Population dynamics of *Brachionus patulus* Muller (Rotifera) in relation to food and temperature

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Abstract. The combined effects of food (*Chlorella*) and temperature on the population growth of a laboratory clone of the rotifer *Brachionus patulus* were studied. The intrinsic rate of increase (*r*) as well as the maximum densities achieved were a function of temperature. While the *r* was negative at 15°C regardless of food level, its magnitude was dependent on food level at medium (25°C) and high (35°C) temperatures, indicating a significant temperature × food interaction. The seasonal variations in the abundance of *Brachionus patulus* in the plankton of a regularly sampled pond are explained in terms of the observed food-temperature effects on the survival and reproduction of the laboratory population.

Keywords. Rotifera; *Brachionus patulus*; population dynamics; food; temperature.

1. Introduction

A thorough knowledge of factors influencing the dynamics of rotifer populations is essential not only for understanding zooplankton community organization in natural freshwater bodies (Dussart *et al* 1984; Herzig 1987), but also for maximizing production of rotifers in aquaculture where they are offered as the first live food for cultured fish and crustaceans (Gatesoupe and Luquet 1981; Lubzens 1987; James and Abu-Rezeq 1989). Another area for application of this knowledge is aquatic ecotoxicology where certain parameters of rotifer population dynamics have been considered ideal for the bioassay of sublethal levels of pollutants (Halbach *et al* 1981; Halbach 1984). Although there have been field and laboratory studies on the effects of temperature and food levels on rotifers (Edmondson 1965; Halbach 1970; Pourriot and Rougier 1975; Hofmann 1977; Rothhaupt 1985; Galkovskaja 1987), very few considered the combined effects of these two factors, particularly for species inhabiting tropical freshwaters (Duncan 1984). Population dynamics, as Halbach *et al* (1981) put it, acts as 'magnifying glass' for small but significant changes in the life history traits of individual organisms, changes which are summed over thousands of individuals and find detectable expression at the population level. Recently we examined the interaction of food and temperature in influencing certain life history traits of *Brachionus patulus*, a ptychoplanktic rotifer commonly found in ponds (Sarma and Rao 1990). This communication reports the combined effects of food and temperature on the population growth of *B. patulus* and attempt to relate the laboratory findings to certain seasonal variations in its abundance in nature.

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2. Materials and methods

2.1 *Laboratory studies*

The experimental animal *B. patulus* was cultured in the laboratory using a starter culture of amictic females cloned from a single individual collected from local plankton. The rotifers were fed with single-celled alga *Chlorella*, mass-cultured in the laboratory, and maintained in a BOD incubator at $27 \pm 2°C$ under diffuse fluorescent illumination. Based on a series of preliminary tests, temperature levels of 15°, 25° and 35°C, and food levels of 1, 2 and 4×10^6 cells (*Chlorella*)/ml, were chosen for the final tests. Earlier dynamics experiments (Sarma 1987) indicated that very low (< 10/ml) initial densities (N_o) could lead to chance extinction of population under certain test conditions (particularly low temperatures). We therefore selected a fairly high N_o of 50 ± 5/ml for the tests, after experimentally confirming that the magnitude of N_o did not significantly influence the reproductive rates and carrying capacities achieved by the rotifer under optimal conditions (Sarma and Rao 1987).

Chlorella in the log phase of their growth were harvested from 10 l culture bottles, centrifuged (5 min at 800 g), rinsed and resuspended in distilled water. Desired food levels were obtained by serial dilution of this stock solution, the *Chlorella* density of which was measured using a hemocytometer. Glass beakers (25 ml) with 20 ml medium with *Chlorella* at one of the test densities (1, 2 or 4×10^6 cells/ml) were maintained at each of the experimental temperatures (15°, 25° and $35° \pm 1°C$) in thermostatically controlled water baths under continuous illumination. Three replicates were set up for each treatment (food-temperature combination). Rotifers at a density of 50 ± 5/ml were introduced into each of the 27 beakers (3 food levels × 3 temperatures × 3 replicates). The initial population in each case included neonates, non-egg bearing adults and ovigerous adults in approximately equal proportions, with an age composition typical of a growing population in stock cultures. Although *B. patulus* in the stock cultures bred mostly parthenogenetically, occasionally males and mictic females with eggs were observed during the tests but were excluded from population counts in view of their very low frequency (0·2–0·4%).

