

Facing Adversity: Dormant Embryos in Rotifers

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Abstract. An in-depth look at the basic aspects of dormancy in cyclic parthenogenetic organisms is now possible thanks to research efforts conducted over the past two decades with rotifer dormant embryos. In this review, we assemble and compose the current knowledge on four central themes: (1) distribution of dormancy in animals, with an overview on the phylogenetic distribution of embryo dormancy in metazoans, and (2) physiological and cellular processes involved in dormancy, with a strong emphasis on the dormant embryos of cyclically parthenogenetic monogonont rotifers; and discussions of (3) the selective pressures and (4) the evolutionary and population implications of dormancy in these animals. Dormancy in metazoans is a widespread phenomenon with taxon-specific features, and rotifers are among the animals in which dormancy is an intrinsic feature of their life cycle. Our review shows that embryo dormancy in rotifers shares common functional pathways with other taxa at the molecular and cellular level, despite the independent evolution of dormancy across phyla. These pathways include the arrest of similar metabolic routes and the usage of common metabolites for the stabilization of cellular structures and to confer stress resistance. We conclude that specific features of recurrent harsh environmental conditions are a powerful selective pressure for the fine-tuning of

dormancy patterns in rotifers. We hypothesize that similar mechanisms at the organism level will lead to similar adaptive consequences at the population level across taxa, among which the formation of egg banks, the coexistence of species, and the possibility of differentiation among populations and local adaptation stand out. Our review shows how studies of rotifers have contributed to improved knowledge of all of these aspects.

Introduction

Dormancy is a state of reduced metabolic activity adopted by many organisms to overcome conditions of environmental stress. It is a widespread adaptation that may imply a temporary suspension of cell division in the case of single-celled organisms such as bacteria (van Vliet, 2015), algae, and protists (Corliss and Esser, 1974; Rengefors *et al.*, 1998). It may also imply the suppression of the cell cycle, growth, development, and/or reproduction at a given life-history stage in multicellular organisms such as plants or metazoans (Keilin, 1959; Alekseev *et al.*, 2007; Hairston and Fox, 2009). The most obvious benefit of dormancy is that it provides safety under both biotic and abiotic stressful conditions while just maintaining basal metabolism to ensure survival (Gremer and Sala, 2013). The expected net benefit of this strategy may explain why dormancy is a widespread trait. Additionally, other effects associated with dormancy should not be overlooked, such as the potential for dispersal and habitat colonization (*e.g.*, Jenkins and Buikema, 1998) or the long-term survival of spores, akinetes, plant seeds, invertebrate cysts, and resting eggs, which serve as “time capsules” and revive in future times (Lubzens *et al.*, 2010). These effects may have important ecological applications (*e.g.*, paleoreconstruction, ecosystem restoration, *etc.*, Weider *et al.*, 2018).

Animal dormancy may occur at any life developmental stage: egg, embryo, larvae, or adult. Developmental arrest at embryonic developmental stages is well known in aquatic

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Abbreviations: 5-HT, serotonin; Akt, protein kinase B; AQP, aquaporins; ATP, adenosine triphosphate; CoA, coenzyme A; COI, cytochrome oxidase c subunit I; E2, estradiol; FoxO, forkhead transcription factor; GABA, γ -aminobutyric acid; GH, growth hormone; hCG, human chorionic gonadotropin; HSF, heat shock transcription factor; HSP, heat shock protein; IDP, intrinsically disordered protein; JH, juvenile hormone; LEA, late embryogenesis abundant proteins; MIP, miosis-inducing protein; NADPH, reduced nicotinamide adenine dinucleotide phosphate; PPP, pentose phosphate pathway; RNAi, RNA interference; ROS, reactive oxygen species; sHSP, small molecular weight heat shock protein; T3, triiodothyronine.

invertebrates, such as rotifers (e.g., *Brachionus* species), Cladocera (e.g., *Daphnia* species), the brine shrimp *Artemia* and copepods (for review, see Alekseev *et al.*, 2007), and insects (Denlinger *et al.*, 2012); and vertebrates, such as fishes (Podrabsky and Hand, 2015) and mammals (Lopes *et al.*, 2004; Ptak *et al.*, 2012; Fenelon *et al.*, 2014; Fu *et al.*, 2014). In short-lived organisms, developmental arrest is typically initiated in a single developmental stage (Vinogradova, 2007). In rotifers, dormancy occurs by two strategies: (1) quiescence, a form of dormancy that is controlled exogenously and induced directly by the occurrence of adverse conditions that may occur at any life stage, as in bdelloid rotifers; or (2) diapause, a form of dormancy that is controlled by an internal mechanism and is initiated in response to an environmental cue, as in monogonont rotifers. Monogononts possess a whole series of biological and ecological features that have recently turned them into remarkable model organisms (Declerck and Papakostas, 2017) and that have led to important contributions in dormancy research (e.g., Denekamp *et al.*, 2009, 2010a, 2011; Franch-Gras *et al.*, 2017; Tarazona *et al.*, 2017). Functional information based on -omics approaches is also now available for rotifers (Clark *et al.*, 2012; Ziv *et al.*, 2017; Franch-Gras *et al.*, 2018; Kim *et al.*, 2018; Rozema *et al.*, 2019).

One of the outstanding features of monogonont rotifers in relation to dormancy is their life cycle. It is designated as cyclical parthenogenesis and implies asexual and sexual reproduction (e.g., Serra *et al.*, 2018). With slight variations, this cycle is found in at least 15,000 animal species (Hebert, 1987), particularly including rotifers, aphids, and cladocerans. Dormancy patterns and their association with life cycle in monogonont rotifers have been previously reviewed (Gilbert, 1974; Pourriot and Snell, 1983; Ricci, 2001; Schröder, 2005). In the case of a typical monogonont rotifer life cycle (Fig. 1), several generations of asexual reproduction are followed by one generation of sexual reproduction, which produces the dormant embryos, popularly known as resting or diapausing eggs. Cyclically parthenogenetic rotifers are typically temporary in the plankton and periodically recolonize (e.g., annually) the water column through the hatching of dormant embryos accumulated in pond and lake sediments. The hatchlings are asexual females that produce diploid, subitaneous eggs (known as amictic eggs) that develop directly into diploid asexual females by ameiotic parthenogenesis, which entails a phase of clonal proliferation. The females laying these eggs, which actually contain diploid embryos, are known as asexual or amictic females. As a response to species-specific environmental cues (see next paragraph), the sexual phase begins with the parthenogenetic production of sexual daughters by asexual mothers. During sexual reproduction, asexual proliferation does not stop, because parthenogenetic females produce both sexual and asexual daughters. Sexual females (known as mictic females) are morphologically indistinguishable from asexual females but produce meiotic haploid oocytes. If these oocytes are not fertilized, they will be extruded as eggs from the sexual females and will develop

into haploid males. If a male inseminates a young sexual female carrying haploid oocytes, fertilization can take place; and oocytes develop into diploid embryos, which enter dormancy and stop their development. While dormant, these embryos can survive adverse conditions. They can enable rotifer populations to recolonize the water column when suitable conditions resume at the site and can also disperse to other habitats.

The transition from asexual to sexual reproduction occurs in rotifer females during oogenesis (Gilbert, 2007) and depends on species-specific environmental cues such as long photoperiod (Pourriot and Clément, 1975), dietary tocopherol (Gilbert, 1980), and high population density (Gilbert, 2004). Of these, population density is the most common cue for sexual reproduction induction in the widely studied genus *Brachionus*. In *Brachionus plicatilis* Müller, 1786, sexual reproduction is triggered by a water-soluble protein called mixis-inducing protein (MIP), which is produced and released by the rotifers themselves and which accumulates in the environment as population density increases (Snell *et al.*, 2006). The induction of sexual reproduction in this rotifer fits with a quorum-sensing mechanism whereby the accumulation of MIP enables a single female to sense and respond to the density of females in the population (Kubanek and Snell, 2008). It is hypothesized that the observed link between population density and sexual reproduction increases the probability of male and female mating and so assures the production of dormant embryos, although alternative explanations exist (discussed in Serra *et al.*, 2004). Besides population density, other environmental factors, such as light wavelength, salinity, temperature, feeding history, and maternal factors, have been found to modulate the onset and level of sexual reproduction in *B. plicatilis* (Hagiwara *et al.*, 1988; Denekamp *et al.*, 2010b; Kim and Hagiwara, 2011; Kim *et al.*, 2013, 2018). Within-species genetic differences in the predisposition of sexual reproduction have been found (Aparici *et al.*, 2001; Schröder *et al.*, 2007; Carmona *et al.*, 2009; Franch-Gras *et al.*, 2017); and, furthermore, even single clones, as a result of the intraclonal production of dormant embryos, have been reported to show genetic variation in this trait (Hagiwara and Hino, 1989; Lubzens, 1989). Also at the intraclonal level, low or no response to the environmental cues has been described in the first generations after leaving dormancy (Gilbert, 2002; Schröder and Gilbert, 2004).

An in-depth look at the basic aspects of dormancy in cyclical parthenogenetic organisms is now possible as a result of research efforts using rotifers that were carried out in the past two decades. Research oriented to rotifer ecology has covered a variety of topics, such as the induction and timing of sexual reproduction for the production of dormant embryos (Snell *et al.*, 2006; Kubanek and Snell, 2008), patterns of abundance and viability in natural egg banks (García-Roger *et al.*, 2006a, b, c), or the factors controlling hatching (Gilbert and Schröder, 2004; Gilbert, 2017). Rooted in this research, progress has been made in the study of the molecular and physiological basis of dormancy—including the identification of genes, proteins,

