



## Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment

Luc Brendonck & Luc De Meester

*Laboratory of Aquatic Ecology, K.U.Leuven, De Bériotstraat 32, B-3000 Leuven, Belgium*

*E-mail: Luc.Brendonck@bio.kuleuven.ac.be*

Received 7 September 2002; in revised form 3 July 2002; accepted 26 July 2002

*Key words:* resting stages, egg banks, structure, ecological dynamics, evolutionary dynamics, historical reconstructions

### Abstract

Many representatives of freshwater zooplankton produce at some stage in their life cycle resting stages. A variable portion of the eggs of the previous growing period will hatch at the next occasion while the remaining ones are added to a persistent egg bank, where they can remain viable for decades or longer. The importance of the study of resting eggs and egg banks in general for such different disciplines as taxonomy, ecological biogeography, paleolimnology, nature conservation, evolutionary ecology and community and population ecology is generally appreciated. The major current and expected future developments in this rapidly expanding field of research are presented here. The structure and dynamics of the egg bank are determined by the life history characteristics of the species (or local population), the hatching phenology of their resting stages, and the characteristics of the habitat. The horizontal distribution of dormant stages is generally patchy, with a greater density in the deeper and/or windward parts of a pond or lake. In sediment cores, most viable (responsive) eggs occur in the upper centimeters, although vertical variation related to the history of fish predation or water quality occurs. The accumulation of resting stages of different species, generations and genotypes with variable regeneration niches results in a mixed egg bank with greater potential biodiversity than the active community sampled at any one moment. Through the benthic–pelagic coupling, this dormant reservoir may have considerable impact on the evolutionary potential of the organisms, the ecological dynamics of the community and the distribution of species. Egg banks can be considered the archive of the local habitat, since the pattern of changes in species assemblage and genotypes from the past up to the present reflect changes due to natural or anthropogenic impact that can be used to reconstruct evolutionary processes or even to restore the local habitat. Overlooking the egg bank as an important component of zooplankton communities may lead to erroneous interpretations in the analysis of community and population genetic structure. This review integrates technical and scientific information needed in the study of the structure and function of egg banks in zooplankton with special focus on the fascinating latest developments in the field.

### Introduction

Organisms that permanently inhabit temporarily variable aquatic environments rely on the production of so-called resting or dormant stages to bridge periods of unsuitable physical (e.g. drought, low or high temperatures, low oxygen) or biological (e.g. bad or limited food, predation, competition) conditions (Cáceres, 1997; Brendonck et al., 1998a). These structures remain in a general state of dormancy, defined

as a state of suppressed development (Danks, 1987). Dormancy is used as a general term regardless of cues required for induction or termination (Cáceres, 1997a), though the term actually encompasses a wide spectrum of physiological states (see Hand, 1991) with quiescence and diapause as the two extremes. Quiescence is defined as an immediate response to a limiting factor, while diapause (also often referred to as the refractory phase) is a state of dormancy where an arrest of development is internally initiated (Bren-

donck, 1996). In quiescent stages, metabolism and development are resumed as soon as conditions are permissible. Diapausing organisms do not resume development, even when conditions are favorable, until diapause is broken.

After deposition, most resting stages sink to the bottom, while some remain afloat or are attached to plants or sediment particles. Depending on the type of habitat and region, these resting stages withstand often-extreme conditions of temperature, oxygen, salinity or drought and remain dormant until favorable conditions are restored after breaking of any diapause. The conditions that are necessary for the breaking of diapause and inducing hatching very much depend on the species and often even vary among populations within the same species (e.g. Wyngaard, 1988). At each occasion, generally only part of the resting stages hatches, the theoretical fraction of which corresponds with the chance of a successful growth and reproduction (Cohen, 1966; Brown & Venable, 1986) and the chance of survival in the diapause state (Ellner, 1985). In nature, resting stages that do not receive the necessary stimulus to hatch (e.g. when covered by sediment when photoperiod and light intensity are important stimuli) will also not hatch even when they are responsive (i.e. when diapause is broken), which results in an even greater dormant fraction than theoretically predicted. When long-term dormancy is the case, the resting stages can survive for many seasons, accumulate with stages produced at different episodes and gradually form a mixed *persistent 'egg bank'* (Fig. 1). Resting stages that are not able to survive for long in a dormant state may form a *transient egg bank*. When considering egg banks, one should consider both the fraction above (e.g. floating or attached) and in the soil surface. Banks of resting stages occur in most ecosystems of the aquatic environment, and particularly in variable systems such as shallow lakes and ephemeral pools (de Stasio, 1989).

Prolonged dormancy of animal resting stages is analogous to seed dormancy (Hairston & Cáceres, 1996). Although the molecular and physiological nature of dormancy may be different among taxa, the consequences of resting stages in the life cycle and the ecological implications of an egg/seed bank are convergent. This is illustrated by the fruitful application and testing of general models on optimal reproduction and germination, species coexistence, and bet-hedging strategies in diverse animal taxa, even though these models of dormancy were initially developed for plants (Brendonck et al., 1998a).

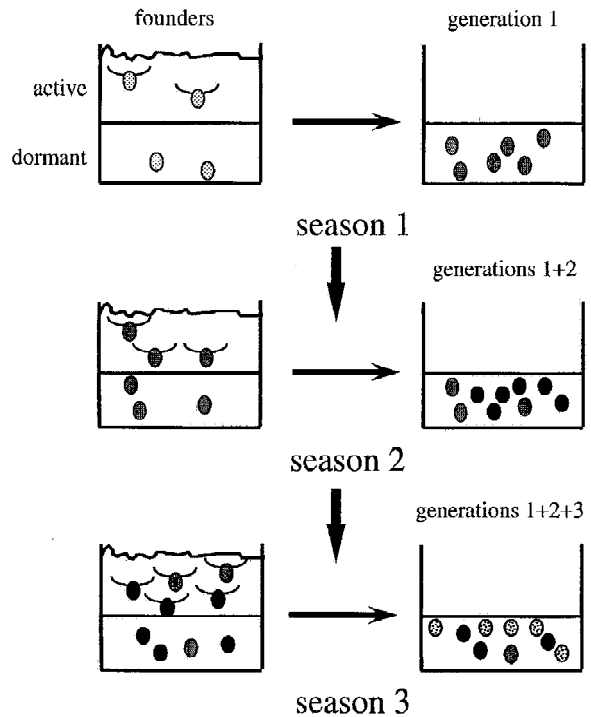


Figure 1. Diagram illustrating the formation of an idealized persistent egg bank during subsequent seasons (or growing periods) in the case of a habitat drying out periodically. At the left side populations are active in the growing period (here illustrated as the wet phase). At the right side populations are only present in a dormant state (e.g. here in the dry phase of the habitat). Dispersed resting eggs or active organisms found the population. At the start of each growing season (or hydrocycle in the case of habitats with several inundation/drought cycles in one season), part of the egg bank hatches while the dormant eggs are added to the egg bank. This ultimately results in a mixed egg bank with generation overlap.

Resting stages are formed by representatives of most freshwater zooplankton taxa, and can be very abundant in the sediment (review in Hairston, 1996), where they can survive for decades or longer (Hairston et al., 1995). Delayed hatching of part of the egg bank, extending the average generation time of the organisms, has been observed in several species, and results in the generation of an egg bank with strong generation overlap (Ellner & Hairston, 1994). In a fluctuating environment, this process can theoretically lead to the generation of an egg bank with a high genetic (Ellner & Hairston, 1994; Hedrick, 1995) and species diversity (Chesson & Warner, 1981; Warner & Chesson, 1985) through a mechanism termed the 'storage effect' (Chesson, 1983). Resting egg banks thus constitute an ecological and evolutionary reservoir that impacts population, community, and ecosystem processes and that offers an invaluable recent tool for the

study of ecological biogeography, biodiversity, evolutionary ecology, paleolimnology, and community and population ecology.

Since the last general contribution to the study of diapause in crustaceans and non-crustaceans (Brendonck et al., 1998a), the field of diapause research has advanced considerably. Especially the recent incorporation of molecular ecology has resulted in important insights in the evolutionary and ecological function of diapause. With this contribution we, therefore, aim at reviewing the state of the art and recent developments in the study of resting stages and egg banks in freshwater zooplankton from temporary pools, ponds and shallow lakes and their application in ecological and evolutionary research. We also summarize different techniques to stimulate the further incorporation of egg bank studies in the analysis of patterns of community and population genetic structure. Finally, some current and potential future applications making use of egg banks to study population and community processes and to reconstruct fluxes in species density and composition or variation in genetic structure in relation to environmental changes are summarized. Although large branchiopods (anostracans, notostracans, 'conchostracans') are not always considered planktonic (large size and active swimmers) they will be included in the present review as egg banks are a dominant feature in their life history and as the observed patterns and processes may help to understand the general importance and consequences of egg banks in a wide variety of aquatic habitats.

### **Types and characteristics of resting stages in freshwater zooplankton**

A brief historical review of the discovery and description of dormant stages in crustacean zooplankton is given in Fryer (1996). In most species, the detection of the dormant structure came many years after species description. The dorsal black spot of the ephippium in daphnids, for example, was long considered a disease before it was recognized as the characteristic dormant structure (Fryer, 1996).

Not all zooplankton make dormant eggs and not all dormant stages have the ability to survive for long in the egg bank (Hairston, 1996). The types of resting stages in freshwater zooplankton are reviewed in Wiggins et al. (1980), Fryer (1996) and Cáceres (1997a) for most groups, in Gilbert (1974) for the rotifers, in Hairston & Cáceres (1996) for the crustaceans

and in Brendonck (1996) for the large branchiopods. Dormant stages are embryonic in the monogonont rotifers, Branchiopoda and most calanoid Copepoda; larval (copepodite stages) in the cyclopoid; and adult in some harpacticoid copepods and in the parthenogenetic bdelloid rotifers. It is not clear if all these types of dormant stages are manifestations of a homologous (monophyletic) process or independent adaptations to cope with similar problems and consequently polyphyletic in origin (Hairston & Cáceres, 1996). The degree of dormancy also varies among groups, ranging from the intense diapause of some branchiopod, rotifer and copepod eggs at one end of the spectrum to larval and adult stages of some copepods with only a reduced metabolism, at the other end. In this latter state of so-called 'active diapause', the organisms may remain motile, and even feed, but at lower intensities than in the normal active individuals.

Resting stages of zooplankton occur in different shapes and sizes (Fig. 2) and in many species they have an outer protective cover which is especially well-developed in the most primitive branchiopods (Fryer, 1996). The shape and external sculpturing or ornamentation are to some extent useful for identification at a higher taxonomic level or even at the species level, a feature that is especially well explored in anostracans (Mura & Thiéry, 1986; Brendonck & Coomans, 1994a, b; Thiéry et al., 1995), in some conchostracans (Belk, 1989; Martin & Belk, 1989), cladocerans (Kokkinn & Williams, 1987; Korínek et al., 1997) and rotifers (Wurdak et al., 1978; Gilbert & Wurdak, 1978; Gilbert et al., 1979; Munuswamy et al., 1996). This character potentially allows researchers to estimate diversity in aquatic habitats solely by analyzing the sediment for specific forms of resting stages. This is a very useful method in aquatic habitats that dry out periodically or for species with only a limited presence in the water column. The structure and size of the eggshell may to some extent also determine the buoyancy of the resting stages after production (e.g. by the formation of a float).

