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RESOURCE LIMITATION AND REPRODUCTIVE EFFORT IN A PLANKTONIC ROTIFER

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Abstract. Individuals that live in resource-limited environments are faced with an allocation problem since they generally do not have enough assimilated energy to fuel each of the processes of reproduction, somatic growth, and storage at the physiological maximum rate. Thus, they have to decide on the proportions at which they allocate energy to the various processes. In laboratory experiments and field observations, I found that the common planktonic rotifer *Synchaeta pectinata* increases the proportion of energy allocated to reproduction (reproductive effort, RE) as food becomes more limited. This change in the allocation scheme along a gradient of food concentrations was inferred from volumetric measurements of egg size and the size of the elliptically shaped ovary. *Synchaeta pectinata* used the contents of its ovary either for reproduction (increasing the size of the individually and consecutively produced eggs) or for storage (enhancing survival during starvation by resorption of this material). As egg size was relatively constant across food levels, the higher RE at low food concentrations was not due to the fact that *Synchaeta* channeled a larger absolute quantity of energy into reproduction, but rather that they lowered the threshold size for reproduction of the ovary and hence reproduced earlier. This pattern was also suggested by the results of the field study: when the resource concentrations declined during the study period, the ovary size of field-caught *Synchaeta* decreased considerably whereas the size of their eggs, collected at the same dates, stayed relatively constant.

The lower reproductive threshold at low food concentrations resulted in a small ovary size after each egg deposition which implied a twofold cost. First, rotifers with small ovaries were less resistant to starvation because they could resorb only a little material from their ovaries. Second, it took longer for them to produce the next egg since a small ovary took longer to recover in size than a large ovary (for a given food concentration).

The plasticity in the allocation scheme of *Synchaeta pectinata* can be interpreted as an adaptive strategy to variable food conditions. By lowering their reproductive threshold when food becomes limited, *Synchaeta pectinata* increase their chance to produce at least one offspring during their lifetime. In contrast, the higher reproductive threshold under good food conditions results in better maternal condition and, therefore, facilitates future reproduction.

Key words: allocation pattern; egg size; food level; life table; ovary size; reproductive effort; reproductive threshold; resource abundance; rotifer; Synchaeta; *trade-off.*

INTRODUCTION

Resource limitation represents an ecological factor that is of key importance to the dynamics of most animal populations. Previous work by ecologists has focused on the assessment of resource limitation and mainly addressed the question of whether the abundance of a particular organism was influenced by resource limitation. This can be shown, for example, by food supplementation experiments on a population level (e.g., Merriman and Kirk 2000). Resource limitation can also be assessed on an individual level. In this case, an increase in food availability should lead to a higher amount of assimilated energy in an individual, which can be measured by one of the various indices of body condition (e.g., a lipid storage index; Tessier and Goulden 1982).

A resource-limited environment can impose a strong selective pressure on individuals, which might lead to evolutionary adaptation. At low food availability, the amount of assimilated energy in individuals is inevitably reduced. This leads to the ''allocation problem'', in which a limited amount of assimilated energy has to be shared among several competing processes. An obligatory part of this energy is required for basic metabolic processes, otherwise the individual would die immediately. The remaining part, hereafter referred to as surplus energy (Ware 1982), can be channeled into three other processes: reproduction, somatic growth, or storage. In most organisms these processes are mutually exclusive, so energy devoted, for example, to reproduction is no longer available for growth or storage. The allocation scheme of an organism describes the

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relative contributions of assimilated energy to each of these processes. It is generally assumed that the allocation scheme is subject to strong selective pressures for it ultimately determines the net reproductive rate of individuals. Hence, it is likely that the allocation scheme for a given environment has been optimized by natural selection (Sibly and Calow 1986).

Life history theory provides a framework that allows for predictions about allocation schemes, especially about one specific aspect—the reproductive effort (RE). The RE is, when defined in purely energetic terms, the proportion of surplus energy devoted to reproduction (Ware 1980). Thus, it scales between zero and one, with an RE of one meaning that all surplus energy is used for the production of offspring. Many theoretical models have been formulated that try to predict the RE for different age classes and under different selective regimes (Stearns 1992). The common assumption of these models is that any increase in the RE (which would increase the current reproductive output) is traded off against decreases in future reproduction either through direct effects on fecundity or through effects on parental survival. The study of such trade-offs, also termed the ''costs of reproduction'' has received considerable attention in recent years (e.g., Patridge and Harvey 1985, Bell and Koufopanou 1986, Reznik 1992, Clutton-Brock 1998). One prediction of such theoretical models is that the RE should increase as the parent's probability of survival to the next reproductive opportunity decreases (Gadgil and Bossert 1970, Michod 1979, Shine and Schwarzkopf 1992). This prediction has been supported by several studies in which a decrease of survival to the next reproductive opportunity was caused by various factors: sudden deterioration of abiotic conditions (Roitberg et al. 1993), the presence of predators (Stibor 1992, Reznick and Bryga 1996, Boersma et al. 1999), or senescence (Clutton-Brock 1984, Part et al. 1992; but see Langley and Clutton-Brock 1998).

Low food levels are another factor that can reduce the parent's probability of survival and should therefore lead to an increased reproductive effort. For example, the reduction of survival probability can be due to a higher starvation risk (especially when food levels are fluctuating) and/or due to a delay in the next reproductive event which causes prolonged exposure to other mortality factors. Very short periods of low resource abundance are not likely to have these effects. However, if the resource levels in a habitat typically fluctuate with a low frequency (relative to the mean starvation time of the organism in question), they should affect the survival of an organism and should therefore provide strong selective pressure. Recent empirical evidence for the hypothesis that the RE increases to the detriment of later reproduction as the food level decreases is provided by the study of Madsen and Shine (1999). These authors found that Australian water pythons reproduce while being in poorer body condition in years of low abundance of rats. Such lowering of the reproductive threshold corresponds to an increased RE. However, the study of Madsen and Shine (1999) is based on field correlations, so factors other than food concentration might also have played a role. So far, no experimental study exists that explicitly tested the hypothesis that the RE increases at low food concentrations.

The purpose of this paper is to provide such an experimental test using the common planktonic rotifer *Synchaeta pectinata* as a model organism. Planktonic rotifers are excellent models for testing hypotheses about adaptation to resource limitation. Like other herbivorous zooplankton, they are subject to extensive variations in food availability in their natural habitats. These variations may include both predictable changes associated with seasonal succession of their resources and unpredictable changes resulting from complex biotic interactions or sudden changes due to weather conditions. Recent experimental evidence has shown that *Synchaeta* is frequently resource limited in the field (Merriman and Kirk 2000). In this paper, I will develop a method to quantify surplus energy and reproductive effort in the planktonic rotifer *Synchaeta pectinata.* Rotifers provide unusual opportunities in this respect, since the anatomy of their reproductive organs allows the ''flow of surplus energy to reproduction'' to be observed directly in living animals. My method is based on the works of Bentfeld (1971*a*, *b*), who found that oocyte growth in rotifers is accomplished by a passive flow of cytoplasm from the vitellarium (yolk gland) into each developing egg. This quantity of cytoplasm can be measured volumetrically in living animals. *Synchaeta pectinata* is especially suited for such studies since its body wall is completely transparent, a feature that facilitates size measurements of interior organs.

