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Population dynamics of cladocerans in Sunfish Lake, Ontario

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Investigation of populations of *Daphnia rosea*, *D. retrocurva*, and *Diaphanosoma leuchtenbergianum* in Sunfish Lake, southern Ontario, during 1969 indicated that, in the absence of predation, food supply was the major factor controlling population size and influencing population parameters. Generally with each species, a population peak was preceded by a rise in fecundity, an increase in birth rate, and a fall in death rate. As the carrying capacity of the environment in terms of food was surpassed the population numbers declined, fecundity dropped off, and the death rate rose. A strong negative correlation between fecundity and death rate was observed.

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L'analyse des populations de *Daphnia rosea*, *D. retrocurva* et *Diaphanosoma leuchtenbergianum* dans le lac Sunfish du sud de l'Ontario en 1969, indique qu'en l'absence de prédateurs, c'est la quantité de nourriture qui contrôle surtout l'effectif des populations et influence les paramètres de ces populations. En général, pour chaque espèce, le sommet d'abondance atteint par la population est précédé par un accroissement de la fécondité, une augmentation du taux de natalité et une réduction du taux de mortalité. Lorsque le stock limite de l'environnement, en ce qui concerne la nourriture disponible, est dépassé, l'effectif des populations décline, la fécondité baisse et le taux de mortalité augmente. On a obtenu une corrélation négative très marquée entre la fécondité et le taux de mortalité. [Traduit par le journal]

Introduction

Studies on laboratory and natural cladoceran populations indicate that seasonal abundance, fecundity, and instantaneous rates of birth, natural increase, and death may be strongly influenced by either food supply (Slobodkin 1954) or predation (Hall 1964; Wright 1965). The present study examines seasonal distribution and population dynamics of *Daphnia rosea*, *D. retrocurva*, and *Diaphanosoma leuchtenbergianum* in Sunfish Lake, where the absence of planktonic predators such as *Leptodora* and *Chaoborus* and the complete restriction of fish to the littoral zone suggested that predation was an unimportant factor. Sunfish Lake is a small (8.3 hectares), deep (max. 20 m), meromictic water body in Waterloo County, southern Ontario. Water chemistry and phytoplankton have already been fully detailed in Duthie and Carter (1970), and the life cycle of the predominant calanoid copepod *Diaptomus oregonensis* is given in Lai and Carter (1970). Water temperatures during the present sampling season are shown in Fig. 1.

Methods

Samples were collected from April 25 through October 30, 1969, with a Schindler-Patalas Plexiglas trap of 22.5-

liter capacity, equipped with a net and collecting bucket of No. 20 mesh (apertures of 76 microns (μ)), at 2-m intervals from 0 to 18 m at the deepest point in the lake. Intervals between sampling trips varied from 2 days to 2 weeks, the shorter sampling intervals occurring during periods of high or rapidly changing population size. Temperatures at 1-m intervals were recorded on each occasion. Samples were preserved in 95% ethyl alcohol, and in the laboratory each sample was counted in its entirety at 20 \times magnification under a binocular microscope. Samples taken by H. C. Lai with a Birge-Juday trap on June 6, 1968 at 5:30 a.m. and 1:00 p.m. were examined to determine whether any major diurnal migration of Cladocera was taking place.

Live specimens of *Daphnia rosea* were collected during the first 2 weeks in July. Immediately on return to the laboratory one non-ovigerous female was transferred to each of 90 culture tubes. The tubes were divided into three batches of 30 each and stored in Hotpack incubators without light at 5.0, 13.3, and 24.0°C. To provide an adequate food supply, portions of Sunfish Lake water were periodically concentrated by a factor of 50 through a 0.45-Millipore filter, and 1 ml of this concentrate was added to each culture every 2 days. The cultures were examined at intervals of from 8 to 48 h, and the presence and numbers of eggs or young were recorded in each case. The egg development time for each temperature was calculated as the mean time period between formation and hatching of eggs.