In large branchiopods, egg shapes are usually (sub-)spherical, but tetrahedral, disc-like, and cylindrical egg shapes do occur (Fig. 2). After deposition, eggs usually sink to the bottom where they build up the egg bank. After the ephemeral pools refill, part of the eggs float (Brendonck et al., 1998b, Brendonck & Riddoch, 2000a). The large and spherical eggs of notostracans are often glued to sediment particles or plant leaves (Linder, 1952; Fryer, 1996). The dormant copepodite or adult stages in cyclopoid and harpactic-

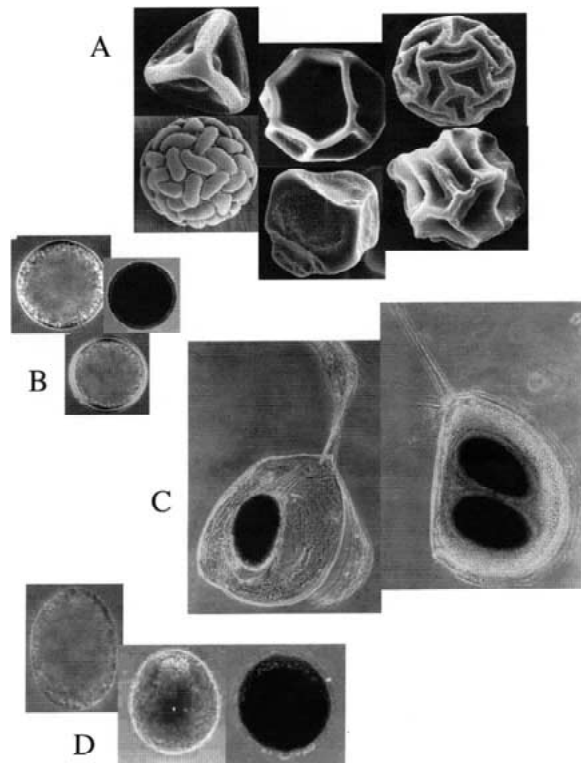


Figure 2. Illustration of the diversity of resting stages that may be encountered in the sediment of lakes, ponds and pools. In some groups the outer sculpturing may help in taxon identification. (A) Resting eggs of large branchiopods (range: 200–400  $\mu\text{m}$ ): (B) Types of spherical resting eggs in calanoid copepods (range: 80–200  $\mu\text{m}$ ) (pictures from Viitasalo & Katajisto, 1994): (C) Ephippia of anomopod cladocerans holding one (as in *Bosmina* sp.) or two (as in *Daphnia*) resting eggs (range: 400–500  $\mu\text{m}$ ) (pictures from Viitasalo & Katajisto, 1994): (D) Types of monogonont rotifer resting eggs (range: 80–200  $\mu\text{m}$ ) (pictures from Viitasalo & Katajisto, 1994).

oid copepods, respectively, are often but not always encased in a kind of transparent gelatinous cyst, sometimes with an outer layer of mud particles (Fryer & Smyly, 1954; Smyly, 1961, 1967; Elgmork, 1962). In calanoid copepods, resting eggs are spherical (Fig. 2) and sink freely to the bottom after deposition (Viitasalo & Katajisto, 1994). Santella & Ianora (1990) and Belmonte & Puce (1994) observed striking differences in the morphology of diapause and subitaneous eggs in some marine calanoids. In the cladocerans, the best known resting stages occur in the Anomopoda with the daphnids having the most specialized resting stages. Here, one or two resting eggs are encapsulated by the carapace valves or parts thereof and form the composite structure known as an ephippium. This ephippium is shed at molting (Fig. 2). Ephippia of *Daphnia*

may become attached to floating debris or vegetation, though most sink to the bottom after a brief floating phase (Carvalho & Wolf, 1989). Chydorids and macrothricids have more primitive ephippia that are often firmly glued to suitable objects. In the open-water Haplopoda and Onychopoda, the usually spherical and naked resting eggs are shed freely and sink to the bottom. Only the eggs of *Polyphemus pediculus* are sticky and are often attached to vegetation (Fryer, 1996). In the Ctenopoda, eggs are generally spherical or ellipsoidal and may have a smooth, protuberant or spiny surface (Korovchinsky & Boikova, 1996). Eggs are usually shed freely but in some species (*Sida crystallina*, *Pseudosida variabilis* and some species of *Diaphanosoma*) the outer envelope is sticky and eggs may become attached to vegetation or other objects (Fryer, 1996; Korovchinsky & Boikova, 1996). In rotifers, the production of dormant eggs occurs in most of the monogononts, where the yolk-filled embryo is surrounded by a thick, multilayered shell (King, 1972; Gilbert, 1974, 1995). In this group, eggs are spherical (Fig. 2) and sink freely to the substrate after deposition. Floating rotifer eggs have been mentioned by Hagiwara (1996).

Many of these resting stages are very resistant and may survive extreme temperatures, high pressure, or drought. The ability to withstand drought is not restricted to the encapsulated resting eggs but is also reported in the dormant copepodite of cyclopoid copepods (e.g. Rzóška, 1961; Champeau, 1970) and adult stages in harpacticoid copepods (e.g. Champeau, 1970). Some of these species even thrive in ephemeral rain pools in arid regions (Rzóška, 1961). Örstan (1995, 1998) mentioned bdelloid rotifer eggs that under some conditions survived several days of drying.

### Structure and dynamics of egg banks

The spatial structure of the eggs in the sediment is important in the analysis of the long-term population dynamics (Cáceres, 1997b), while a basic understanding of the egg bank dynamics is a necessary first step towards quantifying the long-term effects of dormancy on populations and communities (Cáceres, 1998a, b). The structure and dynamics of the egg bank is mainly determined by the timing and amount of resting egg production and the places in the habitat where resting stages are deposited, the timing and amount of hatching, and the rate of loss by senescence, predation, disease and dispersal (de Stasio, 1989; Cáceres

& Hairston, 1998). Finally, the level of disturbance of the sediment has serious impact on the vertical structure of the egg bank. There are only a few studies that have analyzed multiple components that determine egg bank dynamics (e.g. Herzig, 1985; de Stasio, 1989; Cáceres, 1998b), and none has so far made a complete analysis of all aspects determining resting egg budgets simultaneously.

#### *Egg bank size and (vertical and horizontal) structure*

Hatching is mainly restricted to the resting eggs in the upper 2 cm of the sediment (Herzig, 1985) that is indicated as the 'active egg bank' according to Cáceres & Hairston (1998). It is, however, often considered that eggs in the top 10 cm of the sediments have a reasonable chance of being mixed and exposed to hatching triggers (Hairston et al., 2000) and some egg bank counts, therefore, are based on a greater sediment depth. Large pools of dormant stages exist in the active egg bank in all groups of freshwater zooplankton, as shown in rotifers (Nipkow, 1961; Hairston et al., 2000), large branchiopods (Hildrew, 1985; Thiéry, 1997; Brendonck & Riddoch, 2000b), calanoid copepods (de Stasio, 1989; Hairston et al., 2000), cyclopoid copepods (Hairston et al., 2000) and cladocerans (Lampert & Krause, 1976; Smyly, 1977; Herzig, 1985; Carvalho & Wolf, 1989; review in Hairston, 1996; Cáceres, 1998b; Cousyn & de Meester, 1998; Hairston et al., 2000). In zooplankton egg banks, egg densities are usually within the range of  $10^3$ – $10^5$  eggs per  $m^2$ . Egg densities up to  $4 \times 10^7$  were detected in rotifer egg banks (Nipkow, 1961).

The largest fraction of viable eggs generally occurs in the top 4–6 cm of the sediment (Herzig, 1985; Carvalho & Wolf, 1989; Hairston & Van Brunt, 1994; Cáceres, 1998b). As for the total number of eggs, Cousyn & de Meester (1998) found a variable pattern of ephippia densities in the sediment related to the past presence of planktivorous fish in the studied lake, while highest densities of eggs of the halophilic *Daphnia exilis* were found by Hairston et al. (1999b) in depth layers corresponding with a period of particular industrial and salt waste producing activity along the shore of Onondaga Lake. Increased *Daphnia* ephippial densities since the 1940s in the sediments of the Keweenaw Waterway were most probably related to increased eutrophication (Kerfoot et al., 1999). Such historical changes in species composition or densities of eggs in the sediment probably reflect population densities and allow for the demographic reconstruc-

tion in an ecological context when sediment cores are analyzed from habitats with a good historical record of local climatic and ecological conditions and anthropogenic impact (e.g. fisheries, industry). Onbe (1985) and DeStasio (1989) present support for the claim that egg density in the sediments reflects water column population size in marine and freshwater calanoid copepods, respectively, making such reconstructions reliable.

Horizontally, egg banks generally show a patchy distribution and a gradient with highest densities in the deeper parts of the lake (Kankaala, 1983; Herzig, 1985; Moritz, 1987; Carvalho & Wolf, 1989; de Stasio, 1989; Cáceres, 1998b). Differences in egg densities in the littoral versus the pelagic areas can be related to micro-habitat choice in the females (e.g. in cyclopoid copepods; Elgmork & Langeland, 1980), to the fact that near-shore conditions (e.g. more light) stimulate more eggs to hatch (de Stasio, 1989) or to the topography of the pond or lake floor (e.g. drifting of eggs to the deeper parts). By means of hatching traps, Wolf & Carvalho (1989) and Cáceres (1998b) measured higher hatching activity in the shallower parts of the studied lake, despite lower egg densities in this zone. No such difference in hatching rates was noted by Hairston et al. (2000).

#### *Method for assessing the vertical and horizontal structure of egg banks*

With the exception of small ephemeral rock pools where the very thin layer of sediment holding the egg bank can be collected using a spoon (Brendonck & Riddoch, 2000b), the deeper sediment of lakes and ponds is usually sampled by some type of tube corer of which variable diameters exist (minimum should be 5 cm). To collect the sediment, the tube is pushed vertically, avoiding disturbance. For collecting sediment in deeper water, a gravity corer or piston corer operated by a scuba diver can be applied. For a proper quantitative analysis of the horizontal structure and reliable extrapolation to total egg bank size, as many patches as possible should be sampled randomly. To analyze the vertical structure of the egg bank, the entire core is cut in slices of about 1 cm thick. Depending on the density of eggs in the sediment, the depth of the slices may vary with depth, with smallest intervals (e.g. 1 cm) in the top layers and 2 to 4 cm for deeper sediment layers. Sometimes the outer edge of each sediment slice that is dragged along the wall of the core tube is removed with a cookie cutter. In case the collected sediment not only serves for

egg bank counts but also as the source material for experiments with live organisms (e.g. life histories, tolerance), the sediment should be kept in darkness (e.g. by wrapping in aluminum foil) and refrigerated (4 °C) until experiments start (Cousyn & de Meester, 1998). Resting eggs can be isolated from the sediment by washing the sediment slices (or sub-samples thereof) on a series of sieves (mesh size depending on the group, around 30  $\mu\text{m}$  in rotifers, 150  $\mu\text{m}$  in the other groups) and counting all eggs in a tray under the dissection microscope. As it is sometimes hard to remove the eggs from the sediment, additional preparatory steps with sonication before and density centrifugation (e.g. sugar flotation method, Marcus, 1984, 1990) after washing are advisable. Where sonication is useful to remove dirt from resting stages with a hard cover, it is unknown how it affects the more delicate dormant copepodites and adults in some copepods. To make a correction for the variable number of eggs in the ephippial cases of daphnids, a fraction of all ephippia should be opened by means of needles. Examples of the analysis of egg banks are given in Carvalho & Wolf, 1989; de Stasio, 1989; Hairston et al., 1995; Weider et al., 1997; Cáceres, 1998b; Cousyn & de Meester, 1998; Hairston et al., 1999b; Kerfoot et al., 1999; Duffy et al., 2000; Hairston et al., 2000; Cousyn et al., 2001.

#### Timing and amount of hatching

##### Time of hatching (Fig. 3)

To synchronize the life cycle with suitable conditions for growth, avoiding drought, competition and predation, an effective mechanism is necessary for detecting the appropriate time of the year or the stage during an inundation cycle to hatch. These cues differ according to the size and predictability of the aquatic habitat.

In permanent, relatively shallow aquatic habitats, photoperiod and temperature have been shown to be very important for induction and breaking of diapause. Photoperiod (at least in temperate areas) is the most reliable variable to reflect seasonal changes. The importance of such light periodicity for regulating the life cycle has been shown in many zooplankton species (reviewed in Fryer, 1996). Generalist species and clones (e.g. in cladocerans) respond less clearly to seasonal cues or are sensitive to other more subtle environmental factors such as changes in water chemistry, crowding, etc. In deep lakes, the decisive factor for changing the activity state is usually an interaction of temperature and the state of the gaseous regime

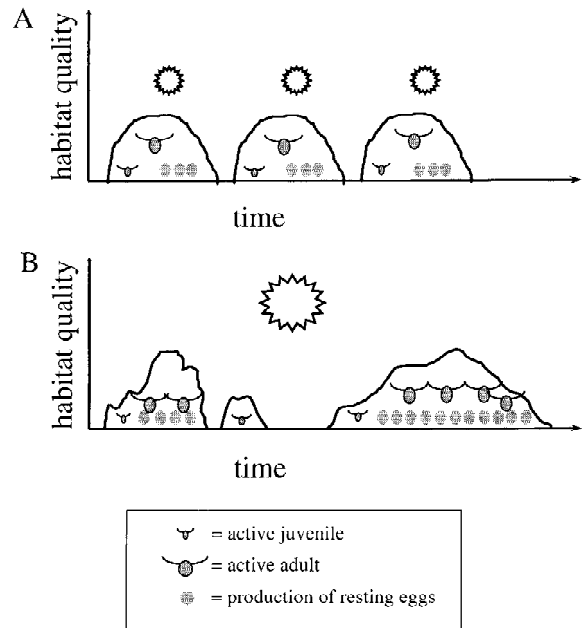


Figure 3. Diagram illustrating the idealized phenology of hatching and egg production of some zooplankton groups in (A) a predictable habitat with one growing season per year and (B) an unpredictable habitat with several inundation cycles in one year (season). In the idealized predictable habitat (e.g. lake in temperate climate), hatching usually starts in spring while egg production starts when environmental conditions deteriorate (decrease in habitat quality). Change in photoperiod (illustrated by the sun-like symbol) is a reliable proximate cue inducing egg hatching and production in this habitat type. This strategy is mainly adopted by cladocerans, rotifers and copepods. In the unpredictable habitat (e.g. desert pool), hatching starts after rains and egg production begins from the moment animals are mature and continues until drying of the pool. In some cases pools dry out before eggs can be produced (abortive hatching). Changes in conductivity and temperature and not day length are reliable cues to induce hatching. This strategy is common in large branchiopods. Both strategies are known in some rotifer species (Carmona et al., 1995).

