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Evolution of rotifer life histories

Claus-Peter Stelzer
Department of Evolutionary Biology, Institute of Animal Evolution and Ecology, Westphalian Wilhelms-University Münster, Hüfferstrasse 1, D-48149 Münster, Germany
E-mail: cpstelzer@web.de

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Abstract

When compared to most other multicellular animals, rotifers are all relatively small, short-lived and fast-reproducing organisms. However among and within different rotifer species there is a large variation in life history patterns. This review accounts for such variation in rotifers, with a strong focus on monogonont rotifers. As the life cycle of monogonont rotifers involves both asexual and sexual reproduction, life history patterns can be examined on the level of the genetic individual, which includes all asexual females, sexual females and males that originated from one resting egg. This concept has been applied successfully in many areas, for example in predicting optimal levels of mictic reproduction or sex allocation theory. The benefits and implications of the view of the genetic individual are discussed in detail. Rotifer life histories can also be viewed on the level of physiological individuals. A large part of this review deals with the life histories of individual amictic females and addresses life history traits like body size, egg size and resource allocation patterns. It asks which trade-offs exist among those traits, how these traits change under the influence of environmental factors like food availability or temperature, and whether these changes can be interpreted as adaptive.

Introduction

The aim of life history theory is to understand how the life history traits (see Table 1) of organisms have evolved. In other words, life history theory is an attempt to account for the tremendous variation of life histories within and among different groups of organisms (Stearns, 1992). For example, why do some organisms take years to mature and produce just one offspring every other year, while others produce a huge number of offspring after a relatively short juvenile phase? In a gross comparison with other animal groups, rotifers seem relatively uniform with regard to their life histories. They all are small, short lived and fast reproducing invertebrates (Allan, 1976). However, within the phylum Rotifera there is a large variation in life histories. One example is body size, which spans almost three orders of magnitude when different rotifer species are considered.

This review addresses life history variation in Rotifera, mostly in monogonont rotifers. The first part will introduce some basic concepts of life history theory, like constraints and trade-offs, and give examples for those in Rotifera. Another part will address the problem that genetic identity and physiological identity are not congruent entities in rotifers (as they are in most sexual diploid organisms). Thus in rotifers it is possible to distinguish between the life history of a physiological individual (individual amictic females, mictic females or males) and a genetic individual (all physiological individuals that derived from a single resting egg). The remaining parts of the review will be devoted to the life history of amictic females, as most of the previous empirical work has focussed

Table 1. The basic life-history traits

The basic life history traits
Egg size, size at birth
Growth pattern (e.g., determinate vs. indeterminate growth)
Age at maturity
Size at maturity
Number, size and sex ratio of offspring
Age- and size-specific reproductive investments
Age- and size-specific mortality schedules
Length of life

on them. Adaptation with respect to several life history traits, like body size or egg size, will be considered here. Finally some recent studies on life history adaptation to resource limitation will be summarized and discussed.

General considerations

Variation in life histories can be assessed on different levels. One example for life history variation at the level of individuals is phenotypic plasticity. Individual females of one clone may show variation in a life history trait depending on the environment they grew up in. Such phenotypic plasticity may be adaptive, as it can result in phenotypes fitter than alternative ones in the development-controlling environment. Life history variation can also be assessed at the population genetic (microevolutionary) level. This would involve a comparison of many different clones of the same rotifer species in a standardised environment. Differences among these clones have a genetic basis and would thus respond to selection. In a comparative analysis, life history traits are compared among the members of some higher level of phylogenetic organisation (e.g., monogononts vs. bdelloids). This type of analysis looks for general patterns that are characteristic for higher taxonomic ranks.

Constraints and trade-offs

A central tenet of life history theory is that individual traits cannot vary independently, but are subject to constraints and trade-offs. An example for a phylogenetic constraint that probably applies to all rotifers is eutely. The fixed cell number at birth sets upper limits to the evolution of the trait body size, since cells cannot grow indefinitely large. Additionally, ciliary propulsion, the basic mode of locomotion in rotifers, may impose a constraint on maximum body size, as it becomes energetically inefficient at large body sizes (Sleigh & Blake, 1977; Epp & Lewis, 1984; Stemberger & Gilbert, 1987). Physiological constraints can occur in individuals within a species. For example, a decrease in egg size at very low food concentrations may be inevitable if there is not enough material for a larger egg. One constraint that applies for all rotifers is that clutch size is fixed at one egg. Even bdelloid rotifers, which possess two ovaries, produce their eggs sequentially, alternating between the two ovaries (Ricci, 1995). Pseudoclutches as they can be observed in egg-bearing genera (e.g., *Brachionus*) are sequentially produced eggs of different ages, whereas a real clutch would be parallel produced offspring. Pseudoclutches can arise when the egg-laying interval is shorter than the period of embryonic development.

