

## NOTES

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### A simple model relating habitat features to a diapause egg bank

*Abstract*—As a way to escape from adverse conditions, many zooplankton populations produce diapausing eggs that accumulate in the sediments and hatch when suitable environmental conditions are restored. While buried in the sediment, diapausing eggs may be affected by several processes (i.e., production, hatching, deterioration, and loss). We present a simple mathematical model for the dynamics of diapausing eggs in the sediment. We were mainly inspired by the model organism *Brachionus plicatilis*, a cyclical parthenogen rotifer, but the model is applicable to other zooplankters. Three diapausing egg categories are used as variables in our model: (1) healthy-looking eggs, assumed to represent the fraction of viable eggs; (2) deteriorated eggs, considered unviable; and (3) hatched eggs, shells remaining in the egg bank from past emergences. The model is used to relate the abundances of these egg categories to production, hatching, deterioration, and loss rates. Then, we propose how relationships between these variables are related to habitat features for temporary populations. Size of the egg bank, here considered as the summation of the three egg categories, is indicative of the quality conditions in the water column (i.e., high production of diapausing eggs). The ratio among deteriorated and healthy-looking eggs is indicative of deterioration rates in the sediment, and high ratios are expected when sediment adversity is high. Our analysis also indicates that the ratio among hatched and healthy-looking eggs is indicative of the hatching rate, which we hypothesize is positively related to both sediment adversity and water-column predictability.

Population zooplankton studies have been classically focused on the population dynamics in the water column. For a long time, limnologists have been aware of the importance of (1) the production of diapausing stages in the water column (Weismann 1876; Sars 1885; both cited by Hairston and Kearns 2002), which allow zooplankters to resist adverse conditions in which they cannot survive and reproduce, and (2) the colonization patterns of the water column from diapausing stages located in the pond and lake sediments, when favorable conditions resume. However, only in the last two decades have the processes affecting diapausing stages in the sediment received increasing attention (De Stasio 1989; Cáceres and Hairston 1998; Hairston and Kearns 2002). It is now recognized that diapausing eggs accumulate and form banks and that these banks have dynamic properties that are coupled to ecological and evolutionary processes occurring in the water column.

Diapausing egg banks influence ecological and evolutionary processes in several ways. First, they are de-

mographic and genetic reservoirs, providing inertia to populations, which in this way resist biotic and abiotic environmental changes. This inertia may have implications for population persistence, zooplankton community diversity, rates of adaptation, and population differentiation (Hairston 1998; Brendonck and De Meester 2003). Second, features exhibited by diapausing egg banks are expected to be at least partially shaped by evolutionary forces. Patterns of production and hatching of diapausing eggs are fitness components, and their evolution can be understood using life-history theory. Therefore, habitat features (e.g., temporality, adversity, predictability) are expected to be correlated with patterns of diapause (Cohen 1970; Cáceres and Tessier 2003, 2004).

In this article, we aim to clarify how demographic processes are related to observable features of the diapausing egg banks, namely, abundances of different categories of diapausing eggs or their remains. For this purpose, we construct a dynamic model on diapausing egg categories. In our model, we omit a number of factors that are likely to affect sediment banks. This simplification makes our model practical and relates it to observed properties of natural sediments. It is thus assumed that the omitted factors exert minor effects if compared with the processes taken into account by our model. By formally modeling the dynamics of diapausing egg banks, we make much more explicit the assumptions needed to interpret field data than when verbal arguments are used. After modeling the dynamics of the egg bank, we use the standard theory of life-history evolution in order to elaborate qualitative expectations for the diapausing egg-bank features in relation to habitat type. Our interest is to show that important insights into the egg-bank dynamics can be gained by studying the abundances of several egg categories and that these dynamics may be the adaptive response to the features of water-column and sediment conditions.

*A simple model for the dynamics of diapausing eggs in the sediment*—We will consider that three categories of diapausing eggs can be distinguished in the sediment: (1) healthy-looking eggs, regarded as viable (He); (2) deteriorated, but still identifiable eggs, regarded as unviable (D); and (3) hatched eggs (Ha). In the rotifer species *Brachionus*, this distinction is easy to observe under the stereomicroscope.