This study covers laboratory experiments and a field study. The laboratory experiments were designed to deduce the basic allocation scheme from measurements of body size, the size of the ovary, and egg size. The experimental conditions covered the full spectrum of resource availability: from ad libitum food conditions to complete starvation. To test whether the basic findings of the laboratory studies also hold under natural conditions, a field study was conducted during the spring maximum of *Synchaeta pectinata.* This time period was characterized by initially high and subsequently decreasing food concentrations. The basic question addressed in this study was: Does the allocation scheme in individuals change with food concentration in the way predicted by life history theory, namely that RE increases at low food concentrations?

Materials and Methods

Egg production in rotifers

Rotifers are iteroparous organisms that produce their eggs individually and consecutively throughout the

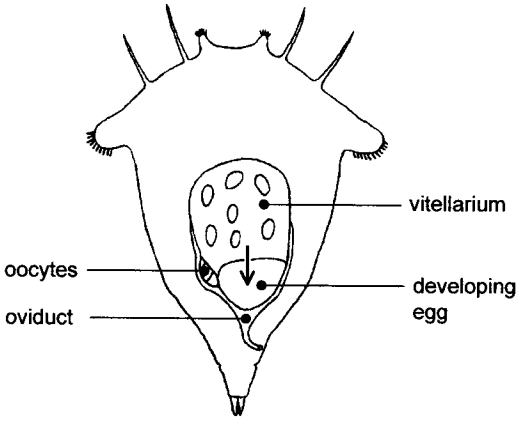

FIG. 1. Schematic drawing of the reproductive system of *Synchaeta pectinata* according to the descriptions of Bentfeld (1971*a*) and Lehmensick (1925). The arrow indicates the flow direction of cytoplasm from the vitellarium into the developing egg. Oocytes, developing egg, and vitellarium comprise the ''ovary,'' as measured in this study.

adult lifespan. ''Clutches,'' such as those observed in egg-bearing species (e.g., *Brachionus* spp.) are actually accumulations of eggs produced consecutively in time intervals shorter than the duration of embryonic development. Oocyte growth between egg depositions is accomplished by flow of cytoplasm from the syncytial vitellarium gland into the oocyte through a small cytoplasmic bridge (Fig. 1). As no transformations occur during this process (e.g., production of yolk proteins), the material within the vitellarium, the growing egg or the fully developed egg is essentially the same—vitellarium plasma. Hence, the amount of resources in, respectively, the energy content of eggs and vitellarium can be measured by simple volumetric approximations. Based on the assumptions that there is no somatic growth in adults and that storage depots like lipid droplets are of minor importance (the validity of these assumptions will be shown in *Discussion: Surplus energy and reproductive effort in* Synchaeta), the surplus energy of an adult *Synchaeta* is represented by the current size of the ovary (vitellarium + oocytes). Accordingly, the reproductive effort (RE) for each egg deposition can be defined as

$$\text{RE} = \frac{\text{egg volume}}{\text{egg volume + residual ovary volume}}.$$

This index can take values between zero and one. It describes the proportion of total vitellarium plasma (ovary size before egg deposition) that has been used for the production of an egg and therefore refers to one egg-laying interval.

Culture conditions

All experiments were carried out with one clone of *Synchaeta pectinata,* which was isolated from Schöhsee, a meso-eutrophic lake in northern Germany. In my culture this clone reproduced solely by parthenogenesis. The animals were cultured in artificial ADaM medium (Klüttgen et al. 1994), which was supplemented with 10% MBL medium (Guillard 1975) and 2.2 mg/L Na_2EDTA to improve the growth conditions for the food alga *Cryptomonas erosa* var. *reflexa* (kindly supplied by J. J. Gilbert). Stock cultures of *Synchaeta* were maintained at 12°C, constant low light and high food concentrations (~2–3 mg C/L) in 1-L glass bottles that were rotated slowly (~0.2 rpm) on a plankton wheel. Every other day 30–50% of the contents of each bottle were replaced by fresh food suspension. To produce cohorts of animals for the experiments, eggs were isolated from one bottle and then kept separately until they hatched.

The food alga *Cryptomonas* was grown in MBL medium in semicontinuous culture and was continuously illuminated (100 μmol quanta·m^{-2}·s^{-1}). Under these culture conditions, the carbon content of one *Cryptomonas* cell was 219 pg/cell (Stelzer 1998). Alga concentrations were measured with a CASY electronic particle counter (Schärfe System, Reutlingen, Germany) and diluted with ADaM and MBL medium to yield the desired food concentration and chemical composition of the rotifer culture medium. All experimental animals were isolated as cohorts and were further cultured individually in 3 mL of food suspension in 12-well tissue culture plates. Previous determinations of clearance rates of *Synchaeta* showed that even at the lowest food concentrations the daily grazing effect in such a system was never >6%, but usually much less. Thus, all measurements can be related to a food concentration rather than a food ration. *Cryptomonas* is a motile alga and therefore does not sink to the bottom of the wells. However, phototactic behavior or orientation to the water surface may result in uneven distribution of *Cryptomonas* cells within the culture wells. To prevent such effects the culture plates were placed on a shaker, which was controlled by an interval timer (2 min on, 15 min off).

Measurements of body and ovary size

Volumetric measurements were done with the analySIS image analysis system (Soft Imaging System, Münster, Germany), connected to an inverted microscope. For the measurements, animals were individually placed into a plankton compression chamber (Hydrobios, Kiel, Germany). The height of the chamber was decreased until the animal had slowed down sufficiently in its movements. When the animal was in a relaxed position, a picture was taken with the ''freeze'' option of the image analyzer. With some practice these procedures take no longer than ~1 min/animal and have no negative effects on survival, growth, or reproduction. Thus, individual animals could be measured repeatedly throughout their lifetimes. The measurements included body length and breadth and ovary size, which was measured as area and afterwards transformed to volume units. The shape of the ovary can

be approximated to an ellipsoid of revolution with a length : diameter relationship of 1.5. However, at very low food concentrations, some individuals carried a fully developed egg and the vitellarium was very small. In these cases, the approximation to a sphere was more realistic. Body volume was calculated from body length and breadth according to the formula suggested by Ruttner-Kolisko (1977). The egg sizes were calculated from measurements of egg diameters (egg shape = sphere).

Five experiments were conducted that all examined the effect of different food concentrations (from very high levels to complete starvation) on various individual traits: somatic growth, ovary growth, ovary size after egg deposition, egg size, survival probability, and others. These data are later (see *Discussion: Surplus energy and reproductive effort in* Synchaeta) used to derive a simplified allocation scheme for adult *Synchaeta pectinata.* Furthermore, they are used to characterize costs associated with a high RE and to test the hypothesis that RE increases at low food concentrations.

Experiment 1: food and growth in juveniles

The first experiment was performed to assess the effect of two food concentrations (0.1 and 1.0 mg C/L) on somatic growth and ovary growth in juvenile and early adult *Synchaeta.* For each food concentration, a cohort of six animals born within a 6-h interval was used. Body size and ovary size were measured in 12-h intervals from birth until the age of 7 d.

