Chapter 9
Seasonal Diphenism in *Daphnia* from Temperate Environments: Organismal Traits and Molecular Regulation

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Abstract In temperate waters, post-diapause and subitaneous offspring in *Daphnia* substantially vary in organismal traits. Post-diapause offspring have elevated metabolic activity. Under rich food, they grow faster, mature at a larger body size and exhibit a greater allocation to progeny resulting in a higher relative fitness. In contrast, subitaneous females are more resistant to starvation and have a higher fitness across limited food concentrations.

These offspring types result from different developmental programs of the same genetic background, representing the phenomenon of phenotypic plasticity. A high-throughput proteomic analysis revealed 176 proteins that were differentially expressed among offspring phenotypes. There were more upregulated proteins with oxyreductase and binding activity in post-diapause offspring, whereas more upregulated proteins with transporter and transferase activity were seen in subitaneous offspring. Over 1.5-fold more of the proteins that were upregulated in post-diapause phenotype are involved in metabolism and biosynthesis. The greatest difference, a fivefold upregulation in post-diapause compared to subitaneous offspring, was recorded for the target of rapamycin-like (TOR) protein. Expression of ribosomal proteins in this offspring phenotype was also increased. These upregulations suggest that the TOR signalling pathway is involved and can be responsible for the regulation of the developmental program underlying post-diapause and subitaneous offspring phenotypes. Gene regulatory patterns observed in post-diapause and subitaneous offspring were in general agreement with observed organismal traits of these *Daphnia* phenotypes.

In temperate waters, *Daphnia* have evolved two alternative seasonal phenotypes matching environmental conditions in which they occur and perform in accordance with predictions of seasonal polyphenism (diphenism in this case). Due to higher metabolic activity, which must lead to increased resource acquisition, post-diapause

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offspring are superior to subitaneous 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.

Keywords Cladocera · Diapause · Metabolism · Allocation · Fitness · Phenotypic plasticity · Proteomic analysis · TOR (target of rapamycin) · Seasonal polyphenism

9.1 Introduction

Diapause is an adaptation enabling many organisms by programmed arrest of development to survive seasonally or at least in short-term predictable adverse conditions (Hairston Jr. 1998). Advantage of the diapause is tightly associated not only with its timely induction but also with the proper time of diapause termination. These processes are governed by environmental cues usually adjusted by internal control (Tauber et al. 1986; Alekseev 1990; Fox and Mousseau 1998). Obviously, diapause termination should happen in a favourable environment, at least in an environment sufficient for living.

In univoltine organisms, the termination of the diapause within a season as soon as environment become suitable for living seems to be advantageous, whilst in multivoltine organisms, a few emergence strategies are possible. If the environment varies unpredictably, the most adaptive emergence strategy may be to disperse the recruitment over the season in pursuit of spreading the risk of occurring in hostile conditions. If the environment can be predicted as favourable, the synchronization of recruitment might be most adaptive. The predictability of environment during activation further implies that selection can favour specific post-diapause traits which increase recruit fitness in a prospective environment. Therefore, a disparity between post-diapause and subitaneous (immediately/directly developing) offspring can evolve, if they use to inhabit varying environmental conditions.

In this chapter, we analyse seasonal phenotypes of *Daphnia* inhabiting temperate waters. We collate organismal traits of post-diapause and subitaneous offspring phenotypes, provide data on probable molecular regulation of this diphenism and qualify this seasonal phenomenon.

9.2 *Daphnia* Life Cycle

In temperate waters, the cyclic parthenogen *Daphnia* propagates mostly by parthenogenesis, producing subitaneous eggs. With deterioration of environmental conditions, which can be predicted from environmental cues, these animals initiate sexual reproduction and produce diapausing eggs encased in an ephippium (Stross and Hill

1965; Carvalho and Hughes 1983; Pijanowska and Stolpe 1996; Slusarczyk 2001; Koch et al. 2009; Deng et al. 2010), although the timing and magnitude of investment into a dormant stage depend upon local conditions (Walsh 2013). Daphnids as all other cladocerans possess an embryonic diapause. Diapausing eggs start to hatch in the next season but, being resistant to external factors, can remain viable for extended periods, forming a sediment egg bank that facilitates temporal population persistence (Hairston Jr. et al. 1995; De Stasio 2007).

