Hatching phenology, life history and egg bank size of fairy shrimp Branchipodopsis spp. (Branchiopoda, Crustacea) in relation to the ephemerality of their rock pool habitat

**Bram Vanschoenwinkel · Maitland Seaman ·
Luc Brendonck**

Abstract In temporary aquatic habitats, permanence and the severe disturbance associated with desiccation are strong selective agents expected to lead to differentiation in life history strategies in populations experiencing different disturbance regimes. Besides optimal timing of hatching of dormant life stages, maturation and reproduction, pool inhabitants also benefit from the acquisition of reliable cues for the quality of the ambient environment. We investigated whether hatching patterns, life history characteristics and egg bank size of *Branchipodopsis* fairy shrimp (Branchiopoda, Anostraca) inhabiting a cluster of temporary rock pools in South Africa reflect variation in habitat stability and hatching cues. Long-term hydrological variation was used to select pools along a gradient of habitat stability. Initial conductivity was a good indicator for the length of inundations. No hatching occurred under elevated conductivities, which may present a mechanism to avoid abortive hatching. Egg bank size was unaffected by habitat size or habitat stability but instead was related to cover by a protective sheet of dry aquatic vegetation, which presumably counteracts egg bank erosion by wind when pools are dry. Life history but not hatching phenology reflected some aspects of habitat stability. Fairy shrimp populations in ephemeral pools started reproduction earlier than populations in more stable habitats. Additional common garden or transplant experiments, however, will be required to assess the relative importance of environmental and genetic components in explaining the observed variation and acquire more insight into the trade-offs that lie at the base of the evolution of life history strategies along the pond permanence gradient.

Keywords Hatching phenology ·
Hydroperiod · Hydroregime · Life history evolution ·
Temporary pools · Dormant egg banks

B. Vanschoenwinkel (✉) · L. Brendonck
Laboratory of Aquatic Ecology and Evolutionary Biology,
Katholieke Universiteit Leuven, Ch. Deberiotstraat 32,
3000 Leuven, Belgium
e-mail: bram.vanschoenwinkel@bio.kuleuven.be

M. Seaman
Centre for Environmental Management, University
of the Free State, Mandela Drive, 9300 Bloemfontein,
South Africa

Introduction

Life history strategies in natural populations are often expected to reflect the disturbance history of the habitat in which they occur (Roff 1992, 2002; Stoks and McPeek 2003). Pond permanence is a well-known example of disturbance (Wellborn et al. 1996). Contrasting life history strategies are expected among species and populations inhabiting different

ranges of a gradient of habitat duration (hydroperiod) (Brendonck and Riddoch 2002; De Block et al. 2008) and across the habitat transition between temporary and permanent ponds (Wellborn et al. 1996; De Block and Stoks 2004). Wissinger et al. (2003) suggested that differences in life histories explained variation in distribution patterns of caddisflies (Trichoptera) among temporary and permanent ponds. Similar observations were made by Johansson and Suhling (2004) who reported that larvae of dragonfly species (Odonata) typical for temporary pools were characterised by faster growth rates than those from permanent ponds.

Temporary aquatic habitats are typically characterised by variation in timing, frequency and duration of inundations; a number of variables that together shape the disturbance regime (i.e., hydroregime) of the habitat (Hulsmans et al. 2008). Permanent inhabitants of these systems, such as fairy shrimps (Anostraca), survive the dry habitat phases by means of dormant life stages in the sediment. Accumulation of these dormant eggs in the sediment results in the formation of an egg bank (Brendonck and De Meester 2003). Fairy shrimps have developed a number of traits to help them persist under often harsh conditions, including early hatching, rapid maturation and early start of egg production (Wiggins et al. 1980; Brendonck et al. 2000). Due to often low predictability of the length of aquatic phases in these habitats, the decision to end diapause or to remain dormant entails important risks. As a result, acquisition of reliable information about the quality of the environment is crucial (Spencer and Blaustein 2001). Emergence during subsequent inundations too short for reproduction (abortive hatching) may lead to egg bank depletion. A number of environmental variables, such as water level (Hall 1959), conductivity (Sam and Krishnaswamy 1979; Brendonck et al. 1998), temperature (Brendonck et al. 1998; Brendonck and Riddoch 2002), oxygen concentration (Moore 1967), and light regime (Mitchell 1990), have been suggested as hatching cues for temporary pool invertebrates. Some resting eggs, however, are not responsive to hatching cues and require desiccation, a critical amount of time or a cold shock before they hatch (reviewed in Brendonck and De Meester 2003).