Rotifer densities in each beaker were measured at 24 ± 2 h intervals by taking 2–3 aliquot samples of 1 ml each and counting rotifers under a stereozoom binocular microscope at 10–20 × magnification. In addition, the numbers of ovigerous adults, neonates and eggs (including those detached from parent body) were recorded. After a 3-week period, all beakers maintained at 15° and 35°C were shifted to the intermediate temperature (25°C) and observations continued for another week.

The intrinsic rate of natural increase (r) in *B. patulus* was calculated for the exponential phase of population growth by using the formula $r = \ln N_t - \ln N_o / t$ (Poole 1974). Where N_o = initial density and N_t = density after time t (in days).

2.2 *Field observations*

Field sampling of plankton was undertaken over one year period to examine the relation between water temperature and population densities of *B. patulus* in nature.

For this study, a small (0·1 ha), perennial, oligotrophic pond adjacent to the University campus was chosen. Plankton samples were collected from the pond at 15 day intervals by filtering 50 l of water from the littoral-benthic regions through a nytex sieve (pore size: 53 μm). The collected plankton was concentrated and preserved in 5% formalin for later analysis. Water temperature was recorded at the sampling time. In the laboratory, *B. patulus* densities were estimated by the method described in the preceding section. The frequency of neonates and egg-bearing adults in each sample was also recorded.

3. Results

3.1 *Laboratory observations*

In the laboratory study, both food and temperature had a significant effect on population growth in *B. patulus* (figure 1). At 15°C, where food effects were not significant, the densities declined sharply in the initial stages, either reaching an equilibrium or showing only a marginal increase subsequently. The average number of eggs/♀ at this temperature was however higher than at 25° or 35°C. When after 3 weeks the temperature was raised to 25°C, there was a rapid increase in the rotifer population density.

The population growth at 25° and 35°C showed clear, food-related trends. Although the growth pattern departed substantially from a sigmoid growth curve, a distinct peak indicating carrying capacity (K), followed by a crash and initiation of a new growth cycle could be noticed (figure 1). The maximum density achieved was influenced significantly not only by temperature and food levels independently but also by their interaction ($P < 0.001$, F-test, 2-way ANOVA). Thus at high food levels, the magnitude of population increase (over the initial density) was nearly 9·6 times at 25°C, but only 4·2 times at 35°C (figure 2). Low food levels (1×10^6 cells/ml) that contributed to a substantial increase in population density at 25°C, could not sustain population beyond 12 days and could not initiate new growth cycle following a crash at 35°C. Shifting of test individuals from 35–25°C resulted in a rapid increase in population size. The average number of eggs/♀ recorded each day was generally lower at 35° than at 25°C. The intrinsic rate of increase (r) was negative at 15°C regardless of food level (figure 3). At 25° and 35°C, food level had a significant effect on r ($P < 0.01$, F-test, 2-way ANOVA). Although between 25° and 35°C, the temperature effect on r was not significant ($P \sim 0.07$), the food × temperature interaction was ($P < 0.01$).