Experiment 2: food and ovary-size dynamics

The second experiment was performed to assess the effect of food concentrations on the dynamics of ovary size (i.e., growth between egg depositions and ovary sizes at egg depositions) in adult *Synchaeta.* Animals were precultured at three food concentrations (0.1, 0.2, and 1.0 mg C/L) until the age of 6 d and were then further cultured at six different food concentrations (0.1, 0.2, 0.3, 0.5, 1.0, and 3.0 mg C/L). Animals precultured at 0.1 mg C/L were only subjected to 0.3 and 3.0 mg C/L. Each treatment was given to four animals (replicates) that were subsequently measured for 3.5 d at intervals of 12 h (0.1, 0.2, and 0.3 mg C/L) and 8 h (0.5, 1.0, and 3.0 mg C/L).

Experiment 3: starvation and ovary-size dynamics

The third experiment was performed to assess the dynamics of ovary size under complete starvation, i.e., to test whether *Synchaeta* continue to produce eggs or whether they resorb material from their ovaries under such conditions. Six-day-old adults previously cultured at 0.3 mg C/L were subjected to complete starvation and the size of their ovary was measured every 6 h until death.

Experiment 4: starvation resistance

The fourth experiment was performed to test the hypothesis that *Synchaeta* which enter a starvation period with larger ovaries can starve longer than animals with smaller initial ovary sizes. A cohort of 54 animals was cultured for 6 d at 0.3 mg C/L and an additional day at 0.05 mg C/L to ensure that the animals did not enter the starvation phase with very high gut fillings and was then subjected to complete starvation. At the beginning of the starvation period, body size and ovary size of each animal were measured. Subsequently, survival and reproduction was assessed every 8 h until the last animal had died. A multiple regression analysis was performed to separate the effects of body size and ovary size on starvation time.

Experiment 5: food and reproductive effort

The fifth experiment was a life table response experiment (LTRE) at different food concentrations (0.1, 0.2, 0.3, and 1.0 mg C/L) with additional measurements on individual traits like body size, ovary size, and egg size. Additionally this experiment tested if RE changes with food concentration.

For each food concentration, a cohort of 24 animals born within a 6-h interval was used. From the age of 4 d on, the animals were checked every 8 h to determine the time of the first egg deposition (AFR = age at first reproduction). Body size (SFR = size at first reproduction), ovary size (OFR = ovary size after first reproduction), and the size of the first egg (FES) in all animals were measured immediately after their first egg deposition. Egg depositions were assumed to have occurred in the middle of a control interval. Therefore, the OFR was corrected for growth that happened within 4 h using the estimates for the ovary growth rate of experiment 2. All animals were cultured until they died and daily controls were made to check for survival and newly produced eggs. Population growth rates were calculated from the l_x and m_x values by solving the Euler-Lotka equation iteratively:

$$\sum e^{-rx} \cdot l_x \cdot m_x = 1$$

where l_x is the survivorship until age x and m_x is the mean number of offspring of a female at age x.

To test whether RE was higher at low food concentrations, the arcsine-transformed values of the RE were plotted against the logarithm of food concentration. If RE was higher at low food concentrations the regression line fitted through these values should have a significantly negative slope.

Field study

A field study was conducted in Schöhsee during the time of the spring maximum of *Synchaeta pectinata* to test whether the relationships among body size, egg size, ovary size, and food concentration observed in the laboratory could also be found under natural con-

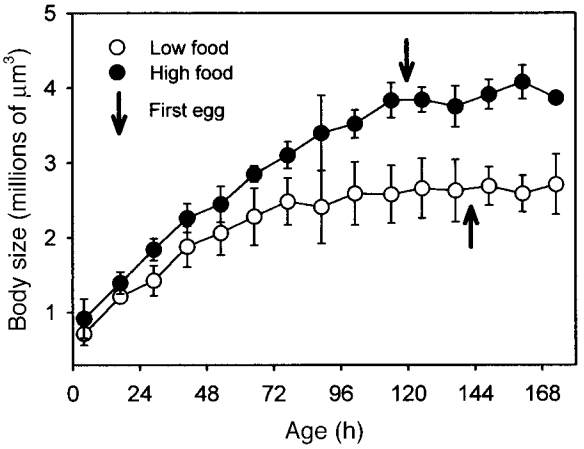

FIG. 2. Somatic growth of *Synchaeta pectinata* during the juvenile and early adult phase at two different food concentrations (open circles, 0.1 mg C/L; filled circles, 1.0 mg C/L). Values are means ± 1 SD, $n = 6$. Arrows indicate the age at first reproduction (as the time when the first egg was laid).

ditions. Samples were taken every fifth day from 6 March until 21 April 1999 at one location in the lake where the depth was 12.5 m.

Synchaeta pectinata was sampled by vertical hauls (12–0 m) using a 30-μm plankton net. Its abundance was determined from samples fixed in 4% formaldehyde using an inverted microscope. Additionally, live specimens were collected. These were separated from large zooplankton with a 500-μm mesh and stored at 4°C to reduce mechanical damage by predation and metabolic stress until the actual measurements were made (~2 h later). From this sample, 30 adult *Synchaeta pectinata* were randomly selected and their body size and ovary size were measured. Additionally, the size of 10 subitaneous (i.e., nondiapausing) eggs was measured.

Phytoplankton was sampled at two depths (1 and 5 m) using a Ruttner water sampler (Hydrobios, Kiel, Germany). Samples of 50 mL were fixed in Lugols solution, allowed to settle, and counted using an inverted microscope at 250× and 400× magnification. Only the abundance of cryptomonads was assessed, as *Synchaeta pectinata* is known to be specialized on these algae (Zimmermann 1974, Gilbert and Bogdan 1984). Four different species of cryptomonads could be found during the sampling period. Measurements of their cell size allowed an estimation of the ''total cryptomonad biovolume'' as an indicator of resource availability. In addition, temperature and oxygen content were measured in 1-m steps at each sampling date.

RESULTS

Experiment 1: food and growth in juveniles

The increase in body size during the juvenile phase followed a typical growth curve (Fig. 2). Animals cultured at low food concentrations (0.1 mg C/L) grew more slowly and achieved a smaller body size than animals kept at high food concentrations (1.0 mg C/L). Somatic growth of adults, i.e., increase in body size after first reproduction (120 h at high food, 144 h at low food) was negligibly small at both food concentrations.

Mean ovary size in juveniles increased steadily until the first reproduction (Fig. 3). At 1.0 mg C/L ovary growth was faster than at 0.1 mg C/L. The growth curve at 1.0 mg C/L had an exponential shape. At 0.1 mg C/L, not all animals reproduced during the experiment. Those that did reproduce had attained higher ovary sizes at the age of maturity. This threshold ovary size was at $\sim 0.4 \times 10^6$ μm³ and occurred in other experiments with low food concentrations as well. This volume equals the sum of an egg of the mean size ($\sim 0.34 \times 10^6$ μm³) and the minimum ovary size observed in adults ($\sim 0.06 \times 10^6$ μm³). In some rare events, egg deposition occurred at a much lower ovary size. In such cases, however, the egg was very small and did not result in a viable offspring.

