Journal of Plankton Research Volume 4 Number 3 1982

Population dynamics of *Simocephalus vetulus* (O.F.Muller)

P.C.Sharma and M.C.Pant

Department of Zoology, Th. D.S.B. Constt. College, Kumaun University, Nainital-263002, India

(Received May 1981; accepted April 1982)

Abstract. Investigations on the population of *Simocephalus vetulus* (O.F.Muller) were carried out both in natural and laboratory conditions, at different temperatures and food concentrations. The temperature and food were found to have a pronounced bearing upon the rate of development and the life span of this zooplankter. The temperature also influenced the rate of growth and the size of population by increasing the instantaneous rate of birth. Besides food and temperature, the hydrogen ion concentration of the water also appeared to influence the size of the population. There was a positive correlation between fecundity and death rate with a strong facultative relationship between fecundity and food supply.

Introduction

Zooplankton constitutes one of the important components of secondary production in a body of water. The problem of effective management needs a detailed knowledge of the various species. Further, the production of aquatic organisms results in the transfer of matter and energy from one trophic level to subsequent ones. The zooplankters belonging to the group Cladocera are important as food for both young and adult fish (Alikuhni, 1952; Welch, 1952; Pennak, 1953; Vass and Vas Van-oven, 1959) and these animals often predominate in the zooplankton.

The seasonal succession of the Cladocera is quite variable among species and within species under different lake conditions (Wetzel, 1975). Some information on the general natural history and population ecology of this group from both temperate and arctic regions is available (Wesenberg-Lund, 1926; Berg, 1931; Slobodkin, 1954; Edmondson, 1955). The dynamic properties of the cladoceran populations, particularly the instantaneous rate of growth, birth rate and death rate have been observed to be strongly influenced either by predation or food supply (Slobodkin, 1954; Hall, 1964; Tappa, 1965; Wright, 1965). Clark and Carter (1974) worked on three species of Cladocera in Sunfish Lake, Ontario and hypothesized that in the absence of predation, food is the most important single factor controlling the population dynamics; in addition to moderating the rates of population change and mortality, it also influences the fecundity. Kwick and Carter (1975) investigated the seasonal cycles and population dynamics of limnetic cladocerans of a pond and suggested that cladoceran community dynamics depended upon either inherent characteristics of each species or an environmental pressure other than predation. Recently Jones *et al.*, (1979) studied the population dynamics and production of *Daphnia hyalina* var *lacustris* in a shallow eutrophic reservoir. They reported a high and positive growth rate in early spring and a negative one with the progress of summer. Some work on this aspect in tropical waters has been conducted by Michael (1962) and Vijayaraghaban (1970).

In the present investigation an attempt has been made to examine the dynamic properties of a common cladoceran zooplankter in a subtropical water body (Bhimtal, India), both in natural (field study) as well as in laboratory conditions.

Materials and Methods

Field methods

Samples of *S. vetulus* were collected weekly from the littoral zone of Bhimtal lake (79°36′E Long.; 9°20′N Lat.). The concentrate from 5 l constituted a single sample. Such samples collected from each of four stations were taken to the laboratory alive, in a half-liter plastic container.

The samples containing particulate matter and animals were poured into beakers and allowed to settle for half an hour. *S. vetulus* and other living animals tend to leave the bottom and come up to the surface water when the beaker containing them is mildly heated at the bottom. The material was then quickly decanted. The process was repeated three or four times. The samples were further concentrated to 10 ml and stored in 90% alcohol. The above technique was found to be quite efficient in separating 90–95% individuals of *S. vetulus* and other invertebrates from field samples.

The samples were adjusted to known volumes and analysed by the examination of 1 ml aliquots in a Sedgwick-Rafter cell using a compound microscope at 40 x and 100 x magnification. The length and width of the zooplankter were measured with a micrometer. The following equation was used to estimate the density of each size group:

$$N = \frac{(a\ 1000)c}{L}$$

Where N = total number of individuals/l of original water, a = average number of individuals in all counts in a counting unit of 1 ml, c = volume of original concentrate in ml, L = volume of water filtered through net, in l.

Laboratory methods

The samples of *S. vetulus* collected from Bhimtal lake were allowed to grow at room temperature in the laboratory on a mixture of algae in glass troughs filled with water.

To study population attributes, five organisms of *S. vetulus* were raised individually from an early stage of development in small Petri dishes at four experimental temperatures (8 ± 1°C, 15 ± 1°C, 21 ± 1°C and 28 ± 1°C) corresponding to the mean temperatures of four seasons, namely, winter, autumn, spring and summer at Bhimtal lake. Four different food concentrations were used at each temperature.

Chlamydomons sp, a green alga, was used as food for the zooplankter. The alga collected from Bhimtal lake was cultured in the laboratory in Beijerinck nutritive medium (NH_4NO_3 0.1%; K_2HPO_4 0.02%; $MgSO_4.7H_2O$ 0.01% and $FeCl_3$ 0.001%) at room temperature in a glass container exposed to natural as well as fluorescent light. The samples of algae from the glass container were filtered, washed and concentrated at each time before feeding the animals.

Four concentrations of food, viz., 25 000, 50 000, 75 000 and 100 000 cells/ml were used in the present investigation. The concentrated algal cells were counted in a Bright Line Haemocytometer, and were diluted with stored tap water to obtain the required concentration of food. The temperature of each food suspension was maintained equal to each experimental temperature. The rearing medium of the zooplankter was renewed daily at higher temperatures (21 and 28°C) and after two days at lower temperatures (8 and 15°C).

The individuals in each experiment were examined daily. The moulting rate was determined by the first appearance of the cast off cuticle covering. The length of the organism was measured after each moult. The number and duration of egg development and its time of hatching into developed young were also recorded at each temperature. *S. vetulus* carries eggs in its brood chamber which are released as fully developed young at the time of moulting. Side by side with the release of young, a batch of fresh eggs also enters the brood chamber. The reproduction was measured in terms of number of new individuals produced/day (before measuring the length of the organism). The young produced by each individual (in the experimental dishes) were removed into separate containers. The quantity and concentration of food were kept constant for each experiment. For size age analysis a separate set of new born individuals were observed at different food and temperature conditions. The size of the individuals, number of eggs and the moulting time were recorded.

