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Zooplankton competition promotes trade-offs affecting diapause in rotifers

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Abstract Facultative diapause should be favoured by natural selection in temporary variable habitats. Diapause patterns are evolutionary constrained because producing diapause is resource demanding, which might have implications for competitive dynamics and competitor coexistence through mechanisms such as the storage effect. Besides these implications, competition intensity might affect the quality of the diapausing stages and the reproductive success of the offspring emerging from them. We experimentally analysed traits involved in diapause in the cyclically parthenogenetic rotifer *Brachionus calyciflorus,* in relation to the presence of its competitor, the cladoceran *Moina micrura*. Under competition with *Moina*, *Brachionus* produced fewer diapausing eggs, most of which possessed visual attributes indicating a higher quality. These diapausing eggs produced under a competitive environment had a higher hatching success; however, the hatchlings exhibited a lower population growth rate. We propose the existence of trade-offs between traits related to diapause: the number of produced eggs, quality of these eggs and hatchling performance. Our results show that interspecific competition may cause fine-tuned changes in the life cycle patterns of the populations. Furthermore, these changes could affect that abundance and performance of competitors and thereby drive back effects on the competitive output. These diapause-driven feedback mechanisms may have strong implications for the dynamics of the natural communities.

Keywords Diapausing quality · Hatching success · Hatchling · Population costs · Resting eggs

Introduction

Diapause is an adaptation of many small invertebrates inhabiting fluctuating environments, which enables them to survive recurrent adverse periods (Hairston 1998; Alver and Hagiwara 2007). Facultative diapause is expected to evolve by natural selection in highly changing conditions where permanence is hazardous (Smith and Snell 2012; Roulin et al. 2013). Nevertheless, this strategy is evolutionarily constrained by trade-offs because, among other costs, production of diapausing stages is metabolically expensive (Hahn and Denlinger 2011). Diapause stages of organisms must have protective features and the organisms must store sufficient reserves in the pre-diapause period to satisfy their maintenance during diapause, and still have reserves to complete development and resume activity (Hahn and Denlinger 2007). Evidence suggests a trade-off between metabolic costs of diapause and adult components of fitness, e.g. reduced fecundity and body size of adult insects emerging from diapause stages (Kroon and Veenedaal 1998; Matsuo 2006; Perez and Noriega 2013). As a result, the performance of individuals leaving diapause is expected to be related to the quality of the environment where the diapause stage was produced.

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Two major zooplankton groups—cladocerans and monogonont rotifers—are cyclical parthenogens. In these groups, facultative production of diapausing eggs is almost always associated with the switching from asexual to sexual reproduction. This implies an additional cost, the production of males (i.e. the twofold cost of sex). It has been proposed that, since sexual reproduction is more resource demanding and takes longer to complete than asexual reproduction (Serra et al. 2004), it should occur under good environmental conditions (resource-demanding hypothesis) (Preston et al. 2000; Serra et al. 2004). In many zooplankters, sex and diapausing stage are induced by chemical signals released to the environment by conspecifics (Carmona et al. 1994; Zadereev 2003; Fussmann et al. 2007). This phenomenon has been considered to be quorum sensing (Kubanek and Snell 2008). A number of environmental factors, including food availability, could have a strong impact on diapause production (Gilbert 1974; Pourriot and Snell 1983; Gilbert and Schröder 2007). Therefore, resource competition, which is known to be a strong driving force for organisms' adaptations and the structure of natural communities (Cody and Diamond 1975; Diamond and Case 1986; Morin 2011), could play a critical role in the determination of diapause features and the concomitant reproductive success of the organisms.

In this vein, diapause not only allows species to avoid adverse physical environments, but also has the potential to be a way for them to temporally escape from a competitive environment. Moreover, diapause has strong implications for the coexistence of competitors, through at least two mechanisms: the so-called 'storage effect' (Chesson and Huntly 1989; Chesson 1994), which explains coexistence invoking, among other factors, a life cycle stage relatively immune to competition; and (2) the production of diapause stages which may affect the proliferation of dominant competitors as well as their competitive ability (Montero-Pau and Serra 2011). Nevertheless, few advances have been made in determining whether interspecific competition shapes the reproductive outcome of diapause.

