Vol. 29: 127–139, 1986 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published February 27

Prenatal mortality in a marine cladoceran, *Evadne nordmanni*

Trevor Platt[1] & Norio Yamamura[2]

[1]Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada
[2]Saga Medical School, 421-6 Nabeshima, Nabeshima-Machi, Saga 840-01, Japan

ABSTRACT: The embryology of the parthenogenetic marine cladoceran *Evadne nordmanni* Lovén is described such that an arbitrary series of developmental stages can be established. A population dynamics is developed for organisms that display the kind of paedogenesis seen in *E. nordmanni,* based on the assumption that the frequency of occurrence of a given developmental stage is an indicator of the time taken to complete it. It is then possible to determine the prenatal mortality. The equations are applied to samples of *E. nordmanni* taken from the coastal waters of Nova Scotia. It is found that prenatal mortality plays a significant role in controlling the population size of *E. nordmanni.* Evolutionary implications are discussed.

INTRODUCTION

Evadne nordmanni Lovén is a cosmopolitan marine cladoceran that occurs seasonally in large numbers in continental shelf waters, as well as in the open ocean (Gieskes 1971). On the coast of Nova Scotia it is an important, and often dominant component of the near-surface, neritic zooplankton between June and October (Platt 1977). The principal mode of reproduction in *E. nordmanni* is by parthenogenesis; developing embryos are carried in the brood pouch of the mother and are subsequently released as free-swimming, but miniature, adults which themselves already carry blastulae in their own brood pouches (Kuttner 1911). Such a life-cycle, an extreme example of paedogenesis (Onbé 1974), is adapted for high rates of population increase when conditions are favourable.

By virtue of the transparency of the carapace and its enclosed brood pouch, and of the large size of the embryos, it is a relatively simple matter in preserved specimens to count the number of embryos and to judge their stage of development. Thus, if an absolute time-scale for development could be established independently, *Evadne nordmanni* would seem to be the ideal organism for estimation of reproductive rate from field samples according to standard methods (e.g. Edmondson 1955, 1960, Hall 1964). Writing on freshwater cladocera, however, Threlkeld (1979a) has stressed the potential error in estimates of birth rate that is incurred by ignoring egg mortality. Moreover, Bainbridge (1958), Gieskes (1970) and Platt (1977) have presented preliminary evidence of prenatal mortality in the developing embryos of *Evadne nordmanni.*

In this paper we first describe the embryology of *Evadne nordmanni* and define the various developmental stages that will be used in the subsequent treatment; then we present a mathematical description of the population dynamics of embryos for organisns with the type of parthenogenetic life cycle exhibited by *E. nordmanni;* next, we illustrate the application of the model to calculation of the prenatal mortality of *E. nordmanni* in the inshore waters of St. Margaret's Bay, Nova Scotia, using weekly samples collected during summer 1968; finally, we discuss the importance of this component of mortality for fluctuations in the population density of *E. nordmanni.*

METHODS

Sampling. The cladocera were sampled weekly from June to October 1968 in St. Margaret's Bay, Nova Scotia at Station A (44° 35′ N, 64° 02′ W). A Clarke-Bumpus net, 12.5 cm in diameter, with mesh-size 153 μm was used. Horizontal tows of 10 min duration (speed ≈ 2 kn) were made at 1, 5, 10, 15, and 20 m. The volume of water filtered (calibrated) was from 1 to 20 m^3 depending on conditions. Depth of towing was

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verified by a Benthos® depth recorder attached to the wire below the net. All tows were made in duplicate.

The samples were preserved immediately in 5 % formalin. Later, their volume was made up to exactly 100 ml with 5 % formol-saline as follows. When brought back from the field the animals usually had settled to the bottom of the jar. If not, this was remedied by adding 1 drop of dilute detergent solution, followed by vigorous shaking. Most of the supernatant formol-saline was pipetted off and the animals transferred to a 50 ml cylinder. The volume of animals and fluid was measured, the volume required to make up 100 ml measured out, and used to wash the animals back into the jar.

Samples were examined using a compound microscope at 100×, total magnification, and a Sedgwick-Rafter cell (minus cover-glass). Sub-samples of exactly 1 ml were dispensed in the cell using a calibrated automatic pipette. A drop of the detergent solution had been added to the jars to prevent the animals clinging to the sides of the pipette.

For population counts at least 5 duplicate counts were made on each sample. All samples were counted. The counts were adjusted to give the number of individuals per cubic metre at each depth and integrated over the 20 m water column using the method of Platt & Irwin (1968) to give a population figure for each sampling day.

Embryonic stages. The embryological development of a related form, *Penilia avirostris,* has been well described by Della Croce & Bettanin (1965) and by Sudler (1899). Della Croce & Bettanin (1965) also divided the embryonic development into stages. Since the embryos of *Evadne nordmanni* are similar in appearance and development to those of *P. avirostris,* the stages were chosen to be consistent with those outlined by Della Croce & Bettanin (1965).

Embryos for description were obtained by placing several preserved adults on a microscope (7.5 cm × 2.5 cm) slide in a drop of formol-saline. Three small spots of silicone grease were arranged on the slide around the liquid drop: these would provide support for a cover-slip after the animals were dissected. The embryos were removed from the brood pouch using very fine needles under a dissecting microscope. A cover-slip was mounted and the preparation examined in a compound microscope at 400× magnification. It was possible to reorient the embryos in 3 dimensions by tapping gently on the cover-slip. The specimens were photographed in a Zeiss photo-microscope, and measured by comparing the photographs against pictures of a micrometer slide photographed at the same magnification. Drawings were made by projecting an image of the embryo onto drawing paper and tracing its outline. Some 150 adult animals were examined.

Other measurements. For every sampling day, 100 animals from the 1 m sample were examined, the body length measured and the number and stage of the embryos were determined. The presence of resting eggs and of male specimens was noted as appropriate. Body length was measured from the caudal furca to the point of attachment of the second antennal muscles to the carapace (Bainbridge 1958), using an eyepiece micrometer.

DEVELOPMENTAL STAGES

Synopsis of embryology

The development of *Evadne nordmanni* (Fig. 1 to 5) has similarities with that of *Penilia avirostris* (described by Sudler 1899, and Della Croce & Bettanin 1965) and that of *Podon leukarti* (described by Gieskes 1970, who also extended his remarks to the development of *E. nordmanni*). Della Croce & Bettanin (1965) divided the development of *P. avirostris* into distinct stages. In describing the embryology of *E. nordmanni,* we have followed their general approach (Fig. 1), but have preferred to distinguish fewer stages (Fig. 1).

The eggs are rounded in shape, approximately 70 µm in diameter. The number of eggs found in the brood pouch varied from 1 to 21, more being found early in the season. As they develop, the eggs elongate, then the head end broadens and the embryo appears T-shaped. At this stage, the second antennae start to form as in Fig. 1, Stage 2. As the embryo increases in length, the mandibles start to develop, and the second antennae lengthen but do not grow past the anterior end of the thoracic region until the thoracic region has differentiated.

