Hydrobiologia (2005) 546:291–306
A. Herzig, R.D. Gulati, C.D. Jersabek & L. May (eds.) Rotifera X: Rotifer Research: Trends, New Tools and Recent Advances
DOI 10.1007/s10750-005-4235-x

Diapause in monogonont rotifers

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Key words: diapause, diapausing eggs, resting eggs, sexual reproduction, cyclic parthenogenesis

Abstract

This review focuses on more recent findings on the diapause in Monogonont rotifers, since the major reviews by Pourriot & Snell (1983, Hydrobiologia 104: 213–224) and Gilbert (1992, Rotifera. In Adiyodi, K. G. & R. G. Adiyodi (eds), Reproductive Biology of Invertebrates, Vol. 5 – Sexual Differentiation and Behaviour. IBH Publishing Co., Oxford: 115–136; Vol. 6A – Asexual Propagation and Reproductive Strategies. IBH Publishing Co., Oxford: 231–263.). It covers diapausing egg formation, diapausing egg survival, and diapausing egg hatching as well as possible strategies involved in these processes. Data from laboratory and field studies exist, but little information is available on diapausing egg hatching in the field. Resting or diapausing egg production can be mictic and in some cases amictic. Mictic diapausing egg production depends on the balance between cues promoting and inhibiting mictic female production. Such cues can be either environmental or endogenous. Our knowledge on factors inducing mixis is still limited to a few species, but effects of crowding on mixis induction may be more widespread. Recent results also show that male mating behavior may play an important role in the successful production of diapausing eggs. Hatching may be induced by factors related to temperature and light conditions; also desiccation may have a role. However, desiccation of temporary habitats may also be damaging to diapausing stages. Although few data are available, those existing point to distinct differences between populations and the importance of clonal variation within populations regarding the initiation as well as the termination of diapause.

Introduction

Diapause has been most intensively studied in insects, where it is defined as a dynamic state of low metabolic activity associated with reduced morphogenesis and increased resistance to environmental extremes. It occurs during a genetically defined stage of the life cycle, usually in response to a number of environmental stimuli that precede unfavorable conditions. Once diapause has begun, metabolic activity is suppressed, even if conditions favorable for development prevail (Tauber et al., 1986). This form of dormancy is in contrast to quiescence, which is a state of suppressed metabolism directly provoked by conditions unfavorable for growth and reproduction, and which can occur during any stage of the life cycle.

Diapause and quiescence are widespread forms of dormancy among animal phyla (Cáceres, 1997). In the phylum Rotifera diapause is limited to the Monogononta, whereas quiescence is found in the Bdelloidea (Ricci, 2001). As in crustaceans, dormant stages of rotifers can serve two purposes, dispersal in space and time (Hairston, 1998): dormancy allows survival during periods of harsh environmental conditions which do not permit the existence of active stages (dispersal in time) and dormant stages are the main propagule stages by which new habitats can be colonized (dispersal in space).

The life cycle of the Monogononta is characterized by cyclic parthenogenesis. Amictic females reproduce parthenogenetically, producing female offspring (amictic reproduction). Diapause is initiated by environmental cues when part of a population starts to reproduce sexually (mictic reproduction). Mictic females are produced, whose oocytes undergo meiosis. Unfertilized mictic females parthenogenetically produce haploid male offspring. If a mictic female is fertilized by a male, it produces diploid diapausing eggs, also called resting eggs. In some species amictic (parthenogenetic) production of diapausing eggs has been reported.

Research on diapause in monogonont rotifers has covered formation, hatching, and survival of resting eggs as well as possible strategies involved in these processes. Factors controlling initiation of mixis in monogonont rotifers have been an important area of diapause research. The second focus of research has been on factors controlling resting egg hatching and affecting resting egg survival. Both processes affect the function of the resting egg bank, which ensures the survival of the population during periods of harsh environmental conditions. This review covers new results on diapause in monogonont rotifers that have been published since the last major reviews by Pourriot & Snell (1983) and by Gilbert (1992, 1993). Resting egg hatching and unique features of the stem females hatching from resting eggs are covered in detail in another review (Gilbert & Schröder, 2004).

Mictic reproduction

Diapause in monogonont rotifers depends on the production of resting eggs by fertilized mictic females. The factors initiating mixis in rotifer populations, but also the frequencies of fertilizable mictic females and males, as well as the ratio of unfertilized male-producing females to resting egg producing females may be important and influence the production of resting eggs. Also mating behavior must be considered in this context because it may critically affect successful resting egg production.

Mixis initiation

Factors that induce the production of mictic females are still poorly known for most species. They include photoperiod in species of *Notommata* and *Trichocerca*, the uptake of α-tocopherol enriched food in many species of the genus *Asplanchna*, and factors related to density in several other species. The work on photoperiod and uptake of α-tocopherol as mixis-inducing factors has been reviewed in detail by Pourriot & Snell (1983) and Gilbert (1992, 1993) and will not be covered here.

Increasing population density induces mixis in species of several genera. Crowding has long been known to affect mictic female production in the *Brachionus plicatilis* species complex and in *B. calyciflorus* (Pourriot & Snell, 1983; Gilbert, 1992, 1993); however, recent studies have demonstrated that increasing population density also induces mictic female production in *Epiphanes brachionus* (Pourriot & Rougier, 1999) and in *Brachionus angularis*, *Epiphanes senta*, and *Rhinoglena frontalis* (Schröder & Gilbert, 2004). Carmona et al. (1993) provided some evidence that mixis in *B. plicatilis* is induced by a chemical cue which is present in the water of dense populations. Stelzer & Snell (2003) definitely showed that this is the case. Their results strongly support the hypothesis that the animals produce a chemical substance which accumulates in the water at high population densities and then induces mixis. This hypothesis would also explain the results of Hagiwara et al. (1994) who found that the addition of water soluble extracts of conspecific rotifers from mass cultures increases mixis in *B. plicatilis*.

