energetically is not very great. It is seldom found in the stomachs of benthos-feeding fishes (M. Viljanen, pers. comm.), or in the guts of invertebrate predators (P. Paasivirta, pers. comm.). The chief importance of *D. stevensoni* is perhaps its contribution to sediment mineralization.

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