Effect of periodical starvation on the life history of *Brachionus plicatilis* O.F. Müller (Rotifera): a possible strategy for population stability

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Abstract

To estimate the changes in the life history of the rotifer *Brachionus plicatilis* O.F. Müller under starvation, we carried out an individual culture and determined the effects of periodical food deprivation on its asexual reproductive characteristics such as lifespan, reproductive period, age at first egg and offspring production, and lifetime fecundity (total number of offspring produced in her lifetime). Rotifers were fed for 1–3 h daily, and were then starved until the next day. Control animals were fed throughout their lifespan. Starved rotifers matured and produced their first offspring at an older age than the control animals. The periodical starvation resulted in a decrease in the lifetime fecundity to less than half that of the non-starved control. The reproductive period and lifespan were 2–3 times longer in the starved animals than in the control animals. The negative relationship between lifespan and lifetime fecundity is interpreted as a trade-off in an alternative life-history strategy of rotifers under starved conditions. The great decrease in fecundity and extension of lifespan enables rotifers to compensate to keep the population in equilibrium.

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1. Introduction

The environment of an organism is affected by a broad range of factors caused by both the organisms themselves and external factors such as climatic changes (Solomon,
Organisms change their life-history traits such as growth, maturation, reproduction, and survivorship to optimize their fitness against such various environmental factors by making trade-offs (Begon and Mortimer, 1986). The ability to modify the life-history traits associated with environmental changes is directly attributed to reproductive plasticity. Phenotypes lacking this ability are rapidly eliminated by natural selection. Therefore, a study of the changes in individual life history in response to various environmental changes is important with respect to both life history evolution and the basis of complex population dynamics.

Resource abundance can be a critical factor in determining the individual life history. The natural environment, however, rarely provides sufficient resources for organisms. For example, the diel vertical migration of zooplankton to escape from predators in both freshwater and marine habitats causes them to face food deprivation hourly (e.g., Hutchinson, 1967; Hanazato et al., 1997). In addition to short-term starvation, the composition of phytoplankton widely fluctuates seasonally, and their zooplankton predators are often undernourished (Tessier, 1986). Therefore, the ability to withstand the starvation appears to be a key element in species persistence and to influence competitive outcome and community structure (Kirk, 1997).

Rotifers have been used as a model organism for the study of laboratory population dynamics because of their small size (generally < 500 μm) and short reproductive cycle (King, 1967; Kirk, 1991, 1997, 1998; Yoshinaga et al., 1999). Monogonont rotifers are known as cyclical parthenogens, and clones can be easily obtained. Rotifers play an important role in nature as well as in the laboratory because they possess the fastest reproductive rates of all metazoans (Nogrady et al., 1993).

The environmental factor caused by the organisms themselves is known as the 'crowding factor'. It generally consists of the following three components: (1) a chemical change in environment caused by accumulation of metabolic wastes, (2) physical interference by neighbors, and (3) a decrease in the food abundance at various time scales caused by the competition for limited food resources (Utida, 1941). We have previously examined the effect of chemical changes (Yoshinaga et al., 1999). In the present study, however, we focused on the last factor, starvation, and conducted an individual culture of the rotifer *B. plicatilis* to examine the effects of periodical food deprivation on individual life-history characteristics. Knowledge regarding the changes in life-history traits under periodical starvation will contribute to the understanding of life-history patterns of rotifers under food-limited conditions.

2. Materials and Methods

2.1. Cultures

We used a clonal *Brachionus plicatilis* established from a single amictic female of the Ishikawa strain and the dietary microalgae *Tetraselmis tetrahele* (Yoshinaga et al., 1999). Both the rotifers and the algae were cultured in Brujewicz artificial seawater (Subow, 1931; salinity, 33 ppt; sterilized by 0.45-μm filter) at 25°C. As nutritive salts, 0.9 mM (NH₄)₂SO₄, 0.06 mM Na₂HPO₄ and 15 mg l⁻¹ Clewat 32 (Teikoku Kagaku
Sangyo) were added to the algal culture medium. The algal cells were suspended in the rotifer culture medium at $0.5 \times 10^6$ cells ml$^{-1}$. Stock and experimental cultures of rotifer were kept under total darkness to prevent algal growth.