Although it is still unknown whether a chemical is also involved in the density-dependent mixis induction of the other species mentioned above, such a possibility is likely. Physical contacts between females at high densities can be excluded as an obligatory mixis stimulus because mixis could be induced in females kept individually in a small volume of medium. In *E. brachionus*, Pourriot & Rougier (1999) found no significant differences in the proportion of mictic offspring of females which were kept individually and females which were grouped with other females at the equivalent density. The density-dependent stimulus appears to be very specific at least in some species, but it may be less specific in others. Gilbert (2003b) found that mixis is not induced in single females of a *B. calyciflorus* strain from Florida if they were crowded with females from a reproductively isolated Australian *B. calyciflorus* strain. However, the mixis inducing signal may be quite unspecific in *B. plicatilis*. Carmona et al. (1993) reported that mixis could be induced by a medium that was preconditioned by an *Artemia* culture.

The induction of mixis at high densities of conspecific females has been considered to be adaptive in several aspects. First, it has been argued that high densities increase the probability of male–female encounters, which seem to be random and depend on males recognizing females only upon contact (Snell, 1998). Second, if high densities are reached by amictic reproduction, and subsequently the reproductive mode switches to mictic reproduction, at a given fertilization rate more resting eggs can be produced simply because the number of sexual females will be higher (Snell & Boyer, 1988; Serra & King, 1999). Gilbert (1993) postulates that factors inducing sexual reproduction reflect favorable conditions which allow rapid population growth, high population densities, and the production of large numbers of energy-rich resting eggs. On the other hand, it has been argued that high population densities may lead to overexploitation of food resources and therefore cause deteriorating conditions in the near future (Serra & Carmona, 1993; Aparici et al., 1996; Ciros-Pérez et al., 2002). In this case, increasing densities would lead to the production of resting eggs in anticipation of the deterioration of the habitat. However, threshold densities inducing mixis are usually well below observed maximum population densities (Gilbert, 2002; Gilbert & Schröder, unpublished data), indicating that resting eggs should be produced when food resources are still sufficient.

While unfavorable environmental conditions such as food limitation may directly induce sexual reproduction in cladocerans (Kleiven et al., 1992; Alekseev & Lampert, 2001; LaMontagne & McCauley, 2001), there has been little experimental evidence so far that this also may be the general case in monogonont rotifers. Mictic reproduction seems to be more inhibited by unfavorable conditions than amictic reproduction (Snell & Boyer, 1988; Snell & Carmona, 1995), and conditions enhancing mictic female production also increase fecundity of fertilized mictic females (Hagiwara et al., 1988). Also, crowding, which is known to induce mixis in several species, was not found to be associated with reduced fecundity (Schröder & Gilbert, 2004). All these findings indicate that mictic reproduction and resting egg production are more likely to take place under favorable conditions, well before the habitat deteriorates and conditions become unfavorable for population growth. However, the possibility that food deprivation associated with imminent habitat deterioration may directly influence mictic reproduction has been raised (Carmona et al., 1993; Aparici et al., 1996; Ciros-Pérez et al., 2002), and it has been shown for *B. plicatilis* that starvation of the stem females promotes mixis induction in later generations (Hagiwara, this volume Part V). This question certainly requires further research, especially since factors inducing mixis are still unknown for most monogonont species.

Exogenous and endogenous factors modifying the mixis response

The response to the mixis cue can be modified by endogenous as well as exogenous factors. First it can be influenced by exogenous environmental factors which inhibit or increase the effect of the actual mixis stimulus in some way. Snell & Boyer (1988) found that mictic female production in *B. plicatilis* is more sensitive to food limitation and to increased ammonia concentration than amictic female production: females individually cultured in small volumes comparable to high population density cease to produce mictic offspring at low food concentrations and high ammonia concentrations, while they are still producing amictic offspring under these conditions. Snell & Hoff (1985, 1987) found that the type of diet also had a large effect on mictic female production in *B. plicatilis* as well as on the fertility of the male offspring produced by unfertilized mictic females. Mictic female production was highest when food was a combination of *Chlorella vulgaris* and Baker's yeast, while on a diet of the cyanobacterium *Schizotrix calcicola* mictic females produced male offspring with significantly reduced fertility.

It has been demonstrated in several species that mixis induction is affected by temperature. In experimental cultures the proportion of mictic offspring of *E. brachionus* females increases to 50% of the population size with increasing population density at 14 °C, whereas at 10 °C it remains at a constant low rate of 5–8% even with increasing density (Pourriot & Rougier, 1999). As a result of the prevailing amictic reproduction at the lower temperature, the population growth rate was higher at 10 °C than at 14 °C. In experiments with females of this species individually isolated in small volumes, the proportion of mictic offspring was higher at 20 °C than at 14 °C. In contrast, Hagiwara et al. (1988) found that the proportion of mictic females of *B. plicatilis* in experimental culture is higher at a temperature of 15 °C than at 20, 25 and 30 °C. Fecundity of fertilized mictic females (i.e. the number of resting eggs produced) increased with decreasing temperatures. However, mictic female production was significantly increased when females were moved from 10 °C to 25 °C (Kogane et al., 1997).