Population dynamics

If one eliminates (as in the present study) immigration and emigration, the rate of increase of the population can be calculated as suggested by Hall (1964) and later followed by Clark and Carter (1974) and Kwick and Carter (1975). The instantaneous birth rate was calculated using the following equation:

$$b = \ln(1+B)$$

where b is the instantaneous birth rate, B, the finite birth rate.

The finite birth rate B, was calculated by,

$$B = Ne/DNi$$

where Ne and Ni are the number of eggs and the number of animals respectively and D is the egg developmental time for the species at the respective temperature. The observed instantaneous rate of population change (r) was calculated by,

$$r = \frac{\ln Nt - \ln No}{t}$$

where Nt is the observed value of N (number of individuals) after an interval of t days. The instantaneous death rate (d) was then, estimated by subtracting r from b,

$$d = b - r$$

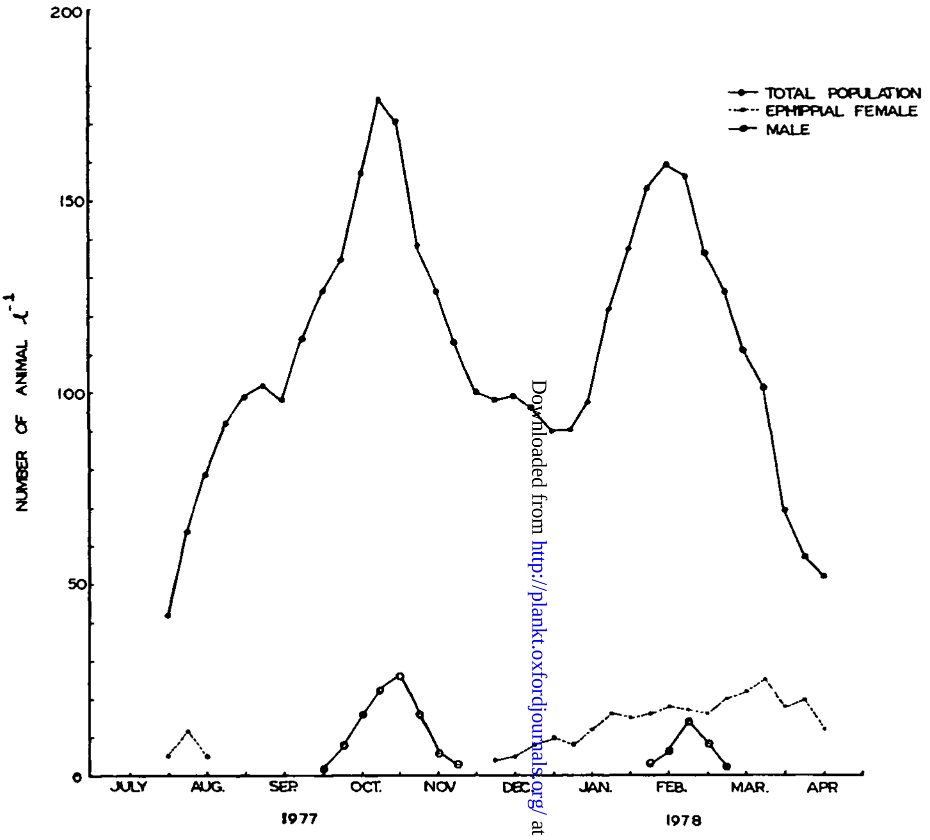

Fig. 1. Seasonal variation in density of parthenogenetic female, ephippial female and male individual *S. vetulus*.

Observations

Natural population (field studies)

Population density. The density of *S. vetulus* expressed as number of individuals/l (Figure 1) showed two maxima, one each in October (176 individuals) and February (159 individuals). The population approached a minimum during the last week of December, disappeared altogether by the middle of April and did not reappear until the last week of July. Individuals carrying ephippia were observed in August and again from the first week of December to mid-April (Figure 1). The maximum number of individuals carrying ephippia (25 individuals) was however, seen during March. The population of male individuals, though small, (Figure 1) also showed two maxima, one each in October (27 individuals) and February (15 individuals).

Size structure. The individuals collected from the lake on different sampling dates

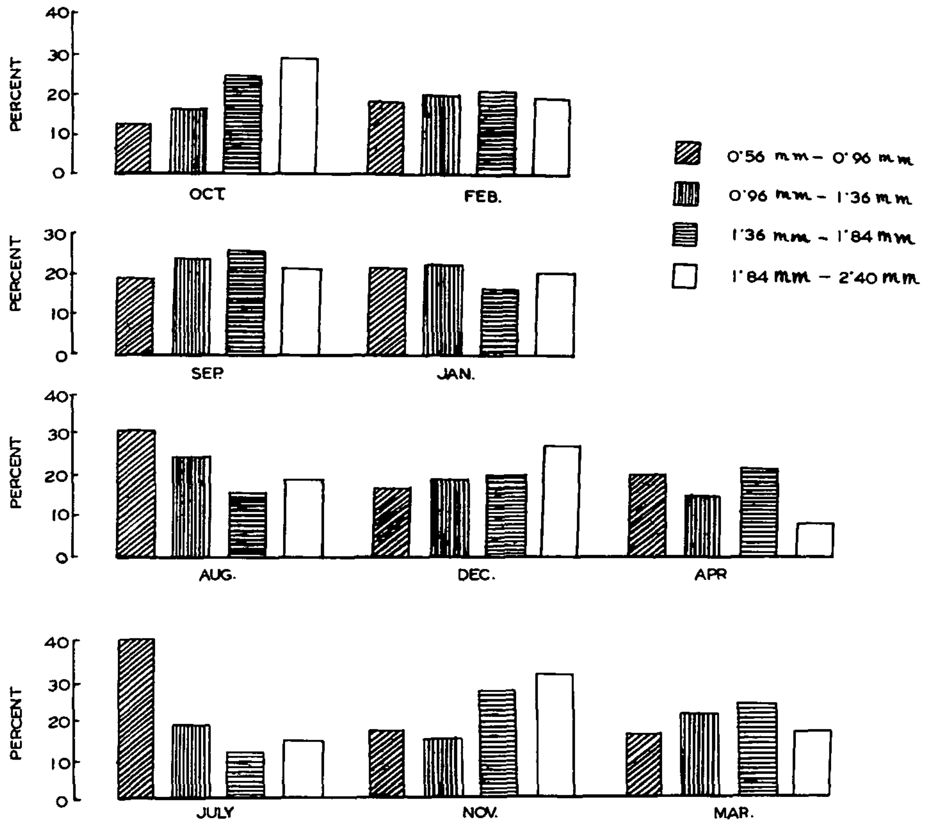

Fig. 2. Percentage composition of different size group individuals of *S. vetulus*.

were examined and grouped into the following categories (based on the size-age categories established from the laboratory experiments):

(i) pre-adult stage (size 0.56 – 0.96 mm);

(ii) early reproductive stage (size 0.96 – 1.36 mm; 7 – 19 eggs/individual);

(iii) peak reproductive stage (size 1.36 – 1.84 mm; 21 – 36 eggs/individual); and

(iv) last reproductive stage (size 1.84 – 2.40 mm; 3 – 9 eggs/individual).