In temporary or strongly fluctuating environments, the long-term fitness of diapausing organisms and the temporal persistence of their populations are directly related to the number of diapausing stages produced over the seasons and their quality, in terms of their survival and reproductive ability. Interspecific competition generates adverse environments that could either hamper the production and/or quality of diapauses, or trigger adaptive responses leading to maintenance, within certain limits, of the long-term fitness of the affected organisms. In this study, we test the hypotheses that interspecific competition exerts an effect on the diapause-driven reproductive outcome of the rotifer *Brachionus calycyflorus*, and that this effect leads to an increased quality of its diapause stages.

The focal species, the freshwater rotifer *B. calyciflorus* Pallas, 1766 and its competitor, the cladoceran *Moina micrura* Kurz, 1874, are common inhabitants of subtropical and temperate lakes (Pagano 2008). *B. calyciflorus* can be found throughout the year in lakes and ponds in Central Chile, whereas *M. micrura* is a species of tropical origin that exhibits a high growth potential at higher temperatures. Because of this, *M. micrura* is a characteristic summer species in temperate Chilean lakes (Ramos-Jiliberto and Aránguiz-Acuña 2007). These two species co-occur and feed over a wide size range of microalgae by filtering them (Rothhaupt 1990; Pagano 2008; Lacerot et al. 2013), although previous studies have shown *B. calyciflorus* to be competitively weaker than *Moina* species (Xi and Hagiwara 2007; Aránguiz-Acuña and Ramos-Jiliberto 2014). Our objective was to determine if interspecific competition affects rotifer investment in diapause by modifying the quantity and quality of diapause eggs produced.

Materials and methods

Cultures of the experimental species

B. calyciflorus and *M. micrura* were collected from temperate lakes of central Chile: Tranque Lo Orozco (33º22′S–71°41′W) and Laguna Carén (33º25′S–70°51′W). One clone of each species was established from a single parthenogenic female and maintained under standard laboratory conditions [pH 7.5 ± 0.1, temperature 20 ± 1 °C, photoperiod 16-h:8-h, light:dark (L:D)] for 2 months before the experiments. Induction of male production was prevented by avoiding a high population density; that is, by removing the excess individuals above the specified crowding cue threshold for each species (Aránguiz-Acuña and Ramos-Jiliberto 2014). The culture medium for maintenance and experiments was COMBO medium (Kilham et al. 1998). The stock cultures of both zooplankters were fed daily with the green alga *Pseudokirchneriella subcapitata* at a density 10^6 cells mL^{-1}, which was cultured in Bold's basal medium (Borowitzka and Borowitzka 1988). The alga was harvested in exponential growth phase, and densities were measured by direct counting.

Production and hatching of diapausing eggs

Diapausing eggs of *B. calyciflorus* were obtained from growing stock populations under two conditions: in the presence of *M. micrura* [at densities lower than 1.5 individuals (ind.) mL^{-1}] and in the absence of this cladoceran. This *Moina* density is approximately twofold the maximum density found in field temperate populations (Ramos-Jiliberto and Aránguiz-Acuña 2007), and about half the maximum levels recently reported in laboratory cultures (Azuraidi et al. 2013). Cultures were maintained in 1,000 mL of COMBO medium, with five replicates for each condition, a photoperiod of 12-h:12-h (L:D) and 20 °C temperature. Every other day the media were fully renewed with the microalgae *P. subcapitata* as food, at a density of 0.25×10^6 cells mL^{-1}. Eggs were harvested every other day, during a period of 18 months. After a variable period of diapause, depending on the date when they were produced, the eggs were scored following García-Roger et al. (2005) and assigned to either high- or low-quality categories, according to their viability-related features. High-quality eggs corresponded to healthy eggs, where the embryo fills between 75 and 100 % of the interior space. Conversely, in low-quality eggs the embryo fills <75 % of the space. After scoring the eggs, hatching was induced by placing the eggs into 96-multiwell dishes with 200 µl of COMBO medium and incubating at 25 °C under white fluorescent constant illumination (150–170 µmol quanta m^{-2} s^{-1}) for up to 10 days. Dishes were checked every 24 h for hatchlings and the hatching day was recorded. Differences in eclosion time between diapausing egg types (low and high quality) and between condition of production (interspecific competition present or absent) were analysed using survival analyses with Cox proportional hazards, where the variable Time to death was replaced by Time to hatch. Counts of hatching eggs were analysed using generalised linear models assuming a Poisson distribution and using log as a link function. Using a χ^2-test we analysed the association between the effect of the presence of *M. micrura* and rotifer diapausing egg quality. Statistical analyses were performed in R 3.0.2 statistical software (R Core Team 2013).