Also varying salinities have a similar effect as varying temperature in *B. plicatilis*: the proportion of mictic females as well as the fecundity of fertilized mictic females was highest at a salinity of 4‰ and decreased with increasing salinity (Hagiwara et al., 1988). Similar results were obtained by Lubzens et al. (1985) and by Pozuelo & Lubián (1993). *Brachionus rotundiformis* displays the reverse trend (Hagiwara et al., 1989): the proportion of mictic females and the fecundity of fertilized mictic females increases with increasing salinity. It should be pointed out, however, that it is difficult to separate effects of salinity and food type and concentration on the one side and effects of crowding on the other. Suboptimal salinity and low food concentration may decrease the crowding response simply because they decrease population growth and metabolic rate relative to controls. Thus they may operate indirectly only by affecting population density.

Hagiwara et al. (1994) demonstrated that the presence of certain bacteria led to increased mictic reproduction in *B. plicatilis*, suggesting that the synthesis of vitamins by the bacteria could enhance mictic female production.

Endogenous factors – Carmona et al. (1994) noted that the proportion of mictic offspring in *B. plicatilis* is also dependent on the age of the mother. The proportion of mictic offspring in young females – during the first 2 days of the reproductive period – was higher than the proportion of mictic offspring in older females.

Endogenous factors may also affect the extent to which amictic females respond to a given mixis cue. It has first been demonstrated for *B. calyciflorus* that the first generations that follow the ex-resting-egg female (stem female) respond not at all, or to a much less extent, to a high population density than do later generations (Gilbert, 2002, 2003a). The offspring of these early generation females are mostly amictic, even when they are crowded. Females of the 12th and later generations produce 50% or more mictic offspring when they are produced in a comparable high density environment. This delay in the mictic response is also found in *B. angularis*, *E. senta*, and *R. frontalis* (Schröder & Gilbert, 2004), all of which respond to population density as a mixis cue.

The mechanisms of these endogenous effects on mictic reproduction are still unknown. However, it has been recently demonstrated that common invertebrate hormones are also present in rotifers (Gallardo et al., 2000a). Serotonin (5-HT) influences mictic female production in *B. plicatilis* (Gallardo et al., 2000b), suggesting that hormonal activity in combination with external mixis stimuli affects mictic female production.

It is important to note that a large amount of variation within many species has been found in the response to mixis cues. Usually mixis stimuli only induce females to produce a certain proportion of mictic offspring and only in a few cases is this close to 100% (Pourriot, 1965; Buchner, 1992; Aparici et al., 1996). The proportion of mictic female offspring can vary remarkably. Variation can be found at three different levels of organization. First there is intraclonal variation: it can often be observed in experiments with a single clone that a few females do not produce any mictic offspring under conditions that otherwise induce mixis. Then there is variation among clones within a population. In *B. calyciflorus*, *B. angularis*, *E. senta*, and *R. frontalis*, the propensity to produce mictic offspring varies significantly among clones of the same strain (Gilbert, 2002; Schröder & Gilbert, in press). Similar results were also found in comparisons of *B. plicatilis* clones from the same strain (Hino & Hirano, 1977). Aparici et al. (2001) detected large variation in the time of mixis initiation after hatching from the resting egg as well in the densities at which mictic females appeared in a number of clones from a *B. plicatilis* strain collected in the Torreblanca Marsh (Spain). However, only a small part of that variation was found to be heritable and therefore clone specific; most of the detected variation was assumed to be phenotypic and of environmental origin.

Not surprisingly, there is variation among strains of different populations. Carmona et al. (1994) found that mictic rates in 13 clones of *B. plicatilis* collected at different sites varied significantly when they were exposed to the same high density stimulus. In the study of mixis delay in *B. calyciflorus*, *B. angularis*, *E. senta*, and *R. frontalis* (Schröder & Gilbert, 2004), significant variation was found among strains: a delay of mixis in the early generation was found in one strain of *B. calyciflorus* from a temporary pond in Florida, but it was absent in another strain from a permanent pond in Georgia. The same was observed for a floodplain strain of *R. frontalis* and a strain from a permanent pond, but strains of *E. senta* from the same habitats as the *Rhinoglena* strains both displayed a delay of mixis in the early generations (Schröder & Gilbert, 2004).

Cyclic parthenogenesis in the life cycle of monogonont rotifers includes important trade-offs between parthenogenetic and sexual reproduction. Population growth and increases in frequency of individual clones relative to other clones within the population depend on parthenogenetic reproduction of amictic females. Therefore, allocating resources to the production of mictic offspring decreases a clone's intrinsic growth rate and thus its frequency within the population (Snell, 1987; Serra & Carmona, 1993; Serra & King, 1999). Results from long-term batch and chemostat cultures show that the propensity for mictic reproduction in a population declines and finally disappears in continuous cultures so that reproduction is completely amictic within 2 months to 3 years (Boraas, 1983; Bennett & Boraas, 1989; Buchner, 1992; Fussmann et al., 2003) and indicate that mixis is under strong selection. Mixis is favored if periods of adverse environmental conditions can only be survived by diapausing resting eggs. But, in the absence of such periods clones with high propensity for mixis will be selected against because they will display a reduced growth rate compared to clones with low propensity for mixis. Selection for exclusive amictic reproduction may also be acting in natural populations. Reproduction was found to be purely amictic in populations of *Keratella cochlearis*, which were perennial in large lakes, whereas in populations inhabiting small ponds sexual periods did occur (Wesenberg-Lund, 1930).

Ciros-Pérez et al. (2002) have also demonstrated trade-offs between mictic and amictic reproduction. They have shown that mictic reproduction associated with reduced population growth affects competitive ability when closely related species compete for food. They found in resource competition experiments with pairs of experimental populations of *B. plicatilis*, *B. rotundiformis* and *B. ibericus* that one species was excluded by the other when its mixis investment was high where that of the other species was low. If mixis investment was intermediate in both species, they were able to coexist. However, mixis investment was always maximal when a species was the inferior competitor and its exclusion was predicted by Tilman's resource competition theory (Tilman, 1982). This led the authors to raise the question whether increased mixis levels are to some extent an adaptive response of the competing species which is excluded. This would require a cue for sexual reproduction which is a predictor of the effects of interspecific competition. The authors conclude that food deprivation could be a possible cue, arguing that in exploitative interspecific competition the species with the lower competitive capability will be food deprived. This argument is consistent with results on *B. plicatilis* (Hagiwara et al., this volume Part V), showing that starvation of stem females positively influences mixis in later generations.