In the natural population, all the size groups were represented with proportions varying from time to time (Figure 2). During July, the individuals of the pre-adult stage contributed maximally (43.0%) by number, whereas the other size-age categories accounted only for 12.2%, 11.8% and 14.2% of the total population, respectively. The early reproductive stage peaked during August, reaching 27.0%, whereas remaining stages accounted for 30.0%, 16.5% and 27.5% of the total population, respectively. The peak reproductive and the last reproductive stages peaked in the month of November and contributed 27% and 32% to the total population, respectively. In general, the pre-adult and early reproductive stages dominated the population for most of the year.

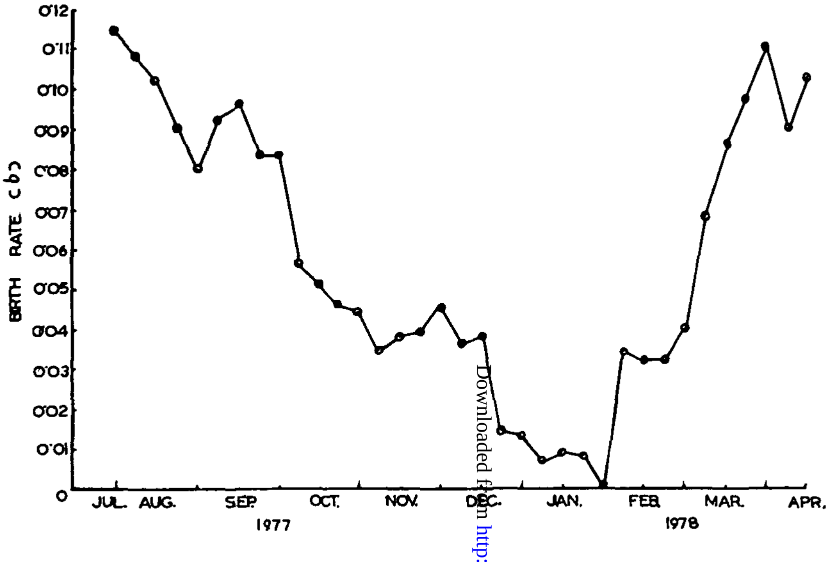

Fig. 3. Seasonal variation in the birth rate (b) of *S. vetulus*.

Population dynamics. The population dynamics are concerned with rate of increase, fluctuation in number and the environmental parameters that influence the population. The growth of population is a function of three factors: birth rate, death rate and movements of individuals in and out of the population.

Birth rates. The seasonal variation in the instantaneous rate of birth (Figure 3) was highest in July (b = 0.17) and March (b = 0.15) and the lowest (b = 0.0006) in January. Starting from an initial peak value of b = 0.17 in the last week of July, the birth rate declined sharply in August, then revealed minor oscillations, ranging from 0.096 – 0.056, from the second week of September to the first week of October. A sharp decline was again observed in the birth rate during October reaching 0.34 by the first week of November.

The birth rate tended to increase slightly, ranging from 0.034 to 0.045, during November. From December onwards, the values became progressively lower and eventually the lowest value (0.0006) was obtained in the last week of January. After falling off, the birth rate increased, at first steadily, then sharply and formed a second peak by the end of March, declining thereafter.

Death rate. The death rate peaked sharply and reached a maximum value (Figure 4) in the first week of August (d = 0.095). It declined for a short period during the second and third weeks of August increasing steadily to a value of 0.091 by the middle of September. From mid-September onwards, there occurred a gradual fall in the death rate ranging from 0.061 to 0.028, till mid-October. This was followed by an increase in death rate (0.041) in the later part of October. A marked fall in the death rate (0.0005) occurred in the first week of November, followed by considerable oscillations in the values (ranging from 0.026 to 0.005) from mid-

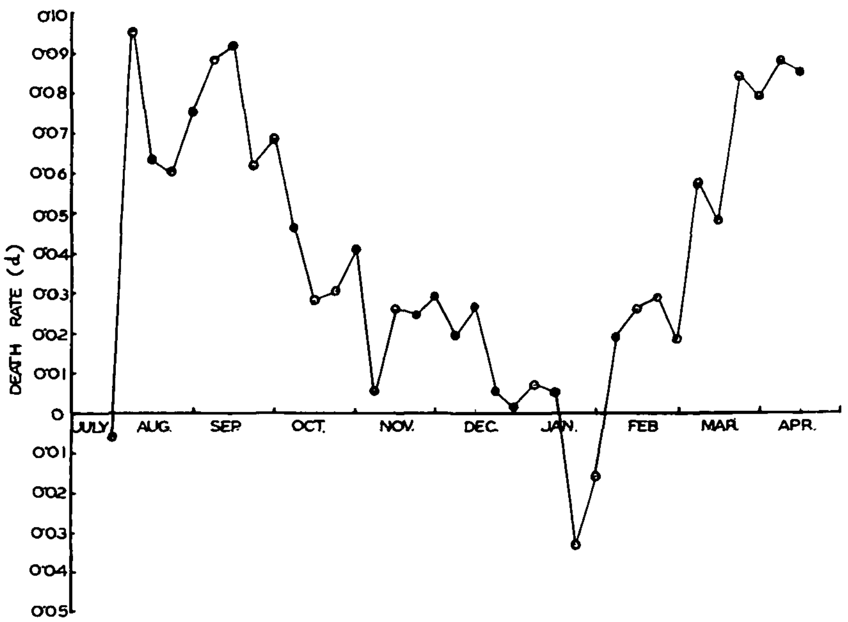

Fig. 4. Seasonal variation in the death rate (d) of *S. vetulus*.