The first antennae are clearly visible as 2 protrusions slightly anterior and dorsal to the second antennae (Fig. 1, Stage 3). The upper lip of the embryo is visible now and grows over the mandibular and maxillary region. The second antennae bifurcate. The differentiation of the thoracic region starts at the anterior end, with 4 thoracic segments forming in sequence. The segments elongate forming 4 pairs of legs which bifurcate into endo- and exopodites (Fig. 1, Stage 4). The maxillae are now visible as are the setae on the second antennae. The digestive tract and the rudiments of the large compound eye can be seen clearly. Dorsally, the carapace appears as 2 more-or-less horizontal outgrowths just above the first pair of legs. All the structures found in the adult now seem to be present, and the embryo develops to assume the form of a miniature adult. If the embryo is female, as is usually the case, the ovary is active and parthenogenetic eggs are laid into the brood pouch before the embryos are released

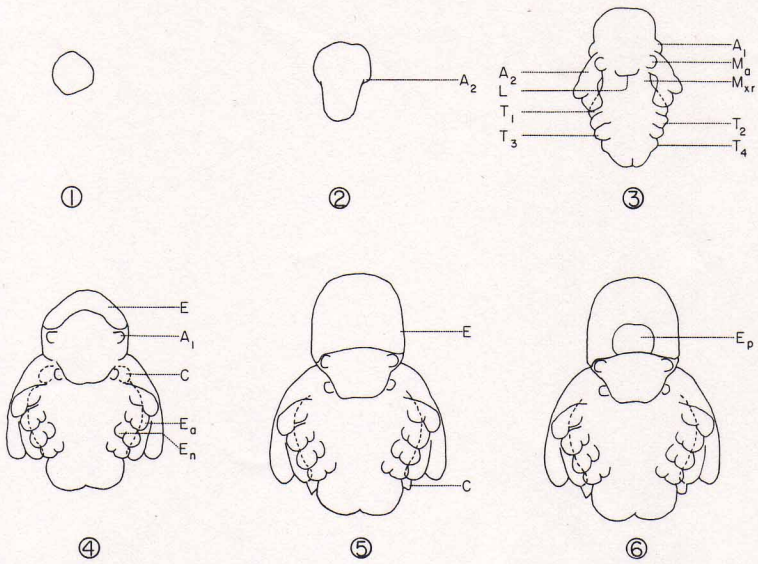

Fig. 1. *Evadne nordmanni.* Arbitrary developmental stages as defined and used in this study. A_1: first antenna; A_2: second antenna; C: carapace; E: eye; E_a: exopodite; E_n: endopodite; E_p: eye pigment; M_a: mandible; M_{xr}: mandibular and maxillary region; T_1 to T_4: thoracic segments

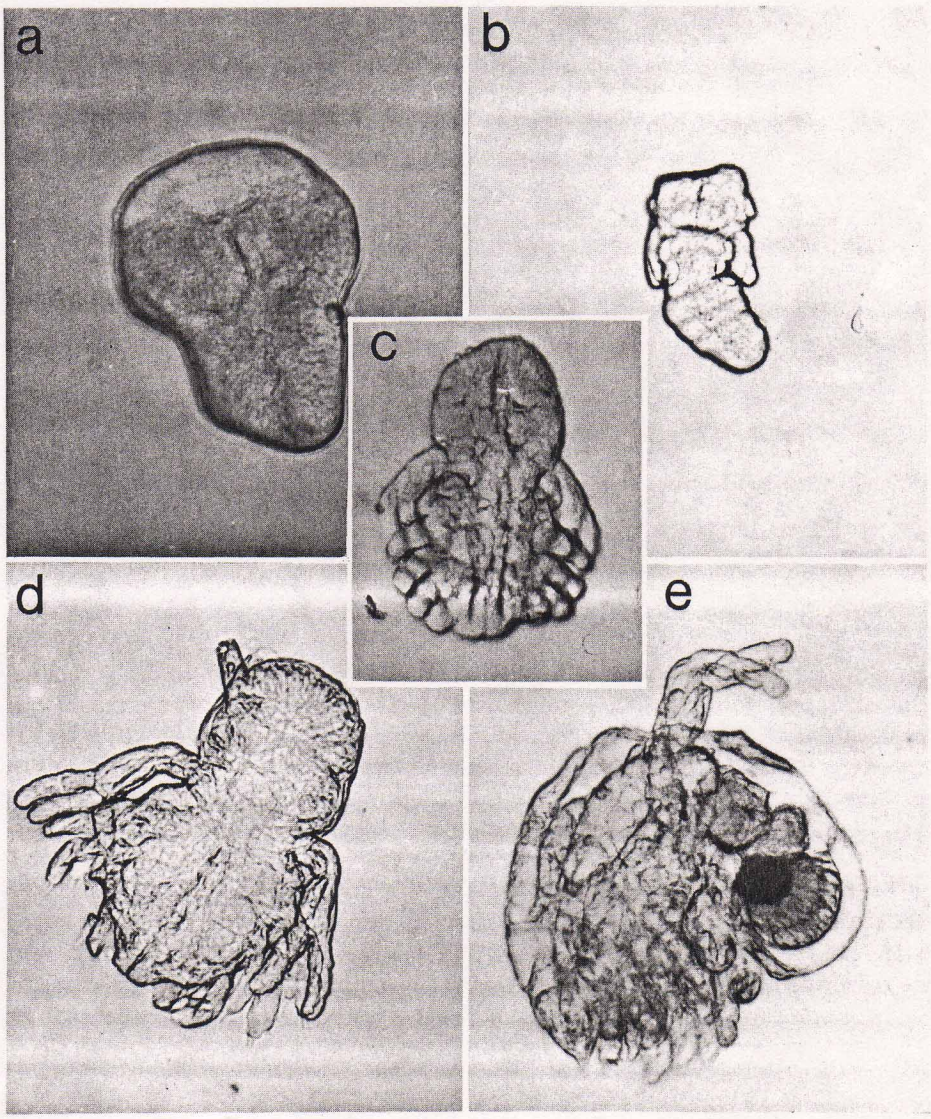

Fig. 2. *Evadne nordmanni.* Parthenogenetic embryos showing Stages 2 to 6. Magnification 208×. (a) Stage 2; (b) Stage 3; (c) Stage 4; (d) early Stage 5; (e) Stage 6

