



*J. Plankton Res.* (2013) 35(4): 707–723. First published online April 7, 2013 doi:10.1093/plankt/fbt032

## REVIEW

# Resistance of dormant stages of planktonic invertebrates to adverse environmental conditions

**JACEK RADZIKOWSKI\***

DEPARTMENT OF HYDROBIOLOGY, UNIVERSITY OF WARSAW ŻWIRKI I WIGURY 101, 02-089 WARSZAWA, POLAND

\*CORRESPONDING AUTHOR: j.radzikowski@uw.edu.pl, jacekasdf@wp.pl

Received November 23, 2012; accepted March 15, 2013

Corresponding editor: Beatrix E. Beisner

Formation of highly resistant dormant forms is a well-known feature that allows inhabitants of unstable water bodies to survive periods of adverse conditions. The resistance of dormant forms of some aquatic invertebrates to different biotic and abiotic factors has been well characterized in recent decades, while the tolerance to desiccation of some rotifers has been recognized since the beginning of the 18th century. Here, I review the literature on the longevity and resistance to environmental extremes of dormant stages of planktonic animals (i.e. cladocerans, copepods, ostracods, monogonont rotifers) and some other aquatic invertebrates. Mechanisms of resistance and the evolutionary forces that shape them are also discussed.

**KEYWORDS:** dormancy; zooplankton; resistance; diapause; longevity

## INTRODUCTION

Dormancy, defined as a state of arrested development (Danks, 1987), is a trait commonly found in organisms that inhabit harsh or unstable environments. The formation of dormant stages permits survival during periods of adverse conditions that are intolerable for active individuals (Ślusarczyk, 1998; Caceres and Tessier, 2003).

The term “dormancy” refers to two distinguishable states: quiescence and diapause. Quiescence is controlled exogenously and induced directly by the occurrence of harsh environmental conditions. A quiescent organism can enter this state in many ontogenetic stages, and remains dormant only until the adverse conditions end. In contrast, diapause is controlled by an internal mechanism that is initiated by various cues, such as temperature or photoperiod, and in short-lived organisms, it is typically initiated only in a single ontogenetic stage. Breaking of diapause requires specific cues, and not necessarily the return of favorable conditions (Danks, 1987; Caceres, 1997; Ślusarczyk, 1998; Ricci, 2001). In this review, diapause and quiescence will not be (at least in the majority of cited cases) distinguished, and both phenomena will be jointly referred to as dormancy.

In different aquatic invertebrates, dormancy, where present, is expressed at various ontogenetic stages, from eggs to adults, but in a given taxon, it commonly occurs at only one of these stages (Dahms, 1995; Alekseev and Starobogatov, 1996). However, some organisms like rotifers of the class Bdelloidea, can enter dormancy (in this case, quiescence) at different ontogenetic stages: as embryos, juveniles or adults (Ricci, 2001). On the other hand, the dormant stages in Copepoda vary among the three orders that are able to enter dormancy. Many calanoid species are able to produce dormant eggs, but some calanoids can enter dormancy as nauplii or copepodids. Dormancy in cyclopoids is restricted to copepodids and adults, while different harpacticoids can enter dormancy as eggs, nauplii, copepodids or adults (Næss and Nilssen, 1991; Dahms, 1995).

It is well known that the dormant forms of many aquatic invertebrates are able to maintain viability despite being exposed to environmental extremes that would kill their active forms. Since van Leeuwenhoek, who in 1701 reported his observation of “animalcules” that survived desiccation and were “resurrected” following the addition of water to a sample of dust from a dry gutter [as suggested by Tunnacliffe and Lapinski (Tunnacliffe and Lapinski, 2003), these were probably quiescent adult bdelloid rotifers *Philodina roseola*], there has been a considerable amount of research on the resistance of dormant forms of aquatic invertebrates.

The aim of this review is to not only describe the survival abilities of dormant forms produced by particular taxa of aquatic (mostly planktonic) invertebrates, but also to relate their resistance to the adverse conditions they typically face in their natural habitats. Animals that inhabit shallow or temporary water bodies, characterized by variable environmental conditions, might experience higher selective pressure on the resistance of their dormant stages to environmental extremes (such as high or low temperatures, desiccation or freezing) than dormant forms of organisms inhabiting more stable habitats, e.g. deep lakes or oceans. On the other hand, extensive tolerance of dormant stages that evolved in prehistoric times could have been gradually lost by lineages that have colonized more favorable habitats. Both of the above scenarios are possible, and the evidence supporting each is presented and discussed below.

Most of the reviewed studies investigated dormant forms of zooplankton (Cladocera, Copepoda, Rotifera), while a few have examined benthic species (e.g. Ostracoda) and some species that dwell in the water retained by mosses and soil (i.e. rotifers of the class Bdelloidea). Crustaceans and rotifers are not the only groups of planktonic organisms that are able to enter dormancy. The production of dormant forms is also a common feature in phytoplankton (Rengefors *et al.*, 1998; McQuoid *et al.*, 2002) and ciliates (reviewed by Corliss and Esser, 1974; Gutiérrez *et al.*, 2001; Verni and Rosati, 2011). Jellyfish from the class Scyphozoa are also able to produce dormant podocysts (Arai, 1997, 2009), but there is a dearth of data on jellyfish dormant stages (Boero *et al.*, 2008; Arai, 2009), so they have not been considered in this review.

## MECHANISMS OF RESISTANCE

A thorough description of the anatomical, biochemical and physiological adaptations contributing to the resistance of dormant stages is beyond the scope of this review, but their most significant traits that allow aquatic invertebrates to survive harsh environmental conditions will be briefly described.

Many planktonic invertebrates (e.g. cladocerans, calanoid copepods or anostracans) that produce diapausing stages survive periods of adverse conditions in the form of dormant eggs or cysts (Dahms, 1995; Ślusarczyk, 1999; Clegg and Trotman, 2002). The dormant eggs of numerous planktonic taxa are produced bisexually, while their subitaneous, directly developing eggs are produced parthenogenetically. Although there are some exceptions, this switch from parthenogenetic to bisexual reproduction is observed in most cladocerans (Fryer, 1996) and in

monogonont rotifers (Gilbert, 1974). On the other hand, the eggs of copepods, both subitaneous (with a few exceptions; Sarvala, 1978) and dormant, are produced bisexually (Dahms, 1995). In Ostracoda, dormant eggs can be produced both bisexually and by parthenogenesis (Dole-Olivier *et al.*, 2000; Vandekerkhove *et al.*, 2013). Among anostracans, notostracans and conchostracans, different taxa are able to produce dormant cysts by parthenogenesis or in a bisexual way (Bell, 1982).

In contrast to subitaneous eggs, diapausing eggs are often shielded by thick envelopes and shells that help to protect them against the negative effects of adverse environmental factors, such as drying, freezing, mechanical damage, microbial invasion, predation, UV radiation or harmful chemicals (Seidman and Larsen, 1979; Fryer, 1996; Tanguay *et al.*, 2004; Makrushin and Lyanguzova, 2006; Alekseev *et al.*, 2010). Dormant eggs have been shown to possess thicker and more complex egg envelopes in freshwater and marine calanoid copepods (e.g. Hairston and Olds, 1984; Santella and Ianora, 1990; Ianora and Santella, 1991; Couch *et al.*, 2001; Dharani and Altaff, 2004), monogonont rotifers (Gilbert, 1974; Pourriot and Snell, 1983; Gilbert and Wurdak, 1978; Wurdak *et al.*, 1978), ostracod *Heterocypris incongruens* (Özuluğ and Suludere, 2012) and freshwater cladocerans of the genus *Daphnia* (Schultz, 1977; Seidman and Larsen, 1979). In contrast to those of monogonont rotifers and calanoid copepods, the dormant eggs of *Daphnia* (as well as some other cladocerans) are also covered by an additional external envelope derived from carapace, called the ephippium (Schultz, 1977; Seidman and Larsen, 1979). Thick and multilayered envelopes, similar to those protecting calanoid, monogonont and cladoceran eggs, also protect diapausing embryos of the anostracan *Artemia* (Morris and Afzelius, 1967; Clegg and Trotman, 2002; Tanguay *et al.*, 2004). In general, dormant eggs/cysts of anostracans and other large phyllopods, i.e. notostracans and conchostracans (Laevicaudata and Spinicaudata), are also covered by thick outer protective shells (reviewed by Fryer, 1996).

