Daphnia

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Kęstutis ARBAČIAUSKAS

Institute of Ecology of Vilnius University, Akademijos St. 2, LT-08412 Vilnius-21, Lithuania
e-mail address: arbas@ekoi.lt

ABSTRACT

Life-history and physiology of post-diapause and directly developing offspring in Daphnia *were compared to determine differences in life-history pattern between offspring origins, identify the basic traits effecting pattern distinction, assess the consequencies of differing life-history for relative fitness, and qualify this seasonal phenomenon. Although the size of ex-ephippial hatchlings was positively correlated with maternal size, ephippia produced by differently sized females of D. magna yielded neonates which body size and it's variation were similar to those for the first-clutch parthenogenetic neonates produced under high food conditions. Otherwise, post-diapause neonates of D. pulex were larger than first-clutch parthenogenetic neonates and varied in size close to that for neonates from the later clutches. Ex-ephippial offspring showed elevated metabolic activity. Under rich food, they grew faster during juvenile development and were larger at maturation than parthenogenetic females. Post-diapause offspring of D. magna showed higher juvenile growth rates also at limited food availability. Female origins during early maturity differed in resource allocation strategy. A greater allocation to progeny in offspring exiting diapause, however, resulted in increased progeny numbers and higher relative fitness only under rich food environments. Whereas, parthenogenetic females of D. magna exhibited a trend for higher fitness across limited food concentrations. For D. pulex, variability of fitness across differing nutritional environments was lower in directly developing females than that for ex-ephippial offspring. Higher metabolic activity in combination with small initial size resulted in lower resistance to starvation of post-diapause offspring of D. magna. Descendants of female origins in this species showed similar fitness. We conclude that although some traits of ex-ephippial offspring in comparison to parthenogenetic ones may differ across* Daphnia *species, the life-history strategy of post-diapause females in* Daphnia *is the same. Ex-ephippial females are adapted to predictable optimal conditions, whereas parthenogenetic females are adapted to unpredictably varying environment.* Daphnia *have evolved two alternative seasonal phenotypes matching environmental conditions in which they occur, and perform in accordance with predictions of seasonal polyphenism. Due to higher metabolic activity, which must lead to increased resource acquisition and probably is associated to larger allocation to progeny, post-diapause females are superior to directly developing offspring under high food conditions, which are expected during early season, but inferior under limiting food environments, which frequently occur later in the season. In seasonal climate, the adjustment of resource acquisition with respect to resource availability may be a general evolutionary trend for multivoltine organisms resulting in a seasonal polyphenism.*

Key words: diapause, seasonal polyphenism, physiology, life-history, fitness, food

1. INTRODUCTION

In temperate waters, the cyclic parthenogen *Daphnia* propagate mostly by parthenogenesis producing subitaneous eggs, which number depends upon feeding conditions. With deterioration of environmental quality, usually in the end of the growing season, these animals initiate sexual reproduction (Stross & Hill 1965; Carvalho & Hughes 1983). It results in two diapausing eggs encased in ephippium, a protective structure modified from carapace. Emergence from diapausing eggs in daphnids takes place in the early season during a relatively short period (Wolf & Carvalho 1989; Caceres 1998; Hairston *et al*. 2000), although these eggs being resistant to external factors can remain viable for extended time periods (Hairston *et al*. 1995). In temperate lakes and ponds, the beginning of growing season with sufficient nutrient and increasing sunlight and temperature results in massive development of edible algae. Hence, post-diapause daphnids are born into a predictable high-food environment. In contrast, their directly developing parthenogenetic offspring live in an unpredictable, highly variable conditions in terms of food availability and quality (Sommer *et al*. 1986). Thus, post-diapause and directly developing offspring of *Daphnia* live in differing seasonal environments which properties must select for different offspring phenotypes.

Higher fecundities of ex-ephippial females and their inability to produce sexual eggs in the first clutch has been already descried by Weismann (1880, cited from Alekseev 1990), but detailed comparative studies of ex-ephippial and parthenogenetic offspring in *Daphnia* have been initiated only recently. In this work, life-history and physiology of post-diapause and directly developing offspring were compared to determine differences in life-history pattern between offspring origins, identify the basic traits effecting pattern distinction, and assess the consequences of differing life-history for relative fitness. Ultimately, we set to qualify this seasonal phenomenon.

2. BACKGROUND

Post-diapause and directly developing offspring in *Daphnia* can be hypothesized to represent different seasonal phenotypes, thus, seasonal polyphenism. This type of phenotypic plasticity describes annually repeating seasonal change of phenotypes within multivoltine organism, classic examples being wing pattern polyphenism in butterflies, phenotypic alterations in a life cycle of aphids, and cyclomorphosis in cladocerans and rotifers (Shapiro 1976). Seasonal polyphenism generally is thought to be adaptive. Commonly it is determined with respect to separate morphological or physiological traits, which are expected to effect life-history pattern and relative fitness.