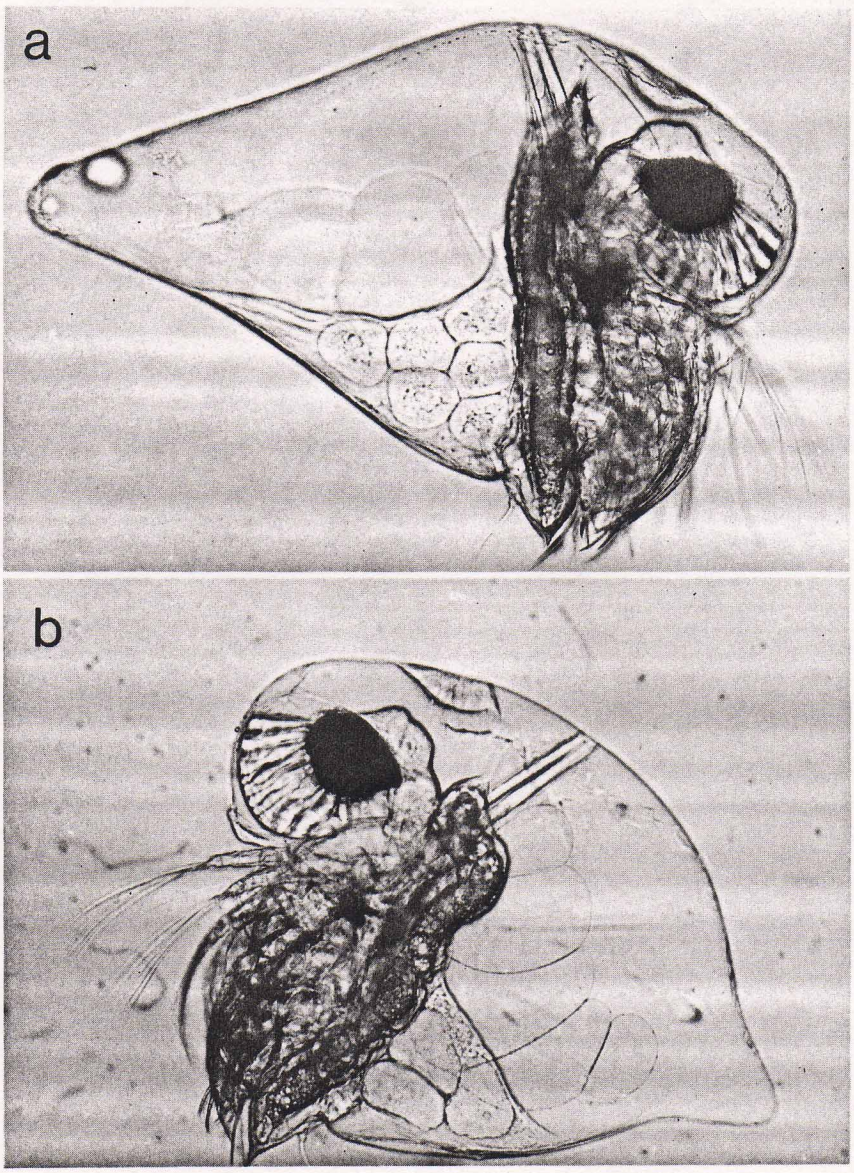

Fig. 3. *Evadne nordmanni.* Adult females with (a) 6 eggs (Stage 1). (b) 3 Stage 2 embryos in their brood pouches. 135×

from their mother's carapace. Kuttner (1911) stated that the eggs pass into the brood pouch just as the eye pigmentation becomes visible.

Definition of developmental stages

The embryonic development was divided into 6 stages based on external morphology (Fig. 1). These stages are arbitrary and convenient divisions of what is in reality a continuous developmental process. For routine staging of the broods of large numbers of adult female *Evadne nordmanni,* easily distinguished characters were chosen as diagnostic criteria. These were (i) the formation of the head region and the second antennae, (ii) the development of the thoracic region, and (iii) the development of the eye. They are cross-referenced against the stages described by Della Croce & Bettanin (1965) for the development of *Penilia avirostris* which appear in Roman numerals, in parentheses, at the appropriate places in the sequence described below.

Stage 1 (Fig. 3a). The egg develops up to the differentiation of the head and second antennae, remaining spherical in shape or only slightly irregular with no visible signs of differentiation (Stages I to II of Della Croce & Bettanin 1965).

Stage 2 (Fig. 2a & 3b). The embryo is elongated and T-shaped with the anterior end forming the crossbar of

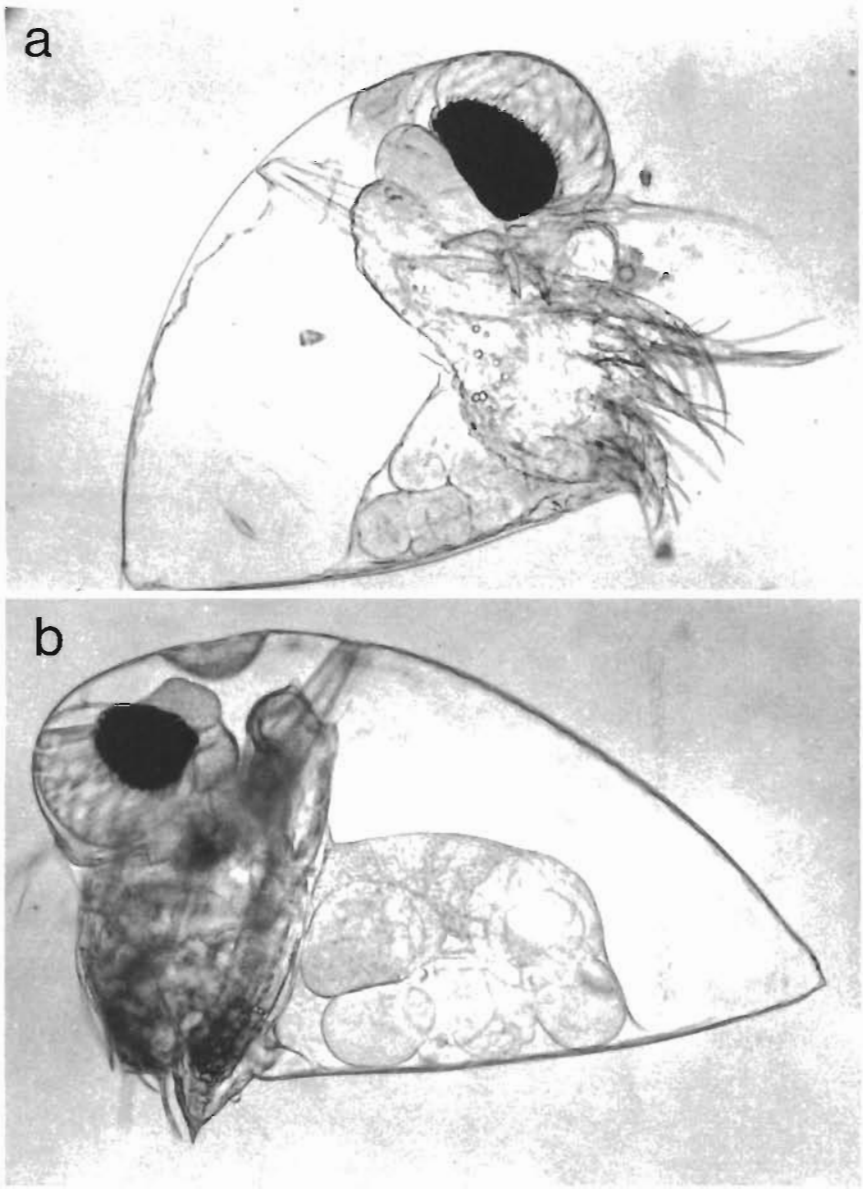

Fig. 4. *Evadne nordmanni*. Adult females with (a) 3 Stage 3 embryos. (b) 3 Stage 4 embryos in their brood pouches. 135×

the T. The head is differentiating. The first antennae can be seen as 2 protrusions anterior to the second antennae. The second antennae develop during this stage and the mandibles form at the end of the stage. No thoracic segments are visible. The mandibular and maxillary regions are forming (III to IV).

Stage 3 (Fig. 2b & 4a). The embryo has elongated further. The first and second antennae are visible. The second antennae have bifurcated and at least 1 thoracic segment can be seen. The number of thoracic segments vary from 1 to 4, depending on the stage of development. At the end of this stage all 4 segments have formed but the legs are not yet seen (V to X).

Stage 4 (Fig. 2c & 4b). The rudimentary eye has appeared. The legs are now visible growing from the thoracic segments, are folded on the ventral side of the thorax, and have bifurcated. The second antennae reach the third thoracic segment and bear setae. The carapace has started to form (XI).