The parental generation with synchronized ages (±1 h) was cultured at 10 ind. ml$^{-1}$ in the medium containing algae. Females carrying their first egg were transferred to the new medium without algae to isolate neonates from the algae. The neonates that hatched within 1 h were used as experimental cohorts. Thus, only animals produced as the first daughters by each parent were used.

2.2. Experimental design

The rotifers (mean age 0.5 h) were cultured individually at 1 ind. ml$^{-1}$. Twenty-four animals were randomly divided into three groups (each $n = 8$) and assigned to the feeding schedule described below. Animals in two starved groups (23 h-starved and 21 h-starved) were placed in artificial seawater without algae and transferred to new media containing algae to feed for 1 or 3 h daily. After feeding, these animals were starved again in new media without algae. Visible feces and uneaten algal cells contaminating the animals were removed by pipetting. The duration of daily starvation (23 and 21 h) was based on the clearance time of algal cells by the animals at a stationary phase (>$1000$ ind. ml$^{-1}$) during daily-renewed batch cultures (Yoshinaga et al., in press). Control animals were fed for 24 h a day throughout their lifespan, but they were also transferred to the new media with food twice a day in order to equalize the handling influence with those of starved groups.

All animals used in the study reproduced asexually; mictic females or males were not observed. The survival and fecundity were recorded once a day until the last animal of all groups died to determine their life-history parameters: age at first egg production, age at first offspring production, reproductive period (the duration between the first and last offspring production), lifetime fecundity (total number of offspring produced in her lifetime), and lifespan (calculated from survival function; see below). The timing of the individual deaths was determined as the mean between the time of two observations before and after death.

2.3. Statistical analysis

To compare the lifespan among three groups with different feeding regimes, survival analysis methods (SAS Institute) were carried out to compute product-limit estimates of survival functions. Differences between survival functions among the three groups were tested using non-parametric log-rank tests for the homogeneity of survival functions.

One-way analysis of variance (ANOVA) was conducted to identify significant differences among the three groups regarding the age at first egg and offspring production, reproductive period, and lifetime fecundity. Multiple comparison was carried out using post-hoc Fisher’s protected least significant difference (PLSD) test to determine which groups were significantly different. The relationships between lifespan and lifetime fecundity, and between lifespan and reproductive period were examined by
a Spearman rank correlation. All statistical analyses were carried out by StatView 5.0 J (SAS Institute).

3. Results

3.1. Lifespan

The lifespans were significantly longer in the two starved groups (mean±S.E., 26.5±1.5 and 23.8±1.5 days for 23 and 21 h-starved, respectively) than in the control group (9.9±1.2 days, log-rank test, each \( P < 0.01 \); Fig. 1). There was no difference in lifespans between the two starved groups.

3.2. The age at first egg and offspring production, lifetime fecundity, and reproductive period

Periodical starvation caused large variations in the life-history parameters. The 21 h-starved and 23 h-starved groups produced their first eggs at means of 3.4 and 5.3 days, respectively, which were at significantly older ages than the control group that had a mean of 1.0 days (each \( P < 0.01 \); Table 1). The 23 h-starved group matured at a significantly older age than the 21 h-starved group (\( P < 0.01 \)). Similarly, the 21 h- and 23 h-starved groups produced their first offspring at means of 4.0 and 6.1 days, respectively. These ages were significantly older than a mean 2.0 days of the control group (each \( P < 0.01 \); Table 1). The 23 h-starved group produced their first neonates at a significantly older age than the 21 h-starved group (\( P < 0.01 \)). The mean lifetime fecundity of the 21- and 23 h-starved groups (9.2 and 8.3 individuals, respectively) were significantly fewer than 23.4 individuals of the control group (each \( P < 0.01 \); Table 1). However, there was no difference in the lifetime fecundity between the two starved groups. The 21 and 23 h-starved groups had mean reproductive periods of 17.3 and 18.2 days, respectively, and these were significantly longer than a mean 6.6 days for the control group (each \( P < 0.01 \); Table 1). There was no difference in the reproductive periods between the two starved groups.