(Fryer, 1996). In shallow and short-lived temporary pools, temperature changes and changes in osmotic and oxygen values during an inundation cycle are the most important indicators of the suitability for growth and reproduction (Brendonck, 1996). It is generally assumed that hatching of resting stages in large branchiopods is triggered by a combination of environmental conditions that relate well to the climatic region and type of habitat inhabited by the organisms concerned (Brendonck, 1996; Blaustein, 1997).

In cladocerans, copepods and rotifers, most hatching takes place in spring at the onset of the growing season (Herzig, 1985; Wolf & Carvalho, 1989; de Stasio, 1989, 1990; Cáceres, 1998a, b; Hairston et al., 2000). Carvalho & Wolf (1989), following the hatch-

ing phenology of a *Daphnia* egg bank by incubating the sediment under laboratory conditions, observed a minimal period before hatching started, followed by a burst over several days, then a phase of variable duration with few, intermittent hatchlings. In the field, hatching began after the thawing of ice and continued for 3–4 weeks. Cáceres (1998b) detected by means of traps and egg bank analyses that emergence of two daphnid species in Oneida Lake is restricted to early spring. Hairston et al. (2000) showed by means of hatching traps that various zooplankton species (rotifers, calanoid copepods and cladocerans) that were dominant only later in the year also hatched early in the season, but remained in low numbers until more favorable conditions were manifested in the water column. Only the cyclopoid copepods hatched at variable times during the year. Herzig (1985) observed that the hatching pattern was also more irregular in *Leptodora* and *Bythotrephes* eggs, which hatched from March until August and from April until September, respectively. In large branchiopods, mainly inhabiting ephemeral pools, hatching is usually restricted to periods of refilling or significant dilution of the pools due to fresh rains (Brendonck et al., 1998b).

#### *Amount of hatching*

Theory predicts that frequent catastrophic mortalities (e.g. by early drying of pools) select for prolonged dormancy with hatching fractions corresponding with the chance for successful recruitment and the probability of survival while dormant (Cohen, 1966; Ellner, 1984; Brown & Venable, 1986). This diversified germination behavior maximizes the geometric mean fitness over time by reducing the variance in fitness, at the cost of the arithmetic mean fitness of each generation (Philippi & Seger, 1989). There is only little empirical evidence for this theory for hatching fractions in zooplankton. In anostracans from arid and semi-arid regions, hatching fractions of less than 20% are frequently measured under laboratory conditions (Hathaway & Simovich, 1996; Simovich & Hathaway, 1997; Brendonck et al., 1998b). In these species, the laboratory hatching fractions were below expected frequencies of adequate inundation lengths as estimated on the basis of a 15-year survey (Moorad, pers. comm.) or on the basis of long-term climatic records extrapolated to local hydroperiods (Brendonck & Riddoch, 2001). Low hatching percentages were also observed in several other large branchiopods from arid regions as reviewed in Brendonck (1996). Hatching percentages of less than 20% were, how-

ever, also observed by Carvalho & Wolf (1989) in the top layer of *Daphnia* egg banks of a temperate lake. Cáceres (1998b) also measured very low hatching rates (between 0 and 25 daphnids per m<sup>2</sup>) in comparison with the large numbers of eggs deposited (between 0 to over 10<sup>4</sup> eggs per m<sup>2</sup>). These low hatching fractions may indicate that besides physical characteristics, other (biotic) density-dependent variables should be considered to estimate chances for successful recruitment (Bulmer, 1984). Intra-specific differences in hatching success and requirements with patterns in accordance with those expected from the hypothesis of local adaptation, have been reported for several aquatic organisms (e.g. Hairston & Olds, 1984).

Several authors presented evidence that eggs that do not hatch at the first occasion do so under similar conditions at a later date. Delayed hatching of part of the egg bank in anostracans, for example, served as a hedge against more than 10 subsequent drought catastrophes (Hildrew, 1985; Brendonck et al., 1998b). Hildrew (1985), Simovich & Hathaway (1997) and Van Dooren & Brendonck (1998), showed that variability in hatching response even occurs in single broods and can, therefore, be considered a diversified bet-hedging strategy. In a calanoid copepod, de Stasio (1989) observed frequent bouts of hatching from the egg bank over a period of 3 years where the addition of new eggs was prevented by hatching traps. In hatching trials with *Daphnia* egg banks, however, Carvalho & Wolf (1989) noted that most ephippia remained dormant even after re-exposure to different hatching conditions. de Meester & de Jager (1993), however, observed that exposure of *Daphnia magna* resting eggs to a second stimulus did result in additional hatching. As these experiments were done using ephippia from experimental lineages sharing the same parents, these results indicate the existence of bet-hedging also for this group of organisms.

#### *Methods to assess hatching phenology*

To measure the time and amount of hatching in the field, hatching traps can be used. These instruments are inverted funnels on which a replaceable collection bottle is mounted. The funnel is pushed a few centimeters in the sediment avoiding any disturbance. Care should also be taken not to enclose any predators or study organisms that might start to reproduce and the funnels should be prevented from moving laterally. Exchange with the environment is ensured through windows covered with 75- $\mu$ m meshes. Hatching in-

individuals are trapped in the vial on top of the funnel. The vials should be checked and replaced frequently, especially at the start of the growing season to avoid any reproduction of hatched organisms inside the funnel. Hatching traps located at different places in a studied pond or lake may furthermore reveal a spatial pattern of emergence. To estimate the hatching fraction, the egg numbers should be quantified from sediment samples in the vicinity of the hatching traps. Alternatively, after hatching has stopped, densities of the unhatched resting stages in the top 2 cm of the sediment that was covered by the funnel could be estimated. Examples of the use of hatching traps are given in de Stasio (1989), Herzig (1985), Wolf & Carvalho (1989), Cáceres (1998b), Hairston et al. (2000). In addition to the use of hatching traps, it is also possible to compare egg bank densities in the sediment before and after the main emergence period. This method, however, most likely overestimates emergence rates due to senescence and predation of the eggs. In shallow waters, one should be careful in using hatching traps, as it is not always clear whether all individuals swim to the surface (i.e. the sampling vial) upon hatching (E. Decaestecker, pers. comm.). The use of large hatching traps is not possible in shallow ephemeral pools. To study in situ-hatching in these habitats, the top layer of sediment can be transferred to vials with bottom and top mesh and left in the pools until inundation. After daily quantification of hatched organisms the numbers of unhatched and viable eggs remaining in the enclosed sediment can be counted and hatching fractions calculated. Where no hatching traps can be deployed it is also possible to incubate at regular intervals freshly collected sediment under field conditions in the laboratory to estimate the amount and duration of hatching in the field (method in Mnatsakanova & Polishchuk, 1996). To obviate interference from artifacts due to incubation in laboratory conditions, one may resort to a more labour-intensive but effective method: isolating at regular time intervals sediments from the natural habitat, followed by incubation during a short time span in the laboratory. All animals that hatch within a time interval that is clearly shorter than egg development time under incubation temperature are known to have been induced in the field.

## Viability

Long-term viability largely determines the depth (age) to which viable eggs can be found in undisturbed

sediments and from which they can continue to seed the pelagic community if they are exposed to suitable hatching triggers. Often viable diapausing eggs are buried in sediments that are stratified temporally. Viable zooplankton eggs (various taxa) have been obtained from sediments dated between 40 and 125 years, and in one instance with calanoid copepods from sediments 330 years old (Hairston et al., 1995). Cáceres (1998b) achieved hatching from ephippia collected from 125-year-old sediment. Besides knowledge of the maximum viability, information on the mortality rate of eggs due to senescence, disease and parasitism are also important variables in modeling the dynamics of the egg bank and more particularly in estimating the impact of ageing eggs in the current population and community dynamics. Herzig (1985) compared the hatching fraction in newly produced resting eggs of the cladocerans *Leptodora kindti* and *Bythotrephes longimanus* with eggs from variable depths in the sediment and found a decreasing hatching fraction with age (depth) of the eggs. A similar negative relationship between hatching success and sediment depth was obtained by Hairston & Van Brunt (1994) and by Hairston et al. (1995) in egg banks of a calanoid copepod. Hairston et al. (1999b) observed that daphnid eggs older than 25 years no longer hatched and suggested that this could be due to heavy metal pollution in that period. Kerfoot et al. (1999) also attributed decreased hatching in zooplankton from deep sediments to the presence of high concentrations of heavy metals in that segment of the core. These estimates of limited viability are specific to these contaminated environments. Some studies, however, found substantial declines in hatching success in eggs older than 30 years without indication of any pollution in that period (Carvalho & Wolf, 1989; Weider et al., 1997). Hairston et al. (1995) estimated the mortality rate at about 1.1–1.5% per year for two lakes inhabited by the copepod *Diatomus sanguineus*. Besides mortality caused by senescence of the eggs, predation may be an often-overlooked variable in estimating egg budgets. Cáceres & Hairston (1998) studied the ability of invertebrates to consume *Daphnia* eggs in the laboratory and found that mainly amphipods readily ingested the ephippia.

### *Methods to assess resting egg long-term viability*

There are different ways for estimating the maximum viability of resting stages. First, eggs could be isolated from specific depths (ages) in undisturbed and dated sediment cores and incubated under standard laborat-



ory conditions (e.g. Hairston et al., 1995; Cousyn & de Meester, 1998; Hairston et al., 1999b; Kerfoot et al., 1999; Cousyn et al., 2001). To establish a chronology for the cores,  $^{210}\text{Pb}$  dating of the sediment is usually performed and dates and sedimentation rates are calculated according to the constant rate of supply model (Appleby & Oldfield, 1983). Alternatively, hatching traps could be followed several years or until no more hatching occurs, herewith avoiding the addition of any new eggs by reproduction of enclosed organisms or by disturbance of the sediment (e.g. de Stasio, 1989). Otherwise, a bulk of freshly produced eggs could be collected and packed in nets with small mesh size (e.g. 50  $\mu\text{m}$ ) and buried at different places in the sediment. Entire artificial egg bank nets or sub-samples thereof should then be checked at specific intervals for their viability (hatchability) in the laboratory. Nets should be buried at different places as there might be an interaction with the local quality of the sediment as is the case for seed emergence and viability (Kalisz, 1991). When soil is also included in the nets, it should first be autoclaved to kill any existing eggs. As eggs are packed in net they are still not exposed to predation, a variable that is often overlooked and difficult to measure.

