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Role of parthenogenetic natality and emergence from diapausing eggs in the dynamics of some rotifer populations

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Abstract

There are few quantitative data on the role of emergence from diapausing eggs in population dynamics of natural populations of zooplankton species; to our knowledge, all these concern copepods and 'cladocerans'. We present here direct estimates of emergence from bottom resting eggs for another important category of freshwater zooplankton, namely rotifers. Three populations of rotifers of the genus *Brachionus* were studied in a lake. During the study period 10 population increases, each corresponding to an individual sampling interval, were detected. For each interval, emergence from immediately hatching, parthenogenetic eggs calculated on the basis of the Edmondson-Paloheimo model and emergence from diapausing bottom eggs determined in short-term experiments were estimated and compared to each other. We found that three of the population increases observed are entirely explained by parthenogenetic natality. In contrast, emergence from diapausing eggs can, on its own, account for none of population increases. For two population increases, however, it accounts for that part of population growth which remains unexplained by the parthenogenetic natality. For rotifer populations studied, emergence from diapausing eggs is generally less important than parthenogenetic births, when both are regarded as an immediate cause of population growth. This is in sharp contrast to the data available for some crustaceans (De Stasio, 1990) where the role of emergence from diapausing eggs in population dynamics has been clearly shown.

Introduction

There is increasing, although mostly indirect, evidence that emergence from bottom diapausing eggs or cysts may be of great importance for population dynamics and seasonal succession in plankton systems (Bogoslovsky, 1969; Marcus, 1984; Kawabata & Ohta, 1989; De Stasio & Hairston, 1992; Yampolsky & Kalabushkin, 1992; Ishikawa & Taniguchi, 1994). However, direct estimates of the emergence in the field are still rare and for planktonic animals are mostly confined to crustaceans (De Stasio, 1989, 1990). As to another important category of freshwater zooplankton such as rotifers, little evidence exists of the role of their bottom resting eggs in population dynamics of active planktonic stages. Information on this process may be important not only for the study of rotifers itself but also for comparison with crustaceans. This may provide better understanding of the whole zooplankton community because copepods, 'cladocerans', and rotifers often coexist.

Several major processes are responsible for local population growth in zooplankton. These are recruitment from immediately hatching eggs which are often attached to the mother's body (in 'cladocerans' and rotifers such eggs are produced by parthenogenesis and referred to below as parthenogenetic eggs), from diapausing bottom eggs, and due to advection. Since all these factors may operate simultaneously they should be studied on the same time scale. We know of no instance, however, where this requirement is entirely fulfilled. Here we present data both on births from planktonic parthenogenetic eggs and on emergence from bottom diapausing eggs obtained concurrently.

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We have no data on advection, so its role will be judged only indirectly.

The normal way to calculate parthenogenetic natality in zooplankton is based on the Edmondson (1968) and Paloheimo (1974) model (for review see Polishchuk, 1986). It provides instantaneous, per capita estimates of the birth rate. In contrast, emergence from diapausing eggs as an empirical characteristic is expressed in terms of finite, absolute values. To make contributions of these two sources of population recruitment comparable, we slightly modify the standard approach to birth rate estimation.

In this paper we present direct estimates of the rate of emergence from the bottom diapausing eggs for three rotifer species. We estimate contributions of population recruitment due to parthenogenetic natality and due to emergence from diapausing eggs to the population increases observed. Finally, we compare our findings with those available in the literature for copepods and 'cladocerans'. Part of the material concerning the emergence from diapausing eggs has already been presented (Mnatsakanova, 1990). For the present work, the data were recalculated and corrected.

Materials and methods

Study area and sampling procedure

The study was carried out at Lake Chirtovo not far from Nizhny Novgorod, in the flood-lands of the Oka River. The lake is subdivided into three highly extended arms (west, north-eastern, and south) with a total area of 62 ha (Fig. 1). The lake is part of a system of slowly moving stretches of water and has an inflow to its west arm and outflow from the north-east. Through the inflow it is fed with treated sewage from a piggery with high concentration of N (N-NH_4, 59 mg l^{-1}) and P (P-P_2O_5, 15.5 mg l^{-1}, see Voroshilov *et al.*, 1985). Samples were taken in the south bay which is clear of the main stream and can be considered semi-isolated (Voroshilov *et al.*, 1985). It is 100 m wide and 2 m maximum depth. The water is thermally uniform, with temperature ranging from 14 to 24 °C during the study period. Zooplankton species composition varies from year to year partly due to whether fish are introduced with the Oka River during spring flood. In the year studied, zooplankton was dominated by brachionid rotifers, although *Daphnia*, *Moina* and several copepod species were also present.