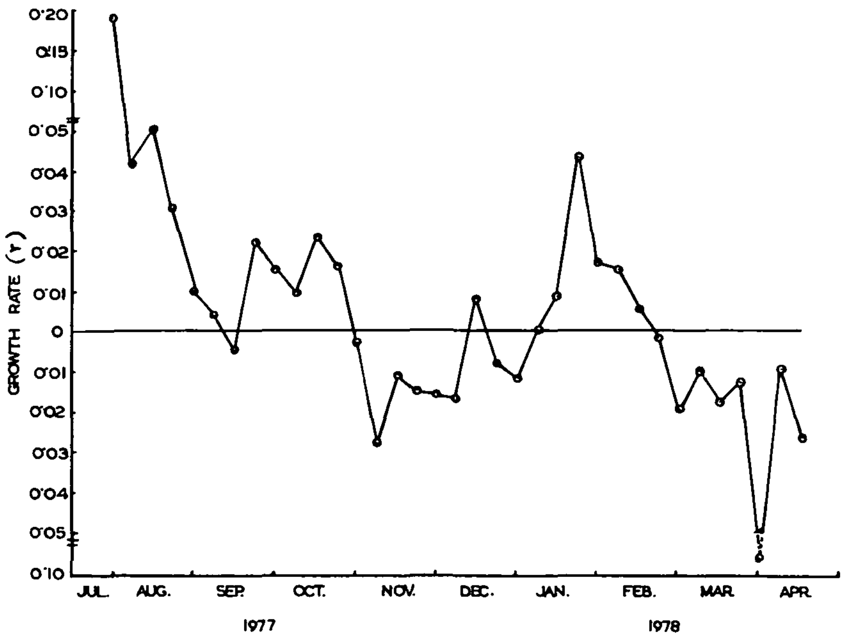

Fig. 5. Seasonal variation in the growth rate (r) of *S. vetulus*.

November to mid-January. The death rate eventually became negative in the later part of January. Hereafter, the values tended to increase with some fluctuations during the lst week of February, mid-March and last week of March till the first week of April.

Growth rate. The time series pattern of growth rate illustrated in Figure 5 showed the maximum rate of growth in the last week of July. Thereafter, the growth rate became progressively lower (except in the second week of August) and eventually approached negative values by the second week of September. The rate again increased in the second week of September and fluctuated between 0.009 and 0.024 in the next four weeks. The values remained negative from the last week of October to the first week of January, with the exception of the third week of December. Starting from a zero value in the second week of January the 'r' increased to 0.043 in the third week of January. Thereafter the growth rate again declined and became negative by the third week of February and remained so till mid-April.

Laboratory population (experimental studies). A number of experiments (see **Materials and Methods**) were set up to study the effects of varying concentrations of food and different temperatures upon reproduction, development, growth and survival of *S. vetulus*. The number of individuals produced, time taken to complete the life span at each temperature and food concentrations are given in Tables I and II.

The intrinsic rate of growth for experimental studies was calculated by the following formula:

$$r = \frac{\ln Nt - \ln No}{t}$$

where No represents the number of individuals at the beginning of each experiment and Nt the total number of individuals at the end of each experiment (including dead organisms).

The total life span of *S. vetulus* was observed to be only 48 ± 1 days at 8 ± 1°C. It gave birth to young at the age of 29 ± 1 days. These offspring (removed in a separate dish) did not reproduce during the lifetime of their parents. Birth rates and death rates were estimated from the material.

Separate values for total birth and total mortality were also obtained by counting the individuals during the experiments. From these values the birth rate 'b' and death rate 'd' were calculated as number of individuals/day/individual. The observed b and d values were related to the calculated birth and death rates using the following linear regressions (Figures 6 and 7):

$$Y = -0.00058 + 1.36818X; \ r = 0.96$$

where Y is calculated death rate and X is the observed death rate.

$$Y = 0.001567 + 0.969230X; \ r = 0.99$$

where Y is calculated birth rate and X is the observed birth rate.

At other temperatures, namely 15°C, 21°C and 28°C, the daughter organisms

Table I. Time devoted to various life span activities, egg developmental time, total juveniles produced, instantaneous growth (r), intrinsic birth (b) and death (d) rates of *S. vetulus* at four experimental temperatures.

	Temperature			
	8 ± 1°C	15 ± 1°C	21 ± 1°C	28 ± 1°C
Total lifespan (days)	49	78	65	32
Pre-adult developmental time (days)	30	25	21	9
Pre-adult moults	5	5	5	5
Post-adult developmental time (days)	19	53	44	23
Post-adult moults	5	14	17	12
Developmental time of egg (days)	12.0	4.11	3.44	1.55
Total juveniles produced by one female	68.0 ± 4.63	138.8 ± 11.2	227.0 ± 25.7	267.0 ± 8.88
Growth rate (r)	0.080	0.098	0.128	0.282
Death rate (d)	0.0051	0.0023	0.0018	0.0023
Birth rate (b)	0.0851	0.1003	0.1298	0.2843
Average of total population at the end of experiment	50.6 ± 5.8	2235.6 ± 18.6	4235.6 ± 36.0	8422.2 ± 21.0

reproduced during the life time of their parent stock but no quantitative record could be kept. Therefore, b and d values could not be calculated by the usual formulae employed by Hall (1964). Since the calculated and observed birth and death rates, as explained above, were significantly related with each other and the observed growth rate (r) and death rate (d) values were known at these temperatures, the birth rate (b) can be calculated as given by:

$$b = r + d.$$

Temperature affects population by influencing the total life span of the animal. Preliminary investigations at different temperatures indicated that the lower limit of temperature tolerance in *S. vetulus* is 5°C. Later it was ascertained that the organism sustained life but failed to reproduce at this temperature. The organisms were ultimately reared at four different temperatures (8 ± 1°C, 15 ± 1°C, 21 ± 1°C and 28 ± 1°C) corresponding approximately to the mean environmental temperatures, during winter, spring, autumn and summer seasons, respectively, at Bhimtal Lake. The nutrition was not taken into account as all the organisms at all the temperatures were supplied with more or less the same quantity of food. The exact quantity of food (number of cells/ml) was not measured, since the same was considered to be in surplus.