Results

Seasonal Abundance

Daphnia rosea was the most abundant species

during the greater part of the year (Fig. 2). A maximum of 270 000/m² was reached at the beginning of May, major fluctuations in numbers occurring during the growth and decline of this peak. During midsummer, all three species began to increase in numbers, resulting in each case in a peak very different in form from the earlier one of *D. rosea*. These peaks were smoothly progressive in their growth and decline, and of considerable duration. Maxima for each of the three species were separated in time. The population of *Diaphanosoma leuchtenbergianum* began to increase around the middle of July and started to decline in mid-August. By the end of October, when sampling ceased, the numbers were reduced almost to zero. *D. rosea* began to increase in numbers around the beginning of August and reached a maximum as *D. leuchtenbergianum*

declined; by the end of October, the population was falling off rapidly, asexual egg production had ceased, and numerous ephippia had formed. The peak in *Daphnia retrocurva* was still later in time, beginning towards the end of August and entering a period of slow decline only by late October, with the production of a few ephippia. All three late summer-autumn peaks were of the same order of magnitude, that of *D. rosea* reaching 74 000 animals/m², *D. leuchtenbergianum* 50 000 animals/m², and *D. retrocurva* 56 000 animals/m². The total number of animals of all three species had a density somewhat smaller than that in spring, when the population was composed mainly of *D. rosea*.

Vertical Seasonal Distribution

Table 1, showing vertical distribution of *D. retrocurva* and *D. rosea* on June 6, 1968 at

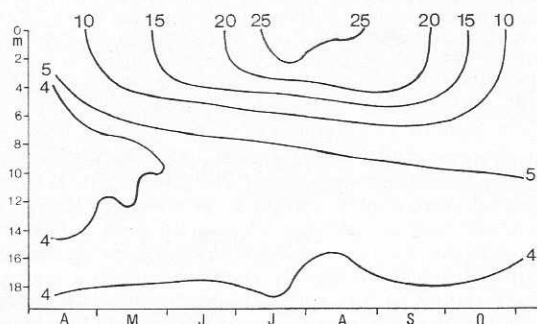


FIG. 1. Sunfish Lake temperatures, 1969. Isotherms in degrees centigrade.

TABLE 1

Vertical distribution of *Daphnia retrocurva* and *D. rosea* per cubic meter at 5:30 a.m. and 1:00 p.m. on June 6, 1968

Depth, m	<i>D. retrocurva</i>		<i>D. rosea</i>	
	5:30 a.m.	1:00 p.m.	5:30 a.m.	1:00 p.m.
1	9000	4540	2180	2267
3	11567	10137	2256	1545
5	12273	13245	1364	682
7	23636	25089	0	1089
9	37545	22272	1545	909
11	10455	10455	683	1136
13	11818	6818	455	227
17	5818	7727	273	455

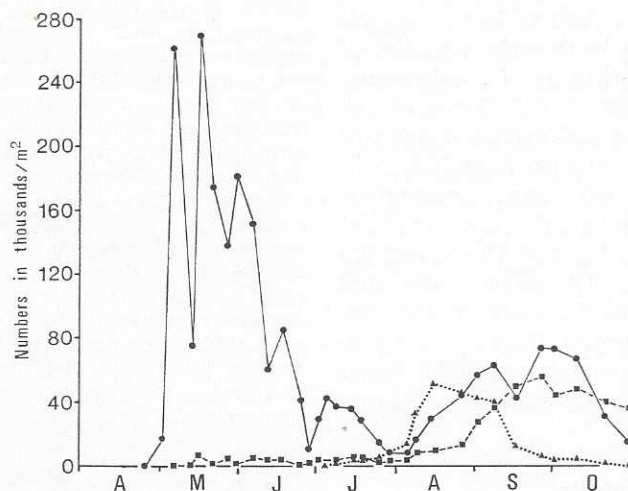


FIG. 2. Total cladoceran populations per square meter, April through November. *D. rosea*, ●; *D. retrocurva*, ■; *D. leuchtenbergianum*, ▲.

