Chapter 8
Mechanisms Facilitating Dispersal of Dormant Eggs in a Planktonic Crustacean

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Abstract While plants are famously known to use their dormant forms for both temporal and spatial dispersal, animals are generally recognized to use them mostly for periodic survival in unfavourable conditions, despite a plethora of animals (sedentary or inhabiting isolated sites) regularly using their dormant forms for spatial dispersal, too. Freely moving planktonic crustaceans of the genus *Daphnia*, inhabiting island-like freshwater habitats, are one of the model examples. While they have low chance to cross terrestrial barriers and reach neighbourhood waterbodies in an active form, they have developed adaptations that facilitate spatial dispersal of their dormant forms. In this chapter, we broadly summarize the ultimate reasons of spatial dispersal of freshwater organisms and the modes and routes of their dislocation. We further focus on the morphological, behavioural and life history adaptations that facilitate spatial dispersal of the dormant forms of a model planktonic crustacean, *Daphnia*. Finally, we evaluate the risks and costs of passive dispersal, assess its effectiveness and describe non-adaptive consequences.

Keywords Dispersal mechanisms, *Daphnia*, Dormant eggs, Ephippial case, Oviposition behaviour

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8.1 Spatial Dispersal of Freshwater Organisms: Causes and Routes

In geological and geographical scales, freshwaters are short living and small-sized habitats. This imposes selective forces on their inhabitants and promotes both dormancy and dispersal. While these are plants that are widely recognized to use their dormant seed stage for dispersal, animal dormant eggs are functionally analogous, and routes of their dispersal are similar.

8.1.1 Ultimate Causes Behind Spatial Dispersal of Freshwater Organisms

Living creatures are relatively fragile structures, yet they have been present on Earth for more than 3 billion years. Their long existence is owed not to their extraordinary endurance, but to their endless replication and their spatial or temporal avoidance of unfavourable conditions (Venable and Lawlor 1980; Mc Peek and Kalisz 1998; Buoro and Carlson 2014). Organisms with effective mechanisms of dispersal may survive by shifting between habitats as long as environmental variations are not correlated between neighbouring locations. All habitat are exposed to some spatial or temporal variation in abiotic conditions. Even in relatively stable abiotic setting, biotic interactions may inevitably cause spatial or temporal fluctuations in environmental conditions. Uneven distribution of resources, interspecific competition (Holt and Barfield 2002), predation (Weisser 2002) or parasitism (Boulinier et al. 2002) may affect fitness of organisms considerably and drive spatial dispersal (Gandon and Michalakis 2002). Moreover, spatial dispersal might be beneficial even in invariable locations due to kin interactions (including sib competition or parent-offspring conflict (Hamilton and May 1977)) or inbreeding depression (Bengtsson 1978; Perrin and Mazalov 1999).

Aquatic organisms inhabiting freshwater sites need to disperse more desperately than their marine counterparts do. Most freshwater lentic habitats are highly isolated, ephemeral habitats in geological and evolutionary timescales that emerge and vanish frequently. Majority of lakes formed in the northern temperate zone after the last glaciation has disappeared within the last ten thousand years (Marszelewski 2005). Shallow temporary waters persist even shorter than large deep lakes. Thus, most if not all species inhabiting freshwater bodies need effective mechanisms of overland dispersal to thrive in time.

Environmental deteriorations may have abiotic or biotic origin, operate at local or regional scale and concern all organisms – mobile and immobile ones. While mobile organisms may seek suitable locations in the active form, the sedentary species or those living in isolated habitats frequently use their dormant forms for passive dispersal (Bohonak and Jenkins 2003; Panov et al. 2004; Panov and Cáceres 2007).

8.1.2 Importance of Dormant Forms in Animal Dispersal in Freshwaters

Most freshwater animals are able to move actively within aquatic habitats. Some of them may also travel between waterbodies along permanent or temporal waterway connections (Michels et al. 2001; Shurin and Havel 2002; Leuven et al. 2009). Yet, many lakes and ponds are island-like habitats, permanently isolated from each other by impenetrable terrestrial barriers. They are not lifeless, though, but inhabited by various aquatic species that colonize them quickly (Louette and de Meester 2005; Juračka et al. 2016). Some animals may actively cross short terrestrial barriers between aquatic habitats, e.g. vertebrates like reptiles, amphibians, or even fish, as well as invertebrates, e.g. most insects and some crustaceans. However, most aquatic species are incapable of moving across terrestrial zone due to sedentary lifestyle or poor moving skills or due to intolerance to overland conditions, e.g. desiccation. While passive dispersal of active forms between water habitats seems feasible on meter-wide distances, most freshwater animals are not able to survive long overland journey. Still, many of them are able to disperse passively across hostile terrestrial habitats once they suspend their development. Dormant forms of freshwater species are well suited for overland dispersal (Panov et al. 2004; Panov and Cáceres 2007). They are tolerant to various abiotic and biotic threats (Radzikowski 2013) and may possess various morphological or physiological adaptations facilitating their dispersal.

8.1.3 Routes of Passive Dispersal of Dormant Aquatic Organisms

Organisms producing resting stages disperse passively via different routes, often with multiple processes and vectors involved (Higgins et al. 2003; Incagnone et al. 2015). From the disperser perspective, that is, from the viewpoint of the challenges the animals encounter on route, and thus the mechanisms, or the adaptations, facilitating dispersal via these routes, dormant propagules of freshwater organisms move between habitats, mainly thanks to different processes such as (1) floating on the water surface, (2) sticking to other surfaces, (3) surviving being eaten or (4) floating in the air. The relative importance of these phenomena to effective dispersal and population establishment naturally varies both between organisms and their propagule characteristics, and between habitats. Also, the contribution of the different processes and vectors varies between studies, and is still unresolved (see Bohonak and Jenkins 2003; Cohen and Shurin 2003; Allen 2007; Vanschoenwinkel et al. 2008a; Coughlan et al. 2017).

8.1.3.1 Floating on Water

Water-air interface is the first gateway out of the aquatic habitat. Floating in water – plankton-wise – distributes the propagules within and between interconnected bodies of water, and may aid encountering animate and inanimate vectors, but in itself is not effective in transporting them between the habitats where waterway connections are scarce. Temporarily entering neuston, in its turn, exposes propagules to further potential vectors of dispersal. For aquatic plants, water-mediated spread of seeds, i.e. hydrochory, is recognized as an important dispersal route (Hopfensperger and Baldwin 2009; Pollux et al. 2009), and there are no reasons to expect it to be otherwise for aquatic animals dispersing via dormant forms. As propagules float, thanks to either of the two acting forces, buoyancy (upthrust) or surface tension, water-borne dispersal is facilitated by traits harnessing either of them. Floatability is even used as a proxy for seed dispersal capacity (Kappes et al. 2014; van Leeuwen et al. 2014). For freshwater invertebrates, the dormant stage floatability has also been linked to dispersal capacity, like the increasing proportion of floatoblasts to sessoblasts produced with increasing ramet size of bryozoans (Karlson 1992), the distinction and phenotypic reversals between floaters and sinkers among resting eggs of an anostracan (Pinceel et al. 2013), or the prevalence of floating and sinking ephippia of cladocerans (Pietrzak and Ślusarczyk 2006; Cáceres et al. 2007; Ślusarczyk et al. 2017a). Furthermore, numbers of propagules attached to birds have been recorded to coincide with their availability on the water surface (Brochet et al. 2010a).

8.1.3.2 Sticking to Surfaces

What makes propagules trapped at the water-air phase boundary makes them also stick to other surfaces. Darwin famously noted minuscule creatures actively crawling onto duck feet immersed in water, but in fact, even surface debris, dead or alive, will stick to a resurfacing object provided both have hydrophobic surfaces. For instance, cladoceran ephippia get easily and firmly attached to hair fringes of the abdomen and legs of a heteropteran insect *Notonecta* sp., and thus are carried away from the water surface, with ephippium floating ability being a critical factor here (van de Meutter et al. 2008). Propagules of many aquatic species have been repeatedly found to be externally transported by vertebrates, especially waterbirds, but also mammals (Maguire Jr. 1963; Bilton et al. 2001; Figuerola and Green 2002a). Plant, fungal and protist spores were reported to disperse between aquatic environments in plumage or on feet of ducks, waders and rails (Vivian-Smith and Stiles 1994; Figuerola and Green 2002b; Brochet et al. 2010b; Raulings et al. 2011; Lewis et al. 2014; Reynolds and Cumming 2016). So were invertebrate eggs, including dormant cladocerans (Figuerola and Green 2002b; Brochet et al. 2010a; Reynolds and Cumming 2016). Finally, the omnipresent and extremely migratory species, humans, now provides a multitude of artificial surfaces frequently moved between waterbodies. Tourism, transportation and research, all these activities involve

adherence and movement of dormant propagules of aquatic organisms between environments, on equipment from vehicles and vessels to boots (see Waterkeyn et al. 2010; Valls et al. 2016; Bullock et al. 2018), where even a hundred of cladoceran ephippia can adhere to a single fishing line (Jacobs and MacIsaac 2007). Indeed, animal-mediated external dispersal of propagules, i.e. ectozoochory, has been frequently evaluated as an important route, at least on local scales (see Coughlan et al. 2017; van Van Leeuwen 2018, for most recent reviews). Still, a lot, including the impact of factors affecting attachment and detachment of the propagules, like bird preening behaviour or the role of sediment type, e.g. encapsulating mud (Figuerola and Green 2002b), is still understudied (Coughlan et al. 2017).