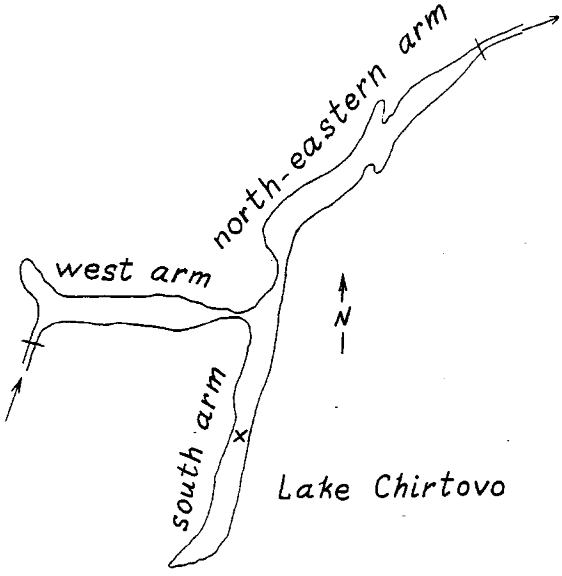

Fig. 1. A map of Lake Chirtovo. Arrows denote the inflow to and the outflow from the lake. The cross indicates the study area.

Zooplankton samples were collected from 23 May to 21 July 1987 every 3 d, with a gap in the observations from 19 June to 4 July. On each occasion samples were taken at about 11 a.m. Four hauls from different stations situated not far from one another (Fig. 1) were made with a plankton net (open area 0.05 m^2, mesh size 100–200 μm) towed from the bottom to the surface. The four samples were pooled, transported to the laboratory and treated immediately. Subsamples of sufficient volume to provide at least 100 animals of each species studied were counted in a Bogorov plankton tray under a dissecting microscope. Formalin was added by drops directly in the tray to prevent egg loss. Counts were made of the number of animals per litre (N) and the number of female parthenogenetic eggs per litre (E) for three rotifer species: *Brachionus calyciflorus*, *B. urceus*, and *B. angularis*. The ratio of eggs to animals, E/N, called the egg ratio was then calculated. Unsmoothed data were used throughout. Resting eggs which were also counted when observed, were not included in E. Males, because of their small size, must have passed through the net and were never seen in the samples. Male-producing parthenogenetic eggs when observed were therefore excluded from calculations of E.

Water temperature was measured every day or every second day. On that basis the egg development time (D, in days) was calculated according to the equation presented by Bottrell *et al.* (1976).

An important source of statistical error involved in population abundance estimates is spatial heterogeneity of zooplankton. Unfortunately, in 1987 we have no data allowing it to be assessed. Such data are available on 18 August 1985 when 9 net samples were taken at different stations simultaneously (within an hour) and each sample was counted separately. All these stations were within the area where samples were taken in 1987. Zooplankton at that time consisted almost entirely of *B. calyciflorus*. Using a program written in BASIC we computed the standard error of population size estimates for all $\binom{9}{4} = 126$ distinct combinations selecting 4 samples out of 9. Then the relative error, that is, the ratio of SE to the mean size, was calculated. It averaged 18% and was applied to the population size estimates in 1987.

Technique for hatching experiments

For taking bottom sediments, we used a corer designed by Sorokin (Chirkova, 1975) which is similar to the Kajak corer (Downing, 1984). The corer has a transparent plastic tube with a 33 mm inner diameter which penetrates the sediments 7–10 cm. On withdrawal, the tube was half or a little less full of sediments, with the above-sediment water filling its upper part. When hoisted to the boat, the tube was immediately closed at the bottom and detached from the frame. To transfer the sediments undisturbed, a glass tube of a smaller diameter of 30 mm was forced through the corer's tube. The corer's tube was then fastened to the frame, and the process was repeated to yield 1 to 4 sample tubes on each sampling occasion. Samples were taken from 5 to 19 June and from 3 to 22 July 1987 every day or every second day from the same area as zooplankton samples.