Life table experiments

Complete life tables were constructed by recording the age-specific survival and reproduction of individual organisms of *B. calyciflorus* from birth to death. The individuals were hatched from diapausing eggs, as was detailed above, in the presence (25 individuals) or absence (33 individuals) of the competitor *M. micrura*. Neonates were transferred into multiwell dishes with 200 µl of food suspension of *P. subcapitata* at a density of 1×10^6 cells mL^{-1} in COMBO medium at 17 °C. Every 24 h, each animal was checked for survival, its offspring were counted and discarded and the medium was renewed. From these data, we estimated age-specific fertility (m_x; computed using the number of live offspring at each age x) and proportion of survivors to a given age (l_x). The finite population growth rate (λ) was calculated using the discrete Euler–Lotka equation:

$$1 = \sum \lambda^{-x} l_x m_x$$

We calculated 95 % confidence intervals for λ by 5,000 bootstrap resampling. Differences in growth rate between treatments (with/without *Moina*) were tested by generating pseudo-samples by means of a permutation test (5,000 runs) of individual life tables, using $\alpha = 0.05$.

Dynamics of diapausing egg production

We monitored the dynamics of *B. calyciflorus* and the production of diapausing eggs in cultures with and without *M. micrura* at a fixed density of 0.05 ind. mL^{-1}. C content was estimated in a known number of individuals from both zooplankton species by isotope δ^{13}C with standard Vienna Pee Dee belemnite. This allowed us to use approximately the same herbivore biomass density (C per volume) in both treatments (with and without *Moina*) as the initial conditions. *B. calyciflorus* was started at densities of 0.1 and 0.2 ind mL^{-1} (presence and absence of *M. micrura*, respectively). The alga *P. subcapitata* was added once at the beginning of the experiment at a density of 1.5×10^5 cells mL^{-1}. The experiment was conducted in 100 mL of COMBO medium in 250-mL glass containers with five replicates per treatment, under continuous light and 22 °C. The containers were continuously shaken in an orbital shaker at low speed (40 r.p.m.).

Adult rotifer density was counted daily in two to three 10-mL samples for each replicate. Rotifer diapausing eggs were counted daily and then removed from the culture. These eggs were induced to hatch as indicated above. Algal density was measured daily spectrophotometrically, and converted to algae density using the equation absorbance $= a(\text{cells} \times \text{ml}^{-1})^b$ where a and b are calibration coefficients (Ribeiro Rodrigues et al. 2011). Experiments were finished after 16 days, when all cultures were extinct. From these data we calculated daily per capita production of diapausing eggs and the hatching success, measured as the percentage of eggs hatched relative to the total number of produced eggs.

Results

In a first experiment we evaluated the effect exerted by the presence of a competitor—*M. micrura*—on the production of diapausing eggs by the rotifer *B. calyciflorus* and the hatching success of these eggs. For this experiment, 284 and 196 eggs were obtained from cultures without and with *Moina*, respectively. No significant differences in hatching times of diapausing eggs were observed, irrespective of the quality score of the eggs or the competition condition under which they were produced. Interestingly, the presence of the competitor *Moina* led to an increased production (by 138 %) of high-quality diapausing eggs and a strongly

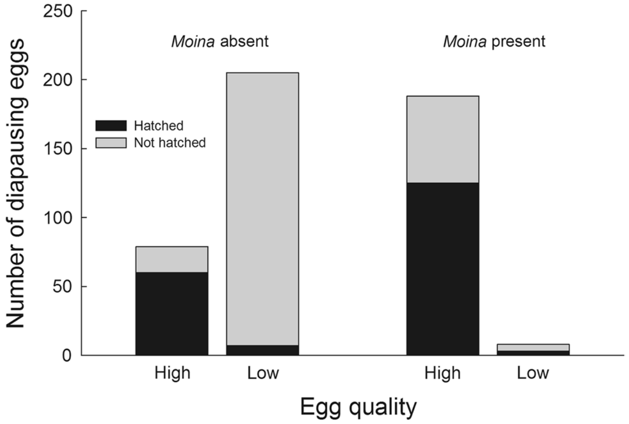

Fig. 1 Diapausing eggs produced by *Brachionus calyciflorus* in conditions with presence and absence of *Moina micrura*; eggs belonging to quality categories (low and high), and whether or not they hatched ($n = 480$)