Stage 5 (Fig. 2d & 5a). The caudal furca can now be seen. The eye is fully developed, but no pigment is present. The embryo has flexed and the thoracic legs curve anteriorly as in the adult. The carapace is complete and the ovaries can be seen (XII).

Stage 6 (Fig. 2e & 5b). The embryo now appears to be fully developed and the eye is pigmented. Pathenogenetic eggs have passed into the brood pouch (XIII).

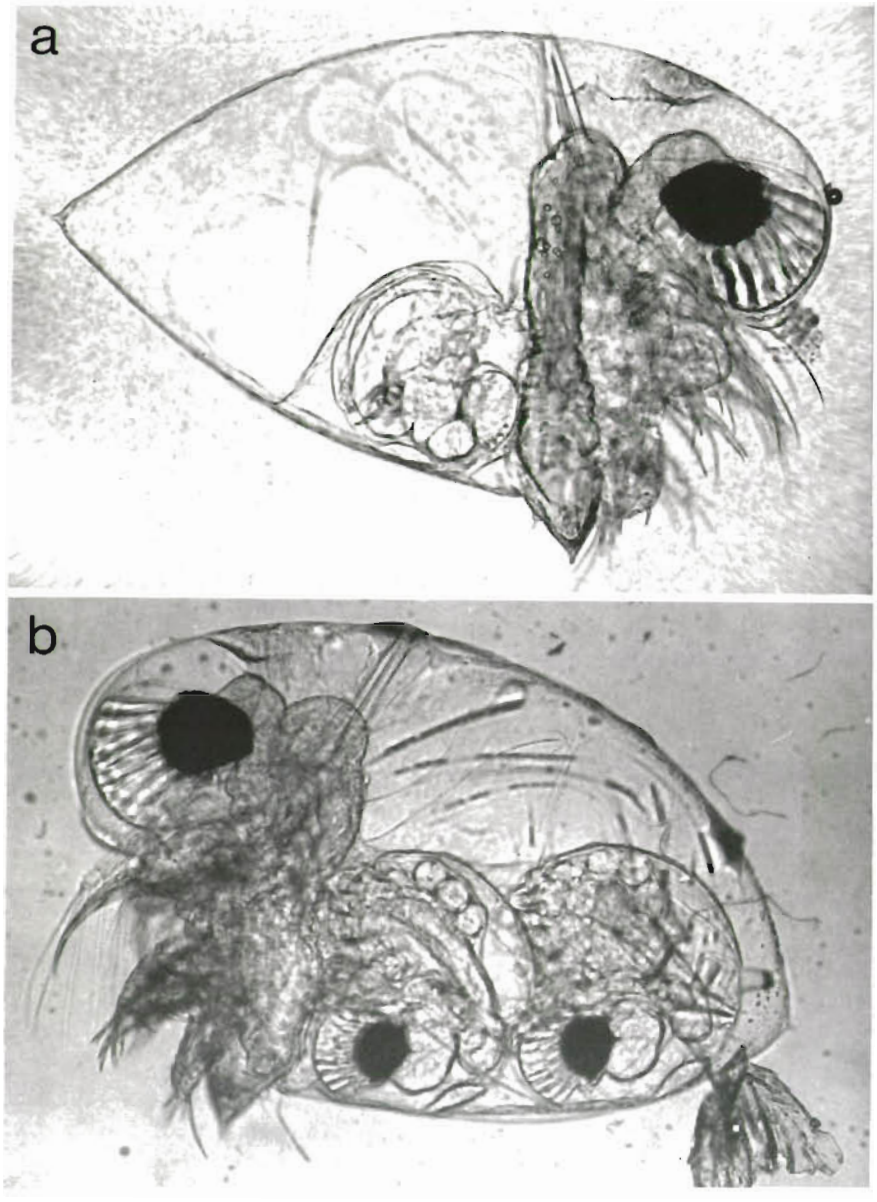

Fig. 5. *Evadne nordmanni*. Adult females with (a) 1 Stage 5 embryo. (b) 2 Stage 6 embryos in their brood pouches. Both are fully developed and have parthenogenetic eggs in their brood pouches. 135×

Mathematical description of relative duration of developmental stages

Let a be the total development time, and x be the age of each individual. We assume that individuals reaching age a release their offspring and return to age 0, i.e. they begin incubating a new brood of embryos, the offspring also falling initially into age class 0. This is justified because we know that when released by the adults, at the time of moulting, the embryos themselves already carry blastulae in their own brood pouches (Kuttner 1911, Gieskes 1970, Onbé 1974, Platt 1977). In other words the age class of the parthenogenetic females can be specified by the age (developmental stage) of the embryos it contains.

The number of individuals in an age interval $(x, x + dx)$ at time t is denoted by $n(x, t)\,dx$. The age distribution, $n(x, t)$, satisfies a von Foerster type equation (Oster 1978);

$$\frac{\partial n(x, t)}{\partial t} = -\frac{\partial n(x, t)}{\partial x} - m(x)\, n(x, t) \text{ for } 0 < x < a, \quad (1)$$

with a particular boundary condition,

$$n(0, t) = (b_f + 1)\, n(a, t), \quad (2)$$

where $m(x)$ = instantaneous mortality at age x; b_f = average number of embryos per female at age a.

Strictly speaking, the solution of (1) and (2) will not approach a stable age distribution for an arbitrary

initial distribution. However, if the moulting period varies over some small interval including a, a stable age distribution will be reached and Eqn (2) is approximately correct. We use Eqns (1) and (2) with this limited interpretation.

The final age distribution is

$$n(x, t) = \tilde{n}(x) \cdot \exp\{rt\} \tag{3}$$

where

$$\tilde{n}(x) = \tilde{n}(0) \exp\{-rx - \int_0^x m(x)\,dx\} \tag{4}$$

From (3) and (4) with the boundary condition (2), we get the rate of increase, r;

$$r = \frac{1}{a}\ln(b_f + 1) - \frac{1}{a}\int_0^a m(x)\,dx. \tag{5}$$

This is a solution of the Euler equation (Lotka 1925) $\int_0^a \exp\{-rx\}\, b(x)\, l(x)\,dx = 1$ when $b(x) = (b_f + 1)\,\delta(x-a)$, where $l(x) = \exp\{-\int_0^x m(x)\,dx\}$ and $\delta(\cdot)$ is a delta function. The first term of the right hand side of Eqn (5) is the instantaneous birth and the second term is average mortality over the total development time. Substituting (5) into (4), the explicit form of the age distribution is

$$\tilde{n}(x) = \tilde{n}(0) \exp\{-\ln(b_f+1) \cdot \frac{x}{a} - (\int_0^x m(x)\,dx - \frac{x}{a}\int_0^a m(x)\,dx)\} \tag{6}$$

This equation means that the stable age distribution is invariant when the mortality varies uniformly with age. Especially when the mortality is independent of the age, the age distribution is not influenced by the magnitude of the mortality;

$$\tilde{n}(x) = \tilde{n}(0) \exp\{-\ln(b_f+1)\frac{x}{a}\} = \tilde{n}(0)\,(b_f+1)^{-x/a} \tag{7}$$