When dealing with seasonal polyphenism, three aspects of this phenomenon should be keystoned. First, polyphenism generally is associated with traits exhibiting discontinuous variation. Such traits are attributed to threshold traits, resulting from switching between alternative developmental pathways (see Roff 1996). Second, although diapause enables organisms to survive also aseasonally unfavourable circumstances such as food shortage or severe predation, the diapause primarily is an adaptation to avoid seasonally harsh conditions (Hairston 1998). Therefore, seasonal polyphenism likely is tightly, even inextricably, linked to diapause (Shapiro 1976). Third, theoretical analysis imply that the temporal change of distinct phenotypes should be favoured only if environment is temporary variable but predictable, in which an organism at the point of the determination of the phenotype can accurately predict future conditions (see Scheiner 1993). Also, to understand the processes underlying the polyphenism, the proximate causes, or factors governing the switch between alternative phenotypes, must be distinguished from the ultimate causes, or factors affecting relative fitness of phenotypes (Moran 1992). Consequently, proximate factors of seasonal polyphenism generally are expected to be good predictors of ultimate factors.

Environmental factors governing the switching between alternative phenotypes, including diapause induction and termination, has been extensively reviewed (Tauber *et al.* 1986; Danks 1987; Alekseev 1990; Hairston 1998). The response to environmental cues generally is adjusted by parental control. Examples of such transgenerational phenotypic plasticity are well-known in insects (Fox & Mousseau 1998). Recently, maternal effects were determined in cladocerans for diapause induction (LaMontagne & McCauley 2001; Alekseev & Lampert 2001) and diapause termination (De Meester *et al.* 1998).

The ultimate cause of seasonal polyphenism must be associated with seasonally changing environment. However, the selection for seasonal switching between alternate phenotypes in addition to temporal change may also depend upon spatial heterogeneity. Hence, two types of seasonal variation, in broad sense, could be distinguished: 1) spatio-seasonal variation, in which spatial variation of selecting factors is essential for the evolution and maintenance of seasonal polyphenism, and 2) seasonal variation, in narrow sense, in which predictable temporal change is sufficient for seasonal polyphenism.

Protective and life cycle polyphenism among directly developing generations of multivoltine organisms commonly exhibit seasonal pattern. For those polyphenism, including cyclomorphosis in planktonic animals or alteration of fully winged and flightless forms in many insects, spatial variation is considered to be important (Roff 1996). Cyclomorphosis in cladocerans and rotifers, which describes seasonal generating of exuberant structures, is presumed to be an adaptation against predators (Dodson 1974; Jacobs 1987). Host-altering life cycle in aphids including winged migrants requires the presence and sufficient quality of host plants, i.e. spatial heterogeneity (Moran 1991).

The scope of this work is a narrow sense seasonal polyphenism, that which ultimate and sufficient cause is predictable annual change of climatic factors. Food availability for consumers, at least herbivorous invertebrates with broad diet, or when the amount of resources similarly vary in all potential habitats, may also operate as ultimate factor, as seasonal change of food quantity and quality is closely associated to climatic factors. The intermitted by diapause change of discontinuous phenotypes definitely belongs to that type of polyphenism. It should be noted, that environmental conditions for post-diapause generation in multivoltine organisms commonly are predictable in long-term, but irrespective of information about parental environment. Under such circumstances, natural selection may favour parents producing progeny that develop into a phenotype opposite from that of the parent, but matching environment in which they will live. This transgenerational effect received a definition of a negative maternal effect (Fox & Mousseau 1998). Thus far, narrow sense seasonal polyphenism when traits are determined by parents, that must occur if embryonic diapause is involved, may be attributed to negative maternal effects.

Post-diapause and directly developing daphnids occur in different seasonal environments, to which they probably are best adapted. So far, if offspring origins represent alternative phenotypes of *Daphnia*, i.e. seasonal diphenism, than that must unfold in threshold traits and distinct life-history pattern resulting in different relative fitness across varying food availability, which likely is the most important seasonal factor determining the relative fitness of planktonic animals in temperate waters (Sommer *et al.* 1986).

3. METHODS

Investigations were performed on population samples, i.e. across multiple clones, of *Daphnia magna* and *D. pulex*. Variation for ephippial length and body length

of ex-ephippial hatchlings in *D. magna* was estimated on a field sample of ephippia. To avoid pseudo-replications in the establishment of relationship between ephippial length and neonate body length, values for hatchlings from the same ephippium were averaged prior to the statistical analysis (Fig. 1). Lengths of ephippia were converted to body lengths of females using the relationship given in Boersma *et al.* (2000). The size of neonates of different origin was compared on animals from experiments in a flow-through system run at 20 °C under one high and two limited food concentrations (see Arbačiauskas & Lampert 2003). Body mass and body length of ex-ephippial hatchlings and forth-clutch parthenogenetic neonates derived under 1.0 and 0.2 mg C l^{-1} food for the initiation of experiments, and first-clutch parthenogenetic neonates produced at 0.2, 0.4 and 1.5 mg C l^{-1} food were analysed (Fig. 2). For the estimate of the smallest body size in parthenogenetic hatchlings, first-clutch neonates produced under high food (1.5 mg C l^{-1}) by mothers derived from the first clutch were also included (Arbačiauskas 2004).

For *D. pulex*, ex-ephippial hatchlings measured during individual hatching of ephippia (Arbačiauskas 2001) were compared with parthenogenetic neonates produced in the life-table experiments. As high food circumstances, parallel experiments for post-diapause and parthenogenetic females at 15 °C in filtered pond water with addition of Scenedesmus (1.85 mg C l^{-1}) and natural pond water were involved (referred as HIGH and POND-HIGH, see Arbačiauskas 1998). For the lower food environment, the life-table survey of ex-ephippial offspring under natural pond water performed during the other season was used (POND-LOW). The lower food concentrations in this experiment indicated 1.5-2.0 times smaller mean size of the first three clutches when comparing with corresponding clutch in ex-ephippial females from POND-HIGH (Arbačiauskas, unpublished results). Differences in body size of first-clutch neonates between HIGH and POND-HIGH within ex-ephippial and parthenogenetic females were not significant, but varied between female origins, thus, measurements were respectively merged (Fig. 3). Measurements across older clutches (clutches 2-4) and different types of mothers were also merged for HIGH and POND-HIGH, as differences due to clutch number and mother's origin were not significant (see Fig. 4 in Arbačiauskas 1998). In POND-LOW, females were raised until the release of the third clutch, thus, values for clutches 2 and 3 were used.