The dynamics of these three egg categories are controlled by the following processes: (1) egg production, which happens in the water column; (2) hatching; (3) degradation,

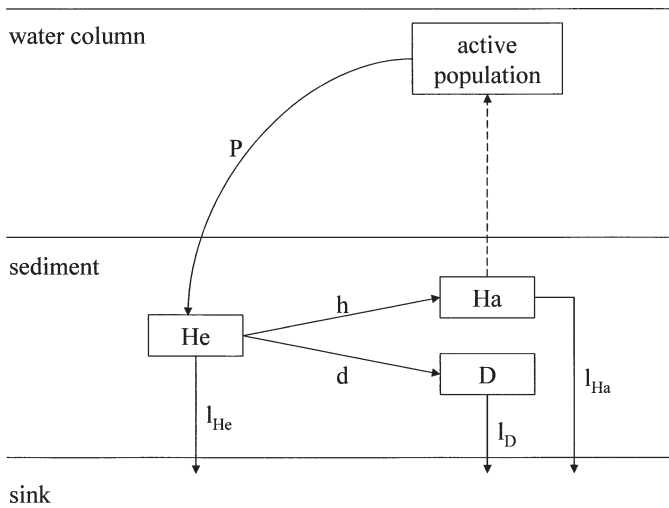


Fig. 1. Diagram of diapausing egg-bank dynamics. Arrows indicate fluxes between egg categories and water-column–sediment system compartments. The dashed arrow represents the emergence of neonates from diapausing eggs in the sediment. Two sediment compartments are considered. A single sediment layer is shown. However, rates can be taken as average values for a structured sediment. Variables: healthy-looking diapausing eggs [He], hatched eggs [Ha], deteriorated eggs [D]. Parameters: egg production rate [ $P$ ] ( $\text{time}^{-1}$ ), per capita hatching rate [ $h$ ], per capita deterioration rate [ $d$ ], per capita loss rate of healthy-looking eggs [ $l_{He}$ ], per capita loss rate of hatched eggs [ $l_{Ha}$ ], per capita loss rate of deteriorated eggs [ $l_D$ ].

assumed to transform viable eggs (i.e., healthy-looking eggs) to deteriorated eggs; and (4) loss, due to burial and mechanical fragmentation, initially assumed to be different for the different types of diapausing eggs.

The conceptual model relating these variables and processes in diapausing egg banks is depicted in Fig. 1. We propose the following equations to describe dynamics of the three egg categories:

$$\Delta \text{He} / \Delta t = P - h\text{He} - d\text{He} - l_{\text{He}}\text{He}$$

$$\Delta \text{Ha} / \Delta t = h\text{He} - l_{\text{Ha}}\text{Ha}$$

$$\Delta \text{D} / \Delta t = d\text{He} - l_{\text{D}}\text{D}$$

where  $P$  is the production rate of eggs in the water column,  $h$  is the per capita hatching rate,  $d$  is the per capita deterioration rate, and the  $l$  parameters are the per capita loss rates for each egg category.

Although we recognize that aging might affect deterioration and hatching and that the location of the eggs in different sediment layers might affect the rates, our model is not an explicit age-structured, depth-structured model. Our model is consistent with the assumption that we are describing a well-mixed upper sediment layer that is sufficiently thin so that hatching is unaffected by the depth within the sediment layer. Equilibrium is asymptotically achieved as we assume that production ( $P$ ) and per capita loss rates ( $l_{\text{He}}$ ,  $l_{\text{Ha}}$ ,  $l_{\text{D}}$ ) are constant rates; that is, total loss will increase with the number of eggs up to balancing egg production.

Despite the aforementioned, our model is also consistent with an ecological scenario where hatching, deterioration, and losses are depth- and egg age-dependent, and eggs move up and down in the sediment. If the rates describing all these processes are time independent, then the composition of the diapausing egg bank regarding (1) egg age, (2) egg depth, and (3) egg category would converge to a stable state, as is well-known from the theory of stage-structured populations (Caswell 2001). Moreover, if the input of eggs in the sediment ( $P$ ) is constant, the composition of the diapausing egg bank would converge to a stationary state. Therefore, an equilibrium is expected to be asymptotically achieved even in a complex structured bank. At that equilibrium, the rates in our model can be interpreted as the result of averaging age-dependent, depth-dependent rates. For instance,  $d = \sum_{ij} d_{ij} (\text{He}_{ij} / [\sum_{ij} \text{He}_{ij}])$ , where  $i$  designates egg age,  $j$  designates egg depth, and  $(\text{He}_{ij} / [\sum_{ij} \text{He}_{ij}])$  is the fraction of healthy-looking eggs of age  $i$  and depth  $j$ . This is analogous to the well-known result that a birth rate can be computed for an age-structured population by using the stable-age structure and the age-specific fecundity rates.

We use difference equations to describe variation because we assume that some of the processes involved act in periodic pulses (e.g., every year). This assumption implies that equilibrium values refer to periodic observations with the same frequency as that for pulses. Therefore, the observed values at equilibrium could be different according to the census timing in a population cycle.