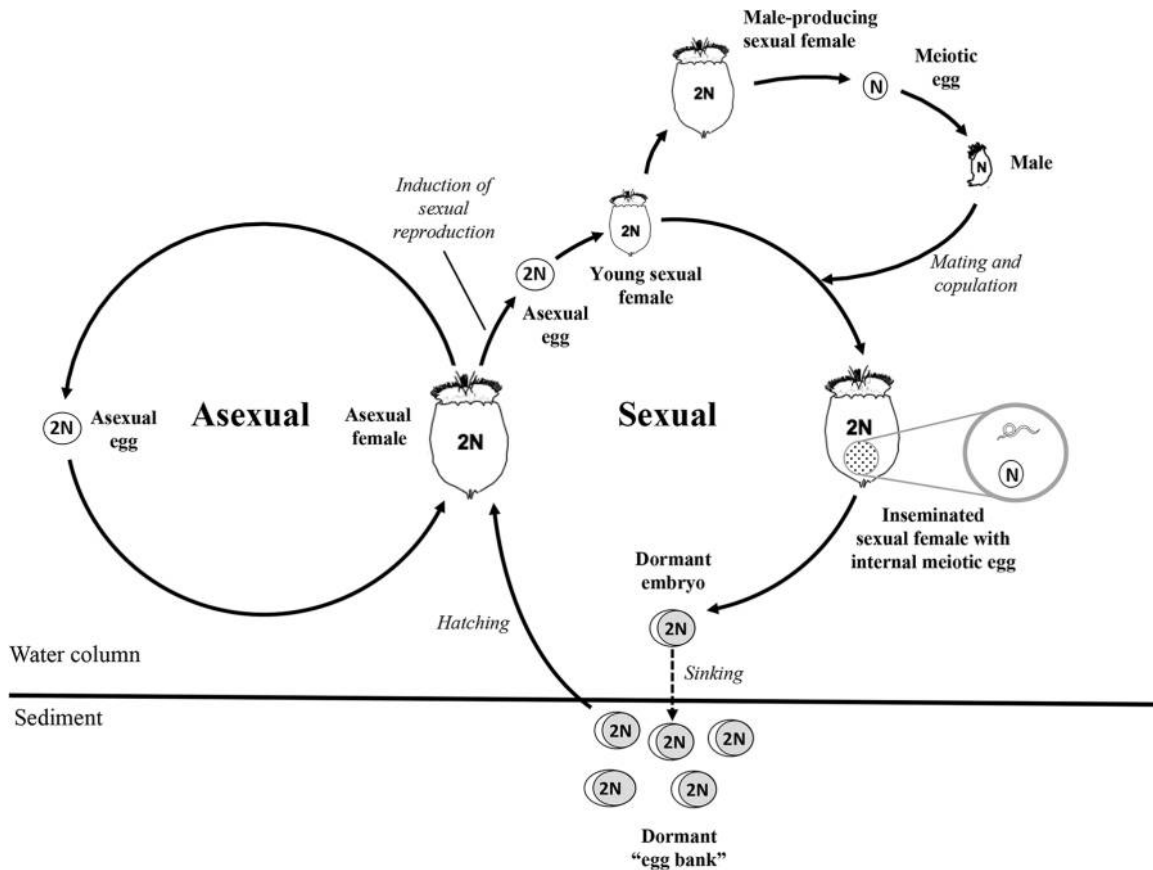


Figure 1. Typical cyclical parthenogenesis life cycle of monogonont rotifers, showing asexual and sexual reproduction and formation of dormant embryos. In the asexual phase, diploid asexual females parthenogenetically produce diploid asexual eggs that develop into genetically identical daughters. The sexual phase is induced by environmental factors and starts with the parthenogenetic production of sexual daughters by asexual mothers as a fraction of their offspring. Sexual females produce meiotic haploid eggs that develop into either haploid males or, if fertilized, diploid dormant embryos. These embryos may sink to the sediments and accumulate, thus forming dormant “egg banks,” while surviving adverse conditions. After receiving appropriate environmental stimuli, a fraction of the dormant embryos hatches into asexual females; and the cycle is restarted. N indicates haploid eggs or individuals; 2N indicates diploids. (Redrawn from original artwork courtesy of África Gómez and María J. Carmona.)

and metabolites with an association with dormancy (Denekamp *et al.*, 2009; Clark *et al.*, 2012; Ziv *et al.*, 2017; Rozema *et al.*, 2019)—and in the adaptive significance of dormancy, especially in the potential strategies involved in coping with environmental uncertainty (Franch-Gras *et al.*, 2017; Tarazona *et al.*, 2017). Progress in both research areas has also benefited from the development of high-throughput sequencing and novel molecular tools applied to rotifer research (Denekamp *et al.*, 2011; Franch-Gras *et al.*, 2018). Placing in context all of these new findings, but also identifying gaps of knowledge and topics that merit special attention, warrants a review.

Our review will assemble the current knowledge on four central themes: (1) distribution of dormancy in animals, with an overview on the phylogenetic distribution of embryo dormancy in metazoans; (2) physiological and cellular processes involved in embryo dormancy, with emphasis on cyclically parthenogenetic rotifers; (3) a discussion of the selective pres-

ures for dormancy in these animals; and (4) the evolutionary and population implications of dormancy. An attempt was made to compare dormancy in monogonont rotifers, using the available knowledge of other organisms, including their sister clade of bdelloid rotifers (Sørensen and Giribet, 2006).

Distribution of Dormancy in Animals

We provide here a brief assessment of the distribution of dormancy capabilities across all Metazoa, in order to place the characteristics of rotifers in context. For each phylum, we gathered data on the presence and/or absence of dormancy in any form and whether dormancy occurs as diapause at a specific developmental stage (*e.g.*, resting egg, dormant embryo, *etc.*) or as quiescence at any life stage (including desiccation, encystation, estivation, coiling, xerosome formation, *etc.*). We started by directly asking for information from two or three experts

on each phylum, and then we confirmed it by searching the primary literature. We searched for the occurrence of dormancy in oceanic habitats (proper marine and brackish habitats connected to the sea) and continental habitats (terrestrial, freshwater, and inland saline), providing examples of species that can enter dormancy in both habitats (Fig. 2). The estimate of the total number of species in each phylum was obtained from Zhang (2013). In order to find experts from all phyla, we consulted the board of experts of online biodiversity databases, such as the World Register of Marine Species (WoRMS; WoRMS Editorial Board, 2019) and Fauna Europaea (de Jong *et al.*, 2014). As a result, out of the 35 extant phyla listed in the most updated overview of animal diversity (Giribet and Edgecombe, 2020), at least 19 phyla have evidence of some form of dormancy. Dormancy occurs more often in continental than in oceanic habitats: out of the 17 phyla with continental representatives, all but 1 (Nematomorpha) are capable of dormancy, whereas only 12 out of the 33 phyla with oceanic representatives are capable of dormancy (Fig. 2). The potentiality for dormancy in Metazoa is high, and the variability in the mechanisms is wide: rotifers are not alone. Our review will focus on the dormant embryos of cyclically parthenogenetic monogonont rotifers, mostly with comparisons to dormancy in other organisms that live in the same habitats as monogononts, such as bdelloid rotifers, tardigrades, nematodes, and several groups of arthropods (*e.g.*, cladocerans, copepods, brine shrimps, and midges), even if they are phylogenetically not closely related.

Physiological and Cellular Processes Involved in Dormancy

The onset of embryo dormancy has to precede adverse environmental conditions, and therefore, it relies on sensing and internally processing reliable cues related to future conditions. It is worth noting that dormancy is a reversible state, with a resumption of development and reproduction in environmentally friendly conditions. Physiological and structural changes occur during entry and exit from dormancy in synchronization with environmental cues (Alekseev, 2007).

As is common in other taxa (*i.e.*, ephippia in cladocerans or diapausing eggs of anostracans and copepods), rotifer dormant embryos are encased in protective shells, often exhibiting spines and/or external sculpturing. Rotifer dormant embryos contain lipid and glycogen stores in higher amounts than the asexual egg (Wurdak *et al.*, 1978; Pourriot and Snell, 1983; Clément and Wurdak, 1991; Walsh *et al.*, 2014; see also fig. 1 in Ziv *et al.*, 2017). In organisms where dormancy is associated with desiccation—such as bdelloids, nematodes, tardigrades (Hashimoto *et al.*, 2015; Boothby *et al.*, 2017; Kaczmarek *et al.*, 2019), springtails (reviewed in Clark and Worland, 2008), the Antarctic midge (Hayward *et al.*, 2007), and the sleeping chironomid (reviewed in Cornette and Kikawada, 2011; Gusev *et al.*, 2014)—there is a formation of a

glassy or vitrified state, which entails an increase in cellular viscosity and leads to a dramatic reduction in biochemical reactions, including metabolism and other functional pathways (reviewed in Berjak, 2006). Numerous metabolites accumulate in organisms prior to desiccation that may ameliorate the harmful effects of dehydration, including sugars as glucose and trehalose; polyols as mannitol, erythritol, and glycerol; and amino acids as alanine, aspartate, and betaine (Crowe *et al.*, 1996; Yancey, 2005; Elnitsky *et al.*, 2008; Petersen *et al.*, 2008). In numerous desiccated organisms, trehalose has been associated with the formation of the glassy state (especially in *Artemia* dormant embryos, where it constitutes 15% of the dry weight; reviewed in MacRae, 2016); however, it was not detected in desiccated bdelloid rotifers or tardigrades (Lapinski and Tunnacliffe, 2003; Boothby *et al.*, 2017). The dormant embryos of cyclically parthenogenetic rotifers also survive desiccation (Gilbert, 2001; Kanagasabapathi and Munuswamy, 2011; Ziv *et al.*, 2017). Only small amounts of trehalose (0.35% of the dry weight) have previously been reported in them (Caprioli *et al.*, 2004), but recent results suggest the occurrence of trehalose in relatively higher abundance in dormant embryos than in non-dormant embryos (a fold change ranging from 1.37 to 61.66) (Rozema *et al.*, 2019). Notwithstanding, two transcripts for trehalose-6-phosphate synthase and four trehalose phosphate synthase proteins were detected in rotifer dormant embryos (Denekamp *et al.*, 2009; Ziv *et al.*, 2017), suggesting the synthesis of trehalose in rotifers. Bdelloid rotifers do not form dormant embryos but simply contract into xerosomes (Wallace and Smith, 2009) by withdrawing the cephalic and caudal extremities into the trunk; then they gradually lose water and undergo anhydrobiosis by reducing their body volume (Marotta *et al.*, 2010). A similar preparatory phase was also reported for tardigrades (Boothby *et al.*, 2017).

While the dormant stage of cyclically parthenogenetic rotifers enters into dormancy, the normal developmental program of the embryo is interrupted, and there is a coordinated down-regulation of complex metabolic processes. This stage of hypometabolism, or “suspended animation,” is sustained even under conditions that would normally promote active metabolism and development (reviewed in Hand *et al.*, 2011a; reviewed in Denlinger *et al.*, 2012). Maintenance or bio-stabilization of the cellular structural and functional competence during the dormant period is essential for exiting dormancy and renewing life activities. The exit from dormancy involves a response to species-specific cues, with light serving as the most important cue in hatching of rotifer dormant embryos (Minkoff *et al.*, 1983). Moreover, higher hatching success was observed in the response to 250–310-nm irradiation during the hatching process (Hagiwara *et al.*, 1995). Temperature, salinity, and peroxidation are also known to modulate hatching success (Minkoff *et al.*, 1983; Hagiwara *et al.*, 1995).

Although embryonic diapause appears in distantly related organisms, similar phenotypes and common functional pathways have been identified, regardless of the diversity and

Phylum	Dormancy Type	Oceanic example	Continental example	Species
Ctenophora	NO	NO	-	187
Porifera	YES	<i>Chalinula loosanoffi</i>	<i>Spongilla lacustris</i>	8659
Placozoa	NO	NO	-	1
Cnidaria	YES	<i>Cyanea lamarcki</i> , <i>Paracoryne huxleyi</i>	<i>Hydra vulgaris</i> , <i>Craspedacista soverbii</i>	10203
Xenoturbellida	NO	NO	-	2
Acoelomorpha	NO	NO	-	428
Echinodermata	YES	<i>Holothuria theeli</i>	-	7550
Hemichordata	NO	NO	-	103
Cephalochordata	NO	NO	-	33
Urochordata	YES	<i>Borysthus schlosseri</i> , <i>Clavelina lepadiformis</i>	-	2804
Cranata	YES	<i>Notonthenia corticeps</i>	<i>Nothobranchius guentheri</i> , <i>Glis glis</i>	65458
Loricifera	NO	NO	-	30
Kimorhyncha	NO	NO	-	196
Priapulida	NO	NO	-	19
Nematoda	YES	NO	<i>Panagrolaimus davidi</i> , <i>Anguina tritici</i>	25033
Nematomorpha	NO	NO	NO	339
Tardigrada	YES	<i>Echiniscoides sigismundi</i>	<i>Paramacrobiotus spatialis</i> , <i>Milnesium</i> sp.	1167
Onychophora	YES	-	Eastern Australian Peripatopsidae	183
Arthropoda	YES	<i>Heteropsyllus numi</i> , <i>Labidocera aestiva</i>	<i>Artemia salina</i> , <i>Onychodiptomus sanguineus</i>	1257040
Orthonecrida	NO	NO	-	29
Rhombzoa	NO	NO	-	107
Chaetognatha	NO	NO	-	170
Gnathostomulida	NO	NO	-	97
Micrognathozoa	YES	-	<i>Limnognathia maerski</i>	1
Rotifera (with Acanthocephala)	YES	<i>Brachionus plicatilis</i>	<i>Macrotrachela quadricornifera</i> , <i>Admetia vaga</i>	3246
Gastrotricha	YES	NO	<i>Lepidodermella squamata</i> , <i>Chaetonotus maximus</i>	794
Platyhelminthes	YES	<i>Monocelis longispila</i>	<i>Bryoplana xerophila</i>	29487
Cycliophora	YES	<i>Symbion pandora</i>	-	2
Mollusca	YES	NO	<i>Eremina desertorum</i>	84977
Annelida	YES	NO	<i>Aulodrilus acutus</i> , <i>Trigaster calwoodi</i>	17733
Nemertea	YES	NO	<i>Argonemertes dendyi</i>	1358
Bryozoa	YES	<i>Bugula neritina</i> , <i>Steghinoporella</i> sp.	<i>Cristatella muscicola</i> , <i>Plumatella</i> sp.	6008
Entoprocta	YES	<i>Barentsia matsushimana</i> , <i>Urnatella gracilis</i>	<i>Urnatella gracilis</i> , <i>Loxosomatoides sirmidhornae</i>	171
Brachiopoda	NO	NO	-	392
Phoronida	NO	NO	-	16