Mictic patterns and timing of mixis

Recent efforts have been made to theoretically predict the optimal time of mixis induction and optimal mictic ratios as well as sex allocation and threshold age of fertilization, after which mictic females can no longer be fertilized and produce only haploid male offspring. The timing of mictic reproduction as well as mictic ratios are critical for the optimal production of resting eggs. Serra & Carmona (1993), Aparici et al. (1996), King & Serra (1998) and Serra & King (1999) theoretically explored whether the optimal mixis strategy for monogonont rotifers is a polyphasic pattern of resting egg production or a 'bang-bang' strategy, and whether it depended on the predictability of the environment. Following Ricci's definition (2001), in a polyphasic pattern resting egg production would start immediately at the beginning of population development with a low proportion of mictic females and continue until the habitat deteriorates. In a 'bang-bang' strategy, resting eggs are produced by a large proportion of the population only after a period of exclusive amictic population growth and just before the environment deteriorates. Continuous mixis starting at low densities decreases population growth rates, but guarantees a continuous production of resting eggs as soon as critical male–female encounter densities are reached. It is therefore not so much dependent on long-term habitat stability as a 'bang-bang' strategy with short periods of mictic reproduction at high population densities only, even though the latter strategy may lead to a higher yield of resting eggs. Aparici et al. (1996) and Spencer et al. (2001) come to the conclusion that polymorphisms in the timing of mixis induction and mixed strategies may be important in environments of high unpredictability.

Clonal diversity in the timing of mixis and the mictic ratio within a population may be maintained by the storage effect of the resting egg bank. Fluctuating selection may favor clones with late mixis initiation in some years and those with early mixis initiation in others, leading to varying success in sexual reproduction and varying recruitment of the different phenotypes to the resting egg bank in different years. The resting egg bank may then act as a buffer in years of poor recruitment of new resting eggs produced by the active stages of the population. In theory, the storage effect can explain the maintenance of genetic variation within a population of a cyclic parthenogen (Hairston et al., 1996) and thus the coexistence of competing clones in a temporally varying environment. A population of coexisting clones with different mixis patterns which may be favorable in some seasons and disadvantageous in others depending on fluctuating selection, may display a mixis pattern that is intermediate between a 'bang-bang' strategy and a recurrent mictic pattern.

Optimal sexual reproduction is dependent on the ratio between males and females. Sex allocation theory predicts that the optimal sex ratio is 1:1 (Charnov, 1982). However, in haplodiploid cyclic parthenogens such as monogonont rotifers the number of males is irrelevant; rather, the ratio of unfertilized and fertilized mictic females is important and should be even (Aparici et al., 1998, 2002; Calsina et al., 2000; Calsina & Ripoll, 2002). In order to maintain an even ratio between the two types of mictic females, the threshold age of fertilization of mictic females is critical. A young threshold age of fertilization will shift the ratio towards male producing females, an old threshold age will cause the opposite. The theoretical findings for sex allocation in rotifers are supported by field and laboratory data (Aparici et al., 2002), although evidence is scarce. Laboratory populations of *B. plicatilis* displayed ratios of fertilized to unfertilized mictic females close to 0.5 at the end of the exponential growth phase; however, it was only close to 0.5 in one of the two natural populations that were investigated. The authors attributed this deviation from the predicted value to environmental random variation. Aparici et al. (2002) argue that insights from the application of sex allocation theory to monogonont rotifers exclude one reason frequently invoked why the induction of mixis is related to high population densities in several species: the argument that higher densities will increase encounter probabilities between males and females and lead to higher insemination rates and subsequently to a higher number of resting egg producing females, is inconsistent with their results. According to the sex allocation theory and their empirical evidence, the number of resting egg producing females integrated over time should always be half the total number of sexual females.

Mictic patterns in natural populations

Only few studies addressed mictic patterns and mictic strategies in natural populations. Very high mictic ratios (close to 100%) seem to be rare in natural populations; they have been reported in *B. plicatilis* (Aparici et al., 1996), in *B. urceolaris* (Buchner, 1992), and in *B. calyciflorus* (Pourriot, 1965). More often, mictic ratios are around 20–30% (Carmona et al., 1995; Miracle &

Armengol-Díaz, 1995). Field data indicate that mixis already occurs at much lower density levels than the laboratory data would suggest as threshold levels (Carmona et al., 1995; Schröder, 2001).

Miracle & Armengol-Díaz (1995) observed different mixis patterns in two species which co-occur in the oxicline of a Spanish lake. Sexual reproduction in *Filinia hofmanni* was observed continuously over the whole period of population development with maxima at the time of highest densities. *Anuraeopsis fissa* produced resting eggs only at the very end of the population development.

Carmona et al. (1995) identified different mictic patterns for three species of the *Brachionus plicatilis* complex in small marsh ponds in Spain. *B. plicatilis* displays a more continuous mictic pattern with sexual reproduction throughout the time of its presence in the ponds. This may be a conservative bet-hedging strategy – suitable in an unpredictable environment – as this species appears in winter and spring, when sudden unpredictable flooding of the marsh with sharp decreases in salinity may occur. In contrast, *B. rotundiformis* and *B. ibericus* showed a punctuated mictic pattern. Especially in *B. rotundiformis*, higher mictic ratios were observed only for brief periods towards the end of population development. Both species are spring-summer species, whose existence in the ponds is limited by gradual desiccation in summer or decreasing temperatures in the fall. Desiccation and falling temperatures are more predictable than floods and the authors hypothesize that a punctuated mixis pattern would be the optimal strategy in these habitats.