Experiment 2: food and ovary-size dynamics

Ovary-size dynamics in adults followed a saw-toothed pattern (Fig. 4). There were sudden drops in ovary size in periods just after an animal had laid an egg. Between two egg depositions, ovary size increased somewhat exponentially until a threshold ovary size was reached or exceeded. The increase in ovary size was steeper at high food concentrations (1.0 mg C/L) than at medium food concentrations (0.3 mg C/L) which led to shorter egg-laying intervals at 1.0 vs. 0.3 mg C/L.

The increase in ovary size at food concentrations of 0.3 mg C/L (Fig. 5) was not significantly different

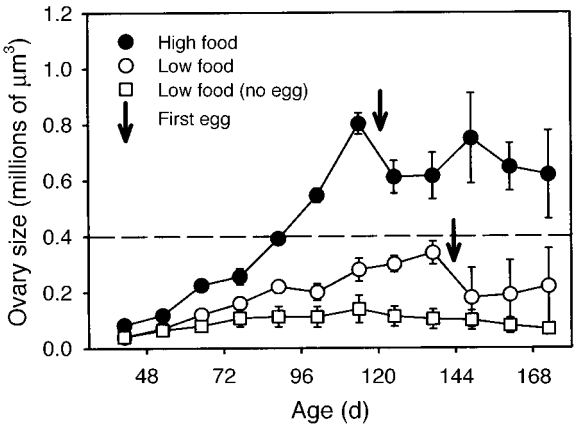

FIG. 3. Ovary size dynamics of juvenile and early adult *Synchaeta pectinata* at two different food concentrations (open circles, 0.1 mg C/L with reproduction; squares, 0.1 mg C/L without reproduction; filled circles, 1.0 mg C/L). Values are means ± 1 SD, $n = 3$–4. Arrows indicate the age at first reproduction (as the time when the first egg was laid). The broken line is the threshold ovary size for reproduction (see *Results*).

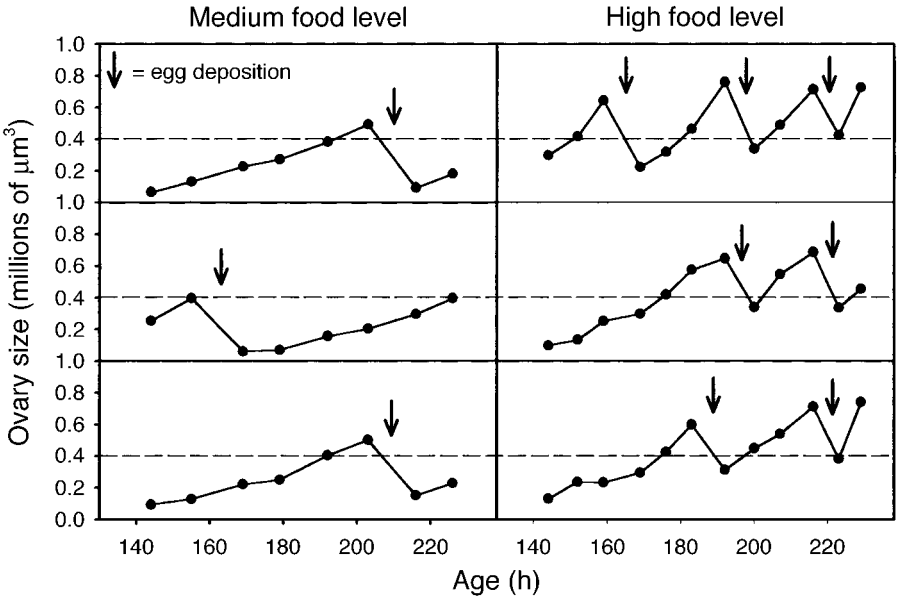

FIG. 4. Ovary size dynamics of individual adult *Synchaeta pectinata* at two different food concentrations (medium = 0.3 mg C/L, high = 1.0 mg C/L). Arrows indicate time intervals in which an egg was laid. All animals were previously cultured at 0.2 mg C/L. The broken line is the threshold ovary size for reproduction (see *Results*).

among animals precultured at 0.1, 0.2, and 1.0 mg C/L (ANCOVA, $F_{2,64} = 1.3$, $P = 0.275$) although these animals had quite different body sizes. However, larger ovaries increased in size to a greater degree as shown by the significant positive slope of the regression line in Fig. 5 ($P < 0.01$).

Since ovary growth was dependent on ovary size, the exponential rate of ovary size increase (oi) was calculated for those intervals in which no egg was laid and the rates were then averaged for each animal. Plotting oi against the food concentration resulted in a curve with a hyperbolic shape (Fig. 6). As there should be a food concentration that is barely sufficient to maintain the basic metabolism but no ovary size increase, a Monod model modified for a threshold for zero growth of the ovary was fitted to the data:

$$\text{oi} = \text{oi}_{\text{max}} \frac{(S - S_0)}{(S - S_0 + k_S)}$$

where oi is the exponential rate of ovary growth, oi_{max}

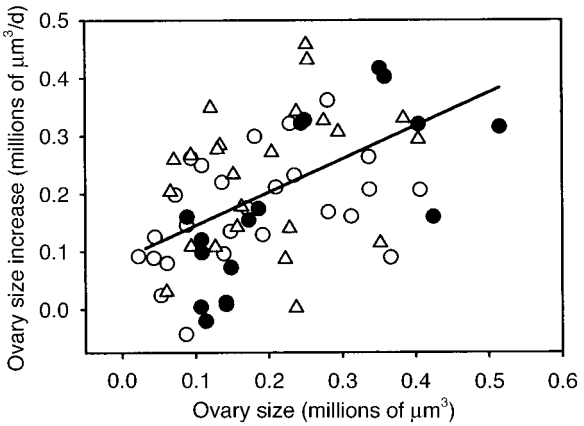

FIG. 5. Ovary size increase as a function of the current ovary size at a food concentration of 0.3 mg C/L. The symbols indicate the different preculturing food treatments (open circles, 0.1 mg C/L; triangles, 0.2 mg C/L; filled circles, 1.0 mg C/L). There was no significant difference among the preculturing food treatments (ANCOVA, $F_{2,64} = 1.317$, $P = 0.275$); however, the slope of the overall regression line was significantly positive ($t = 4.736$, $P < 0.001$).

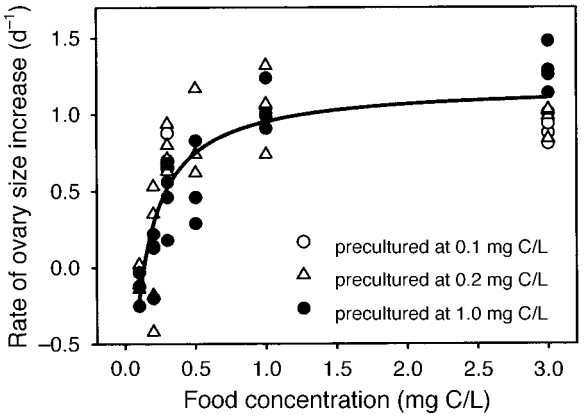

FIG. 6. Relationship between the exponential rate of ovary growth and food concentration. The symbols indicate the different preculturing food treatments (open circles, 0.1 mg C/L; open triangles, 0.2 mg C/L; filled circles, 1.0 mg C/L). Each symbol represents the measurement on one individual animal during 3.5 d. The line fitted to the values is a Monod function, modified for a threshold food concentration (see *Results*).