Figure 2. Overview of the occurrence of dormancy across the 35 currently recognized phyla (Giribet and Edgecombe, 2020). For each phylum, there is information on the presence or absence of dormancy, type of dormancy (three groups: 1, diapause, at a specific developmental stage, e.g., resting egg, dormant embryo, etc.; 2, quiescence, at any life stage, e.g., desiccation, encystation, estivation, etc.; or 3, both), examples of species with dormancy in oceanic and continental habitats, and total number of species. The phylogenetic tree is modified from Giribet and Edgecombe (2020). The columns with "NO" means that the phylum is present in the habitat but without dormancy, whereas the columns with a dash mean that the phylum is not present in the habitat. References to support the dormant species are as follows: Fell (1974, 1995) for Porifera; Thein *et al.* (2013) for Cnidaria; Da Silva *et al.* (1986) for Echinodermata; De Caralt *et al.* (2002) for Urochordata; Campbell *et al.* (2008) for Craniata; Perry (2011) for Nematoda; Guidetti *et al.* (2011) for Tardigrada; Monge-Nájera (1994) for Onychophora; Dahms (1995) for Arthropoda; Kristensen and Funch (2000) for Micrognathozoa; Ricci (2001) for Rotifera; Ricci and Balsamo (2000) for Gastrotricha; Van Steenkiste *et al.* (2010) for Platyhelminthes; Funch and Kristensen (1995) for Cycliophora; Grant (1889) for Mollusca; Ohtaka (2018) for Annelida; Moore and Gibson (1985) for Nemertea; Palumbi and Jackson (1983), and Hengherr and Shill (2011) for Bryozoa; and Scholz (1987) and Emschermann (1987) for Entoprocta.

complexity in the survival strategies of organisms displaying dormancy. Dormant organisms share physiological patterns, or “hallmarks of dormancy,” in their life histories. These include a coordinated depression of adenosine triphosphate (ATP)-producing and ATP-consuming metabolic pathways, depression of numerous metabolic pathways, changes in carbohydrate and lipid metabolism, suspension of the cell cycle, depression in the rate of protein turnover, resistance to stress, and protection and bio-stabilization of cellular structures (reviewed in Lubzens *et al.*, 2010; MacRae, 2010, 2016; Denlinger *et al.*, 2012; Lubzens, 2015; Hand *et al.*, 2016). Surprisingly, there is little transcriptional similarity among dormancies across species (Ragland *et al.*, 2010), suggesting that there are many ways to alter cellular functions to support the basic physiological requirements for entrance into and exit from dormancy (reviewed in Podrabsky and Hand, 2015; Ziv *et al.*, 2017). Moreover, in the rotifer *Brachionus plicatilis*, only a modest correlation was found between the transcriptome and proteome profiles in asexual eggs and dormant embryos, highlighting a limitation of transcriptome studies in reflecting the functional events within dormant and non-dormant embryos (Ziv *et al.*, 2017). General conclusions reached from proteome profiling on changes in functional pathways during dormancy have been recently supported by metabolome profiling (Rozema *et al.*, 2019).

Molecular information on the functional pathways associated with the entry into the dormant stage and the revival during hatching in rotifers is limited. There is also no detailed molecular information on the processes and functional pathways associated with dehydration and rehydration in desiccation-tolerant bdelloid rotifers. Extensive studies were carried out on the pathways associated with entry into dormancy in *Artemia* embryos (hereafter referred to as cysts because of deep-rooted usage), but investigations into the exit from dormancy are also missing in this highly used and easily available dormant form (reviewed in Hand *et al.*, 2016). In the following subsections we report on dormancy hallmark pathways that were investigated in rotifer dormant embryos, thus highlighting the need for more extensive studies.

Metabolic arrest during entry into dormancy and its renewal during hatching

The long-term survival of dormant organisms depends on reducing energy expenditure by suppression of production through oxidative pathways and suppression of energy consumption (reviewed in Hand *et al.*, 2011a). A deep metabolic depression is suggested by the undetectable levels of ATP in *B. plicatilis* dormant embryos (Ziv *et al.*, 2017; Rozema *et al.*, 2019). In *Artemia* cysts, ATP is about fivefold lower compared with post-diapause embryos (Patil *et al.*, 2013). In addition, *Artemia* cysts display a rapid decrease in respiration rate during the first 3 days after the release from oviparous females, followed by a slower decline through day 26, when it reaches less

than 1% of day 0 (Patil *et al.*, 2013). There is no information at this stage on the course of decrease in metabolism during the formation and maturation of dormant rotifer embryos. Development continues for about eight days after the start of embryo formation (Hagiwara *et al.*, 1995), suggesting an ongoing metabolism during this period. The metabolic depression in rotifer dormant embryos may be attributed to a putative down-regulation of the tricarboxylic acid (TCA) cycle and pyruvate metabolism (Ziv *et al.*, 2017; Rozema *et al.*, 2019). The pyruvate dehydrogenase E1 component, which catalyzes the carbon flow from pyruvate to Acetyl coenzyme A (CoA), has not been detected in rotifer dormant embryos (Ziv *et al.*, 2017). Down-regulation of this enzyme is also involved in curtailing the supply of carbon substrate to mitochondria in *Artemia* cysts (Patil *et al.*, 2013). In addition, lower abundance of numerous proteins was observed in the oxidative phosphorylation pathway, suggesting that this pathway was also compromised in the mitochondria. Other sources of cellular energy include degradation of lipids and proteins, but lower abundance of key proteins in these pathways in rotifer dormant embryos suggests that these pathways were also reduced (Ziv *et al.*, 2017). Most of the proteins of the glycolysis/gluconeogenesis and the pentose phosphate pathway (PPP) showed similar abundance in the dormant embryos and asexual eggs, suggesting that either these pathways yield energy during dormancy or they could be recruited quickly during the exit from it. The PPP branches from glycolysis at the first committed step of glucose metabolism (Cho *et al.*, 2018) and is required for the synthesis of ribonucleotides (of importance at the exit from dormancy). It is also a major source of reduced nicotinamide adenine dinucleotide phosphate (NADPH). NADPH is required for and consumed during fatty acid synthesis and the scavenging of reactive oxygen species (ROS), during dormancy, or at the resumption of oxidative phosphorylation.

Currently, there are no direct measurements of the resumption of metabolism at the exit from dormancy during the rotifer dormant embryo hatching process. Information on functional processes that are associated with renewal of metabolism in dormant stages from other species is also scarce. Illumination is commonly used in experimental studies as a dormancy-terminating cue (Hagiwara *et al.*, 1995). Transcriptome studies in rotifer dormant embryos (Kim *et al.*, 2015) revealed the differential displayed expression of Acyl-CoA dehydrogenase after 30 minutes of illumination. This enzyme catalyzes the initial step of fatty acid β -oxidation in mitochondria, suggesting degradation of lipids as one of the initial steps in renewal of metabolism. A putative role for lipid metabolism during exit from dormancy was also demonstrated by the expression of genes encoding enoyl-CoA hydratase and 3-oxoacid CoA-transferase subunit B, after 33 hours of illumination in dormant embryos hatched at high salinity (Han *et al.*, 2018). In addition, a gene encoding for α -amylase—which is involved in the hydrolysis of polysaccharides, such as glycogen, that yield glucose and maltose—showed differential expression

after four hours of illumination (Han *et al.*, 2018). Interestingly, vacuolar H⁺-inorganic pyrophosphatase (V-PPase)—an enzyme with a function in proton pump, transmembrane proton transport, and hydrogen-translocating pyrophosphatase activity—was expressed after 30 minutes of dormant embryo illumination (Kim *et al.*, 2015).

A question arises as to whether metabolism occurs in rotifer dormant embryos, in *Artemia* cysts, or in organisms including bdelloid rotifers, tardigrades, and insects, where desiccation occurs at any age (Ricci, 1998; Clark *et al.*, 2009; Gusev *et al.*, 2014). As mentioned before, desiccation is associated with a high cellular viscosity that may hamper chemical reactions (reviewed in Berjak, 2006).

The cell cycle arrest

The arrest of the cell cycle, one of the characteristics of dormancy (Podrabsky and Hand, 2015), occurs in rotifer dormant embryos, because they contain 39 or 40–60 nuclei (Hagiwara *et al.*, 1995; Boschetti *et al.*, 2011), compared with ~1000 nuclei of adult females (Hyman, 1951). Notwithstanding, the above-mentioned studies did not disclose whether dormancy occurs at the early or late stages of gastrulation. Nor has it been established whether the pattern of development in dormant embryos relies on maternal or zygotic gene expression. From the study of Smith *et al.* (2010) on the expression pattern of the *nanos* (*BpNos*) gene of asexual developing embryos, the expression of this maternal gene is reduced in embryos at around 16 cells, which is the stage suggested for gastrulation in rotifers by Heinol (reviewed in 2015). *Artemia* cysts enter dormancy at the gastrula stage at the ~4000-cell stage (Clegg and Conte, 1980); in *Daphnia pulex*, the cell cycle is stopped at ~1000 cells (early gastrula stage); and in *Daphnia magna* is stopped at the 3500-nuclei stage (Chen *et al.*, 2018). In *Artemia*, the cell cycle is arrested before the downregulation of metabolism (reviewed in Hand *et al.*, 2011a), but similar information is not available for rotifer dormant embryos. In *Artemia*, the cell cycle remains arrested (probably at the G2/M phase), throughout pre-emergence development, until after hatching; and cell differentiation occurs without cell division or DNA synthesis (reviewed in Clegg and Conte, 1980; Dai *et al.*, 2008).

Adaptation to stress

Rotifer dormant embryos have adapted to stress through several strategies, including additional eggshell coats, desiccation tolerance, higher abundance of heat shock proteins (HSPs; or other molecular chaperones), antioxidants and oxydoreductases, and facilitated water transport through aquaporins. Below we discuss the role and review the current state of knowledge regarding these strategies.

A. Egg shell coats. Rotifer dormant embryos are surrounded by three coats, with the innermost containing chitin (Wurdak *et al.*, 1978; Clément and Wurdak, 1991). There is a thicken-

ing of the shell envelopes during dormant egg formation (Hagiwara *et al.*, 1995), but there is almost no information on the permeability or biochemical and physiological properties of the egg coats except that dormant embryos are impermeable to molecular probes such as double-strand RNA (dsRNA) (Snell *et al.*, 2010).