Measurements of respiratory rate and survival under starvation of post-diapause and directly developing offspring in *D. magna* are described in Arbačiauskas & Lampert (2003). In figure 4 for neonates of both origins, only measurements which are comparable with respect to body mass and conditions before measurements are included. Life-history characteristics and relative fitness

of ex-ephippial and parthenogenetic offspring, and their descendents, in *D. magna* were measured in a flow-through system under high and limited food concentrations (Arbačiauskas & Lampert 2003; Arbačiauskas 2004). Estimates of life-history traits and fitness, and their variability across differing food, in *D. pulex*, were derived from life-table experiments (Arbačiauskas 1998, 2001). Reproductive effort during early maturity in offspring origins under high and limited food, being illustrated here (Fig. 5), was estimated as the ratio of generative to total production over the first two adult instars. Experiments under 1.5 and 0.4 mg C l^{-1} food indicated high and limited food environments for *D. magna*. Treatments HIGH and POND-HIGH were used as high food conditions, and the survey in filtered pond water was considered as limited food conditions for *D. pulex* (see Arbačiauskas 1998).

4. RESULTS AND DISCUSSION

4.1. Start characteristics of ex-ephippial and parthenogenetic neonates

The body length (*BL*) of ex-ephippial hatchlings was significantly related to the length of ephippium (*EL*) (Fig. 1; $BL = 0.634 + 0.110 \times EL$, $r^2 = 0.25$, $F_{1,127} = 41.3$; $P < 0.001$), indicating the correlation between body sizes of mothers and post-diapause neonates, which was also reported earlier (Boersma *et al.* 2000).
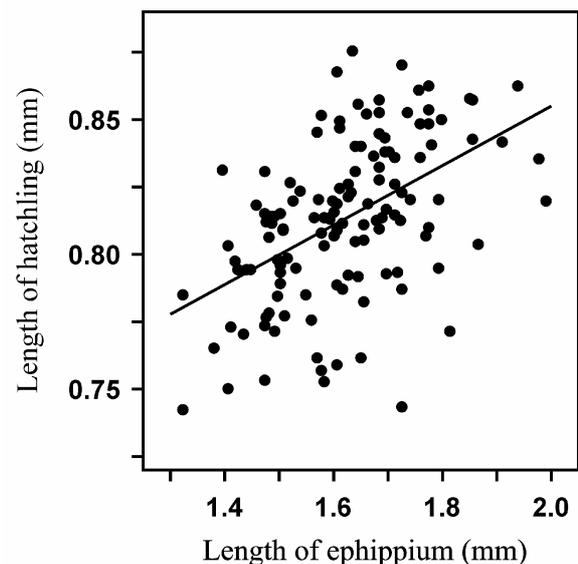

g . Variation of ephippial length and body size of hatchlings in the field population of *D. magna*.

In our study, ephippia which yielded hatchlings varied in size between 1.32 and 1.99 mm. This range in *D. magna* corresponds variation in body length of females approximately between 2.8 and 4.5 mm. Consequently, daphnids of various size and age were contributing to a bank of diapausing eggs. However, diapaus-
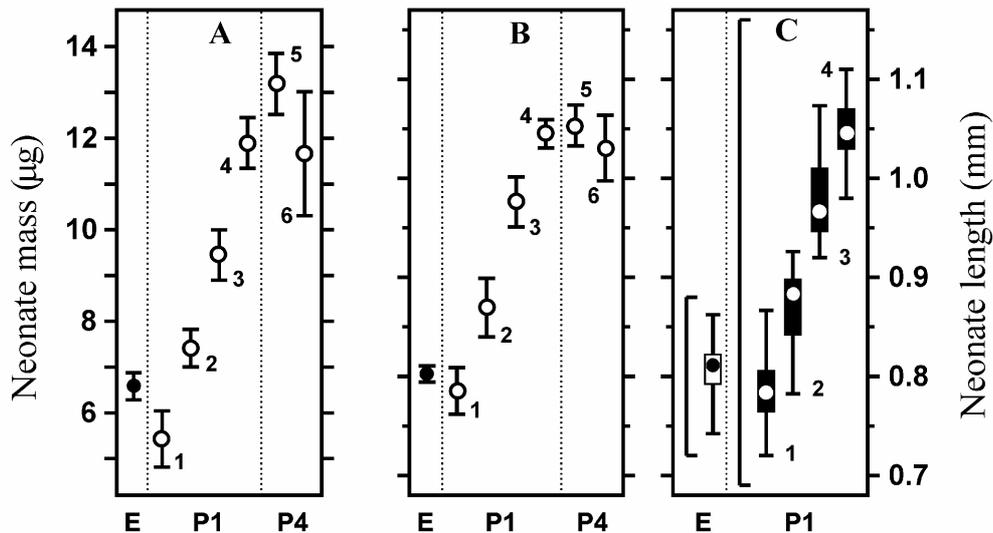
g . Body mass ( ), body length ( ) (mean ±1SD) and Body length variation (, range for individual measurements, and median, quartiles and range across means for individual clutches) in *D. magna* for ex-ephippial hatchlings (E) and parthenogenetic neonates produced in the first (P1) and the fourth (P4) clutch under differing food concentrations. A and B; E: $n = 12$; P1: mothers' origin clutch 1, food 1.5 mg C l^{-1}, $n = 6$ (1); ex-ephippial and clutch 4, 1.5 (2), 0.4 (3) and 0.2 mg C l^{-1} (4), $n = 6$; and P4: ex-ephippial, 1.0 mg C l^{-1}, $n = 9$ (5); clutch 4, 0.2 mg C l^{-1}, $n = 3$ (6). C; variation across individual clutches is estimated for E on $n = 72$, and P1 on n between 21 and 23.