Previous research on hatching and life history adaptations of freshwater invertebrates along the pond permanence gradient were limited to comparisons of a relatively low number of independent observations. In most cases, studies were limited to a comparison of two or three populations from contrasting habitats (Hamer and Appleton 1991; Mura 2001; Mura et al. 2003). Published work also focused mainly on inter- rather than intra-specific variation (Johansson and Suhling 2004; De Block et al. 2008). Overall, studies covering a larger number of populations along a gradient of hydrological stability are lacking. Finally, quantification of hydrological variation in study systems is typically limited to short-term observations of water presence (Mura 2001; De Block et al. 2008) or indirect estimators such as depth or surface to volume ratio (Marcus and Weeks 1997). Since long-term observations are usually required to cover inter- and intra-annual variation in the number (inundation frequency) and the duration (hydroperiod) of inundations of temporary pools (Bauder 2005), short-term measurements probably do not allow to reliably characterise the selection regime.

Here, we investigate differences in hatching phenology (start, duration and peak of hatching), early life history characteristics (maturation rate, day of first reproduction, daily egg production) and population size variables (population density, egg bank size, egg bank density) in *Branchipodopsis* fairy shrimp inhabiting temporary rock pools situated on an isolated mountaintop. Additionally, we also evaluate the feasibility of different abiotic variables (pH, conductivity, temperature) as hatching cues. Four consecutive inundations were monitored during the 2005 rainy season. Recent advances in hydrological modelling have made it possible to estimate historic variation in lengths and frequencies of inundations, and hence to reliably reconstruct the disturbance regime of individual habitat patches (Vanschoenwinkel et al. 2009a). Making use of this approach, we selected 15 temporary rock pools along a natural disturbance gradient characterised by a reduction in hydroperiod and increase in desiccation frequency. We hypothesise that differences in disturbance regime (hydroregime) among pools impose a strong selective pressure that is reflected in the hatching patterns, early life history characteristics and egg bank size of fairy shrimp. We expect that selection in short-lasting patches promoted rapid maturation and early start of reproduction. In more stable patches, however, trade-offs might stimulate individuals to allocate more energy to growth and postpone

reproduction. Finally, habitat size and the proportion of inundations long enough for reproduction were hypothesised to be the main determinants of egg bank size.

Materials and methods

Study system

The experiment was carried out in a cluster of temporary rock pools at the summit of the Korannaberg mountain (Free State Province, South Africa). The pool cluster consists of 36 large pools and several smaller depressions that intermittently hold water after rains. Pools range from small, ephemeral pools that usually only keep water for several days to larger, long-living pools that can retain water for several months or more. Fifteen pools were selected to cover a permanence gradient. The hydrology of the Korannaberg rock pools was modelled and hydrological characteristics were reconstructed based on long-term climate data (Vanschoenwinkel et al. 2009a). Based on model reconstructions integrating 80 years of available climate data, pools were divided into four groups experiencing different hydroregimes; E: ephemeral pools ($n = 5$), S: short-lasting pools ($n = 4$), M: medium-lasting pools ($n = 3$) and L: long-lasting pools ($n = 3$) using cluster analysis. Cluster analysis was performed using the PRIMER statistical package (PRIMER-E, 2000) based on a similarity matrix of normalised Euclidean distances using standardised values of mean hydroperiod and mean desiccation frequency. As linkage rule, we used unweighted pair-group average (Sneath and Sokal 1973). Descriptive statistics (median, mean, SD) of hydrological variables for the different pool types identified via cluster analysis are provided in the Table 1. The percentage of inundations longer or equal to 7 days was used as an estimate for the chance of successful reproduction. This is the critical time period for egg production of the studied taxa based on field and laboratory observations (Seaman et al. 1995).

Study species

Anostracans of the genus *Branchipodopsis* are permanent rock pool inhabitants that survive dry periods

as dormant cysts (encysted embryos, commonly referred to as resting eggs) in the sediment. They reproduce sexually and can mate and produce small clutches of eggs repeatedly during their lifetime. Eggs typically require a period of desiccation before they can hatch (Vanschoenwinkel unpublished data). *Branchipodopsis* fairy shrimp have developed several traits including rapid growth and early reproduction that enable them to survive in ephemeral pools (Brendonck and Riddoch 2002). For Korannaberg fairy shrimp, eggs are typically deposited as early as 6–7 days after hatching (Botha unpublished data, Seaman et al. 1995). Genotyping *Branchipodopsis* individuals from the Korannaberg pools (mitochondrial COI gene) revealed that the resting eggs used in our experiments belong to two different *Branchipodopsis* species (Vanschoenwinkel unpublished data): *B. drakensbergensis* Hamer and Appleton 1996 and a closely related undescribed lineage, which is morphologically almost identical, with the exception of a microscopic antennal appendage exclusively observable in adult males. No differences between the two species were found in morphologies of eggs, juveniles and females. Laboratory hatching revealed strictly unimodal hatching patterns, and adult males of both species were detected at the same time in active populations, suggesting that both species adopt the same hatching strategy. Combination of sampling of active communities and genotyping of resting eggs furthermore revealed that both species are probably present in all pools. Due to high similarity among the two species, we expect that they will respond similarly to the studied selection regime.