B. Desiccation tolerance by late embryogenesis abundant (LEA) proteins. LEA proteins have been found in most organisms that survive desiccation, including desiccation-tolerant cyanobacteria, bacteria, Archaea, nematodes, tardigrades, rotifers, and arthropods (reviewed in Tunnacliffe *et al.*, 2010; reviewed in Hand *et al.*, 2011b). LEA proteins are hydrophilic, mostly unstructured, flexible proteins and are a part of the group of intrinsically disordered proteins (IDPs), which assume structural changes upon drying (reviewed in Wise and Tunnacliffe, 2004; Shimizu *et al.*, 2010; reviewed in MacRae, 2016; reviewed in Boothby and Pielak, 2017; Boothby *et al.*, 2017). LEA proteins inhibit protein aggregation either by chaperoning or by molecular shielding and the formation of electrostatic and/or physical barriers that prevent protein interactions (Chakrabortee *et al.*, 2012; Hatanaka *et al.*, 2013). Moreover, LEA proteins and other IDPs contribute to vitrification without the presence of trehalose (reviewed in Tunnacliffe *et al.*, 2010; Boothby *et al.*, 2017). Two genes coding for LEA proteins were identified and expressed in dormant embryos of *B. plicatilis* and females forming them, but not in other female forms or males (Denekamp *et al.*, 2010a). *In silico* analysis revealed that the two proteins resemble group-3 LEA proteins based on the repeats for 11-mer motifs, although they also display several putative amino acids typical of the 20-mer motif of group-1 LEA proteins. LEA proteins were also identified in asexual eggs, but their abundance in resting eggs ranged between a fold change of ~1000 and 1400 with asexual eggs (Ziv *et al.*, 2017). LEA transcripts and proteins degrade during hatching in *B. plicatilis* (Denekamp *et al.*, 2010a, 2011), suggesting a specific role in dormant embryos. LEA transcripts were also identified in dormant embryos of *Brachionus manjavacas*, and also in this species they degrade during hatching (Han *et al.*, 2018). In *Artemia*, 14 LEA and LEA-like genes were identified, with some localized to specific cellular regions (*e.g.*, *AfrLEA3m* in the mitochondria); but it is possible that some of them do not have a specific function during stress (reviewed in MacRae, 2016).

C. Molecular chaperones or heat shock proteins (HSPs). Many proteins of the cellular chaperone system are expressed ubiquitously in the normal cell state to aid in folding of native polypeptides and their translocation to different cellular compartments (reviewed in Feder and Hofmann, 1999; reviewed in Hartl and Hayer-Hartl, 2002). The most extensively studied HSPs are the molecular chaperones that function intracellularly in an ATP-dependent manner and include HSP 60 kDa/HSP 10 kDa (HSP60/HSP10, chaperonins) (HSPD/HSPE), HSP40 (DNAJ), HSP70 (HSPA), HSP90 (HSPC), HSP100, and HSP110 (HSPH) families. The expression of many of these

HSPs is regulated by heat shock transcription factors (HSFs), of which HSF1 is the best studied (reviewed in Edkins *et al.*, 2017). During stress response, they may be upregulated to further assist misfolded proteins to attain or regain their native states, and also to target degraded proteins and regulate their removal from the cell, thus preventing the formation of cytotoxic aggregates (reviewed in Parsell and Lindquist, 1993). Transcripts associated with the HSP70 pathway (HSP with DNAJ co-chaperones and the HSP70/HSP90 organizing protein) were upregulated in *B. plicatilis* dormant embryos, suggesting a role for a cellular stress response (Clark *et al.*, 2012). In addition to the HSPs, dormant stages contain small-molecular-weight heat shock proteins (sHSPs). They may play a particularly important role in dormant organisms, because they act as ATP-independent chaperones, without the expenditure of important ATP reserves, preventing the irreversible denaturation of other proteins; but they are not otherwise actively engaged in their subsequent processing in stressful conditions. In *Artemia*, sHSPs constitute a protective network during dormancy (King *et al.*, 2013, 2014; reviewed in MacRae, 2016). Four sHSPs were identified in dormant-destined embryos of *Artemia*—p26, artemin (which is a ferritin homolog), ArHsp21, and ArHsp22—and they contain an α -crystalline domain (reviewed in MacRae, 2016). sHSP transcripts and proteins were also identified in *B. plicatilis* dormant embryos (Denekamp *et al.*, 2009; Clark *et al.*, 2012; Ziv *et al.*, 2017). One HSP20 protein was identified only in dormant embryos; and others show higher abundance in dormant embryos, with a fold change ranging from 1200 to 4000 compared to asexual eggs (Ziv *et al.*, 2017). Ferritin is one of the most abundant proteins in *B. plicatilis* dormant embryos (Ziv *et al.*, 2017). Artemin appears in the cytosol of cyst-destined embryos in *Artemia* and constitutes 7% of the soluble protein in mature cysts, but the function of this protein in rotifers has yet to be resolved. It was proposed that it functions in elevated stress resistance and tolerance to desiccation. Purified artemin prevents heat-induced denaturation of other proteins in the absence of added ATP, an activity shared by ferritin (reviewed in MacRae, 2016). Recently, Tan and MacRae (2018, 2019) showed that HSF1 regulates the expression of p26, ArHsp21, ArHsp22, and artemin in *Artemia* cysts. Diapausing cysts with diminished amounts of HSF1 were significantly less stress tolerant than cysts containing normal levels of HSF1. Also, sHSP transcripts were degraded during hatching, suggesting a specific role in rotifer dormant embryos (Denekamp *et al.*, 2011).

D. Antioxidants. Rotifer dormant embryos contain a large array of transcripts and proteins with a function against ROS. These include peroxiredoxin, catalase, glutathione-s-transferase, superoxide dismutases, thioredoxins, and ferritin (Clark *et al.*, 2012; Ziv *et al.*, 2017). In all life stages ROS are toxic because they directly damage DNA, lipids, and proteins; and they are involved in numerous biological processes (reviewed in MacRae, 2010; Clark *et al.*, 2012). The occurrence of a large array of proteins functioning against ROS would be an advantage

during the exit from dormancy, with the start of oxidative phosphorylation, which could occur before the onset of transcription and translation in the embryo. Surprisingly, recent studies showed that elevated ROS levels at non-physiological levels promote the extension of lifespan, characteristic of diapause in insect pupae, through the regulation of protein kinase B (Akt) and forkhead transcription factor (FoxO) pathways (Zhang *et al.*, 2017; see also *Regulation of dormancy*, below).

E. Oxidoreductases. This category comprises a range of different enzyme families, including alcohol dehydrogenases, cytochrome P450s, and selenium-binding proteins. A selenium-binding protein was one of the most abundant proteins in rotifer dormant embryos, and the transcript was upregulated in diapausing insects (Robich *et al.*, 2007; Ziv *et al.*, 2017). About 26 transcripts with a putative association with oxidoreductase activity were overexpressed in dormant embryos compared to asexual eggs in *B. plicatilis* (see table S3 in Clark *et al.*, 2012). Numerous other proteins with similar putative functions were also highly abundant in dormant embryos (see table 1 in Ziv *et al.*, 2017). The proteins in this category play critical roles in the intermediate metabolism of many cellular substrates, such as lipids, carbohydrates, and amino acids and also in detoxification processes and degradation of xenobiotics (especially the cytochrome P450 family).

F. Aquaporins (AQPs). These are transmembrane proteins that serve as channels for water and small soluble molecule transport. They are of importance in cellular water management under normal conditions and have specific functions during dehydration, freezing, and desiccation (see Goto *et al.*, 2011). Three different putative AQP transcripts were identified in *B. plicatilis* expressed sequence tag (EST) libraries, but their function has not yet been resolved. With respect to other organisms, an AQP capable of transporting water was reported in the Antarctic midge (*Belgica antarctica*), which tolerates the loss of ~70% of body water content (Goto *et al.*, 2011). A homolog of this AQP was also reported for the sleeping chironomid (*Polypedilum vanderplanki*), which tolerates desiccation (Kikawada *et al.*, 2008).

Transcription, translation, degradation, and proteome remodeling

Proteome profiling revealed that proteins that are associated with transcription, translation, degradation, and proteome remodeling were at lower abundance in rotifer dormant embryos compared with asexual eggs, putatively suggesting an impairment of these processes in the former (Ziv *et al.*, 2017). Moreover, thymidine and uracil have not been detected in dormant embryos, suggesting the cessation of DNA synthesis, transcription, and, plausibly, translation (Rozema *et al.*, 2019). In *Artemia*, direct measurements by radiolabeled isotopes showed that protein synthesis was severely depressed in diapausing embryos, and there was no evidence for proteolysis. In addition, nucleic acid synthesis was also depressed (Clegg *et al.*, 1996;

reviewed in Hand *et al.*, 2016). These studies stress the importance of the maintenance of cellular structural and molecular integrity during dormancy, which can last for years, and the putative functional importance of HSPs, sHSPs, and LEA proteins during this period.

Regulation of dormancy

Rotifer dormant embryos are produced in the course of sexual reproduction, but the signals and cascade of functional and molecular events for this mode of reproduction have not been fully elucidated. Numerous environmental and internal factors were mentioned (see the *Introduction*) as modulators of sexual reproduction. The effect of a few invertebrate and vertebrate hormones associated with regulation of reproduction was tested on *Brachionus plicatilis* (Gallardo *et al.*, 1997, 1999, 2000) and *Brachionus calyciflorus* (Yang and Snell, 2010). For *B. plicatilis*, these include juvenile hormone (JH), serotonin (5-HT), 20-hydroxyecdysone, human chorionic gonadotropin (hCG), growth hormone (GH), triiodothyronine (T3), estradiol (E2), and γ -aminobutyric acid (GABA). T3 and hCG had no effect on sexual female production. Inconsistent effects were found for GH, E2, GABA, and 20-HE, but JH increased the production of sexual females (Gallardo *et al.*, 2000). Only 5-HT and GABA have been detected so far in *B. plicatilis* (Gallardo *et al.*, 2000). For *B. calyciflorus*, the total number of dormant embryos produced by rotifers exposed to progesterone, E2, or testosterone (at $1000 \mu\text{g L}^{-1}$) decreased significantly in all treatments (Yang and Snell, 2010) but had a variable effect on asexual reproduction. Recently, a ligand-activated estrogen-like receptor was shown to regulate asexual reproduction of females in *B. manjavacas*, suggesting a role for E2 in rotifers (Jones *et al.*, 2017). A JH esterase-binding protein was detected in asexual eggs and dormant embryos, with a higher abundance in asexual eggs (Ziv *et al.*, 2017), supporting a role for JH in rotifers; but its specific function was not determined. In the cladocerans *Daphnia* and *Moina*, methyl farnesoate, a JH precursor molecule, is responsible for programming developing oocytes into male offspring; and it denotes the first step in the switch from asexual parthenogenetic reproduction to sexual reproduction (Olmstead and LeBlanc, 2001; Lampert *et al.*, 2012; LeBlanc and Medlock, 2015; Toyota *et al.*, 2015). In these organisms, photoperiod is a critical cue in creating permissive conditions for male production; and under these conditions, male sex determination is temperature dependent.