ing eggs produced by differently sized females yielded neonates of relatively close size, while parthenogenetic neonates spanned a much wider range of sizes due to well established maternal effects (Fig. 2). The size of directly developing neonates grows with the increase of clutch number and maternal size, and decrease of food level for mothers (Tessier & Consolatti 1991, Glazier 1992; Gliwicz & Guisande 1992; Ebert 1993; Lampert 1993). Ex-ephippial neonates in *D. magna* were closest in size to first-clutch parthenogenetic neonates produced under high food environment. Ephippia from another field population of *D. magna* yielded hatchlings of close body mass (Arbačiauskas & Lampert 2003). In another study (Boersma *et al.* 2000), ex-ephippial neonates of this species derived from a field sample of ephippia and ephippia obtained by crosses between clones from different populations exhibited the same range of variation in body length under even a larger range of ephippial length. Thus, it seems that post-diapause neonates of *D. magna* in general are close to the first-clutch parthenogenetic neonates from high food environments.

Meanwhile, ex-ephippial hatchlings of *D. pulex* were significantly larger than the first-clutch parthenogenetic neonates and even those from the later clutches produced under high food conditions (Fig. 3). In this species, post-diapause neonates exhibited mean body sizes close to those measured in the later than the first clutches under feeding conditions which can be considered as limiting when compared with high food treatments. In comparison to *D. magna*, variation for body size in ex-ephippial hatchlings of *D. pulex*, when related to parthenogenetic neonates, was substantially larger.

They varied in body size similarly to that measured for directly developing neonates across the clutches produced after the first one (Fig. 3). Thus, *D. magna* and *D. pulex* differed in relative investment per diapausing egg. *D. magna* use to live in more productive environments than *D. pulex*, therefore, established difference may reflect the evolutionary response to species-specific inhabitable environments.

In comparison to directly developing neonates, post-diapause hatchlings differ also in other characteristics. As indicated by measurements for *D. magna*, the mass density per body volume in ex-ephippial neonates is some 23% higher than that in parthenogenetic neonates (Arbačiauskas, unpublished results). Diapausing and subitaneous eggs in *Daphnia* substantially differ biochemically and with respect to enclosed energy reserves (Zaffagnini 1987). Consequently, neonates of differing origin must also differ biochemically. The larger energetic value of diapausing eggs in comparison to directly developing ones has been determined for rotifers (Wurdak *et al.* 1977) and calanoid copepods (Williams-Howze *et al.* 1998). Thus, different biochemical quality of post-diapause and directly developing neonates may be common in various taxa of planktonic animals.