Trade-offs arise when an increase in one trait, e.g., current reproduction, causes a decrease in another trait, e.g., future survival. On the physiological level a trade-off will arise when a limited amount of resources has to be allocated among competing processes, such as somatic growth, reproduction or the accumulation of storage tissue. On the genetic level, trade-offs can be caused by antagonistic pleiotrophy, e.g., there may be genes that increase fecundity at an early adult age but are also detrimental to survival at an older age. Trade-offs may also arise as a consequence in particular ecological situations, e.g., if bearing eggs (reproduction) decreases survival due to a higher susceptibility to predators. Trade-offs, where an increase in current reproduction is paid by a decrease of future survival and/or fecundity are often called "costs of reproduction" (e.g., Snell & King, 1977; Sarma et al., 2002). Trade-offs can manifest themselves in negative phenotypic correlations between two life history traits. However, as correlation does not prove causation, a negative correlation itself does not prove the existence of a trade-off. To be sure that two functions are traded off against each other, direct experimental manipulations are necessary (Reznik, 1992). In this case, an artificially induced increase in one trait will result in a significant decrease of the other trait. This can happen either on the physiological level (e.g., manipulations of brood size or egg size) or on the genetic level (e.g., artificial selection experiments). None of these manipulations have been carried out on rotifers yet, although artificial selection experiments seem feasible in species that readily produce sexual stages (e.g., *Brachionus*).

The genetic individual and the physiological individual

In monogonont rotifers there are different perspectives from which life histories can be viewed. Traditionally, most of the work has been done on the life history of amictic females (this topic will be addressed later in this review). Other studies have compared the life histories of amictic females with those of mictic females (King, 1970) or males (Snell & Childress, 1987). All these studies focus on physiological individuals, i.e., units that are physically separated and have their own metabolism. A completely different way of looking at rotifer life histories is to focus on the genetic individual, which in case of a monogonont rotifer are all descendents of a single resting egg (i.e., all amictic females, mictic females and males). All these physiological individuals share the same genome (although males have just half of it), barring mutations that may have occurred in the germ line during asexual reproduction.

There are several analogies between the genetic individual of a monogonont rotifer and a typical diploid sexual organism. Amictic females represent the somatic tissue whereas mictic females and males represent the reproductive tissue. This analogy has been pointed out by Serra & King (1999). Whereas the life of a physiological individual ends with the death of the body, a genetic individual would die when the last amictic female of the clone has died. Genetic individuals therefore live considerably longer. In pond species of temperate regions this may be up to one season and in lake species which are not subject to draught or freezing, it may be even longer.

One may argue that over several successive asexual generations rotifers will accumulate mutations, which is at odds with the concept of genetic identity (Loxdale & Lushai, 2003). Strictly speaking, genetic identity is destroyed after only one mutation in the germline. However, from the standpoint of evolutionary adaptation within a rotifer clone these changes are completely irrelevant. Even with some mutations that may have occurred during asexual reproduction, the coefficient of relatedness among members of a clone is still essentially one. The genetic divergence due to mutations on these time scales is too minor to cause a conflict among the physical individuals of one clone.

The view of the genetic individual and the view of the physiological individual are not mutually excluding concepts. They just focus on different aspects and time scales. However they imply different measures of fitness. In the physiological individual (usually the amictic female) the population growth rate r is the relevant measure of fitness, whereas for the clone the relative genetic contribution (relative contribution of haploid genomes) to the resting egg bank is more appropriate.

