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Short review

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THE FATE OF THE EPHIPPIA – *DAPHNIA* DISPERSAL IN TIME AND SPACE

ABSTRACT: When conditions deteriorate, freshwater cladocerans from the genus *Daphnia* switch to production of diapausing eggs encased in chitinous shells called ephippia. Ephippia may serve for temporal escape and recolonisation of the habitat or for geographical dispersal and colonisation of other habitats. While dormancy and dispersal of ephippia have been well studied, initial factors determining the fate of the ephippia have remained unknown.

We first consider the fate of an ephippium that sinks to the bottom of the water body, where it enriches the egg bank present in the sediments. We then discuss the potential and evidence for dispersal of ephippia, which is probably facilitated by their flotation on the water surface. Finally, we concentrate on the moment of the release of the ephippium showing a likely mechanism that determines its further fate – temporal or spatial dispersal – and we demonstrate it to be accomplished through maternal behaviour.

KEY WORDS: *Daphnia*, ephippium, diapause, dispersal, maternal influence

1. INTRODUCTION

For annual plants, only two strategies are possible when unsuitable conditions arise: escape in time or escape in space. Annuals may escape in time by fractional

or delayed seed germination or they may escape spatially to new patches via seed dispersal (Venable and Lawlor 1980). Whether a seed is destined for dispersal or not is maternally determined, either by seed morphology or morphology of the mother plant (Venable and Brown 1988, Donohue 1998). Similarities of these two escape mechanisms and maternal determination may be found in the animal kingdom.

Freshwater planktonic cladocerans (Crustacea, Branchiopoda) produce dormant eggs which may serve these two functions: they provide a mode of avoiding harsh periods by seeking refuge in time and they get dispersed between non-contiguous bodies of water. These diapausing eggs are encased in protective chitinous shells called ephippia. Ultimate reasons for diapause in cladocerans from the genus *Daphnia*, proximate factors inducing ephippia production, their resistance to various environmental conditions, as well as ecological and evolutionary consequences of their production, have been well studied (Bohonak and Jenkins 2003, Brendonck and De Meester 2003, Gyllström and Hansson 2004, for recent reviews). However, factors determining their fate, destining them for

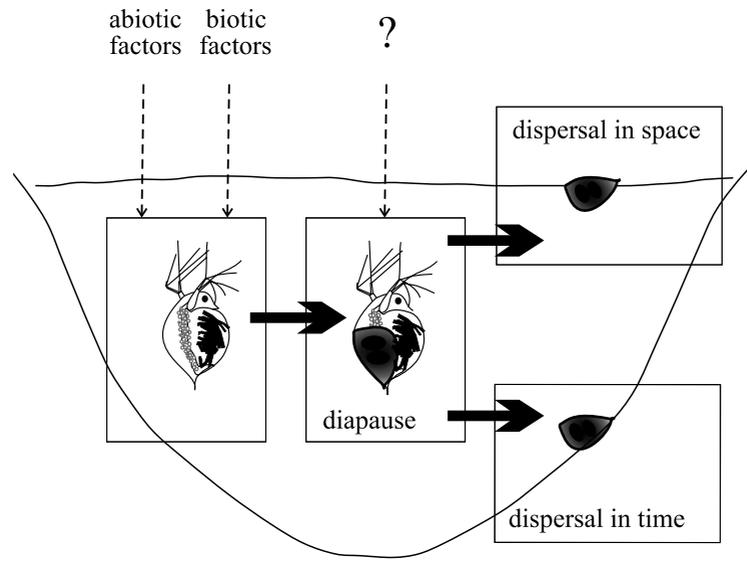


Fig. 1. Part of the *Daphnia* life cycle: from active to dormant stage (ephippium) and its further fate. Ehippia sinking to the sediments serve as a means of temporal dispersal and ehippia floating at the water surface as a means of spatial dispersal.

prolonged dormancy or for dispersal, have not yet been identified.

We suggest that the overriding factor determining whether ehippial eggs would serve as a means of temporal escape or of geographical dispersal might be the place of their deposition, i.e. sinking to the sediments or floating on the water surface (Fig. 1). We observed that this might be determined by the mother's behaviour.