If the total development time is divided in n stages at ages $x_0 = 0, x_1, x_2, \ldots, x_n = a$, the probability of finding the ith stage is

$$p_i = \frac{\int_{x_{i-1}}^{x_i} \tilde{n}(x)\,dx}{\int_0^a n(x)\,dx} \tag{8}$$

and the cumulative probability is

$$\Phi_i = \sum_{j=1}^{i} p_j = \frac{\int_0^{x_i} \tilde{n}(x)\,dx}{\int_0^a \tilde{n}(x)\,dx} \tag{9}$$

When the mortality is constant through the development, applying (7) to (9),

$$\Phi_i = \frac{b_f+1}{b_f}\,[1 - \exp\{-\ln(b_f+1) \cdot \frac{x_i}{a}\}] \tag{10}$$

Rewriting (10), we obtain a representation of relative terminal age of the ith stage, y_i, in terms of the cumulative frequency Φ_i;

$$y_i = \frac{x_i}{a} = \frac{-1}{\ln(b_f+1)} \cdot \ln\left(1 - \frac{b_f}{b_f+1} \cdot \Phi_i\right) \tag{11}$$

The relative duration of the ith stage is

$$\tau_i = y_i - y_{i-1} \tag{12}$$

If b_f is small, we get $y_i \simeq \Phi_i$ and therefore $\tau_i \simeq p_i$. In this case, the frequency in each stage is almost equal to the relative duration of the stage because the age distribution is nearly uniform.

Duration of developmental stages

It is a central assumption of the analysis followed here that the relative duration of a particular embryonic stage is correlated with the frequency of occurrence of that stage as seen in embryos examined from a large number of adult females.

Histograms were constructed for the frequency of occurrence of embryonic stages in each sample. In addition to the 6 stages defined above, 3 other categories were used. These were: first, the presence of amorphous eggs or embryos (Fig. 6) which presumably had failed to develop completely after passing into the brood pouch (Bainbridge 1958); second, the presence of a resting egg (Fig. 7a); and the third possibility, that the adult was a male rather than a female (Fig. 7b). The

Table 1. Relative occurrence of females with embryos of a given stage

Data #	Date	Stage 1	2	3	4	5	6	Total #
1	12 Jun	21	20	17	31	5	6	100
2	20 Jun	17	13	36	23	9	1	99
3	26 Jun	27	10	37	16	9	0	99
4	10 Jul	24	12	21	28	12	0	97
5	18 Jul	15	7	39	11	25	2	99
6	24 Jul	21	9	26	33	4	1	94
7	1 Aug	32	9	26	18	13	0	98
8	8 Aug	56	12	16	9	7	0	100
9	15 Aug	36	8	22	19	11	1	97
10	21 Aug	40	14	19	18	6	0	97
11	29 Aug	18	9	37	27	4	1	96
12	5 Sep	68	1	10	13	3	0	95
13	13 Sep	23	6	18	25	13	0	85
14	18 Sep	38	5	18	15	18	0	94
15	26 Sep	22	17	24	13	6	7	89
16	30 Oct	12	4	17	28	14	24	97

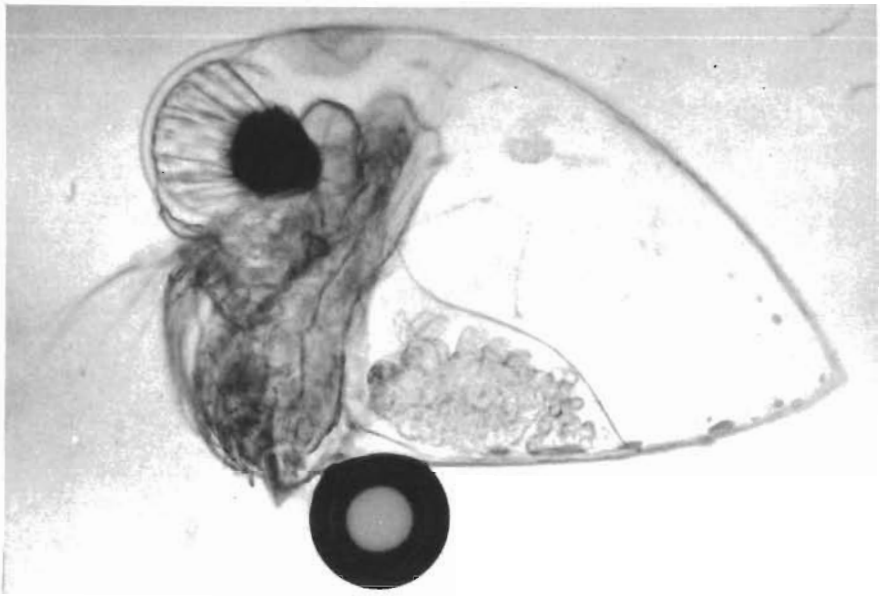

Fig. 6. *Evadne nordmanni.* Adult female with a disintegrating embryo(s)? in her brood pouch

frequency distributions of embryonic stages are presented in Platt (1977: Fig. 13 to 16).

The first question that arises is whether or not the frequency of occurrence of the stages (Table 1) is consistent among the 16 samples. The nonparametric Kendall concordance test was made on the frequency rankings under the Null Hypothesis that the 16 sets of rankings are independent (Siegel 1956). We found $W = 0.67$ with $S = 4480$, such that the Null Hypothesis could be rejected with $P < 0.01$. Thus the frequency of occurrence of stages is consistent from sample to sample and pooling of samples is justified. Stage 3 is most frequent, followed by Stages 1, 4, 5, 2, and 6.

Estimation of relative duration of developmental stages

The seasonal change in abundance of *Evadne nordmanni* is shown in Fig. 8, based on samples from St. Margaret's Bay taken about every week from May to October in 1968 (Platt 1977). The population increases until early summer and decreases rather suddenly in autumn. From each sample from 1 m depth (12 Jul to 3 Oct), 100 individuals were inspected and classified into 1 of 6 developmental stages, and the number of embryos in each individual counted.

All the individuals had embryos and therefore could be classified into the 6 stages, except for a small

Table 2. The number of embryos per individual for each stage

Week	Date	Stage					
		1	2	3	4	5	6
1	12 Jun	10.10 ± 5.41	8.10 ± 2.47	9.41 ± 3.27	9.52 ± 1.21	10.00 ± 0.89	9.17 ± 2.27
2	20 Jun	10.24 ± 3.08	8.46 ± 2.21	8.28 ± 3.49	8.35 ± 2.16	8.56 ± 3.65	4.00
3	26 Jun	9.22 ± 2.42	8.70 ± 1.55	8.30 ± 1.47	9.13 ± 2.09	7.67 ± 1.94	–
4	10 Jul	4.54 ± 1.50	4.17 ± 0.80	3.95 ± 0.84	3.18 ± 0.97	3.25 ± 0.92	–
5	18 Jul	4.07 ± 1.24	3.14 ± 1.25	2.85 ± 1.08	2.18 ± 0.94	2.04 ± 0.66	1.50 ± 0.50
6	24 Jul	3.95 ± 0.95	2.33 ± 0.47	2.81 ± 1.04	2.48 ± 0.99	1.75 ± 0.43	1.00
7	1 Aug	4.38 ± 0.96	3.22 ± 0.79	3.42 ± 0.84	2.78 ± 0.85	2.92 ± 1.07	–
8	8 Aug	3.71 ± 0.94	3.08 ± 0.86	2.38 ± 1.05	2.11 ± 0.87	1.86 ± 0.64	–
9	15 Aug	3.44 ± 1.01	2.63 ± 0.86	2.45 ± 0.89	2.63 ± 1.09	2.55 ± 0.78	3.00
10	21 Aug	4.05 ± 0.86	3.79 ± 1.01	3.26 ± 0.96	2.94 ± 0.78	2.17 ± 0.69	–
11	29 Aug	4.56 ± 1.12	3.33 ± 0.47	2.83 ± 0.94	2.78 ± 0.79	3.00 ± 0.71	2.00
12	5 Sep	4.41 ± 0.88	4.00	3.70 ± 0.78	3.31 ± 0.61	3.67 ± 1.25	–
13	13 Sep	4.09 ± 0.88	2.67 ± 0.69	2.61 ± 0.76	2.08 ± 0.74	1.92 ± 0.47	–
14	18 Sep	4.26 ± 0.64	5.00 ± 1.17	3.33 ± 0.88	2.53 ± 0.81	2.61 ± 0.68	–
15	26 Sep	2.91 ± 0.95	1.94 ± 0.64	2.08 ± 0.57	1.31 ± 0.46	1.00 ± 0	1.00 ± 0
16	3 Oct	4.33 ± 0.62	3.25 ± 0.43	3.00 ± 0.59	2.04 ± 0.57	1.79 ± 0.77	1.29 ± 0.45