Experimental design

We selected 15 pools covering a broad permanence gradient (average hydroperiod range: 8–57 days). Some pools on the study site are subject to high dispersal rates via temporary overflows (Vanschoenwinkel et al. 2008). These pools were not included in this study as incoming dispersal may distort patterns. The 15 selected pools and their resting egg bank coverage were drawn to scale and the surface area calculated. Cover by aquatic macrophyte species (%) was estimated and average thickness of the sediment containing resting eggs. In each pool, we collected three random samples of a standard circular surface of resting egg bank (28 cm^2; corresponding to the

Table 1 Descriptive statistics (median, mean, SD) of hydrological variables for pools assigned to different disturbance regimes (hydroregimes) via cluster analysis

Disturbance class	N	Hydroperiod (days)		Desiccation frequency (dryings/year)	
		Median (range)	Mean (SD)	Median (range)	Mean (SD)
E	5	5	8 ± 8	15	16 ± 3
S	4	7	16 ± 25	12	12 ± 3
M	3	8	28 ± 19	8	8 ± 3
L	3	13	57 ± 95	6	6 ± 3

surface area of a hatching chamber) using a spoon and a fine brush. Each sample was transferred into a hatching chamber, which consisted of a plastic cup with a lid, lined at the bottom with fine netting (20-μm mesh). The lid of the cup was also lined with netting (200-μm mesh) to allow filling of the cups during rain. In each pool, we set up three hatching chambers by fitting them into a 30- by 20-cm Styrofoam plate, which enabled the hatching chambers to float when pools were full.

All hatching chambers were put in the field on October 1st, 2005 and again on November 1st when all pools were dry. From the onset of the first rains, they were checked daily for nauplii each morning from 7 a.m. until 10 a.m. during three consecutive inundations. All nauplii were counted and transferred to the respective pool. At the end of the third monitored inundation, just before pools dried up and the resting egg bank in the chambers was still moist, the contents (residual egg bank) of each chamber was transferred to a sample vial with 7% formaldehyde and transported to the laboratory. All unhatched egg bank samples were counted under a stereomicroscope. Eggs were deemed viable when a well-defined embryo popped out when squeezed (for details of the method see Brendonck and Riddoch 2000). Using average egg bank densities from the hatching chambers (number of hatchlings + residual viable eggs) and estimated surface area of resting egg banks in each pool, we calculated resting egg bank size and egg bank density (eggs/cm^2) for each pool. Variation in hatching fractions is not discussed here and, together with results from long-term laboratory hatching experiments, this will be discussed in the light of bet hedging strategies in another manuscript.

From the moment the first juveniles (post nauplius stage) started to appear, active population density was estimated each day using quadrats (bottomless plastic box; dimensions: 13 × 13 × 10 cm). The quadrat was placed in the water column in one swift movement and the total number of enclosed anostracans (juveniles, females and males) was counted. A total of eight quadrats were taken randomly in each pool. A minimum of 100 individuals was collected daily with an aquarium net (500-μm mesh) to determine maturation. The day of first reproduction was recorded for each population.

To compare maturation rates among pools, we used the percentage of adults as measured on November 20 (day first mature individuals were spotted in some pools), 21 and 22 (day some pools dried out). Due to differences in timing of hatching and population build up in different pools, we could not directly compare population densities at specific dates. We therefore compared population density among pools based on the maximum population density reached during the observation period.

From the moment first adults appeared, we randomly sampled 30 females each day using a dipnet. Ten females were subsequently transferred to plastic lidded cups (three replicates) placed in the pool basin. Cups were lined at the bottom with fine gauze (20-μm mesh) to allow transfer of water and nutrients. After 24 h, the number of deposited eggs was counted and used to estimate the daily egg production.

Environmental variables

Rainfall was measured each morning at 8 a.m. using a rain gauge placed in the centre of the studied pool cluster. From the day of inundation onwards, oxygen, water temperature, conductivity and pH were measured in the 15 pools between 7 and 9 a.m., using WTW metres (conductivity metre 330i, oxygen metre 315i, pH metre 340; WTW, Weilheim, Germany).

Data analysis

To search for possible trade-offs among measured life history and hatching phenology variables, Pearson product moment correlations were calculated. When the assumption of normality was not met, non parametric Spearman Rank correlations were used instead. All correlations were performed in Statistica 8.1 (StatSoft, Inc., Tulsa, Oklahoma). To test for differences in hatching traits: hatching start, hatching period, hatching peak (days after inundation) general linear models were built in SAS (Version 9.1; SAS Institute, Cary, NC). Predictor variables known to vary along the pond permanence gradient included hydrological variables related to the hydroregime (mean and SD hydroperiod, mean and SD inundation frequency), chance of successful reproduction (proportion of inundations longer or equal to 7 days), pool morphometrical variables related to habitat size (surface area, maximum depth and volume of the pool basin) and vegetation cover. Similar models were built to explain variation in measured early life history traits: day of first reproduction, mean and maximal daily egg production and egg bank size. Pool E12 was excluded from the models presented in the results section due to aberrant hatching behaviour. In this pool, hatching was initiated after a small shower on November 11 well before hatching started in all other pools i.e., after heavy rains on November 13.