These shells and envelopes allow latent eggs of some planktonic invertebrates to survive passage through the guts of many invertebrates and vertebrates. *Artemia* cysts, which are resistant to avian digestive enzymes (Horne, 1966), can survive gut passage in various (mostly water) birds (Proctor, 1964; Malone, 1965; Proctor and Malone, 1965; Green *et al.*, 2005; Sánchez *et al.*, 2007) and crayfish (Moore and Faust, 1972). Dormant embryos of other anostracans, such as fairy shrimps *Streptocephalus texanus* and *Thamnocephalus platyurus*, *Streptocephalus seali* and *Branchinecta coloradensis*, may survive gut passage in ducks (Proctor *et al.*, 1967), crayfish (Moore and Faust, 1972)

and salamanders (Bohonak and Whiteman, 1999), respectively.

Latent eggs of cladocerans of the genera *Daphnia*, *Moina*, *Latonopsis*, *Macrothrix* and *Sida* were found to survive passage through water bird guts (Proctor, 1964; Proctor and Malone, 1965; Mellors, 1975), and the dormant eggs of some species (of the genera *Bythotrephes* and *Daphnia*) can also survive passage through the guts of fish (Mellors, 1975; Jarnagin *et al.*, 2000), rats and newts (Mellors, 1975).

Resistance to digestion in the digestive tracts of birds is also a property of the latent eggs of ostracods of the genus *Cypris*, *Cypridopsis* and *Cyprinotus* (Proctor, 1964; Proctor and Malone, 1965), and calanoid copepods of the genus *Eudiaptomus* (Bartholmé *et al.*, 2005). Latent eggs of the calanoid species *Labidocera aestiva* were also shown to survive passage through polychaete guts (Marcus, 1984). However, invulnerability to predator gut passage is not restricted to the dormant eggs of aquatic invertebrates. Survival of various adult and juvenile ostracods has been observed after they had been eaten and expelled by frog tadpoles and mice (Lopez *et al.*, 2002), fish (Vinyard, 1979; Aarnio and Bonsdorff, 1997) and birds (Proctor *et al.*, 1967; Frisch *et al.*, 2007).

Frisch *et al.* (Frisch *et al.*, 2007) also observed survival of adult harpacticoid copepods after passage through bird guts, and subitaneous eggs of two monogonont rotifers (*Brachionus calyciflorus* and *Epiphanes macrourus*) remained viable following gut passage in fish larvae (Saint-Jean and Pagano, 1995). Moreover, there are numerous records of subitaneous eggs of cyclopoid, harpacticoid and calanoid copepods (freshwater and marine) surviving passage through the guts of fish (e.g. Gliwicz and Rowan, 1984; Redden and Daborn, 1991; Conway *et al.*, 1994; Saint-Jean and Pagano, 1995; Bartholmé *et al.*, 2005). In contrast, there have been no reports that the subitaneous eggs of cladocerans are resistant to digestion; Bartholmé *et al.* (Bartholmé *et al.*, 2005) and Saint-Jean and Pagano (Saint-Jean and Pagano, 1995) observed 100% mortality of these eggs of *Daphnia*, and *Moina* and *Diaphanosoma*, respectively, after fish gut passage.

Resistance to digestion in the predator gut may facilitate dispersal (by animal vectors, especially birds) of the aforementioned dormant forms, thus allowing aquatic invertebrates to colonize isolated water bodies, a feat that cannot be achieved by active forms (e.g. Malone, 1965; Proctor and Malone, 1965; Moore and Faust, 1972; Sánchez *et al.*, 2007).

While the robust structure of egg envelopes can permit survival under many adverse conditions, neither ephippia nor the outer coverings of latent eggs can assure complete resistance to drying (Fryer, 1996); they

only slow down this process (Clegg, 2005; Dobrynina, 2011). When taken out of their aquatic environment, latent eggs do lose their internal water and desiccate. In some species, dried dormant eggs lose their viability, but in many others, they are able to remain viable and give hatchlings after rehydration. The ability to survive in a desiccated state is probably correlated with the egg's yolk structure: drought-resistant eggs typically have a homogeneous fine-grained yolk without vacuoles, while the yolks of drought-vulnerable species, such as the cladocerans *Leptodora*, *Holopedium* and *Sida*, are coarse grained and have vacuoles (e.g. Makrushin 1978, 1981; Fryer, 1996; Korovchinsky and Boikova, 1996). Makrushin (Makrushin, 1978) suggested that vacuole membranes and coarse yolk grains are mechanically damaged by forces generated during the drying process (leading to egg death), while homogenous, fine-grained yolk is not damaged by desiccation.

The presence of particular proteins (e.g. heat-shock proteins HSP60, p26), disaccharides (trehalose) and other compounds (e.g. glycerol) that can act as cryoprotectants is also crucial for the survival of latent eggs in a dry state (Clegg, 2001; Clegg and Trotman, 2002; Lapinski and Tunnacliffe, 2003; Tunnacliffe and Lapinski, 2003; Tunnacliffe *et al.*, 2005; Watanabe, 2006). For more information on molecular properties of diapause, see the review by MacRae (MacRae, 2010). The occurrence and protective role of such compounds has been fairly well studied, especially in *Artemia* cysts (reviewed by Clegg and Trotman, 2002), but also in monogonont rotifer eggs (e.g. Caprioli *et al.*, 2004; Clark *et al.*, 2012), the cladoceran *Daphnia* (e.g. Pauwels *et al.*, 2007) and notostracan *Triops* eggs (e.g. Hengherr *et al.*, 2011a).

The biochemical mechanisms of resistance in dormant adult bdelloid rotifers are fairly similar to those observed in dormant eggs of planktonic crustaceans and monogononts, except that a late embryogenesis protein rather than trehalose is probably responsible for their anhydrobiotic abilities (Caprioli *et al.*, 2004; Tunnacliffe *et al.*, 2005). While drying, the bdelloid adult withdraws its head and foot and contracts its body into a compact shape called a "tun". The dormant animal is not protected by any kind of cyst and remains permeable to gases and liquids (Hickernell, 1917; Gilbert, 1974; Ricci and Caprioli, 2005).

Copepods that enter dormancy as adults or copepodids usually lower their metabolism, empty their guts and reduce movements of the intestines. The production of digestive enzymes is also reduced, and the size and number of lipid globules in the body increases. In some taxa, the body can be encysted, while in others, dormant animals are not protected by cysts, but they

may become rigid and colorless (Dahms *et al.*, 1990; Næss and Nilssen, 1991; Dahms, 1995).

## THE LIMITS OF TOLERANCE

The anatomical and physiological traits described above allow some aquatic invertebrates to produce dormant forms that can tolerate many kinds of environmental extremes, including stresses that they will never encounter in their natural habitats (Table I).