A mass emergence from diapausing eggs in *Daphnia* in temperate lakes and ponds almost exclusively takes place in the early season over a relatively short time (Wolf and Carvalho 1989; Caceres 1998; Hairston Jr. et al. 2000; Gyllström 2004; Rother et al. 2010; Perez-Martınez et al. 2013), although hatching also may happen years later during any seasons and in a strongly altered environment (Frisch et al. 2014). In temperate waters, as suggested by the Plankton Ecology Group (PEG) model, early seasons with abundant nutrients and increasing sunlight and temperature result in massive development of algae suitable for *Daphnia* nutrition – the spring algal bloom (Sommer et al. 1986). Investigations of cues inducing diapause termination suggest temperature is the dominant cue for emergence (reviewed in Gyllström and Hansson 2004), reducing the probability of a mismatch between daphnids exiting diapause and their algal food (Rother et al. 2010). Hence, the majority of post-diapause *Daphnia* offspring hatch into a predictable high-food environment, whereas during the season their subitaneous descendants encounter environments with greatly variable conditions in terms of food quality and availability. These features of living conditions must affect traits of post-diapause and subitaneous offspring in *Daphnia* inhabiting temperate seasonal environments.

9.3 Organismal Traits of Post-diapause and Subitaneous Offspring

Post-diapause offspring hatch from bisexually produced diapausing eggs (although diapausing eggs also can be produced parthenogenetically) in which development is arrested at early embryogenesis and resumes after hatching cues are received, whilst subitaneous offspring hatch from parthenogenetically produced eggs. The two egg types substantially vary in morphology and histology (Zaffagnini 1987). They also differ in biochemical composition and fatty acid profiles (Arbačiauskas 2007, unpublished data). When comparing neonates of differing origin, post-diapause offspring have higher carbon content, which is consistent with the higher content of triglyceride lipids. They also contain larger amounts of nitrogen indicating higher protein levels. Thus, post-diapause and subitaneous offspring clearly vary in their quality and enclosed substances and energetic resources.

The main disparity between offspring origins, however, is associated with their metabolism. The comparison of respiration showed that post-diapause females had respiratory rates about ~11% higher than those of subitaneous females (Fig. 9.1;

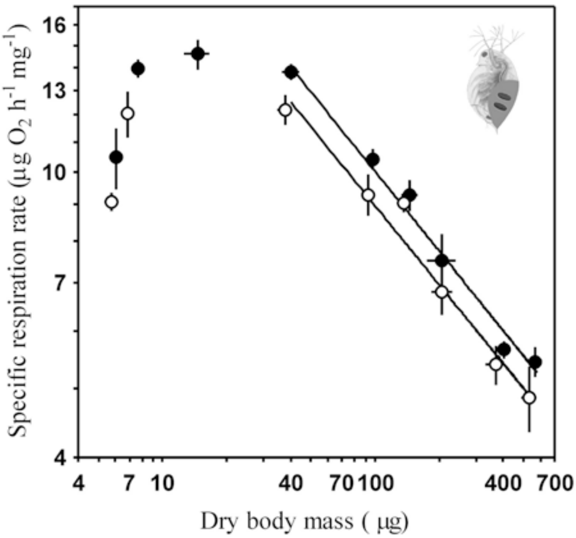

Fig. 9.1 Mass-specific respiration rates (mean ±1SD) in differently sized post-diapause (closed circles) and subitaneous (open circles) offspring of *Daphnia magna*. Note logarithmic scale. (Modified from Arbačiauskas and Lampert 2003)

Arbačiauskas and Lampert 2003). It seems that the metabolic activity is the basic organismal trait distinguishing post-diapause and subitaneous *Daphnia* offspring and affecting their life histories. Higher activity of metabolism in post-diapause females must be related to higher feeding rate, and obviously is adaptive during low water temperatures and abundant food, as is the case in the beginning of the season when hatching from diapausing eggs occurs.

Elevated metabolism, however, can be disadvantageous during severe food shortage. When subjected to starvation, post-diapause neonates as well as adult females exhibit lower survival than subitaneous individuals (Arbačiauskas and Lampert 2003; Arbačiauskas unpublished data).