A role for JH and the insulin-signaling (IS) pathways in dormancy has been established for diapause in insects. A discussion of the role of JH in dormancy is relevant to rotifers in view of the increased production of sexual females after exogenous application of JH and the identification of a JH esterase-binding protein in asexual females (see above). A shutdown in the production of JH is a nearly universal endocrine mechanism for insect diapauses that occur in the adult stage (Sim

et al., 2015), but JH is at high levels in diapausing nymphal stages (Yin *et al.*, 2018). Insulin-signaling and JH-signaling pathways appear to collaboratively mediate expression of FoxO, which generates the diapause phenotype. The forkhead box (Fox) proteins form a diverse family of transcription factors with a conserved DNA-binding domain. FoxO is the main transcriptional effector of the IS pathway and is normally suppressed in the presence of insulin. High insulin levels activate the phosphatidylinositol 3-kinase/protein kinase B (P13K/Akt) pathway, which in turn phosphorylates FoxO, leading to the inactivation of FoxO. A low level of IS represses P13K/Akt and increases the FoxO activity, which generates the diapause phenotype. In the mosquito *Culex pipiens*, the shutdown of the IS pathway activates FoxO and leads to the adult diapause phenotype (Sim *et al.*, 2015). High FoxO levels were also found in insects with diapause in nymphal stages; although, as mentioned, in these stages the JH level is high (Yin *et al.*, 2018). FoxO as a transcription factor functions downstream of IS and JH; and its targets include genes with functional relevance to diapause, including those that are associated with metabolism, development and/or cell cycle, intra- and extracellular signaling, transcription, translation, protein modification, stress response, cell death, and apoptosis (Sim *et al.*, 2015). The genetic pathway involving IS and FoxO appears to also play a critical role in regulating dauer formation in the nematode *Caenorhabditis elegans* and reproductive diapause in the fruit fly *Drosophila melanogaster* (reviewed in Hand *et al.*, 2016), thus suggesting a common mechanism regulating these diverse forms of developmental arrest (Sim *et al.*, 2015). The FoxO transcription factor has not been identified so far in rotifers. An association with the FoxO pathway can be suggested in rotifer dormant embryos by the higher abundance of the regulatory proteins 14-3-3 ϵ and 14-3-3 ζ in asexual eggs (Ziv *et al.*, 2017). The 14-3-3 proteins constitute a highly conserved protein family, with more than 100 signaling proteins serving as ligands for other proteins (reviewed in Darling *et al.*, 2005; and in Morrison, 2009). Interactions are regulated by the phosphorylation state of the ligand, and 14-3-3 proteins can alter the function of a bound protein. They essentially regulate every major cellular function, including signal transduction, apoptosis, cell cycle progression, regulation of the Ras/Raf/MAPK cascade (*i.e.*, a chain of cell proteins that propagates a signal from a receptor on the cell surface to the DNA in the nucleus), and the anterior-posterior axis during embryonic development; and they serve as checkpoint activators within eukaryotic cells. The 14-3-3 proteins participate in light signaling and bind to phytochrome-interacting factors in plants (Adams *et al.*, 2014) and melatonin synthesis in mammals (Ganguly *et al.*, 2005). In addition, 14-3-3 proteins showed differential abundance in the comparison of dormant and non-dormant silkworm eggs (Fan *et al.*, 2013). Moreover, phosphorylated FoxO binds to 14-3-3, and this binding inhibits the interaction between FoxO and the target DNA (Silhan *et al.*, 2009). In addition, HSF1 was reported to bind to 14-3-3 ϵ (Wang *et al.*, 2003). The exact role

of 14-3-3 proteins in dormancy is far from being resolved, but the results in rotifers and the silkworm suggest a role in the regulation of numerous processes during dormancy.

The identification of a progesterone membrane receptor in *B. manjavacas* supports progesterone chemoreception as a key regulatory step involved in rotifer reproduction (Stout *et al.*, 2010). Progesterone is a steroid hormone that acts through specific nuclear receptors to play a critical role in regulating vertebrate reproductive processes; it is also involved in multiple non-reproductive processes, such as neuroprotection and neurogenesis. Progesterone also activates non-nuclear, membrane-associated receptors in vertebrates and invertebrates, with impacts on behavior and reproduction (reviewed in Valadez-Cosmes *et al.*, 2016). The 82-kDa rotifer progesterone receptor protein band is consistent with the size of many membrane progesterone receptors belonging to the progestin and adiponectin receptor family. This membrane receptor was localized to sex organs within female and male rotifers. RNA interference (RNAi) studies showed a 64% decrease in induction of sexuality in daughters of females exposed to RNAi probe; but other biological functions, such as mating behavior, were unaffected (Stout *et al.*, 2010). Exposure of rotifers to low concentrations of progesterone enhanced dormant embryo production. In addition, the hatching success of dormant embryos produced by females exposed to progesterone was higher than in untreated controls (Snell and DesRosiers, 2008). However, the response to progesterone treatment differed markedly in four brachionid species, and exposure to progesterone did not enhance dormant embryo production in *B. plicatilis* or *B. calyciflorus* (Snell and DesRosiers, 2008). The abundance of a progesterone receptor was 34-fold higher in asexual eggs than in dormant embryos (Ziv *et al.*, 2017). These reports suggest that production of dormant embryos is not regulated only by progesterone, and additional studies are required to identify the regulating pathways leading to dormant rotifer embryo production.

Dormancy as an Adaptation

Rotifer adaptation to time-varying environments

Decades of limnological surveys suggest that the activity of rotifer populations in the water column is temporary and typically restricted to a season in the year (*e.g.*, Wallace *et al.*, 2006)—the so-called growing season—although the occurrence of some permanent populations with low-density phases cannot be ruled out. At the timescale of one or a few years, unsuitable periods in a locality can occur in the case of pools and ponds, due to their desiccation, with this event defining the length of the so-called hydroperiod. More generally, physical and chemical changes in temperature, salinity, water turbulence, and so forth have been associated with the end of the growing season, although these causes might act indirectly and may be mediated by food availability and antagonistic interactions (Yoshida *et al.*, 2003). Compared with other zoo-

plankters (cladocerans and copepods), cyclically parthenogenetic monogonont rotifers are regarded as poor competitors but good colonizers (Allan, 1976; Gilbert, 1988). Therefore, even if long periods of constant favorable water conditions occur, a restriction of the growing season is expected for rotifers, because it would end when slower colonizers of the water column but better competitors (*e.g.*, cladocerans) proliferate. Thus, the environments typically inhabited by rotifers impose the need of a stage in the life cycle allowing survivorship through unsuitable periods. Rotifer dormant embryos escape from competition and resist harsh conditions. As detailed above (in *Metabolic arrest during entry into dormancy and its renewal during hatching*), it is due to metabolic arrest, in addition to structures and metabolites whose function it is to protect against adverse conditions and to provide resource reserves. The costs of producing these structures and metabolites can be inferred indirectly by measuring the fecundity of dormant-embryo-producing females relative to the fecundity of females that produce subitaneous asexual eggs (Gabaldón and Carmona, 2015). Although scarce, data on relative fecundities have been retrieved for particular species of the three major groups of the zooplankton after a search in Clarivate Analytics' ISI Web of Science for “(dorm* OR diapaus*) AND (subitaneous) AND (fecundity)” in the topic search query for the period 1996–2019 (see Table 1). Results suggest phylogenetic differences in the cost of producing dormant stages, with particularly high costs in the case of rotifers.

Besides the extra costs of producing dormant stages, the metabolic arrest associated with dormancy results in increased generation time. Thus, entering dormancy during favorable environmental conditions would be expected to decrease fitness, assuming that all other conditions are equivalent. To some extent, this cost is expected to occur as a result of the incapability of organisms to accurately predict forthcoming conditions (for the increased costs of sex, see below and *The interplay between sex and dormancy*). A shortened dormancy, that is, fast return to activity, might partially counteract this fitness cost if dormancy is initiated at a time earlier than is optimal. For instance, despite reports that obligate dormant periods of months to years occur in some genotypes of the rotifer *Brachionus* (Gilbert, 2007), Stelzer (2017), using other genotypes, reported that the first hatchling appeared after 72 hours of dormant stage production. This short dormancy still imposes a cost *via* generation time increase, because these animals are able to produce offspring in less than 48 hours, which adds up to the above-mentioned metabolic and structural investment.

As in cladocerans, an additional cost of cyclically parthenogenetic rotifer dormancy occurs because the production of dormant propagules is almost always associated with sexual reproduction in a life cycle where asexual reproduction is prevalent. In these cases, the specific cost of sex—namely, the production of males—adds up. Using a monogonont rotifer model parameterized with observed values, Stelzer (2017) assumed the shortest dormancy he observed and compared the

Table 1

Relative fecundities of subitaneous to dormant stages in representative taxa of the major zooplankton groups

Taxa	Relative fecundity	References	Observations
Cladocera			
<i>Daphnia pulicaria</i>	1.83–4.62	Conde-Porcuna <i>et al.</i> , 2011	
Copepoda			
<i>Acartia biflosa</i>	1.03	Castro-Longoria and Williams, 1999	
<i>Paracartia latisetosa</i>	1.26	Belmonte and Pati, 2007	Amphoteric females excluded from calculations
Rotifera			
<i>Brachionus manjavacas</i>	8.5	Gabaldón and Carmona, 2015	
<i>Brachionus plicatilis</i>	6.4–7.3	Lubzens and Zmora, 2003; Gabaldón and Carmona, 2015	
<i>Keratella hiemalis</i>	10–20	Gilbert, 1993	Pseudosexual diapausing eggs
<i>Synchaeta pectinata</i>	1	Gilbert, 1995	Asexual diapausing eggs

Database: ISI Web of Science; date of searching: March 5, 2019; searching criteria: TOPIC: ((dorm* OR diapaus*) AND (subitaneous) AND (fecundity)); timespan: 1996–2019; output: 7 papers.

hypothetical proliferation rate of an obligate asexual lineage with an obligate sexual lineage (*i.e.*, incurring in dormancy every single generation), the latter being lower than 25% of the former. Not surprisingly, this implies a strong selective factor against sex and dormancy, with all other things being equal (Serra and Snell, 2009). The evolutionary result is selection of a decreased propensity for sex, and a decrease in the production of dormant embryos, or even sex loss, during the growing season in the wild (*i.e.*, before adverse conditions occur) (Carmona *et al.*, 2009) and also when these animals are maintained in constant laboratory conditions (*e.g.*, Fussmann *et al.*, 2003).

Dormant stages are not invincible. Contrarily, loss of a high proportion of these propagules, particularly if disseminated (see *The role of dormancy as a strategy for spatial dispersion*, below), is expectable. If not disseminated, dormant stages tend to accumulate in the lake sediments, where their fate is jeopardized by a number of factors (*e.g.*, losses due to burial, predation, *etc.*) (García-Roger *et al.*, 2006c). In order to study the main demographic features of dormant egg banks across taxa, we performed another search in Clarivate Analytics' ISI Web of Science, this time using “(dorm* OR diapaus OR rest*) AND egg AND bank AND (abundance OR density) AND (water OR aquatic)” in the topic search query. This search yielded 154 records to be inspected for the period 1996–2019, from which we extracted data, when available, on the density of dormant stages in the sediments, viability, and deterioration rate (Table 2). Often, density of viable dormant stages decreases with sediment depth. In the case of zooplankters, the largest fraction of viable dormant embryos generally occurs in the upper 4–6 cm of sediment (Herzig, 1985; Carvalho and Wolf, 1989; Hairston and Van Brunt, 1994; Cáceres, 1998), with rotifers being no exception (García-Roger *et al.*, 2006a, b; Piscia *et al.*, 2012, 2016). When sedimentation rates are available, the annual mortality of dormant stages in the sediments (estimated from the regression slope of log density of viable stages against time) has been observed to vary from

1% to 64%, thus revealing that the fraction of non-viable dormant stages in the sediments can be very high (Table 2). Interestingly, García-Roger *et al.* (2006b) reported percentages of deteriorated dormant embryos in the egg banks of the rotifer *Brachionus plicatilis* ranging 74%–99% for the uppermost 10 cm of sediment. Laboratory studies confirm that deterioration rates may be high even at relatively short timescales (22%–53% mortality during the first year, depending on population) (García-Roger and Ortells, 2018). Comparisons between two cryptic rotifer species have shown that dormant embryos of *Brachionus manjavacas* start to deteriorate just in the first week after production, which is much earlier than in *B. plicatilis*, which keeps viability for about six months and then deteriorates quickly (Gabaldón *et al.*, 2015). These results have been interpreted in terms of a trade-off between dormant embryo survival and hatchability. In an environment where the survival of the dormant embryos would be more compromised, a greater propensity for hatching would be expected; and investing resources for a long dormancy would not be required.

With respect to habitat type, dormant embryos in the sediments of shallow ponds, if compared to deep lakes, might be exposed to extreme environmental conditions (*e.g.*, desiccation, compacting pressure while buried in the sediment, high exposure to radiation, damage produced by salt crystals when the pond dries out, predators, *etc.*), which may accelerate deterioration processes (García-Roger *et al.*, 2006b). Notice, however, that this does not imply higher success rates in deep lakes. On the contrary, burying and lack of hatching stimuli in deep lakes might promote low hatching rates, except after re-suspension of the sediments, whereas dormant eggs in shallow-water sediments are more likely to experience conditions conducive to hatching (Gilbert, 2017).