The dormant forms of some planktonic invertebrates are among the most highly resistant ontogenetic stages in the whole animal kingdom, and Clegg and Trotman (Clegg and Trotman, 2002) have suggested that the most resistant of these is probably the cyst of the anostracan *Artemia*. Luyet and Gehenio (Luyet and Gehenio, 1940) reported [after Gilchrist, 1939 (unpublished)] the survival of dried *Artemia* cysts after exposure to liquid air ( $-195^{\circ}\text{C}$  to  $-215^{\circ}\text{C}$ ). Subsequently, Skoultchi and Morowitz (Skoultchi and Morowitz, 1964) exposed dry *Artemia* cysts, derived from the Great Salt Lake, to temperatures near absolute zero ( $-271^{\circ}\text{C}$ ) for 6 days and then observed hatching levels similar to untreated controls. A smaller proportion of wet-frozen *Artemia salina* cysts was found to survive exposure to temperatures as low as  $-196^{\circ}\text{C}$  (Hempel-Zawitkowska, 1971a, b). *Artemia* cysts have also been shown to be resistant to high temperatures. More than one-quarter of dried *A. salina* cysts hatched after 1.5-h-long exposure to  $103.5^{\circ}\text{C}$  (Hinton, 1968), and after being held at  $110^{\circ}\text{C}$  for 10 min, 99% of dried *Artemia franciscana* cysts gave hatchlings (Mertens *et al.*, 2008). In the same study, a small percentage of dried cysts of *A. franciscana* survived slow heating to  $130^{\circ}\text{C}$  (Mertens *et al.*, 2008). *Artemia* cysts can also withstand levels of desiccation that do not occur naturally (residual water content of  $<0.0069$  g/g), without any loss of viability, compared with controls (Clegg *et al.*, 1978). It is noteworthy that to achieve such a low water content, cysts were subjected to repeated cycles of gas bombardment at temperatures as low as  $-196^{\circ}\text{C}$ .

The dormant forms of some other anostracan, but also notostracan and conchostracan species, are also highly resistant to environmental extremes. Dried cysts of the anostracan *Branchipus schaefferi* survived slow heating to  $110^{\circ}\text{C}$  (99% hatching) and almost 10% were found to remain viable after 10-min exposure to  $130^{\circ}\text{C}$  (Mertens *et al.*, 2008), while dried eggs of the notostracan *Triops* could withstand temperatures of up to  $1^{\circ}\text{C}$  below boiling point for at least 16 h (Carlisle, 1968). Hempel-Zawitkowska (Hempel-Zawitkowska, 1971b) held desiccated eggs of *Triops cancriformis* at extremely low temperatures ( $-79^{\circ}\text{C}$  and  $-196^{\circ}\text{C}$ ) and observed

Table I: Thermal resistance of dormant forms of some aquatic invertebrates

Species	Dormant stage	Dry/wet	Temp.	Exposure time	Source	Comments
Crustacea: Anostraca						
<i>Artemia</i> sp.	Embryo	Dry	-271°C	6 days	Skoultschi and Morowitz (1964)	Probably <i>A. fertilis</i> (now <i>A. franciscana</i> )
<i>A. salina</i>	Embryo	Wet	-196°C	6 h	Hempel-Zawitkowska (1971a, b)	
<i>A. salina</i>	Embryo	Dry	103.5°C	1.5 h	Hinton (1968)	
<i>A. franciscana</i>	Embryo	Dry	110°C	10 min	Mertens <i>et al.</i> (2008)	
<i>A. franciscana</i>	Embryo	Dry	130°C	Seconds	Mertens <i>et al.</i> (2008)	Cysts heated (~4°C min <sup>-1</sup> ) to this temperature from 22°C and cooled after reaching 130°C
<i>Branchipus schaefferi</i>	Embryo	Dry	130°C	10 min	Mertens <i>et al.</i> (2008)	
Crustacea: Notostraca						
<i>Triops cancriformis</i>	Embryo	Dry	-196°C	5 h	Hempel-Zawitkowska (1971b)	
<i>Triops</i> sp.	Embryo	Dry	99°C	16 h	Carlisle (1968)	After moving the boiling point (change of pressure) to 105°C, cysts survived exposure to 104°C
Crustacea: Conchostraca						
<i>Eocyclus orientalis</i> and <i>Leptestheria dahalacensis</i>	Embryo	Dry	70°C	Unknown	Dobrynina (2011)	
Crustacea: Cladocera						
<i>Daphnia magna</i>	Embryo	Dry	-84°C	3 h	Radzikowski (unpublished data)	
<i>D. magna</i>	Embryo	Dry	110°C	2.5 h	Radzikowski (unpublished data)	Ephippia with eggs were heated slowly (3°C min <sup>-1</sup> ) from 20°C to 110°C, with a total exposure time of 3 h
Crustacea: Ostracoda						
<i>Eucypris virens</i>	Embryo	Dry	-72°C	3 weeks	Vandekerkhove <i>et al.</i> (2013)	
Rotifera: Bdelloidea						
<i>Philodina acuticornis odiosa</i>	Adult	Dry	-150°C	10–15 min	Koehler (1987)	
<i>Habrotrocha constricta</i> and <i>Philodina roseola</i>	Adult	Dry	-273.1°C	~2 h	Becquere (1950) (in Keilin, 1959, Crowe, 1971)	
<i>Adineta gracilis</i> , <i>Rotifer vulgaris</i> , <i>Callidina angusticollis</i>	Adult	Dry	-269°C	~8 h	Becquerel (1936) (in Luyet and Gehenio, 1940)	Liquid helium temperature may vary from around -269°C to -272°C
<i>Callidina</i> sp. and <i>Adineta</i> sp.	Adult	Dry	151°C	15 min	Rahm (1924) (in Crowe, 1971)	
<i>Philodina roseola</i>	Adult	Dry	130°C	10 min	Mertens <i>et al.</i> (2008)	
Rotifera: Monogononta						
<i>Brachionus plicatilis</i>	Embryo	Dry	-80°C	24 h	Balompapueng <i>et al.</i> (1997)	

In each case, at least one specimen exposed to presented temperatures survived the treatment (or at least one egg/cyst gave hatching)

rates of hatching that were even higher than in untreated controls, whereas all *Triops* eggs frozen in water failed to survive any of these low temperature treatments. Dormant forms of conchostracan species are also highly thermoresistant; dry eggs of *Eocyclus orientalis* and *Leptestheria dahalacensis* were found to survive periodic exposure to 70°C (Dobrynina, 2011).

The bdelloid rotifers that often inhabit water stored by mosses, lichens and soils (Ricci and Caprioli, 2005) represent another phylogenetically distinct group of aquatic invertebrates that is resistant to drying and other abiotic extremes (Ricci *et al.*, 1987; Ricci and Caprioli, 1998). In contrast to the dormant embryos of anostracans and notostracans, bdelloids survive periods of adverse conditions as quiescent individuals at many

stages of their ontogenetic development. Studies on the resistance of bdelloid rotifers to unfavorable abiotic conditions, starting with the classic observation of *P. roseola* “resurrection” by van Leeuwenhoek, were conducted by scientists as early as in the 18th and 19th centuries (reviewed by Keilin, 1959; Tunnacliffe and Lapinski, 2003). One of the most significant of these early studies is described in Broca’s report from 1860. Desiccated adult bdelloid rotifers survived 82-day-long storage under vacuum and a subsequent 30-min exposure to 100°C. Even more surprising results were obtained by Murray (Murray, 1909), who studied Antarctic bdelloids found in melted ice with pieces of plant matter derived from a frozen (probably for many years) shallow lake. Many of these dormant animals not only withstood

Antarctic temperatures (approx.  $-40^{\circ}\text{C}$  at that time), but also tropical temperatures (as they were sent to Sydney, Australia) and cycles of freezing and thawing, drying and freezing, or drying and heating to temperatures of  $\sim 100^{\circ}\text{C}$ .