Male mating behavior

Recent studies have shown that male mating behavior may also play an important role in maximizing resting egg production. Mictic females are fertilizable only for a short period after hatching (Buchner et al., 1967; Snell & Childress, 1987; Hagiwara et al., 1988); after that period, they are only able to produce males by parthenogenesis. Males who copulate with older females or with amictic females are wasting their sperm, which may be relevant at least in some species such as *B. plicatilis* where male sperm reserves are limited (Snell & Childress, 1987). Therefore, there should be a strong selection for male copulation only with fertilizable females. Gómez & Serra (1996) have shown that males of *B. plicatilis* initiate mating behavior significantly more often when they encounter young females rather than females aged 1 day or older and they rarely finish mating and copulate with females that are 1 day or older. Males also tend to prefer mictic rather than amictic females. Mating behavior is initiated significantly less often, when males encounter amictic females. However, they still start to exhibit mating behavior and copulate with a large proportion of amictic females they encounter.

Males of *Epiphanes senta* display a behavior that resembles mate-guarding known from many arthropods (Schröder, 2003). Males who encounter a female egg attend it until the female hatches and then copulate with the newborn. However, this behavior differs from mate-guarding in arthropods in that *Epiphanes* males do not show any antagonistic behavior against other males who approach the egg. Males do not attend male or resting eggs. Also, they are able to discriminate between female eggs which have just recently been deposited and mature eggs which will hatch within a short period of time. By preferentially attending eggs that are going to hatch soon, males minimize the amount of time they spend waiting on the eggs. Such a behavior could have two interpretations. First, it would ensure that males only mate with females in their susceptible period, since they only mate with newborn females. Second, this behavior could be a time investment strategy to maximize mating success, if the probability of encountering a fertilizable female during the time period necessary to wait on the egg is lower than 1. Interestingly, males are not able to discriminate between eggs of mictic and amictic females. Similarly, males of *Asplanchna brightwelli* and *Brachionus calyciflorus* seemed unable to discriminate between mictic and amictic females (Gilbert, 1963; Aloia & Moretti, 1973).

Amictic diapausing eggs

Amictic production of diapausing eggs has only been documented for very few species. Ruttner-Kolisko (1946) reported the production of diapausing eggs without fertilization by males in *Keratella* *hiemalis*. These amictic diapausing eggs are morphologically very similar to fertilized resting eggs, dark in color and with a multi-layered shell. Factors that induce the production of these amictic diapausing eggs as well as conditions of hatching, are unknown. Production of amictic diapausing eggs that are morphologically similar to the fertilized resting eggs has also been observed in *Notholca squamula* (Schröder, 1999). The amictic diapausing eggs of *N. squamula* hatch several weeks after being produced when kept in the same culture conditions as those in which the eggs were produced. The factors inducing the production of amictic diapausing eggs in *N. squamula* are also unknown.

The production of amictic diapausing eggs in *Synchaeta pectinata* is better understood. These diapausing eggs differ from the fertilized resting egg (Gilbert, 1995). Their shells consist only of a single layer. Females produce as many amictic diapausing eggs as amictic subitaneous eggs (Gilbert, 1995), indicating that the production of amictic diapausing eggs does not require more resources than the production of subitaneous eggs.

The amictic diapausing egg in *S. pectinata* is the only diapausing stage in monogonont rotifers known to be directly induced by deteriorating environmental conditions. Amictic females that are starved for a certain time period are induced to produce diapausing eggs (Gilbert, 1995; Gilbert & Schreiber, 1995). Short periods of food limitation already induce some females of a clone to produce diapausing eggs and longer periods of more severe food limitation lead to strong diapause response, where 75% of all eggs produced are diapausing (Gilbert & Schreiber, 1998). Food concentrations inducing the production of diapausing eggs are still above threshold concentrations for population growth, but reduced food concentrations may be predicting deteriorating resource conditions (Gilbert & Schreiber, 1998). Amictic females which are cultured in a food-limiting environment vary in their response of diapausing egg production. While some females of a clone are induced to produce some or only diapausing eggs, others continue to produce only subitaneous eggs under the same inducing conditions; this may be considered a bet-hedging strategy (Gilbert, 1998; Gilbert & Schreiber, 1998). It may allow positive population growth if food conditions remain above threshold concentration. At the same time the production of diapausing eggs provides a refuge if food concentrations fall below levels sustaining positive population growth.

There is also considerable genetic variation in the production of amictic diapausing eggs (Fradkin, 1997). *S. pectinata* produces two types of diapausing eggs that differ in their morphology and in the length of diapause. The production of different diapausing egg types is clone specific. Some clones only produce long-term diapausing eggs with a diapause of at least 3 months, while others produce short-term diapausing eggs which invariably hatch after a diapause of only 2 weeks. The diapausing egg types differ in their number of blastomeres. Both have thicker shells than the subitaneous eggs, but the shell of the long-term diapausing egg is much thinner compared to that of the short-term diapausing egg (Fradkin, 1997). Fradkin (1997) found that both types of diapausing eggs were produced in a population in Star Lake (Vermont). The population collapsed over a 3-month period in winter when food concentrations were very low. Over 80% of the population produced long-term diapausing eggs at the beginning and at the end of that period.