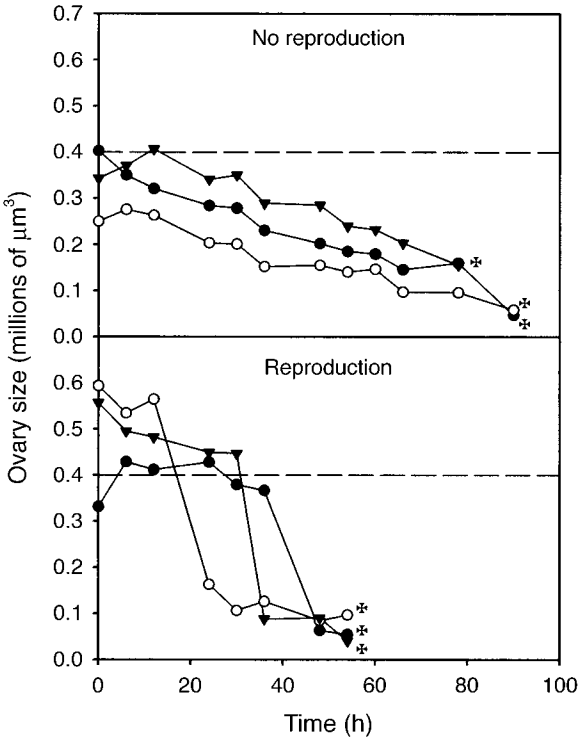

FIG. 7. Ovary size dynamics of young adults that were subjected to complete starvation (upper graph, animals that did not reproduce during starvation; lower graph, animals that reproduced once during starvation). The broken line is the threshold ovary size for reproduction (see Fig. 5). Each animal was followed until it died of starvation (marked with a cross). Symbols indicate different individual animals.

is the maximum rate of ovary growth, S_0 is the threshold food concentration for zero growth of the ovary, k_S is the half saturation constant, and S is the food concentration. The estimated values for the parameters were $oi_{max} = 1.192 d^{-1}$, $S_0 = 0.133$ mg C/L, and $k_S = 0.216$ mg C/L. At all food concentrations below 3.0 mg C/L, oi was not affected by the food concentration at which the animals were precultured. However, at 3.0 mg C/L animals precultured at 1.0 mg C/L had a significantly higher ovary-growth rate than those precultured at 0.1 and 0.2 mg C/L, respectively (t test; $P < 0.01$).

Experiment 3: starvation and ovary-size dynamics

Animals that experienced sudden complete starvation showed two distinct patterns in their ovary-size dynamics depending on the initial size of their ovaries. Animals with an ovary smaller than the above-mentioned ''threshold size'' (see *Experiment 1*) showed a continuous decrease in their ovary size until they died (Fig. 7a). This decrease affected the size of the vitellarium as well as the size of the developing egg. Any reasons for mortality other than starvation were unlikely since the animals were young adults aged ~6 d. All animals with an ovary larger than the threshold size reproduced during starvation and therefore experienced an additional loss of material (Fig. 7b). Furthermore these animals died ~1.5 d earlier than those that did not reproduce during starvation. The observation that a few animals showed a slight increase in ovary size during the first hours of the starvation phase might be attributed to the gut contents that were present at the beginning of the experiment. Body size remained constant during the starvation period (not shown), except for the last 6–12 h before death where most animals had a ''bloated'' appearance. This was probably due to passive inflow of water because these emaciated animals may have lost the ability to regulate their osmotic pressure.

Experiment 4: starvation resistance

Starvation times ranged from 12 to 84 h. The ovary size at which a particular animal entered the starvation period could account for much of this variation, as there was a clear positive relationship between initial ovary size and starvation time (Fig. 8). A multiple regression analysis revealed a significant effect of ovary size on starvation time ($n = 54$, $P < 0.001$), but no effect of body size ($P = 0.192$).

Experiment 5: food and reproductive effort

The survival curves in all food concentrations were similar (Fig. 9b). Mortality during the juvenile phase was very low but increased after the onset of reproduction (day 6–8). Survival times for the four different food treatments were not significantly different from each other (Gehans Wilcoxon test, $n = 96$, $P = 0.192$).

Fecundity strongly increased with food concentration (Fig. 9b). This was due to a shortening of the egg laying intervals at higher food concentrations. Animals cultured at 1.0 mg C/L laid up to 23 eggs during their

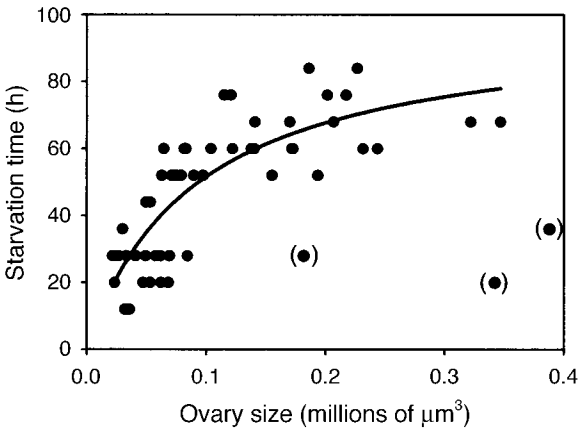

FIG. 8. Survival times of animals entering starvation with different initial ovary sizes (nonreproducing animals only). The line shows a nonlinear regression (Michaelis-Menten model) fitted through the values of 51 animals; three outliners (in parenthesis) that deviated strongly from this pattern were not included in the nonlinear regression.

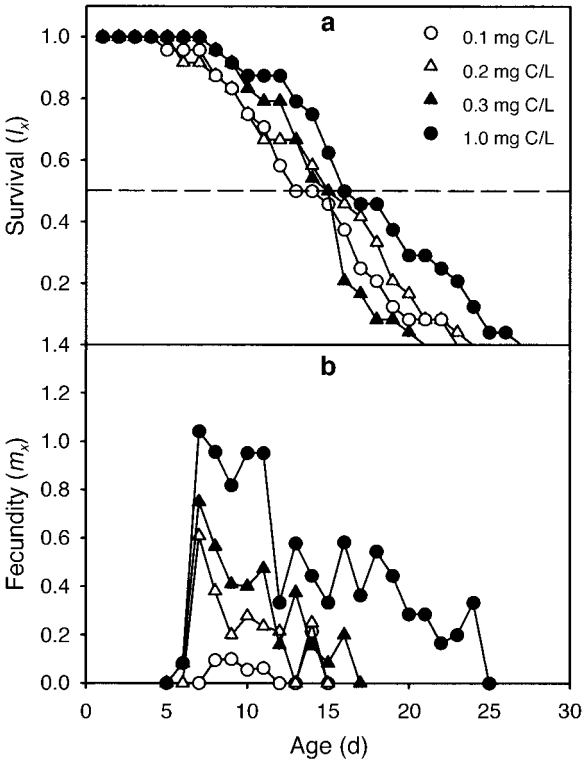

FIG. 9. (a) Survival (proportion of initial cohort alive) and (b) fecundity (offspring per surviving female per day) of *Synchaeta pectinata* at four different food concentrations (open circles, 0.1 mg C/L; open triangles, 0.2 mg C/L; filled triangles, 0.3 mg C/L; filled circles, 1.0 mg C/L). The dashed line indicates 50% of the initial cohort.

lifetime whereas those cultured at 0.1 mg C/L laid either one egg or did not reproduce at all. Animals that did reproduce at the low food concentrations lived for a significantly shorter time than the ones that did not reproduce (Gehans Wilcoxon test, $P < 0.05$, mortality of animals younger than 6 d was not included in the analysis). Many of them also showed the bloated appearance shortly after reproduction.