Other studies on the resistance of dormant forms of bdelloid rotifers to extreme temperatures and other unfavorable conditions were conducted in the first half of the 20th century. The experiments of Rahm (Rahm, 1920, 1921, 1922, 1923, 1924, 1926, after Crowe, 1971 and Luyet and Gehenio, 1940) showed that dry adult bdelloid rotifers (Rahm used *Adineta* and *Callidina* species in part of his studies, and he also tested tardigrades, which exhibited similar resistance) could tolerate high doses of UV and X radiation, exposure to temperatures of liquid air ( $-190^{\circ}\text{C}$  to  $-200^{\circ}\text{C}$ ) for 21 months, liquid hydrogen ( $-253^{\circ}\text{C}$ ) for 26 h and liquid helium ( $-269^{\circ}\text{C}$  to  $-272^{\circ}\text{C}$ ) for almost 8 h. He also observed viable bdelloids after 15-min exposure to  $151^{\circ}\text{C}$ .

Similar experiments to those of Rahm were later conducted by Becquerel, who demonstrated the survival of dried rotifers of species *Habrotrocha constricta* and *P. roseola* after cooling to temperatures slightly above ( $0.05^{\circ}\text{C}$ ) absolute zero (Becquerel, 1950 after Crowe, 1971). Previously, he reported that dry bdelloids (*Adineta gracilis*, *Callidina angusticollis* and *Rotifer vulgaris*) could survive exposure to liquid nitrogen ( $-196^{\circ}\text{C}$ ) for 20 days followed by transfer to liquid helium ( $-269^{\circ}\text{C}$ ) for 7.5 h (Becquerel, 1936 after Luyet and Gehenio, 1940).

Further studies on bdelloid resistance to extreme abiotic conditions have been conducted in recent years. Dry adult rotifers *Macrotrachela quadricornifera* were found to be able to withstand 1-h-long exposure to 180 nm UV radiation (Ricci *et al.*, 2005), altered gravity (hypergravity: 20 G), temperature changes from  $-80^{\circ}\text{C}$  to  $+70^{\circ}\text{C}$ , extreme conditions experienced during an ascent in a stratospheric balloon (40 km above ground with accompanying changes in temperature, radiation and pressure) and transport in a space shuttle, where they were subjected to hypogravity and strong vibrations (Ricci and Caprioli, 1998; Caprioli *et al.*, 2002).

High thermal resistance was also demonstrated in another bdelloid rotifer, *P. roseola*: a high percentage of desiccated adults of this species survived both slow and rapid heating to  $110^{\circ}\text{C}$  and 10-min-long exposure to this temperature, while  $\sim 2\%$  remained viable after similar treatment with a final temperature of  $130^{\circ}\text{C}$  (Mertens *et al.*, 2008). On the other hand, Newsham *et al.* (Newsham *et al.*, 2006) found that under dry conditions, an unspecified bdelloid rotifer could tolerate exposure to  $-80^{\circ}\text{C}$  for more than 6 years. Also Koehler (Koehler, 1987) observed that after slowly cooling medium

containing *Philodina acuticornis odiosa* adults to  $-100^{\circ}\text{C}$  and then placing them at a temperature of  $-150^{\circ}\text{C}$  for 10–15 min, 10–15% of the treated animals survived.

The resistance of the dormant stages of another rotifer class, Monogononta, has been studied far less extensively than that of the bdelloids (Ricci and Caprioli, 2005). Some data on the resistance of monogonont diapausing eggs are available from studies on storage methods for dormant eggs of rotifers of the genus *Brachionus*, which are widely used in aquaculture as fish food. The latent eggs of *Brachionus plicatilis* and *B. rotundiformis* survived lyophilization and canning without reduction in their viability (Hagiwara *et al.*, 1997). Dry diapausing eggs of *B. plicatilis* could survive 24-h-long exposure to  $-80^{\circ}\text{C}$  (Balompapueng *et al.*, 1997), while wet eggs were able to tolerate storage at  $-14^{\circ}\text{C}$  for at least 3 months (Lubzens *et al.*, 1980). The tolerance of diapausing *Brachionus* (and other monogonont rotifers) eggs to high temperatures remains to be determined.

Few studies have examined the thermal resistance of dormant forms of cladocerans. Meijering (Meijering, 2003) reported that the latent eggs of some cladocerans from arctic regions (*Daphnia pulex*, *Macrothrix hirsuticornis*, *Chydorus arcticus* and *Alona quadrangularis*) could survive at least 18 years of storage at  $-18^{\circ}\text{C}$ , which is not surprising. On the other hand, dried dormant stages of many cladoceran species can survive tropical temperatures of Australia (Sars, 1885, 1888). The only thorough studies to identify the limits of cladoceran thermoresistance have examined *Daphnia*; Turowska (Turowska, 2012) reported hatching of *D. pulex* species complex neonates after 30-min-long exposure of dry ephippia to temperatures of  $-84$  and  $+90^{\circ}\text{C}$ . The production of hatchlings has also been observed after 3 h exposure of dry *D. longispina* ephippia to these temperatures (Radzikowski, unpublished data). In the same experiment, dry dormant eggs of *D. magna* were found to survive exposure to  $110^{\circ}\text{C}$  in addition to the aforementioned high and low temperatures (Radzikowski, unpublished data).

Data on the thermal resistance of copepod dormant forms are even more scarce. Brewer (Brewer, 1964) simulated winter and summer conditions of vernal-autumnal ponds near Chicago and subjected latent eggs of the calanoid copepod *Diaptomus stagnalis* to temperatures ranging from  $-25^{\circ}\text{C}$  to  $+35^{\circ}\text{C}$  for periods of up to 35 days. A proportion of the eggs were still viable in both cases, but other results from the same study suggested that slightly higher and lower temperatures probably kill all of them.

The available studies conducted on ostracods have concentrated mainly on their resistance to conditions typical of harsher climates rather than extreme and unusual temperatures. For example, latent eggs of

*H. incongruens*, an ostracod species that inhabits both ephemeral and permanent ponds in temperate parts of North America, remained viable after being dried at 40°C or frozen (wet and dry) at -18°C for 48 h (Angell and Hancock, 1989). In addition, other ontogenetic stages of Ostracoda have been shown to survive drying and exposure to high and low temperatures; Horne (Horne, 1993) exposed juveniles of the meiobenthic species *Candona patzcuaro*, present in dry soil samples from a temporary playa lake in Texas, to -20°C for 30 months or +32°C for 18 months and observed their survival (some surviving animals were also recorded after 24 months at 32°C, but all died with longer exposure). Recently, Vandekerkhove *et al.* (Vandekerkhove *et al.*, 2013) exposed dormant eggs of ostracods to more extreme factors. Dry *Eucypris virens* eggs remained viable after exposure to low temperatures (3 weeks; -72°C) and UV-B radiation (10 h), while wet eggs survived exposure to avian digestive enzymes and highly saline water.

## HOW LONG CAN THEY WAIT?

From an evolutionary point of view, the formation of long-lived dormant forms of aquatic invertebrates is probably an adaptation for survival in temporarily uninhabitable environments, where dormant forms represent a multiannual egg bank, an assemblage of dormant stages that lie in the sediments, similar to a plant seed bank (De Stasio, 1989; Lampert, 1995). The optimal length of dormancy and the possible use of bet-hedging strategies should be correlated with the level of environmental variability (for more information on bet-hedging and optimal dormancy length, see Cohen, 1966; Ellner, 1985; Caceres and Tessier, 2003; Evans and Dennehy, 2005; Lalonde and Roitberg, 2006). However, there is some evidence, presented later in this review, that dormancy may persist for decades or even centuries, which raises the question of whether this extra long dormancy is really adaptive, or is just an artifact. One example is the case of viable latent copepod or cladoceran eggs that can survive in lake sediments, probably without any chance of being unburied, for many decades (e.g. Hairston *et al.*, 1995; Caceres, 1998).