8.1.3.3 Being Eaten

Even if not directly preyed upon, adherence to various organic substrates will make the dormant stages more easily an unintended prey (Green et al. 2002; Reynolds and Cumming 2016). Wherever on the tree of life, if an aquatic organism produces dormant stages, some of them are likely to survive being eaten and being defecated at another location. Chances of surviving such internal transport might be even larger than chances of surviving external one (Reynolds and Cumming 2015). Comparing to ectozoochory, dispersal involving passage through the gut, i.e. endozoochory, of aquatic invertebrate resting stages and plant seeds may play even a more important role in terms of number and diversity of propagules dispersed between water bodies (Brochet et al. 2010b; Sánchez et al. 2012; Costa et al. 2014; Lewis et al. 2014; Moreno et al. 2019). However, their relative roles may change seasonally with the availability of floating propagules (ingestion and adherence) as opposed to constant availability of sediment propagule bank (ingestion) (Brochet et al. 2010a; Reynolds and Cumming 2015). Viable organisms, from freshwater algae (Proctor 1959) to cladocerans (Brochet et al. 2010a) are found in the lower digestive tracts of migrating birds, and a meta-analysis showed that roughly one in three waterbird droppings collected in the field contains a viable propagule, of which macroinvertebrates are almost as frequent as plant seeds (van Leeuwen et al. 2012).

8.1.3.4 Floating in the Air

As much as for the endozoochory, the presence of dormant forms is considered a prerequisite for effective wind dispersal, i.e. anemochory, of small aquatic metazoans (Panov et al. 2004). Once at the surface, or as soon as the temporary basin dries out, they are exposed to wind. Not only the resistant dormant state gives them good chances for survival outside their aquatic medium, but also, in anhydrobiosis they are lighter, and thus more easily than the hydrated forms taken into and moving in the air (Ricci and Caprioli 2005; Ptatscheck et al. 2018). This is important, as adaptations like ballooning – using silk to fly – have evolved only on land, in spiders, mites and moths (Bell et al. 2005). Recently, nematodes have been found as an

exception to the general rule, readily dispersing in the air in active form, their aquatic taxa included (Ptatscheck et al. 2018). Copepods, cladocerans, ostracods and others have been caught moving in the air (Vanschoenwinkel et al. 2008b, 2009), yet, though considered to be an important mechanism of dispersal, the actual rates of airborne transport or the distances thus covered are hardly known (Ptatscheck et al. 2018). Since the early suggestions that winds are the 'most important means of spread' of minute dormant stages of both animals and plants (McAtee 1917), not much has been resolved on how often and how far do aquatic animals in diapause move in reality. A century later, it is proposed that, more specifically, during the dry phase of temporary ponds, wind is the most important dispersal vector of their inhabitants (Incagnone et al. 2015). The floating of the propagules aids to the wind importance (Ślusarczyk et al. 2017a; Sirianni 2017). Not only taxa themselves differ in their 'flying' propensity and its dependence on environmental conditions, but their measured dispersal rates also vary greatly both between studies and methods used (Ptatscheck et al. 2018).

8.2   *Daphnia* as a Model Animal with passively Dispersing Dormant Forms

A good single crustacean taxon to study the mechanisms behind dispersal of its dormant forms will (1) rely only or mostly on the dispersal of dormant forms; (2) disperse via different routes, giving opportunities to study various adaptations; (3) be found in large numbers on at least some of these routes, enabling quantitative sampling for comparative analyses; (4) have wide distributions; and (5) have a record of recent and contemporary invasions, both proxies for effective dispersal. We focus here on the genus *Daphnia*, animals (1) which rarely, if ever, are found dispersing between waterbodies in active form; (2) whose resting eggs are carried over the surface of fresh waterbodies, inside and outside other animals, and in the air; (3) whose resting forms in thousands are periodically found forming near shore carpets covering the surface (Ślusarczyk and Pietrzak 2008; Kaya et al. 2014; Incagnone et al. 2015; Ślusarczyk et al. 2017a), and which together with other cladocerans have been found to be the most abundant group emerging from samples collected from waterbirds (Brochet et al. 2010a); (4) whose species have worldwide distributions (Forro et al. 2008); and (5) which are repeatedly found invading new freshwater habitats of all kinds, natural and artificial, including those experimental (see Sect. 8.2.3). Taking this all together with its being a widely used model in various fields of ecological research, from ecotoxicology to environmental genomics and evolutionary biology, *Daphnia* provides a well-suited model for an aquatic animal dispersing via its dormant forms.

8.2.1   Roles of Dormant Eggs in the life of Daphnia

Daphnia dormant eggs together with the encapsulating protective shell form an ephippium, a structure which functionally resembles a plant seed (Pietrzak and Ślusarczyk 2006): a well-protected, by default sexually produced, embryo, ready to endure both temporal challenges of the local environment and those encountered on dispersal routes outside of the native habitat. Thus, these eggs play an important role in both re-establishing local populations and colonizing new habitats.

Daphnia dormant eggs are most often, and primarily, the result of sexual reproduction. When conditions deteriorate, these animals switch from parthenogenetic production of subitaneous eggs to sexual reproduction inseparably linked with dormancy. The development of sexually produced fertilized egg is halted at the early gastrula stage (Zaffagnini 1987). Though some lineages from regions where the growing season is short, like high latitudes and altitudes, skip the sexual part and produce dormant eggs parthenogenetically (Decaestecker et al. 2009), still each genotype newly emerging after recombination first switches on the dormancy developmental program.

Dormant eggs are produced by *Daphnia* in anticipation of regular fluctuations and in response to direct challenges: before summer drying out and winter freezing down of shallow ponds; before winter formation of ice cover on lakes; before periods of intensive predation risk (Ślusarczyk et al. 2006); and under increasing population densities (Berg et al. 2001; Fitzsimmons and Innes 2006). This may occur once a year (Ślusarczyk 2009) after the first or the second summer in life of an individual (Pietrzak et al. 2013) or more often, and at irregular intervals (Mikulski and Grzesiuk 2019, submitted manuscript), according to the actual conditions. At a single sampling up to 80% of the females may be found carrying an ephippium (Ślusarczyk 2009), and in the laboratory up to 100% of the experimental females may produce them under certain conditions (Ślusarczyk 1995; 2004). Individuals hatching from dormancy (females exclusively) may supply overwintering active population of *Daphnia* or re-establish it after seasonal extinction (Cáceres 1998b).

The ephippial eggs in order to hatch need to pass through a refractory period (initial phase of suspended development when embryo remains insensitive to hatching stimuli; Ślusarczyk et al. 2019, submitted manuscript) and receive a still undefined set of environmental triggers including temperature and light (Davison 1969; Radzikowski et al. 2018; Ślusarczyk and Flis 2019).

Their resistance and other features discussed in the next section make them perfect vehicles for overland transport. Though the existence of a general and direct relationship between the ability of producing dormant forms and dispersal efficiency is still controversial (Incagnone et al. 2015), still, we can discuss many of their associated traits as – if not direct dispersal adaptions – traits effectively facilitating their spatial dispersal. Their morphology, as well as maternal life history and behaviour associated with their production and disposal, and life history of dispersing individual itself, as traits aiding the dispersal capacity, are discussed in the next section.

8.2.2   Adaptations Facilitating Passive Dispersal of Resting Eggs in Daphnia

Passive dispersal of dormant forms to be effective should (1) coincide in space and time with the occurrence of their vectors and (2) be based on resistance to withstand specific challenges encountered while on travel via different routes. Pinpointing particular traits as being under direct dispersal-driven selection may be difficult, though. Many traits that affect dispersal have other functions (Burgess et al. 2016). Research on plants also shows that long distance dispersal events might be rare and driven by nonstandard mechanisms, and is across adaptations (Higgins et al. 2003). Still, multiple adaptations do exist and work on shorter scales. We focus here on the challenges and the facilitating mechanisms specific to spatial dispersal of these forms, discussing still unverified hypotheses, and giving less attention to mechanisms equally facilitating dispersal both in space and in time.

In the case of *Daphnia*, the time of ephippia production and the place of their deposition by the mother are vital for the dispersing propagule and the dispersal vector coincidence. As for the ephippium itself, its internal and external wall structure providing toughness and aiding its floatation, its sticky appendages aiding both floatation and adherence to other structures, and its size itself are the most important traits.

8.2.2.1   Reaching Water Surface: Oviposition Behaviour

Few vectors of ephippial eggs operate deep in the open water, in the life zone of *Daphnia*, while most of them operate close to the water surface – the dangerous zone for planktonic organisms. Therefore, the resting eggs of *Daphnia* should appear close to the water surface in the right moment to be dispersed between water habitats. We consider two likely options of their transfer to the water surface, these linked to animal properties and not to external forces, like water current movements or air bubbles leaving the sediments, neither of which has been to our knowledge reported to bring *Daphnia* either in active or dormant form to the surface.