5:30 a.m. and 1:00 p.m., suggests that diurnal migration in Sunfish Lake, if it exists, is on a very small scale. This is in keeping with the results of Lai (1969) and Bhajan (1970), who report only limited diurnal movement of *Diaptomus oregonensis* and *Bosmina longirostris* respectively, and it probably relates to the high turbidity and consequently low light penetration in the lake.

The cladoceran populations in 1969 were not spatially homogeneous, and seasonal fluctuations were strongly depth-dependent (Fig. 3). Oscillations in the growth and decline of the spring peak in *D. rosea* were evident at all depths, but neither these oscillations nor the period of maximum abundance were synchronous between depths. The population maximum in the epilimnion occurred in early to mid-May; that at

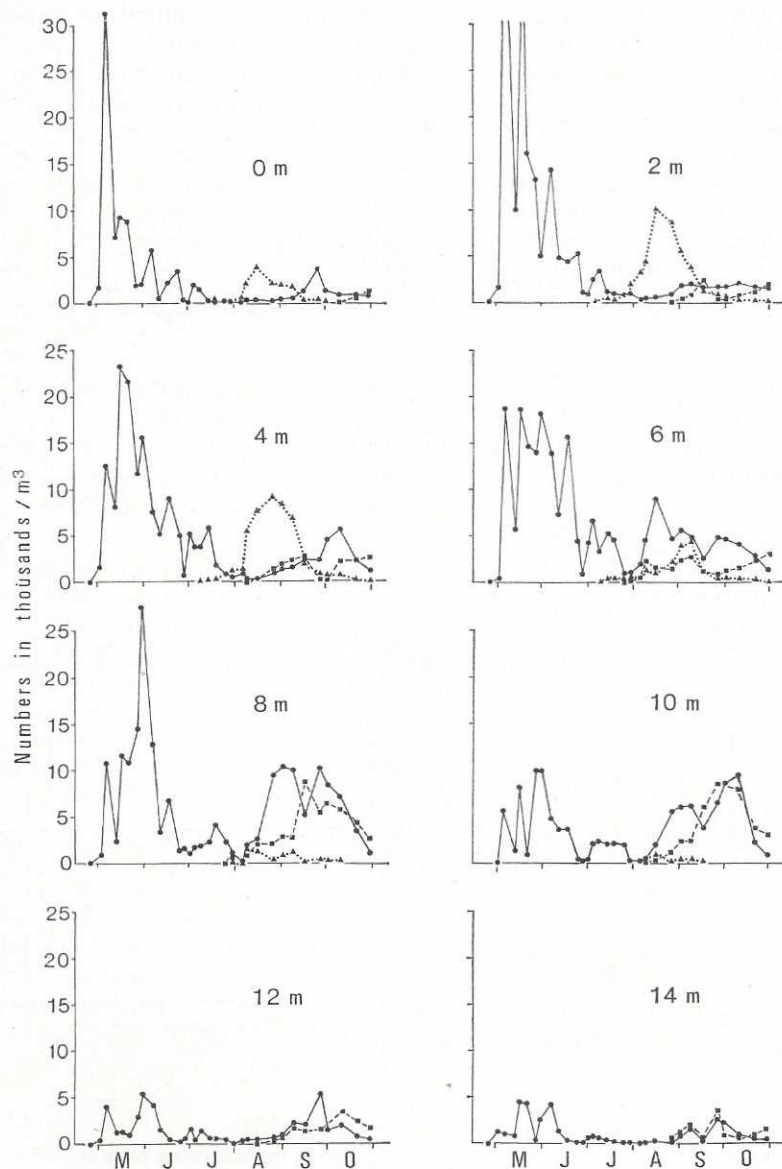


FIG. 3. Cladoceran distributions at eight depths per cubic meter, on all occasions, April through November. *D. rosea*, ●; *D. retrocurva*, ■; *D. leuchtenbergianum*, ▲.