Clones also vary in their propensity to produce diapausing eggs, some producing 82–100% diapausing eggs when induced by starvation and others producing only 16–38% after a starvation period, the latter having significantly higher net reproductive rates as a consequence (Fradkin, 1997). This creates the potential of an ecological trade-off, where different clones may be favored depending on food level. Fradkin (1997) showed that clones with a low propensity are favored due to their higher growth rates, if food resources reach inducing levels but remain above threshold levels. If food levels drop from inducing concentrations to levels below threshold concentrations, clones with a strong propensity are favored, because they produce more diapausing eggs at inducing food levels, and these escape periods of very low food that inflict high mortality on non-diapausing stages.

Resting eggs

The fertilized resting eggs of monogonont rotifers do not seem to fall in two distinct categories of short-term diapause and long-term diapause as the amictic diapausing eggs of *Synchaeta pectinata*. However, the latency period, i.e. the minimum period of dormancy during which hatching is not possible, seems to be very variable both among and within species. Resting eggs may hatch after a latency period of only a few days as in *Brachionus quadridentatus* from an Australian billabong (Gilbert, 2001), but in other species the latency period may last as long as 5–6 months such as in some species of the genus *Polyarthra* (Nipkow, 1952). Pourriot et al. (1982) found differences in the latency period of two clones of *B. calyciflorus*: in one clone, the period was only a day, whereas the resting eggs of the other clone had a latency period of 1 week.

Resting egg hatching and hatching patterns

Factors influencing or inducing hatching of fertilized resting eggs have been extensively investigated experimentally in *Brachionus rubens*, *B. calyciflorus*, *B. angularis*, *B. budapestinensis*, and *B. plicatilis*. The major factors are temperature and light (Pourriot et al., 1980, 1981, 1982, 1983; Blanchot & Pourriot, 1982a, b) and salinity for the *B. plicatilis* species complex (Blanchot & Pourriot, 1982b; Minkoff et al., 1983; Hagiwara & Hino, 1989; Hagiwara et al., 1989). These studies have been reviewed in detail by Pourriot & Snell (1983) and Gilbert (1993).

Rotifers hatch within certain ranges of temperatures which are species specific and correspond to the thermal preference range of these species. For example, resting eggs of the thermophilic species *B. budapestinensis* do not hatch at temperatures of 5 °C and below, and resting eggs of a cold-water strain of *B. angularis* show decreased hatching rates at 18 °C and above (Pourriot et al., 1983). May and coworkers (May, 1987; May et al., 2001) showed that different temperatures induce different species to emerge from sediment samples of Loch Leven/Scotland. Temperature-dependent hatching rates also reflected seasonality and temperature preferences of the different species. Perennial species as *Keratella cochlearis*, *Synchaeta grandis* and *S. kitina* hatched over the whole range of temperatures tested, whereas hatching of the spring and summer species *Asplanchna priodonta*, *Trichocerca pusilla*, and *Pompholyx sulcata* was restricted to temperatures of 10 °C and above. The cold-stenotherm species *Notholca squamula* and *Polyarthra dolichoptera* whose populations almost always developed in the lake at temperatures not higher than 15 °C, only hatched in majority at the colder temperatures tested (5 and 10 °C).

In other species, however, there is no evidence for a connection between temperatures that promote hatching and temperatures suitable for population development. *Cephalodella hoodi*, inhabiting an acidic mining lake in East Germany, is most abundant in spring and summer, but it could only be induced to hatch from sediments at 5 °C, but not at 20 °C (Bell & Weithoff, 2003).

Recent investigations have shown that temperature conditions inducing resting egg hatching may involve the temperature changes which occur across seasons. *Rhinoglena frontalis* is a cold-stenotherm species present in winter and spring in small ponds and in temporary floodplain habitats when water temperatures range between 1–17 °C (Wesenberg-Lund, 1930; Schröder, 2001). In the floodplains of the Oder River, resting eggs are produced in April and May shortly before the waters dry up (Schröder, 2001). Resting eggs produced by a floodplain clone hatched at 6 °C, but only after they were exposed to an intermittent period of high temperature. Virtually no hatching occurred, if the resting eggs were kept constantly at 6 °C, or at 20 °C (Schröder, 1999). The requirement of a high-temperature signal could ensure that resting eggs produced in the spring would not hatch before the flooded areas dried out, but only when they are flooded again the following season.

Also, resting eggs of species inhabiting temporary habitats may be induced to hatch in the next season by the intermittent terrestrial period, independent of temperatures. Experiments with resting eggs produced by a clone of *B. calyciflorus* from the temporary Oder River floodplain showed that these eggs would hatch after they had been exposed to terrestrial conditions at a relative humidity ranging from 55 to 100% for 10–30 days. Only very few eggs hatched when the resting eggs were kept continuously in water (Schröder, 1999).

Light may be another factor which influences hatching of resting eggs. It has little or no effect on hatching in *B. angularis* and *B. budapestinensis*, but it is important in *B. plicatilis* (Blanchot & Pourriot, 1982b; Minkoff et al., 1983; Hagiwara & Hino, 1989) and *B. rubens* (Pourriot et al., 1980, 1981). Hatching increases under short wavelengths 400–480 nm in *B. rubens* (Blanchot & Pourriot, 1982a) and 347–400 nm in *B. plicatilis* (Hagiwara et al., 1995), but UV light had no effect in *B. calyciflorus* (Schröder, 1999).