All life history traits investigated were significantly affected by food concentration (see the one-way ANOVAs in Table 1). However, some traits changed gradually over the whole range of food concentrations (SFR, OFR), whereas others remained constant at food concentrations >0.1 mg C/L (AFR, FES) and no significant differences were found among them by a Tukey test.

Reproductive effort decreased substantially at higher food concentrations (Fig. 10a), a result that supports my original hypothesis. RE ranged from 0.36 to 0.92 and was highest at the lowest food concentrations. Determinations of RE for an earlier experiment (experiment 2) revealed similar patterns with food concentration (Fig. 10b, c). There was a significant negative relationship between RE and food concentration for each of the three data sets ($P < 0.01$ in all cases).

Field study

In spring 1999, a field study was conducted on a *Synchaeta pectinata* population in Schöhsee. During the sampling period, the water temperatures ranged between 4 and 8°C and the oxygen content ranged between 70 and 130%. There was no stratification of the water body during this time. Four cryptomonad species were abundant: *Rhodomonas minuta* (mean cell volume = 120 μm^3), an unidentified *Cryptomonas* sp. (432 μm^3), and two large Cryptomonas species: *Cryptomonas erosa* and *Cryptomonas ovata* (2229 μm^3). Of all cryptomonads, *Cryptomonas* sp. reached the highest abundances.

During the sampling period, there was a continuous decrease in the concentration of cryptomonads (Fig. 11a). Their concentrations in 1 and 5 m depth were very similar as suggested by the small standard deviations. The population of *Synchaeta pectinata* grew fast during the first 3 wk (population growth rate (r) $\approx$ 0.1/d) and reached its maximal abundance of 2.3×10^5 individuals/m^2 on 31 March. During the following weeks the population declined steadily until the end of the sampling period (7.6×10^3 individuals/m^2 on 21

TABLE 1. Life history characteristics of *Synchaeta pectinata* at different food levels.

Treatments	Food level (mg C/L)	Growth rate, r (d^{-1})	SFR (μm^3) ($\times 10^{-6}$)†	AFR (d)	FES (μm^3) ($\times 10^{-6}$)†	OFR (μm^3) ($\times 10^{-6}$)†
a	0.1	−0.098	2.36	9.4	0.273	0.039
b	0.2	0.067	2.67	5.9	0.345	0.246
c	0.3	0.129	2.93	5.6	0.323	0.278
d	1.0	0.213	3.27	5.5	0.348	0.462
ANOVA						
df			64	66	73	42
F			14.91	40.91	10.84	30.92
P			<0.001	<0.001	<0.001	<0.001
Tukey groups			a–b, b–c, d	a, b–d	a, b–d	a–b, b–c, d

Note: SFR = size at first reproduction, AFR = age at first reproduction, FES = size of the first egg, OFR = ovary size after the first egg deposition.
† That is, table entries are reported as millions of μm^3.

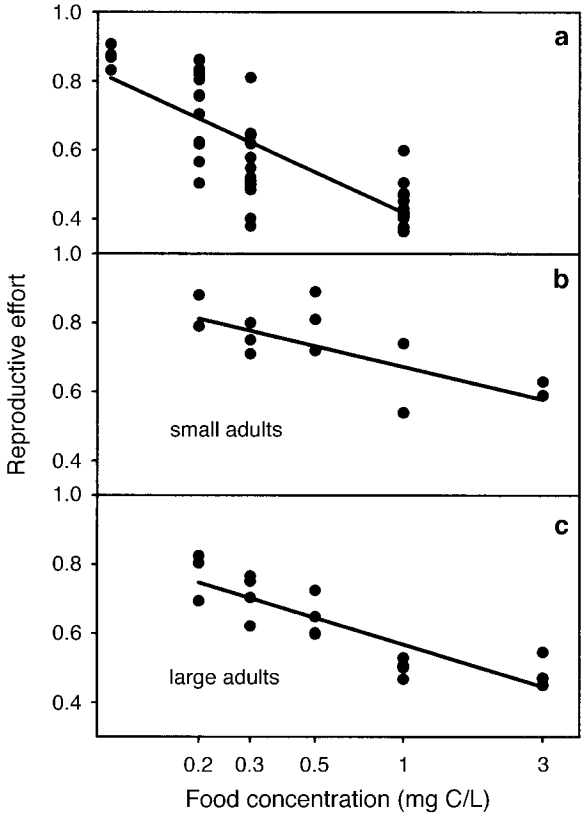

FIG. 10. Relationship between reproductive effort (the proportion of surplus energy devoted to reproduction) and food concentration. (a) Data from experiment 5, where the animals grew up at constant food concentrations; (b) and (c) data from experiment 2, where animals grew up at (b) low food concentration (0.2 mg C/L) and (c) high food concentration (1.0 mg C/L) and were then subjected to different food concentrations. Note the logarithmic scaling of the *x*-axis.

April). The size of subitaneous eggs was relatively constant during long periods of the field study but decreased after 11 April (Fig. 11b). On the last sampling date (21 April), no subitaneous eggs were found at all. Ovary sizes were large during the first two weeks and decreased afterwards. At the last two sampling dates, almost no animal had an ovary size larger than the mean egg size. Adult body size of the field-caught animals was larger at the beginning of the study than at the end (not shown). Although animals with large body size may also have a larger ovary, this did not solely cause the pattern of the decreasing ovary size during the study period, since the relative ovary size (ovary volume in relation to body volume) also declined (Fig. 11c).

The effects of resource limitation become more evident if the different trait values are plotted against the total cryptomonad biovolume at the various sampling dates (Fig. 12a–c). This reveals that the mean ovary size increased with the ambient resource availability following the pattern of a saturation curve (Fig. 12a). Egg sizes showed the same qualitative relationship to food concentration as in the laboratory experiments (Fig. 12b; for comparison see Table 1). They remained constant for a wide range of food concentrations but decreased at very low food concentrations. It was not possible to calculate the RE in the same way as was done in the laboratory experiments for the field data, as egg sizes could not be attributed to individual animals. Nevertheless, the following approximation might give a crude estimate of the mean reproductive effort (RE_{field}) at one particular sampling date during the field study:

$$RE_{field} = MES/MOS_R$$

where MES is the mean egg size and MOS_R is the mean ovary size of animals with an ovary larger than the mean egg size (i.e., those animals that were capable of producing an egg). Fig. 12c shows that RE_{field} increased at low food concentration ($P < 0.01$).