Ephippia might be either displaced to the surface due to positive buoyancy, like they are in sessile bryozoans (Karlson 1992), or due to their oviposition by mobile ephippium carrying females (Ślusarczyk and Pietrzak 2008). The first option has been proposed (e.g. by Cáceres et al. 2007), yet not proved so far. Active *Daphnia* are negatively buoyant and must swim constantly, otherwise they sink (Vega and Clausse 1998). Positive buoyancy of ephippia would affect overall buoyancy of ephippia carrying females and would change their swimming behaviour (e.g. hop and sink rate), which, according to our knowledge, has not been reported so far. On the contrary, experimental tests made on three common species of *Daphnia* (*D. magna*, *D. pulex*, *D. longispina*) revealed that all freshly shed ephippia were negatively buoyant, likewise active forms, and sank to the bottom when being shed by females below the water surface (Ślusarczyk and Pietrzak 2008). All ephippia that appeared at the water surface in further tests were left there by ephippial mothers

during moulting, despite surface threat imposed on them during the tests (high UV radiation). While all tested ephippial females remained far from the risky water surface for most of the UV exposition period, some of them swam toward the water-air interface a few seconds ahead moulting, where they moulted shedding ephippium and dived down shortly after (Ślusarczyk and Pietrzak 2008).

Daphnia, like most other planktonic organisms, avoid surface zone of aquatic habitats (Dawidowicz and Pijanowska 2018). Close to the water surface, *Daphnia* may be exposed to harmful UV radiation (Alonso et al. 2004), enhanced predation risk of visual predators (Gliwicz 2003), or desiccation if being caught by surface tension and then thrown ashore (personal observation). While ephippial eggs are highly resistant to these surface threats (Radzikowski 2013), active individuals are more vulnerable. To reduce some of these threats, ephippia oviposition at the water surface might occur during night, when both fish predation and UV radiation-associated risks are negligible. Such cyclicity of ephippia deposition at the water surface would be reflected in a higher proportion of ephippial compared to non-ephippial females in subsurface zone during night vs. daytime (Fig. 8.1), or by a higher density of ephippia at the water surface at night and dawn compared to the other periods of a day at a calm weather (Fig. 8.2).
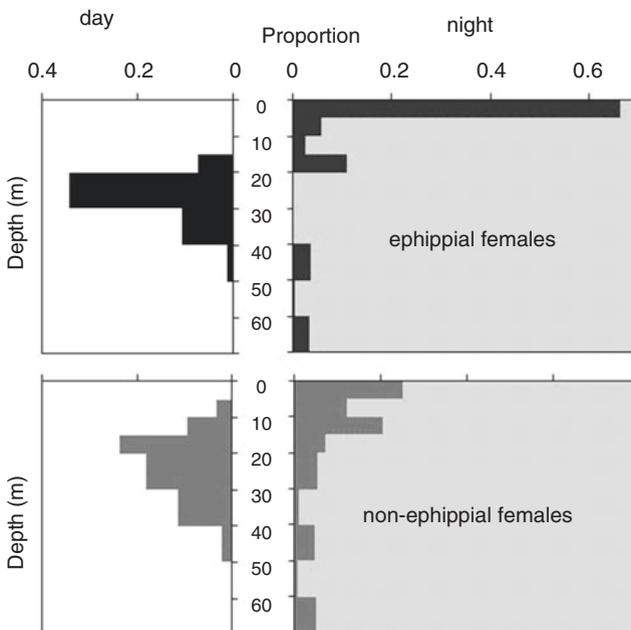
Fig. 8.1 Vertical distribution of *Daphnia pulicaria* females in the deep fishless mountain lake Czarny Staw in the High Tatras, Poland (49°11′18.1″N; 20°04′33.8″E), during the period of ephippia production: top - (black bars) ephippium carrying females; bottom (grey bars) non-ephippial females of the same lineage; during the day (left, white panels) and at night (right, shaded panels). (After Ślusarczyk et al. 2017a, modified)
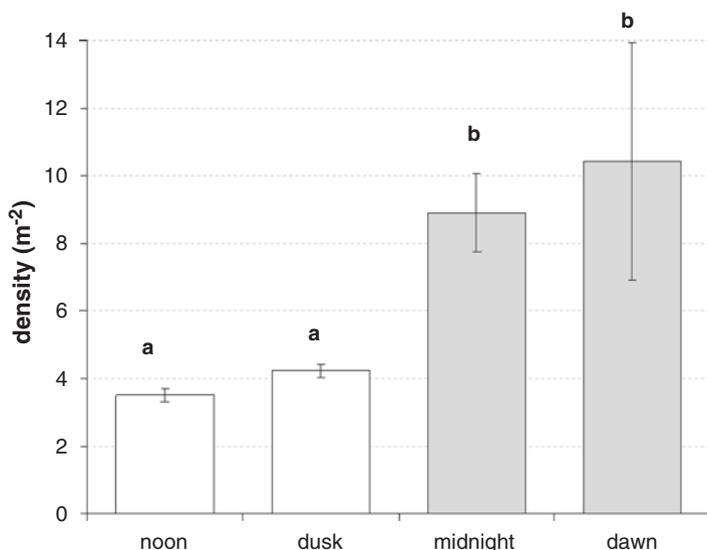
Fig. 8.2 Diurnal changes in ephippia density (mean ± 1SE) of *Daphnia* of the *longispina* group at the water surface in the middle of the small Kociołek Lake (station 5) collected in a single day of an autumn period of ephippia formation. Letters above the bars indicate homogenous groups with similar values according to ANOVA model simplification

8.2.2.2 Floating on Water Surface: External Morphology

Most of the ephippia left by females at the water surface retain negative buoyancy, yet stick to the water plane thanks to weak surface tension, suggesting hydrophobic properties of their outer wall. The role of surface tension was evidenced by sinking of ephippia after water-drop-induced disruption of the water surface or by applying a detergent that reduced surface tension and lowered the proportion of floating ephippia (Ślusarczyk and Pietrzak 2008). The elongated shape (Bormashenko 2016), flattening with protruding edges and relatively small size, all aid in their surface tension-induced floating.

Some ephippia left by *Daphnia* at the water surface gain positive buoyancy due to atmospheric air absorption. Anatomical analysis of the outer structure of the ephippium revealed possible way of air absorption (Bernatowicz et al. 2018). The ephippium of *Daphnia* is made of two concave chitinous shells that enclose the resting eggs. Each shell is made of double walls (Hiruta and Tochinai 2014) interconnected by cellular integuments of various shapes (Bernatowicz et al. 2018). In Ctenodaphnia (*D. magna, D. lumholtzi*), the integument has sponge-like structure that hardly absorbs air unless ephippium dries completely. In other Daphnidae (*longispina* or *pulex* group), the wall has a honeycomb structure with hollow cells that readily absorb air after even brief contact with the atmosphere, what makes them positively buoyant. Air probably does not penetrate through external wall,
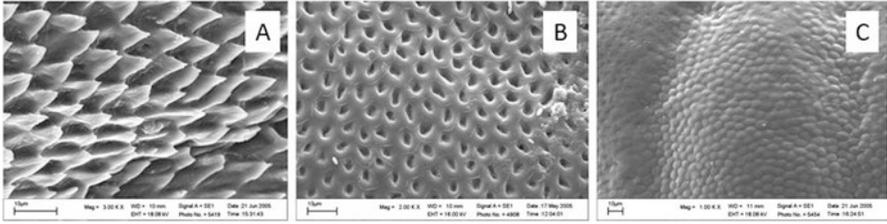
Fig. 8.3 Divergent morphology of the ephippium surface in different groups of *Daphnia* revealed by scanning microscopy. (**a**) *D. magna*, (**b**) *D. pulex*, (**c**) *D. rosea*

which seems impermeable, but most likely enters integuments through a ventral gap then hollows in the internal wall. The surface of the external wall differs considerably between species, which might translate into differences in floating ability: in some species, the wall is dotted with convexities (e.g. *D. rosea*) or with concavities (*D. pulex*, *D. longispina*) or is covered by scaly shaped structures (e.g. *D. magna*) in others (Fig. 8.3).

8.2.2.3   Sticking to Other Surfaces: External Morphology Continued

What makes them hydrophobic and easily caught at the water-air phase boundary makes them also stick to other surfaces. *Daphnia magna*, which hardly ever sheds ephippia at the water surface and is expected to use other mechanisms aiding dispersal, has ephippia that are equipped with tacky filaments, remnants of the moulted carapace which are not seen in other species (Mergeay et al. 2006a), that stay with the ephippium and act as hooks, sticking readily to solid objects (personal observations).

8.2.2.4   Time of Reaching Water Surface: Timing of Life History Events

Ephippia appearance at the water surface was reported not only in laboratory studies but also in the field. Mass occurrence of ephippia at the water surface reaching thousands per square meter in the middle of the lake (Ślusarczyk and Pietrzak 2008) or getting even higher densities on the downwind shore of the waterbodies (Fig. 8.4). It would be tempting to associate seasonal occurrence of ephippia at the water surface with timing of operation of their putative vectors, e.g. with bird migrations period, which seem to us the most effective vectors of ephippial eggs dispersal. However, this would need to be disentangled from the effect of the timing of the environmental deterioration, which might be a stronger selection force than dispersal vector availability.