4.2. Physiology: respiration and resistance to starvation

Measurement of respiration in offspring origins of *D. magna* revealed that consistently about 11% elevated respiratory rates are the characteristic of ex-ephippial females (Fig. 4, Arbačiauskas & Lampert 2003).
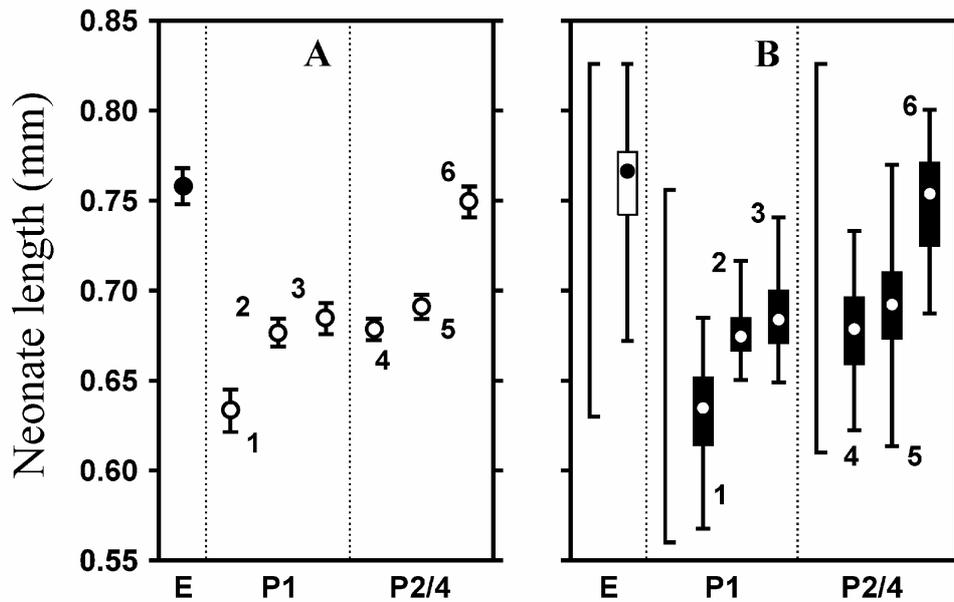
g . Mean body length of individual clutches ( ) (mean ±95%CI) and body length variation (, range for individual measurements, and median, quartiles and range across means for individual clutches) in *D. pulex* for ex-ephippial hatchlings (E, *n* = 42) and parthenogenetic neonates produced in the first clutch (P1) and across clutches 2-4 (P2/4) under differing food conditions. Mothers' origin and food conditions for P1: ex-ephippial, HIGH and POND-HIGH, *n* = 28 (1); parthenogenetic, HIGH and POND-HIGH, *n* = 20 (2), ex-ephippial, POND-LOW, *n* = 25 (3); and P2/4: ex-ephippial and parthenogenetic, HIGH, *n* = 72 (4), and POND-HIGH, *n* = 77 (5); ex-ephippial, POND-LOW, *n* = 49 (6).
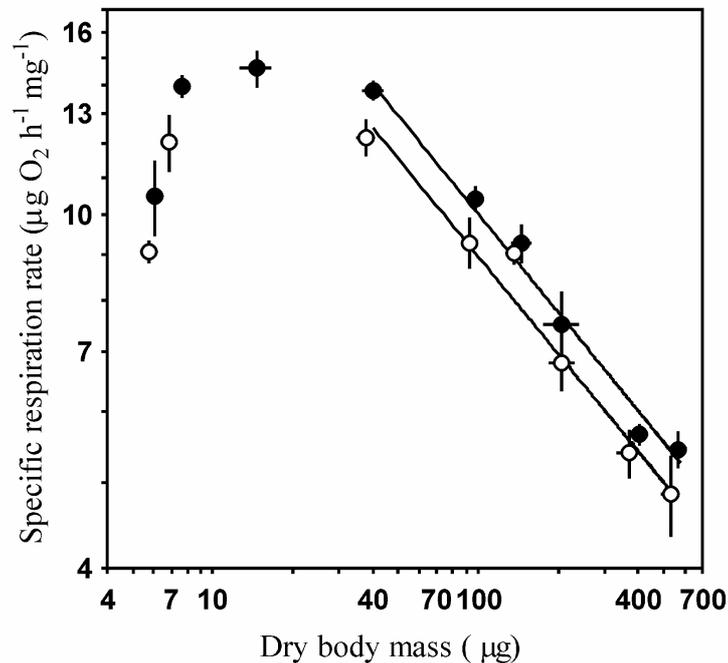
g . Mass-specific respiration rates (mean ±1SD) in differently sized post-diapause (●) and directly developing (○) offspring of *D. magna*. Note logarithmic scale. For neonates included only ex-ephippial hatchlings born into filtered lake water, and ones overnight maintained in 1.0 mg C l⁻¹ food suspension; and parthenogenetic neonates from the first clutch born into filtered water or 1.0 mg C l⁻¹ food suspension (modified from Arbačiauskas & Lampert 2003).

Metabolic activity most probably is the basic physiological trait distinguishing post-diapause and directly developing offspring of *Daphnia*. Higher intensity of metabolism in ex-ephippial individuals must be associated to higher feeding rate and general activity, which can be easily noted when simultaneously observing freely swimming ex-ephippial and parthenogenetic newborns. Higher metabolic activity of post-diapause offspring obviously is adaptive during low water temperatures and abundant food, as is the case in the beginning of the season when daphnids are exiting diapause.

However, elevated metabolism could be detrimental during severe food shortage. When starved, ex-ephippial neonates showed significantly lower survival than parthenogenetic neonates. A 50% survival in post-diapause offspring was even 39% shorter than that in offspring of another origin (5.1 *vs* 7.1 days, respectively) (Arbačiauskas & Lampert 2003). For survival comparison in *D. magna*, the fourth-clutch parthenogenetic neonates were used, thus, they were significantly larger than ex-ephippial hatchlings (Fig. 2). Although the initial size of neonate is important for starvation resistance (Gliwicz & Guisande 1992), it seems that elevated metabolic activity was largerly responsible for lower survival rates in post-diapause neonates. At least clearly detectable heart function in ex-ephippial neonates during the last day of their life in contrast to near absence of that in parthenogenetic neonates suggest the importance of metabolic activity for survival under starvation. The higher metabolic activity of post-diapause offspring probably is common for daphnids, at least those inhabiting temporal waters. Thus, the lower starvation resistance of offspring exiting diapause in comparison to directly developing ones may be expected also in another *Daphnia* species.

4.3. Life-history, allocation and relative fitness

Under rich food environments, juvenile ex-ephippial females grow faster and, consequently, mature at larger body sizes than parthenogenetic females (Arbačiauskas & Gasiūnaitė 1996). When comparing with parthenogenetic neonates of close size, ex-ephippial offspring in *D. pulex* matured with about 10% larger body length (Arbačiauskas 1998). The same difference in body lengths was observed also in *D. magna*, despite in this comparison parthenogenetic offspring initially were twice as heavy. In comparison to parthenogenetic offspring, the faster somatic growth in ex-ephippial offspring, which enabled them to compensate the size difference until maturity, was observed in this species also under limited food concentrations (Arbačiauskas & Lampert 2003). Thus, not body size, but the initial biochemical quality of hatchlings and increased metabolic activity leading to higher feeding rates, which must be beneficial if food is not severely limiting, seems to be primarily important for the fast body size increase in post-diapause females of *Daphnia* during juvenile development.