4–6 m, from early May to mid-June; that at 8–10 m, in late May and early June. After the spring maximum, the epilimnetic population of *D. rosea* declined, and during the rest of the year the greater part of the population remained below the thermocline, with the largest number most consistently at 8 m. *D. retrocurva*, which peaked only in late summer and autumn, was largely restricted to the 8- to 10-m region. *D. leuchtenbergianum* was largely restricted to the epilimnion; very few animals were present below 6 m, while the population maximum was at 2 m.

Population Dynamics

In view of the evidence that the relationship between egg development time and temperature is very similar for different species of Crustacea (Edmondson *et al.* 1962; Schindler 1972), and since the development times which were estimated for *D. rosea* agree very closely with those obtained by Hall (1964) for *D. g. mendotae*, development times of the three species in the present study were calculated from a graph derived by curvilinear extrapolation from Hall's experimentally determined points (Fig. 4).

Using Hall's (1964) method, the instantaneous birth rate was calculated:

$$[1] \quad b = \ln(1 + B),$$

where b is the instantaneous birth rate. B , the finite birth rate is given by the formula:

$$[2] \quad B = Ne/DN_i,$$

in which Ne and N_i are the number of eggs and the number of animals respectively for one species in a sample from a depth i ; and D is the

egg development time for the species at the respective temperature.

From the 10 values of b obtained from the 10 depths for each date, a weighted mean, b' , was calculated for the total population by the equation:

$$[3] \quad b' = \left(\sum_{i=1}^{10} b_i N_i \right) / N,$$

where b_i is the instantaneous birth rate at depth i , and N is the total number of animals at all depths. Since vertical migration is likely to have been minor, as suggested above, and since temperature varied markedly with depth, the total procedure should give a reasonably accurate reading for b'

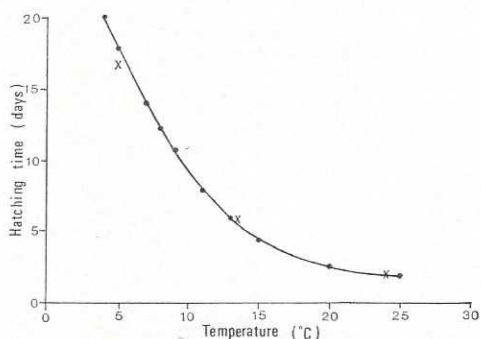


FIG. 4. Egg development times for *Daphnia galeata mendotae*; data from Hall (1964). The three values for *D. rosea* obtained in the present study are marked by \times .

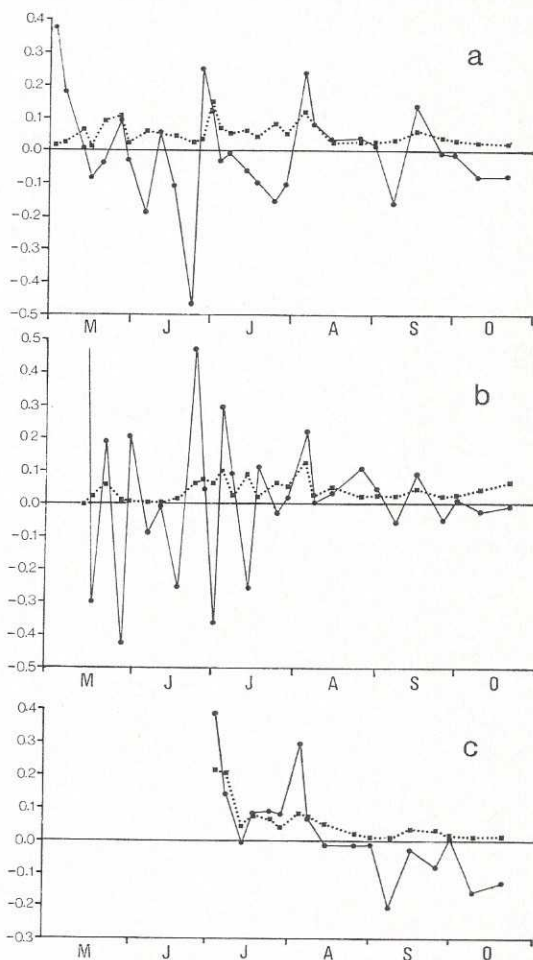


FIG. 5. Instantaneous birth rate (b') and observed rate of population increase (r). Fig. 5a, *Daphnia rosea*; b, *D. retrocurva*; c, *Diaphanosoma leuchtenbergianum*. b' , \blacksquare ; r , \bullet .