#### *Timing and amount of egg production*

##### *Timing of egg production (Fig. 3)*

Most cladocerans and monogonont rotifers are cyclically parthenogenetic and sexual resting eggs are generally only produced when environmental conditions deteriorate. In clonal groups of the rotifer *Brachionus plicatilis*, Carmona et al. (1995) observed a continuous production of resting eggs alongside parthenogenetic reproduction, with the proportion of mictic females varying with clonal lineage and population density. Gilbert (1995), in turn, noticed the production of a diapausing stage in amictic females of the monogonont rotifer *Synchaeta pectinata*. In copepods, reproduction is sexual during the entire life cycle, but different types of eggs can be produced. In calanoid copepods, a change takes place during the life cycle from the production of subitaneous to the production of diapausing eggs. Subitaneous eggs are defined as eggs that hatch within a few days at suitable ambient conditions but that can be induced to become quiescent in response to adverse conditions (Marcus, 1996). The stimulus that triggers the production of diapausing eggs in the above organisms usually acts prior to the onset of deteriorating environmental conditions and

includes token stimuli such as photoperiod, population density, predator density, or food (Hutchinson, 1967; Stross, 1969; Kleiven et al., 1992; Gilbert, 1995; Hairston & Kearns, 1995; Santer & Lampert, 1995; Slusarczyk, 1995; Piercey & Maly, 2000; Alekseev & Lampert, 2001). Hairston & Munns (1984) established a close match between the theoretically optimal and observed diapause timing in copepods, while Hairston & Walton (1986) observed changes in the timing of diapause in response to an altered selection (predation) regime. Resting eggs can, however, also be produced under apparently suitable growing conditions by the presence of predator-specific kairomones (Pijanowska & Stolpe, 1996). In freshwater copepods (eg *Eurytemora affinis*), diapausing eggs were observed in crowded cultures under long day lengths that normally resulted in subitaneous egg production, indicating that crowding or inadequate food levels alone might also induce diapause. Large branchiopods sexually produce dormant eggs during their entire life cycle. Although intra-brood variation exists in the time of rest needed before hatching, subitaneous eggs have never been recorded in this group (Brendonck, 1996).

##### *Amount of egg production*

Depending on depth, de Stasio (1989) measured average values between about 150 000 and 400 000 eggs per  $\text{m}^2$  per year settling in sedimentation traps in the calanoid copepod *Diatomus sanguineus*. As part of a long-term study, Cáceres (1997b) observed temporal variation in the recruitment to the egg bank of competing *Daphnia* species with maxima of 4000 eggs per  $\text{m}^2$  per year in *Daphnia pulicaria* and of about 250 eggs per  $\text{m}^2$  per year in *D. galeata mendotae*. In some years there was even total recruitment failure for one of the two species.

##### *Methods to assess the phenology of egg production*

To quantify and time the production of resting stages, sedimentation traps with a height/diameter ratio larger than 3 (Håkanson et al., 1989) can be placed at several positions in the studied lake or pond. Average numbers of eggs caught per trap can then be extrapolated to the entire surface of the study system. This method may also reveal spatial variation in diapausing egg production and deposition. Examples of studies where sediment traps were used to characterize seasonal egg production are in de Stasio (1989) for copepods and Cáceres (1998b) for daphnids. Alternatively and in shallow pools, daily egg production can be estimated by assessing the size of the active population and by

quantifying the numbers of eggs produced by a sample of the population (e.g. corresponding to a specified, rather large volume of medium) during a given time interval, which is shorter than the time for induction and formation of the resting egg. All resting eggs that are deposited during this time interval are thus induced in the field.

### *Dispersal*

It is unknown and very difficult to measure what the effects of dispersal are on the dynamics of local egg banks. Depending on the type of habitat, resting stages can be dispersed to a variable degree by wind, water movements, waterfowl, amphibians, or humans. Especially in ephemeral pools that frequently dry out, some chance impact of wind action is expected, especially by local whirlwinds. In an attempt to quantify dispersal by wind of resting eggs in an anostracan inhabiting shallow rock pools in southern Africa, Brendonck & Riddoch (1999) captured only a limited number of viable eggs during a whole month in the dry season. The year-to-year fluctuations in egg numbers in these egg banks were not correlated among individual pools. This lack of synchrony in the observed pattern of egg bank dynamics may indicate that chance processes in general might be important in controlling egg bank dynamics in these rock pools (Brendonck & Riddoch, 2000b). In pools where the egg bank was covered by vegetation, protecting the eggs from being blown away, reduced variance in egg bank size over the years was observed.

### *Methods to assess dispersal among egg banks*

It is almost impossible to quantify the impact of wind on local egg banks, except if these eggs could be marked (genetically or with color paint) and trapped in the vicinity of the pools. Trapping of windborne eggs can be done by using sticky traps that are mounted at several heights around the studied pools. Trapping devices should be installed at different heights to catch not only the eggs that bounce on the surface (saltation) but also those eggs that are lifted by wind. Examples of the use of sticky egg traps are given in Brendonck & Riddoch (1999) and in Brendonck & Riddoch (2000b). Alternatively, one could count eggs in the top layer of the sediment at different moments during the dry season and quantify the decrease in egg density. In addition to the impact of wind, degeneration and predation of eggs could also partly be responsible for the detected pattern and should be corrected with controls

(e.g. by protecting parts of the sediment from wind impact). Dispersal by means of overflows or rivulets can be quantified by the installation of traps at the connection points or points of overflow. The rate of dispersal could then be estimated by emptying traps and counting the viable eggs at specific intervals. An example of the use of traps to estimate the amount of dispersal (of active zooplankton) via ditches and small channels is given in Michels et al. (2001). PCR assisted genetic techniques (amplification of diagnostic DNA sequences) may also become useful to detect dispersal patterns (random or structured) among known populations making use of the extracted DNA from individual eggs instead of the adults. Deriving dispersal patterns from patterns of gene flow as revealed by neutral markers rests on many assumptions, and it has been argued that effective gene flow does not reflect dispersal rates in a straightforward way (de Meester et al., 2002).

### *Disturbance of the sediment*

The type and frequency of disturbance of the sediment determines to what extent any buried eggs will be re-suspended and exposed to suitable hatching triggers, and hence will be part of the so-called active egg bank as defined by Cáceres & Hairston (1998). The extent of bioturbation by benthic invertebrates is typically found to be 2–5 cm (Kearns et al., 1996). On the basis of a  $^{210}\text{Pb}$  profile, Cáceres (1998b) concluded that frequent sediment mixing in Oneida Lake occurred down to 7 cm, whereas Hairston et al. (2000) documented mixing down to 10 cm. Sediment cores taken several months after polystyrene beads with similar characteristics to the eggs of a studied copepod species were distributed in the water, illustrated that the beads had moved down to 7 cm in the sediment (Cáceres & Hairston, 1998). The most common disturbance is bioturbation by fish (eating and nest building), burrowing worms, insects, mollusks, etc. Serious disturbance can also be caused by fisheries activities. In temporary pools, disturbance is more the rule than the exception as they are the main watering places for birds, cattle and large game. The level of disturbance also determines to what extent the sediment will be suitable for use in the historical reconstruction of species assemblages and genotype structuring.

### *Methods to measure disturbance of the sediment*

Cáceres & Hairston (1998) seeded the sediment surface of the pool with glass beads having about the

same size and specific gravity as the resting eggs of the copepod *Diaptomus sanguineus* and checked the depth of these particles after a specific period of time. An alternative method could be to use the eggs themselves but with colored surface or with a genotype distinct from the one of the studied local population. The pattern of  $^{210}\text{Pb}$  data in sediment cores may also give an indication of the extent of mixture in the sediment.

### Egg banks and ecological dynamics

The structure and hatching characteristics of egg banks have potentially important consequences for the structure and dynamics of the pelagic community (benthic–pelagic coupling; Marcus, 1995; Marcus & Boero, 1998). Despite their general importance in the ecological dynamics of zooplankton communities, egg banks are, however, only rarely included in freshwater zooplankton population and community studies (Wolf & Carvalho, 1989; de Stasio, 1990; Cáceres, 1997b; Cáceres, 1998b; Hairston et al., 2000).

By emergence from the mixed egg bank at the start of, or during each growing season, the current population and community dynamics are to a large extent uncoupled from the immediate effects of the previous season (de Stasio, 1989). At the population level, the overlapping of generations and the increase of generation time in species with an egg bank slows the rate of population increase when the population is growing and the rate of population decrease when a population is in decline (Caswell & Hastings, 1980). Neglecting seed or egg bank dynamics in demographic models can, therefore, lead to erroneous estimates of the intrinsic rate of population increase and of the stable age distribution (Kalisz, 1991 and references therein).

As hatching is often confined to a restricted period at the beginning of the growing season in permanent pools or after filling of ephemeral pools, hatching from the mixed egg bank (in terms of several species) determines the early composition of the community but is generally not responsible for major changes later during the growing season. Wolf & Carvalho (1989), for example, found that most hatching in lake *Daphnia* species and hybrids was confined to the first 3 to 4 weeks of the growing season and was minimal compared to egg bank size. The authors therefore concluded that hatching could not explain the seasonal changes in the species composition of the *Daphnia* community. Cáceres (1998b) found variable but usually low hatching confined to a restricted

period in the beginning of the growing season in daphnids, and concluded that the contribution of emergence to the development of the spring populations varies among years depending on the hatching fractions and the numbers of overwintering individuals. Hairston et al. (2000) confirmed this pattern of peak hatching in spring and a clear seasonal succession of dominant species throughout the growing season in rotifers, calanoid copepods and cladocerans in Oneida Lake. Only the seasonal dynamics of the cyclopoid copepods, having short-lived copepodite stages, largely depended on direct recruitment from the egg bank. Zooplankton population shifts during the season generally seem to result from the interaction of predation and competition (Gliwicz & Pijanowska, 1989), while temporal variability in abiotic factors (e.g. water temperature) may also interact to produce the observed dynamics (Cáceres, 1998a).

At the community level, the carry-over of some eggs from one generation during multiple years buffers the effect of local extinction of the population and preserves the representation of the species within the community even when several consecutive demographic catastrophes occur due to chance or progressive habitat change (Kalisz, 1991). Egg banks also promote the coexistence of competing species in a temporally variable environment (Fig. 4). Here, egg banks function as a filter (*sensu* Templeton & Levin, 1979) whereby for each species good reproduction at favorable moments may compensate for losses due to a poor growing season, while the long-lived stage allows species to persist through periods when its recruitment is poor. When different competing species are favored at different moments, extinction may be delayed ‘indefinitely’ (Fig. 4) (cf. the storage effect; Chesson, 1983). This process is a powerful mechanism for maintaining species diversity within communities (Chesson & Warner, 1981; Chesson, 1994) and eventually leads to the coexistence of a greater number of species than expected by traditional equilibrium models (e.g. Bonis et al., 1995; Cáceres, 1997b). Storage comes here from the repeated hatching over a sequence of growing seasons by the eggs produced in any one season. Indications for the storage effect in zooplankton were found in different instances. May (1986), for example, observed an assemblage of diapausing rotifer eggs that contained a species diversity that was greater than that measured in the water column in any single year, but fully concordant with the assemblage observed over a 6-year period. Likewise, Donald (1983) observed year-to-year dif-

ferences in an anostracan community followed over 10 years. Species occurrences were mainly determined by the sequence of climatic conditions during the previous dry season. Often, some species were absent during several years but occurred in large population sizes in others. Cáceres (1997b) empirically demonstrated that two competing natural populations of *Daphnia* could only coexist through the storage effect with long-lasting egg banks. According to Hairston (1996, 1998), not only the mere diversity, but also the number and type of organisms (e.g. belonging to different trophic niches) hatching from the egg bank may have a significant impact on the functioning of the ecosystem (e.g. trophic transfer efficiencies, nutrient dynamics, etc.). A species-specific difference in requirements for egg hatching may furthermore help to explain species distribution patterns in zooplankton populations as was illustrated for North-American anostracans (Eng et al., 1990).

Since only part of the species represented in the egg bank are present in the active community at any one time, the species pool of a given area can be divided into two components: the realized biodiversity represented by the active specimens and the potential biodiversity represented by the resting stages only (Marcus & Boero, 1998). Baskin (1994) described the dormant fraction during the dry season in temporary pools as the 'crawl-on-your-belly-and-wait-for-the-rain biodiversity'.