The glass tubes with the sediments were immediately transported to the laboratory. After 20 min standing, the water in the tubes was carefully removed with a siphon to prevent disturbing the sediment. In order to remove every zooplankter from the remainder of the above-sediment water some 100 ml of carbon dioxide saturated soda-water was poured into the tube. Highly concentrated soda-water kills zooplankters (Mudretsova-Wiss, 1933; pers. obs.). After 10 to 30 min standing, the soda-water was siphoned off and fresh, filtered lake water was poured into the tube.

The tubes were allowed to stand undisturbed in the lab or, on several occasions, in the lake. Temperature in the lab was no different from that in the lake. After 1 to 2 d, the above-sediment water was drawn off and any rotifer hatchlings present were counted by species. We never used the tubes once examined for further examination of hatching; instead, fresh samples of sediments were regularly taken and emergence of newly hatched rotifers was recorded.

All hatching rates symbolized below as V were expressed as animal numbers per litre per day. We first calculated the number of animals found in a tube to the number per square metre per day and then converted this to a litre basis, taking a lake depth in the study area to be 2 m.

Contribution of input from the sediments and parthenogenetic births to population increase

In zooplankton, recruitment from parthenogenetic eggs is commonly estimated from the Edmondson (1968) and Paloheimo (1974) model which yields an estimate for the instantaneous per capita birth rate b,

$$b = (1/D)\ln(1+q)\,, \tag{1}$$

where D is the egg development time (d), $q = E/N$ is the egg ratio. Two other characteristics routinely calculated in combination with birth rate are the instantaneous per capita rate of population change r and death rate d,

$$r = (\ln N_t - \ln N_0)/t\,, \tag{2}$$

$$d = b - r\,, \tag{3}$$

where N_0 and N_t are the population abundances at the beginning and at the end of sampling interval t, respectively. Equation 1 is supposed to be based on the exponential model of population growth (for general discussion see Polishchuk, 1986), although when $t = D$ this assumption is shown to be unnecessary (Voronov, 1991). In our study, as it is typical when studying rotifers, $t = 3$ d is several times larger than D which is about 1 d at the temperatures observed in the lake, so the assumption concerning the exponential growth remains essential.

An important assumption underlying Equations 1 and 3 is that the population is closed, that is, there occurs no immigration or emigration. This assumption is, of course, violated when a population experiences an inflow from diapausing eggs deposited in the sediments which is actually the case for the rotifer populations studied. We will show, however, that the contribution of emergence from diapausing eggs to the population growth is relatively small, so Equation 1 can, we believe, be used to estimate birth rate.

A problem with comparison between the contribution of emergence from resting eggs and that of parthenogenetic births to population growth is that the hatching experiments give a value of emergence which corresponds to an absolute population increase such as $N_t - N_0$ or $(N_t - N_0)/t$, whereas birth rate from Equation 1 corresponds to the instantaneous per capita population growth rate. Contribution of emergence from resting eggs relative to an absolute population increase can be expressed as

$$V\,t(N_t - N_0)^{-1}\,, \tag{4}$$

where $V\,t$ represents an absolute number of individuals entering the planktonic population from diapausing eggs over sampling interval $(0, t)$. Given the exponential population growth model, the number of individuals coming from parthenogenetic eggs over interval $(0, t)$ is given by

$$B = \int_0^t bN\,\mathrm{d}t = b\,r^{-1}(N_t - N_0)\,. \tag{5}$$

Contribution of parthenogenetic natality found by analogy with Eq. 4, takes the form

$$b\,r^{-1}\,. \tag{6}$$

The normal practice is to employ the egg ratio in Equation 1 specific to the beginning of sampling interval. When sampling interval equals the egg development time, this practice is certainly valid since it is justified by the arguments underlying the Edmondson-Paloheimo model (Polishchuk, 1986; Voronov, 1991). However, when $t > D$, it is probably better to use the average q and D. We use here the arithmetic means of q and of D over each sampling interval.