Results

Hatching cues

The first two inundations of the rainy season were initiated by showers on October 7 (10 mm; average (±SD) conductivity: 295.85 ± 236 µS/cm) and October 16 (4.5 mm; average conductivity: 224.89 ± 238 µS/cm). Although these small showers resulted in some standing water, no hatching took place. Pools first filled up after heavy rains (25 mm; average conductivity in pools: 40 ± 15 µS/cm) on October 20, which resulted in hatching. Due to severe evaporation, however, all pools dried up before any fairy shrimp could mature. We were only able to collect hatching and life history data during the fourth inundation, which was initiated by a rainstorm on

November 11 (6.5 mm) (average conductivity: 236 ± 147 µS/cm). No hatching was observed at that time, except in pool E12 (conductivity 142 µS/cm). Additional rainfall (36 mm) on November 13 (3 days after initial inundation) resulted in a drop in pool conductivity (average conductivity: 45 ± 23 µS/cm) in all pools (Fig. 1a) coinciding with initiation of hatching (Fig. 2). Other measured environmental variables (pH, water temperature) did not show any variation potentially related to hatching phenology). Initial conductivity was inversely proportional to the length of subsequent inundations (Spearman $R = -0.62$; $P < 0.01$) (Fig. 1b).

Hatching and life history variation

Hatching was initiated hours after heavy rains resulted in a conductivity shock (3 days after initial inundation) and eggs continued to hatch for 4 days (Fig. 2). Populations that hatched early, exhibited slower maturation rates (Spearman rank $R = -0.91$; $P < 0.01$), and a significant negative correlation was found between length of the hatching period and the number of days after initial inundation that hatching was initiated (Spearman $R = -0.81$; $P < 0.01$). Means and standard errors of different measured hatching, life history and population size variables along the pond permanence gradient are summarised in Fig. 3. Due to early desiccation, no fairy shrimp reached maturity or reproduced in certain pools (all E pools except E12).

None of the tested environmental variables could explain variation in start of hatching, duration of hatching (hatching period) or the day of maximal hatching (hatching peak). (all $P > 0.05$). Day of first reproduction was positively related to the chance of successful reproduction ($ß = 21.2$, $P = 0.03$, $r^2 = 0.31$). No significant general linear models could be built to explain variation in average and maximum daily reproduction, maturation, population density or egg bank density.

Egg bank size

Resting egg bank sizes ranged between 6×10^3 and 5.6×10^6 eggs per pool, which corresponds to egg densities ranging from 6.2×10^3 up to 2.5×10^5 eggs per m^2. Egg bank size was shown to be positively related to vegetation cover (Fig. 4) ($ß = 35560$,

Fig. 1 **a** Conductivity of the 15 studied pools during the first 9 days after initial inundation (mean ± SD). Arrows indicate rainfall events. **b** Relation between initial conductivity and the duration of subsequent inundations
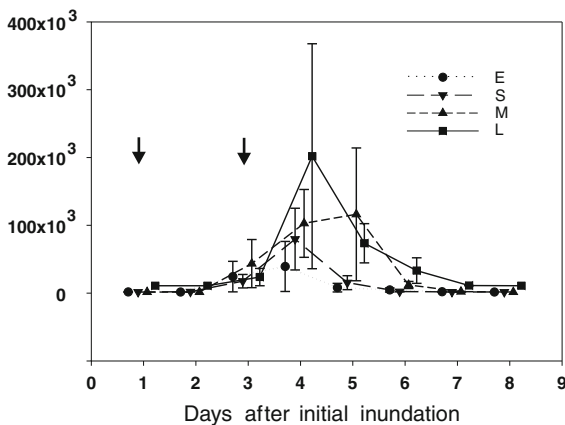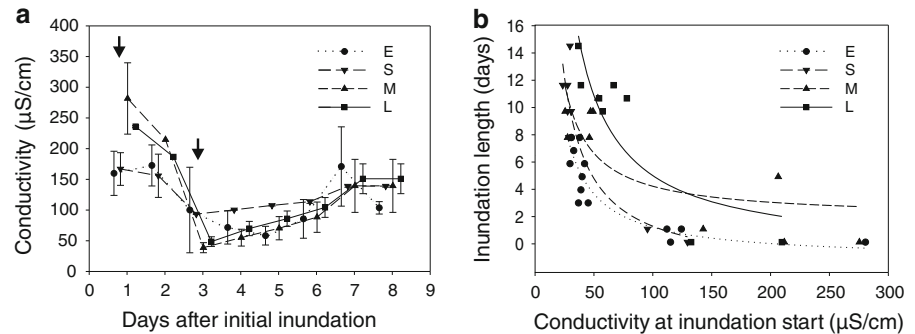

Fig. 2 Number of anostracan nauplii (mean ± SD) hatched from the 15 studied pools during the first 8 days after initial inundation: *E*: ephemeral pools, *S*: short-lasting pools, *M*: medium-lasting pools and *L*: long-lasting pools. *Arrows* indicate rainfall events

$P = 0.002$) independently of pool surface area (ß = 328649, $P = 0.09$), which was also included in the model ($r^2 = 0.77$). Egg bank densities were correlated with population densities (Spearman $R = 0.59$, $P = 0.02$).