DISCUSSION

Surplus energy and reproductive effort in Synchaeta

A key assumption in my paper is that surplus energy is mainly represented by the current size of the ovary in adult *Synchaeta.* This assumption seems to be realistic. Since these rotifers essentially did not grow as adults (Fig. 2), allocation to body growth was approximately zero. Hence, surplus energy was either devoted to reproduction or remained in the body for later re-

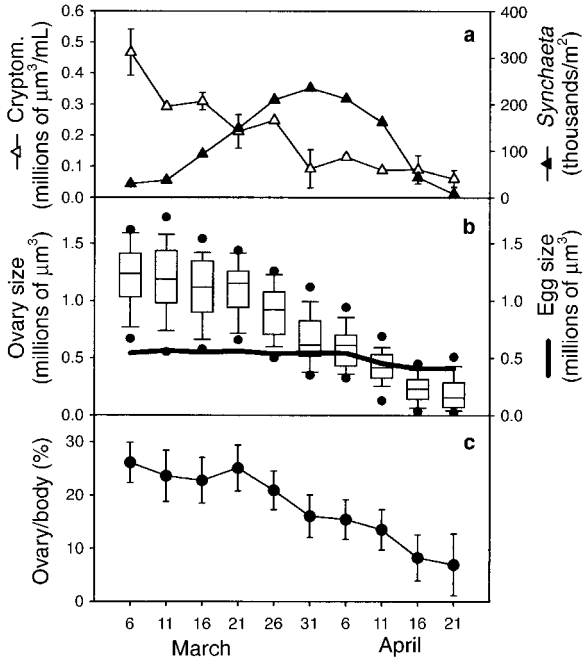

FIG. 11. Temporal changes during the field experiment. (a) Concentration of cryptomonad algae (''Crytom.'') (open triangles; mean ± 1 SD) and abundances of *Synchaeta pectinata* (filled triangles). (b) Ovary size (box plot; dots are 5 and 95 percentiles) and mean egg size (heavy line). (c) Relative ovary size (ovary volume divided by total body volume; mean ± 1 SD).

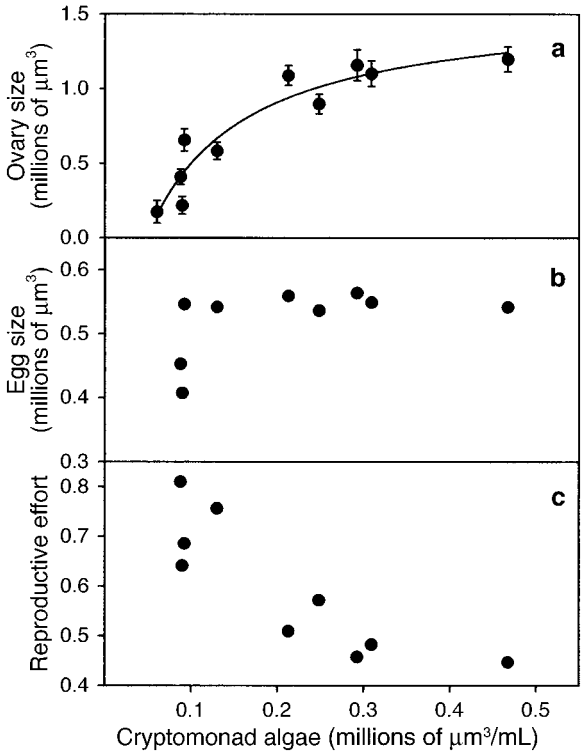

FIG. 12. Various physiological traits of *Synchaeta pectinata* in relation to food concentration (concentration of cryptomonad algae) during the field experiment. (a) Ovary size vs. food concentration (mean ± 1 SD). (b) Egg size (mean; standard deviation is too small to be visible). (c) Reproductive effort.

production. The ovary seems to be the most important storage organ in the body of *Synchaeta.* The only additional possibilities for energy storage are lipid droplets (sometimes found attached to the stomach wall) and the mixocoel fluid. Both are probably of minor importance in the energy budget. Lipid droplets were present in small amounts, but only when the animals were cultured at very high food concentrations (>1 mg C/L), levels typically not experienced by individuals in lakes and ponds. Mixocoel fluid is not likely to be an important pool of energy storage since larger amounts of dissolved substances (e.g., sugars) in it would produce high costs for osmoregulation. Furthermore, there was no effect of body size on starvation time in experiment 4, which one would have expected if mixocoel was the main storage pool. Thus, the predominant amount of surplus energy must have consisted of vitellarium plasma.

Individual *Synchaeta pectinata* acquired surplus energy at a slower rate when they were cultured in low food concentrations as shown by a positive relationship between ovary growth rate and food concentration (Fig. 6). For the most part, this pattern was not influenced by the body size of the individuals, however at the highest food concentration (3 mg C/L) larger animals (those precultured at 1 mg C/L) had a significantly higher ovary growth rate. This may be due to higher maximum ingestion rates of large *Synchaeta pectinata.* To date, there is no study demonstrating such a relationship between body size and maximum ingestion rate in a rotifer. However, for other zooplankters, like *Daphnia,* it has been shown that maximum ingestion rates increase proportionally with body length (summarized in McCauley et al. 1990).

On average, *Synchaeta pectinata* that were growing at low food concentrations had a smaller ovary size both under laboratory and field conditions (Figs. 4 and 12a). As ovary size represents the surplus energy currently available to an adult animal, it can be used as an indicator of the animal's physiological condition allowing a crude estimate of the reproductive potential in the near future and of the resistance to starvation. In other organisms, scores based on the body weight/body length ratio (Shine and Madsen 1997) or indices of lipid storage (Tessier and Goulden 1982) have been used for such purpose. An advantage of ovary size is that it relates to reproduction in a particularly straightforward way.

In rotifers, the energy devoted to reproduction is exactly the amount of plasma that has been flowing from the vitellarium into the egg (Bentfeld 1971*b*). Therefore, the definition of RE (egg volume/[egg volume + residual ovary size]) seems to be appropriate. In *Synchaeta,* the RE was determined at each egg deposition, since these were the moments when energy was irreversibly allocated to reproduction. Between two egg depositions, this was not the case as the contents of a developing egg could also be resorbed during starvation. At very low food concentrations, some animals with an ovary smaller than the minimum ovary size for reproduction did not reproduce at all. At first sight, one could argue that these had an RE of zero. However, such reasoning neglects that animals with a very small ovary suffer a serious constraint. Even if they tried to reproduce, they would produce an egg far too small to yield viable offspring. This would be analogous to not reproducing at all. In their case, it is pointless to make any statement about the RE. It would be equally pointless to argue, e.g., that juvenile animals have an RE of zero because they do not reproduce. Juveniles do not have the option to reproduce, because their reproductive organs are not fully developed.