2. SINKING EPHIPPIA

The active part of a *Daphnia* population dwells in the pelagial zone, whereas large numbers of ehippia are found in the sediments. Therefore, most ehippia are believed to be shed in the water column and sink directly to the bottom of water bodies, where they form egg banks. Such egg banks in the sediments are analogous to seed banks of plants in the ground and may reach densities of tens of thousands of ehippia per square metre (Cáceres 1998, Vandekerckhove *et al.* 2005a). The horizontal distributions of ehippia in the lake beds are reported to be concentrated in deep waters (Carvalho and Wolf 1989). This is often explained by higher deposition

of ehippia in places where the overlying water column contains a larger population (Brendonck and De Meester 2003).

Production of ehippia marks the beginning of what can be thought of as a time travel (Hairston 1998). Resting eggs of *Daphnia* will resume activity when conditions improve at a later, more favourable time, most likely in spring (Cáceres and Schwalbach 2001). Hatching usually takes place at the onset of the growing season when the opportunity for growth and reproduction appears, and before the lake stratifies, when environmental cues such as light or rise in temperature are cut off (Wolf and Carvalho 1989). However, not all ehippial eggs resume development at the first suitable occasion. Some remain dormant for longer periods, thus possibly "hedging bets" against future unpredictable catastrophes (Cáceres and Tessier 2003).

Theory predicts the fraction of ehippia hatching each year, but the observed emergence in the field is well below the predicted values (Cáceres 1998). Reduced light penetration, low oxygen levels and consistently low temperatures in deeper waters can prolong diapause (Carvalho and Wolf

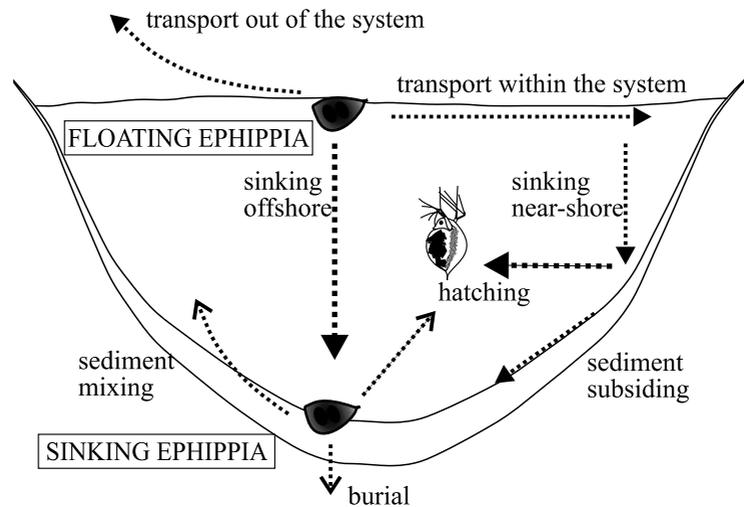


Fig. 2. Possible fate of ephippia sinking to the sediments and floating on water surface (see Cáceres and Hairston 1998, Gyllström and Hansson 2004 for comparison).

1989), however this might not be adaptive. In addition, there is a risk of rapidly being buried in deeper strata with submergence into the sediment. In eutrophic lakes sedimentation rates may be as high as several centimetres per year, whereas hatching only takes place near the sediment-water interface (Cáceres 1998). As Cáceres and Tessier (2003) point out, the majority of the egg bank is likely never to receive the hatching stimulus in most lakes.

Burial in the sediments, however, does not necessarily preclude the ephippium from hatching later (Fig. 2). Chances for reappearance of the ephippium at the sediment surface decrease with its burial depth, but sediment mixing by bioturbation and water movements may bring it back close to the surface or even to the water column, and while deep sediment mixing may be rare, viable ephippia have been found in sediments dated over one hundred years old (Cáceres 1998). Whether staying viable in diapause for decades is an adaptation to unpredictable environmental conditions or a consequence of egg burial (Hairston *et al.* 1995), sinking to the sediments creates opportunities for temporal but not for spatial dispersal.

3. FLOATING EPHIPPIA

Cáceres (1998) reported that estimates of annual production of ephippia at times were more than double the numbers of those effectively deposited into the sediments and hatching annually. The missing ephippia could probably be found floating at the water surface or attached to vegetation, both of which have been reported anecdotally in the literature. According to Brendonck and De Meester (2003) these ephippia should be considered a regular part of the egg bank despite the fact that their fates may be considerably different from that of ephippia deposited in the sediments. Ephippia deposited in deep spots have a low chance of receiving hatching stimuli and production of floating ephippia might enable their passive surface transport towards the shores. Sinking to the sediments near-shore may be advantageous because of the exposure to more pronounced environmental cues absent in deep waters and thus the ability to hatch at the appropriate time for successful recolonisation of the habitat. It has been claimed already that hatching takes place mainly in shallower waters (Wolf and Carvalho 1989) and some authors have suggested that the littoral zone

may play an important role in the recruitment of *Daphnia* in large lake populations (Weider et al. 1997, Jankowski 2003). Furthermore, if they are buried near-shore, they are more likely to be brought back to the sediment surface through mixing.