Using Equations 1, 2, 4, and 6, we calculated the contribution of emergence from diapausing eggs and that of parthenogenetic natality for each sampling interval where the populations were found to increase. Only population increases are analysed here because emergence manifests itself, as a factor of population dynamics, most clearly when the population is increasing. Only summer increases are considered because data on emergence from diapausing eggs are available beginning on 5 June.

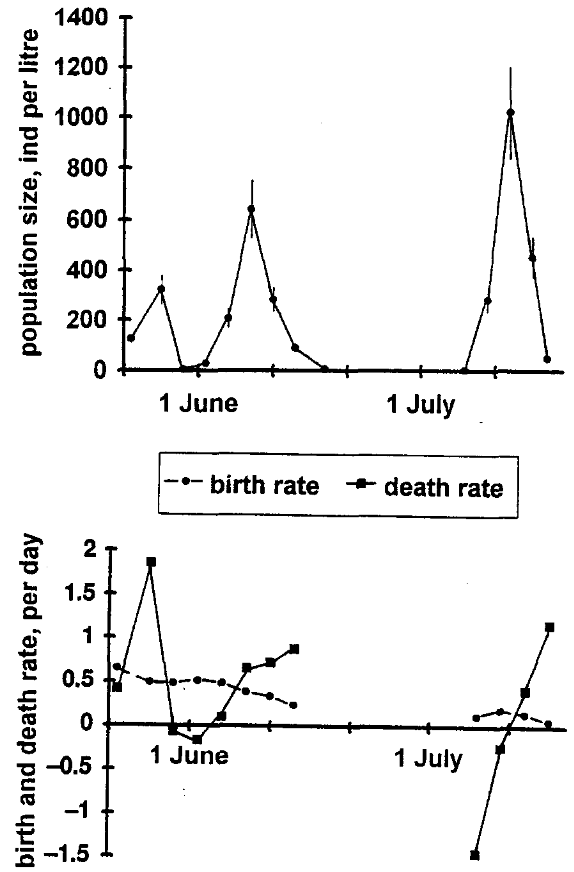

Fig. 2. Seasonal dynamics of *Brachionus calyciflorus* in summer 1987. *Upper panel* – Population size. Error bars indicate ± SE, and, if not shown, are smaller than the symbol size. *Lower panel* – Birth and death rates. See text for detail.

Results

Seasonal changes in population sizes and contribution of parthenogenetic births to population growth

At the beginning of summer we observed two peaks in *Brachionus calyciflorus*, in late May and early June. Maximum population size reached 640 ind l^{-1} (Fig. 2). Following the gap in observations, a sharp peak of population abundance of about 1000 ind l^{-1} occurred in mid July. *B. angularis* and *B. urceus* each exhibited only one population peak of about 1500 ind l^{-1} in early June (Figs 3 and 4). Also, seasonal changes in birth and death rates calculated by Equations 1 and 3 are shown in Figs 2 to 4.

For the three rotifer species studied, ten summer population increases, each relating to an individual