on each date. These values of b' are plotted for each species in Fig. 5, together with the observed instantaneous rates of increase of the total population, r , given by:

$$[4] \quad r = (\ln N_t - \ln N_0)/t,$$

where N_t represents the observed value of N after an interval of t days. By subtraction of r from b' , a series of values for d , the estimated death rate, was derived and is shown for each species in Fig. 6.

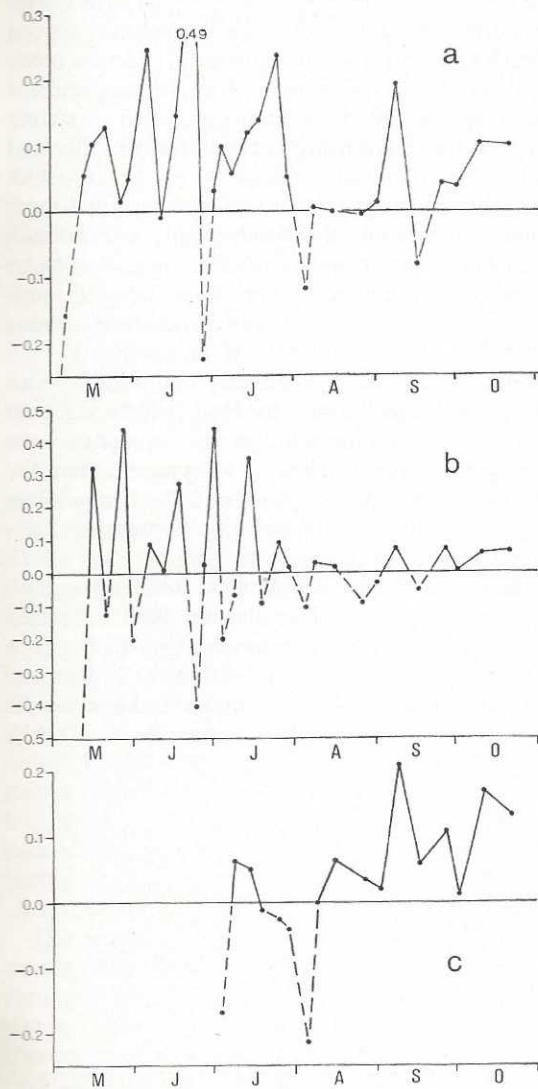


FIG. 6. Instantaneous death rate (d). Fig. 6a, *Daphnia rosea*; b, *D. retrocurva*; c, *Diaphanosoma leuchtenbergianum*.

The number of eggs produced by the adults of a *Daphnia* population has been shown to be largely a function of their nutritional state (Banta *et al.* 1939; Slobodkin 1954; Hall 1964). Since the proportion of adults was not determined in the present study, seasonal changes in mean fecundity of ovigerous animals were used as a comparative measure of seasonal changes in nutrition (Fig. 7). These values are naturally somewhat higher than conventional estimates of brood size, as animals without eggs were excluded.

After marked oscillations, the estimated death rate of *D. rosea* reached a maximum value of almost 0.5 during mid-June as the spring population peak was declining (Fig. 6). After falling off sharply, the death rate then increased steadily in