On the other hand, deposition of ephippia at the water surface may be a mechanism promoting *Daphnia* dispersal between lakes. By migrating to new habitats *Daphnia* might a) avoid local deterioration of environmental conditions, b) reduce parent-offspring conflict (Ellner 1986) or c) simply spread its genes. Since most animals (birds, amphibious animals, humans) and inanimate (wind, outflow) potential vectors of ephippia dispersal operate in the surface or sub-surface zone of freshwater habitats, ephippia floating at the water surface have facilitated contact with these vectors.

Whether ephippia do get dispersed frequently has been often discussed. Discrepancies between the high potential for dispersal and low levels of gene flow inferred from genetic variation between populations have given rise to much controversy and promoted a debate on the ecological and evolutionary significance of dispersal in freshwater zooplankton (Bohonak and Jenkins 2003, Havel and Shurin 2004, for critical reviews). Recent studies give evidence for ongoing effective dispersal of cladocerans (Figuerola et al. 2005, Louette and De Meester 2005). High colonization rates observed for newly created habitats show ephippia move frequently between water bodies (Vanderkhove et al. 2005b), but the establishment success may be constrained by local interactions, as predicted by De Meester et al. (2002).

Whether aimed at within lake or between lakes dispersal, ephippia staying at the water surface, as well as those transported overland, might be exposed to environmental factors not present in deep waters. Ephippia show resistance to desiccation and freezing (Fryer 1996), and passage through the guts of fish, birds and mammals (Proctor 1964, Proctor et al. 1967, Mellors 1975), which is also important for surviving the dry phase in temporary water bodies.

4. DETERMINING THE FATE

The phenomenon of ephippia floating at the water surface is probably more widespread than previously thought and it is doubtful that mere physical processes such as winter storms (Kerfoot et al. 2004) or acquiring positive buoyancy in the sediments could be responsible for mass floating of ephippia observed in water bodies of different morphology and trophy (M. Slusarczyk and B. Pietrzak – unpublished). The hydrophobic outer structure of the ephippium makes it adhere to the water surface and increases its probability of being trapped by the forces of surface tension. How an ephippium carried by a female dwelling in the pelagial zone gets to the surface has only been investigated recently.

We studied (M. Slusarczyk and B. Pietrzak – unpublished) the mechanism of emergence of *Daphnia* ephippia at the water surface. With the use of an experimental set and video recordings we revealed that *Daphnia* females brought ephippia to the surface despite the direct threat of ultraviolet radiation which has been demonstrated to make *Daphnia* stay deeper in the water column. The females approached the surface only at the time of moulting and on having contact with the water-air phase boundary they were easily trapped due to the hydrophobic character of the ephippium. They freed themselves after moulting leaving the moult and the ephippium at the surface. All newly formed ephippia were negatively buoyant, but they could become buoyant after deposition at the surface, due to air penetrating the ephippial structure.

While all ephippia found at the surface had been brought there by the mothers, not all females shed the ephippium at the interface. Some females did not approach the surface and moulted in the water column, giving rise to the following questions: What influences a *Daphnia* female to moult at the surface or not? Is this behaviour indeed an adaptive mechanism facilitating dispersal? Do genes or environmental cues determine it? How are the further life histories of the animals different?

5. CONCLUSIONS

Whether entering diapause in *Daphnia* will provide a mechanism for dispersal in time, through survival over long periods of time, or dispersal in space, through the ability to be transported across otherwise uninhabitable parts of the environment, as put by Hairston (1998), might depend on the place of the deposition of the ephippium. This seems to be determined by the mother's behaviour, although we do not exclude the involvement of additional morphological traits. Floating poses different risks and advantages to the ephippium than sinking directly to the bottom. Whether these are two alternative survival strategies, remains an open question. If they are, prevalence of one or the other, accordingly to the theory, should depend on spatial and temporal variability of the habitat.

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