Life history theory of the genetic individual

There are several studies on monogonont rotifers that incorporate both asexual and sexual stages of the life cycle. In these studies the concept of the genetic individual is often implicit. One example is a theoretical analysis of optimal mictic ratios in the rotifer *Brachionus plicatilis* by Serra & King (1999). If a rotifer clone induces mixis very late (at high population densities), it may enjoy a much higher population size when it finally starts to produce mictic females and may therefore increase its contribution to the resting egg bank. However, it may also risk its own extinction if the habitat deteriorates before resting eggs can be produced. This conflict bears striking similarity with the trade-off between early vs. late reproduction in other organisms. Another conflict that can arise is the question whether the descendants of a single resting egg, once they switched to sexual reproduction, should produce 100% mictic daughters or continue to produce also some amictic ones. In an environment where density-dependent growth can occur, the model of Serra & King (1999) predicts mixis to be induced as soon as the population comes close to its carrying capacity and intermediate mixis ratios thereafter. However, the exact conditions that rotifers will encounter in their natural habitats are temporally and spatially highly variable. Hence it is not surprising that there is considerable variation in the propensity of different *Brachionus* clones to produce mictic daughters (e.g., Gilbert, 2003).

Another phenomenon where the analogy between the genetic individual and a "real" individual comes in mind, are trans-generational effects in successive generations of amictically reproducing *Brachionus*. Gilbert (2002) found that females newly hatched from resting eggs showed extremely low propensity for mixis induction by the mixis factor, and that this effect gradually disappeared in successive generations. Only after 12 parthenogenetic generations, the different clones reached their maximum propensity for mixis induction. This pattern can be interpreted as a developmental programme of the genetic individual to delay its own reproduction.

Another example where it makes more sense to look at the genetic individual is sex allocation. In rotifers, a treatment of sex allocation is actually impossible from the perspective of the physiological individual, as one mictic female will either produce male or female offspring (Serra & Snell, 1998), but not both (except for the rare cases of amphoteric reproduction, see King & Snell, 1977). The life history trait that affects sex allocation in monogonont rotifers is the threshold age at which a mictic female can be fertilised (Aparici et al., 1998). If a female is fertilised before this age, she will produce (female) resting-eggs, otherwise she will produce male offspring. Aparici et al. (1998) developed a model to predict the evolutionary stable strategy for the threshold age of fertilisation in a population at equilibrium (zero net-growth, but constant supply of mictic females). They found that the only evolutionary stable strategy was a threshold age of fertilisation where the number of fertilised and unfertilised females was equal. This means that selection will favour clones which invest equally into male and female function. This theoretical prediction was validated in a subsequent experimental study (Aparici et al., 2002).

The genetic individual is a simultaneous hermaphrodite, as it possesses both male and female reproductive function (i.e., unfertilised and fertilised mictic females respectively, see Aparici et al., 1998). Unfertilised mictic females are analogous to the male reproductive organs. This is because meiosis, the process that initiates the production of male gametes happens already in the body of mictic females. Although the haploid egg cells first develop into males, there is no relevant additional event from the genetic view. Meiotic recombination and segregation happen when the mictic female produces her haploid egg cells. Each male develops by mitotic cell divisions only, thus its sperm are genetically identical. The analogue to a rotifer male in a diploid sexual organism would be an individual spermatozoon, because genetically male rotifers are the vehicle for one single spermatozoon that has been multiplied 20-fold (there are about 20 sperms per one male *Brachionus plicatilis*, Snell & Hoff, 1987).

From the view of the physiological individual the fertilisation mode in rotifers is internal fertilisation. On the other hand, the gametes of one genetic individual are widely dispersed in the environment and fertilisation among them is mostly governed by random encounters. In a rotifer clone, the female gametes are the haploid egg cells inside the body of a mictic female (the ones that will be fertilised). In *Brachionus*, a fertilised mictic female can typically grow just 2–3 of her fertilised oocytes into a resting egg (Snell & Childress, 1987). In some species within the *Brachionus plicatilis* species complex, the resting egg stays inside the body of the female (Gomez & Snell, 1996). In this case just one resting egg is produced per female, hence every mictic female body carries just one gamete. Thus, although the gametes of rotifers are not shed free into the water, genetically the fertilisation system in rotifers bears more resemblance to broadcast spawning than to internal fertilisation. At one time, fertilisation can occur massively parallel, among and also within many different genetic individuals.

Life history theory of amictic females

The following paragraphs deal with the life histories of amictic females only. Amictic females are the life history stage of rotifers that is exposed to natural selection most of time. Thus it is of great importance to study the life history adaptations that allow these units to efficiently replicate themselves.