On the other hand, as stated by Hinton (Hinton, 1968), the maximal viability of a dormant organism (i.e. an organism in the cryptobiotic state) could be indefinite if it is protected against incidental oxidations and reductions. Therefore, under specific conditions, dormant forms might remain viable for an indeterminate time. Since such protective conditions presumably do not occur in nature, the survival of dormant stages

decreases with time. For this reason, the record values cited in this review are taken only from studies in which no special storage conditions, which would eliminate the processes described above, were employed.

It is clear that Hinton's statement should only be true in cases in which the metabolism of the dormant organism is halted. Otherwise metabolic activity would, in time, lead to the total exhaustion of energy storage components and, as a consequence, to death. For this reason, metabolically active dormant forms of the cladocerans *Bythotrephes longimanus* and *Leptodora kindtii*, kept in water containing dissolved oxygen, survived only ~9 and 12 months, respectively (Andrew and Herzig, 1984). Also, quiescent eggs of three marine calanoid copepod species (*Acartia tonsa*, *Centropages hamatus*, *L. aestiva*) were found not to halt their metabolic processes, even when maintained in anoxic water (they had probably switched to anaerobic metabolism), which caused the death of a significant proportion after 32 days of exposure to these conditions (Marcus *et al.*, 1997).

On the other hand, Clegg (Clegg, 1997) observed signs of metabolism in fully hydrated *A. franciscana* cysts kept in anoxic conditions, but only for the first few days of the experiment. He subsequently failed to detect any signs of metabolism, although at least 60% of the cysts tested survived for 4 years under these conditions. It was suggested that a similar reversible metabolic standstill under anoxic conditions occurs in the dormant stages of other organisms (e.g. copepods).

Field research combined with accurate dating is the only, though not completely reliable, way to assess the maximum longevity of dormant forms under natural conditions. Some old and viable dormant forms are also occasionally found in laboratory storage rooms, where they avoid temperature changes, freezing/thawing or drying/wetting cycles that occur in nature, which makes the data on their longevity incomparable with that obtained from field work. The main problem in assessing the longevity of dormant stages of aquatic invertebrates is the difficulty in identifying their maximum "natural" longevity. It is impossible to know whether the observed "record age" is near the maximal value, or if the oldest viable dormant forms of a particular type have yet to be found. While dormant bacteria and embryonic dormant forms of plants (their seeds) have been found to be extremely long-lived, the maximum longevity data obtained for aquatic invertebrate dormant stages are less striking, but still impressive.

*Bacillus* sp. bacteria have been resurrected from dormant stages isolated from a 250-million-year-old salt crystal (Vreeland *et al.*, 2000), while Schubert *et al.* (Schubert *et al.*, 2009) cultured *Archaea* that survived as "starvation-survival forms" for ~30 000 years.

The oldest seeds to have been germinated and grown into healthy plants were claimed to be from the arctic tundra lupine (*Lupinus arcticus*) that were initially dated at 10 000 years old (Porsild *et al.*, 1967). However, more recent radiocarbon dating of seeds from the same excavation revealed that they originated from the modern age (Zazula *et al.*, 2009). There are also reports (as yet undisputed) describing the germination of 1000-year-old seeds of sacred lotus *Nelumbo nucifera* (Shen-Miller *et al.*, 1995) and 2000-year-old palm *Phoenix dactylifera* seeds (Sallon *et al.*, 2008). The oldest known viable dormant forms of planktonic invertebrates are considerably younger (Table II).

Hairston *et al.* (Hairston *et al.*, 1995) estimated that the oldest viable dormant eggs of the calanoid copepod *Diaptomus sanguineus* found in Bullhead Pond, RI, USA, were 332 years old, while the oldest viable dormant eggs of the calanoid copepod *Boeckella poppei*, found in shallow Xihu Lake on King George Island, Antarctica, were estimated to be 195 years old (Jiang *et al.*, 2012). Hairston and Van Brunt (Hairston and Van Brunt, 1994) found viable eggs of another calanoid, *Leptodiaptomus minutus*, that were 22 years old, in Oneida Lake, NY, USA. The oldest viable calanoid dormant forms from a marine/brackish water ecosystem were isolated in the Pettaquamscutt estuary, and these were found to be at least 40 years old, but the hatchlings died before they could be identified to the species level (Marcus *et al.*, 1994). Also Katajisto (Katajisto, 1996) reported the hatching of *Acartia bifilosa* and *Eurytemora affinis* from brackish Baltic Sea sediments, estimated to be up to 19 years old.

The oldest known viable cladoceran ephippial eggs are those of *Daphnia pulicaria* and *Daphnia galeata mendotae* found in sediments of Oneida Lake by Caceres (Caceres, 1998). Hatching of eggs older than 125 years was observed for both of these species (Caceres, 1998). Several years earlier, Carvalho and Wolf (Carvalho and Wolf, 1989) found viable latent eggs of *D. galeata* and *D. hyalina* in Kellerssee (north Germany), which were estimated to be up to 70 years old.

For diapausing eggs of cladocerans other than *Daphnia*, there have been claims of viability remaining for up to 14 years for *Ceriodaphnia pulchella* (Moritz, 1987), 55 years for *Macrothrix* sp. (el Moghraby, 1977), 30 years for *Polyphemus pediculus* (Pesta, 1925 after Butorina, 2003), 15–21 years for *Bosmina* sp. (Katajisto, 1996; Piscia *et al.*, 2012) and 8–10 years for *Podon* sp. and *Evadne* sp. (Viitasalo and Katajisto, 1994).

Dormant anostracan forms have been found to maintain viability for at least a dozen years. A small fraction (0.8%) of dry *A. salina* cysts stored at room temperature, hatched after 15 years (Clegg, 1967). Long-term survival

of dry cysts kept at room temperature (within samples of dried mud) has also been recorded for *Branchinecta packardii* (16 years), *B. mackini* (14 years) and *T. platyurus* (13 years; Dexter, 1973). On the other hand, 19% of wet-stored cysts of *S. seali*, kept in darkness at room temperature, displayed viability after 15 years (Moore, 1979).

Dexter (Dexter, 1973) observed 14-year-long survival of dry notostracan *Triops longicaudatus* cysts, while Hann and Lonsberry (Hann and Lonsberry, 1991) obtained hatchlings from dry cysts of *Lepidurus couesii* that had been stored for 2 years. The only data on the longevity of latent conchostracan eggs are those of Mattox and Velardo (Mattox and Velardo, 1950), who observed hatching from eggs of *Caenestheriella gynecia* stored under laboratory conditions for 8 years in water or 5 years dry, and Dobrynina (Dobrynina, 2011), who obtained hatchlings from *E. orientalis* and *L. dahalacensis* eggs kept for more than 10 years in cold (2–5°C) water in the laboratory.

The study of Boulton and Lloyd (Boulton and Lloyd, 1992), which appears to be the only one to have examined ostracod longevity, detected the emergence of unidentified ostracods (among many other aquatic invertebrates) from soil samples collected from a floodplain in South Australia, which had last experienced flooding 14 years before sampling.