It is apparent from Table I, that the temperature has a greater influence upon the rates of population parameters and time devoted to various lifespan activities than does food in *S. vetulus*. A maximum life span of 78 days was recorded at 15°C and a minimum of 34 days at 28°C. The egg and pre-adult developmental time decreased with increase in temperature whereas post-adult developmental

Table II. Time devoted to various life span activities, egg developmental time, total juveniles produced, instantaneous growth (r), intrinsic birth (b) and death (d) rates of *S. vetulus* in given food concentration at four experimental temperatures.

	Temperature 8 ± 1°C				15 ± 1°C		
Food concentration (cells/ml)	25 000	50 000	75 000	100 000	25 000	50 000	75 000
Total lifespan (days)	47	49	48	48	71	74	78
Pre-adult developmental time (days)	28	30	29	29	23	22	25
Pre-adult moults	5	5	5	5	5	5	5
Post-adult moults	5	5	5	5	14	14	14
Post-adult developmental time (days)	19	19	19	19	48	52	52
Developmental time of egg (days)	12	12	12	12	4.11	4.11	4.11
Average number of juveniles produced by one female	52.8	63.0	62.6	78.2	126.0	163.6	154.2
S.D. (±)	7.08	3.80	3.50	2.59	3.81	4.39	4.60
Growth rate (r)	0.078	0.081	0.082	0.087	0.108	0.104	0.099
Death rate (d)	0.0052	0.0036	0.0034	0.0028	0.0011	0.0009	0.0011
Birth rate (b)	0.0832	0.0844	0.0854	0.0898	0.1091	0.1049	0.1001
Average total population at the end of experiment	40.6	52.6	53.2	68.2	2152.6	2214.2	2290.0
S.D. (±)	5.8	10.0	8.0	12.8	23.0	12.0	8.0

time did not show any definite pattern and was maximum at 15°C. There were 5 pre-adult moults at each temperature; however, post-adult moults varied from a minimum of 5 at 8°C to a maximum of 17 at 21°C. In general, birth, death and growth rates did not show any marked variation at different food concentration in a given temperature. However, instantaneous growth rate (r), intrinsic birth rate (b), average number of juvenile produced, and total population tended to increase with increasing temperature from 8°C to 28°C. The death rate was highest at 8°C and did not show much variation at other given temperatures.

To ascertain the effect of nutrition on the different parameters of population, four different concentrations of food, *viz.*, 25 000, 50 000, 75 000 and 100 000 cells/ml were tested at each of the four different temperatures, e.g., 8°C, 15°C, 21°C and 28°C separately. Table II depicts the effect of the above food concentrations on various life span activities, the birth, growth and death rate of *S. vetulus*.

Discussion

In general, the cladoceran population consist entirely of parthenogenetic females for most of the year. (Pennak, 1953, Hutchinson, 1967). Several authors

	21 ± 1°C				28 ± 1°C			
100 000	25 000	50 000	75 000	100 000	25 000	50 000	75 000	100 000
74	63	64	65	65	34	34	34	35
23	23	23	21	22	9	9	9	9
5	5	5	5	5	5	5	5	5
14	14	14	17	17	12	12	12	12
51	40	41	44	44	25	25	25	25
4.11	3.47	3.47	3.47	3.47	1.55	1.55	1.55	1.55
181.4	205.0	228.6	222.8	231.0	244.4	242.3	266.4	283.4
3.13	6.08	5.85	6.30	5.09	2.02	3.85	4.39	4.97
0.104	0.131	0.130	0.128	0.128	0.265	0.265	0.265	0.257
0.0013	0.0018	0.0007	0.0008	0.0007	0.0028	0.0022	0.0026	0.0026
0.1063	0.1328	0.1307	0.1288	0.1287	0.2678	0.2673	0.2679	0.2605
2326.4	4036.8	4239.2	4291.6	4327.4	8191.0	8216.0	8295.0	8322.0
11.0	15.0	10.8	8.6	16.0	12.4	28.8	21.4	12.9

reported the absence of males from the cladoceran population (Apstein, 1907; Brook and Rzosk, 1954; Byers, 1960; Michael, 1962). In *S. vetulus*, as reported by Pennak (1953), the sexual phase was limited and the males were found only for a short period during peak population of parthenogenetic females. The presence of males was attributed to the crowding of females, shortage of food and to the change in temperature (Banta, 1939; Pennak, 1953; Clark and Carter, 1974; Kwick and Carter, 1975). The occurrence of ephippial eggs immediately after the decline of the male population could probably be attributed to the production of these eggs by sexual activity. Berg (1931) noticed the presence of the ephippial females during or just before the onset of adverse environmental conditions in certain species of *Daphnia*. Pennak (1953) hypothesized that the production of ephippial eggs during unfavourable conditions is a device for the preservation of the population for a long period. In the present study, a few ephippial females occurred during the period of the maximum density of the parthenogenetic females. The maximum density of such females was, however, recorded during the periods of the drying of the shoreline of the lake. Similar observations have also been made recently by Clark and Carter (1974) and Kwick and Carter (1975).

In a population, the frequency of a particular size-age group depends upon the

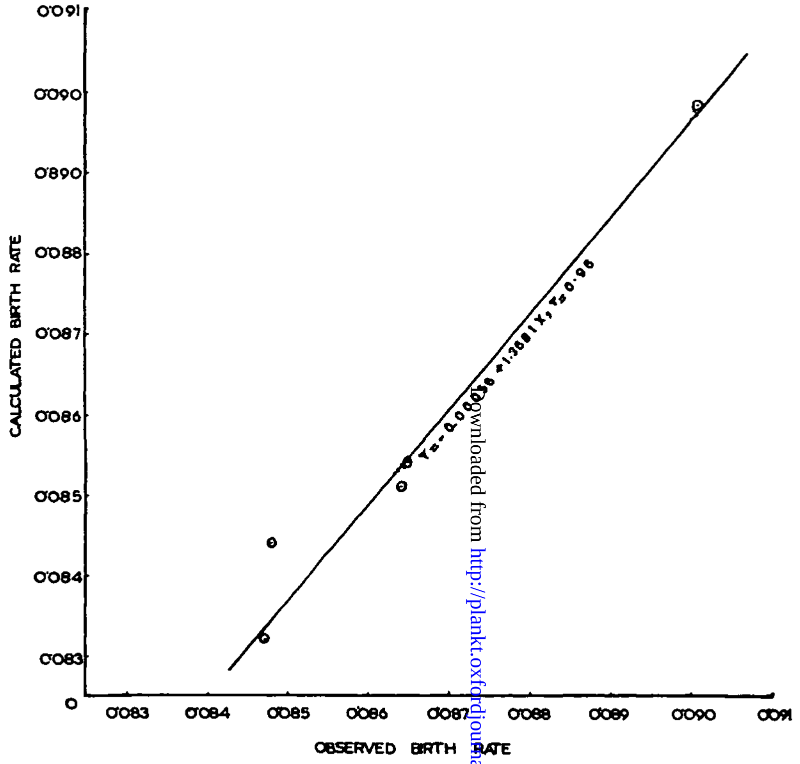

Fig. 6. Relationship between observed and calculated birth rate values of *S. vetulus*.