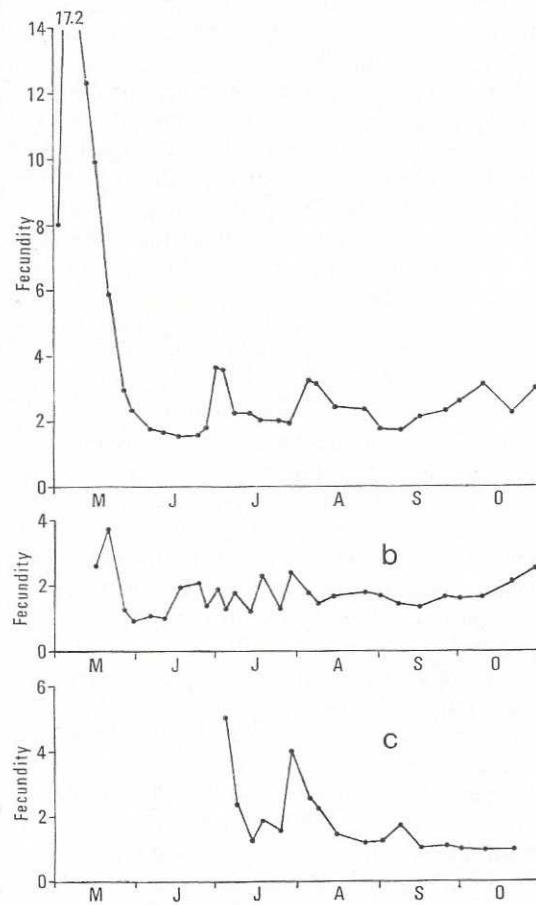


FIG. 7. Fecundity (mean number of eggs/ovigerous female). Fig. 7a, *Daphnia rosea*; b, *D. retrocurva*; c, *Diaphanosoma leuchtenbergianum*.

July, accompanying the steady decrease in population size (Fig. 2). At the end of July, as the population size reached a minimum value, the death rate fell sharply and, with the exception of one possibly erroneous fluctuation in mid-September, remained close to zero through the duration of the autumn peak. It then steadily increased as population size declined in October.

The birth rate of *D. rosea* remained low throughout, values exceeding 0.1 only during the two population minima at the end of June and in late July-early August (Fig. 5). Since no estimate could be made of the numbers of hatching ephippia, birth rates calculated during early spring are likely to be gross underestimates, this probably being the reason for the theoretically impossible negative death rates calculated for early May. Negative values of d occurring later in the year all occur during periods of rapidly changing rates of increase, and may be explained as sampling error.

Fecundity of *D. rosea* after reaching values of up to 20 eggs per ovigerous female during the growth of the spring peak declined rapidly and remained for the most part low during the rest of the season (Fig. 7). Slight increases occurred at the times of the two summer increases in b' mentioned above and also during the autumn population pulse.

Values of r and d in *D. retrocurva* are for the most part little value, particularly during the first part of the year; the violent fluctuations in r , and consequently in d , are almost certainly the result of the large sampling errors, consequent on the very low population density. During the autumn peak, the fluctuations decreased somewhat and an increase in death rate may be detected as the peak reached its maximum and declined. Birth rates and fecundity were for the most part very low; birth rates only sporadically exceeded 0.1 while fecundity, after reaching a maximum of 3.7 in May, remained between 1.5 and 2 during most of the year.

The rapid increase of *D. leuchtenbergianum* during late July and early August was preceded by a period of relatively high birth rate (reaching values in excess of 0.2) and apparent negative death rate which probably indicates the hatching of resting eggs. The death rate then rose through the autumn, with some oscillations, as the population declined. Fecundity rose as high as five eggs per ovigerous female, when the species first

appeared in early July, then decreased sharply, and rose again to four as the population began to increase at the end of July. Values then became progressively lower, remaining around 1.0 during the period of population decline.

Discussion

The data suggest that nutrition plays a large part in determining seasonal population patterns in Sunfish Lake. In the case of *Daphnia rosea*, a strong negative correlation may be seen between fecundity and death rate (Fig. 8). This indicates a corresponding negative correlation between death rate and state of nutrition. If factors other than food were the primary limiting mechanisms in a species such as *D. rosea*, with a strong facultative relationship between food supply and fecundity, then the converse would be expected. As the mortality because of non-nutritional causes increased, the food supply per animal, and hence the mean number of eggs, would be expected to increase. This hypothesis is supported by the very low egg production during summer. The estimates of fecundity in the present study are not directly comparable with the brood sizes quoted by Hall (1964), since no analysis of the population age structure was attempted. Nevertheless, it is apparent that the *D. rosea* population in Sunfish Lake is much less fecund than other *Daphnia* populations described in the literature. In a population of *D. galeata mendotae*, which was suffering a high mortality because of predation, Hall estimated the mean brood size of adults as varying between two and five through the summer. Equivalent values for *D. rosea* in Sunfish Lake must lie between 0.6 and slightly more than 2.0 (the