Fig. 8.4 Floating ephippia accumulating in high densities on a downwind shore within foam or debris

8.2.2.5 Harsh Physical Conditions: Resistance

While the structure of the wall of the ephippia varies greatly between species (Bernatowicz et al. 2018), it invariably gives them toughness and endurance. Also, unlike the subitaneous egg, the dormant embryo invariably has a yet another protective layer: the inelastic and highly impermeable outermost egg shell (chorion). The embryo also contains high concentrations of the heat shock protein Hsp60, and cryoprotective glycerol (Pauwels et al. 2007) and possibly trehalose (Smirnov 2014).

Dormant embryo enclosed in the protective ephippial case of some species of *Daphnia* may withstand prolonged desiccation, extremely high or low temperature, anoxic conditions and passage through the gut of fish or birds (for review, see Radzikowski 2013). For instance, ephippia from northern *Daphnia* from Greenland hatched with success after being keep at –18°C for 18 years (Meijering 2003).

We might expect some differences between resident and dispersal ephippial eggs in their resistance to environmental extremes since different selective forces may shape properties of the two groups. The ephippial eggs of the individuals predestined for passive overland dispersal might be expected to be more resistant to extreme abiotic threats than the resident ones. The latter remain at the bottom of the native habitats where they may never face desiccation nor extreme thermal conditions, which dispersion forms have to cope with. Indeed, ephippial eggs collected at the water surface (dispersing) revealed higher tolerance to elevated temperature and desiccation compared to the resident ones collected at the bottom of some deep lakes in Poland (see Radzikowski 2019 for more details).

Risk of mechanical damage of the resting eggs is relatively low in "soft" aquatic lentic habitats. Unlike, overland dispersing resting eggs are exposed to abrasion and much greater mechanical forces not balanced by water buoyancy or viscosity. Therefore, the ephippial case seems redundant for resident resting eggs residing in deep permanent lakes, more useful in temporarily drying habitats, while vital for those passively dispersing. In this light, the ephippial case could be viewed as a structural adaptation for overland dispersal. Indeed, cladocerans which possess

well-developed ephippial case are among the first invaders to newly formed isolated waterbodies (Louette and de Meester 2005). The most advanced ephippial structures may be found in Daphnidae (including Moinidae), while poorly developed cases are found in other Anomopoda (e.g. Bosminidae, Chydoridae, Macrothricidae) and non-existent in other Cladocera: Ctenopoda, Haplopoda or Onychopoda (Fryer 1996).

8.2.2.6 Unknown Hatching Habitat: Sensitivity and Hatching Phenology

The resident and dispersal ephippial eggs might also differ in some other features related to their distinct functions, like hatching phenology or longevity, which has not been probably tested so far. According to Venable and Levin (1985), who compared hatching phenology of dispersal and resident seeds of some terrestrial plants inhabiting unpredictably changing desert habitats, the dispersal seeds equipped with morphological adaptations for spatial dispersal germinated readily and synchronously while the resident seeds germinated more gradually. Some proportion of resident seeds postponed germination until a further favourable occasion as if they hedged against risk of unpredictable environmental deterioration (Venable and Lawlor 1980; Venable and Levin 1985). Diversified revival from the periodic rest (asynchronous germination or hatching) is considered the adaptive mechanism reducing risk of failed decision to resume development at uncertain conditions (Cohen 1966; Seger and Brockmann 1987; Ślusarczyk et al. 2017b).

It is hard to guess which ephippial eggs, either dispersal (shed at the water surface) or resident (released in the water column), should reveal higher longevity since both of them may be exposed to unpredictable environmental fluctuations. The dispersal hitchhikers may be displaced into unpredictable sites before they luckily reach some suitable location. Yet, the fate of the resident ephippia might not be defined either, once most of them may be buried for indefinite time in lake sediments before some external force (burrowing animal, gas bubbles, etc.) bring them back to the sediment surface, only where their development is feasible (Radzikowski et al. 2016). Large quantities of ephippia reside deep in lake sediments (Carvalho and Wolf 1989; Cáceres 1998a; Kerfoot et al. 2004) and may never hatch. For the above reasons, both dispersal and resident ephippial eggs might feature long viability, helping them to survive to a rare occasion for reactivation. While dispersal ephippia might possibly hatch at first favourable occasion (as it might be the last one), the resident should be more careful and reveal bet-hedging way of reactivation to cope with temporal variability of environmental conditions. The uncertainty receives now a new dimension under increasing intensity and scope of anthropogenic hydrological disturbances in the freshwater habitats (Brendonck et al. 2017).

So far we know little about *Daphnia* hatching phenology, length of latency included. We are aware that ephippial eggs of some lake *Daphnia* have very long dormancy periods reaching decades (Cáceres 1998a) or even centuries (Frisch et al. 2014), while those from temporary ponds reveal bet-hedging way of reactivation (Radzikowski 2019) which may prevent coincident resurrection off all resting eggs and diversify the risk of the failed choice in unpredictably changing habitats. We do

not know, however, the hatching phenology of ephippial eggs of the lake *Daphnia* nor longevity of ephippial eggs in temporary waters, not mentioning the differences between resident and dispersing ones in that field.

8.2.2.7   More Challenges and Mechanisms

Many more potentially important selective forces can be identified and adaptive mechanisms speculated on. Surviving gut passage demands particular chemical and mechanical resistance. Anemochory and ectozoochory are facilitated by small size of the propagule (van de Meutter et al. 2008), which in case of *Daphnia* is directly linked to mother body size, and female-size-corrected variation in ephippium size has not been shown so far. Lethal effect of ultraviolet light is a vital factor not only for airborne propagules (Maguire Jr. 1963) but also to all exposed for longer periods to direct sunlight. Hydrophobic ephippial case offers enhanced protection against desiccation, and honeycomb-like structure offers enhanced protection against mechanical damage (Bernatowicz et al. 2018) and – when incrusted with black protective pigments – to UV radiation (Shan 1970). Indeed, pigmentation of the shell varies between ephippia (Gerrish and Cáceres 2003), and its association with dispersal versus resident phenotype has neither been shown yet.

8.2.3   *Effectiveness of Passive Dispersal*

For a long time, it was thought that plankton organisms producing resting stages have high dispersal capacities, enabling them to successfully colonize waterbodies and be widespread in ponds and lakes across large-scale extent (Mayr 1970; Cohen and Shurin 2003). The wide geographical ranges of many freshwater taxa are testimony that passive dispersal by resting stages can be effective for dispersal-gene flow and make many aquatic taxa essentially cosmopolitan and genetically similar.

This assumption was questioned following detailed morphological studies (Frey 1982) and molecular work (Lynch and Spitze 1994; Colbourne and Hebert 1996; De Meester 1996a; Schwenk et al. 1998; Gómez et al. 2000, 2002). Comparison of patterns in gene flow in freshwater taxa with different life cycles support the scenario that high dispersal of organisms favour an effective monopolization of waterbody resources by newly invading species (and genotypes), yielding a strong priority effect (De Meester et al. 2002). This founder effect increases genetic differentiation among zooplankton populations inhabiting nearby ponds and reduces gene flow among populations and waterbodies. Boileau et al. (1992) proposed that the high levels of genetic differentiation in cyclic parthenogenetic species such as *Daphnia* reflect their potential to colonize habitats from a few resting eggs that are resistant to decay for dozens of generations, and their capacity for rapid population growth upon hatching. Such founder effects were illustrated by the persistence of non-indigenous species (*Daphnia exilis* and *D. lumhotzi* in USA; *D. ambigua* and *D. parvula* in

Europe) as resting eggs in sediments and their rapid colonization only promoted by human disturbances (Hairston et al. 1999; Havel et al. 1995; Maier 1996).

De Meester et al. (2002) examined the potential mechanisms causing a discrepancy between high dispersal rates and reduced level of gene flow (the monopolization hypothesis and dispersal-gene flow paradox) in cyclical parthenogens such as *Daphnia*. Founder events upon colonization of waterbodies followed by rapid population growth and local adaptation of daphnids as well as buffering effect of resting eggs banks result in an effective monopolization of resources and a strong priority effect, creating high genetic differentiation among nearby populations (see also Boileau et al. 1992; Jenkins and Buikema 1998; Palsson 2000). Pronounced genetic differentiation among daphnid populations was detected for neutral markers as well as ecological relevant traits (De Meester 1996a, b). Thus, patterns of regional genetic differentiation in daphnid populations may often reflect historical colonization of new habitats via dispersal and priority effect rather than contemporary gene flow. In addition, strong local selection also favours genetic divergence among nearby populations even if dispersal rates are high (Michels et al. 2001; De Meester et al. 2002).