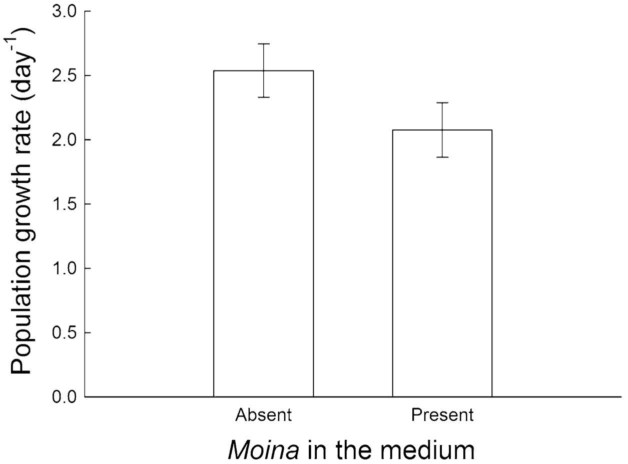

Fig. 2 Population growth rates [mean values ±95 % confidence interval (CI), five replicates] of *B. calyciflorus* individuals hatched from diapausing eggs produced without and with the cladoceran competitor *M. micrura* (significant differences, 5,000 randomizations, $\alpha = 0.05$)

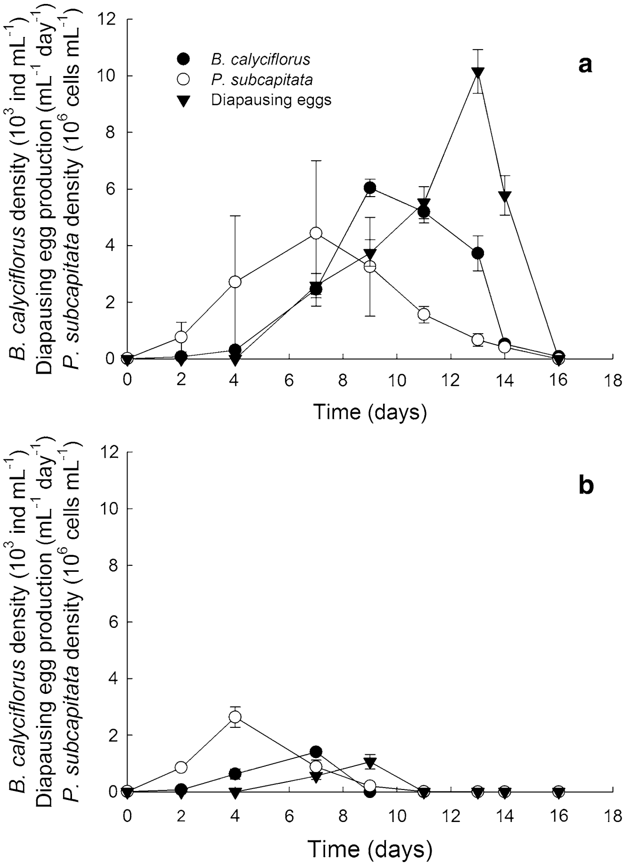

Fig. 3 Time course of the density of *Pseudokirchneriella subcapitata* (*open circles*), *B. calyciflorus* (*closed circles*) and *B. calyciflorus* diapausing eggs (*closed triangles*). **a** In the absence of *M. micrura*, and **b** in the presence of *M. micrura*. Mean values of five replicates and 95 % CI are shown

decreased production (96 %) of low-quality diapausing eggs (Fig. 1). From the diapausing eggs produced, a variable fraction of them were hatched, depending on the competition treatment and their quality ($\chi^2 = 24.496$, $df = 2$, $P < 0.001$). The total number of hatched eggs was larger in presence of *Moina*, and both the absolute number and the proportion of hatched eggs—over the number of produced eggs—were markedly higher in eggs of higher quality (Fig. 1).