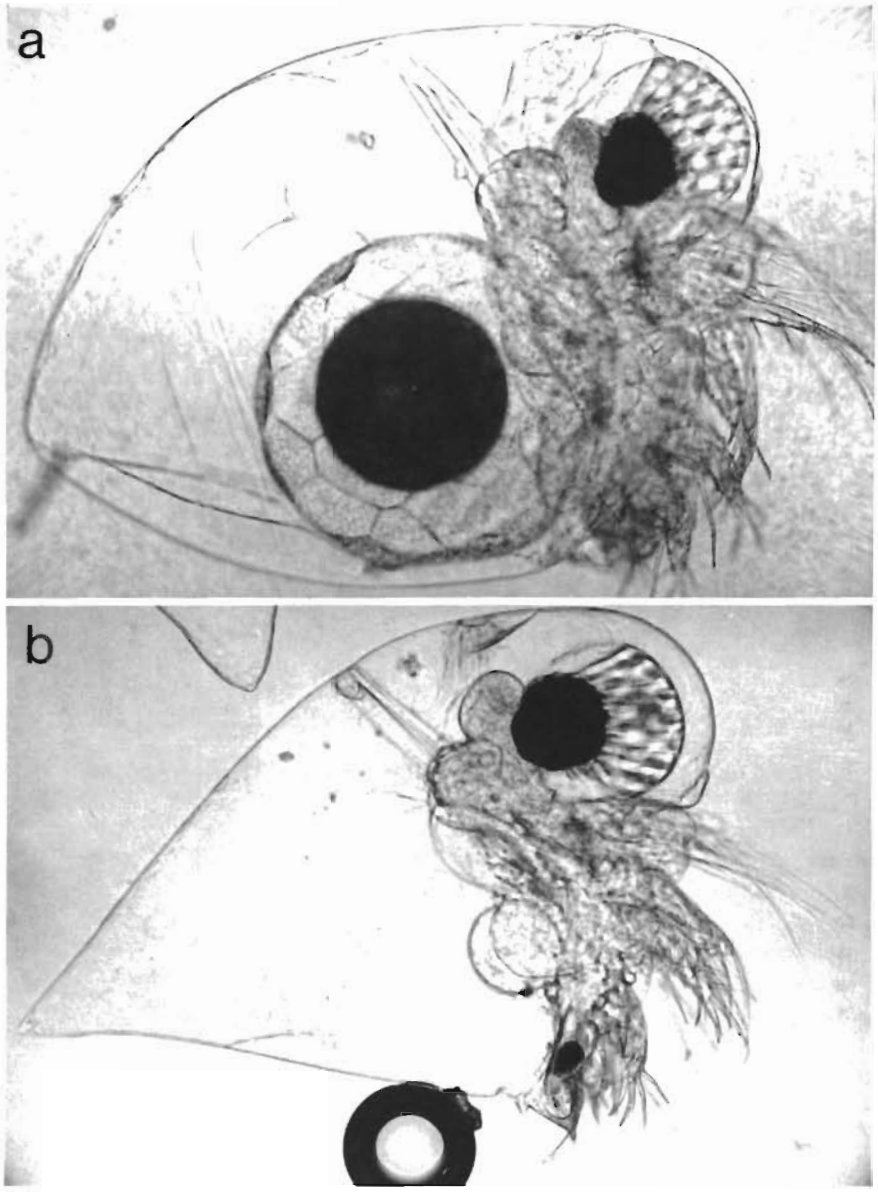

Fig. 7. *Evadne nordmanni*. (a) Adult female with a developing resting (sexual) egg. (b) Adult male

number of males, those having resting eggs, and those having amorphous eggs. The frequency of the 6 developmental stages and the average number of embryos per female in such stage are given in Table 1 and Table 2, respectively.

The following analysis is based on the average frequency of occurrence from 10 July to 18 September; the abundance of animals in this period is uniformly high, and the number of early stage embryos relatively constant. Since the frequency of occurrence of the 6th stage was very small in almost all samples, we pooled the 5th and 6th stages into a composite stage.

The average frequency in each stage and the cumulative frequency are shown in Table 3. The embryo number at age a, b_i, in Eqn (11), was given by the average number of embryos per female in the 5/6th stage in the same period from 10 July to 18 September (Table 2). The calculated value is 2.4. We have assumed here that the average frequency distribution represents the stage distribution deduced from a stable age distribution with the parameter value, b_i, which is the average number of embryos in the final stage.

From Eqn (11) and (12), the relative terminal age, y_i, and the relative duration, τ_i, of each age are calculated and shown in Table 3.

In the fresh water cladoceran *Daphnia*, the relative duration of developmental stages of the embryos is surprisingly constant in many different species (Threlkeld 1979a), though the absolute duration depends on temperature (Bottrell 1974, Bottrell et al. 1976). We

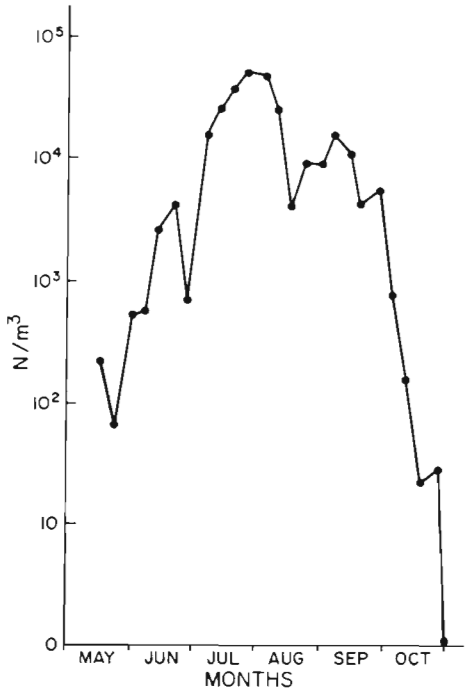

Fig. 8. *Evadne nordmanni*. Abundance: seasonal variation in 1968, St. Margarets Bay, Nova Scotia

have therefore assumed that the relative duration is also constant through seasons also in the marine cladoceran *Evadne*.