Life table analysis

A life table summarises several life history traits, such as age-specific mortalities and fecundities, including the age at first reproduction. Life tables have been a popular tool since the early days of rotifer biology. They are conducted over the life span of a cohort of amictic females and the data are usually obtained in daily intervals. The data can be used to calculate important measures, such as the population growth rate r but also for more specific questions about survival patterns and trade-offs between fecundity and survival (Snell & King, 1977; Sarma et al., 2002).

The calculation of the population growth rate r can be done in different ways. The simplest way uses the formulae (Begon et al., 1991):

$$r \approx \frac{\ln R_0}{T} \quad \text{and} \quad T \approx \frac{\sum x \cdot l_x \cdot m_x}{\sum l_x \cdot m_x}$$

where R_0 is the average number of offspring per female per lifetime, x is the age class (e.g., 1 for the first 0–24 h), m_x are the age-specific fecundities (offspring per female per 24 h), and l_x is the age-specific survivorship (proportion of females still alive at age class x). As rotifers are continuously producing offspring, it is actually more accurate to use $x - 0.5$ instead of x (when calculating r based on daily observations). This assumes that all births happened exactly in between the observation intervals, whereas using x assumes that all births and deaths happened just before the census.

A more accurate method to calculate r is the Lotka–Euler equation:

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

This equation has to be solved iteratively, usually by the use of a computer. An example for an algorithm in the computer language PASCAL can be found in Stearns (1992) but other computer languages, or even calculations in Excel spreadsheets can be used for this purpose.

The population growth rate r can also be calculated from Leslie matrices (Caswell, 1989; Stelzer, 2002). Although computationally more elaborate than the above methods, Leslie matrices allow a more detailed analysis of the life table data. For example, the sensitivity of r to changes in vital rates of different ages can be calculated analytically (using specialised software packages like MATLAB®). This analysis allows identifying which of the many differences in age-specific survivorship and fecundity between two life tables are actually responsible for the observed difference in the population growth rate. Additionally, Leslie matrices can also be used to model the influence of age-structure fluctuations on population dynamics (Caswell, 1989).

For comparison of survivorship data (e.g., to compare starvation times or life spans), specialised statistical methods have been developed (e.g., Serra et al., 1994). Since survivorship data are not normally distributed, standard parametric tests are not appropriate (Fox, 2001). Alternative tests have been used in several studies with rotifers (Kirk, 1997a; Stelzer, 2001; Yoshinaga et al., 2003).

To test whether the population growth rates obtained from two life tables are significantly different from each other, confidence intervals for r have to be calculated (Conde-Porcuna, 1998; Stelzer, 2002). These can be estimated by re-sampling methods (the Bootstrap or the Jackknife method, Meyer et al., 1986) For these methods the use of a desktop computer is inevitable, as for each life table r has to be calculated multiple times from a subset of the data (Meyer et al., 1986; Caswell,1989).

Life tables will continue to be an important tool in the research on rotifers. Often they are the first type of analysis that is done with a newly cultured species. However, if the only relevant measure taken out of such a study is the population growth rate r, it is often easier to directly measure r from the growth of semi-continuous cultures (for methods, see Rothhaupt, 1990).

Body size

Body size is an adaptive trait, shaped by various selective pressures during its evolution (Roff, 1981). During juvenile growth many organisms face a trade-off between reproducing early at a smaller size and reproducing late at a larger size. Rotifers grow by increase in cell size only. The fact that there are no cell divisions after hatching certainly sets upper limits to body size. Despite this rather theoretical constraint there is a large variation in body size among different rotifer species

(Stemberger & Gilbert, 1985; Telesh et al., 1998), among species within genera (Rougier et al., 2000), among clones (Snell & Carrillo, 1984), and within a clone due to phenotypic plasticity (Stelzer, 2002).

Size differences among species of different genera can be immense. In terms of body volume, *Asplanchna priodonta* is 2000-fold bigger than *Keratella cochlearis tecta* (Telesh et al., 1998). However, large rotifers often contain more intercellular space, whereas the tissues of small rotifers are more "dense" in terms of the ratio between cellular and intercellular space. In the carbon content the difference between *A. priodonta* and *K.c. tecta* is only 87-fold (Telesh et al., 1998).