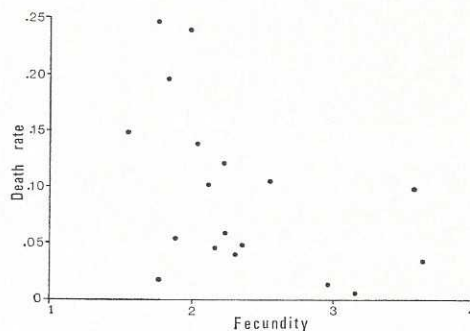


FIG. 8. *Daphnia rosea*. Fecundity in relation to instantaneous death rate.

approximate mean values for brood size per total animals, and for the fecundity of ovigerous animals respectively through June, July, and August). That these low values were not due to a genetic characteristic of the population is indicated by the very high fecundity observed during the spring peak, when values as high as 20 were noted. Stross *et al.* (1961) report values of brood size below 1.0 in *Daphnia* populations where food shortage might be expected.

As pointed out by Hall, a very low mean brood size is to be expected in a population which has reached the carrying capacity of its environment in terms of food. At equilibrium, only one egg, on the average, will be produced by each animal, and since the life expectancy of *Daphnia* includes more than one reproductive instar, the equilibrium brood size must be less than unity. Slobodkin (1954) found, in fact, that the average brood size in an equilibrium, food-limited laboratory population of *Daphnia obtusa* was less than 0.5 eggs per adult. He hypothesized that, because of the length of time required to attain equilibrium, this situation would rarely, if ever, exist in nature. In the present situation, *D. rosea* did not approach equilibrium in the spring though the evidence seems to indicate that at least an approximation to the equilibrium situation took place during the latter part of the summer. Thus, the rapid growth of the spring peak in Fig. 2 suggests that the population, hatching from ephippia, grew very rapidly in the presence of an ample food supply. The initial high fecundity values then fell off very sharply as the food supply was reduced by grazing, to the point where the population was almost eliminated on June 27. During this period, the death rate was very high, the average values being around 0.25, corresponding with a population turnover time of 4 days (Fig. 6). This situation appears to correspond almost exactly with that observed by Slobodkin (1954) during the initial establishment of laboratory cultures of *D. obtusa* under constant food conditions.

The secondary peak of *D. rosea* observed during July followed a transitory increase in fecundity at the point of minimum population size, and both fecundity and death rate remained somewhat lower than in May. The average death rate was 0.12 for the month of July, giving a turnover time of about 8 days. This data, coupled with the absence of the large fluctuations

which had characterized the spring peak, suggest that a more stable relationship with the food supply was being established. This is confirmed by the events occurring during the growth and decline of the autumn peak. A second transitory increase in fecundity during early August indicates the probability that the population fell below the carrying capacity of the environment in terms of food. Simultaneously the death rate fell almost to zero, where it remained for over a month as the population size gradually increased. This increase, which was only about 3% per day, suggests that the population was reasonably close to equilibrium.

The data for the other two cladocerans are more difficult to interpret, since the populations were so small for much of the season. However, in the case of *D. leuchtenbergianum*, a very marked increase in fecundity, from 1.5 to 4.0, and a very low death rate (mean = about 0.01) at the start of the autumn maximum is strong evidence in favor of a link between population size and available food; during late September and October, fecundity remained consistently at around 1, the theoretical minimum value, suggesting that the decline in the autumn peak took place under conditions of very low food supply. It is possible that *D. leuchtenbergianum*, which was largely epilimnetic (Fig. 3), lived off algae which were unavailable to the other two species.

Acknowledgments

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