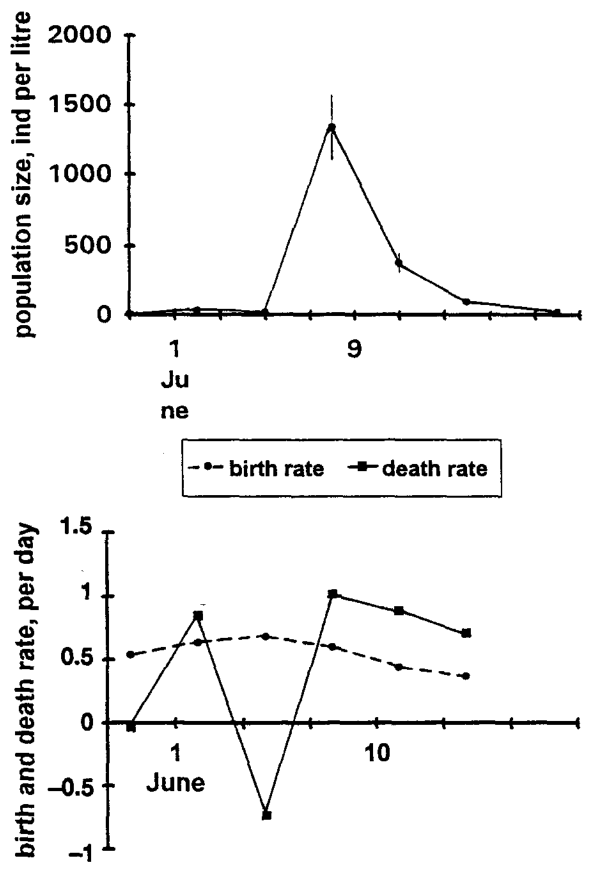

Fig. 3. As Fig. 2, but for *Brachionus angularis.*

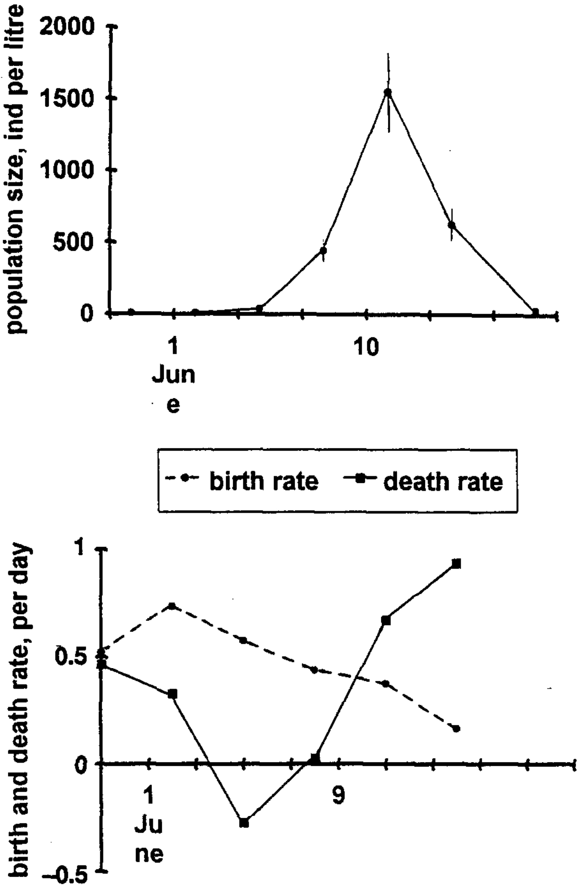

Fig. 4. As Fig. 2, but for *Brachionus urceus.*

sampling interval, have been analysed (Table 1). We consider only those increases which appear to be real, given the range of population size variation over individual sampling intervals and possible errors of population size estimates. Contributions of parthenogenetic natality to population increases vary from 8% to more than 100% (three intervals out of 10, Table 1). The latter means that $b > r$ so that the increases where contributions exceed 100% can be entirely attributed to parthenogenetic natality. Excluding figures higher than 100%, parthenogenetic natality is responsible on average for 62% of the magnitude of population increases.

Contribution of emergence from diapausing eggs to population growth

Emergence from diapausing eggs was rare (there were zero to 5 hatchlings per tube per day for *Brachionus calyciflorus*, for example), and so it is hard to discuss temporal changes in the emergence rate. Emergence rates in the tubes left in the laboratory did not significantly differ from the rates obtained in the tubes concurrently suspended in the lake. In three cases with synchronous determination of emergence rates in the laboratory and in the lake, differences between average rates are 44%, 9%, and 12% (all the data for *B. calyciflorus*). This appears to be rather small taking into account that the maximum and minimum emergence rates observed in individual tubes which were run concurrently and held in the laboratory sometimes differ by a factor of 10. Here we use only the average emergence rate for periods of continuous observation.