With regard to rotifers, the age of the oldest known viable latent eggs of monogononts is several times that of quiescent bdelloid adults. Probably, the oldest eggs that have produced hatchlings are those of *B. plicatilis*, found by Fu (Fu, 1991 after Kotani *et al.*, 2001) in sediments from Kai-ike Pond located in Japan, that were up to 100 years old and those of *B. calyciflorus*, dated to be  $98 \pm 11$  years old, found in sediments from deep Lake Orta in north Italy (Piscia *et al.*, 2012). Kotani *et al.* (Kotani *et al.*, 2001) hatched one *Brachionus* sp. individual from eggs taken from the aforementioned pond in Japan, which were estimated to be 65–69 years old. A noteworthy case of long-lived latent monogonont eggs originating from a freshwater habitat is that of *Polyarthra dolichoptera* raised from eggs of around 35 years old obtained from Lake Zurich, Switzerland (Nipkow, 1961). Individuals of *Brachionus* sp. have been hatched from sediments dated at more than 40 years old collected from a brackish water estuary (Marcus *et al.*, 1994), and viable dormant eggs of *Synchaeta* sp. were found in brackish Baltic Sea sediments estimated to be 18–22 years old (Katajisto, 1996).

As mentioned previously, quiescent bdelloid adults lose viability much faster than diapausing monogonont eggs. Hickernell (Hickernell, 1917) mentioned “authenticated records” showing that *Philodina* sp. specimens withstood 27-year-long desiccation, while one modern study



Table II: The maximal reported age of viable dormant forms of selected aquatic invertebrates

Species	Dormant stage	Storage place and conditions	Age/storage length	Source	Comments
Crustacea: Anostraca					
<i>Artemia franciscana</i>	Embryo	Cysts stored in deoxygenated water, laboratory conditions, room temperature (20–23°C)	4 years	Clegg (1997)	
<i>Thamnocephalus platyurus</i>	Embryo	Cysts stored in dry mud; room temperature	13 years	Dexter (1973)	
<i>Branchinecta mackini</i>	Embryo	Cysts stored in dry mud; room temperature	14 years	Dexter (1973)	
<i>Artemia salina</i>	Embryo	Dry cysts stored in room temperature	15 years	Clegg (1967)	
<i>Streptocephalus seali</i>	Embryo	Cysts stored in water, at room temperature and in darkness	15 years	Moore (1979)	
<i>Branchinecta packardii</i>	Embryo	Cysts stored in dry mud; room temperature	16 years	Dexter (1973)	
Crustacea: Notostraca					
<i>Lepidurus couessi</i>	Embryo	Dry eggs stored in room temperature	2 years	Hann and Lonsberry (1991)	
<i>Triops longicaudatus</i>	Embryo	Eggs stored in dry mud; room temperature	14 years	Dexter (1973)	
Crustacea: Conchostraca					
<i>Caenestheriella gynecia</i>	Embryo	Eggs stored in dry mud; room temperature	5 years	Mattox and Velardo (1950)	
<i>Caenestheriella gynecia</i>	Embryo	Eggs stored in water, at room temperature and in darkness	8 years	Mattox and Velardo (1950)	
Crustacea: Cladocera					
<i>Evadne</i> sp. and <i>Podon</i> sp.	Embryo	Sea bottom sediments	8–10 years	Viitasalo and Katajisto (1994)	
<i>Ceriodaphnia pulchella</i>	Embryo	Lake bottom sediments	14 years	Moritz (1987)	
<i>Bosmina longirostris</i>	Embryo	Lake bottom sediments	18 years	Piscia <i>et al.</i> (2012)	± 3 years
<i>Polyphemus pediculus</i>	Embryo	Dry eggs	30 years	Pesta (1925) (in Butorina, 2003)	The source of eggs and other storage conditions are not described in detail in Butorina's paper
<i>Macrothrix</i> sp.	Embryo	Trapped in old mud wall	55 years	el Moghraby (1977)	
<i>Daphnia galeata</i> and <i>D. hyalina</i> ,	Embryo	Lake bottom sediments	70 years	Carvalho and Wolf (1989)	
<i>D. pulicaria</i> and <i>D. galeata mendotae</i>	Embryo	Lake bottom sediments	125 years	Caceres (1998)	
Crustacea: Copepoda					
<i>Acartia bifilosa</i> and <i>Eurytemora affinis</i>	Embryo	Sea bottom sediments	19 years	Katajisto (1996)	
<i>Leptodiaptomus minutus</i>	Embryo	Lake bottom sediments	22 years	Hairston and Van Brunt (1994)	
Unspecified calanoid copepods	Embryo	Estuary bottom sediments	40 years	Marcus <i>et al.</i> (1994)	Animals died being too young to be identified to species level
<i>Boeckella poppei</i>	Embryo	Shallow Arctic lake sediments	195 years	Jiang <i>et al.</i> (2012)	
<i>Diaptomus sanguineus</i>	Embryo	Pond bottom sediments	332 years	Hairston <i>et al.</i> (1995)	Age estimated by <sup>210</sup> Pb sediment dating + extrapolation
Rotifera: Bdelloidea					
<i>Mniobia</i> sp.	Adult	Found in dry moss sample	9 years	Guidetti and Jönsson (2002)	
Rotifera: Monogononta					
<i>Synchaeta</i> sp.	Embryo	Sea bottom sediments	18–22 years	Katajisto (1996)	
<i>Polyarthra dolichoptera</i>	Embryo	Lake bottom sediments	35 years	Nipkow (1961)	
<i>Brachionus calyciflorus</i>	Embryo	Lake bottom sediments	98 years	Piscia <i>et al.</i> (2012)	± 11 years
<i>Brachionus plicatilis</i>	Embryo	Pond bottom sediments	100 years	Fu (1991) (in Kotani <i>et al.</i> , 2001)	

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has claimed that rotifers of the genus *Mniobia*, which were “resurrected” after rewetting of a dry 9-year-old moss sample, are probably the oldest known viable anhydrobiotic bdelloids (Guidetti and Jönsson, 2002).

## RECENT ADAPTATIONS OR ANCIENT ABILITIES?

Gyllström and Hansson (Gyllström and Hansson, 2004) have stated that if diapause is an adaptive response to harsh environmental conditions, its patterns should differ between organisms inhabiting permanent and temporary habitats. High resistance of the dormant forms of planktonic invertebrates seems to be a necessary adaptation for survival in harsh and highly unpredictable environments (especially those in which periods of drought and extreme temperatures occur). Therefore, the high thermal resistance of diapausing *Triops* eggs originating from temporary rainpools near Khartoum, Sudan, where the dried mud might be exposed for many days to temperatures as high as 80°C, is not surprising (Carlisle, 1968). The great richness of planktonic life (many anostracan, conchostracan, notostracan, copepod, rotifer and cladoceran species) described by Rzóška (Rzóška, 1961) that hatched from dormant stages in Sudanese ephemeral rainpools a few days after seasonal downpours and later disappeared for the majority of year, being covered by hot sand and dust, also represents a good example of the evolution of drought- and thermo-resistant dormant stages as an adaptation to life in harsh environments. The case of *Macrothrix* sp. raised from a 55-year-old mud wall in the same region (el Moghraby, 1977) supports this notion. Similar adaptation of the dormant forms of planktonic invertebrates in order to survive desiccation and extreme temperatures may be found in temporary water bodies, not only in arid regions (e.g. communities described in desert playas in California; Brown and Carpelan, 1971), but also in temperate climates (e.g. Hay and Hay, 1889; Mozley, 1932; Ranade, 1957).