Effectiveness of passive dispersal in freshwater organisms is still debated because it varies among species due to specific differences in functional traits such as body size, resting egg features, resistance to environmental threats during dispersal and adaptation to local habitat (Cohen and Shurin 2003). There is now a substantial amount of evidence that daphnids exhibit significant potential for passive dispersal via long distance transport through wind (Michels et al. 2001; Cáceres and Soluk 2002), direct water flow among connected waterbodies (van de Meutter et al. 2006) or animal vectors such as waterfowl (Proctor and Malone 1965; Figuerola et al. 2003, 2005; Moreno et al. 2019) or aquatic insects (van de Meutter et al. 2008). However, several studies have suggested that aquatic microcrustaceans are relatively efficient dispersers in a variety of landscapes, whereas others have indicated dispersal limitation at large and small spatial scales or under specific circumstances (Juračka et al. 2016; Horváth et al. 2016).

Supporters of effective dispersal have shown that species of cladocerans can disperse effectively over short distance (<1 km) and colonize suitable habitats quickly depending on their ability to tolerate local conditions, such as water acidity and the presence of fish. Louette and De Meester (2005) monitored cladoceran colonization in 25 newly created waterbodies and isolated pools over a wide geographic area. They found high effectiveness of passive dispersal via transport of dormant stages. Daphnids (*D. obtusa*, *Ceriodaphnia* spp., *Simocephalus vetulus* and *Scapholeberis mucronata*) were the most frequently found, representing almost 50% of the colonization events. Experimental studies also gave strong evidence of high dispersal and colonization effectiveness of cladoceran zooplankton, as 60–75% of the regional species pool can be captured in mesocosms after between less than two months and two years depending on the distance to the nearest pond (Cáceres and Soluk 2002; Cohen and Shurin 2003; Lopes et al. 2016). Recently, dispersal limitation was suggested not important in the Arctic young freshwater habitats, where the structure of asexual *Daphnia* populations reflected environmental gradients and differences in clonal ecology (Haileselasie et al. 2016). In another study conducted in Ethiopian

reservoirs, these were the founder effects again suggested to structure regional population (Haileselasie et al. 2018).

Effectiveness of passive dispersal of cladocerans has also been evaluated by quantifying the build-up of the dormant egg bank in the sediment during the first six months in newly created egg-free pools over Flanders, Belgium (Vandekerkhove et al. 2005). High densities (60–10000 eggs per m^2) of cladoceran egg banks were observed in the new pools. In parallel, the temporal dormant egg bank on the water surface, reaching densities of hundreds to thousands of ephippia per m^2, has been suggested as another proxy for this high potential (Ślusarczyk et al. 2017a). The high prevalence of floating ephippia in *Daphnia* may make it a more effective disperser than some other cladocerans (Sirianni 2017).

Supporters of dispersal limitation found multiple indications of dispersal limitation affecting the community assembly of microcrustacean communities. On a large-scale survey, spatial patterns in zooplankton community composition were better explained by the geomorphological structure of the landscape than by mere geographic distances between waterbodies (Juračka et al. 2016), suggesting that ridges separating the network of valleys act as dispersal barriers and may channel the dispersal routes of the taxa. Furthermore, dispersal limitation was reflected by a strong positive relationship between species richness and the number of neighbouring waterbodies. On a small-scale extent, although the effect of wind lessen dispersal limitation along its prevailing direction, it persists that dispersal limitation may constraint community assembly in highly mobile organisms even at spatial scale below 5 km (Horváth et al. 2016). Most probably, different processes dominate at different spatial and temporal scales. Heino et al. (2015) suggested dispersal limitation to be increasing with distances between habitats, contrary to the importance of mass effects, and the spatial extents of different processes to be affected by the dispersal ability of organisms. More recently, the need of using novel tools to assess the role of dispersal in shaping communities has been proposed (Heino et al. 2017).

8.2.4   Consequences of Dispersal of Dormant Eggs

Several phenomena associated with the passive dispersal of ephippial eggs may have far reaching non-adaptive implications for these organisms.

8.2.4.1   Ephippia Exploitation

During periods of intense ephippia formation, high quantities of ephippia may accumulate along the downwind shore of the waterbodies (Figs. 8.4 and 8.5). This supra- and meso-littoral aggregation of resting eggs constitutes an underestimated bank of *Daphnia* resting forms in freshwater habitats. The accumulation of the resting eggs of *Daphnia* may be intense enough to exploit it commercially in aquacultures likewise floating eggs of the brine shrimps *Artemia franciscana* and has already been suggested as a source for exploitation for chitin extraction (Kaya et al. 2014).

Fig. 8.5 Mean densities of ephippia of *Daphnia* of the *longispina* group at the water surface of the small eutrophic Lake Kociołek (54°03′01″N 22°19′54″E), collected with half-submerged neuston net kept in front of cruising boat at noon at five sampling stations located along prevailing wind directions reported week ahead of sampling period. Letters below the density values indicate homogenous groups with values similar according to ANOVA model simplification
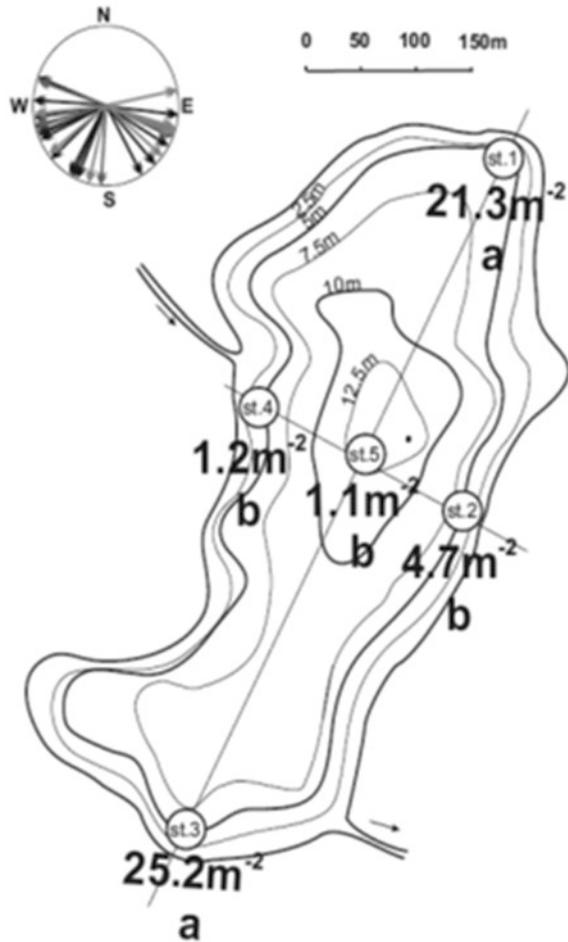
8.2.4.2 Trap More Than Shelter

Ephippia accumulate in deep locations. The resident ephippia which are shed below the water surface, and those oviposited at the water surface that sink with time become unevenly distributed over the lake bottom. The highest densities of ephippia frequently occurs in the deepest zones of lakes (Carvalho and Wolf 1989; Jankowski 2003; Kerfoot et al. 2004) either because of the higher number of females shedding ephippia in cumulated volume of water above those places or, what is more likely, due to their slipway from shallower locations along the bottom slopes. Controversy exists if bottom sediments are shelter for the resting eggs or rather a trap that disable their hatching (Cáceres and Hairston 1998). Dormant forms of aquatic species may reside in lake sediments for long time not deliberately, but due to their burrowing by lake sediments. According to Radzikowski et al. (2016), even a thin sediment layer (less than 2.5 mm) may hamper development of resting eggs of *Daphnia*. This might

provoke a significant question on the ultimate function of ephippia deposition at the water surface: is it dispersion between, or rather within aquatic habitats? *Daphnia* could shed ephippia at the water surface not to colonize other waterbodies, but to let them be rafted toward the shallow littoral zone and try to escape the sediment trap of the profundal zone. Higher proportion of ephippia left by Daphnidae at the water surface in shallow lakes with frequently mixed sediments than deep ones with stagnant bottom (Ślusarczyk et al. 2017a) indicate, however, that between-lake dispersal is the more likely selective force behind this phenomenon.

8.2.4.3 Anthropogenic Invasions

Local mass aggregations of ephippia, together with their clinginess to different surface, and with carelessness on the human part, has led to unprecedented dispersal events. Intensified transport of dormant forms by anthropogenic vectors (e.g. by regional and global trades) broke existing intercontinental barriers and facilitated colonization of freshwater habitats by invasive species. This includes encroachment of alien species of *Daphnia* originating from remote locations in a recent time (Havel and Shurin 2004; Panov et al. 2004; Panov and Cáceres 2007), e.g. ongoing invasion of *D. lumholtzi* in North America (Havel et al. 2002) or *D. pulex* in Africa (Mergeay et al. 2006b).

8.2.4.4 Enhanced Biotic Diver sity and Slower Evolutionary changes

The spatial dispersal of dormant forms may enhance biotic diversity on a local (alfa diversity) and regional scale (gamma diversity) due to immigration of novel or recolonization of exterminated genotypes from neighbourhood locations (Chesson 2000) and reduce biotic dissimilarities between habitats within a region (i.e. lower beta diversity). The immigration of dormant forms from neighbourhood locations, like resurrection from the native bank of resting eggs, may slow down competitive exclusion of suboptimal competitors by superior ones and slow down evolutionary changes within genetic pool and species sorting within local habitats (Hairston and de Stasio 1988).