The basic life-history difference between ex-ephippial and parthenogenetic offspring likely is associated to allocation strategy. Under rich food environments, post-diapause offspring demonstrate significantly larger reproductive effort during early maturity (Fig. 5). In *D. pulex*, reproductive effort for the first clutch was estimated to be at 11-16% greater than that in parthenogenetic females (Arbačiauskas 1998). When food is limiting, difference in early reproductive effort between offspring origins decreased, and was undetectable when comparing population samples (Fig. 5). However, measurements of reproductive investment and body condition in *D. magna* suggest that larger allocation to reproduction in comparison to body, at least body condition, persists in ex-ephippial offspring during early maturity across high and limited, leastwise not severely limiting, food environments (Arbačiauskas, unpublished results).
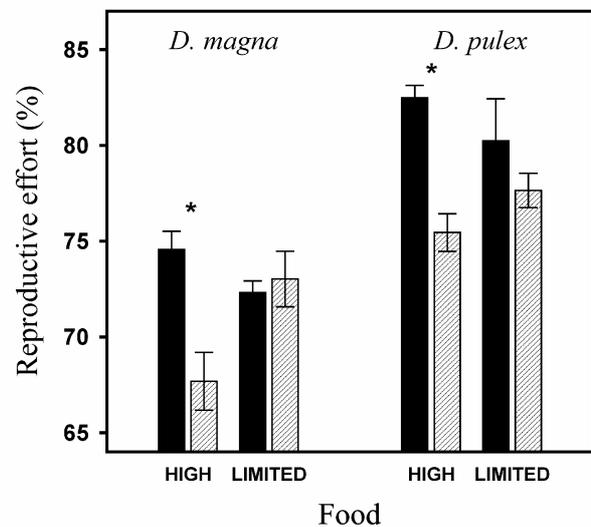

g . Reproductive effort (mean ±1SE) over the first two adult instars in post-diapause (black columns) and directly developing (hatched columns) offspring of *D. magna* and *D. pulex* raised under high and limited food conditions (see Methods). Asterisks denote significant differences between offspring origins (Tukey HSD test: *D. magna*, *P* = 0.015; *D. pulex*, *P* <0.001).

A greater allocation to reproduction results in significantly larger progeny numbers only under rich food concentrations. Ex-ephippial females of *D. pulex* produced a first clutch which on mean was more than twice that of parthenogenetic females (Arbačiauskas 1998). In *D. magna*, that difference comprised 1.6 times, while progeny numbers between offspring origins during early maturity were the same under limited food availabilities (Arbačiauskas & Lampert 2003).

In comparison to parthenogenetic offspring, a shorter time until first clutch release was recorded for females exiting diapause in *D. pulex*, but in contrast, ex-ephippial females in *D. magna* showed a significant

trend for a latter time of first reproduction (Arbači-auskas 1998, unpublished results). Ex-ephippial hatchlings of the later species were substantially smaller in size than parthenogenetic neonates used in experiments (Fig. 2), thus, they may had one additional instar until maturity.

Larger numbers of progeny and shorter time until first reproduction were estimated to result in an increase in relative fitness of post-diapause offspring of *D. pulex* by 20%, while the decrease of food availability significantly stronger suppressed the rate of population increase in this offspring origin as compared to directly developing females (Arbačiauskas 1998). Higher early fecundity despite slightly longer time to reproduction resulted in significantly higher relative fitness of ex-ephippial females under rich food also in *D. magna* (Arbačiauskas & Lampert 2003). In this species, a significant trend for higher rates of population increase was detected in parthenogenetic offspring across limited food concentrations (Arbačiauskas, unpublished results). Thus, post-diapause offspring in *Daphnia* will perform better only under rich food environment. When food is limiting, they show no advantage, and even may be loosing to parthenogenetic offspring.

Across differing nutritional environments, directly developing females of *D. pulex* exhibited the lower than post-diapause offspring variation in reproductive characteristics associated to the first adult instar, consequently lower variability in relative fitness (Arbačiauskas 2001). This pattern can be interpreted as adaptation of parthenogenetic offspring to an unpredictability and lower quality of their environment, in comparison to that for ex-ephippial offspring (Roff 1992; Stearns 1992). Thus, life-history pattern of post-diapause and directly developing offspring in *Daphnia* suggests that offspring origins are adapted to different environments with respect to availability and predictability of food.

4.4. Descendents of ex-ephippial and parthenogenetic females

Ex-ephippial females of *D. pulex* in treatments with high food in the first clutch were constantly producing neonates, which individual size was significantly smaller (6% in body length) than that for the first-clutch neonates from parthenogenetic females (Arbačiauskas 1998). As parental fitness depends upon both, the number of progeny and the individual fitness of progeny in the environment where they will live, and fitness of parthenogenetic offspring is related to initial size, the life-history characteristics of descendents of post-diapause and directly developing females were studied in *D. magna* under high and limited food concentrations. Although small but significant difference in egg characteristics was detected for the first clutch produced under high food, it did not translate into size difference of first-clutch neonates and variation in fitness between offspring from ex-ephippial and parthenogenetic moth-ers. In general, post-diapause females responded in egg size to differing food in common to parthenogenetic females. Consequently, a significant ex-diapause effect on fitness in successive parthenogenetic generations may not be expected in *D. magna* at the population level (Arbačiauskas 2004). However, such effect may be present in *D. pulex* living at rich food environments, and result in some loss of fitness related to offspring quality in post-diapause females compared to parthenogenetic ones, as neonate size in *Daphnia* is positively correlated with fitness (Lampert 1993). The pattern of allocation per offspring in daphnids exiting diapause may differ across species and environments, and this aspect warrants further investigation.