Under high food concentrations, juvenile post-diapause females grow faster and, consequently, mature at larger body sizes than subitaneous females (Arbačiauskas and Gasiūnaitė 1996; Arbačiauskas 1998). The faster somatic growth of post-diapause offspring, which enabled them to compensate until maturity about twofold smaller initial body size, was observed in *Daphnia magna* also under limited food quantities (Arbačiauskas and Lampert 2003). Thus, when food is not severely limiting, the higher metabolic activity and initial biochemical quality of neonates must be responsible for the fast somatic growth in post-diapause females during juvenile development.

After maturation, at least during early maturity, the somatic growth of post-diapause females under rich food is slower than that in subitaneous females (Arbačiauskas 1998). This pattern is due to the different resource allocation strategy. Under abundant food environments, post-diapause females possess significantly higher reproductive effort during early maturity. When food is limiting, differences in early reproductive effort between offspring origins decrease, and were undetectable when comparing population samples (Arbačiauskas 1998, 2004b).

A greater allocation into reproduction results in increased progeny numbers only under abundant food concentrations. Post-diapause *Daphnia* females produced a first clutch which was from 1.6-fold to more than twice that of subitaneous females (Arbačiauskas 1998; Arbačiauskas and Lampert 2003). Progeny numbers in offspring origins during early maturity were close under limited food availabilities.

The relative fitness of post-diapause offspring in *D. pulex* under rich food was estimated to be ~20% higher than that for subitaneous offspring (Arbačiauskas 1998). The larger early fecundity at high food concentrations resulted in higher fitness of post-diapause females also in *D. magna*; however, a trend for a higher fitness in subitaneous offspring was measured over reduced food concentrations (Arbačiauskas and Lampert 2003). Obtained data clearly suggest that post-diapause offspring in *Daphnia* are superior to subitaneous offspring only under rich food environments, whereas subitaneous offspring perform better when food is limiting.

It seems also that across differing food environments, subitaneous females exhibit a lower than post-diapause female variation in reproductive characteristics, consequently, lower variability of relative fitness in response to feeding conditions (Arbačiauskas 2001). This pattern may be interpreted as an adaptation of subitaneous offspring to unpredictability and lower quality of their environment, i.e. bet-hedging strategy (see Roff 1992).

It is noteworthy that specific post-diapause organismal traits generally are not transferred to the successive subitaneous generations, at least they were not seen when comparing population samples (Arbačiauskas 2004a). The propensity to sexual reproduction of *Daphnia* in post-diapause generation may be reduced in comparison with successive subitaneous generations, as has been detected for rotifers (Gilbert 2002) and aphids (Lees 1960).

9.4 Molecular Regulation of Development of Offspring Phenotypes

Post-diapause and subitaneous offspring types in the same clone must result from different developmental programs of the same genetic background, representing the phenomenon of phenotypic plasticity. To explore the molecular mechanism of this phenotypic plasticity in *D. pulex*, a high-throughput proteomic analysis and expression analysis of several genes were applied. The study revealed 176 proteins that were differentially expressed among offspring phenotypes; 89 proteins were overexpressed in post-diapause offspring and 87 proteins were upregulated in subitaneous offspring (Kaupinis et al. 2017). There were more upregulated proteins with oxyreductase and binding activity in post-diapause offspring, whereas more upregulated proteins with transporter and transferase activity were seen in subitaneous offspring. In comparison with subitaneous phenotype, over 1.5-fold more of the proteins that were upregulated in post-diapause phenotype are involved in metabolism and biosynthesis (Fig. 9.2). Expression levels of several selected genes linked