Despite the high mortality rate of dormant embryos, high maximum longevities have been reported: 65 years in *Brachionus calyciflorus* (Piscia *et al.*, 2012), 80 years in *B. plicatilis*

Table 2

Features of dormant egg banks in the sediments across taxa

Taxa	Density (per cm ²)	Depth sampled (cm)	Viable/total (%)	Deterioration rate (per year)	Reference	Habitat
Anostraca						
<i>Branchinella ornata</i>	0.66–5.06	0–11	–	0.245–0.304 ^d	Hulsmans <i>et al.</i> , 2006	Wetland
<i>Branchipodopsis wolffi</i>	0.10–2.20	Surface	–	–	Brendonck and Riddoch, 2000	Ephemeral rock pool
<i>Branchipus schaefferi</i>	0.03–0.15	Surface	–	–	Thiéry, 1997	Rainfall pond
<i>Chirocephalus ruffoi</i>	0.08–44.00	0–15	80 ^a	–	Mura, 2004	Shallow pond
	0.10–3.00	0–2.5	–	–	Mura, 2005	Shallow pond
<i>Phallocryptus spinosa</i>	0.02–0.11	Surface	–	–	Moscatello <i>et al.</i> , 2002	Pond
	0.08–3.15	0–13	85 ^a	0.190 ^d	Hulsmans <i>et al.</i> , 2006	Wetland
<i>Streptocephalus vitreus</i>	0.20–1.30	Surface	–	–	Hildrew, 1985	Rainfall pond
<i>Tanymastigites perrieri</i>	0.01–0.06	Surface	–	–	Thiéry, 1997	Rainfall pond
Cladocera						
<i>Bytotrephes longimanus</i>	4.00	Surface	36 ^a	0.640	Brown and Branstrator, 2011	Lake Reservoir
	0.18	0–6	–	–	Katajisto <i>et al.</i> , 2013	Marine (Baltic Sea)
<i>Cercopagis pengoi</i>	0.46–0.88	0–6	–	0.471 ^d	Sopanen, 2008	Marine (Baltic Sea)
	0.30–2.60	0–13	<50 ^a	0.096–0.167 ^d	Katajisto <i>et al.</i> , 2013	Marine (Baltic Sea)
<i>Daphnia hyalina</i> - <i>Daphnia galeata</i> complex	3.00–14.00	0–40	70 ^a	0.053	Weider <i>et al.</i> , 1997	Lake
	0.10–24.00	0–100	50 ^a	–	Jankowski and Straile, 2003	Lake
<i>Daphnia galeata mendotae</i>	2.504	0–10	–	–	Cáceres, 1998	Lake
<i>Daphnia longispina</i>	0.15–77.00	0–40	<1 ^b	–	Faustová <i>et al.</i> , 2004	Glacial acidified lakes
<i>Daphnia magna</i>	16.50–187.00	0–20	55 ^a	–	Cousyn and De Meester, 1998	Shallow ponds
<i>Daphnia obtusa</i>	0.01–1.00	Surface	>80 ^a	–	Hotovy and Petrussek, 2007	Rainfall pond
<i>Daphnia pulicaria</i>	8.00	0–10	–	–	Cáceres, 1998	Lake
<i>Moina macrocopa</i>	0.01–1.00	Surface	>80 ^a	–	Hotovy and Petrussek, 2007	Rainfall pond
Copepoda						
<i>Acartia</i> sp.	0.45	0–3	100 ^b	–	Pati <i>et al.</i> , 1999	Shallow pond
<i>Acartia bifilosa</i>	1000.00	0–30	60 ^a	–	Uriarte and Villate, 2006	Estuary
<i>Acartia grani</i>	19.00–660.00	0–23	–	–	Guerrero and Rodríguez, 1998	Marine (coastal)
<i>Acartia pacifica</i>	0.23–38.50	0–30	–	0.141	Jiang <i>et al.</i> , 2004	Marine (coastal)
<i>Acartia spinicauda</i>	70.60	0–14	–	0.366 ^d	Wang <i>et al.</i> , 2016	Marine (coastal)
<i>Acartia tonsa</i>	80.00	0–1	85 ^{a,c}	–	Berasategui <i>et al.</i> , 2013	Estuary
<i>Boeckella poppei</i>	7.20–9.20	0–10	–	0.016	Jiang <i>et al.</i> , 2012	Maritime lakes
<i>Onychodiptomus sanguineus</i>	4.00–8.00	0–30	–	0.011–0.015	Hairston <i>et al.</i> , 1995	Lake
<i>Eurytemora americana</i>	78.90	0–1	80–100 ^{a,c}	–	Berasategui <i>et al.</i> , 2013	Estuary
<i>Tortanus forcipatus</i>	2.40–6.00	0–37	–	0.135	Dahms <i>et al.</i> , 2006	Marine (coastal)
Rotifera						
<i>Brachionus</i> sp.	0.16	0–3	92 ^b	–	Pati <i>et al.</i> , 1999	Shallow pond
	2.00–115.00	0–10	5 ^b	0.047–0.136 ^d	García-Roger <i>et al.</i> , 2006b	Shallow ponds
<i>Synchaeta</i> sp.	10.00	0–3	66 ^b	–	Pati <i>et al.</i> , 1999	Shallow pond
	<1.00	0–12	–	–	Wang <i>et al.</i> , 2016	Marine (coastal)
Nematoda						
Unidentified nematodes	0.04–0.55	0–3	93–100 ^b	–	Pati <i>et al.</i> , 1999	Shallow pond

Database: ISI Web of Science; date of searching: March 5, 2019; searching criteria: TOPIC: ((dorm* OR diapaus* OR rest*) AND egg AND bank AND (abundance OR density) AND (water OR aquatic)); timespan searched: 1996–2019; output: 154 papers.

^a Egg viability assessed by hatching.

^b Egg viability assessed by color and morphology.

^c Egg viability assessed after neutral red staining.

^d Estimated here from raw data reported by the author(s). Calculated as the parameter *b* in the regression model $\ln(\text{“viable egg density”}) = a + b \text{ “time”}$, only sampling sites where $R^2 > 0.7$ is included. Time was estimated from sedimentation rates.

(García-Roger *et al.*, 2006b), and 65–100 years in *Brachionus rotundiformis* (King and Serra, 1998; Kotani *et al.*, 2001). These values are comparable to those reported in other zooplankters: 125 years in the cladoceran *Daphnia* (Cáceres, 1998) and 330 years in the copepod *Onychodiptomus sanguineus*

(Hairston *et al.*, 1995). Although recent research has reported outstanding long-term survival in *Daphnia pulicaria* ephippia of about 700 years (Frisch *et al.*, 2014), longevity of rotifer dormant embryos is among maximum reported ages in aquatic invertebrates (Radzikowski, 2013). These long-lasting dormant

propagules might be important in evolutionary studies and dynamics (see *Evolutionary and Population Implications of Dormancy*, below).

Unpredictable environmental fluctuations and dormancy

The optimal timings to start and leave dormancy in determinist environments are straightforward, while sophisticated strategies are expectable in uncertain scenarios (Ellner *et al.*, 1999; Spencer *et al.*, 2001; Serra *et al.*, 2005). Based on classical models for seed dormancy of annual plants (Cohen, 1966; King and Roughgarden, 1982), risk-spreading strategies associated with dormancy traits have been hypothesized to occur in rotifers (García-Roger *et al.*, 2017). Therefore, since active animals cannot predict the end of the growing season, then producing dormant stages as soon as the end might occur would avoid the risk of a zero-fitness event. Studies with rotifers provide results that support this hypothesis. Franch-Gras *et al.* (2017) observed that, as measured in standard laboratory conditions, *B. plicatilis* genotypes living in unpredictable ponds initiated sexual reproduction at lower density thresholds, as a way of producing dormant embryos early to successfully face an unexpectedly short growing season. The results provided by Franch-Gras *et al.* (2017) confer correlational evidence for the hypothesis put forward. Consistent with this study, but additionally providing causal evidence by using an experimental evolution approach, Tarazona *et al.* (2017) found that *B. plicatilis* lab populations subject to an unpredictable selective regime evolved lower density thresholds (*i.e.*, higher propensity) for sexual reproduction than rotifer populations subject to a predictable selective regime.

An early timing of entering dormancy is not the only way to cope with unpredictable environmental fluctuations. Intermediate hatching fractions of dormant stages are expected if cues predicting future conditions are not completely accurate. Otherwise, if the growing season turns out to be unexpectedly too short for a new cohort of these stages to be produced, the genotype will have zero fitness. Bet-hedging strategies for hatching are predicted in these circumstances (Cohen, 1966; Seger and Brockmann, 1987; Philippi and Seger, 1989; Simons, 2011). Consistently, the aforementioned study of experimental evolution conducted by Tarazona *et al.* (2017) found that *B. plicatilis* rotifer populations subject to an unpredictable length of the growing season evolved a decreased hatching fraction of the dormant embryos. Similar results have been reported for other zooplankters. Pinceel *et al.* (2017) observed decreased hatching fractions in dormant embryos of natural populations of *Branchinella longirostris* (Anostraca) and *Paralimnadia badia* (Spinicaudata) along an aridity gradient where the probability of reproductive success was progressively lower.

The role of dormancy as a strategy for spatial dispersal

Rotifer habitats (lakes, ponds, lagoons, *etc.*) are “islands” in an “ocean” with adverse (dry) conditions. As in other aquatic

invertebrates whose active stages cannot survive for long periods out of the water (Panov and Cáceres, 2007), dormant embryos are thought to be key determinants of spatial dispersal in rotifers (Fontaneto, 2019). Evidence has documented dormant stages of aquatic organisms being dispersed by the wind (Jenkins and Underwood, 1998; Brendonck and Riddoch, 1999; Cáceres and Soluk, 2002; Vanschoenwinkel *et al.*, 2008, 2009; Moreno *et al.*, 2016; Rivas *et al.*, 2018, 2019), water flows (Michels *et al.*, 2001; Shanks *et al.*, 2003; Hulsmans *et al.*, 2007), and other animals (Figuerola and Green, 2002; Van de Meutter *et al.*, 2006; Muñoz *et al.*, 2013; Moreno *et al.*, 2019). Overall, among the most abundant passive dispersers appear to be the dormant embryos of monogonont rotifers, which are only sometimes overtaken by xerosomes of bdelloid rotifers (Rivas *et al.*, 2019), followed by cladoceran ephippia (Cáceres and Soluk, 2002; Cohen and Shurin, 2003; Moreno *et al.*, 2016). This is particularly interesting because a unique stage serves simultaneously for both spatial and temporal dispersal; both types of dispersal are recognized as risk-spreading strategies for persisting through randomly changing environmental conditions (Levin *et al.*, 1984; McPeck and Kalisz, 1998; Bohonak and Jenkins, 2003; Gremer and Venable, 2014).

On general grounds, the fact that both spatial and temporal dispersal can reduce the risk of reproductive failure suggests that they are alternative, competing life-history strategies across species (Snyder, 2006; Buoro and Carlson, 2014). The prevalence of one of the two strategies may result from a potential evolutionary trade-off imposed by physical and biochemical constraints (Rees, 1993), with the result that betting on one of these strategies compromises the alternative one. This is expected to depend on the particular traits exhibited by the propagules (*e.g.*, morphology, size), the spatial structure of the habitat (*e.g.*, isolated *vs.* connected), and the scale and predictability of temporal environmental fluctuations (Cohen and Levin, 1987; Venable and Brown, 1988; Snyder, 2006). Interestingly, Venable and Brown (1988) modeled the spatial and temporal dispersal of seeds in environments that vary both spatially and temporally in order to find the optimal allocation between the two fates in the seeds of a population. They concluded that these strategies could be partly substitutable, depending on environmental conditions. Thus, for instance, increasing either the number of patches in a spatially heterogeneous landscape or the probability of favorable conditions would cause an increase of the optimal fraction of spatial-dispersal propagules, while decreasing the effective dispersal distance and/or increasing positive spatial autocorrelation would decrease it. An optimal fraction of spatial-dispersal propagules could be achieved through phenotypic variation in the propagules, with some being oriented to spatial (*vs.* temporal) dispersal. However, it is worthy to note that there are also traits promoting a positive covariation between the two types of dispersal. For instance, some zooplankters that produce long-lasting dormant propagules would disperse greater distances by better surviving ingestion by waterfowl (Figuerola and

Green, 2002). Positive covariation might be due to genetic linkage or pleiotropy (Peiman and Robinson, 2017), or it may also arise as a joint adaptation to both spatially and temporally unpredictable environments (Venable and Brown, 1988; Snyder, 2006).