The dispersal ability of resting eggs may influence the dynamics of local communities and the distribution of particular species. The effectiveness of passive dispersal by resistant resting eggs in zooplankton is often demonstrated by their ability to colonize even remote oceanic islands (Brendonck et al., 1990; Peck, 1994) and by the broad distributions of some species (Banareescu, 1990; Havel & Hebert, 1993; Hamer & Brendonck, 1997) or genotypes (Weider et al., 1999). Wind and animal vectors have been suggested as important dispersal agents, but few direct measurements have been made (Brendonck & Riddoch, 1999; Bohonak & Whiteman, 1999; Michels et al., 2001). Despite their apparently high dispersal capabilities, basins in the vicinity of inhabited pools of apparently equal quality are often empty (Boileau & Hebert, 1991; Boileau & Taylor, 1994; Jenkins, 1995) or contain a structurally different community (Jenkins & Buikema, 1998). In addition, significant genetic variation is often observed among (often nearby) local populations of pond invertebrates (in anostracans: Davies et al., 1997; Bohonak, 1998; Brendonck et al., 2000; in

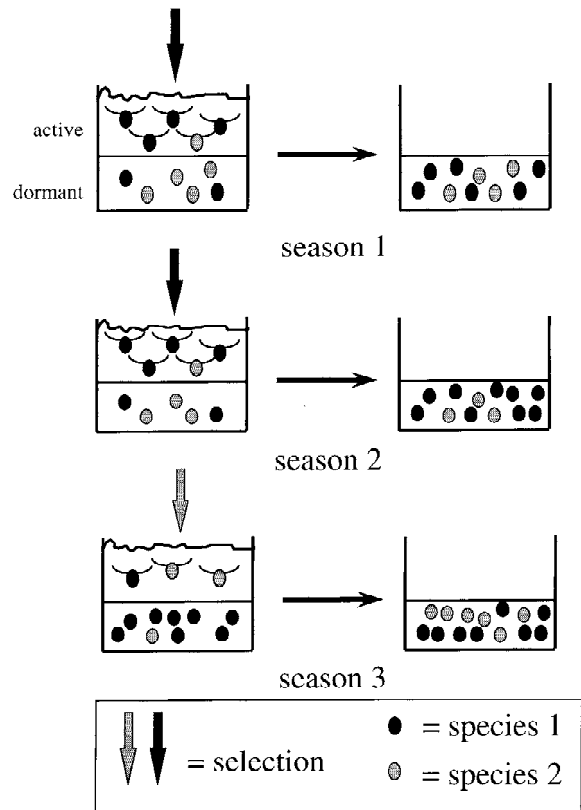


Figure 4. Diagram illustrating how, through the storage effect, two competing species with different regeneration niches can co-exist in a variable environment (variable selection regimes in subsequent seasons visualized by the different gray shading). At the left side, populations are active in the growing period (here illustrated as the wet phase). At the right side, populations are only present in a dormant state (e.g. here in the dry phase of the habitat). Each species has its own favorite environment (corresponding color in selection regime) during which recruitment is successful. Eggs in the sediment bridge the unfavorable time span in a dormant state. Species can in this figure also be replaced by genotypes to illustrate the maintenance of genetic diversity in the egg bank by the same process.

*Daphnia*: Declerck et al., 2001). There is also no clear relationship between dispersal inferred from local genetic divergence and species distributions (Boileau et al., 1992). Whether these observations result from chance effects associated with dispersal or from unsuccessful colonization related to competition with resident populations is an issue of controversy (e.g. review in de Meester, 1996; de Meester et al., 2002). It should be noted that, as mentioned above, eggs are sometimes attached to firm substrata that reduces the chances of dispersal. According to Fryer (1996), it is often more advantageous to ensure persistence of a population in a habitat that has proved favorable

than to subject eggs to the hazards involved in chance dispersal.

### Egg banks and evolutionary dynamics

In general, the effects of a pool of dormant stages on evolutionary dynamics within populations are expected to be substantial, particularly when the distribution of dormant genotypes is different from that in the active population. In the case of delayed diapause and long-term viability of the dormant fraction, both directional and fluctuating selection will result in a gradual accumulation of genotypes in the egg (seed) bank that differ from those expressed at any one time in the active population (Levin, 1990; Hairston et al., 1996b). In the case of directional selection, the mean genotype in the dormant pool is expected to differ from that in the active population, whereas fluctuating selection should result in greater genotypic variance in the resting egg bank than in the active population (Hairston et al., 1996b). The impact of this mixed egg bank (in terms of generations) on the evolution of the population as a whole will then depend on the intensity of the selection pressure, the amount of generation overlap in the egg bank (which in turn is dependent on hatching fraction and long-term viability of the eggs), the intensity of disturbance of the sediment, and the hatching characteristics of different age classes of eggs (e.g. those produced in the last season *versus* 'old' eggs).

As resting stages are not exposed to the same selective forces as adults, they remove a fraction of the gene pool from the influence of micro-evolutionary forces in each generation and as such are theoretically predicted to slow down micro-evolutionary processes such as response to natural selection and drift (Templeton & Levin, 1979; Hairston & de Stasio, 1988; Ellner et al., 1999).

Another theoretical result of overlapping generations in the dormant egg pool is the maintenance of genetic variation in a temporally varying environment, over a broad range of conditions (Ellner & Hairston, 1994; Hedrick, 1995). As with the maintenance of species diversity within communities, the storage effect is also a powerful mechanism for maintaining genetic diversity within populations by buffering the effects of local extinctions of genotypes in the active portion of the population (Fig. 4) (Chesson, 1985; Seger & Brockmann, 1987; Ellner & Hairston, 1994; Hairston et al., 1996a). In the same way as egg banks are reservoirs of species, they can function as stocks of genes

and gene complexes. This genetic variation increases the evolutionary potential of the population (Levin, 1990).

There is some evidence that generation overlap promotes maintenance of genetic variation in a population of the copepod *Diaptomus sanguineus* (Hairston et al., 1996b). A large inter-population variability for timing of diapause was found in *D. sanguineus* as well as a substantial heritability of traits related to the production and timing of diapausing eggs. The importance of the egg bank for the maintenance of genetic variation is also suggested by Sadler & Spitze (1995) who found lower levels of genetic variation in the subtropical cladocerans *Simocephalus serrulatus* in contrast to *Daphnia* populations. They speculated that this difference was due to the fact that *Simocephalus* species only produce one resting egg at a time, in contrast to the two eggs, typical for *Daphnia* individuals, and as such have only half the effective population size and half of the effects of dispersal events. Another indication for the importance of egg banks in maintaining genetic diversity is the fact that intermittent populations of *Daphnia* in small ponds that rely entirely on resting eggs for repopulation are largely in Hardy–Weinberg equilibrium (Hebert, 1978, 1987), in contrast with the large deviations from H–W equilibrium in ponds where some adults survive throughout the year, rendering the contribution from the egg bank less important (Hebert, 1978, 1987), and where prolonged periods of clonal selection erode genetic diversity (Mort & Wolf, 1986). The situation is less clear in large populations in lakes where some individuals may also overwinter as adults but where a large diversity is often measured (Carvalho & Crisp, 1987), resembling more closely the situation in intermittent pond populations (Mort & Wolf, 1985, 1986). According to de Meester (1996), this can be explained by the high genetic diversity in large populations at the start of the growing season, minimizing the impact of subsequent clonal selection. Where deviations from H–W equilibrium occur in temporary populations, it is often due to a deficiency of heterozygotes. This can be explained by a Wahlund effect following simultaneous hatching from a mixed egg bank (Hebert, 1987; Brendonck et al., 2000; Gómez & Carvalho, 2000).

Kalisz (1991) speculates that the time resting stages spend dormant in the seed or egg bank could act to purge out the inferior genotypes (e.g. due to inbreeding) if they are more likely to senesce and die in the seed bank without germinating. This sieving mechanism would have significant consequences

for the fitness of the genotypes represented in the active population and may also result in different genotypes represented in the seed bank versus the active population. Gómez and Carvalho (2000) measured a difference in allele frequencies between hatched individuals and resting eggs of the rotifer *Brachionus plicatilis*, and suggested that this could indicate genetic differences in the hatching of resting eggs or drift or selection after hatching.

The duration of dormancy may itself evolve as a function of traits expressed in the active stage, which may in turn alter the direction or intensity of selection on the active traits (Hairston et al., 1996b). These authors compared the switch to production of diapausing eggs between individuals from active and diapausing sub-populations of a freshwater copepod with a long-lived egg bank. The mean timing of diapause was significantly later in the season for copepods reared from individuals collected from the water column. They hypothesized that their results are explained by adaptive covariance between traits that influence how long an egg spends in the sediments before hatching and traits that influence the seasonal timing of diapause.

### Current and future applications

#### *Historical (genetic and demographic) reconstruction and resurrection ecology*

One field that is in full development is the use of molecular and ecologically relevant (life history and behavioural) markers to study the genetic structure of resting egg banks and to reconstruct evolutionary changes in the recent past. As egg banks integrate annual and seasonal variation, they are representative of the entire community and are becoming key elements in the study of species diversity. Lake sediments in general archive histories of population and community dynamics for many organisms with tissues resistant to decomposition (Kerfoot et al., 1999; Jeppesen et al., 2001). The fact that many aquatic sediments are stratified historically and can be dated using standard radio-isotope techniques or by direct counting of varves in the case of laminated sediments (Viitasalo & Katajisto, 1994) makes historical reconstruction possible (see above). As resting eggs in the sediment can remain viable for decades or centuries, the long-lived dormant stages of zooplankton additionally offer a unique source of living historical information (e.g.

Weider et al., 1997; Hairston et al., 1999a,b; Kerfoot et al., 1999; Cousyn et al., 2001; Limburg & Weider, 2002), the study of which was denoted as resurrection ecology by Kerfoot et al. (1999). Detailed morphological or genetic analysis of the resting stages in the sediment cores from habitats with known history allows one to reconstruct changes in species assemblage and population genetic structure of zooplankton communities in an ecological context. Such a reconstruction may, for example, reveal patterns in species composition in relation to climatic conditions as well as the potential of some species to disperse and colonize. It is also possible to use such data to address questions about evolutionary rates, to infer rates of genetic drift, rates of response to natural selection, or rates of immigration from external sources or from earlier dormant stages from within the system (e.g. by bioturbation). Egg banks also provide opportunities to study genetic processes related to founder events (Hairston et al., 1999b).

Ancient eggs may be exposed to (a range of) hatching conditions in order to study the life history characteristics of such 'living fossils'. Weider et al. (1997) revealed significant shifts in allele frequencies in the egg bank of a *Daphnia* population which paralleled concomitant shifts in the trophic state of Lake Constance during the past 25–35 years. Hairston et al. (1999a) studied the genetic variation in an ecologically relevant character, resistance to toxins of cyanobacteria, in adults hatched from the same egg bank and found increasing resistance in those periods of intense eutrophication. In another case study, Hairston et al. (1999b) and Duffy et al. (2000) illustrated the presence of two *Daphnia* species (*D. curvirostris* and *D. exilis*) in the egg bank of Onondaga Lake that were absent from the active population for more than 15 years. The peak abundance of both species coincided with increased production of salt wastes due to industrial activities along the shores of the lake excluding zooplanktivorous fish and native *Daphnia* species. Kerfoot et al. (1999) found changes in the tolerance for heavy metals in *Daphnia*, concordant with periods of variable pollution loads. Cousyn et al. (2001) combined the study of changes in microsatellite allele frequencies (as a neutral marker) and changes in vertical migration (as an ecologically relevant character related to predator avoidance) in eggs isolated from episodes that corresponded with variable predation pressure during the last 30 years in a shallow Belgian pond. Genetic differentiation for the ecologically relevant character was about ten times higher than

*Table 1.* The five main conditions that need to be met to enable a successful reconstruction of micro-evolution from a resting propagule bank. The combination of these requirements at present strongly constrain the questions that can be studied and the populations (localities, habitats) and taxa to which the approach can be applied

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(1)	One needs to select a habitat or population with a well-documented history with respect to the (environmental) variable in relation to which evolutionary changes are being studied.
(2)	One needs an undisturbed sediment record that can be properly dated.
(3)	The sediment core(s) should contain sufficient resting propagules for a proper analysis.
(4)	For an analysis of genetic changes at neutral marker loci, one needs high resolution genetic markers that can be applied on small amounts of tissue (e.g. microsatellite loci).
(5)	For an analysis of evolutionary changes in ecologically relevant traits, the resting propagules need to be viable and responsive to hatching stimuli.

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for the neutral marker. These data indicate that micro-evolutionary shifts related to anthropogenic changes in ponds and lakes have occurred in a short period and are revealed by the diapausing eggs, the archive in the sediment. In addition to the study of the effects of eutrophication (Hairston et al., 2000) and fish predation (Cousyn et al., 2001) one could think about studying the changes in tolerance to heavy metals and persistent pesticides, changes in the tolerance to UV-irradiation as an indication of the increasing hole in the ozone layer, study of the response to lake restoration efforts through biomanipulation, etc.

The reconstruction of micro-evolution using resting propagule banks as archives of past genetic changes involves the integration of different techniques and approaches, such as radio-dating, historical reconstruction, the use of molecular tools and experimental quantitative genetics (Hairston et al., 1999; Cousyn et al., 2001). Providing a detailed survey of these methods is out of the scope of this review. Table 1, however, provides a list of conditions that need to be fulfilled for a successful reconstruction of micro-evolution from resting propagule banks. This table shows that one should select potential case studies carefully, as it is not obvious that all these conditions are met.