Since most rotifer species, especially those of different genera, have evolved under very different ecological conditions, it is hard to establish a general relationship between body size and its selective value. For example, whereas a large body size can be expected to protect against predation by invertebrate predators like *Asplanchna* or copepods (Lapesa et al., 2002) and against interference competition by *Daphnia* (Gilbert, 1989), there are also examples for alternative solutions (e.g., the escape response of *Polyarthra*) that retain a relatively small body size (Wickham & Gilbert, 1991).

One popular generalisation is that animals with a large body size have a higher fecundity than small animals. Thus, during juvenile growth there is a trade-off between reproducing early and staying small and reproducing later at a larger body size while having a higher fecundity (Roff, 1981). The mechanistic explanation for the higher fecundity in larger females is often that they can carry more offspring per brood (e.g., in *Daphnia*, Glazier, 1992; Lampert, 1993). In rotifers the situation is more complex. As eggs are produced individually and sequentially, the argument with the larger brood is not valid. One advantage of a large body size could be that it allows more eggs to be attached to the outside of the body (Walz et al., 1995). On the other hand, there are many rotifer species that do not carry their eggs but release them into the water. So the question remains, whether larger females in a particular rotifer species can produce offspring at a higher speed than smaller females. One way to test this hypothesis is to compare the fecundity of differentially sized females within one species (i.e., either clones of different size or individuals with phenotypically induced size-differences within one clone). To my knowledge, no such study has been performed yet. There are, however, studies that report positive correlations between body size and birth rate in comparisons among species of different genera (Lewis, 1979; Walz, 1995).

Reproduction and its costs

There are two characteristics of rotifer reproduction that are fundamentally different from many other organisms. First, the number of oocytes is fixed at birth. This feature can sometimes be observed in life table experiments due to the existence of a distinct post-reproductive phase, often after a characteristic number of eggs have been laid (e.g., ~20 in *Brachionus*, Halbach, 1970). Even when cultured under the most benign conditions, rotifers stop reproduction at some age, presumably because they have depleted their reservoir in oocytes. It is currently unknown whether the limited oocyte supply has any significance under natural conditions. Another question is, whether there is variability in total oocyte number (i.e., maximum possible number of offspring per female) among different species. It is possible that in some rotifer species, where the expected number of offspring per female is low under natural conditions, the number of oocytes is also reduced. A second characteristic of rotifer reproduction is that there is no parallel production of offspring (clutch size = 1). This complicates the analysis of trade-offs between offspring size and number. Theoretically a trade-off between offspring size and the speed of reproduction is possible, since offspring size may only be increased at the cost of longer egg laying intervals. However, confounding variables such as age-related changes in food intake or other age-specific effects may influence this trade-off or even influence egg size directly.

Several studies have addressed costs of reproduction in rotifers, both on the physiological and on the population genetic level. Demonstrations of reproductive costs often involve life table analyses. Current reproductive output is correlated with measures of later reproduction and/or survival. A negative correlation indicates reproductive costs. In their pioneering study Snell & King (1977) showed that in *Asplanchna brightwelli* both the residual reproductive value and survival after 24 h were negatively correlated with age-specific fecundity. The study involved 21 different clones and Snell & King (1977) extracted two basic life history patterns: some clones produced a lot of offspring in a short time and had a short lifespan, while others reproduced slower but lived longer. A similar study by Sarma et al. (2002) addressed the cost of reproduction in four rotifer species and found evidence in the form of negative correlations between fecundity and survival in the majority of cases. Stelzer (2001) measured the costs of reproduction arising from resource allocation in individual *Synchaeta pectinata*. *Synchaeta* can use the cytoplasm in their vitellarium for either the production of eggs and or to maintain their metabolism during starvation. In animals with a similar amount of cytoplasm in the vitellarium, those that reproduced during starvation died on average one day earlier than those that did not reproduce. This demonstrated the cost of reproduction on the level of individual physiology.