A second experiment was conducted to evaluate the effect of the competitive environment on the fitness of rotifers hatched from diapausing eggs, measured as the finite population growth rate. These results indicated that rotifers hatched from eggs produced in the presence of *Moina* had a lower population growth rate, estimated from complete life tables, as compared to rotifers produced in the absence of the competitor (Fig. 2). In summary, the two first experiments indicated that under competition with *Moina*, the rotifer *B. calyciflorus* produced more eggs of high quality, which was translated into an increased hatching rate, which produced more offspring but with lower average reproductive success.

We conducted a final experiment to evaluate the production of diapausing eggs and their hatching success under a more realistic competition (and its control) scenario by allowing the density of the shared algal resource to vary according to its consumption rate by *Moina* and *Brachionus*. We evaluated the per capita production of diapausing eggs and the hatching success under both competition and control scenarios. The resource dynamics exhibited a unimodal shape, followed by a similarly shaped and delayed dynamics of *B. calyciflorus* and then by the production of diapausing eggs (Fig. 3). Under the competition scenario, the dynamics were accelerated. The increased consumption

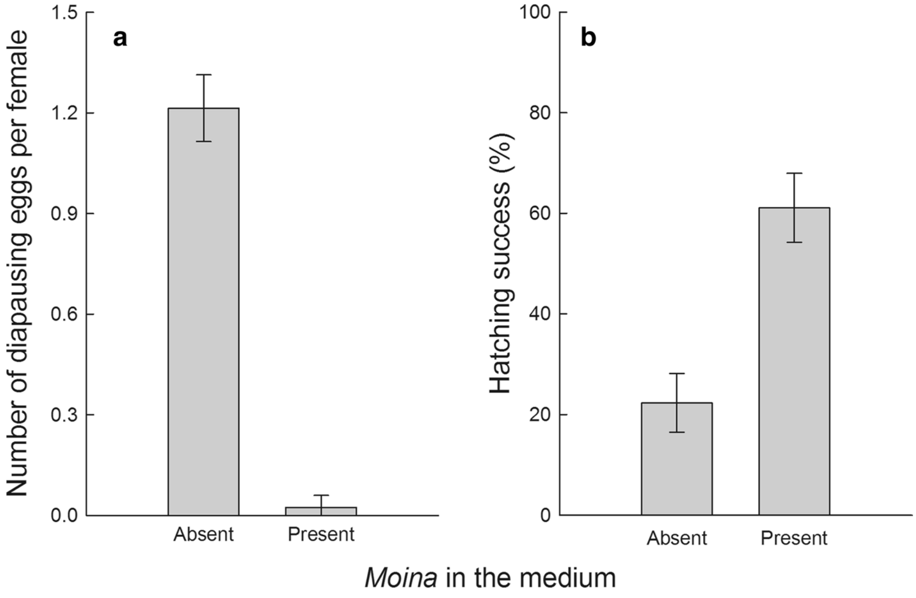

Fig. 4 Number of diapausing eggs produced per *B. calyciflorus* female ($n = 14{,}700$ females) (**a**) and hatching success of diapausing eggs in two competitive environments ($n = 1{,}000$ eggs) (**b**); mean values and 95 % CI are shown

of algae due to *Moina* inclusion shortened the temporal dynamics of algae, rotifer and diapausing egg production, but their qualitative trend remained unaltered (Fig. 3). Per capita production of diapausing eggs was strongly suppressed (repeated-measures ANOVA, $F = 5.51$, $df = 1$, $P = 0.046$) and hatching success was significantly increased (174 %) by *Moina* competition (*t*-test, $t = 8.449$, $df = 8$, $P < 0.001$; Fig. 4). Thus, rotifer competition with *Moina* promoted hatching success, an effect caused by the presence of the competitor and reinforced by the resource depletion driven by competition.