Discussion

Hatching cues

Rock pools in semi arid regions are among the most extreme aquatic habitats in the world. Due to erratic rainfall and high evaporation rates, wet phases often do not allow sufficient time for maturation and reproduction of aquatic organisms (Hulsmans et al. 2008). Model reconstructions indicate that in the Korannaberg pool cluster on average 45% of

inundations are too short (<7 days) for fairy shrimp to reach maturity and allow for reproduction (Seaman et al. 1995; Vanschoenwinkel et al. 2009a). For an activated dormant egg, the decision to remain quiescent (Drinkwater and Clegg 1991) or to hatch and join the active community therefore holds important risks and may prove to be fatal. During this study, individuals in a number of populations (in four out of five E pools and in one out of four S pools) hatched but never reached maturity due to premature desiccation of the habitat. Repeated periods of hatching followed by reproductive failure (abortive hatching) may therefore be costly. Consequently, it is expected that evolution will select for genotypes responding to hatching cues providing reliable information about the quality (e.g., duration) of inundations (Spencer and Blaustein 2001). Field observations suggest that elevated conductivities inhibited hatching of *Branchipodopsis* fairy shrimp. No hatching was observed during the first two very short inundations initiated by little rainfall and characterised by conductivities > 100 µS/cm. Similarly, with a single exception (population in the pool E12), no hatching was observed at the beginning of the third inundation. Only when sufficient additional precipitation resulted in a drop in conductivities, hatching was initiated (Fig. 1a). As demonstrated in the current study, low initial conductivities can be predictors for the length of inundations (Fig. 1b), pointing to the adaptive value of low conductivity as a hatching cue in temporary pool crustaceans. A laboratory study by Sam and Krishnaswamy (1979) also reported that hatching of the fairy shrimp *Streptocephalus dichotomus* was inhibited by elevated conductivities (>80 µS/cm). Brendonck et al. (1998) likewise demonstrated that low conductivities promoted hatching of the fairy shrimp *Branchipodopsis wolfi*. The
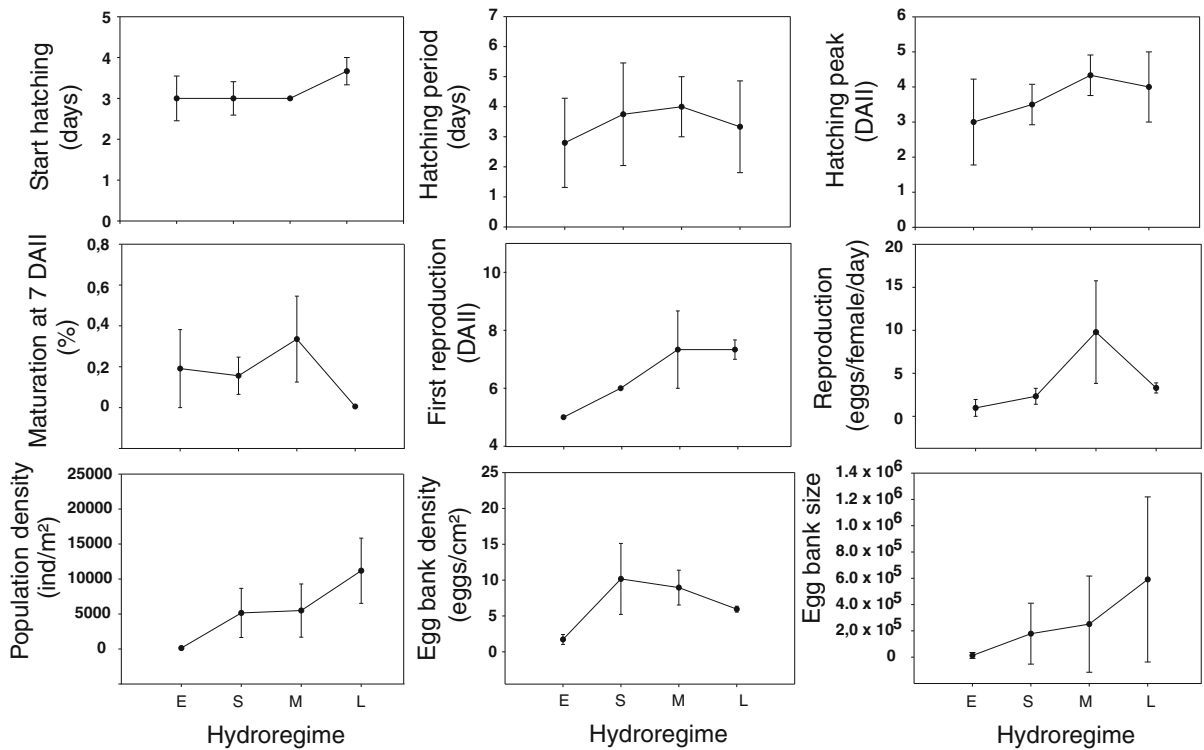
Fig. 3 Differences in hatching phenology (start, duration and peak of hatching), early life history characteristics (maturation, day of first reproduction, reproduction) and population parameters (population density, resting egg bank density and size) in hydrologically different pools. DAII = days after initial inundation. Means are given ±1 SE
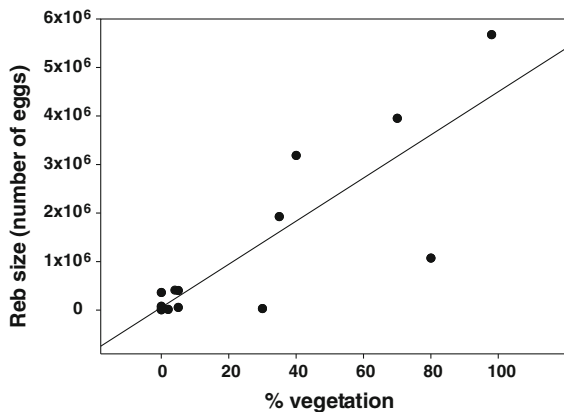