B. calyciflorus hatched throughout the whole study period, while *B. angularis* and *B. urceus* hatched only in June. This correlates with the fact that the two latter species were not found in the plankton in July. Mean emergence rate ranges from 0.6 to 2.1 ind l^{-1} d^{-1},

Table 1. Population size and contribution of parthenogenetic births to population increase for three rotifer species. Notation: N_0 = actual population size at the beginning of sampling interval, N_t = actual population size at the end of sampling interval, SE = standard error, D = mean egg development time, q = mean egg ratio (E/N), b = birth rate, $b = (1/D)\ln(1+q)$, r = rate of population increase, $r = (\ln N_t - \ln N_0)/t$, where $t = 3$ d is sampling interval, Cont = contribution of parthenogenetic births to population increase, Cont = $b\,r^{-1}$ 100%. If contribution is less than 100% the observed population increase cannot be explained by the recruitment from parthenogenetic eggs.

Sampling interval	$N_0 \pm$ SE (ind l^{-1})	$N_t \pm$ SE (ind l^{-1})	D (day)	q	b (d^{-1})	r (d^{-1})	Cont (%)
			Brachionus calyciflorus				
30 May – 2 June	5.4 ± 1.0	27.5 ± 5.0	1.6	1.2	0.48	0.54	89
2 – 5 June	27.5 ± 5.0	206.1 ± 37.1	1.2	0.9	0.51	0.67	76
5 – 8 June	206.1 ± 37.1	640.0 ± 115.2	1.0	0.6	0.48	0.38	128
7 – 10 Jule	2.6 ± 0.5	282.7 ± 50.9	0.9	0.1	0.12	1.57	8
10 – 13 July	282.7 ± 50.9	1019.4 ± 183.5	0.8	0.2	0.20	0.43	46
			Brachionus angularis				
30 May – 2 June	6.5 ± 1.2	35.8 ± 6.4	1.6	1.3	0.54	0.57	94
5 – 8 June	18.9 ± 3.4	1337.4 ± 240.7	1.0	1.0	0.72	1.42	51
			Brachionus urceus				
2 – 5 June	10.3 ± 1.8	34.9 ± 6.3	1.2	1.5	0.74	0.41	180
5 – 8 June	34.9 ± 6.3	445.2 ± 80.1	1.0	0.8	0.61	0.85	72
8 – 11 June	445.2 ± 80.1	1548.6 ± 278.7	0.9	0.5	0.44	0.42	106

Table 2. Rate of emergence from bottom diapausing eggs expressed on a litre basis. Notation: n = number of observations, V = emergence rate, SD = standard deviation, CV = coefficient of variation. Emergence rate presents the mean value for the periods indicated.

Period	n	V (ind l^{-1} d^{-1})	SD (ind l^{-1} d^{-1})	CV (%)
		Brachionus calyciflorus		
5 – 19 June	21	1.64	1.21	73
3 – 22 July	12	0.59	0.37	63
		Brachionus angularis		
5 – 19 June	14	0.92	0.59	64
		Brachionus urceus		
5 – 19 June	17	2.13	2.15	101

with a coefficient of variation between 60 and 100% (Table 2).

Such a low hatching rate as compared with the population increases observed (Table 3) implies that recruitment due to emergence from diapause eggs can only play a part in population growth if population size is low. Indeed, all three sampling intervals where emergence makes a sizeable contribution of 10 to 25% to population increase comprise the very early stage of the population growth (Table 3). In the other seven intervals where the populations increase, the contribution of emergence is less then 3%. A mean contribution of emergence from diapausing eggs, for all ten sampling intervals, comprises 6.5%. Emergence from diapausing eggs on its own accounts for none of the population increases. It might be important, however, as an additional factor when parthenogenetic natality alone fails to explain population increase.

Consider the role of emergence from diapausing eggs for those sampling intervals where the contribution of parthenogenetic natality is less than 100%, that is, the birth rate is lower than the actual rate of population growth. We estimated the extent to which emergence from diapausing eggs can close the gap between actual population increase and the number of individuals hatched from parthenogenetic eggs. That is, we calculated the quantity $V\,t\,[(N_t - N_0) - B]^{-1}$ where B is taken from Equation 5. In two cases out of seven, emergence from diapausing eggs contributes more than 100% to that gap (Table 3), thus being the sec-