Moreover, highly resistant dormant forms of planktonic invertebrates are also found in seasonally (thus predictably) changing permanent habitats. For example, *Artemia* cysts that can survive freezing to temperatures near absolute zero were derived from the thermally stable Great Salt Lake (Skoultchi and Morowitz, 1964). In addition, 9 planktonic crustacean (e.g. cyclopoid copepods and cladoceran *Daphnia cucullata*) and 59 rotifer (bdelloid and monogonont) species were isolated as hatchlings from frozen sand collected from the shore of a deep lowland lake in Poland (Kalinowska *et al.*, 2010). In both cases, the high resistance of the dormant forms

may still be adaptive; those forms that float or are deposited in shallow near-shore waters could be subjected to rapid temperature changes, drying or freezing, so their resistance might be vital for their survival. As indicated by Pietrzak and Ślusarczyk (Pietrzak and Ślusarczyk, 2006; Ślusarczyk and Pietrzak, 2008), diapausing forms deposited on the water’s surface may be employed by planktonic crustaceans for dispersal between lakes. The high risk of disappearance of freshwater habitats may exert pressure on species inhabiting isolated waterbodies, both temporary and permanent, to produce desiccation-tolerant and thermally resistant diapausing forms that may facilitate their overland passive dispersal by external vectors (e.g. birds or wind).

Nevertheless, the resistance of dormant forms originating from permanent habitats seems to be lower than that of their relatives from more variable and harsher habitats. The bdelloid rotifers provide one of the best examples of this phenomenon (Ricci, 1998). Adults, eggs and embryos of 15 bdelloid species, representing four families and six genera (inhabiting both waterbodies and water retained by mosses), were desiccated and kept dry for 7 days. After this treatment, higher recovery rates were observed for the moss species, i.e. those frequently subjected to desiccation events. While some aquatic bdelloids were found to survive desiccation (*P. acuticornis* or *Rotatoria neptunoida*), individuals of two other typically aquatic species, *Rotaria neptunia* and *R. rotatoria*, which inhabit permanent water bodies that do not dry out very often, did not survive this treatment. Interestingly, other representatives of the genus *Rotatoria*, closely related to the aforementioned species, but derived from moss and soil habitats, could survive desiccation very well. In a subsequent study, Caprioli and Ricci (Caprioli and Ricci, 2001) subjected specimens of three bdelloid rotifer species to desiccation and harsh thermal conditions (−80°C) and observed that the aquatic *P. roseola* recovered from such treatments less well than the moss-inhabiting *M. quadricornifera* and *Adineta oculata*.

As suggested by Ricci (Ricci, 1998), differences in the desiccation tolerance of individual bdelloid species might be related to the occurrence of dry periods in their natural habitats. However, the ability of some aquatic species to survive desiccation suggests that the anhydrobiotic capabilities of bdelloids are not an effect of recent adaptation to life in unpredictable habitats, but were once a trait common to all bdelloid rotifers, which some of those that inhabit relatively stable, permanent water bodies have now lost (Ricci, 1998).

The properties of different *Artemia* species provide another example that may support a correlation between high thermal resistance of dormant stages and the

presence of harsh conditions in their native habitats. Dry cysts of *A. franciscana*, isolated from different locations, were found to exhibit different levels of thermal tolerance when subjected to a temperature of 80°C (Hengherr *et al.*, 2011b). Half of the cysts originating from the large, predictable Great Salt Lake died after 2.3 h of exposure to this elevated temperature, while half of the cysts derived from the less predictable and warmer San Francisco Bay salterns managed to survive 44.3 h under similar conditions. Thermal adaptation (genetic or epigenetic) of *A. franciscana* seems to occur very rapidly: cysts from the tropical Mekong Delta region, where the brine shrimp was introduced from San Francisco Bay a few years earlier, were found to exhibit 50% mortality after 54.8 h at 80°C. The greater thermal tolerance of the cysts from Vietnam was associated with higher content of stress-related proteins and trehalose (Hengherr *et al.*, 2011b). Similar results were obtained by Clegg *et al.* (Clegg *et al.*, 2001) for cysts of *Artemia* species kept in a wet state and slowly heated to 50°C. The highest thermal resistance was found for *A. franciscana* cysts obtained from the Mekong Delta, just one to three seasons after introduction of this species from the San Francisco Bay region (cysts from the third season showed 10% survival after 105 min of exposure). Cysts originating from the San Francisco Bay region and those of *A. sinica* from Mongolia were more vulnerable to moderate temperatures (10 and 20% survival after 60 min at 50°C, respectively; no survival after >75 min of exposure), but cysts of *A. tibetiana*, a species found at high altitudes in Tibet, where the average water temperature varies from 1 to 2°C, showed dramatically lower rates of survival. Half of the *A. tibetiana* cysts tested died before the water temperature reached 50°C, and after 15 min under these thermal conditions, all of them were dead. Levels of protective molecules were found to be much lower in the dormant forms in *A. tibetiana* than in the cysts of other species. It was therefore suggested that under cold water conditions that predominate in high mountains, there is no need for the production of protective proteins, which is costly for the organism, and so the reduction in their content might be an effect of natural selection, resulting in lower thermal tolerance of the cysts (Clegg *et al.*, 2001; Van Stappen *et al.*, 2003; Tanguay *et al.*, 2004).

In the case of both the aquatic bdelloids that are unable to survive desiccation and *Artemia tibetiana*, the lower resistance of dormant forms probably results from the loss of some costly abilities by these species, rather than the acquisition of new abilities by other, more resistant, species. The high plasticity of *A. franciscana* indicates that individuals of this species have the ability to produce cysts containing more protective molecules in

response to changes in the habitat water temperature (like those from the Mekong Delta). Nevertheless, even the cysts of this species produced in the milder environments of the Great Salt Lake and San Francisco Bay salterns are still highly resistant. The evolutionary source of the high resistance of the dormant stages of some species, which is in some cases unnecessary for survival, remains to be elucidated. The aforementioned cases suggest that the high tolerance of dormant stages evolved in the early history of both bdelloids and anostracans (and also other planktonic crustaceans), and is not an effect of later adaptation to life in harsher habitats.

There is some evidence that the phenomenon of dormancy alone and also the high resistance of dormant forms might have evolved millions of years ago, when the predecessors of today's aquatic invertebrates left the oceans and started to penetrate inland water habitats.

In the review of Caceres (Caceres, 1997), it was noted that dormancy is a trait that is far less common in marine invertebrates than in those that have representatives in freshwater or terrestrial habitats, with prolonged dormancy being almost absent in exclusively marine taxa. This author suggested that such distribution of the trait of dormancy might have been shaped either by (I) past evolution, as a prerequisite for the colonization of non-marine habitats, or as an effect of selective pressure on animals that had recently moved from the seas and oceans to new, harsh and unpredictable habitats, or by (II) more recent evolution, promoted by the conditions prevailing in some current habitats. These two scenarios are not mutually exclusive and dormancy might have evolved independently many times. The first hypothesis, where the production of dormant stages is treated as a very old trait, seems to be more widely accepted and is supported by the fact that these stages may show resistance to temperatures far higher than any that are encountered in temporary inland water basins, even in the dry phase.

The apparent lack of dormancy in marine forms was also highlighted by Crowe (Crowe, 1971), who noted that among bdelloid rotifers, tardigrades and nematodes, only the specialized terrestrial forms, not the primitive marine ones, were capable of anhydrobiosis. Alekseev and Starobogatov (Alekseev and Starobogatov, 1996) linked patterns of diapause with the invasion of invertebrates (i.e. crustaceans) from marine to freshwater habitats. These authors observed that the dormancy length of a given taxon correlated with the historical time of its penetration into inland waters. The earlier the taxon left the oceans, the longer the possible period of dormancy in the life histories of species representing them. Most marine crustacean species are unable to