Fig. 4 Positive relationship between vegetation cover (%) and the size of fairy shrimp egg bank in the studied pools

deviant patterns found for pool E12 probably resulted from the fact that it is characterised by lower conductivities than the other pools included in this study. Initial rains on November 11 therefore may have triggered hatching in pool E12 but not in the other pools with a higher concentration of dissolved salts.

Hatching and life history variation

In short-lasting pools, time stress is expected to select for early hatching and a short period of hatching (Brendonck 1996). In the current study, however, hatching was restricted to the first 4 days after initiation of hatching. No clear differences in start of hatching, hatching peak or hatching period among populations could be demonstrated. It seems that it is generally advantageous for fairy shrimp to hatch as soon as possible, independent of the average disturbance regime of their habitat since this may lead to longer lifespans and production of more clutches of eggs before the pool dries up. Additionally, this strategy also helps to avoid higher predation pressure later during the inundation (Jocqué et al. 2007; Spencer et al. 1999). Another factor that probably contributes to explaining the lack of differences in

start of hatching between populations in short—versus long-lasting pools is that pools which, on average, experience longer hydroperiods (Table 1; Vanschoenwinkel et al. 2009a), often also experience short inundations when basins are only filled to a limited extent.

Selection in short-lasting patches is believed to promote rapid maturation and early start of reproduction (Roff 1992). Based on our data, we found some support for this hypothesis. Fairy shrimp inhabiting more ephemeral rock pools started reproduction earlier than populations in more stable pools, which experience more suitable inundations. As mentioned by Hildrew (1985), producing a small clutch early on reduces the risk of not producing any progeny. Slower maturation, on the other hand, can be beneficial when, via evolutionary trade-offs, this leads to the production of more or higher quality offspring (Stearns 1992; Roff 2002). In more stable patches, for example, trade-offs might stimulate individuals to allocate more energy to growth and postpone reproduction (Mura et al. 2003; Johansson and Suhling 2004). This strategy may have advantages in securing a larger total egg production or making individuals less susceptible to invertebrate predation (Zaret 1980).

There were, however, no clear indications for evolutionary trade-offs among the limited set of traits measured. Our findings do suggest that populations which hatch early, exhibit a slower maturation. This could suggest a cost of early hatching. Perhaps, feeding conditions immediately after inundation were not optimal due to lower densities of live food sources such as bacteria and algae (Boven et al. 2008). It must also be noted that those populations that hatched early also continued to hatch over a longer time period (5–6 days instead of 3–4 days) and that the presence of late hatching individuals may partly explain slower overall maturation rate of the population. We found no significant correlations with daily egg production but this may be due to the fact that we could not monitor long enough. When pools were drying out, adults only recently appeared in the monitored populations and reproduction had only just begun. Laboratory experiments raising fairy shrimp from different populations under standardised conditions would allow better measurements of fitness-related traits (longevity, daily fecundity and the lifetime production of eggs).

We found some indications that life history traits of fairy shrimp populations, notably start of reproduction, reflect the disturbance regime of their habitat. These patterns may be indicative of local adaptation; however, it cannot be excluded that the measured traits are plastic and expressed in response to local environmental conditions. Reciprocal transplant or common garden experiments (Van Dooren and Brendonck 1998) may help to unravel the relative importance of local environmental stimuli, maternal effects or genetic variation generating variation in hatching phenology and life history strategies along the pond permanence gradient. Finally, it must be noted that due to the cryptic morphologies of the species involved, this study presents patterns observed at the level of the assemblage. Even though both species were most likely present in every pool and are likely to respond similarly to local hydrological conditions, we cannot exclude that the two species might slightly differ in some life history traits (e.g., maturation time). Therefore, subtle changes in taxon frequencies among pools may have contributed to the observed variation.