A cost of reproduction that specifically applies to egg-bearing species may be a decrease in swimming performance when the number of carried eggs is high (J. J. Gilbert, personal communication). Decreased swimming speed will result in lower energy intake rates because the volume searched for food decreases. Yufera et al. (this volume Part V) report that ovigerous females exhibit higher oxygen consumption than it is expected from the sum of the oxygen consumption of non-ovigerous females and that of isolated eggs. Additionally, the absolute swimming speed declined in all treatments (although not significantly) in ovigerous females. Both findings indicate that carrying a large number of eggs may be an additional cost that has to be considered in egg-bearing species. However, before final conclusions can be drawn, a wider range in the number of eggs carried needs to examined. In the study of Yufera et al. (this volume Part V) up to two eggs per female were considered, whereas under good conditions *Brachionus* females often carry 3–4 eggs.

Egg size

Egg size is under the simultaneous influence of many factors (Bernardo, 1996). For example it may co-vary with factors like maternal age or size. Also environmental factors, such as food availability or temperature can influence egg size. It is an important question whether this variability in egg size has any adaptive significance.

Egg size and offspring fitness

It is often assumed that offspring size and offspring fitness are positively correlated and that this results in a trade-off between producing few large or many small offspring (Smith & Fretwell, 1974; Glazier, 1992). This hypothesis has been addressed in rotifers with regard to egg size (e.g., Kirk, 1997b; Orsenigo et al., 1998). Egg size within a rotifer clone is known to vary with environmental factors like food concentration or temperature. One question would be whether this phenotypic plasticity is adaptive. For example, it may be beneficial to produce larger, starvation resistant offspring at low food concentrations (Glazier, 1992). This problem has actually two parts. First, are larger offspring produced at low food concentrations and, second, are these larger offspring fitter at low food concentrations/under starvation? These two hypotheses have been addressed by Kirk (1997a) in a study using *B. calyciflorus* and *S. pectinata*. The two species responded differently along the gradient of food concentrations. Egg size in *Brachionus* increased with food concentration (see also Sarma & Rao, 1987; Walz & Rothbucher, 1991), whereas it stayed relatively constant in *Synchaeta*. Constant egg sizes along a wide range of food concentrations in *Synchaeta* were also observed by Stelzer (2001). In *Synchaeta*, egg size seems to increase not as a function of food level, but as a function of the mother's age and possibly size. For example three day old females produce larger eggs than two day old females (Kirk, 1997b). Both in *Brachionus* and *Synchaeta*, a larger egg size seems to be advantageous, as offspring from large eggs had longer starvation times (Kirk, 1997b). Similar questions were addressed in a study on the bdelloid rotifer *Macrotrachela quadricornifera* (Santo et al., 2001). In this study differentially sized eggs were produced by culturing the mothers at high vs. low food concentrations. Large eggs were obtained at the higher food concentration. Offspring from large eggs developed faster, having a significantly shorter embryonic development and juvenile period. Recovery from desiccation, a fitness-related trait in bdelloids, was not affected by the difference in egg size (Santo et al., 2001). The shorter embryonic development of large eggs as observed by Santo et al. (2001) is not a general pattern though. Studies with other rotifers have shown that embryonic development time can increase or also be unaffected by egg size (summarised in Walz, 1995).

Temperature is another factor that can influence egg size in rotifers (Green, 1998; Stelzer, 2002). Large eggs are usually produced at low temperatures, whereas small eggs are produced at high temperatures. Stelzer (2002) showed that when *S. pectinata* were cultured at 4 °C they produced eggs that were 35% larger than those of animals cultured at 12 °C. This is in strong contrast to the apparent constancy of *Synchaeta*'s egg size across different food concentrations (see above). However, offspring from large eggs did not exhibit a greater fitness than those of small eggs (Stelzer, 2002). In fact it seemed that offspring from large and small eggs had a slightly higher growth rate at the temperature at which they were produced. Offspring from small eggs were growing significantly faster at high temperatures than offspring from large eggs (Stelzer, 2002). Offspring from large eggs did slightly better at low temperatures, but the difference was non-significant. Therefore the higher investment into individual offspring at low temperatures does not seem to be rewarded by higher offspring fitness.