Table 3. Contribution of emergence from bottom diapausing eggs to population increase or to the gap between population increase and the number of parthenogenetic births over sampling interval. Notation: N_0 and N_t = population sizes at the beginning and end of sampling interval. Cont 1 = contribution of emergence from diapausing eggs to population increase; Cont 1 = $V\,t(N_t - N_0)^{-1}$ 100%, where V is emergence rate from Table 2 and $t = 3$ d is sampling interval. B = number of individuals coming from parthenogenetic eggs over sampling interval; $B = b\,r^{-1}(N_t - N_0)$, where b is birth rate, r is the rate of population increase, both are taken from Table 1. G = the gap between population increase and the number of individuals coming from parthenogenetic eggs, $G = (N_t - N_0) - B$. Cont 2 = contribution of emergence from diapausing eggs to gap G, Cont 2 = $V\,t\,G^{-1}$ 100%. PR means that population increase can be entirely attributed to parthenogenetic births, that is, $B > N_t - N_0$ and $b > r$.

Sampling interval	$N_t - N_0$ (ind l^{-1})	Cont 1 (%)	B (ind l^{-1})	G (ind l^{-1})	Cont 2 (%)
		Brachionus calyciflorus			
30 May – 2 June	22.1	22	19.7	2.5	200.8
2 – 5 June	178.6	2.8	136.5	42.1	11.7
5 – 8 June	433.9	1.1	554.4	PR	–
7 – 10 Jule	280.1	0.6	21.3	258.8	0.7
10 – 13 July	736.8	0.2	339.1	397.7	0.4
		Brachionus angularis			
30 May – 2 June	29.3	9.5	27.5	1.8	153.3
5 – 8 June	1318.6	0.2	670.9	647.7	0.4
		Brachionus urceus			
2 – 5 June	24.6	26	44.4	PR	–
5 – 8 June	410.3	1.6	295.8	114.5	5.6
8 – 11 June	1103.4	0.6	1169.7	PR	–

ond most important factor of population growth. We consider it the second on those two sampling intervals, as compared with parthenogenetic natality, because parthenogenetic natality taken alone explains 89 and 94% of the amount of the population increases, whereas emergence from diapausing eggs taken alone, only 22 and 10% (Tables 1 and 3). For five remaining intervals parthenogenetic births and emergence from resting eggs even taken together are insufficient to explain the population increases observed.

Discussion

We have analysed population increases for three species of brachionid rotifers over ten sampling intervals. Parthenogenetic natality on its own explains population increases over three intervals, whereas emergence from diapausing eggs on its own explains none at all. On average, parthenogenetic natality is responsible for 62% of the amount of population increases while emergence from diapausing eggs for 6.5% only. Notice that for parthenogenetic natality it is a conservative estimate because values larger than 100% were excluded when the average was calculated. Hence for the populations studied, parthenogenetic natality is a more important factor of population growth than emergence from diapausing eggs.

A role of emergence from diapausing eggs in population growth is revealed in two intervals where parthenogenetic natality taken alone cannot explain the population increases while both these factors operating simultaneously can. Nevertheless on five sampling intervals out of ten, population increases remain uninterpreted. We speculate that one more factor such as horizontal transport of animals within the lake affected the population growth.

It may be that our observations yield biased estimates of emergence rate. Temperature which is known to be among the factors inducing rotifer resting eggs to hatch (May, 1987), was approximately the same in the lake and laboratory. Yet other conditions in the experimental tubes may differ from those in the lake: diapausing eggs in the tubes are affected by increased aeration due to sediment disturbance which cannot be completely avoided, by additional light when tubes are being taken from the bottom and left standing in the laboratory (though we observed no marked difference when holding the tubes in the lake), and by a 30-min exposure to carbon dioxide. For crustaceans, all these influences are known to stimulate emergence from diapausing eggs (Alekseev, 1990), although for *Diaptomus sanguineus*, a freshwater calanoid copepod, low oxygen shock is reported to stimulate emergence (Hairston & Munns, 1984; De Stasio, 1989 but see Lutz *et al.*, 1992 for stimulating effect of high oxygen concentrations on hatching from diapausing eggs in marine calanoid copepods). If our experimental perturbation stimulates hatching from diapausing eggs, the observed emergence rates tend to be overestimated, and an actual recruitment from diapausing eggs becomes still less important for population growth.