The estimated values of the relative duration will be only approximate, but they are good enough as tentative estimates for analysing the prenatal mortality of the embryos.

Change in number of embryos

In Table 2, we can see a characteristic pattern of change in the number of embryos through developmental stages. In the 3 samples from 12 to 26 June, the average number of embryos in all stages is uniformly high, while in the rest of the samples (10 July to 3 October), the embryo number in the first stage is much smaller than that of the earlier samples and there is a general tendency for number to decrease with increasing age.

The standard deviation of the embryo numbers is so small (ranges of the embryo numbers in first and last stages do not overlap in most of the samples) that the decrease of the average number of embryos could not be interpreted as resulting from a higher embryonic mortality in those individuals with a higher number of Stage 1 embryos. Therefore, we can conclude with confidence that there is a finite prenatal mortality of embryos themselves. The seasonal changes in the number of embryos in the 1st stage, b_1, and in the 5/6th stage, $b_{5,6}$, are shown in Fig. 9.

Next, we estimate the prenatal mortality by the least squares method, as the slope of the logarithmic regression of the number of embryos on the mid-time points

Table 3. Average frequency of occurrence and relative duration of each stage

	1	2	3	4	5,6
p_i	0.35	0.09	0.24	0.20	0.12
Φ_i	0.35	0.44	0.68	0.88	1.00
y_i	0.23	0.30	0.54	0.81	1.00
τ_i	0.23	0.07	0.24	0.27	0.19
t_i	0.12	0.27	0.42	0.67	0.90

where

$\Phi_i = \sum_{j=1}^{i} p_i$

Φ_i is cumulative probability of occurrence up to the ith stage

$b_f = 2.41$, $y_i = \frac{-1}{1.23} \ln (1-0.707\ \Phi_i)$

where b_f is the average number of embryos per female at age a

$\tau_i = y_i - y_{i-1}$

τ_i = relative duration of the ith stage

$t_i = (y_{i-1} + y_i)/2$

p_i = probability of finding the ith stage

y_i = relative terminal age of the ith stage

Table 4. Vital statistics of adult cladoceran populations by weeks (see also Fig. 8)

Data #	Date	N_i	r_i	μ
1	12 Jun	2677	0.052	−0.16
2	20 Jun	4055	−0.290	0.25
3	26 Jun	717	0.245	0.14
4	10 Jul	22055	0.058	0.62
5	18 Jul	35120	0.055	0.86
6	24 Jul	48782	−0.005	0.87
7	1 Aug	47040	−0.092	0.64
8	8 Aug	24785	−0.264	1.08
9	15 Aug	3894	0.133	0.43
10	21 Aug	8637	0.000	0.65
11	29 Aug	8667	0.076	0.73
12	5 Sep	14770	−0.041	0.46
13	13 Sep	10637	−0.185	1.03
14	18 Sep	4220	0.029	0.75
15	26 Sep	5335	−0.288	1.25
16	3 Oct	712	−0.218	1.60
	10 Oct	155		

$r = \frac{1}{D} \ln \frac{N_{i+1}}{N_i}$

r = rate of increase (d^{-1})

D = number of days between successive samples

N_i = number in the ith sample (m^{-3})

μ = embryo mortality (d^{-1})

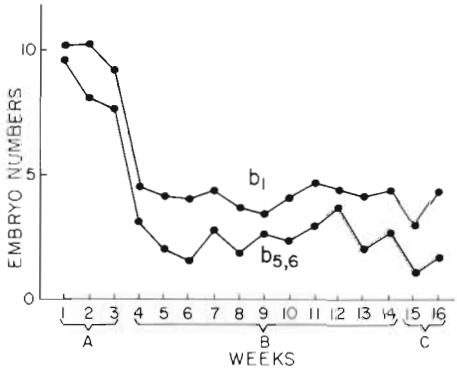

Fig. 9. *Evadne nordmanni*. Seasonal changes in embryo number, early and late stages

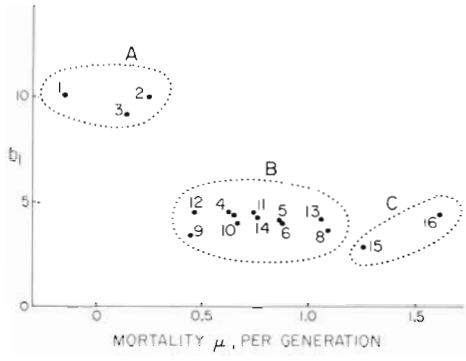

Fig. 11. *Evadne nordmanni*. Number of embryos in Stage 1 as function of prenatal mortality. Periods A, B, C are early, middle and late season as defined in text. Numbers 1 to 16 refer to weekly samples

of the developmental stages. This method is based on the assumption that the mortality is constant with age. The estimated mortality, μ, is the value per generation, and it is the product of the mortality per unit time and the development time, a.

The seasonal change in the mortality, μ, is shown in Fig. 10 and Table 4. The mortality has a tendency to increase as the season advances. We divided all samples into 3 seasonal groups. The first 3 samples (Group A) show lower mortality than any of other samples, the last 2 samples (Group C) show higher mortality than the others, and in the rest of the samples (Group B) the mortality is intermediate, but the magnitude fluctuates. In this division, Group A corresponds to high values of b_1, and Group B and C to low values of b_1. Referring to Fig. 8, we can see that Group A occurs in the population-increasing season and Group C in the population-decreasing season. In the season of Group B, the population fluctuates about a high average level.

We calculated correlations between the prenatal mortality, μ, and the number of embryos in the first stage, b_1, and between μ and the number of embryos in the last stage, $b_{5,6}$ (Fig. 11 & 12).

In Group B, there is no significant correlation between μ and b_1 ($\varrho = -0.12$, $p > 0.25$) but there is a significant correlation between μ and $b_{5,6}$ ($\varrho = -0.76$, $p < 0.005$). Considering that the standard deviation of b_1 (0.34) is considerably smaller than that of $b_{5,6}$ (0.61) in this Group ($F = 2.98$, $p < 0.05$), we can characterise the fluctuation by saying that b_1 is relatively constant and that it is the fluctuation of μ that brings about the fluctuation of $b_{5,6}$.

Fig. 13 shows the correlation between μ and the average rate of increase $\bar{r}$ of the population from 1 sampling to the next defined by

$$\bar{r} = \frac{1}{D} \ln \left(\frac{N_{i+1}}{N_i} \right) \qquad (13)$$

where N_i is the abundance in the ith sample (see Fig. 8 and Table 4) and D is the number of days between the successive samplings.