increase and decrease of one size-age group individuals or the other (Edmondson, 1955). In contrast to the regular shifting of different size-age groups recorded by Edmondson (1955), no definite pattern of shifting of the various size-age group individuals could be made out in the present study. The probable reason for such a disorderly pattern of size-age group individuals could be assigned to the continuous recruitment of the individuals to the populations from both hatching of ephippial eggs and release of juveniles from the parthenogenetic females.

The influence of temperature on the rate of development and on life span as observed by Hall (1964) in *Daphnia galeata mendotae* has been found valid in the present investigation on *S. vetulus* (Table I). The highest number of instars were observed at 21°C. The lowest life span was at 28°C and 8°C, with 5 pre-adult instars at each temperature. Michael (1962) observed a life span of 12 days for *Ceriodaphnia corunata* in the laboratory at a temperature range of 28°C to 31°C, with 5 pre-adult instars. Anderson *et al.* (1937) recorded 5 pre-adult instars in temperate *Daphnia pulex* at a temperature range of 15 – 22°C. Incidentially, the same number of pre-adult instars were also found in the arctic *D. middendorffiana* at a lower range of temperature from zero to 10°C by Edmondson (1955). The presence of 5 pre-adult instars at different temperatures and climatic conditions in the different species of *Daphnia* and *S. vetulus*, probably indicate the cosmopolitan nature of the group in general. However, the number of post-adult

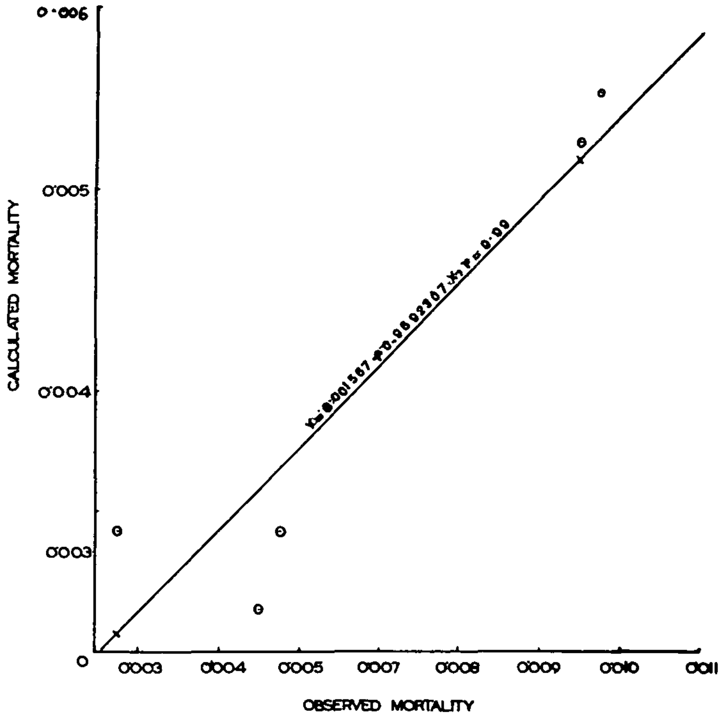

Fig. 7. Relationship between observed and calculated death rate values of *S. vetulus*.

instars in these species varies with the maximum occurring in the temperate (15 – 22°C) forms and the minimum in the arctic ones (0 – 10°C). The tropical species (28 – 31°C) more or less occupy an intermediate position. In *S. vetulus*, minimum and maximum number of post-adult instars were found at 8°C and 21°C, respectively. At a higher temperature, i.e., 28°C, a moderate number of instars were recorded. It appears, therefore, that the lesser number of instars in arctic and temperate forms as well as in *S. vetulus* at lower temperatures is probably a device to complete the life cycle before unfavourable environmental conditions set in. In certain cases hereditary factors and even differences in culture media may also cause variation in the number of instars (Anderson and Jenkins, 1942). However, these factors were not taken into consideration in the present study.

The egg production varies from species to species. In *S. vetulus* the production of eggs increased from first to fifth or sixth adult instars and decreased thereafter. This observation is similar to that recorded for many temperate daphnids like *D. pulex* (Anderson *et al*, 1937), *D. magna* (Anderson and Jenkin, 1942) and *D. longispina* (Green, 1955). Navanethakrishnan and Michael (1971), studying *D. carinata*, observed the increased production of eggs from first adult instar to the last instar. The variation in the egg production in different species may be caused by differences in temperature (McArthur and Baillie, 1929) or concentrations of food (Dunhan, 1938; Anderson and Jenkins, 1942) or genetic differences (Banta, 1979). In *S. vetulus* the number of eggs produced varied at different temperatures and food concentrations, however, it was always high in fifth or sixth instars (third instar at 8°C) at all temperatures and food concentrations in the laboratory, suggesting that the fecundity is perhaps age-specific in this species.

Navanethakrishnan and Michael (1971) suggested that, in the case of *D. carinata*, a tropical species, it is advantageous to produce eggs in increasing number until the last instars which may be a device to build up the population rapidly during favourable environmental conditions. According to them, in the temperate *D. pulex* there is a trend towards a decrease in egg production even during the middle of the reproductive period, but these organisms appear to have much larger life span and more adult instars (15 – 20); thereby their total egg production may exceed that of the tropical species. In *S. vetulus*, considering its longer life span, the production of higher number of eggs at fifth or sixth post-adult instars would enable the species to produce more and more eggs and build up its population before unfavourable conditions (shortage of food, lowering of temperature, etc.) set in.

In general, the population increased with an increase in food concentration at all temperatures in the laboratory (Slobodkin, 1954; Hall, 1964). Similar observations were also made for *S. vetulus* population in the laboratory.