In a heterogeneous patchy environment with regular dispersal such as the studied pool cluster, one might expect that the influx of maladapted genotypes would counteract the possibility of local adaptation. Still, the presented data indicate a good match between fairy shrimp life histories and local hydrological conditions despite high dispersal rates measured at the site notably via wind (Vanschoenwinkel et al. 2008). This could suggest that fairy shrimp eggs are either able to adequately respond to local conditions (phenotypic plasticity) or that gene flow is limited due to a low establishment success of incoming migrants adapted to other conditions (De Meester et al. 2002).

Egg bank size

Larger habitats typically house bigger populations due to a larger carrying capacity. The data, however, suggest that habitat size and habitat stability were relatively unimportant in determining size of dormant egg banks. Instead, vegetation cover emerged as the most important explanatory variable. The idea that vegetation could stabilise egg banks was proposed earlier by Brendonck and Riddoch (2000). In that study, a lower variance in egg

densities was measured over a period of 4 years in pools with vegetation compared to pools without vegetation. Additional information was provided by Vanschoenwinkel et al. (2009b), who measured high dispersal rates, not only of resting eggs but also of resting egg bank fragments in this study system. The authors also hinted at the potential of aquatic vegetation to decrease wind erosion of the egg bank. The current results thus support this hypothesis. Mass movement of resting eggs and sediment via wind may explain why aquatic vegetation that forms a protective crust during the dry periods may be more important in determining egg bank size than basin size or hydroregime. Fairy shrimp egg bank densities were quite variable but, with exception of the highly exposed unvegetated pools that sometimes only held a couple of hundred eggs, recorded densities fell within the range of 10^3–10^5 eggs per m^2, which is typical for freshwater zooplankton (Brendonck and De Meester 2003). Using an experimental vacuum cleaner, Graham and Wirth (2008) showed that large branchiopod eggs from dry potholes in Utah (USA) are more easily picked up by wind from disturbed than from undisturbed egg banks. In disturbing the protective crust, human activities therefore could adversely affect populations of temporary pool invertebrates including fairy shrimp, which for their survival are highly dependent on the buffering capacity of the dormant egg bank. Many inselbergs, notably in Southern Africa and Australia, but also rock pools in other areas such as the potholes on the sandstone flats in Utah are popular tourist destinations; and in some cases, hiking trails and four by four tracks pass right through pool sites damaging the egg banks (Graham and Wirth 2008; Vanschoenwinkel personal observation). Conservation managers should therefore consider better regulating these activities.

References

Bauder ET (2005) The effects of an unpredictable precipitation regime on vernal pool hydrology. Freshwater Biol 50:2129–2135

Boven L, Stoks R, Forro L, Brendonck L (2008) Seasonal dynamics in water quality and vegetation cover in temporary pools with variable hydroperiods in Kiskunsag (Hungary). Wetlands 28:401–410

Brendonck L (1996) Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea:Branchiopoda:Anostraca, Notostraca, Conchostraca). In: International symposium on diapause in the Crustacea. Kluwer, St Petersburg, pp 85–97

Brendonck L, De Meester L (2003) Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. Hydrobiologia 491:65–84

Brendonck L, Riddoch BJ (2000) Egg bank dynamics in anostracan desert rock pool populations (Crustacea: Branchiopoda). Arch Hydrobiol 148:71–84

Brendonck L, Riddoch BJ (2002) Hatching characteristics of the fairy shrimp Branchipodopsis wolfi in relation to the stochastic nature of its habitat, desert rock pools. In: Williams WD (ed) Verh Internat Verein Limnol 27:3931–3935

Brendonck L, Riddoch BJ, Van de Weghe V, Van Dooren T (1998) The maintenance of egg banks in very short-lived pools—a case study with anostracans (Branchiopoda). In: Brendonck L, De Meester L and Hairston NG Jr. (eds), Evolutionary and ecological aspects of crustacean diapause. Arch Hydrobiol 52:141–161

Brendonck L, Hamer M, Riddoch B, Seaman M (2000) *Branchipodopsis* species: specialists of ephemeral rock pools. Afr J Aquat Sci 25:98–104

De Block M, Stoks R (2004) Life-history variation in relation to time constraints in a damselfly. Oecologia 140:68–75

De Block M, McPeek MA, Stoks R (2008) Life history plasticity to combined time and biotic constraints in *Lestes* damselflies from vernal and temporary ponds. Oikos 117:908–916

De Meester L, Gomez A, Okamura B, Schwenk K (2002) The Monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. Acta Oecologica 23:121–135

Drinkwater LE, Clegg JS (1991) Experimental biology of cyst diapauze. In: Browne RA, Sorgeloos P, Trotman CNA (eds) Artemia biology. CRC Press, Boca Raton Ann Arbor Boston, pp 93–117