8.3 Conclusions

While the old paradigm of panmictic occurrence of planktonic species due to their easy colonization of aquatic habitats has eroded, the frequent spread of aquatic organisms has not yet been seriously questioned. What stops their successful invasions seems abiotic and biotic filters rather than dispersal barriers (Shurin 2000; De Meester et al. 2002; Incagnone et al. 2015). Frequent overland dispersal may be attributed to dormant forms used not only for temporal but also for spatial dispersal.

Freshwater dormant forms can survive long voyage across hostile terrestrial zone and may hitchhike using various animate or inanimate vectors, especially when aided by behavioural or morphological adaptations. Planktonic crustaceans of the genus *Daphnia* are among the first colonizers of newly founded waterbodies (Louette and de Meester 2005). Ephippial case of resting eggs may boost their spatial dispersal by offering positive buoyancy facilitating their hitchhiking by surface vectors and enhanced protection against mechanical damages or UV radiation. During periods of intense ephippia formation, high quantities of ephippia often accumulate along the downwind shore, where the wind blows them to. The supralittoral and meso-littoral banks of resting eggs may be an underestimated source not only for passive dispersal between waterbodies but possibly also as a refuge preventing their dislocation to the deep trap of profundal sediments.

Daphnia is undoubtedly the best-studied cladoceran species. The question remains, how effective is dispersal of other cladocerans with poorly developed ephippia or no ephippia at all, and what mechanisms of dispersal they utilize instead. An open question remains also, if dormant eggs used for only temporal dispersal differ structurally or physiologically from ones used for spatial dispersal.

References

Allen MR (2007) Measuring and modelling dispersal of adult zooplankton. Oecologia 153:135–143

Alonso C, Rocco V, Barriga JP, Battini MÂN, Zagarese H (2004) Surface avoidance by freshwater zooplankton: Field evidence on the role of ultraviolet radiation. Limnol Oceanogr 49(1):225–232

Bell JR, Bohan DA, Shaw EM, Weyman GS (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bull Entomol Res 95:69–114

Bengtsson BO (1978) Avoiding inbreeding: at what cost? J Theor Biol 73:439–444

Berg LM, Pálsson S, Lascoux M (2001) Fitness and sexual response to population density in *Daphnia pulex*. Freshw Biol 46:667–677

Bernatowicz P, Radzikowski J, Paterczyk B, Bebas P, Ślusarczyk M (2018) Internal structure of *Daphnia* ephippium as an adaptation to dispersion. *Zool Anz* 277:12–22

Bilton DT, Freeland JR, Okamura B (2001) Dispersal in freshwater invertebrates. *Annu Rev Ecol Syst* 32:159–181. https://doi.org/10.1146/annurev.ecolsys.32.081501.114016

Bohonak A, Jenkins D (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol Lett 6(8):783–796

Boileau MG, Hebert PDN, Schwartz SS (1992) Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. J Evol Biol 5:25–39

Boulinier T, McKoy KD, Sorci G (2002) Dispersal and parasitism. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) Dispersal. Oxford University Press, Oxford, pp 169–180

Bormashenko E (2016) Surface Tension Supported Floating of Heavy Objects: Why Elongated Bodies Float Better? J Colloid Interface Sci 463:8–12

Brendonck L, Pinceel T, Ortells R (2017) Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools. Hydrobiologia 796:201–222

Brochet AL, Gauthier-Clerc M, Guillemain M, Fritz H, Waterkeyn A, Baltanás Á, Green AJ (2010a) Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). Hydrobiologia 637:255–261

Brochet AL, Guillemain M, Fritz H, Gauthier-Clerc M, Green AJ (2010b) Plant dispersal by teal (*Anas crecca*) in the Camargue: duck guts are more important than their feet. Freshw Biol 55:1262–1273. https://doi.org/10.1111/j.1365-2427.2009.02350.x

Bullock JM, Bonte D, Pufal G, DaSilva-Carvalho C, Chapman DS, Garcia C, Garcia D, Matthysen E, Delgado MM (2018) Human-Mediated Dispersal and the Rewiring of Spatial Networks. Trends Ecol Evol 33(12):958–970

Buoro M, Carlson SM (2014) Life-history syndromes: Integrating dispersal through space and time. Ecol Lett 17(6):756–767

Burgess SC, Baskett ML, Grosberg RK, Morgan SG, Strathmann RR (2016) When is dispersal for dispersal? Unifying marine and terrestrial perspectives. Biol Rev 91:867–882. https://doi.org/10.1111/brv.12198

Cáceres CE (1998a) Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. Ecology 79(5):1699–1710

Cáceres CE (1998b) Seasonal dynamics and interspecific competition in Oneida Lake *Daphnia*. Oecologia 115:233–244

Cáceres CE, Hairston NGJ (1998) Benthic-pelagic coupling in planktonic crustaceans: the role of the benthos. Arch Hydrobiol Spec Issue Adv Limnol 52:163–174

Cáceres C, Christoff A, Boeing W (2007) Variation in ephippial buoyancy in *Daphnia pulicaria*. Freshw Biol 52:313–318

Cáceres CE, Soluk DA (2002) Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* 131:402–408

Carvalho GR, Wolf HG (1989) Resting eggs of lake *Daphnia* I. Distribution, abundance and hatching of eggs collected from various depths in lake sediments. Freshw Biol 22:459–470

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31(1):343–366

Cohen D (1966) Optimizing reproduction in a randomly varying environments. J Theoret Biol 12:119–129

Cohen GM, Shurin JB (2003) Scale-dependence and mechanisms of dispersal in freshwater zooplankton. Oikos 103(3):603–617

Colbourne JK, Hebert PDN (1996) The systematics of North American *Daphnia* (Crustacea: Anomapoda): a molecular phylogenetic approach. Philos Trans R Soc Lond B 351:349–360

Costa MJ, Ramos JA, da Silva LP, Timoteo S, Araujo PM, Felgueiras MS, Rosa A, Matos C, Encarnacao P, Tenreiro PQ, Heleno RH (2014) Endozoochory largely outweighs epizoochory in migrating passerines. J Avian Biol 45:59–64. https://doi.org/10.1111/j.1600-048X.2013.00271.x

Coughlan NE, Kelly TC, Davenport J, Jansen MA (2017) Up, up and away: bird-mediated ectozoochorous dispersal between aquatic environments. Freshw Biol 62:631–648. https://doi.org/10.1111/fwb.12894

Dawidowicz P, Pijanowska J (2018) Chapter 9: Diel vertical migration of aquatic crustaceans – adaptive role, underlying mechanisms, and ecosystem consequences. In: Thiel M, Welborn G (eds) The natural history of crustaceans, life histories, vol 5. Oxford University Press, Oxford, pp 231–256

Davison J (1969) Activation of the Ephippial Egg of *Daphnia pulex*. J Gen Physiol 53:562–575

Decaestecker E, De Meester L, Mergeay J (2009) Cyclical Parthenogenesis in *Daphnia*: sexual versus asexual reproduction. In: Lost sex: the evolutionary biology of parthenogenesis. Springer Netherlands, Dordrecht, pp 295–316

De Meester L (1996a) Local genetic differentiation and adaptation in freshwater zooplankton populations: patterns and processes. Ecoscience 3:385–399

De Meester L (1996b) Evolutionary potential and local genetic differentiation in a phenotypically plastic trait of a cyclical parthenogen, *Daphnia*. *Evolution* 50:1293–1298

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

Figuerola J, Green AJ (2002a) Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshw Biol 47:483–494

Figuerola J, Green AJ (2002b) How frequent is external transport of seeds and invertebrate eggs by waterbirds? A study in Doñana, SW Spain. Arch Hydrobiol 155(4):557–565. https://doi.org/10.1127/archiv-hydrobiol/155/2002/557

Figuerola J, Green AJ, Santamaria L (2003) Passive internal transport of aquatic organisms by waterflow in Doñana, south-west Spain. Glob Ecol Biogeogr 12:427–436

Figuerola J, Green AJ, Michot TC (2005) Invertebrate eggs can fly: Evidence of waterflow-mediated gene flow in aquatic invertebrates. Am Nat 165:274–280

Fitzsimmons JM, Innes DJ (2006) Inter-genotype variation in reproductive response to crowding among *Daphnia pulex*. Hydrobiologia 568(1):187–205

Forro L, Korovchinsky NM, Kotov AA, Petrusek A (2008) Global diversity of cladocerans (Cladocera; Crustacea) in freshwater. Hydrobiologia 595:177–184

Frey DG (1982) Questions concerning cosmopolitanism in Cladocera. Arch Hydrobiol 93:484–502

Frisch D, Morton PK, Chowdhury PR, Culver BW, Colbourne JK, Weider LJ, Jeyasingh PD (2014) A millennial-scale chronicle of evolutionary responses to cultural eutrophication in *Daphnia*. Ecol Lett 17(3):360–368

Fryer G (1996) Diapause, a potent force in the evolution of freshwater crustaceans. Hydrobiologia 320:1–14

Gandon S, Michalakis Y (2002) Multiple causes of the evolution of dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) Dispersal. Oxford University Press, Oxford, pp 155–168

Gerrish G, Cáceres C (2003) Genetic versus environmental influence on pigment variation in the ephippia of *Daphnia pulicaria*. Freshw Biol 48(11):1971–1982