As mentioned before (in *Physiological and Cellular Processes Involved in Dormancy*, above), rotifer dormant embryos have morphological features (e.g., spines, external sculpturing, internal extra-embryonic chambers, and lipid droplets) that may contribute to enhancing buoyancy (Wurdak *et al.*, 1978; Walsh *et al.*, 2014). To study the extent of the buoyancy trait in the rotifer dormant embryos and other aquatic organisms, we searched in Clarivate Analytics' ISI Web of Science for “(dorm* OR diapaus* OR rest*) AND (float* OR buoyn*) AND egg” in the topic search query for the period 1996–2019 (Table 3). In several species, it has been reported that some dormant stages are able to float at the water surface, while others sink to the bottom. Floating dormant embryos may have a higher probability of being dispersed to other aquatic ecosystems than do the dormant embryos that sink to the sediment (Green and Figuerola, 2005; Cáceres *et al.*, 2007). The latter typically remain in the same pond or lake in which they are produced and so function as “time travelers” (Hairston, 1998). Hagiwara (1996) observed that desiccation or aeration seemed to cause the appearance of floating dormant embryos in *B. plicatilis* and *B. rotundiformis*. Thus, habitat differences, such as the frequency and duration of hydroperiods in temporary ponds, may be critical for the incidence of escaping in time (by sinking to the sediments) or in space (by floating on the water surface) in different populations, even within the same species (Table 3). In other zooplankters additional evidence exists. Cáceres *et al.* (2007) reported that the production of sinking versus floating phenotypes in *Daphnia* ephippia may be driven by both genetic and environmental factors. In addition, Ślusarczyk *et al.* (2017) suggested that the place of deposition of ephippia is determinant for sinking or floating and that this might be determined by the mother's behavior (Ślusarczyk and Pietrzak, 2009). Pinceel *et al.* (2013) observed that the dispersal phenotype in dormant cysts of the branchiopod *Branchiopodopsis wolffi* can switch between inundation cycles, which could be considered a form of repeated coin-flipping bet hedging.

Evidence of dispersal of dormant stages has been traditionally anecdotal (Darwin, 1859; Maguire, 1963; Proctor, 1964), and it has been only recently that attempts have been made to estimate colonization rates (Jenkins and Buikema, 1998; Brendonck and Riddoch, 1999; Cáceres and Soluk, 2002). In the case of rotifers, Moreno *et al.* (2016) estimated numbers up to 7000 diapausing embryos per day raining down in Spanish ponds (where the surface area of the ponds is about 6–40 ha) and quite similar numbers when considering the dispersal by waterfowl (Moreno *et al.*, 2019). Wilson and Sherman (2013) recorded rotifers in 88% of their wind-dispersed samples in a wetland area, tardigrades in 10%, and nematodes in 7.5%. Recent research has shown that rotifer dormant stages can

Table 3

Buoyancy of dormant eggs across aquatic taxa

Taxa	Proportion of buoyant eggs (%)	References
Anostraca		
<i>Artemia</i> spp.	~100	Abatzopoulos <i>et al.</i> , 2002
<i>Artemia franciscana</i>	~10%	Podrabsky and Hand, 2015
<i>Branchiopodopsis wolffi</i>	Observed	Brendonck and Riddoch, 2000
	Observed	Hulsmans <i>et al.</i> , 2007
	30	Pinceel <i>et al.</i> , 2013
<i>Thamnocephalus platyurus</i>	Observed	Mura and Nagorskaja, 1995
Notostraca		
<i>Lepidurus apus lubbocki</i>	95	Kuller and Gasith, 1996
<i>Triops cancriformis</i>	>95	Kuller and Gasith, 1996
<i>Triops granarius</i>	Observed	Kashiyama <i>et al.</i> , 2010
<i>Triops longicaudatus</i>	Observed	Scott and Grigarick, 1979
Spinicaudata		
<i>Eulimnadia antlei</i>	Observed	Belk, 1972
<i>Eulimnadia baueriana</i>	Observed	Wang <i>et al.</i> , 2014
Cladocera		
<i>Bosmina</i> sp.	Observed	Gyllström and Hansson, 2004
<i>Ceriodaphnia</i> sp.	Observed	Gyllström and Hansson, 2004
<i>Ceriodaphnia quadrangula</i>	Observed	Kaya and Erdoğan, 2014
<i>Daphnia</i> sp.	Observed	Carvalho and Wolf, 1989
	Observed	Fryer, 1996
	Observed	Wetzel, 2001
	Observed	Kerfoot <i>et al.</i> , 2004
<i>Daphnia cucullata</i>	Observed	Vaničková <i>et al.</i> , 2010
	10–80	Ślusarczyk <i>et al.</i> , 2017
<i>Daphnia galeata</i>	Observed	Keller and Spaak, 2004
	Observed	La <i>et al.</i> , 2014
	Observed	Vaničková <i>et al.</i> , 2010
<i>Daphnia hyalina</i>	Observed	Keller and Spaak, 2004
<i>Daphnia laevis</i>	Observed	Brandão <i>et al.</i> , 2014
<i>Daphnia longispina</i>	Observed	Cáceres <i>et al.</i> , 2007
	30	Ślusarczyk and Pietrzak, 2009
	Observed	Vaničková <i>et al.</i> , 2010
	Observed	Kaya and Erdoğan, 2014
<i>Daphnia magna</i>	0	Ślusarczyk and Pietrzak, 2009
	Observed	Kaya and Erdoğan, 2014
<i>Daphnia pulex</i>	20	Ślusarczyk and Pietrzak, 2009
<i>Daphnia pulex-Daphnia pulicaria</i> complex	>80	Siriani, 2017
<i>Daphnia pulicaria</i>	<10	Ślusarczyk and Pietrzak, 2009
	80	Ślusarczyk <i>et al.</i> , 2017
<i>Moina macrocopa</i>	0	Siriani, 2017
Copepoda		
<i>Centropages typicus</i>	Observed	Gaudy, 1971
Rotifera		
<i>Brachionus</i> sp.	14–16	Ito, 1958
<i>Brachionus plicatilis</i>	~10	Hagiwara, 1996
<i>Brachionus rotundiformis</i>	<5–90	Hagiwara, 1996

Database: ISI Web of Science; date of searching: March 5, 2019; searching criteria: TOPIC: ((dorm* OR diapaus* OR rest*) AND (float* OR buoyn*) AND egg); timespan: 1996–2019; output: 133 papers.

be washed far away by windstorms (Rivas *et al.*, 2018, 2019); but perhaps because of the difficulty in estimating direct rates, genetic analyses have gained popularity in estimating gene flow—a lower bound for dispersal—and in showing phylogeographies (Gómez *et al.*, 2000). Population structure studies have found evidence suggesting long-distance colonization events (Gómez *et al.*, 2000; Xiang *et al.*, 2011; Obertegger *et al.*, 2014; Fontaneto, 2019). However, correlation between genetic and geographic distances is frequently found in rotifers (Suañoni *et al.*, 2006; Gómez *et al.*, 2007; Fontaneto *et al.*, 2008). Because dormant stages are likely the main dispersion stages, this correlation suggests, on the contrary, that successful migration occurs frequently at relatively short distances (Bohonak and Jenkins, 2003; Brendonck *et al.*, 2017).

Evolutionary and Population Implications of Dormancy

The interplay between sex and dormancy

A frequent observation in facultative sexual organisms is that dormancy and sexual reproduction are often intertwined (Walsh, 2013; Gerber and Kokko, 2018). Thus, in aquatic cyclical parthenogens, sexually produced embryos typically undergo dormancy, whereas parthenogenetic eggs are subitaneous. This is the typical case of monogonont rotifers, despite the exception reported by Gilbert and Schreiber (1998), where asexual eggs going into a short dormant period were found in *Synchaeta pectinata* (for a similar case in *Artemia parthenogenetica*, see Zhang and King, 1993; or in obligately asexual populations of the cladoceran *Daphnia*, see Weider *et al.*, 1997; Innes *et al.*, 2000). A reason for the association between sex and dormancy can be found in Williams (1975, p. 23), who stated, “Sexuality should occur where there is minimal fitness heritability and maximum likelihood of new genotypes [created by recombination] being of greatest fitness.” In other words, genetically diverse offspring—the result of sexual reproduction—should be produced when environment is uncertain, and natural selection is needed to enable evolutionary adaptation. From our point of view, the prevalent association between dormancy and sex makes a “natural history” case in the controversy of the advantages of sex (*e.g.*, environmental hypotheses *vs.* genetic hypotheses) (West *et al.*, 1999).

The sex-dormancy association has a two-sided cost. On one side, it makes dormancy more costly than if rotifer dormant embryos were produced asexually (Serra and Snell, 2009); on the other, it makes sex more costly than if it were to occur without dormancy. Interestingly, when laboratory rotifer populations faced a new, experimentally controlled environment, they evolved a higher propensity to sex (Becks and Agrawal, 2010, 2012), so that the strict cost of dormancy (additional amount of resources allocated in the egg and increased generation time) plus the strict cost of sex (*e.g.*, the twofold cost) are both compensated by the advantage of fueling selection by providing genetically variable offspring.

Worthy of mention is whether dormancy might protect against sex loss. This effect has been postulated for other cyclical parthenogens (aphids, Simon *et al.*, 2002; cladocerans, Decaestecker *et al.*, 2009) and considered for the case of monogonont rotifers (Serra and Snell, 2009; Stelzer and Lehtonen, 2016). Cyclical parthenogenesis is regarded as retaining the advantages of both sexual and asexual reproduction. Asexual reproduction allows for fast population growth during most generations, while occasional sex might allow for sufficient recombination to avoid the genetic costs of asexuality (Peck and Waxman, 2000; D’Souza and Michiels, 2010). Such occasional sex is thought to provide most of the benefits of sex while avoiding most of its cost (Hurst and Peck, 1996; D’Souza and Michiels, 2010). The surprisingly low frequency of this life cycle in nature is interpreted to be due to its evolutionary instability, because the transition to an obligate asexual cycle is relatively easy (loss of sexual function, rather than the change from sexual to asexual). If the transition occurs in a genotype, its short-term advantage would drive the cyclical parthenogenetic counterparts to extinction, as observed in laboratory rotifer cultures (Fussman *et al.*, 2003). However, if sex is required for dormancy, dormancy might act as a protection against sex loss at an appropriate timescale. Recent theoretical research (Stelzer and Lehtonen, 2016) has shown that in a fluctuating environment, if sex is linked to dormancy, the “total” costs of sex (*i.e.*, accounting for the advantages provided by dormancy when conditions are bad) are decreased. The hypothesis that the association between dormancy and sex stabilizes the cyclically parthenogenetic cycle opens the question of which, if any, molecular mechanisms link sex and dormancy, and how the link is protected and how it acts as a constraint.