Graham TB, Wirth D (2008) Dispersal of large branchiopod cysts: potential movement by wind from potholes on the Colorado Plateau. Hydrobiologia 600:17–27

Hall RE (1959) The development of eggs of *Chirocephalus diaphanus* Prevost in relation to depth of water. Hydrobiologia 14:79–84

Hamer ML, Appleton CC (1991) Life-history adaptations of phyllopods in response to predators, vegetation and habitat duration in North-Eastern Natal. Hydrobiologia 212:105–116

Hildrew AG (1985) A quantitative study of the life-history of a fairy shrimp (Branchiopoda, Anostraca) in relation to the

temporary nature of Its habitat, a Kenyan rainpool. J Animal Ecol 54:99–110

Hulsmans A, Vanschoenwinkel B, Pyke C, Riddoch BJ, Brendonck L (2008) Quantifying the hydroregime of a temporary pool habitat: a modelling approach for ephemeral rock pools in SE Botswana. Ecosystems 11: 89–100

Jocqué M, Riddoch BJ, Brendonck L (2007) Successional phases and species replacements in freshwater rock pools: towards a biological definition of ephemeral systems. Freshwater Biol 52:1734–1744

Johansson F, Suhling F (2004) Behaviour and growth of dragonfly larvae along a permanent to temporary water habitat gradient. Ecol Entomol 29:196–202

Marcus V, Weeks SC (1997) The effects of pond duration on the life history traits of an ephemeral pond crustacean, *Eulimnadia texana*. Hydrobiologia 359:213–221

Mitchell SA (1990) Factors affecting the hatching of *Streptocephalus macrourus* Daday (Crustacea, Eubranchiopoda) eggs. Hydrobiologia 194:13–22

Moore WG (1967) Factors affecting egg-hatching in *Streptocephalus seali* (Branchiopoda—Anostraca). Proceed Symp on Crustacea, Part II, pp. 724–735

Mura G (2001) Life history strategy of *Chirocephalus ruffoi* (Crustacea, Anostraca) in Mediterranean temporary mountain pools. Hydrobiologia 462:145–156

Mura G, Fancello G, Di Guiseppe S (2003) Adaptive strategies in populations of Chirocephalus diaphanus (Crustacea, Anostraca) from temporary waters in the Reatine Apennines (Central Italy). J Limnol 62:35–40

Roff DA (1992) The evolution of life histories: theory and analysis. Chapman and Hall, New York

Roff DA (2002) Life history evolution. Sinauer, Massachusetts

Sam ST, Krishnaswamy S (1979) Effect of osmomolarity of the medium upon hatching of undried eggs of *Streptocephalus dichotomus* Baird (Anostraca, Crustacea). Arch Hydrobiol 86:125–130

Seaman MT, Kok DJ, Meintjes S (1995) The description and preliminary prediction of the inundation pattern in a temporary habitat of Anostraca, Notostraca and Conchostraca in South-Africa. Hydrobiologia 298:93–104

Sneath PHA, Sokal RR (1973) Numerical taxonomy. Freeman, San Francisco

Spencer M, Blaustein L (2001) Hatching responses of temporary pool invertebrates to signals of environmental quality. Isr J Zool 47:397–417

Spencer M, Blaustein L, Schwartz SS, Cohen JE (1999) Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence. Ecol Lett 2:157–166

Stearns SC (1992) The evolution of life histories. Oxford university press, Oxford

Stoks R, McPeek MA (2003) Predators and life histories shape *Lestes* damselfly assemblages along a freshwater habitat gradient. Ecology 84:1576–1587

Van Dooren T, Brendonck L (1998) The hatching pattern of *Branchipodopsis wolfi* (Crustacea: Anostraca): phenotypic plasticity, additive genetic and maternal effects. In: Brendonck, L, De Meester L, Hairston NG Jr (eds) Evolutionary and ecological aspects of crustacean diapause. Arch Hydrobiol 52:219–227

Vanschoenwinkel B, Gielen S, Vandewaerde H, Seaman M, Brendonck L (2008) Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. Ecography 3:567–577

Vanschoenwinkel B, Hulsmans A, De Roeck ER, De Vries C, Seaman M, Brendonck L (2009a) Community structure in temporary freshwater pools: disentangling effects of habitat size and hydroregime. Freshwater Biol 54:1487–1500

Vanschoenwinkel B, Gielen S, Seaman M, Brendonck L (2009b) Wind mediated dispersal of freshwater invertebrates in a rock pool metacommunity: differences in dispersal capacities and modes. Hydrobiologia 635:363–372

Wellborn GA, Skelly DK, Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. Ann Rev Ecol Syst 27:337–363

Wiggins GB, Mackay RJ, Smith IM (1980) Evolutionary and ecological strategies of animals in annual temporary pools. Arch Hydrobiol 58:97–206

Wissinger SA, Brown WS, Jannot JE (2003) Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (USA). Freshwater Biol 48:255–270

Zaret TM (1980) Predation and freshwater communities. Yale University Press, New Haven