Noteworthy also that post-diapause females in *Daphnia* never produce diapausing eggs in the first brood, while that may be induced in the later clutches. Generally, the propensity to sexual reproduction in post-diapause generation of daphnids may be decreased in comparison to successive parthenogenetic generations, as it has been shown for rotifers (Gilbert 2002) and aphids (Lees 1960). That pattern likely is adaptive in the aspect that reduces sensitivity of post-diapause generation to stochastic environmental fluctuations, and enables population increase and transition to diapause at larger numbers. Under special circumstances, however, the life cycle including production of males by ex-ephippial females and sexual reproduction during the early reestablishment of a population could occur even under favourable feeding conditions, as it has been observed in *D. pulex* inhabiting permanent pond with fish (Arbačiauskas, personal observations).

5. CONCLUSIONS

Our data clearly indicate that the performance of post-diapause and directly developing offspring in *Daphnia* inhabiting temporal waters is consistent with seasonal polyphenism, which predicts threshold traits, distinct life-history pattern and fitness trade-offs across varying environments. Due to negative maternal effect elevated metabolic activity of ex-ephippial offspring probably is the basic threshold trait associated to distinct life-history pattern and relative fitness of offspring origins. Post-diapause and directly developing females demonstrate during early maturity different allocation strategy, which persists at various, at least not severely limiting, food availabilities. However, the greater allocation to progeny in offspring exiting diapause results in increased relative fitness only under rich food conditions. On limited nutrition, when comparing population samples no advantage can be discovered over parthenogenetic offspring, which even may tend to be superior. As suggests starvation resistance, the post-diapause offspring would be at a disadvantage under severe food shortage. It should be also noted that some life-history traits of the post-diapause phenotype, when compared to phenotype of directly developing individuals, may differ

between *Daphnia* species. Such variability could result due to selection under species-specific circumstances.

The cyclic parthenogen *Daphnia* has evolved two alternative seasonal phenotypes matching environmental conditions in which they occur. Different adaptation of post-diapause and directly developing offspring in *Daphnia* imply their occurrence at the matching season, hence, selection must favour the emergence of ex-ephippial offspring in one burst at the beginning of the season (Arbačiauskas & Lampert 2003). The evolution of post-diapause traits and timing of the transition to active state in organisms has been linked (Evans & Cabin 1995). Therefore, when the change of seasonal phenotypes is intermitted by diapause, the proximate factors and processes underlying the activation at the right season are equally or even more important for the evolution and maintenance of narrow sense seasonal polyphenism, as those which trigger the induction of diapause, which is known to be an adaptation to escape also aseasonally occurring harsh conditions (Hairston 1998).

For another animal taxa, the adaptive significance of narrow sense seasonal polyphenism likely is best studied in butterflies. In temperate climate, the seasonal change of wing pattern in butterflies is important for thermoregulation and increases fitness of alternative phenotypes in seasons in which they occur (Brakefield 1996 and references therein). The seasonal polyphenism in butterflies, in common to *Daphnia*, is associated to alteration of metabolic activity which must lead to the enhancement of resource acquisition in certain phenotypes. Hence, in seasonal climate, the alteration of resource acquisition with respect to resource availability, or potential to utilize it, may be a general evolutionary trend for multivoltine organisms resulting in a narrow sense seasonal polyphenism.

ACKNOWLEDGMENTS

REFERENCES

Alekseev, V.R. 1990. *Diapause in crustaceans: Ecological and physiological aspects*. Nauka, Moscow: 144 pp (in Russian).

Alekseev, V.R. & W. Lampert. 2001. Maternal control of resting-egg production in *Daphnia*. *Nature*, 414: 899-901.

Arbačiauskas, K. 1998. Life-history traits of exephippial and parthenogenetically derived daphnids: indicators of different life-history strategies. *Arch. Hydrobiol. Special Issues Advances in Limnology*, 52: 339-358.

Arbačiauskas, K. 2001. Life-history variation related to the first adult instar in daphnids derived from diapausing and subitaneous eggs. *Hydrobiologia*, 442: 157-164.

Arbačiauskas, K. (2004). Life-history characteristics and fitness in descendents of parthenogenetic and ex-ephippio females of *Daphnia magna*. *Hydrobiologia*: in press.

Arbačiauskas, K. & Z.R. Gasiūnaitė. 1996. Growth and fecundity of *Daphnia* after diapause and their impact on the development of a population. *Hydrobiologia*, 320: 209-222.

Arbačiauskas, K. & W. Lampert. 2003. Seasonal adaptation of ex-ephippio and parthenogenetic offspring of *Daphnia magna*: differences in life-history and physiology. *Functional Ecology*, 17: 431-437.

Boersma, M., H. Boriss & S.E. Mitchell. 2000. Maternal effects after sexual reproduction in *Daphnia magna*. *J. Plankton Res.*, 22: 279-285.

Brakefield, P.M. 1996. Seasonal polyphenism in butterflies and natural selection. *Trends in Ecology and Evolution*, 11: 275-277.