Gliwicz ZM (2003) Between hazards of starvation and risks of predation: the ecology of offshore animals. International Ecology Institute, Oldendorf/Luhe

Gómez A, Carvalho GR, Lunt DH (2000) Phylogeography and regional endemism of a passive dispersal zooplankter: mitochondrial DNA variation in rotifer resting egg banks. Proc R Soc Lond B 267:2189–2197

Gómez A, Adcock GA, Lunt DH, Carvalho GR (2002) The interplay between colonization history and gene flow in passively dispersing zooplankton: microsatellite analysis of rotifer resting egg banks. J Evol Biol 15:158–171

Green AJ, Figuerola J, Sánchez MI (2002) Implications of waterbird ecology for the dispersal of aquatic organisms. Acta Oecol 23:177–189

Haileselasie TH, Mergeay J, Weider LJ, Sommaruga R, Davidson TA, Meerhoff M, Arndt H, Jürgens K, Jeppesen E, De Meester L (2016) Environment not dispersal limitation drives clonal composition of Arctic *Daphnia* in a recently deglaciated area. Mol Ecol 25:5830–5842. https://doi.org/10.1111/mec.13843

Haileselasie TH, Mergeay J, Vanoverbeke J, Orsini L, De Meester L (2018) Founder effects determine the genetic structure of the water flea *Daphnia* in Ethiopian reservoirs. Limnol Oceanogr 63:915–926. https://doi.org/10.1002/lno.10678

Hairston NGJ, Lampert W, Cáceres CE (1999) Rapid evolution revealed by dormant eggs. Nature 401(30):446

Hairston NGJ, de Stasio BTJ (1988) Rate of evolution slowed by a dormant propagule pool. Nature 336(17):239–242

Hamilton WD, May RM (1977) Dispersal in stable habitats. Nature 269(13):578–581

Havel JE, Mabee MR, Jones JR (1995) Invasion of the exotic *Daphnia lumhotzi* into North American reservoirs. Can J Fish Aquat Sci 52:151–160

Havel JE, Shurin JB (2004) Mechanisms, effects, and scales of dispersal in freshwater zooplankton. Limnol Oceanogr 49:1229–1238

Havel JE, Shurin JB, Jones JR (2002) Estimating dispersal from patterns of spread: spatial and local control of lake invasions. Ecology 83(12):3306–3318

Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshw Biol 60:845–869. https://doi.org/10.1111/fwb.12533

Heino J, Alahuhta J, Ala-Hulkko T, Antikainen H, Bini LM, Bonada N, Datry T, Erős T, Hjort J, Kotavaara O, Melo AS, Soininen J (2017) Integrating dispersal proxies in ecological and environmental research in the freshwater realm. Environ Rev 25:334–349. https://doi.org/10.1139/er-2016-0110

Higgins SI, Nathan R, Cain ML (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84:1945–1956. https://doi.org/10.1890/01-0616

Hiruta C, Tochinai S (2014) Formation and structure of the ephippium (resting egg case) in relation to molting and egg laying in the water flea *Daphnia pulex* De Geer (Cladocera: Daphniidae). J Morphol 275:760–767

Holt RD, Barfield M (2002) On the relationship between the ideal free distribution and the evolution of dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) Dispersal. Oxford University Press, Oxford, pp 83–96

Hopfensperger KN, Baldwin AH (2009) Spatial and temporal dynamics of floating and drift-line seeds at a tidal freshwater marsh on the Potomac River, USA. Plant Ecol 201:677–686

Horváth Z, Vad CF, Ptacnik R (2016) Wind dispersal results in a gradient of dispersal limitation and environmental match among discrete aquatic habitats. Ecography (Cop) 39(8):726–732

Incagnone G, Marrone F, Barone R, Robba L, Naselli-Flores L (2015) How do freshwater organisms cross the "dry ocean"? A review on passive dispersal and colonization processes with a special focus on temporary ponds. Hydrobiologia 750:103–123

Jacobs MJ, MacIsaac HJ (2007) Fouling of fishing line by the waterflea *Cercopagis pengoi*: a mechanism of human-mediated dispersal of zooplankton? Hydrobiologia 583:119–126

Jankowski T (2003). From diapause to sexual reproduction – evolutionary ecology of the daphnia hybrid complex from lake constance. PhD thesis, Universität Konstanz, Konstanz.

Jenkins DG, Buikema AL (1998) Do similar communities develop in similar sites? Ecol Monogr 68:421–443

Juračka PJ, Declerck SAJ, Vondrak D, Beran L, Cerny M, Petrusek A (2016) A naturally heterogeneous landscape can effectively slow down the dispersal of aquatic microcrustaceans. Oecologia 180(3):785–796

Karlson RH (1992) Divergent dispersal strategies in the freshwater bryozoan *Plumatella repens*: ramet size effects on statoblast numbers. Oecologia 89(3):407–411

Kappes H, Tackenberg O, Haase P (2014) Differences in dispersal- and colonization-related traits between taxa from the freshwater and the terrestrial realm. Aquat Ecol 48:73–83

Kaya M, Baran T, Saman I, Ozusaglam MA, Cakmak YS, Menteş A (2014) Physicochemical characterization of chitin and chitosan obtained from resting eggs of *Ceriodaphnia quadrangula* (Branchiopoda: Cladocera: Daphniidae). J Crustac Biol 34:283–288. https://doi.org/10.1163/1937240X-00002221

Kerfoot WC, Wells Budd J, Eadie B, Vanderploeg H, Agy M (2004) Winter storms: Sequential sediment traps record *Daphnia* ephippial production, resuspension, and sediment interactions. Limnol Oceanogr 49(4):1365–1381

Leuven R, van der Velde G, Baijens I, Snijders J, van der Zwart C, Lenders HJR, de Vaate AB (2009) The river Rhine: a global highway for dispersal of aquatic invasive species. Biol Invasions 11(9):1989–2008

Lewis LR, Behling E, Gousse H, Qian E, Elphick CS, Lamarre JF, Bêty J, Liebezeit J, Rozzi R, Goffinet B (2014) First evidence of bryophyte diaspores in the plumage of transequatorial migrant birds. Peer J 2:e424. https://doi.org/10.7717/peerj.424

Lopes PM, Bozelli R, Bini JLM, Santangelo M, Declerck SAJ (2016) Contributions of airborne dispersal and dormant propagule recruitment to the assembly of rotifer and crustacean zooplankton communities in temporary ponds. Freshw Biol 61:658–669

Louette G, de Meester L (2005) High dispersal capacity of cladoceran zooplankton in newly founded communities. Ecology 86(2):353–359

Lynch M, Spitze K (1994) Evolutionary genetics of *Daphnia*. In: Real LA (ed) Ecological genetics. Princeton University Press, Princeton, NJ, pp 109–128

Maguire B Jr (1963) The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol Monogr 33:161–185

Maier G (1996) *Daphnia* invasion: population dynamics of *Daphnia* assemblages in two eutrophic lakes with particular reference to the introduced alien *Daphnia ambigua*. J Plankton Res 18:2001–2015

Marszelewski W (2005) Zmiany warunków abiotycznych w jeziorach Polski północno-wschodniej. Wydawnictwo Uniwersytetu Mikołaja Kopernika, Toruń

Mayr E (1970) Populations, species, and evolution. Belknap Press of Harvard University Press, Cambridge

McAtee WL (1917) Showers of Organic Matter. Mon Weather Rev 45:217

Mc Peek MA, Kalisz S (1998) On the joint evolution of dispersal and dormancy in metapopulations. Arch Hydrobiol Spec Issue Adv Limnol 52:33–51

Meijering MPD (2003) The long-lasting resistance of diapausing eggs from Arctic Cladocera at -18°C. Pol Polar Res 24:167–172

Mergeay J, Verschuren D, de Meester L (2006a) *Daphnia* species diversity in Kenya, and a key to the identification of their ephippia. Hydrobiologia 542(1):261–274

Mergeay J, Verschuren D, de Meester L (2006b) Invasion of an asexual American water flea clone throughout Africa and rapid displacement of a native sibling species. Proc R Soc B Biol Sci 273(1603):2839–2844

Michels E, Cottenie K, Neys L, de Meester L (2001) Zooplankton on the move: first results on the quantification of dispersal of zooplankton in a set of interconnected ponds. Hydrobiologia 442:117–126

Mikulski A. & Grzesiuk M. 2019, Sex and sex dependent reproduction strategies in cyclic partenogen - a case study from astatic urban pond. Submitted manuscript.