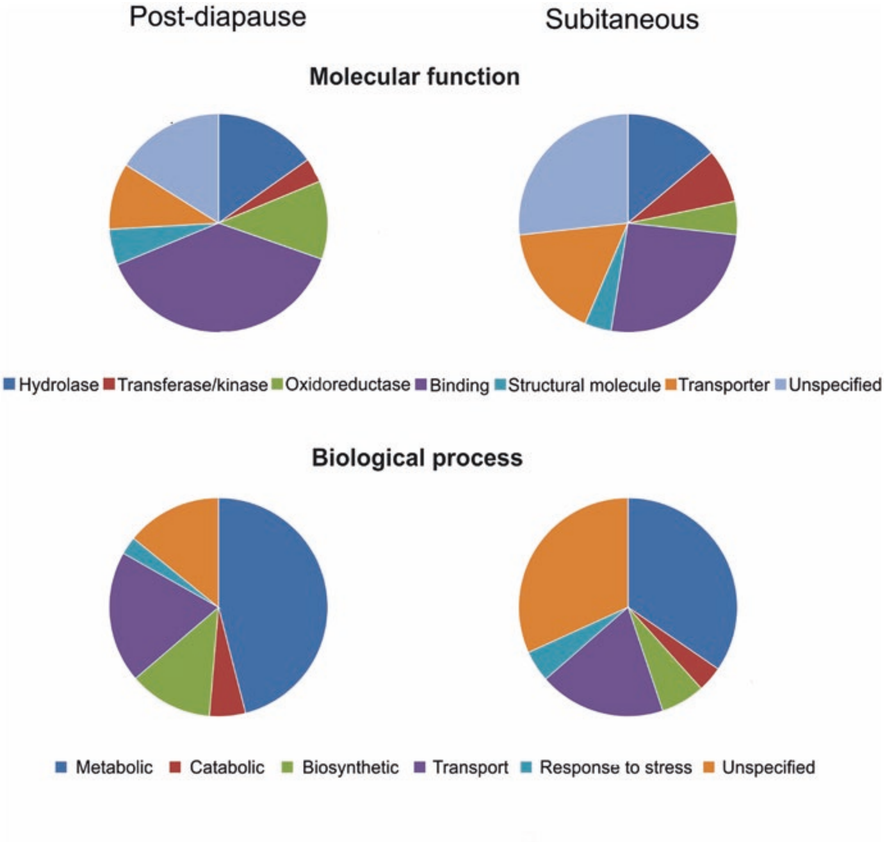

Fig. 9.2 Ontology analysis of upregulated proteins in post-diapause and subitaneous offspring of *Daphnia pulex*. Classification was performed according to the gene ontology terms 'Molecular function' and 'Biological process'. (Modified, for more details see Kaupinis et al. 2017)

to cellular metabolism were also higher in post-diapause females. This pattern perfectly corresponds to previously established higher metabolic rates and faster somatic growth (under rich food) in daphnids exiting diapause. Proteomic data also generally support the previously presumed higher resistance to stress in subitaneous offspring. There were six upregulated proteins related to response to stress, in contrast with only three such proteins upregulated in post-diapause offspring (for details, see Kaupinis et al. 2017).

The greatest difference, a fivefold upregulation in post-diapause compared to subitaneous offspring, was recorded for the target of rapamycin-like (TOR) protein. This nutrient- and energy-sensing kinase is the central component of the conserved eukaryotic signalling pathway that regulates cell and organismal growth (Oldham and Hafen 2003). The TOR signalling pathway is important in the regulation of energy homoeostasis and the control of intracellular metabolic processes in mammals (Andre and Cota 2012); it regulates the synthesis of ribosomal components including transcription and processing of pre-rRNA, expression of ribosomal proteins and synthesis of 5S rRNA (Mayer and Grummt 2006). In association with higher TOR levels, there was a 1.7–1.9-fold overexpression of five ribosomal proteins (Fig. 9.3; Kaupinis et al. 2017). These upregulations of the TOR and ribosomal proteins strongly suggest that the TOR signalling pathway is involved in and can be responsible for the formation of post-diapause and subitaneous phenotypes in *Daphnia*.

The TOR pathway has been reported as having key importance in the regulation of diphenic caste development (queen and worker formation) in the honey bee (Patel et al. 2007), although insulin/insulin-like signalling is considered also to be involved in caste determination (Wolschin et al. 2011; Mutti et al. 2011). TOR-dependent caste determination in the honey bee is conditioned by a rich rather than moderate larval diet (Patel et al. 2007), whilst the involvement of food quality in determining offspring phenotype in *Daphnia* is unlikely, as the phenotype seems to depend upon the egg type from which it originates. Sexually produced diapausing eggs and parthenogenetically produced subitaneous eggs vary substantially in *Daphnia* with respect to biochemical composition. Thus, these eggs types should contain an internal factor switching between developmental programs resulting in post-diapause or subitaneous offspring phenotype.