The rapid increase in the population from late July to early August was preceded by a period of relatively high birth rates (reaching values in excess of 0.1) and apparent negative death rates, indicating the hatching of resting eggs, that grew very rapidly in the presence of ample food supply. Similar observations were made also by Clark and Carter (1974) and Kwick and Carter (1975) in various species of Cladocera. The present study confirms a direct relationship between food supply and birth rate under laboratory conditions. After this phase, the size of the population decreased gradually untill the first week of January. The growth rate assumed negative values, mainly because individuals were continuously lost through mortality. The values of mortality always exceeded birth rates. The subsequent increase in the population between the second week of January and mid-February was due to positive growth rates, i.e., natality exceeded mortality. Subsequently a decline in the field population of *S. vetulus* was accompanied by a low growth rate which eventually became negative due to a sharp increase in death rate.

The bimodal curve representing the population size of *S. vetulus*, for a period of one year, is typical of many zooplankton populations. The two peaks in the population of this zooplankton were associated with the two troughs in the chlorophyll *a* concentration. The rapid increase in the size of the population from July to October could possibly be attributed to the high concentration of chlorophyll-bearing organisms during the corresponding period. The death and birth rates were high during this period, but the former never exceeded the values of the latter. The population peaked during October, declining sharply thereafter by overshooting the carrying capacity of the food-limited environment. The food and population remained quite low untill January. Corresponding with the increase in temperature, the population also increased in size and reached a second peak during February. This peak was, however, characterized by a smaller

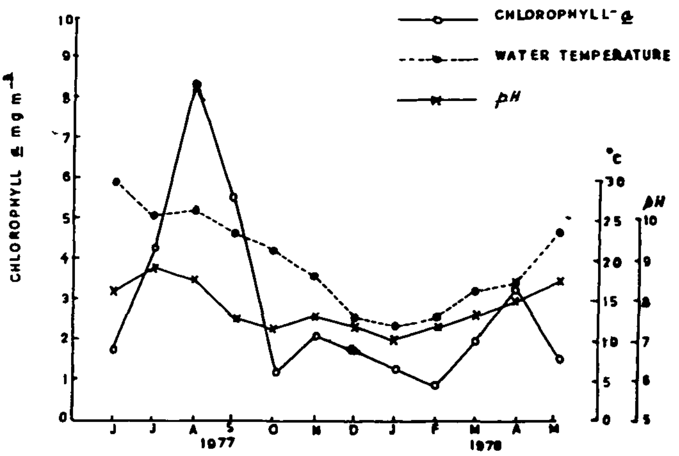

Fig. 8. Seasonal variation in chlorophyll *a* concentration, water temperature and water pH at Bhimtal lake.

number than the peak that occurred during October. The temperature, of course, exhibited an increasing upward trend all through spring and onwards, but the population declined after February and finally vanished with the onset of unfavourble conditions during summer. The food concentration in the form of chlorophyll- bearing organisms was quite low but the level of the total food (contributed by non-chlorophyll-bearing organisms) appeared to be enough to sustain or support the total but low population of *S. vetulus* during the winter. However, as the grazing pressure on the food was over during early spring after the levelling off of zooplankton population, the chlorophyll concentration exhibited another trough towards the end of April.

Besides food and temperature, the hydrogen ion concentration of the water also appeared to influence the size of the population. The pH of the water varied all through the year ranging from 7.0 to 8.7. However, both the peaks in the*S. vetulus* population occurred at a time when the pH ranged between 7.0 to 7.5. Hutchinson (1967) while reviewing the world literature also reported the maximum population of cladocerans at the above range of pH.

There was a positive correlation between fecundity and death rate (Figure 9) with a strong facultative relationship between the former and the food supply. This can be accounted for by differences in age specific death rates combined with a high relative frequency of young in a growing population. Since death rate is negatively correlated with the food supply, it therefore appeared that besides food some other factors also regulated the population size in *S. vetulus*. The fecundity was directly related with different levels of food at given temperatures in the laboratory. Clark and Carter (1974), while working on *D. rosea* found a strong negative correlation between fecundity and death rate, with a corresponding negative correlation between death rate and state of nutrition. The food is considered to be primary limiting mechanisms in *Daphnia rosea* (Clark and Carter, 1974). However, in *S. vetulus*, contrary to Clark and Carter (1974), food alone is not the limiting factor, but temperature also influences the size of

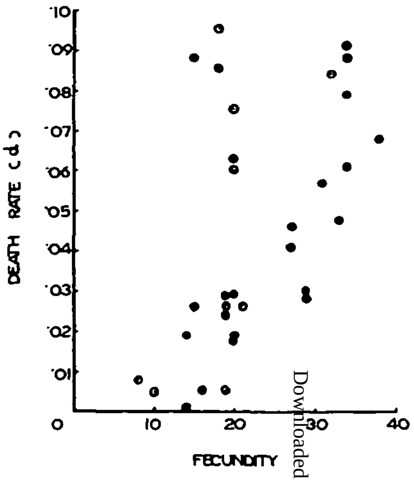

Fig. 9. Relationship between fecundity and death rate values of *S. vetulus*.

population by affecting the birth and growth rate. It is interesting to note that the pre-adult developmental time, pre-adult moults, and the death rate at 15°C and 21°C is more or less the same (recall that birth rate and growth rate tends to increase with increase in temperature), yet the life-span has decreased from 78 days (15°C) to 63 days (21°C). The number of post-adult moults increased on one hand and the post-adult developmental time decreased; this probably indicated the age-specific mortality.

In natural as well as in laboratory conditions, the intrinsic growth and birth rates were influenced by the temperature. In general, an increase in temperature results in an increase in growth and birth rates. However, at high temperatures (above 28°C) the mortality increases whereas the natality decreases. Similar trends in natality and mortality were also observed below 8°C. The population declined very sharply as higher and lower limits of temperature were exceeded during summer and winter, respectively. During summer, the other conditions including shortage of food, lowering of water level and drying of the shore line also became unfavourable. These together resulted in population declines and eventually their elimination from the lake. In *S. vetulus* temperature influenced growth rate more strongly than the food level, under the conditions examined. Frequency of moulting and reproduction and duration of egg development were influenced principally by temperature, whereas growth/instar and brood size appeared to be influenced mainly by food. These observations were similar to those reported by Hall (1964) for *D. galeata mendotae*.