There is a negative correlation between μ and $\bar{r}$, except for 1 unusual sample in Group A for which N_3 takes an extraordinarily small value. Even in Group B, there is a significant correlation ($\varrho = -0.70$, $p < 0.01$), which means that the prenatal mortality plays an important role in the fluctuation pattern of this species. We suggest that a temporal fluctuation of some environmental conditions caused the change in the

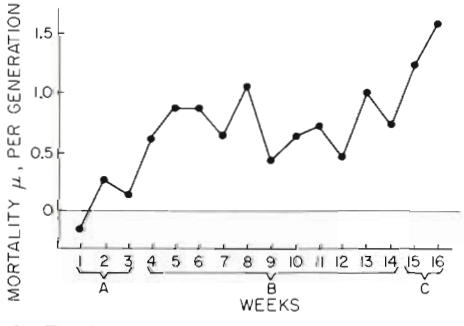

Fig. 10. *Evadne nordmanni*. Seasonal changes in prenatal mortality

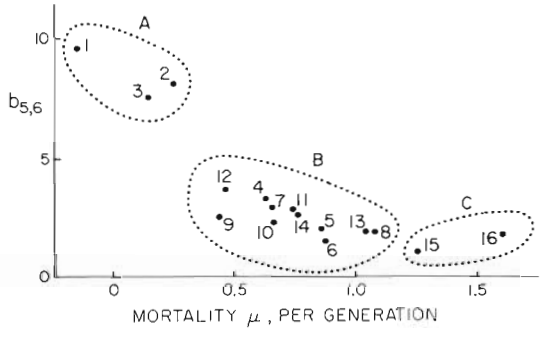

Fig. 12. *Evadne nordmanni*. Number of embryos in final stage as function of prenatal mortality. Periods A, B, C, and numbers 1 to 16 as in Fig. 11

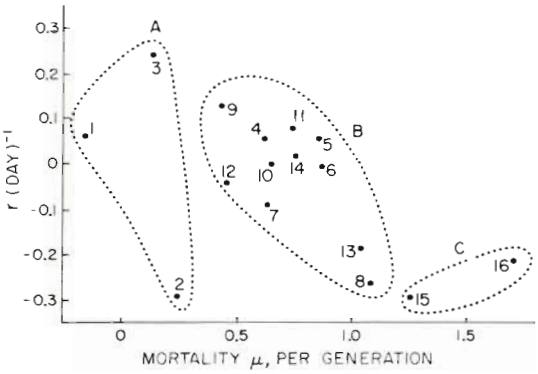

Fig. 13. *Evadne nordmanni*. Intrinsic rate of population increase as a function of prenatal mortality. A, B, and C as in Fig. 11

prenatal mortality. The subsequent fluctuation of fecundity caused the change in the population rate of increase.

DISCUSSION

Evadne nordmanni occurs from late spring to autumn in temperate seas, e.g. the Clyde Sea (Bainbridge 1958), the North Atlantic and North Sea (Gieskes 1971), and the Scotian Shelf (Platt 1977); but its season occurs before summer in warmer seas, e.g. Mediterranean (Thiriot & Vives 1969, Thiriot 1972) and the Seto Inland Sea in Japan (Onbé 1974), after which it is succeeded by other cladoceran species. *E. nordmanni* seems to be adapted to rather cold water temperatures.

It is evident that the number of embryos in the initial stage is under some control, either intrinsic or environmental, because the differences between the numbers in Group A and Groups B and C are pronounced. We consider it to be a response of the organisms to seasonal changes in environmental conditions such as temperature and food. One might expect a smaller number of embryos to be produced when conditions were less favourable: under such conditions, also, an overall reduction of development rate has been suggested for freshwater cladocera by Romanovsky (1984).

Seasonal changes in embryo number per individual have been described for marine cladocerans (Della Croce & Bettanin 1964–65, Bainbridge 1958, Pavlova 1959), and for freshwater cladocerans (Hall 1964, Green 1966, Johnsen 1983). The patterns are generally similar with higher numbers in the beginning period. Bainbridge (1958) reported on the embryo number of *Evadne nordmanni* classified in 2 developmental stages, early-stage and late-stage. There seems to be evidence for prenatal mortality in his data.

The decrease in the number of embryos through developmental stages could be interpreted as an adaptive strategy to unpredictable fluctuations in the environmental conditions. It would be an advantageous strategy if, starting with a certain number of embryos, the adults could decrease the number if and when conditions deteriorated. It would be further advantageous if the nutrients of aborted embryos could be utilised by the remaining embryos. In *Podon* and *Evadne* spp., the eggs are nourished by the mother through the fluid bathing the embryos in the closed brood pouch via glandular cells in its wall (Gieskes 1970). This provides a possible mechanism for the resorption of nutrients from an aborted embryo by its siblings. The possibility of abortion in *Daphnia* spp. was suggested by Threlkeld (1979b). In this case, the organism seems to abort all the embryos at the time of moult when either the temperature or food supply is unfavourable. In the heterostylous perennial plant *Cryptantha flava,* not all embryos mature, the rest being aborted. The number matured depends partly on resources available (Casper 1984). It was pointed out by Casper & Wiens (1981) that the development system in *C. flava* has the potential to permit selective abortion of young ovules based on some assessment of embryo quality.

Since Edmondson first published his model for estimating birth rate, $F = 1/a$ (Edmondson 1960), where F = frequency of the eggs that are going to hatch within 24 h and a = egg development time, many workers have suggested modifications to it, taking into consideration egg mortality and population growth rate (Edmondson 1968, 1972, Paloheimo 1974, Threlkeld 1979a, Taylor & Slatkin 1981). These modifications are based on the assumption of a stable age distribution, including an implicit parameter r.

In our model for a marine cladoceran, the population growth rate, r, was given explicitly in Eqn (5), and

$$F = \frac{\int_t^{t+1} \tilde{n}\,(a,\,t)\,b_t\,dt}{\int_0^a \tilde{n}\,(x,\,t)\,b_0\,e^{-\mu' x}\,dx} \qquad (14)$$

where b_0 and b_t = the average embryo number per adult at the age 0 and the age a, respectively; μ' = the embryo mortality per day in a living adult. Under the assumption of a constant adult mortality $m\,(x) = m$, application of (3), (4) and (5) for (14) gives an explicit form;

$$F = \frac{\beta + \mu'}{\beta - m} \cdot \frac{\{e^{\beta - m}\} - 1}{\{e^{(\mu + \mu')a}\} - 1} \qquad (15)$$

where $\beta = \ln (b_t + 1)/a$.

When $|r| = |\beta - m| \ll 1$ and $|(\beta + \mu')| \ll 1$, Eqn (15) reduces to the original form, $F = 1/a$. Although we estimated b_t and the embryo mortality per generation ($\mu = \mu' \cdot a$), we do not know a and m and therefore cannot estimate F.

Johnson (1983) explored a more direct method for estimation of F, which does not require the assumption of a stable age distribution. It does, however, require that we know the absolute duration of the developmental stages. If we could confirm the relative duration of stages and the dependence of the total development time on temperature, the method would be applicable also to our data.

We have shown by mathematical analysis that the relative duration of embryonic stages can be inferred from the frequency distribution of stages observed in large samples, and that the decrease in embryo number per stage can be used as the basis of a calculation of prenatal mortality. This mortality has to be expressed on a 'per generation' basis instead of in absolute time units because at the moment we do not know the total development time (presumably a function of temperature) in absolute units. One can expect this information to become available if and when techniques improve for handling marine cladocera in the laboratory. Meanwhile, absolute rates could be estimated using data published for freshwater forms. The prenatal mortality, as calculated here, is appreciable and appears to play a significant role in controlling the abundance of this organism in Nova Scotia waters.

Acknowledgements. We thank Jean White for excellent technical support in the embryological part of this work, and Elizabeth Boulding for help in the preparation of the manuscript. Drs. A. Okubo and J. E. Paloheimo were kind enough to check all the mathematics. Drs. A. R. Longhurst, K. H. Mann, T. Onbé, M. Reeve and Dr. W. Silvert all made constructive comments on the mansucript.

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This paper was submitted to the editor; it was accepted for printing on November 22, 1985