Moreno E, Perez-MartĂnez C, Conde-Porcuna JM (2019) Dispersal of rotifers and cladocerans by waterbirds: seasonal changes and hatching success. Hydrobiologia 834(1):145–162. https://doi.org/10.1007/s10750-019-3919-6

Palsson S (2000) Microsatellite variation in Daphnia pulex from both side of the Baltic Sea. Mol Ecol 9:1075–1088

Panov VE, Cáceres C (2007) Role of diapause in dispersal of aquatic invertebrates. In: Diapause in aquatic invertebrates theory and human use. Springer Netherlands, Dordrecht, pp 187–195

Panov VE, Krylov PI, Riccardi N (2004) Role of diapause in dispersal and invasion success by aquatic invertebrates. J Limnol 63. (Suppl. 1:56–69

Pauwels K, Stoks R, Verbiest A, de Meester L (2007) Biochemical adaptation for dormancy in subitaneous and dormant eggs of *Daphnia magna*. Hydrobiologia 594:91–96. https://doi.org/10.1007/s10750-007-9091-4

Perrin N, Mazalov V (1999) Dispersal and Inbreeding Avoidance. Am Nat 154(3):282–292

Pietrzak B, Ślusarczyk M (2006) The fate of ephippia - *Daphnia* dispersal in time and space. Pol J Ecol 54:709–714

Pietrzak B, Bednarska A, Markowska M, Rojek M, Szymanska E, Ślusarczyk M (2013) Behavioural and physiological mechanisms behind extreme longevity in *Daphnia*. Hydrobiologia 715:125–134

Pinceel T, Vanschoenwinkel B, Brendonck L (2013) Flexible dispersal dimorphism in zooplankton resting eggs: an example of repeated phenotypic coin flipping? Biol J Linn Soc 110:749–756

Pollux BJA, Verbruggen E, Van Groenendael JM, Ouborg NJ (2009) Intraspecific variation of seed floating ability in *Sparganium emersum* suggests a bimodal dispersal strategy. Aquat Bot 90:199–203

Proctor VW (1959) Dispersal of fresh-water algae by migratory water birds. Science 130:623–624

Proctor VW, Malone CR (1965) Further evidence of the passive dispersal of small aquatic organism via the intestinal tract of birds. Ecology 46:728–729

Ptatscheck C, Milne PC, Traunspurger W (2018) Is stemflow a vector for the transport of small metazoans from tree surfaces down to soil? BMC Ecol 18:43. https://doi.org/10.1186/s12898-018-0198-4

Radzikowski J (2013) Resistance of dormant stages of planktonic invertebrates to adverse environmental conditions. J Plankton Res 35(4):707–723

Radzikowski J (2019). Properties of the resting stages of Daphnidae inhabiting aquatic habitats of varying degrees of variation in environmental conditions. PhD thesis, University of Warsaw, Warszawa.

Radzikowski J, Sikora A, Ślusarczyk M (2016) The effect of lake sediment on the hatching success of *Daphnia* ephippial eggs. J Limnol 75(3):597–605

Radzikowski J, Krupińska K, Ślusarczyk M (2018) Different thermal stimuli initiate hatching of *Daphnia* diapausing eggs originating from lakes and temporary waters. Limnology 19:81–88

Raulings E, Morris K, Thompson R, Mac Nally R (2011) Do birds of a feather disperse plants together? Freshw Biol 56:1390–1402

Reynolds C, Cumming GS (2015) The role of waterbirds in the dispersal of freshwater cladocera and bryozoa in southern Africa. Afr Zool 50:307–311. https://doi.org/10.1080/15627020.2015.1108164

Reynolds C, Cumming GS (2016) Seed dispersal by waterbirds in southern Africa: comparing the roles of ectozoochory and endozoochory. Freshw Biol 61:349–361. https://doi.org/10.1111/fwb.12709

Ricci C, Caprioli M (2005) Anhydrobiosis in bdelloid species, populations and individuals. Integr Comp Biol 45:759–763

Sánchez MI, Hortas F, Figuerola J, Green AJ (2012) Comparing the potential for dispersal via waterbirds of a native and an invasive brine shrimp. Freshw Biol 57:1896–1903. https://doi.org/10.1111/j.1365-2427.2012.02852.x

Schwenk K, Sand A, Boersma M, Brehm M, Mader E, Offerhaus D, Spaak P (1998) Genetic makers, genealogies and biogeographic patterns in the cladoceran. Aquat Ecol 32:37–51

Seger J, Brockmann JH (1987) What is bet-hedging? In: Harvey PH, Partridge L (eds) Oxford surveys in evolutionary biology. Oxford University Press, Oxford, UK, pp 182–211

Sirianni KM (2017) Differential wind dispersal of cladoceran ephippia in a rock pool metacommunity. Aquat Ecol 51:203–218. https://doi.org/10.1007/s10452-016-9611-2

Shan RKC (1970) Influence of light on hatching resting eggs of chydorids (Cladocera). Internationale Revue der gesamten Hydrobiologie und Hydrographie 55(2):295–302

Shurin JB (2000) Dispersal limitation, invasion resistance and the structure of pond zooplankton communities. Ecology 81:3074–3086

Shurin JB, Havel JE (2002) Hydrologic connections and overland dispersal in an exotic freshwater crustacean. Biol Invasions 4:431–439

Ślusarczyk M (1995) Predator-induced diapause in *Daphnia*. Ecology 76(3):1008–1013

Ślusarczyk M (2004) Environmental plasticity of fish avoidance diapause response in *Daphnia magna*. J Limnol 63. (Suppl. 1:70–74

Ślusarczyk M (2009) Extended lifespan traded for diapause in *Daphnia*. Freshw Biol 54(11):2252–2262

Ślusarczyk M, Pinel-Alloul B, Gelinas M (2006) On ultimate reasons for summer diapause of *Daphnia* in a permanent lake. Verh Internat Verein Limnol 29:1440–1442

Ślusarczyk M, Grabowski T, Pietrzak B (2017a) Quantification of floating ephippia in lakes: a step to a better understanding of high dispersal propensity of freshwater plankters. Hydrobiologia 798(1):61–72

Ślusarczyk M, Starzynski J, Bernatowicz P (2017b) How long to rest in unpredictably changing habitats? PLoS ONE 12(4):e0175927

Ślusarczyk M, Pietrzak B (2008) To sink or float: the fate of dormant offspring is determined by maternal behaviour in *Daphnia*. Freshw Biol 53:569–576

Ślusarczyk M, Flis S (2019) Light quantity, not photoperiod terminates diapause in the crustacean *Daphnia*. Limnol Oceanogr 64(1):124–130

Ślusarczyk M, Chlebicki W, Pijanowska J, Radzikowski J (2019) The role of the refractory period in diapause length determination in a freshwater crustacean. Submitted manuscript.

Smirnov N (2014) Physiology of the cladocera. Academic Press, London, p 352

Valls L, Castillo-Escrivà A, Mesquita-Joanes F, Armengol X (2016) Human-mediated dispersal of aquatic invertebrates with waterproof footwear. Ambio 45:99–109. https://doi.org/10.1007/s13280-015-0689-x

Vandekerkhove J, Louette G, Brendonck L, de Meester L (2005) Development of cladoceran egg bank in new and isolated pools. Arch Hydrobiol 162:339–347

Van de Meutter F, Stoks R, de Meester L (2006) Lotic dispersal of lentic macroinvertebrates. Ecography 29:223–230

Van de Meutter F, Stoks R, de Meester L (2008) Size-selective dispersal of *Daphnia* resting eggs by backswimmers (*Notonecta maculata*). Biol Lett 4:494–496

Van Leeuwen CHA, Sarneel JM, van Paassen J, Rip WJ, Bakker ES (2014) Hydrology, shore morphology and species traits affect seed dispersal, germination and community assembly in shoreline plant communities. J Ecol 102:998–1007

Van Leeuwen CHA, Velde G, Groenendael JM, Klaassen M (2012) Gut travellers: internal dispersal of aquatic organisms by waterfowl. J Biogeogr 39:2031–2040. https://doi.org/10.1111/jbi.12004

Van Leeuwen CHA (2018) Internal and external dispersal of plants by animals: an aquatic perspective on alien interference. Front Plant Sci 9:153. https://doi.org/10.3389/fpls.2018.00153

Vanschoenwinkel B, Gielen S, Vandewaerde H, Seaman M, Brendonck L (2008a) Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. Ecography 31:567–577

Vanschoenwinkel B, Gielen S, Seaman M, Brendonck L (2008b) Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. Oikos 117:125–134. https://doi.org/10.1111/j.2007.0030-1299.16349.x

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

Vega MP, Clausse A (1998) Hydrodynamic characteristics of *Daphnia middendorffiana*. Int Rev Hydrobiol 83(4):267–277

Venable DL, Lawlor L (1980) Delayed germination and dispersal in desert annuals: escape in space and time. Oecologia 46:272–282

Venable DL, Levin DA (1985) Ecology of achene dimorphism in *Heterotheca latifolia*: I. Achene structure, germination and dispersal. J Ecol 73(1):133–145

Vivian-Smith G, Stiles EW (1994) Dispersal of salt marsh seeds on the feet and feathers of waterfowl. Wetlands 14:313–319

Waterkeyn A, Vanschoenwinkel B, Elsen S, Anton-Pardo M, Grillas P, Brendonck L (2010) Unintentional dispersal of aquatic invertebrates via footwear and motor vehicles in a Mediterranean wetland area. Aquat Conserv Mar Freshwat Ecosyst 20:580–587

Weisser WW (2002) The effects of predation on dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) Dispersal. Oxford University Press, Oxford, pp 180–191

Zaffagnini F (1987) Reproduction in *Daphnia*. Memorie Dell'Istituto Italiano Di Idrobiologia Dott Marco De Marchi 45:245–284