#### *The study of biodiversity, reconstruction of the pristine state, and restoration ecology*

By quantifying and characterizing resting stages in the surface layer of the sediment (e.g. upper 2 cm), it is possible to compare the potential species and genetic diversity among lakes or ponds. Given the extended lifetime of most resting stages and the incomplete hatching of the egg bank at any given point in time, the egg bank integrates both seasonal and inter-annual

variation in the community. Egg bank diversity measured at a single occasion before the start of the growing season may therefore be a faster and more reliable estimator of biodiversity than biodiversity estimates based on intensive whole-season sampling. Identifying the resting stages can assess species diversity, where possible on the basis of their morphology, or by hatching sediment under a range of laboratory conditions. Havel et al. (2000) applied this method to compare the diversity in old remnant oxbows and young scour sites in the floodplain of the Missouri River. To further optimize this method, more information is needed on the morphology of the resting stages of different species so that eggs could be identified immediately without having to incubate the sediment first to obtain adults that can be identified. By means of image analysis it could furthermore be possible to automate this identification process to some extent.

The historical reconstruction of species composition and diversity from cores of the egg bank against the known history of a pool may also deliver a reliable estimator of the pristine state of that particular pool in a specific regional setting. This method might be more reliable than the use of habitats in a geographically distinct area as a reference for so-called pristine conditions for a particular type of aquatic habitat. The presence of a long-lived egg bank also has potentials for restoration of any deteriorated pools or re-establishment of threatened or endangered species.

Prolonged dormancy is also significant in the context of environmental change. As some species and genotypes may be excluded at some occasions, their egg banks act as reservoirs for seeding the active community when favorable conditions for that species return (Hairston, 1996). Due to changing environmental conditions (e.g. global warming), the frequency of favorable occasions (growing seasons) for a particu-

lar species may change and influence its potential for existence by changing the size of the egg reservoir. Another problem may be the continuous eutrophication, that, through the increase of organic matter in the soil, may lead to an increase in the numbers and activity of soil organisms. In addition to eating and destroying eggs, these animals can move eggs in the sediment and deposit waste products around them. These deposits may contain chemicals that may affect egg dormancy. These changes at the level of the resting egg bank may have an impact on the amount of biotic diversity (species richness / genetic variation) maintained in the future. Knowledge of the structure and dynamics of egg banks and how these relate with community composition may help to develop a tool for monitoring community changes due to global change.

#### *Phylogeography*

The more complete representation of genotypes in the sediment, integrating seasonal and annual variations of a species as well as the impact of drift and local extinctions, has recently also resulted in the approach to use directly the egg banks instead of the active individuals to study the phylogeny (Gómez et al., 2000) or patterns of genetic differentiation (Ortells et al., 2000) of zooplankton populations. The comparison of egg bank diversity with the diversity in the active pelagic community component within the same lake may furthermore contribute substantially to our understanding of processes that may result in high biodiversity in certain habitats.

#### *Aquaculture and aquatic toxicology*

In contrast to the many studies in *Artemia* (e.g. Clegg, 1997; Clegg & Jackson, 1998; Hontoria et al., 1998; MacRae & Liang, 1998), not many studies have examined the biochemical and physiological basis of quiescence or diapause in zooplankton. Better knowledge of these processes may ultimately result in the manipulation of these physiological phases and in more predictable hatching results in the application of resting eggs in aquaculture and aquatic toxicology.

In environmental toxicology with zooplankton, most attention has been paid to the effects of the chemicals used on the active component populations of various species (Lahr, 1998). Most of these organisms, however, rely on egg banks for recovery. To date, not much information is available on the effects of e.g. insecticide treatments and herbicides on the survival

and hatching response of the dormant fraction of the populations that may eventually result in long-lasting side effects.

#### **Summary**

Long-lived and mixed egg banks form an essential component of zooplankton communities. As egg banks integrate seasonal and year-to-year variations in environmental conditions, they represent much better the total species and genetic diversity in any community or population than the active community component sampled at any one point in time. Overlooking the composition of the egg bank in studies of biodiversity, biogeography or phylogeography may therefore result in incomplete or even erroneous patterns and interpretations of the underlying processes. By revising the fundamental processes that generate, maintain and characterize egg banks in zooplankton, and by concisely summarizing the most important techniques to study various aspects of egg bank structure and function, we hope to stimulate additional research in this expanding and fascinating field of limnological and evolutionary research. Especially the fact that egg banks archive historical changes offers intriguing opportunities for studying the deterministic and random processes that structure populations and communities.

#### **Acknowledgements**

This study was partly financed by the research grant G.0260.97 provided by the F.W.O.-Flanders (Belgium), grant OT/00/14 provided by the Catholic University of Leuven (K.U.Leuven), and EU project BIOMAN (EVK2-CT-1999-00046).

#### **References**

- Alekseev, V. & W. Lampert, 2001. Maternal control of resting egg production in *Daphnia*. *Nature* 414: 899–901.
- Appleby, P. G. & F. Oldfield, 1983. The assessment of <sup>210</sup>Pb data from sites with varying sediment accumulation rates. *Hydrobiologia* 103: 29–35.
- Banarescu, P., 1990. Vol. 1. General distribution and dispersal of freshwater animals. *Zoogeography of Fresh Waters*. Aula-Verlag Wiesbaden.
- Baskin, Y., 1994. California's ephemeral vernal pools may be a good model for speciation. *BioScience* 44: 384–388.
- Belk, D., 1977. The evolution of egg size strategies in fairy shrimps. *S. West. Nat.* 22: 99–105.



- Belk, D., 1989. Identification of species of the conchostracan genus *Eulimnadia* by egg shell morphology. *J. Crust. Biol.* 9: 115–125.
- Belmonte, G. & M. Puce, 1994. Morphological aspects of subitaneous and resting eggs from *Acartia josephinae* (Calanoida). *Hydrobiologia* 292/293: 131–135.
- Blaustein, L., 1997. Non-consumptive effects of larval *Salamandra* on crustacean prey: can eggs detect predators? *Oecologia* 110: 212–217.
- Bohonak, A. J., 1998. Genetic population structure of the fairy shrimp *Branchinecta coloradensis* (Anostraca) in the Rocky Mountains of Colorado. *Can. J. Zool.* 76: 1–9.
- Bohonak, A. J. & H. H. Whiteman, 1999. Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. *Limnol. Oceanogr.* 44: 487–493.
- Boileau, M. G. & P. D. N. Hebert, 1991. Genetic consequences of passive dispersal in pond-dwelling copepods. *Evolution* 45: 721–733.
- Boileau, M. G. & B. E. Taylor, 1994. Chance events, habitat age, and the genetic structure of pond populations. *Arch. Hydrobiol.* 132: 191–202.
- Boileau, M. G., P. D. N. Hebert & S. S. Schwartz, 1992. Nonequilibrium gene frequency divergence: persistent founder effects in natural populations. *J. Evol. Biol.* 5: 25–39.
- Bonis, A., J. Lepart & P. Grillas, 1995. Seed bank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. *Oikos* 74: 81–92.
- Brendonck, L., 1996. Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). *Hydrobiologia* 320: 85–97.
- Brendonck, L. & A. Coomans, 1994a. Egg morphology in African Streptocephalidae (Crustacea: Branchiopoda: Anostraca). Part 1: South of Zambezi and Kunene rivers. *Arch. Hydrobiol. / Suppl.* 99 (3): 313–334.
- Brendonck, L. & A. Coomans, 1994b. Egg morphology in African Streptocephalidae (Crustacea: Branchiopoda: Anostraca). Part 2: North of Zambezi and Kunene rivers, and Madagascar. *Arch. Hydrobiol. / Suppl.* 99 (3): 335–356.
- Brendonck, L. & B. J. Riddoch, 1999. Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). *Biol. J. linn. Soc.* 67: 87–95.
- Brendonck, L. & B. J. Riddoch, 2000a. Dispersal in the desert rock pool anostracan *Branchipodopsis wolffi* (Crustacea: Branchiopoda). *Crust. Iss.* 12: 109–118.
- Brendonck, L. & B. J. Riddoch, 2000b. Egg bank dynamics in anostracan desert rock pool populations (Crustacea: Branchiopoda). *Arch. Hydrobiol.* 148: 71–84.
- Brendonck, L. & B. J. Riddoch, 2001. Hatching characteristics of the fairy shrimp *Branchipodopsis wolffi* in relation to the stochastic nature of its habitat, desert rock pools. *Verh. int. Ver. Limnol.* 27: 3931–3935.
- Brendonck, L., L. de Meester & N. G. Hairston, Jr. (eds), 1998a. Evolutionary and Ecological Aspects of Crustacean Diapause. *Arch. Hydrobiol. (Special Issues)* 52: 561 pp.
- Brendonck, L., L. de Meester & B. J. Riddoch, 2000. Regional structuring of genetic variation in short-lived rock pool populations of *Branchipodopsis wolffi* (Crustacea: Anostraca). *Oecologia* 123: 506–515.
- Brendonck, L., B. J. Riddoch, V. van de Weghe & T. van Dooren, 1998b. The maintenance of egg banks in very short-lived pools – a case study with anostracans (Branchiopoda). In Brendonck, L., L. de Meester & N. G. Hairston, Jr. (eds), Evolutionary and Ecological Aspects of Crustacean Diapause. *Arch. Hydrobiol.* 52: 141–161.
- Brendonck, L., A. Thiery & A. Coomans, 1990. Taxonomy and biogeography of the Galapagos branchiopod fauna (Anostraca, Notostraca, Spinicaudata). *J. Crust. Biol.* 10: 676–694.
- Brown, J. S. & D. L. Venable, 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. *Am. Nat.* 127: 31–47.
- Bulmer, M. G., 1984. Delayed germination of seeds: Cohen's model revisited. *Theor. Pop. Biol.* 26: 367–377.
- Cáceres, C. E., 1997a. Dormancy in invertebrates. *Inv. Biol.* 116: 371–383.
- Cáceres, C. E., 1997b. Temporal variation, dormancy, and coexistence: A field test of the storage effect. *Proc. natn. Acad. Sci. U.S.A.* 94: 9171–9175.
- Cáceres, C. E., 1998a. Seasonal dynamics and interspecific competition in Oneida Lake *Daphnia*. *Oecologia* 115: 233–244.
- Cáceres, C. E., 1998b. Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology* 79: 1699–1710.
- Cáceres, C. E. & N. G. Hairston, Jr., 1998. Benthic-pelagic coupling in planktonic crustaceans: the role of the benthos. *Arch. Hydrobiol.* 52: 163–174.
- Carmona, M. J., A. Gómez & M. Serra, 1995. Mictic patterns of the rotifer *Brachionus plicatilis* in small ponds. *Hydrobiologia* 313/314: 365–371.
- Carvalho, G. R. & D. J. Crisp, 1987. The clonal ecology of *Daphnia magna* (Crustacea: Cladocera). I. Temporal changes in the clonal structure of a natural population. *J. anim. Ecol.* 56: 453–468.
- Carvalho, G. R. & H. G. Wolf, 1989. Resting eggs of lake-*Daphnia*. I. Distribution, abundance and hatching of eggs collected from various depths in lake sediments. *Freshwat. Biol.* 22: 459–470.
- Caswell, H. & A. Hastings, 1980. Fecundity, developmental time, and population growth rate: an analytical solution. *Theor. Pop. Biol.* 17: 71–79.
- Champeau, A., 1970. Recherches sur l'écologie et l'adaptation à la vie latente des copépodes des eaux temporaires Provençales et Corses. Thesis. Univ. Aix-Marseille, 360 pp.
- Chesson, P. L., 1983. Coexistence of competitors in a stochastic environment: The storage effect. In Freeman, H. I. & C. Strobeck (eds), *Population Bbiology*, Springer: 188–198.
- Chesson, P. L., 1985. Coexistence of competitors in spatially and temporally varying environments: A look at the combined effects of different sorts of variability. *Theor. Pop. Biol.* 28: 263–287.
- Chesson, P. L., 1994. Multispecies competition in varying environments. *Theor. Pop. Biol.* 45: 227–276.
- Chesson, P. L. & R. R. Warner, 1981. Environmental variability promotes coexistence in lottery competitive system. *Am. Nat.* 117: 923–943.
- Clegg, J. S., 1997. Embryos of *Artemia franciscana* survive four years of continuous anoxia: the case for complete metabolic rate depression. *Br. J. exp. Biol.* 200: 467–475.
- Clegg, J. S. & S. A. Jackson, 1998. The metabolic status of quiescent and diapause embryos *Artemia franciscana* (Kellog). In Brendonck, L., L. de Meester & N. G. Hairston, Jr. (eds), Evolutionary and Ecological Aspects of Crustacean Diapause. *Arch. Hydrobiol.* 52: 425–439.
- Cohen, D., 1966. Optimizing reproduction in a randomly varying environment. *J. theor. Biol.* 12: 119–129.
- Cousyn, C. & L. de Meester, 1998. The vertical profile of resting egg banks in natural populations of the pond-dwelling cladoceran *Daphnia magna*. In Brendonck, L., L. de Meester, & N. G. Hairston, Jr. (eds), Evolutionary and Ecological Aspects of Crustacean Diapause. *Arch. Hydrobiol.* 52: 127–139.