In summary, although there is considerable phenotypic plasticity for egg size in rotifers, the question whether these patterns are adaptive remains unanswered. Currently there is no good support for the claim that offspring of a certain egg size do best in the environment in which they were induced. There may be several explanations for this. First, constraints may prevent rotifers from adjusting their egg size optimally (Kirk, 1997a). For example, it could be that *Synchaeta* already produces the minimum viable egg size (for a given temperature), so that it would be very disadvantageous to decrease egg size further at high food concentrations. In fact, offspring from small eggs (produced at extremely low food concentrations) often develop very slowly and have a reduced fecundity (C.P. Stelzer, personal observation). Another possibility that may explain the lack of fit between theory and data lies in the nature of the optimality model itself. Models on optimal offspring investment usually assume equilibrium, i.e., offspring will experience the same environment as their mother. This may not be true for rotifers. Especially resource conditions can be extremely variable, both in space and in time (Steward & Wetzel, 1986). The results of studies on offspring fitness also depend on the measure of fitness being employed. These measures have been quite diverse: neonate starvation time (Kirk, 1997a), population growth rate (Stelzer, 2002), duration of embryonic and juvenile development, and resistance to desiccation (Santo et al., 2001).

Large-scale patterns in relative egg size

Comparative analysis has revealed an interesting large scale pattern in rotifers. Although the volume of amictic eggs increases with body volume in a comparison across species, the ratio of egg volume to body volume (REV = relative egg volume) does not stay constant. Instead, small rotifer species consistently show a larger REV than large species (Walz et al., 1995). This indicates that small rotifers have a higher reproductive effort (Walz et al., 1995). The basic pattern was independently confirmed in other studies, e.g., in the taxa Collothecidae and Flosculariidae (Wallace et al., 1998), and in several marine *Synchaeta* species (Rougier et al., 2000). For bdelloid rotifers too few data are available at this time. In one study, involving a comparison between two differentially sized species, the smaller one had a larger REV (Ricci & Fascio, 1995), whereas in another study with two bdelloid species REV was equal (Ricci, 1995). The pattern of REV indicates that small rotifers show, on average, a higher investment in individual offspring than large rotifers. The ubiquity of this phenomenon suggests a common explanation. Current explanations for the higher REV in small rotifers relate the phenomenon to selection for low food demands in small rotifers (Walz et al., 1995). One advantage that small rotifers may gain through their large REV is that they have to grow less to reach adult size (Walz et al., 1995).

Life history adaptations to resource limitation

Resource limitation is one of the most important environmental factors experienced by rotifers (Gonzalez & Frost, 1992; Merriman & Kirk, 2000). Several studies have addressed life history adaptations to conditions of low resource availability on both theoretical and empirical grounds. Kirk (1997b) examined the life history responses to starvation in nine different rotifer species. Starvation times ranged from 0.4 to 5 days. Some species, like *Keratella* or *Brachionus*, immediately stopped allocating resources towards reproduction after food deprivation, whereas others, like *Synchaeta* or *Asplanchna*, continued to produce offspring, sometimes at an even higher rate than the fed controls, but with reduced survival. The differences in reproductive behaviour explained the variation in starvation times among species much better than other variables, e.g., body size. The main finding of this study was that species that reproduced after being deprived of food had considerably shorter starvation times than those which stopped reproduction. Kirk et al. (1999) extended these findings by showing that respiration rates of non-reproducing rotifers drop shortly after food deprivation whereas those of reproducing rotifers stay high for a longer time.

The two diametrically different responses to starvation were confirmed in studies with *Brachionus plicatilis* (Yoshinaga et al., 2003) and *Synchaeta pectinata* (Stelzer, 2001). When *B. plicatilis* was deprived of food at an age of 2 days they not only did stop to lay eggs, but also lived significantly longer than the fed controls (Yoshinaga et al., 2003). Periodical starvation, i.e., feeding *Brachionus* for just 1–3 h and starving them for the rest of each day resulted in lifespans 2–3 times longer than those of non-starved animals (Yoshinaga et al., 2000). According to the authors this strategy may pay off because it increases the probability that females survive adverse conditions to reproduce later in life when food concentrations recover. In contrast to *Brachionus*, *S. pectinata* will continue reproducing under starvation, provided that they have an ovary size large enough to produce at least one more egg (Stelzer, 2001). Although this behaviour decreases the survival chances of the mother, it also helps the clone to persist through periods of starvation. First, because the embryo stage itself is protected from starvation (it does not need to feed) and second, because juvenile rotifers can starve longer than adults (Kirk, 1997b). As *S. pectinata* do not carry their eggs, egg development time may be further prolonged if the eggs sink to the colder depths in a stratified lake.