A negative relationship between lifespan and lifetime fecundity was found (Spearman rank correlation coefficient, \( r_s = -0.50, n = 20, P < 0.03 \); Fig. 2a). Long-lived females had a tendency to produce larger number of offspring, although, these relationships were not significant (each \( P > 0.05 \)). A positive relationship between lifespan and reproductive period was found (\( r_s = 0.92, n = 20, P < 0.01 \); Fig. 2b).

4. Discussion

4.1. Reproduction under starvation

The most significant finding of this study is the delayed responses of reproductive life-history parameters to the diel starvation. Even though the periodic starvation
Fig. 1. Survival (solid line) and fecundity (dotted line) of the rotifer *Brachionus plicatilis* in 23 h-starved (a), 21 h-starved (b), and control (c) groups. Survival curves show the product-limit estimates (mean±SE) of the proportion surviving. Fecundity is the age-specific fecundity.
markedly decreased the lifetime fecundity, the starved rotifers survived longer than the control animals. Consistent with previous studies (Snell and King, 1977; Enesco et al., 1989; Kirk, 1997), there were relationships between lifespan and both the length of the reproductive period and lifetime fecundity (Fig. 2). The end of the reproductive period has been suggested to signal the end of the lifespan in the rotifer *Asplanchna brightwelli* (Enesco et al., 1989), and a trade-off between lifespan and fecundity, which shows a negative correlation in Fig. 2a, has been suggested in freshwater rotifers, including three genera of *Brachionus* (Snell and King, 1977; Kirk, 1997).

Reproduction during starvation has been studied in many taxa of organisms, from zooplankton (Tessier et al., 1983; Kirk, 1997) to mammals (Keys, 1950; Atkinson and Ramsey, 1995). Most organisms cease to allocate energy to reproduction under
starvation conditions, which may increase their chances for future survival. For the nine species of freshwater rotifers, including five *Brachionus* species, Kirk (1997) has suggested that species with relatively longer lifespans cease to reproduce just after the onset of the starvation, while species with shorter lifespans continue to reproduce during starvation. In this study, reproductive suppression under starvation was shown to bring about a longer reproductive period and lifespan. Prolonged lifespans may enable animals to reproduce at older ages if there is a recovery of resource abundance. This prediction may support ‘the Reproductive Suppression Model’ (Wasser and Barash, 1983), in which females can optimize their lifetime reproductive success by suppressing reproduction when the future conditions for the survival of offspring are likely to be sufficiently better than present ones as to exceed the costs of the suppression itself. Based on the above, it might be hypothesized that the periodically starved rotifers limit their energy expenditure for reproduction, extending their reproductive period and lifespan betting that future conditions will be better than current ones.

4.2. Stability of population

Periodical starvation is a common phenomenon, as are changes in the chemical environment caused by diel vertical migration or increases in the population density. By using RAMAS/time software (Applied Biomathematics), Snell and Serra (1998) have conducted time-series analyses on rotifer populations in natural waters, finding that all populations examined were in a stationary phase fluctuating at around a constant mean with constant variance. A similar overall time series has been observed in rotifer populations cultured in laboratory chemostat cultures (Kirk, 1998). Although this method involves the possibility of constructing realistic models and forecasting population-density fluctuations, research on a detailed mechanism that maintains population equilibrium or leads a population to complex dynamical behaviors remains necessary for further comprehensive understanding.

The periodically starved rotifers had lifespans 2–3 times longer than the controls fed throughout their lifespans. The extension of an individual’s lifespan in the cohort results in a decrease in the death rate of a high-density population. Moreover, the reduction in the lifetime fecundity of an individual caused by the periodical starvation will lead to a lower birth rate in the population than that in a food-rich environment. Accordingly, the changes in the individual life-history characteristics in response to periodical starvation will bring about both reduced birth and death rates in the population; consequently, the amplitude of the population density fluctuation may be moderated. The rotifers are likely to maintain populations in steady-state by changing their life-history characteristics, and this flexibility in life history traits may be a mechanism to maximize lifetime reproduction in an environment with temporally varying resources.

References