3.2 *Field observations*

Summer temperatures of the pond water were 30–35°C while winter temperatures were in the range of 14–17°C. Maximal densities of *B. patulus* were recorded during Sept.–Oct. period when water temperatures were 26 ± 1°C (figure 4). A declining trend starting in December continued till March after which no *B. patulus* were represented in plankton collections for nearly 3 months (April–June). During a greater part of this period the pond temperatures were > 30°C. *B. patulus* reappeared in plankton samples starting with July and continued with an increasing trend. On the average, about 30% of the individuals of *B. patulus* in the field
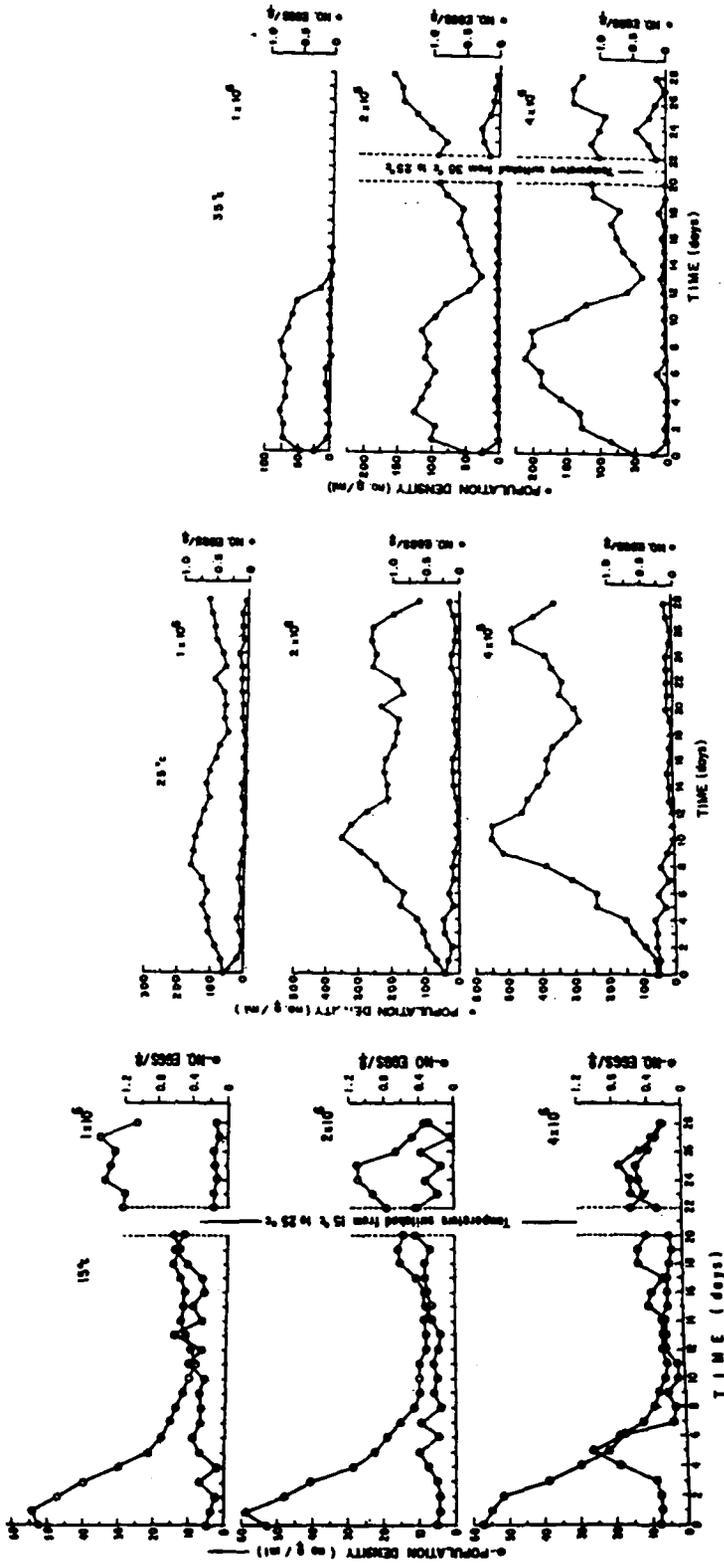
Figure 1. Population growth (○) and number of eggs/♀ (●) in *B. patulus* grown at 3 food levels at 15°, 25° and 35°C. Test populations held at 15° and 35°C were shifted to 25°C separately after 21 days. Each point represents the mean of 3 replicates.
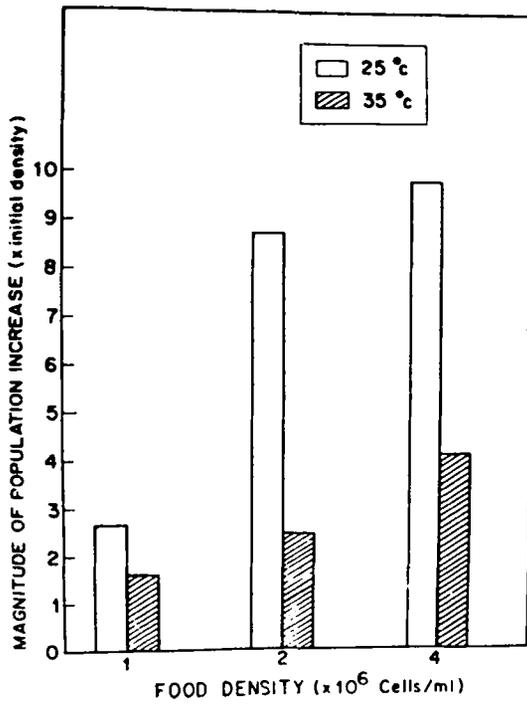
Figure 2. Magnitude of population increase (maximum density reached/initial density) as a function of food level in *B. patulus* held at 25° and 35°C. Values shown are the mean of 3 replicates.
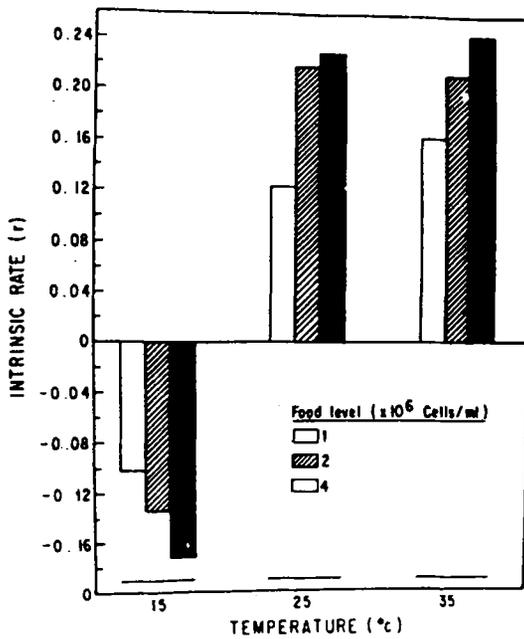