The birth rate values obtained in the laboratory at different temperatures coincided well with the values obtained for natural populations during different periods of the year. The lower birth rates in the field population during the winter season, corresponding to the laboratory temperature of 8°C, were probably due to the decrease in the concentration of food during these months, from July to November, when the average temperature of the lake water was 18.3°C. The average value of birth rate (0.09) obtained for this temperature appeared to be quite close to the observed values of birth rate (0.11) at corresponding temperature ranging between 15°C and 21°C. The minor differences, could probably be due to the diurnal fluctuations in field temperature which were, however, kept constant in the laboratory.

The growth rates were generally higher in the laboratory population in comparison to the natural ones due to the fact that the food did not act as a limiting factor in the laboratory and the temperature was kept constant. Mortalities directly counted in the laboratory were considerably lower than in the field population because they were raised under controlled temperature and food conditions. The other environmental conditions (such as predation) affecting the field population were also eliminated in the laboratory.

Acknowledgements

The authors express their appreciation to Dr.J.S.Singh, Department of Botany and Dr. H.B.Tripathi, Physics Department, Kumaun University, Naintal for critically going through the manuscript. P.C.S. is also thankful to D.S.T. New Delhi and C.S.I.R. New Delhi for providing the fellowships during the period of study.

References

Alikunhi,K.H.: 1952, 'On the food of young carp fry', *J. Zool. Soc. India*, **4**, 77-84.

Anderson,B.G. and Jenkins,J.C.: 1942, 'A time study of events in the life span of *Daphnia magna*', *Biol. Bull.*, **83**, 260-272.

Anderson,B.G., Lumer,H. and Zupancic,L.J.,Jr.: 1937, 'Growth and variability in *Daphnia pulex*', *Biol. Bull.*, **73**, 444-463.

Apstein,C.: 1907, 'Das Plankton im Colombo See auf Ceylon', *Zool. Jb. (Abt. Syst.)*, **25**, 201-244.

Banta,A.M.: 1939, 'Studies on the physiology, genetics and evolution of some Cladocera', *Carnegie Inst. Wash. Publ.*, **513**, 285.

Berg.K.: 1931, 'Studies on the genus *Daphnia* O.F.Muller with special refrence to the mode of reproduction', *Vidensk. Medd. Dansk. Matlerh. Forem. Kbh.*, **19**, 1-222.

Brook,A.J. and Rzosk,J.: 1954, 'The influence of the Gebel Aulyia Dam on the development of Nile plankton', *J. Anim. Ecol.*, **24**, 101-114.

Borecky,G.W.: 1956, 'Population density of the limnetic Cladocera of Pymulancing Reservoir', *Ecology*, **37**, 719-727.

Byers, J.A.; 1960, 'A freshwater pond in New Zealand', *Aust. J. Mar. Freshwater Res.*, **11**, 222-240.

Clark,A.S. and Carter,J.C.H.: 1974, 'Population dynamics of cladocerans in Sunfish Lake, Ontario, *Can. J. Zool.*, **52**, 1235-1242.

Dunham,H.H.: 1938, 'Abundant feeding followed by restricted feeding and longevity in *Daphnia*', *Physiol. Zool.*, **11**, 399-407.

Edmonson,W.T.: 1955, 'The seasonal life history of *Daphnia* in an arctic lake, *Ecology*, **36**, 439-455.

Green,J.: 1955, 'Studies on a population of *Daphnia magna*', *J. Anim. Ecol.*, **24**, 84-97.

Hall,D.J.: 1964, 'An experimental approach to the dynamics of natural population of *Daphnia galeata mendotas*', *Ecology*, **45**, 94-112.

Harbosch,P.: 1920, 'Die süsswasser-entromestrecen Gronlands, eine faunistische, oecologische, untiergeograpische Studie', *Z. Hydorol.*, **1**, 136-184.

Jones,H.R., Lack,T.J. and Jones,C.S.: 1979, 'Population dynamics and production of *Daphnia hyalina* var *lacustris* in Farmoor I, a shallow eutrophic reservoir, *J. Plankton Res.*, **1**, 45-65.

Kwick,J.K. and Carter,J.C.H.: 1975, 'Population dynamics of Limnetic Cladocera in a beaver pond', *J. Fish Res. Board Can.*, **32**, 341-346.

McArher,J.W. and Baillie,W.H.T.: 1929, 'Metabolic activity and duration of life. I. Influence of temperature on longevity in *Daphnia magna*', *J. Exp. Zool.*, **53**, 243-268.

Michael,R.G.: 1962, 'Seasonal events in a natural population of the cladoceran *Ceriodaphnia cornuta* Sars and observations on its life cycle', *J. Zool. Soc. India,* **14**, 211-218.
Navenethankrishnan,P. and Michael,R.G.: 1971, 'Egg production and growth in *Daphnia carinata* King', *Proc. Indian Acad. Sci.,* **73**, 117-123.
Pennak,R.W.: 1953, '*Fresh water invertebrates of United States*', 2nd edition, published by John Wiley and Sons, Inc., 763 pp.
Slobodkin,L.B.: 1954, 'Population dynamics in *Daphnia obtusa* Kurz', *Ecol. Monogr.,* **24**, 69-88.
Tappa,D.W.: 1965, 'The dynamics of the association of six limnetic species of *Daphnia* in Aziscoos Lake', *Maine Ecol. Monogr.,* **35**, 395-423.
Vess,K.F. and Vas Van-oven,A.: 1959, 'Studies on the production and utilization of natural food in Indonesian Cart. ponds', *Hydrobiologia,* **21**, 308-392.
Vijayaraghaban,S.: 1970, 'Seasonal events in a natural population of *Daphnia carinata* King', *Proc. Ind. Acad. Sci.,* **5**, 193-293.
Welch,P.S.: 1952, '*Limnology*', published by McGraw-Hill Co., New York, 511 pp.
Wetzel,R.G.: 1975, '*Limnology*', published by W.B.Saunders Co., Philadelphia, 743 pp.
Wesenberg-Lund,C.: 1926, 'Contributions to the biology and morphology of the genus *Daphnia* with some remarks on heredity', *Mem. Acad. R. Sci. Lett. Dan., Sect. Sci., Ser. 8,* **11**, 89-251.
Wright,J.C.: 1965, 'The population dynamics and production of *Daphnia* in Canyon Ferry Reservoir', *Mentana. Limnol. Oceanogr.,* **10**, 583-591.