Light also increased resting egg hatching in *Epiphanes senta* strains from the temporary floodplains of the Oder River/Germany and neighboring permanent ponds (Schröder, unpublished data), although the main factor that induced hatching was low temperature. *Epiphanes senta* occurs in floodplain waters in winter and spring but is absent in summer (Schröder, 1999). Resting eggs produced by several clones were induced to hatch after 3.5 months at 20 °C if exposed to 10 °C. However, resting eggs produced by some clones could also be induced to hatch at 20 °C, if they were exposed to light, although the hatching rates were much lower than at 10 °C and did not exceed 15%. Hatching rates at the low temperature were significantly different when the resting eggs produced by the different clones were compared. They fell into two groups: hatching rates of eggs produced by some clones reached 90–95%, whereas hatching rates of egg produced by the other clones ranged between 45 and 70%. Resting eggs produced by some clones hatched synchronously within a few days, while resting eggs produced by other clones hatched over a longer period of time. Parental clones of both groups could be found within the same strain, indicating the existence of a genetic polymorphism in the hatching pattern of the strain (Schröder, unpublished data).

Studies estimating the densities of resting eggs in the sediments by counting eggs recovered with sugar floatation methods or by measuring emergence of rotifers from flooded sediments in the laboratory, show that the egg bank in the sediments can contain very large numbers of resting eggs (Nipkow, 1961; Snell et al., 1983; May 1986, 1987; Mnatsakanova & Polishchuk, 1996; Schröder, 2001; Duggan et al., 2002). Snell et al. (1983) recorded as many as 194 *B. plicatilis* resting eggs cm^{-3} at the sediment surface in a brackish-water pond in Florida. However, when densities derived from resting egg counts are compared with numbers of emerging rotifers, densities exceed hatching rates by 1–2 orders of magnitude. Duggan et al. (2002) counted both numbers of resting eggs in the sediments and recorded hatching rates from sediment samples of two New Zealand lakes; they found a twofold to 10-fold difference, depending on the incubation temperature of flooded sediments. Such a difference may reflect the function of the egg bank: if only some of the resting eggs are induced to hatch at a time, those remaining dormant carry the population through years of poor recruitment to the egg bank (Hairston & de Stasio, 1988; de Stasio, 1989).

There may be several reasons why only a fraction of the eggs hatches at a given time. One of them certainly is that a large number of eggs may face conditions that inhibit hatching. Such conditions could be low oxygen concentrations, low temperatures, lack of light, or high concentrations of hydrogen sulphide and methane and may vary with sediment depth. Thus, hatching of buried eggs may require that the eggs are suspended in the water by strong currents or bioturbation (Gilbert & Schröder, 2004).

Another reason may be a bet-hedging strategy involved in the hatching of resting eggs. Experiments with resting eggs derived from single clones of *R. frontalis* and *B. calyciflorus* have shown that conditions inducing hatching in the two species do not induce all exposed resting eggs to hatch. However, if the still dormant eggs are exposed to the same conditions again later, another fraction of the dormant resting eggs could be induced to hatch (Schröder, 1999). Such a bet-hedging mechanism, which could be caused either by a genetic polymorphism or by a polyphenism, could contribute to the long-term survival of populations if conditions for population growth and production of new resting eggs are unpredictable. It should be expected that hatching rates would be lower in less predictable habitats. However, there is almost no evidence to support this prediction. Pourriot et al. (1982) compared hatching rates of two clones of *B. calyciflorus* and attributed large differences in hatching fractions to different strategies in a predictable and an unpredictable habitat. They did not, however, take into account the possibility of existing polymorphisms in hatching patterns within the populations, since they only examined one clone of each population. That such a polymorphism within a population may exist, has been shown in *E. senta* as described above (Schröder, unpublished data).

In most laboratory studies, synchronous hatching of a significant fraction of resting eggs was observed under certain environmental conditions, but in other cases sporadic hatching over extended periods was found (Pourriot & Snell, 1983). In shallow temporary waters, where recolonization after reflooding obviously has to take place via hatching from resting eggs, it seems likely that large numbers of resting eggs hatch within a short period of time, as soon as the previously dried sediments are submerged again. The flooding of the dried sediments of shallow temporary waters constitutes an environment with well oxygenated water and light which should be favorable for hatching (Gilbert, 2001), and a large diversity of rotifers has been found to hatch from dried sediments of floodplains and billabongs (Boulton & Lloyd, 1992; Nielsen et al., 2000; Langley et al., 2001; Schröder, 2001). The fact that Gómez & Carvalho (2000) found an extraordinarily high genetic diversity in planktonic populations of *B. plicatilis* in a shallow temporary pond (Poza Sur/Spain) also supports the hypothesis of synchronous hatching of many different clones, rather than the hatching of a few stem females which then found a large population consisting only of a small number of clones.

Still the question remains whether synchronous mass hatching over a short period of time also occurs in field populations of large permanent lakes, where a large fraction of the resting egg bank is contained in sediments at greater depth, or whether continuous hatching of only few resting eggs takes place over longer periods of time, especially since field studies on resting egg hatching are rare (Gilbert & Schröder, in press). Indirect evidence exists for massive resting egg hatching in the littoral induced by drought-associated desiccation, intense light and high oxygen concentrations at the sediment surface. Arnott et al. (2001) observed an increase in species richness associated with a drought event. This may be indicating that substantial numbers of resting eggs hatched from previously dried sediments after they were reflooded.