The length of the expected starvation period, in the natural systems where the species have evolved, may explain the difference between the two different responses of *Brachionus* and *Synchaeta*. The "*Brachionus* response" (stop reproduction and lower the metabolism in order to preserve the mothers body) will only pay off if the starvation period is quite short. At 20 °C adult *B. calyciflorus* can starve for two days at maximum (Kirk, 1997b). If the starvation period is longer, the mother will die without leaving any further offspring. Longer starvation periods seem to be the conditions that favour the "*Synchaeta* response". Depending on the duration of embryonic development, Stelzer (2001) estimated that using this strategy asexually reproducing *Synchaeta* can span up to 1 week of adverse resource conditions. Even longer periods of starvation can be bridged if embryonic development is "intrinsically" prolonged. This is the case for some strains of *S. pectinata*, which have evolved amictic eggs with a diapausing stage that can be induced by low food concentrations (Gilbert & Schreiber, 1998).

In a modelling study, Shertzer & Ellner (2002) tried to predict optimal allocation among somatic growth, reproduction and storage under conditions of variable resource supply. Life history data from *B. calyciflorus* was used in the model and some of its boundary conditions reflect this, e.g., it was assumed that allocation to reproduction stopped when food intake dropped below the maintenance threshold. Shertzer & Ellner's model predicts that the optimal body size should be smaller if animals evolve under variable resource concentrations and that optimal body size decreases further as the length of "bad periods" increases. Other adaptations to variable resource conditions were increased allocation to storage, delayed maturity, and indeterminate growth. The model correctly predicted starvation times in animals that were starved at different age classes or acclimatised to different food levels prior to starvation. However, the predictions regarding the above mentioned life history characteristics still await empirical validation. This could be done by artificial selection experiments in which *B. calyciflorus* is cultured under constant vs. variable resource conditions.

A more general model for resource allocation under variable food conditions would need more relaxed boundary conditions than the one of Shertzer & Ellner (2002). First, the model should allow allocation to reproduction to continue, even when animals are starved (as this seems to be the case in some rotifer species). Second, it would be more realistic if stored energy could be used both for maintenance of the metabolism and for reproduction in animals that experience starvation. Third, longer periods of starvation should be examined. In Shertzer & Ellner (2002) they are only up to 2 days (this is approximately the starvation time of *Brachionus*). If a starvation-protected embryonic stage would be incorporated, the model might produce a similar dichotomy than we see in the starvation response of planktonic rotifers (Kirk, 1997b).

Conclusions and future perspectives

Life history theory in rotifers has made much progress in recent years. It has been increasingly common to consider the adaptive significance of life history patterns and to relate them to selective pressures that rotifers are exposed to in their natural habitats. In some cases it has been relatively easy to find plausible adaptive explanations (e.g., resource allocation, mixis strategies). In other cases, the adaptive significance is still unclear (e.g., egg size). Such traits may be determined mainly by constraints and some of these constraints may be very specific to rotifers. There is certainly more work needed on the influence of constraints on rotifer life histories.

Several lines of research seem particularly promising for future studies:

Due to their asexual mode of reproduction, rotifers are ideal study objects to look at the reaction norms of genotypes (clones). In most studies so far, phenotypic plasticity has been assessed only for one or few clones. This is probably insufficient, since a lot of genetic variation for the norm of reaction probably exists in nature. Therefore, several clones of a species should be tested when studying a particular question. Since some rotifers form cryptic species complexes (Gomez et al., 2002), an analysis of one or two phylogenetic informative genes may be necessary to confirm that the studied clones do indeed belong to the same species.

In the future it may be worthwhile to adopt techniques that are already standard in other organisms, for instance artificial selection experiments. *Brachionus* would be a suitable organism for this approach as they are easy to culture and readily reproduce sexually. Interesting selective regimes would be environments with constant vs. variable resources (to test the predictions of Shertzer & Ellner, 2002) or the selection for large vs. small body size/egg size.

Life history studies are usually performed with monogonont rotifers or bdelloid rotifers, but not with both. It would be interesting to have more data on both of these groups, especially those bdelloid and monogonont species that occur in the same habitat. Such studies could establish the basic differences in life history evolution of facultative vs. obligate asexual organisms. Rotifers are probably the only phylum where such a comparison is possible.

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