The highest upregulation (fourfold) in subitaneous offspring was recorded for sideroflexin (Fig. 9.3). This mitochondrial transmembrane protein has been reported to be responsible for skeletal abnormalities and the haematological phenotype of flexed-tail mice and is suggested to be a transporter important in mitochondrial iron metabolism; it may not necessarily transport iron but could mediate the uptake of other metabolites essential for heme synthesis (Fleming et al. 2001). Thus, sideroflexin may be linked to haemoglobins, which also were overexpressed in subitaneous females. Recently, it has been shown that sideroflexin family genes can be important in embryonic development in the clawed frog *Xenopus laevis* (Li et al. 2010). The specific role of upregulation of sideroflexin and haemoglobins in subitaneous *Daphnia* offspring needs further investigation. Haemoglobins are directly related to metabolism via oxygen delivery, and induction of haemoglobins is known to be a response to hypoxia (Zeis et al. 2009; Gerke et al. 2011).

The proteomic study revealed 47 proteins which exhibited at least a 1.5-fold difference (Fig. 9.3). The functions of some of these proteins remain unknown and the roles of many others in relation to fitness traits are not well understood. However, the revealed protein patterns support our findings that metabolic and somatic growth rates are higher in post-diapause offspring, whereas subitaneous offspring are more resistant to stress thus better adapted to unpredictable environments. The most important result, however, is the finding of upregulation of TOR and ribosomal proteins in the post-diapause offspring phenotype, suggesting that the TOR signalling pathway is involved and presumably responsible for the regulation of phenotypic plasticity underlying the determination of post-diapause and subitaneous phenotypes in *Daphnia*.