Figure 3. The intrinsic rate of increase (*r*) in *B. patulus* grown under different food-temperature conditions. Values shown are the mean of 3 replicates.
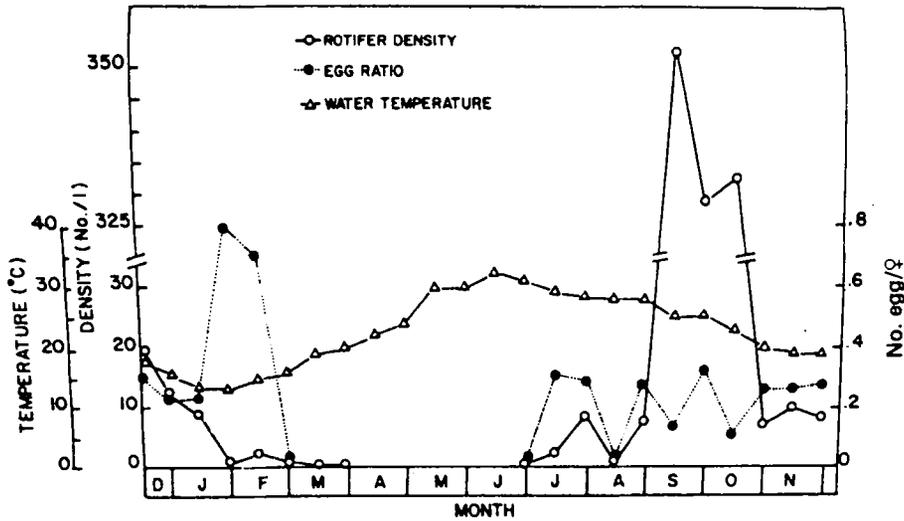
Figure 4. Seasonal variation in abundance (O) and egg ratio (●) of *B. patulus* in a pond sampled at fortnightly intervals. Also shown (△) is the surface water temperature recorded at each sampling time.

samples were ovigerous. The lowest frequency of egg-bearers was recorded in summer months and the highest in winter months (figure 4).

4. Discussion

The pattern of population growth in *B. patulus* did not follow faithfully a typical Verhulst-Pearl logistic model observed by others for different brachionid species (Halbach and Halbach-Keup 1974; Halbach 1979; Rothhaupt 1985; Walz 1987). In particular, the absence of a clearly defined lag phase in our study is probably due to the high initial densities used in the tests. Certain irregularities observed in the later growth phase could be attributed to the fact that the starter group in our study were not all of the same age class but included neonates, juveniles and ovigerous adults.

The equilibrium density (K) achieved by rotifer populations is a function of the quantity of food available (Halbach 1970) while the duration of each cycle and the amplitude of oscillations around K are known to be temperature-dependent (Halbach 1979). Temperature influences egg developmental time (Duncan. 1983; Herzig 1983; Sarma and Rao 1990) and incorporation of developmental time lags into logistic growth model has indeed been shown to generate oscillations in population density around K (Krebs 1985).