Population differentiation and local adaptation

The high potential for dispersal of dormant stages would lead to widespread distributions of aquatic invertebrates. However, molecular marker studies have accumulated evidence for local-scale population differentiation in rotifers (Ortells *et al.*, 2000; Gómez *et al.*, 2002, 2007; Derry *et al.*, 2003), as in other aquatic invertebrates (Lynch and Spitze, 1994; De Meester, 1996; Ventura *et al.*, 2014). These findings contributed to the formulation of the so-called dispersal-gene flow paradox. As an explanatory factor preventing immigration that would blur an initial differentiation due to a founder effect, Boileau *et al.* (1992) stated that the founder effect persisted because of the achievement of large, rather constant population sizes shortly after a new locality is colonized. This picture was completed by the monopolization hypothesis (De Meester *et al.*, 2002), which added the consideration of fast local adaptation of the founders. In fact, when studying rotifer populations in Spanish lakes, Gómez *et al.* (2002) reported levels of population differentiation consistent with colonization by a single dormant egg; and Badosa *et al.* (2017) observed that typically

low numbers of founding clones were responsible for the settlement of *Brachionus plicatilis* populations in newly built pond habitats. In this way, dormant eggs play two roles. On the one hand, they favor immigration and act against population differentiation. On the other hand, the dormant egg bank in the sediment works as a demographic and genetic buffer against newly invading genotypes and, in this manner, enhances priority effects (Hairston, 1996; Brendonck and De Meester, 2003; Latta *et al.*, 2010). Priority effects seem to predominate over forces that homogenize populations.

Genotype rescue

Dormant eggs buried in the sediment might occasionally find conditions that induce their hatching, with the result of slowing evolutionary rates if their genotypes are selected against. However, this also fuels adaptation by (1) providing genetic diversity, or (2) providing pre-adapted genotypes in conditions of fluctuating selection. These issues have not been empirically studied, yet studies have addressed whether dormant stages buried in layered lake sediments trace climate- and human-driven environmental changes (reviewed in Amsinck *et al.*, 2007). In these so-called resurrection ecology studies, dormant stages produced in historical times are induced to hatch and so uncover changes in biological traits (behavioral, physiological, or morphological or in genetic markers) that are associated with the tolerance of specific ecological conditions (Weider *et al.*, 1997; Kerfoot *et al.*, 1999; Sommer *et al.*, 2016). For instance, Weider *et al.* (1997) documented that the frequency of a genetic marker (an allele of the enzyme phosphoglucose isomerase) in the dormant population of *Daphnia galeata* in the sediments of Lake Constance (Germany) was positively related to phosphorus enrichment throughout a 35-year historical period in the lake. Also studying *Daphnia ephippia*, Kerfoot *et al.* (1999) reported historical population genetic changes related to changes in copper exposure.

Whereas there is potential for paleolimnological research in almost all aquatic organisms producing dormant stages, it has been only recently that rotifers have been used in this kind of study (Epp *et al.*, 2010; Montero-Pau *et al.*, 2011; Piscia *et al.*, 2012; Zweerus *et al.*, 2017). Paleoecological research in rotifers has been enabled, in part, by recent development of molecular techniques allowing the isolation of DNA from single rotifer dormant embryos (Montero-Pau *et al.*, 2008). The extraction of ancient DNA from dormant stages or from their remains also allows the reconstruction of microevolutionary dynamics in order to study the effects of egg banks on the genetic diversity of natural populations (*e.g.*, Limburg and Weider, 2002) or the testing of evolutionary hypotheses (*e.g.*, Red Queen hypothesis on predator-prey/host-parasite co-evolution; Kerfoot and Weider, 2004; Decaestecker *et al.*, 2007); this is now also open to rotifers. For instance, Epp *et al.* (2010) studied historical changes in the genetic structure of a *Brachionus* sp. population in Lake

Sonachi (Kenya) from dormant embryos in the sediment record. These authors showed that changes in haplotype dominance for the cytochrome oxidase *c* subunit I (COI) 153-bp amplicon were correlated with changes in sediment composition of the core that corresponded to major environmental events, such as the deposition of volcanic ash in the lake and a period of low water level. More recent research in Lake Orta (Italy) has related the abundance and genetic diversity of dormant *Brachionus calyciflorus* embryos in the sediments of the lake to its history of copper pollution and recovery (Piscia *et al.*, 2012, 2016; Sommer *et al.*, 2016; Zweerus *et al.*, 2017). Again based on COI sequencing, Piscia *et al.* (2012) found that all of the dormant embryos of *B. calyciflorus* isolated from the sediments from the pre-pollution phase to the present belonged to a unique clone, suggesting a physiological pre-adaptation of this successful clone to high levels of copper. In spite of such a low genetic variability, a later study by Zweerus *et al.* (2017) has revealed that clonal lineages established from dormant embryos isolated from sediment layers corresponding to low- to high-pollution periods performed differently under different experimental copper concentrations, but in a direction contrary to expectation under an adaptive evolution hypothesis.

Coexistence of competitors

As stressed above, rotifer dormancy can be a mechanism to avoid competition. Interestingly, when a competitor invests in dormancy and/or facultative sex, it weakens its current competition capability as a result of decreasing its growth rate; and it opens a window for its exclusion by, or coexistence with, another competitor (Montero-Pau and Serra, 2011).

A more general explanation for species diversity is the “storage effect” theory (Chesson, 2000), which explains stable coexistence of competitors by a combination of (1) environmental fluctuation, (2) specialization of competitors in relation to the values embraced by that fluctuation, and (3) the occurrence of a stage of the life cycle relatively free of competition, as in the case of dormant eggs. As evidenced by Montero-Pau *et al.* (2011), these three necessary conditions are present in monogonont rotifers. These authors studied two co-occurring cryptic species of the rotifer *Brachionus* (*B. plicatilis* and *B. manjavacas*) by counting dormant embryos in sediment cores isolated from Pétrola Lake (Spain). The two species were euryhaline and overlapped by some extent in their tolerance ranges; but, in particular, *B. manjavacas* tended to occur at higher salinities than *B. plicatilis*, which has implications for competition. Although not being a critical test for the storage effect, the study by Montero-Pau *et al.* (2011) provides evidence of a difference in the variance of dormant embryo recruitment between both species (higher for *B. plicatilis* than for *B. manjavacas*). Based on the frequencies of dormant embryos in the sediment, these authors claimed that *B. manjavacas* was the dominant competitor; and they found that,

consistent with the prediction of the storage effect theory (Chesson, 2003), this species showed lower recruitment variance. Going further, Gabaldón *et al.* (2015), using the same rotifer species, investigated differences in life-history traits related to dormancy. These authors found that *B. plicatilis* showed a higher propensity for sexual reproduction—and, thus, an earlier production of dormant embryos—as well as longer survival and a more extended hatching pattern of the dormant embryos than *B. manjavacas*, suggesting that the same lake is perceived as more uncertain by the former species. A more direct test in favor of the storage effect has been reported only once previously, in the case of two competing species of *Daphnia* with overlapping generations and variable annual recruitment to dormant egg banks (Cáceres, 1997).

Conclusions and Future Directions

Monogonont rotifer dormancy is a many-fold phenomenon implying deep metabolic changes, important effects on fitness, and implications for evolution and ecological community diversity. Despite its independent evolution in many taxa, dormancy shares many fundamental features among monogonont rotifers and other animal groups.

Embryonic dormancy appears in distantly related organisms. However, common functional pathways have been identified at molecular and cellular levels. These include arrest of similar metabolic pathways, general changes in carbohydrate and lipid metabolism, suspension of the cell cycle and stabilization of cellular structures, depression in the rate of protein turnover, and stress resistance (for review see Lubzens, 2015; Hand *et al.*, 2016; MacRae, 2016). This points out that the different metazoan phyla share a basic molecular toolbox from which they take the mechanisms needed to evolve dormancy as an organism-level trait. Despite this constraint on evolvability, monogonont dormancy shows essential particular traits, as expected from a polyphyletic phenomenon.

As a whole, dormancy seems to have evolved many times in response to important selective pressures. Faced with the question of what kind of environments have favored dormancy, it seems well established that dormancy traits are adaptations to fluctuating habitats characterized by an alternation between favorable and adverse periods. The acquisition of dormancy opens an ecological opportunity that enables organisms to colonize not only habitats that would otherwise lead to the extinction of populations at one time or another but also new environments. In this way, the adaptive value of dormancy can be understood as a case of niche expansion (*i.e.*, organisms take advantage of a new niche space previously unavailable or unattainable) that favors the *per capita* rate of increase of the population. Note that even if there were no risk of local extinction, the production of dormant stages as spatial dispersion devices would still be expected, because dispersal is an evolutionarily stable strategy (Johnson and Gaines, 1990). An even greater challenge in adapting to the temporality of habitats is environ-

mental uncertainty, by which organisms cannot anticipate the arrival of adverse conditions or whether a growing season will be favorable or unfavorable. Regarding this, recent research has shown that environmental unpredictability in growing season length is a major selective force shaping dormancy patterns in rotifers (Franch-Gras *et al.*, 2017; Tarazona *et al.*, 2017). Increased unpredictability (1) promotes the early production of dormant embryos, and (2) selects for longer dormancy, as expected from bet-hedging theory (Franch-Gras *et al.*, 2019). Short growing seasons have a similar effect (Smith and Snell, 2012). Actually, because dormancy is an adaptation to survive through conditions where fitness would be otherwise zero or close to zero, it is the target of powerful selective pressures.

In all taxa in which dormancy has evolved, it is an adaptation that allows for a high degree of isolation from the environment and resistance against severe adverse conditions without apparent aging. Indeed, while not a feature unique to monogonont rotifers, dormant embryos may serve for dispersal in both space and time. What makes these observations important is that these same adaptations across taxa lead to similar ecological consequences, among which the formation of egg banks, the coexistence of species, and the possibility of differentiation between populations and local adaptation stand out. Dormancy may also have important consequences for evolution (Hairston and De Stasio, 1988; Shoemaker and Lennon, 2018), although much less is known about how dormancy influences evolutionary forces such as genetic drift or recombination. The association between the production of dormant embryos and sexual reproduction in cyclically parthenogenetic rotifers is notable and occurs similarly in cladocerans.

Gaps and future directions

The mechanistic linkage between sexual reproduction and dormancy and the adaptive consequences of this relationship are still largely unknown. For example, with respect to the sex-blocking effect occurring after dormancy (which constrains an organism's own production of dormant embryos), it is unknown for how many generations it extends in relation to what type of habitat (Schröder and Gilbert, 2004). Also, the question is unresolved of how much sexual reproduction is enough to optimize the production of dormant embryos and generate genetic variability while avoiding its costs (Peck and Waxman, 2000). Monogonont rotifers offer an appropriate study system to address these issues.

In general, our review shows that research with rotifer dormant embryos has allowed the formulation of qualitative predictions, in the sense stated by Levins (1966): for example, when is it optimal to produce the dormant embryos—whether early or later, but not the exact timing—or when should the duration of the diapause be more or less prolonged (García-Roger *et al.*, 2017)? This is a first step, but the message we are sending here is the need for greater precision. On the one hand, it is needed for the integration of the currently unconnected bundle

of molecular mechanisms involved in dormancy to produce an organism-level trait; and, on the other hand, precision is also required to shed light on how these mechanisms allow the fine-tuned adjustment of dormancy patterns in relation to environmental and adaptive constraints. The need for a greater degree of quantification is also critical to understand the optimal combination between risk-spreading strategies (spatial or temporal) in which dormancy is involved. This is particularly interesting in those organisms in which dormant embryos serve for both spatial and temporal dispersal—as is the case with monogonont rotifers. Of major interest is the mechanistic association between sexual reproduction and dormancy. This would shed light on whether this association implies a major constraint, that an unlikely linking results in a short-term protection against sex loss and stabilizes the cyclical parthenogenesis life cycle.

Another issue that remains unresolved is the study of the effects of dormancy on metapopulation and metacommunity dynamics. Some important processes have been identified that relate dispersion, local adaptation, priority, or storage effects; but more research—fundamentally empirical—is needed for their integration. Despite all of these outstanding gaps and research challenges, we emphasize here that the solid background achieved in the study of rotifer dormant embryos augurs progress in physiological, demographic, and evolutionary frameworks. This is true especially in those topics we have identified as priorities, which must be explored in order to enhance our understanding of escaping adversity in space and time.

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