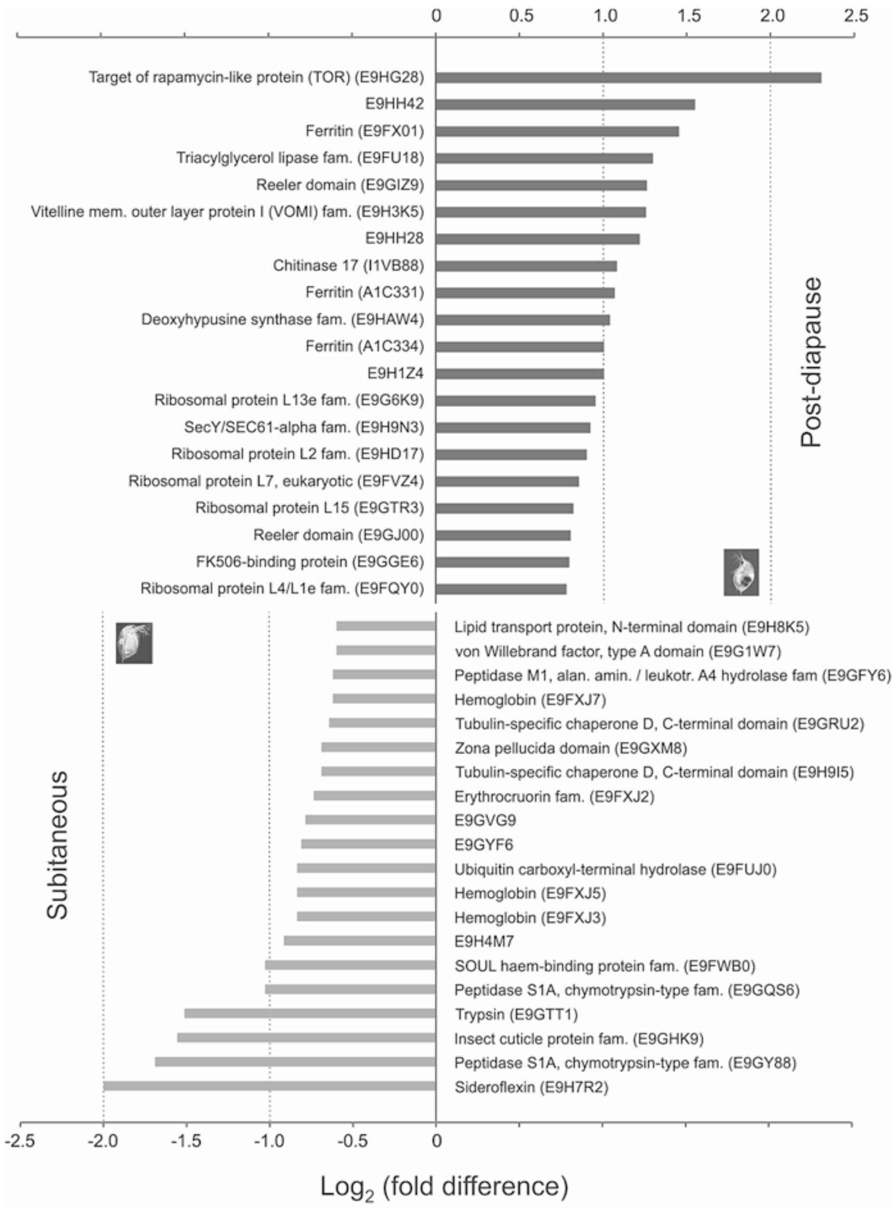

Fig. 9.3 Fold difference (Log_2-transformed) in protein levels between post-diapause and subitaneous offspring of *Daphnia pulex*. Positive values indicate a higher level in the post-diapause phenotype and negative values indicate the opposite. Shown are 20 proteins with largest difference for each phenotype. Protein names (family membership/description) and accession numbers are from the UniProt (Universal Protein Resource database, http://www.uniprot.org/uniprot). (Modified, for more details see Kaupinis et al. 2017)

9.5 Conclusions

Life-history patterns substantially differ between post-diapause and subitaneous offspring in *Daphnia*. Differential gene expression resulting in elevated metabolic activity of post-diapause offspring are primarily responsible for distinction in organismal traits and life-history strategy between offspring phenotypes. During early maturity, post-diapause and subitaneous females possess different resource allocation strategy. The greater allocation to progeny in post-diapause offspring, however, results in increased relative fitness only under rich food environments. On limited nutrition, no advantage over subitaneous females was seen, which even may be superior.

Post-diapause and subitaneous offspring in *Daphnia* are adapted to different environments. Post-diapause offspring are adapted to a favourable environment without food limitation, which is expected during early season when emergence from diapause is observed, whilst subitaneous offspring are adapted to unpredictable and variable food conditions, which are expected later in the season (Arbačiauskas 1998, 2001). This pattern, in turn, implies that selection should favour the synchronous hatching of diapausing eggs in the beginning of the season when the spring algal bloom is to be expected (Arbačiauskas and Lampert 2003).

In temperate environments, the cyclic parthenogen *Daphnia* has evolved two alternative phenotypes matching environmental conditions in which they occur. This seasonal performance of *Daphnia* is consistent with the phenomenon of seasonal polyphenism (specifically diphenism in *Daphnia* case), which predicts the presence of threshold traits affecting life-history patterns and fitness trade-offs across varying environments. The elevated metabolic activity of post-diapause offspring is the threshold trait which determines disparity between offspring phenotypes (see Arbačiauskas 2004b). The transgenerational effect responsible for different quality and, consequently, different life-history patterns of post-diapause offspring in comparison with their mothers has received a definition of a negative maternal effect, which is to be expected when environment for progeny is predictable in long-term, but irrespective of parental environment (see Fox and Mousseau 1998).

Among another animal taxa, the adaptive significance of seasonal polyphenism probably is best examined in butterflies. The seasonal change of wing patterns in butterflies is important for thermoregulation under temperate climate and increases fitness of alternative phenotypes in seasons in which they occur (Brakefield 1996 and references therein). In common with *Daphnia*, seasonal polyphenism of butterflies is associated with metabolic activity, which should condition the enhancement of resource acquisition. The adjustment of resource acquisition with respect to resource availability might be a common evolutionary trend resulting in seasonal polyphenism of multivoltine organisms inhabiting seasonal environments.

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