Caceres, C.E. 1998. Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology*, 79: 1699-1710.

Carvalho, G.R. & R.N. Hughes. 1983. The effect of food availability, female-density and photoperiod on ephippia production in *Daphnia magna* Straus (Crustacea, Cladocera). *Freshwat. Biol.*, 13: 37-46.

Danks, N.V. 1987. *Insect Dormancy: An Ecological Perspective*. Tyrell Press, Gloucester: 439 pp.

De Meester, L., C. Cousyn & J. Vanoverbeke.1998. Chemical interactions, maternal effects and the hatching of *Daphnia* diapausing eggs. *Arch. Hydrobiol. Special Issues Advances in Limnology*, 52: 253-262.

Dodson, S. I. 1974. Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. *Limnol. Oceanogr.*, 19: 721-729.

Ebert, D. 1993. The trade-off between offspring size and number in *Daphnia magna*: The influence of genetic, environmental and maternal effects. *Arch. Hydrobiol. Suppl.*, 90: 453-473.

Evans, A.S. & R.J. Cabin. 1995. Can dormancy affect the evolution of post-germination traits? The case of *Lesquerella fendleri*. *Ecology*, 76: 344-356.

Fox, C.W. & T.A. Mousseau. 1998. Maternal effects as adaptations for transgenerational phenotypic plasticity in insects. In: T.A. Mousseau & C.W. Fox (Eds), *Maternal effects as adaptations*. Oxford University Press, New York: 159-177.

Gilbert, J. J. 2002. Endogenous regulation of environmentally induced sexuality in a rotifer: a multigenerational parental effect induced by fertilization. *Freshwat. Biol.*, 47: 1633-1641.

Glazier, D.S. 1992. Effects of food, genotype, and maternal size and age on offspring investment in *Daphnia magna*. *Ecology*, 73: 910-926.

Gliwicz, Z. M. & C. Guisande. 1992. Family planning in *Daphnia*: resistance to starvation in offspring born to mothers grown at different food levels. *Oecologia,* 91: 463-467.

Hairston, N.G. Jr. 1998. Time travelers: What's timely in diapause research? *Arch. Hydrobiol. Special Issues Advances in Limnology*, 52: 1-15.

Hairston, N.G. Jr., A.-M. Hansen & W.R. Schaffner. 2000. The effect of diapause emergence on the seasonal dynamics of zooplankton assemblage. *Freshwat. Biol.*, 22: 471-478.

Hairston, N.G. Jr., R.A. van Brunt, C.M. Kearns & D.R. Engstrom. 1995. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology*, 76: 1706-1711.

Jacobs, J. 1987. Cyclomorphosis in *Daphnia*. *Mem. Ist. ital. Idrobiol.*, 45: 325-352.

LaMontagne, J.M. & E. McCauley. 2001. Maternal effects in *Daphnia*: what mothers are telling their offspring and do they listen? *Ecology Letters*, 4: 64-71.

Lampert, W. 1993. Phenotypic plasticity of the size at first reproduction in *Daphnia*: the importance of maternal size. *Ecology*, 74: 1455-1466.

Lees, A.D. 1960. The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Bucton – II. The operation of the "interval timer" in young clones. *J. Insect Physiol.*, 4: 154-175.

Moran, N.A. 1991. Phenotype fixation and genotypic diversity in the complex life cycle of the aphid *Pemphigus betae*. *Evolution*, 45: 957-970.

Moran, N.A. 1992. The evolutionary maintenance of alternative phenotypes. *Am. Nat.*, 139: 971-989.

Roff, D.A.1992. *The evolution of life histories*. Chapman and Hall, New York: 535 pp.

Roff, D.A. 1996. The evolution of threshold traits in animals. *Quarterly Review of Biology*, 71: 3-35.

Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, 24: 35-68.

Shapiro, A.M. 1976. Seasonal polyphenism. *Evolutionary Biology*, 9: 259-333.

Sommer, U., Z.M. Gliwicz, W. Lampert & A. Duncan. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.*, 106: 433-471.

Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford: 249 pp.

Stross, R.G. & R.G. Hill. 1965. Diapause induction in *Daphnia* requires two stimuli. *Science*, 150: 1462-1464.

Tauber, M.J., C.A. Tauber & S. Masaki. 1986. *Seasonal adaptations of insects*. Oxford University Press, New York: 411 pp.

Tessier, A.J. & N. Consolatti. 1991. Resource quantity and offspring quality in *Daphnia*. *Ecology*, 72: 468-478.

Williams-Howze, J., B.E. Taylor, P.M. Biesiot & G. Seaborn. 1998. Lipid analysis of *Aglaodiaptomus stagnalis* Forbes and their desiccation resistant diapausing eggs. *Arch. Hydrobiol. Special Issues Advances in Limnology*, 52: 493-506.

Wolf, H.G. & G.R. Carvalho. 1989. Testing eggs of lake-*Daphnia* II. *In situ* observations on the hatching of eggs and their contribution to population and community structure. *Freshwat. Biol.*, 22: 471-478.

Wurdak, E., J.J. Gilbert & R. Jagels. 1977. Resting egg ultrastructure and formation of the shell in *Asplanchna sieboldi* and *Brachionus calyciflorus*. *Arch. Hydrobiol. Special Issues Advances in Limnology*, 8: 298-302.

Zaffagnini, F. 1987. Reproduction in *Daphnia*. *Mem. Ist. ital. Idrobiol.*, 45: 245-284.