Discussion

Presence of the competitor *M. micrura* accelerated the processes of exclusion of *B. calyciflorus* in the experiments, which affected their patterns of diapause production. Our long-term culture experiment suggests that more eggs of lower quality are produced in the absence of *Moina*, and more high-quality eggs are produced with the competitor. Resource competition imposed by the presence of *Moina* accelerated food depletion and resulted in lower rotifer per capita diapausing egg production. Those diapausing eggs produced in the presence of *Moina* had better hatching success than those produced in the absence of *Moina*, but the females hatched from the former had poorer performance.

Diapause and sex are associated in the life cycle of cyclically parthenogenetic rotifers, and more resources are allocated to a diapausing egg than a subitaneous egg (Wurdak et al. 1978; Clark et al. 2012). All these factors result in an important cost of diapause, and one of its effects is a decrease of the short-term population growth rate (Spencer et al. 2001; Serra et al. 2005). However, diapause is required for genotype persistence. Our results point out that the trade-off between current growth and diapause investment is not the only one operating in the sexual phase of the rotifer life cycle. In our two experiments we observed a higher hatching success of the rotifer diapausing eggs produced in the presence of the superior competitor, and our first experiment suggests lower deterioration rates of these eggs. This suggests that high-quality diapausing eggs were produced at the cost of producing fewer eggs per female. Moreover, hatchlings emerging from eggs produced in cultures with *Moina* had better performance.

We propose a trade-off model for traits related to diapause. The traits involved in the trade-off would be production rate (*P*), egg durability, expressed as high quality and hatching success of diapausing eggs (*D*), and hatchling performance (*H*). When *Moina* is absent, the average rotifer produces many low-quality diapausing egg having high neonate performance; when *Moina* is present, the average rotifer phenotype invests more in greater durability of the eggs produced. Although a relationship between quantity/quality of diapause eggs has not been assessed in rotifers yet, there is broad general evidence that variation in dietary intake mediates a trade-off between egg quantity and quality (Roff 1992). In the cladoceran *Daphnia* few but relatively large-sized neonates are produced at low food levels, suggesting that qualitative changes in the production of offspring can result from quantitative changes in resource abundance (Tessier and Consolatti 1991).

Some hypotheses could explain the observed variation in diapausing egg production patterns, some of them not invoking a specific, advantageous response to *Moina*. First, it could be hypothesized that *Moina* creates an adverse environment due to food depletion, hence constraining the production and quality of diapausing eggs. This seems to us an unlikely explanation, because we observed that some effects of *Moina* on rotifer diapausing eggs were not negative, and eggs produced in the presence of *Moina* had higher durability (i.e. high hatching rates of high-quality eggs).

A second hypothesis appeals to a bet-hedging evolutionary strategy. Rotifer diapausing eggs face environmental uncertainty, and it would be adaptive for a single genotype to produce several types of eggs, some of them very durable to overcome a long adverse period, and many others not so durable suited to rapid colonization after a short adverse period. Patterns of diapausing egg production could be dependent on the phase of population dynamics in which eggs are formed. The presence of *Moina* changes this dynamics, i.e. restricting the presence of *B. calyciflorus*, limiting their exposition to only a part of environmental stimulus, and therefore diapausing egg production patterns could be modified accordingly. Proximate factors could be food concentration (Pourriot and Snell 1983), concentrations of intraspecific signals (Snell et al. 2006) and changes in the rotifer age structure [see Hagiwara and Hino (1989) and Alver and Hagiwara (2007) for the relationship between age of parental individuals and diapausing egg production]. Recently, the adaptive potential of bet-hedging strategies to enable organisms to face the uncertainty of the rotifer environment has been stressed (Roger-García et al., in press). Heterogeneity in sexual investment among females in response to an environmental signal has been previously noted as a component of a diversified bet-hedging strategy for a clonal population (Gilbert and Schröder 2007).

Finally, our results suggest that the competitive dynamics among zooplankton are complex because the presence of competitors may cause fine-tuned changes in the life cycle of the interacting populations. In turn, these changes should have effects on the competitive output in the water column. For instance, two alternative responses are possible: to try to resist the competitor by avoiding the diversion of resources into diapausing stages, or to escape from competition by investing more in diapause. In addition to their effects in the water column, the competitive dynamics could have effects on the features of the diapausing egg banks in the sediment, which could determine the fate—persistence or not—of the populations in the next recruiting seasons.

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