Although it is widely appreciated that emergence from diapausing eggs may play a significant role in ensuring the existence of zooplankton populations on both ecological and evolutionary time scales (Hairston & De Stasio, 1988; De Stasio & Hairston, 1992; Marcus *et al.*, 1994), we know of no instance of estimating the rate of hatching of diapausing eggs from lake sediments in natural populations of rotifers (for review of the state of the art see Hollowday, 1993). Generally speaking, much more is known about the density of resting eggs in sediments and cues inducing hatching in the laboratory (for rotifers see e.g. Smirnova, 1985; May, 1987 and the literature therein) than about the natural input from resting eggs to the pelagial.

Pioneer research by De Stasio (1989, 1990) has shed new light on the role of emergence from diapausing eggs in seasonal dynamics of some planktonic freshwater crustaceans. Nauplii of calanoid copepods *Diaptomus sanguineus* and *Epischura nordenskioldi* from Bullhead Pond (Rhode Island, USA) appear in the plankton in late autumn every year. The start of emergence from diapause eggs, after a period of lack of emergence, was detected directly. Moreover, all nauplii that emerge in late autumn are from the bottom diapausing eggs as there have been no adult females in the plankton during a 2- (for *Epischura*) or 6-month (for *Diaptomus*) period before the first nauplii appear. Emergence from diapausing eggs thus determines the start of the annual population cycle. De Stasio (1990) also found that the timing of peak abundance of *Ceriodaphnia reticulata*, an anomopod 'cladoceran', in the plankton coincides well with peak emergence from the diapausing eggs. For another anomopod, *Eubosmina longispina*, emergence from diapausing eggs seems rare, with no correspondence between population dynamics in the plankton and emergence from the sediments. Note that De Stasio (1990) correlates the timing of planktonic and bottom events but does not compare numerically the magnitude of recruitment from those sources.

For the *Brachionus* species studied here, the situation in June and July appears similar to that for *Eubosmina*. Although emergence from diapausing eggs occurred during the whole study period, comparison of the contributions of parthenogenetic natality and diapausing eggs leads us to the conclusion that parthenogenetic, immediately hatching eggs play a bigger part in seasonal population growth than diapausing eggs.

When studying zooplankton population dynamics, one often comes up against the so-called "negative death rate" (Polishchuk, 1982). It arises when the difference between birth rate and the actual rate of population growth which normally serves as an estimate of the death rate (see Equation 3) turns out to be negative. For our data set we observed negative death rates on seven sampling intervals (Figs 2 to 4). These intervals are exactly those on which the contribution of parthenogenetic natality to population increase is less than 100% (Table 1). This is because $b/r < 1$ entails $d < 0$, and vice versa.

Negative death rate is commonly attributed to an input of individuals into the population (Polishchuk, 1982). Here we examine one possible source of such input, emergence from diapausing eggs deposited in sediments. We find that while the input from sediments does actually occur, in the majority of cases it is insufficient to explain that part of population growth which remains unexplained by the parthenogenetic natality. Hence some additional source of population recruitment must have been involved. Moreover, based on the percentage of sampling intervals where parthenogenetic natality and emergence from diapausing eggs taken together do now allow us to explain population increases (five out of ten intervals), we suggest that an unknown factor may play a rather large role in the population dynamics.

An important, while not well studied, agent in population recruitment of zooplankton is water movements and horizontal transport of animals (Threlkeld, 1987).

It is well documented for a natural re-establishment event for *Bosmina longirostris* in Lake Tahoe which resulted from wind-induced advection from a semi-isolated embayment (Threlkeld, 1981). We did not measure the water movement at the locality studied. Thus we can only suggest that in our water body horizontal transport may also have an effect on the population dynamics.

Since in nature diverse factors operate concurrently a better understanding can be attained when different aspects of population dynamics are studied simultaneously. Our study is the first to quantify the relative importance of input from bottom diapausing eggs and from planktonic, immediately hatching, eggs to population growth in zooplankton. However, half of the population increases observed cannot be accounted for by either of the processes considered. More comprehensive studies are needed to get more insight into the population dynamics of planktonic animals, whether they be crustaceans or rotifers. When both immediately-hatching and diapausing eggs are involved, the same principles apply to both groups.

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