- Cousyn, C., L. de Meester, J. K. Colbourne, L. Brendonck, D. Verschuren & F. Volckaert, 2001. Rapid, local adaptation of zooplankton behavior to changes in predation pressure in the absence of neutral genetic changes. *PNAS* 98: 6256–6260.
- Danks, H. V., 1987. *Insect Dormancy: An Ecological Perspective*. Tyrell Press, Gloucester, 439 pp.
- Davies, C. P., M. A. Simovich & S. A. Hathaway, 1997. Population genetic structure of a California endemic branchiopod, *Branchinecta sandiegonensis*. *Hydrobiologia* 359: 149–158.
- Declerck, S., C. Cousyn & L. de Meester, 2001. Evidence for local adaptation in neighbouring *Daphnia* populations: a laboratory transplant experiment. *Freshwat. Biol.* 46: 187–198.
- de Meester L., 1996. Local genetic differentiation and adaptation in freshwater zooplankton populations: patterns and processes. *Ecoscience* 3: 385–399.
- de Meester, L. & H. de Jager, 1993. Hatching of *Daphnia* sexual eggs: 2. The effect of age and a second stimulus. *Freshwat. Biol.* 30: 227–233.
- de Meester, L., A. Gómez, B. Okamura & K. Schwenk, 2002. Dispersal, monopolisation and gene flow in continental aquatic organisms. *Acta Oecologia*. 23: 121–135
- de Stasio, B. T., Jr., 1989. The seed bank of a freshwater crustacean: copepodology for the plant ecologist. *Ecology* 70: 1377–1389.
- de Stasio, B. T., Jr., 1990. The role of dormancy and emergence patterns in the dynamics of a freshwater zooplankton community. *Limnol. Oceanogr.* 35: 1377–1389.
- Donald, D. B., 1983. Erratic occurrence of anostracans in a temporary pond: colonization and extinction or adaptation to variations in annual weather? *Can. J. Zool.* 61: 1492–1498.
- Duffy, M. A., L. J. Pery, C. M. Kearns, L. J. Weider & N. G. Hairston, Jr., 2000. Paleogenetic evidence for a past invasion of Onondaga Lake, New York, by exotic *Daphnia curvirostris* using mtDNA from dormant eggs. *Limnol. Oceanogr.* 45: 1409–1414.
- Elgmork, K., 1962. A bottom resting stage in the planktonic freshwater copepod *Cyclops scutifer* Sars. *Oikos* 13: 306–310.
- Elgmork, K. & A. Langeland, 1980. *Cyclops scutifer* Sars: one- and two-year cycles with diapause in the meromictic lake Blankvatn. *Arch. Hydrobiol.* 88: 178–201.
- Ellner, S., 1984. Asymptotic behavior of some stochastic difference equation population models. *J. Math. Biol.* 19: 169–200.
- Ellner, S., 1985. ESS germination strategies in randomly varying environments. I. Logistic-type models. *Theor. Pop. Biol.* 28: 50–79.
- Ellner, S. & N. G. Hairston, Jr., 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *Am. Nat.* 143: 403–417.
- Ellner, S. P., N. G. Hairston, Jr., M. Kearns & D. Babiš, 1999. The roles of fluctuating selection and longterm diapause in microevolution of diapause timing in a freshwater copepod. *Evolution* 53: 111–122.
- Eng, L. L., D. Belk & C. H. Eriksen, 1990. Californian Anostraca: distribution, habitat, and status. *J. Crust. Biol.* 10: 247–277.
- Fryer, G., 1996. Diapause, a potent force in the evolution of freshwater crustaceans. *Hydrobiologia* 320: 1–14.
- Fryer, G. & W. J. P. Smyly, 1954. Some remarks on the resting stages of some freshwater cyclopoid and harpacticoid copepods. *Ann. mag. Nat. Hist. Ser.* 12: 65–72.
- Gilbert, J. J., 1974. Dormancy in rotifers. *Trans. am. microsc. Soc.* 93: 490–512.
- Gilbert, J. J., 1995. Structure, development and induction of a new diapause stage in rotifers. *Freshwat. Biol.* 34: 263–270.
- Gilbert, J. J. & E. S. Wurdak, 1978. Species-specific morphology of resting eggs in the rotifer *Asplanchna*. *Trans. am. microsc. Soc.* 97: 330–339.
- Gilbert, J. J., C. W. Birky, Jr. & E. S. Wurdak, 1979. Taxonomic relationships of *Asplanchna brightwelli*, *A. intermedia*, and *A. sieboldi*. *Arch. Hydrobiol.* 87: 224–242.
- Gliwicz, Z. M. & J. Pijanowska, 1989. The role of predation in zooplankton succession. In Sommer, U. (ed.), *Plankton Ecology*. Springer, Berlin Heidelberg New York: 253–298.
- Gómez, A. & G. R. Carvalho, 2000. Sex, parthenogenesis and genetic structure of rotifers: microsatellite analysis of contemporary and resting egg bank populations. *Mol. Ecol.* 9: 203–214.
- Gómez, A., G. R. Carvalho & D. H. Lunt, 2000. Phylogeography and regional endemism of a passively dispersing zooplankton: mitochondrial DNA variation in rotifer resting egg banks. *Proc. R. Soc. Lond.* 267: 2189–2197.
- Hagiwara, A., 1996. Appearance of floating resting eggs in the rotifers *Brachionus plicatilis* and *B. rotundiformis*. *Bull. Fac. Fish., Nagasaki Univ.* 77: 111–115.
- Hairston, N. G., Jr., 1996. Zooplankton egg banks as biotic reservoirs in changing environments. *Limnol. Oceanogr.* 41: 1087–1092.
- Hairston, N. G., Jr., 1998. Time travellers: What's timely in diapause research? In Brendonck, L., L. de Meester & N. G. Hairston, Jr. (eds), *Evolutionary and Ecological Aspects of Crustacean Diapause*. *Arch. Hydrobiol.* 52: 1–15.
- Hairston, N. G., Jr. & C. E. Cáceres, 1996. Distribution of crustacean diapause: micro – and macroevolutionary pattern and process. *Hydrobiologia* 320: 27–44.
- Hairston, N. G., Jr. & B. T. de Stasio, 1988. Rate of evolution slowed down by a dormant propagule pool. *Nature* 336: 239–242.
- Hairston, N. G. & C. M. Kearns, 1995. The interaction of photoperiod and temperature in diapause timing: A copepod example. *Biol. Bull.* 189: 42–48.
- Hairston, N. G., Jr. & W. R. Munns, Jr., 1984. The timing of copepod diapause as an evolutionarily stable strategy. *Am. Nat.* 123: 733–751.
- Hairston, N. G., Jr. & E. J. Olds, 1984. Population differences in the timing of diapause: adaptation in a spatially heterogeneous environment. *Oecologia* 61: 42–48.
- Hairston, N. G., Jr. & R. A. Van Brunt, 1994. Diapause dynamics of two diaptomid copepod species in a large lake. *Hydrobiologia* 292/293: 209–218.
- Hairston, N. G., Jr. & W. E. Walton, 1986. Rapid evolution of a life history trait. *Proc. natn. Acad. Sci. U.S.A.* 83: 4831–4833.
- Hairston, N. G., Jr., S. Ellner & C. M. Kearns, 1996a. Overlapping generations: the storage effects and the maintenance of biotic diversity. In Rhodes, O. E., Jr., R. K. Chesser & M. H. Smith (eds), *Population Dynamics in Ecological Space and Time*: 109–145.
- Hairston, N. G., Jr., A-M Hansen & W. R. Schaffner, 2000. The effect of diapause emergence on the seasonal dynamics of a zooplankton assemblage. *Freshwat. Biol.* 45: 133–145.
- Hairston, N. G., Jr., C. M. Kearns & S. P. Ellner, 1996b. Phenotypic variation in a zooplankton egg bank. *Ecology* 77: 2382–2392.
- Hairston, N. G., Jr., W. Lampert, C. E. Cáceres, C. L. Holtmeier, L. J. Weider, U. Gaedke, J. M. Fischer, J. A. Fox & D. M. Probst, 1999a. Rapid evolution revealed by dormant eggs. *Nature* 401: 446.
- Hairston, N. G., Jr., R. A. Van Brunt & C. M. Kearns, 1995. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 76: 1706–1711.
- Hairston, N. G., Jr., L. J. Perry, A. J. Bohonak, M. Q. Fellows, C. M. Kearns & D. R. Engstrom, 1999b. Population biology of a failed invasion: Paleolimnology of *Daphnia exilis* in upstate New York. *Limnol. Oceanogr.* 44: 477–486.