enter dormancy and, as noted by Caceres (Caceres, 1997), the majority of marine invertebrates that produce dormant stages are those that are secondarily marine, i.e. their ancestors “returned” to oceans from inland waters. Among neolimnic crustaceans that invaded inland waters most recently, some can remain dormant for less than a year, while the majority are unable to enter dormancy at all. On the other hand, long-term dormancy (mostly embryonic) is a trait common to Anostraca, Cladocera, Conchostraca and Notostraca, i.e. the crustaceans that were the first to leave marine habitats (Alekseev and Starobogatov, 1996). Slow and large representatives of the most primitive crustacean taxa (Anostraca, Conchostraca and Notostraca), which are thought to have colonized fresh water in the Paleozoic era, were extremely vulnerable to predation, and so were most likely restricted to predator-free temporary pools that are probably the most permanent, in a geological scale, type of fresh water body (Alekseev and Starobogatov, 1996; Fryer, 1996). At this time, highly resistant latent eggs were essential for survival in periods of drought, and since the beginning of inland water colonization, aquatic invertebrates have had a lot of time to adapt to the extreme conditions prevailing in this kind of water body (Alekseev and Starobogatov, 1996; Fryer, 1996; Williams, 1998). The colonization of fresh water might have happened via estuaries that mix marine and fresh water conditions (Alekseev and Starobogatov, 1996), but perhaps small near-shore brackish and fresh water pools were also an “intermediate stop” for invertebrate colonizers of inland waters. Regardless of which of these hypothetical colonization scenarios occurred in reality, it is highly probable that not only the phenomenon of prolonged dormancy, but also the great resistance of dormant forms has its roots in the Paleozoic era. Beladjal *et al.* and Mertens *et al.* (Beladjal *et al.*, 2007; Mertens *et al.*, 2008), who subjected dry adults of the bdelloid rotifer *Philodina* and cysts of anostracans *Artemia* and *Branchipus* to temperatures exceeding 100°C and observed their survival, speculated that this extremely high thermal resistance arose in the early evolution of these organisms. They suggested that thermal tolerance might have evolved in some organisms in the Paleozoic era, Devon or earlier, when their new habitats after leaving the oceans often became dry and extremely hot. These abilities might have been retained by some species, facilitating their survival in the most dry and hot modern environments. For other species inhabiting less extreme environments, the maintenance of this expensive trait was not necessary, so it was lost by natural selection and the energy required for the production of protective compounds was allocated elsewhere. This loss of resistance to

extreme temperatures can be seen in the cases of *A. tibetiana* (Clegg *et al.*, 2001) and truly aquatic bdelloid rotifers (Ricci, 1998), as discussed above.

However, there is still a lack of studies on other closely related organisms that might fully confirm the hypothesis that the greater resistance of dormant forms of species inhabiting harsher/less predictable habitats is due to abandoning expensive genetic mechanisms of resistance by closely related species coming from more predictable and benign environments. Among the few studies that have addressed this question are those examining the latent eggs of calanoid copepods. Such eggs of species originating from the coastal waters of Norway were found to be vulnerable to temperatures as low as  $-15^{\circ}\text{C}$ , or as high as  $+20^{\circ}\text{C}$  (Næss, 1991), whereas fresh water calanoid species inhabiting temporary ponds were shown to form dormant eggs that could survive exposure to temperatures both higher and lower than this (Brewer, 1964).

Also, the cysts of lake forms of *Artemia* seem to be less resistant than those coming from variable habitats (Clegg *et al.*, 2001). However, there is still a lack of examples of fresh water species that inhabit a wide spectrum of water bodies, characterized by a different amplitude and predictability of environmental extremes, which produce dormant stages that vary in resistance in correlation with the conditions prevailing in these habitats. Comparison of the resistance of the dormant stages of invertebrates inhabiting deep, dimictic fresh water lakes with those of closely related species present in the smallest, highly variable fresh water bodies (e.g. puddles, small temporary ponds) is required to test the hypotheses of Beladjal and Mertens.

While the thermal resistance of the dormant stages of planktonic invertebrates may be explained by ancient or recent adaptations, an evolutionary explanation of their longevity is less straightforward.

Alekseev and Starobogatov (Alekseev and Starobogatov, 1996) correlated the maximum length of dormancy of given taxa with their time of invasion of inland waters, and, as mentioned above, the application of mathematical models has proven that prolonged dormancy and bet-hedging strategies are adaptive in temporarily varying habitats (Cohen, 1966; Ellner, 1985; Evans and Dennehy, 2005; Lalonde and Roitberg, 2006). Thus, prolonged dormancy of planktonic animals is considered to be an adaptation to life in temporary water bodies such as vernal pools or small ponds. Also successful existence in habitats such as floodplains, which are covered by water once every few years, requires the production of long-lived dormant forms that hatch immediately after flooding (Boulton and Lloyd, 1992; Schröder, 2001). The selective

advantage of diapause lasting hundreds or thousands of years remains a mystery.

Two of the best examples of this extremely long dormancy in permanent and highly predictable water bodies are the aforementioned ephippial eggs of *Daphnia* from Oneida Lake that were hatched 130 years after their deposition (Caceres, 1998) and neritic marine calanoid and monogonont rotifer eggs that remained viable for at least 40 years (Marcus *et al.*, 1994). Hairston *et al.* (Hairston *et al.*, 1995) suggested that although the evolution of prolonged diapause in habitats where the survival of dormant eggs is high could be promoted by even minor fluctuations in the successful yearly recruitment from the egg bank, prolonged dormancy may, in some cases, be a consequence of egg burial. This may permit survival during the unpredictable period before their reappearance at the sediment surface caused by some external force (e.g. bottom dwellers).

The existence of long-lived dormant forms even in marine habitats raises the question of whether the trait of longevity of latent eggs, evolved while organisms were leaving the oceans, and probably expensive to maintain, can disappear (like the extreme thermal resistance of dormant stages) in habitats where it is no longer required. Although near-coast marine environments and lakes are not very variable from year to year, in terms of environmental conditions, the phenomenon of prolonged dormancy still exists in these habitats. However, there remains a lack of examples that confirm the loss of prolonged dormancy by zooplankters inhabiting environmentally stable and predictable water bodies.

## CONCLUSIONS

The phenomenon of dormancy is undoubtedly one of the most important features allowing aquatic invertebrates to survive in temporarily variable habitats. Production of highly resistant dormant stages enables planktonic animals to disperse, both in time (i.e. wait until adverse conditions end) and space, by means of passive transport facilitated by wind or animal vectors (Pietrzak and Ślusarczyk, 2006). The high tolerance of dormant forms to abiotic factors (e.g. extreme temperatures, desiccation) allows aquatic invertebrates to persist in habitats where the aquatic phase, in comparison with the terrestrial one, is extremely short. In highly unpredictable environments, such as vernal pools or other temporary reservoirs, the production of long-lived dormant forms is probably an element of a bet-hedging strategy that secures the survival of the population despite the occurrence of seasons when there is insufficient time for active animals exiting dormancy to

produce new dormant forms before they die (Caceres and Tessier, 2003). The levels of thermal tolerance and longevity of dormant forms of a given taxa correlate with its time of invasion of inland waters: aquatic animals that produce the most tolerant dormant stages left the oceans in the Paleozoic era and in some cases have maintained their ancient features until today (Alekseev and Starobogatov, 1996; Beladjal *et al.*, 2007; Mertens *et al.*, 2008). There are some instances where organisms have lost their enormous thermal tolerance after colonization of environmentally stable and milder habitats, indicating that thermal resistance has been shaped by more recent evolution. Moreover, extreme longevity of dormant stages could also have been lost in a similar way by certain species or strains inhabiting predictable environments. However, the available data are currently too sparse to draw any far-reaching conclusions on this topic. To fully understand the relationships between habitat unpredictability and the resistance/longevity of dormant forms of planktonic invertebrates, detailed comparisons of the dormant forms of closely related species inhabiting significantly different (in terms of stability) habitats are required.

## ACKNOWLEDGEMENTS

I thank M. Ślusarczyk and two anonymous reviewers for making many insightful comments that improved the manuscript.

## FUNDING

This study was supported by Polish National Science Centre (grant 2012/05/B/NZ8/01232).

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