Resting egg survival

Little is known about the time periods for which resting eggs remain viable in sediment egg banks. In sediments of permanent habitats, they may still hatch after several decades (Marcus et al., 1994; Viitasalo & Katajisto, 1994). Fu (1991, in Kotani et al., 2001) was even able to hatch resting eggs of *B. rotundiformis* from sediments up to 100 years old. Marcus et al. (1994) were able to hatch resting eggs of *Brachionus* sp. from sediments that were more than 40 years old. However, hatching rates of 40-year old eggs represented only 5–10% of the hatching rates of resting eggs in the sediment egg bank which were less than 15 years old. Chittapun et al. (this volume Part V) demonstrated that resting egg viability in the sediments of a tropical swamp was already significantly reduced after resting eggs had been buried in the sediments for only 12–24 months. The factors that affect long-term survival of rotifer resting eggs in sediments of permanent waters are mostly unknown. In cultures of *B. plicatilis* Balompapueng et al. (1997a, b) found that resting eggs whose surface is colonized by bacteria during diapause show drastically decreased hatching rates. Hatching rates increase when bacteria are removed by chemical treatment. The authors conclude that bacteria affect the hatchability possibly by clogging pores of the egg shell and interfering with the gas exchange of the developing embryo after diapause has been terminated. It is possible that bacterial growth may also affect the viability of resting eggs in natural sediments. Nothing is known about the impact of predation on survival of resting eggs in sediment egg banks.

In sediments of temporary waters resting eggs may lose viability after much shorter periods than in permanent waters. Boulton & Lloyd (1992) found no hatching of rotifers from floodplain sediments of the River Murray (Australia) which were flooded only on an average of every 22 years, whereas rotifers hatched from sediments that were flooded annually or on an average of 7 or 11 years. The viability of resting eggs of some rotifer species occurring in temporary habitats may be significantly affected by severe drought stress. Experiments on *Rhinoglena frontalis*, *Brachionus urceolaris* and *B. calyciflorus*, exposing resting eggs to terrestrial conditions at controlled relative humidity for different times revealed that the eggs of *B. urceolaris* were much more vulnerable to drought stress than those of *B. calyciflorus* and *R. frontalis* (Schröder, 1999). Hatching rates of

B. urceolaris eggs decreased significantly even after short exposure to dry periods lasting 1–10 days at low relative humidities of 76 and 33%, compared to hatching after terrestrial conditions at a relative humidity of 100% and to hatching of resting eggs which were kept in water permanently. Resting eggs of *B. calyciflorus* and *R. frontalis* proved to be much more resistant to drought stress. Resting eggs of *R. frontalis* were not negatively affected by terrestrial periods of 20 days at relative humidities of 55.5 and 33%, but almost no hatching occurred if the treatment was prolonged for 60 days. Resting egg hatching in *B. calyciflorus* was not negatively affected by terrestrial periods of 30 days at 55.5% relative humidity, but hatching rates decreased significantly after a 30 day terrestrial period at 33% relative humidity.

The viability of resting eggs may also be affected by the conditions under which they were produced. Hagiwara & Hino (1990) have shown that resting egg hatching of *B. plicatilis* and *B. rotundiformis* is strongly affected by the diet of the resting egg producing mothers. Resting eggs produced in cultures that were fed with *Chlamydomonas* sp. would hatch at a lower percentage than resting eggs produced by females fed *Tetraselmis tetrahele*. Also, the hatching females differed significantly in their fecundity: those hatching from resting eggs produced on the *Chlamydomonas* diet were less fecund than those hatching from resting eggs produced on the *Tetraselmis* diet.

The long-term survival of rotifer populations in unpredictable environments relies on the existence of a resting egg bank, but the work reviewed above suggests that the functioning of the resting egg bank may be limited in many cases. Local extinction of subpopulations and recolonization events within the metapopulation may be important, but hardly any data exist for monogonont rotifers and more research is needed here.

Conclusions

It seems evident that monogonont rotifers exhibit an immense variety of diapausing patterns with a number of different ways to induce mixis and subsequent resting egg production, as well as varying hatching patterns. This holds true even if the fact is taken into account that most research has been done on a small group of species; it can be expected that diversity will increase if more species are considered. Interestingly, of the relatively few species that have been investigated, many respond to high densities as a cue for mictic female production and subsequent production of resting eggs. In these cases high density is not associated with reduced fecundity due to food limitation. This is in agreement with the argument made by Gilbert (1993) and others that resting egg production in monogonont rotifers is likely to take place under favorable conditions in advance of habitat deterioration. However, the results of Hagiwara et al. (this volume Part V) indicate that starvation as caused by habitat deterioration can also trigger resting egg production in other cases. It seems possible that both factors are synergistic, since crowding may lead to overexploitation of food resources.

Since the production of resting eggs involves a trade-off between mictic and amictic reproduction, populations of the same species are likely to display different mixis patterns depending on the specific conditions of the habitat. Selection for early sexual reproduction should be more intense in populations in short-lived temporary ponds than in seasonal populations of large lakes. The more unpredictable a habitat is, the more likely are bet-hedging strategies involved in mictic and amictic reproduction as well as genetic polymorphisms maintained by storage effects of the sediment egg bank, which may also lead to a wide variety of mixis patterns.

Resting egg hatching patterns may also involve bet-hedging strategies and may be influenced by genetic polymorphisms. Therefore, synchronous hatching within a short time period, continuous hatching over a longer period or a combination of both – some clones of a population producing resting eggs that hatch synchronously and other clones producing resting eggs that hatch erratically – may be found in different populations. The sediment egg bank obviously plays a crucial role for the persistence of populations in temporary habitats. However, the long-term viability of resting eggs may be more limited than previously thought and differ significantly among species. Some species seem to be more vulnerable than others to adverse conditions affecting the sediment egg bank such as drought or an anoxic environment. Thus, specific species assemblages in temporary habitats may be determined by environmental conditions during diapause as well as during population development of active stages. The relationships between environment and population dynamics of the sediment egg bank (i.e. recruitment, hatching rates and mortality rates) are poorly understood. Exploring these relationships would contribute to a better understanding of diapause patterns in monogonont rotifers.

Acknowledgments

I thank John Gilbert and an anonymous referee for valuable comments that helped to improve the manuscript. The work was funded by a postdoctoral fellowship from the Deutsche Forschungsgemeinschaft.

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