- Håkanson, L., S. Floderus & M. Wallin, 1989. Sediment trap assemblages – a methodological description. *Hydrobiologia* 176/177: 481–490.
- Hamer, M. & L. Brendonck, 1997. Diversity, distribution and conservation of Anostraca in southern Africa. *Hydrobiologia* 359: 1–12.
- Hand, S. C., 1991. Metabolic dormancy in aquatic invertebrates. *Comp. Environ. Physiol.* 8: 2–50.
- Hathaway, S. A. & M. A. Simovich, 1996. Factors affecting the distribution and co-occurrence of two southern Californian anostracans (Branchiopoda), *Branchinecta sandiegonensis* and *Streptocephalus woottoni*. *J. Crust. Biol.* 16: 669–677.
- Havel, J. E. & P. D. N. Hebert, 1993. *Daphnia lumholtzi* in North America: another exotic zooplankton. *Limnol. Oceanogr.* 38: 1823–1827.
- Havel, J. E., M. Eisenbacher & A. A. Black, 2000. Diversity of crustacean zooplankton in riparian wetlands: colonization and egg banks. *Aquat. Ecol.* 34: 63–76.
- Hebert, P. D. N., 1978. The population biology of *Daphnia* (Crustacea, Daphniidae). *Biol. Rev.* 53: 387–426.
- Hebert, P. D. N., 1987. Genotypic characteristics of the Cladocera. *Hydrobiologia* 145: 183–193.
- Hedrick, P. W., 1995. Genetic polymorphism in a temporally varying environment: effects of delayed germination or diapause. *Heredity* 75: 164–170.
- Herzig, A., 1985. Resting eggs – a significant stage in the life cycle of crustaceans *Leptodora kindti* and *Bythotrephes longimanus*. *Verh. int. Ver. Limnol.* 22: 3088–3098.
- Hildrew, A. G., 1985. A quantitative study of the life history of a fairy shrimp (Branchiopoda: Anostraca) in relation to the temporary nature of its habitat, a Kenyan rainpool. *J. anim. Ecol.* 54: 99–110.
- Hontoria, F., J. H. Crowe, L. M. Crowe & F. Amat, 1998. Trehalose prevents imbibitional damage in anhydrobiotic cysts of *Artemia* by depressing the phase transition temperature in lipids. In Brendonck, L., L. de Meester & N. G. Hairston, Jr. (eds), *Evolutionary and Ecological Aspects of Crustacean Diapause*. *Arch. Hydrobiol.* 52: 451–462.
- Hutchinson, G. E., 1967. *A Treatise on Limnology*. Volume II. Introduction to Lake Biology and the Limnoplankton. John Wiley and Sons, New York.
- Janssen, G. M. C., M. Brandsma & W. Möller, 1998. Termination of quiescence in Crustacea: the role of transfer RNA aminoacylation and intracellular pH in the brine shrimp *Artemia*. In Brendonck, L., L. de Meester & N. G. Hairston, Jr. (eds), *Evolutionary and Ecological Aspects of Crustacean Diapause*. *Arch. Hydrobiol.* 52: 411–423.
- Jenkins, D. G., 1995. Dispersal-limited zooplankton distribution and community composition in new ponds. *Hydrobiologia* 313/314: 15–20.
- Jenkins, D. G. & A. L. Buikema, Jr., 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecol. Monogr.* 63: 421–443.
- Jeppesen, E., P. Leavitt, L. de Meester & J. P. Jensen, 2001. Functional ecology and paleolimnology: using cladoceran remains to reconstruct anthropogenic impact. *TREE* 16: 191–198.
- Kalisz, S., 1991. Experimental determination of seed bank age structure in the winter annual *Collinsia verna*. *Ecology* 72: 575–585.
- Kankaala, P., 1983. Resting eggs, seasonal dynamics and productivity of *Bosmina longispina maritime* (P.E. Müller) (Cladocera) in the northern Baltic proper. *J. Plankt. Res.* 5: 53–69.
- Kearns, C. M., N. G. Hairston, Jr. & D. H. Kesler, 1996. Particle transport by benthic invertebrates: its role in egg bank dynamics. *Hydrobiologia* 332: 63–70.
- Kerfoot, W. C., J. A. Robbins & L. J. Weider, 1999. A new approach to historical reconstruction: combining descriptive and experimental paleolimnology. *Limnol. Oceanogr.* 44: 1232–1247.
- King, C. E., 1972. Adaptations of rotifers to seasonal variation. *Ecology* 53: 408–418.
- Kleiven, O. T., P. Larsson & A. Hobæk, 1992. Sexual reproduction in *Daphnia magna* requires three stimuli. *Oikos* 65: 165–206.
- Kokkinn, M. J. & W. D. Williams, 1987. Is ephippial morphology a useful taxonomic descriptor in the cladocera? An examination based on a study of *Daphniopsis* (Daphniidae) from Australian salt lakes. *Hydrobiologia* 145: 67–73.
- Korínek, V., V. Sacherová & L. Havel, 1997. Subgeneric differences in head shield and ephippia ultrastructure within the genus *Bosmina* Baird (Crustacea, Cladocera). *Hydrobiologia* 360: 13–23.
- Korovchinsky, N. M. & O. S. Boikova, 1996. The resting eggs of the Ctenopoda (Crustacea: Branchiopoda): a review. *Hydrobiologia* 320: 131–140.
- Lahr, J., 1998. An ecological assessment of the hazard of insecticides used in desert locust control, to invertebrates in temporary ponds in the Sahel. *Aquat. Ecol.* 32: 153–162.
- Lampert, W. & I. Krause, 1976. Züri Biologie der Cladocere *Holopedium gibberum* Zaddach im Windgefallweiher (Schwarzwald). *Arch. Hydrobiol.* 48: 262–286.
- Levin, D. A., 1990. The seed bank as a source of genetic novelty in plants. *Am. Nat.* 135: 563–572.
- Limburg, P. A. & L. J. Weider, 2002. “Ancient” DNA in a microcrustacean resting egg bank can serve as a paleolimnological database. *Proc. R. Soc. Lond. Series B.* 269: 281–287.
- Linder, F., 1952. Contributions to the morphology and taxonomy of the branchiopod Notostraca, with special reference to the North American species. *Proc. Unit. St. Nat. Mus.* 102: 1–69.
- MacRae, T. H. & P. Liang, 1998. Molecular characterization of p26, a cyst-specific, small heat shock/a-crystallin protein from *Artemia franciscana*. In Brendonck, L., L. de Meester & N. G. Hairston, Jr. (eds), *Evolutionary and Ecological Aspects of Crustacean Diapause*. *Arch. Hydrobiol.* 52: 393–409.
- Marcus, N. H., 1984. Recruitment of copepod nauplii into the plankton: importance of diapausing eggs and benthic processes. *Mar. Ecol. Prog. Ser.* 15: 47–54.
- Marcus, N. H., 1990. Calanoid copepod, cladoceran, and rotifer eggs in sea-bottom sediments of northern Californian coastal waters: identification, occurrence and hatching. *Mar. Biol.* 105: 413–418.
- Marcus, N. H., 1995. Seasonal study of planktonic copepods and their benthic resting eggs in northern California coastal waters. *Mar. Biol.* 123: 459–465.
- Marcus, N. H., 1996. Ecological and evolutionary significance of resting eggs in marine copepods: past, present, and future studies. *Hydrobiologia* 320: 141–152.
- Marcus, N. H. & F. Boero, 1998. Minireview: The importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnol. Oceanogr.* 43: 763–768.
- Martin, J. W. & D. Belk, 1989. *Eulimnadia ovalunata* and *E. ovisimilis*, new species of clam shrimps (Crustacea, Branchiopoda, Spinicaudata) from South America. *Proc. Biol. Soc. Wash.* 102: 894–900.
- May, L., 1986. Rotifer sampling—a complete species list from one visit? *Hydrobiologia* 134: 117–120.

- Michels, E., K. Cottenie, L. Neys & L. de Meester, 2001. Zooplankton on the move: first results on the quantification of dispersal of zooplankton in a set of interconnected ponds. *Hydrobiologia* 442: 117–126.
- Mnatsakanova, E. A. & L. V. Polishchuk, 1996. Role of parthenogenetic natality and emergence from diapausing eggs in the dynamics of some rotifer populations. *Hydrobiologia* 320: 169–178.
- Moritz, C., 1987. A note on the hatching and viability of *Ceriodaphnia ephippia* collected from lake sediment. *Hydrobiologia* 145: 309–314.
- Mort, M. A. & H. G. Wolf, 1985. Enzyme variability in large-lake *Daphnia* populations. *Heredity* 55: 27–36.
- Mort, M. A. & H. G. Wolf, 1986. The genetic structure of large-lake *Daphnia* populations. *Evolution* 40: 756–766.
- Munuswamy, N., A. Hagiwara, G. Murugan, K. Hirayama & H. J. Dumont, 1996. Structural differences between the resting eggs of *Brachionus plicatilis* and *Brachionus rotundiformis* (Rotifera, Brachionidae): an electron microscopic study. *Hydrobiologia* 318: 219–223.
- Mura, G. & A. Thiery, 1986. Taxonomical significance of scanning electron microscopic morphology of the euphyllopods' resting eggs from Morocco. Part 1. Anostraca. *Vie Milieu* 36: 125–131.
- Murugan, G. & H. J. Dumont, 1995. Influence of light, DMSO and glycerol on the hatchability of *Thamnocephalus platyurus* Packard cysts. *Hydrobiologia* 298: 175–178.
- Nipkow, F., 1961. Die Rädertiere im Plankton des Zürichsees und ihre Entwicklungsphasen. *Schweiz. Z. Hydrol.* 23: 398–461.
- Örstan, A., 1995. Desiccation survival of the eggs of the rotifer *Adineta vaga* (Davis, 1873). *Hydrobiologia* 313/314: 373–375.
- Örstan, A., 1998. Microhabitats and dispersal routes of bdelloid rotifers. *Scientiae Naturae* 1: 27–35.
- Ortells, R., T. W. Snell, A. Gómez & M. Serra, 2000. Patterns of genetic differentiation in resting egg banks of a rotifer species complex in Spain. *Arch. Hydrobiol.* 149: 529–551.
- Peck, S. B., 1994. Diversity and zoogeography of the non-oceanic Crustacea of the Galapagos Islands, Ecuador (excluding terrestrial Isopoda). *Can. J. Zool.* 72: 54–69.
- Piercey, D. W. & E. J. Maly, 2000. Factors influencing the induction of diapausing egg production in the calanoid copepod *Diaptomus leptopus*. *Aquat. Ecol.* 34: 9–17.
- Philippi, T. & J. Seger, 1989. Hedging one's evolutionary bets, revisited. *TREE* 4: 41–44.
- Pijanowska, J. & G. Stolpe, 1996. Summer diapause in *Daphnia* as a reaction to the presence of fish. *J. Plankton Res.* 18: 1407–1412.
- Rzóska, J., 1961. Observations on tropical rainpools and general remarks on temporary waters. *Hydrobiologia* 17: 265–286.
- Sadler, T. D. & K. Spitze, 1995. Genetic variation in subtropical populations of *Simocephalus* (Crustacea: Cladocera). *Heredity* 123: 1–7.
- Santella, L. & A. Ianora, 1990. Subitaneous and diapause eggs in Mediterranean populations of *Pontella mediterranea* (Copepoda: Calanoida): a morphological study. *Mar. Biol.* 105: 83–90.
- Santer, B. & W. Lampert, 1995. Summer diapause in cyclopoid copepods: Adaptive response to a food bottleneck? *J. anim. Ecol.* 64: 600–613.
- Seger, J. & H. J. Brockmann, 1987. What is bet-hedging? *Oxford Surveys in Evolutionary Biology* 4: 182–211.
- Simovich, M. A. & S. A. Hathaway, 1997. Diversified bet-hedging as a reproductive strategy of some ephemeral pool anostracans (Branchiopoda). *J. crust. Biol.* 17: 38–44.
- Slusarczyk, M., 1995. Predator-induced diapause in *Daphnia*. *Ecology* 76: 1008–1013.
- Stross, R. G., 1969. Photoperiod control of diapause in *Daphnia*. II. Induction of winter diapause in the arctic. *Biol. Bull.* 136: 264–273.
- Smyly, W. J. P., 1961. The life-cycle of the freshwater copepod *Cyclops leuckarti* Claus in Esthwaite Water. *J. anim. Ecol.* 30: 153–171.
- Smyly, W. J. P., 1967. A resting stage in *Cyclops dybowskii* Lande (Crustacea: Copepoda). *Naturalist* 92: 125–126.
- Smyly, W. J. P., 1977. A note on the resting egg of *Holopedium gibberum* Zaddach (Crustacea: Cladocera). *Microscopy (Lond.)* 33: 170–171.
- Templeton, A. R. & D. A. Levin, 1979. Evolutionary consequences of seed pools. *Am. Nat.* 114: 232–249.
- Thiéry, A., 1997. Horizontal distribution and abundance of cysts of several large branchiopods in temporary pool and ditch sediments. In Simovich, M. A., C. Sassaman & D. Belk (eds), *Studies on Large Branchiopod Biology and Conservation*. *Hydrobiologia* 359: 177–189.
- Thiéry, A., J. Brtek & Ch. Gasc, 1995. Cyst morphology of European branchiopods (Crustacea: Anostraca, Notostraca, Spinicaudata, Laevicaudata). *Bull. Mus. Natl. Hist. Nat.* 4 eme Ser. 17 (1–2): 107–139.
- Van Dooren, T. & L. Brendonck, 1998. The hatching pattern of *Branchiopodopsis wolffi* (Crustacea: Anostraca): phenotypic plasticity, additive genetic and maternal effects. In Brendonck L. L. de Meester & N. G. Hairston, Jr. (eds), *Evolutionary and Ecological Aspects of Crustacean Diapause*. *Arch. Hydrobiol.* 52: 219–227.
- Viitasalo, M. & T. Katajisto, 1994. Mesozooplankton resting eggs in the Baltic Sea: identification and vertical distribution in laminated and mixed sediments. *Mar. Biol.* 120: 455–465.
- Warner, R. R. & P. L. Chesson, 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* 125: 769–787.
- Weider, L. J., A. Hobæk, P. D. Hebert & T. J. Crease, 1999. Holarctic phylogeography of an asexual species complex – II. Allozymic variation and clonal structure in Arctic *Daphnia*. *Mol. Ecol.* 8: 1–13.
- Weider, L. J., W. Lampert, M. Wessels, J. K. Colbourne & P. Limburg, 1997. Long-term shifts in a microcrustacean egg bank associated with anthropogenic changes in the Lake Constance ecosystem. *Proc. R. Soc. London B.* 264: 1613–1618.
- Wiggins, G. B., R. J. Mackay & I. M. Smith, 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Arch. Hydrobiol.* 58: 97–206.
- Wolf, H. G. & G. R. Carvalho, 1989. Resting eggs of lake-*Daphnia*. II. In situ observations on the hatching of eggs and their contribution to population and community structure. *Freshwat. Biol.* 22: 471–478.
- Wurdak, E. S., J. J. Gilbert & R. Jagels, 1978. Fine structure of the resting eggs of the rotifers *Brachionus calyciflorus* and *Asplanchna sieboldi*. *Trans. am. Micr. Soc.* 97: 49–72.
- Wyngaard, G. A., 1988. Geographical variation in dormancy in a copepod: evidence from population crosses. *Hydrobiologia* 167/168: 367–374.