The growth patterns, maximum densities achieved and intrinsic rate of increase for *B. patulus* in our study were all influenced by temperature and food levels; in many cases the temperature × food interaction was a significant component of the overall effect. Except at 15°C, the magnitude of effect of one factor on the population parameters was dependent on the level of the other factor acting in concert; for instance, the maximum densities achieved by the rotifer at 25° and 35°C

were directly related to the food level, but the food effect was proportionately less at 25°C. In an attempt to explain similar temperature × food interaction effects on the net reproductive rate of *B. patulus* in a life table study, we suggested that the extremely high metabolic rates at 35°C necessitate a greater portion of intake energy to be channelled into metabolism at the expense of reproductive output (Sarma and Rao 1990). The same mechanism is responsible here for the observed temperature-dependent food effects at the population level. In the present study the low food level which at 25°C did contribute to an increase in population size and to sustained population cycles, could not support the rotifer population for long at 35°C and caused its eventual extinction (figure 1). Transfer of the declining population at 35°C to the optimal 25°C resulted in a rapid increase in population density, lending further support to our metabolic explanation.

The absence of food effect on population growth at 15°C indicates that low temperature *per se* was responsible for the observed effects. At 15°C, which is probably the lower limit for *B. patulus* in nature (Jyoti and Sehgal 1979), food intake and utilization appeared to be poor. Although eggs were being produced at 15°C, the extremely long developmental time at that temperature (Sarma and Rao 1990) contributed to birth-rates far below death rates, leading to a negative *r* (figure 3). Prolonged developmental time must also account for the relatively high frequency of ovigerous females were observed in the population kept at 15°C as well as in natural populations in winter.

The relative abundances of many rotifer species in nature have been known to be strongly correlated with the temperature and trophic condition of the waters they inhabit (Hofmann 1977; Radwan 1980), although their absolute magnitude might be influenced by biotic factors such as invertebrate predation (Williamson 1983) and interference competition with cladocera (Gilbert 1988). In the present study, seasonal variations in the abundance of *B. patulus* in the sampled pond showed strong correlation with those in temperature (figure 4). Maximum densities of this species recorded by us and others (Vasisht and Sharma 1976; Jyoti and Sehgal 1979) were during the months when water temperatures were in the range of 22–27°C, a range that includes the temperature level we found to be optimal (25°C) in the present study. Our observations suggest that the extremely low densities of *B. patulus* observed in peak winter are probably due to low temperatures *per se*, while the low densities observed during summer months are due to the food × temperature interaction discussed earlier. *B. patulus* being tolerant of a wide range of temperatures (12–40°C) (Arora 1966), winter temperatures of waters in Delhi probably do not affect adversely its survivorship as much as they do their reproductive output. The low fecundity, coupled with long developmental time, does not permit build-up of a large population during winter months even if food were abundant. At the other extreme, it was found that *B. patulus* can thrive at temperatures approaching 40°C, provided food concentrations were high (Sarma 1987). Because of high metabolic demands, high fecundity in summer months is possible only under high food conditions. Thus the observed decline in the abundance of *B. patulus* during periods of water temperatures above 32°C is probably due to limitingly low food levels. Compared to temperature, food factor in the life of *B. patulus* is more difficult to assess quantitatively because of wide variations in tropical waters in not only the concentration but also in the diversity of phytoplanktonic algae that are potential food to this species. Information on rotifer food concentrations in tropical

waters is rather scanty, but considering as typical of tropical freshwater bodies, Duncan's (1984) data on rotifer food levels in Parakrama Samudra, Sri Lanka, it may be suggested that during certain periods of the year, natural food levels could be low enough to be limiting for the growth of *B. patulus* populations.

Although the maximum population densities of *B. patulus* recorded in nature, except during occasional blooms, are generally low (< 100/l) (Jyoti and Sehgal 1979; Nogrady 1982), the densities (~550/ml) we obtained under laboratory conditions are typical of intensive mono-cultures of brachionids (Hirata 1979; James *et al* 1983; Lubzens 1987) used as live food for fish and crustacean larvae, and attest to the paramount role of temperature and food in maximizing rotifer production in aquaculture.

Acknowledgements

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