The timing of egg depositions is an important aspect of the RE of *Synchaeta pectinata.* As a simplification concerning the allocation scheme, the amount of resources devoted to reproduction was invariant, since egg size was constant for a wide range of food concentrations (Table 1, Fig. 12b). Only at the lowest food concentration of 0.1 mg C/L did egg size decrease, which was probably caused by insufficient amounts of vitellarium plasma, preventing the production of larger eggs. Constant egg sizes were also found by Kirk (1997*a*) although the food concentrations in his study

were much higher. A high RE was not the result of a larger absolute quantity of energy being allocated towards reproduction, but rather because *Synchaeta* lowered the ovary size at which they reproduced (i.e., they lowered their reproductive threshold). Thus, they reproduced earlier than they would have done in the case of a fixed reproductive threshold.

Costs of increased reproductive effort

Several results of this study indicate that there were demographic costs associated with a high reproductive effort (a low reproductive threshold).

1) Ovary growth did not only depend on food concentration but also on the current ovary size. The reasons for this nonlinear ovary growth are unknown, but transport processes at the surface membrane of the vitellarium might be responsible for this pattern. The larger surface area of the vitellarium in large ovaries might contain more transport proteins and hence material could be transported at a higher rate from the coelom into the vitellarium. An implication of nonlinear ovary growth for individual reproduction is that a high RE decreases future reproduction because it results in a small, slowly growing ovary.

2) When subjected to complete starvation, *Synchaeta* resorbed material from their ovaries. Furthermore, animals that entered a starvation period with larger ovary sizes lived considerably longer, provided that they did not produce an egg during that time. These results indicate that vitellarium plasma is not only used to produce eggs but is also an important energy storage in adults. Consequently, high RE leads to animals that have lower resistance to starvation and it should therefore incur a survival cost in environments with fluctuating resource levels.

3) The highest RE occurred at 0.1 mg C/L. At this food concentration, the animals that reproduced had a significantly shorter lifespan than those that did not reproduce. Most of these animals died soon after egg deposition. Therefore, it seems that a very high RE (close to 1) can lead to immediate death in *Synchaeta*.

Test of the hypothesis: RE increases at low food concentrations

The prerequisite for my reproductive-effort hypothesis was that the probability of survival to a later reproductive opportunity is reduced at low food concentrations. Such a pattern occurred in my experiments: Since egg-laying intervals increased at low food concentrations (due to slower ovary growth) and survival remained constant, the probability that an individual survived to the next egg deposition was reduced at low food levels. This was further confirmed by the fact that animals in the life table response experiment (experiment 5) had fewer reproductive events (egg depositions) during their lifetime. Increasing time intervals between egg depositions at low food concentrations were also found in other studies with rotifers (e.g., Robertson and Salt 1981, Schmid-Araya 1991). However, this is not necessarily the case for all iteroparous organisms. Intervals between reproductive events can be constrained by factors other than food level. Examples include seasonal breeders or organisms in which reproduction is coupled to specific developmental stages (like *Daphnia*, which can only reproduce at the end of a molt cycle).

The hypothesis that RE increases at low food concentrations was confirmed by the experimental data. In experiment 5, the animals cultured at low food concentrations had a higher RE. One could argue that these animals were also smaller in body size and that the higher RE was therefore a consequence of constant egg size and constraints on ovary size caused by small space in the body cavity. Although ultimately such a size constraint must exist, it cannot be the reason for the patterns observed in RE. First, the maximal relative ovary size in animals cultured at high food levels was up to 30% of body volume, whereas the mean relative ovary sizes of animals cultured at 0.1 and 0.2 mg C/L were only 11.7% and 22.1%, respectively. Second, animals that were cultured at high and low food concentrations during their juvenile phase (and therefore attained different adult body sizes) both showed the same relationship between RE and food level (experiment 2). Thus, the observed pattern in RE seems to be explained as an active life history decision by the animals rather than as an unavoidable consequence of size constraints.

The results of the field study also confirmed my hypothesis. In Schöhsee, *Synchaeta* laid eggs of constant size while the food concentration and the mean ovary size were decreasing. The most obvious explanation for this pattern is that the animals in the field lowered their reproductive threshold at low food concentrations as did those in laboratory. However, it has to be noted that the agreement between laboratory and field data is qualitative, since the ranges of food concentration were different. Assuming a carbon content of 0.2 pg C/μm^3 for cryptomonads (Rocha and Duncan 1985), the highest concentrations in the field were 0.1 mg C/L, which is equal to the lowest food concentration, used in the laboratory experiments. Yet, under field conditions, *Synchaeta* did not seem to be limited at this food concentration. A possible explanation for this discrepancy is that *Synchaeta* used additional food sources in the field. Ciliates would be candidates for this, as some studies suggest that these may also be ingested by *Synchaeta* (Gilbert and Jack 1993).

Adaptive significance of increasing RE at low food concentrations

The fact that *Synchaeta pectinata* expended proportionally more energy when lower amounts were available seems paradoxical at first sight, especially since the costs in terms of reduced adult performance were high. Nevertheless, this pattern is predicted as an op-

timal strategy (in terms of maximizing the reproductive output) by models of life history theory. *Synchaeta* seems to be selected for a strategy of ''risky reproduction'' at low resource levels. This strategy may pay off in that it is better to produce one offspring as soon as possible and die as a consequence of this than to wait with reproduction and eventually die later of starvation (if the food levels do not rise within a critical time). In extreme cases of this strategy, an iteroparous organism may become essentially semelparous (as *Synchaeta* did at 0.1 mg C/L).

One might argue that the offspring of eggs produced in such a suicidal act of reproduction is less likely to survive, as the food levels may remain low for some time. The duration of the embryonic development of *Synchaeta pectinata* at 12°C was ~1 d, which is probably not sufficient to span the time until recovery of the food conditions. However, when these eggs were stored at 4°C it lasted ~5 d (*personal observation*). As *Synchaeta pectinata* do not carry their eggs, this situation might well apply in natural systems where the eggs would sink to strata with low temperatures. Additionally, juvenile rotifers can starve longer than adult ones (Kirk 1997*b*). Therefore, by producing subitaneous eggs *Synchaeta* can possibly span a starvation period of ~1 wk.

Other empirical studies suggest that there are alternative adaptations to fluctuating food concentrations. An organism might stop reproduction when facing sudden starvation and use the surplus energy to maintain its metabolism, thus prolonging adult life for later reproduction. An example for this strategy is the perennial triclad *Dugesia lugubris* (Calow and Woollhead 1977). A further strategy to deal with fluctuating food concentrations is the production of diapausing eggs when facing low food levels, which was also shown for some clones of *Synchaeta pectinata* (Gilbert and Schreiber 1998). Such eggs typically hatch after ~14 d, although some clones may also exhibit longer diapause (S. C. Fradkin, *personal communication*).

The reproductive strategy favored by natural selection might depend both on a set of individual constraints (physiological or genetic) and on the scale of the resource fluctuations present in the habitat. If the resource levels typically fluctuate with high frequency relative to the mean starvation time of the organism, a strategy that conserves survival of the parent should be favored. The respective organism should stop reproduction and wait until the food situation improves. However, if the resource levels fluctuate at a low frequency, i.e., if the periods of starvation are longer than the mean starvation time, strategies like ''risky reproduction'' should be favored. In such cases, the probability that an individual survives until another reproductive opportunity decreases considerably, and offspring should be produced as soon as possible. Further studies might directly test the hypothesis that the particular reproductive behavior of an organism can be considered as local adaptation to resource fluctuations within its habitat.

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