Contrary to our assumption of parameter constancy, we admit that the parameters in our model are most likely to be noisy in the field. In fact, we will use the model to address ecological scenarios where  $P$  varies among years. Therefore, the parameters in our model can be conceptualized as average values. Because the sediment integrates a number of years, it is reasonable to assume that the observed abundances of egg categories are close to the parameters' average values.

The values at the equilibrium of the three egg categories are found by setting their variation rates to zero ( $\Delta \text{He} / \Delta t = \Delta \text{Ha} / \Delta t = \Delta \text{D} / \Delta t = 0$ ), which allows us to express each egg category abundance as related to processes rates:

$$\text{He} = P / (h + d + l_{\text{He}}),$$

$$\text{Ha} = (h / l_{\text{Ha}}) [P / (h + d + l_{\text{He}})],$$

$$\text{D} = (d / l_{\text{D}}) [P / (h + d + l_{\text{He}})].$$

In order to relate diapausing egg categories with processes, the following ratios and summations can be used for the values at equilibrium:

$$\text{Ha} / \text{He} = h / l_{\text{Ha}}$$

$$\text{D} / \text{He} = d / l_{\text{D}}$$

$$E = P [1 + (h / l_{\text{Ha}}) + (d / l_{\text{D}})] / (h + d + l_{\text{He}})$$

where  $E = \text{Ha} + \text{He} + \text{D}$ , at equilibrium.

These quite complex relationships largely simplify if we assume that loss rates are the same for the different egg

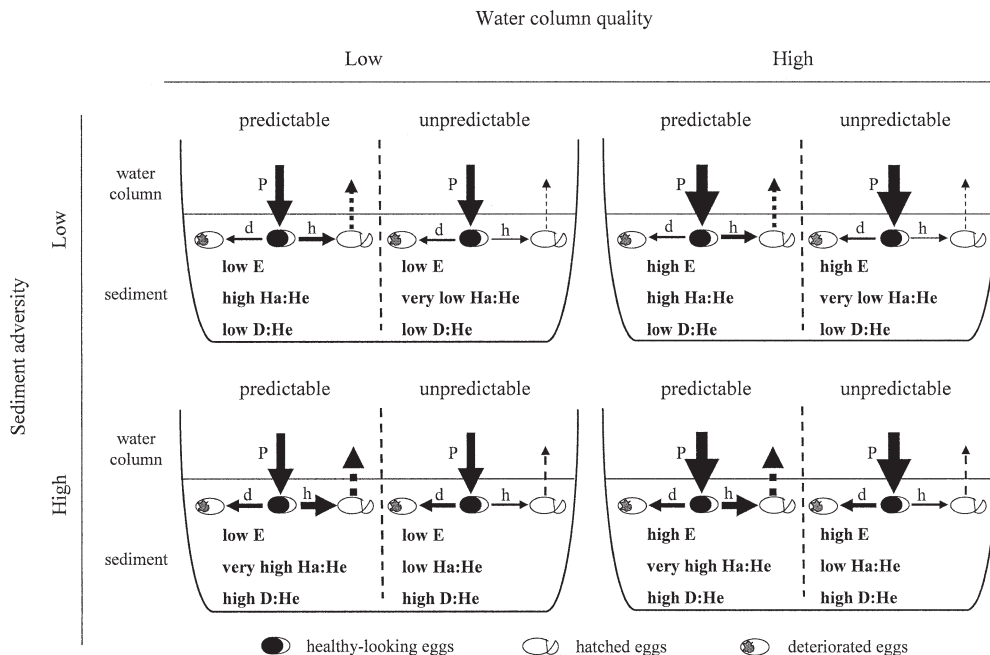


Fig. 2. Intensity of processes (indicated by arrows of different thicknesses (low, medium, high) taking place in diapausing egg banks as related to habitat features. (*P*: egg production rate (time<sup>-1</sup>); *h*: per capita hatching rate; *d*: per capita deterioration rate; *l*: per capita loss rate.) Dotted arrows represent the emergence of neonates from resting diapausing eggs in the sediment. Note that when sediment adversity and water-column predictability are expected to have opposing effects on hatching rate, water-column predictability is assumed to have dominating effects (see text). The expected composition of the egg bank, expressed as ratios among egg categories, is also included (Ha : He, ratio of hatched to healthy-looking diapausing eggs; D : He, ratio of deteriorated to healthy-looking diapausing eggs; *E*, abundance of all types of diapausing eggs [i.e., egg-bank size]). Pictures of diapausing egg types are inspired in the monogonont rotifer *Brachionus plicatilis*.

categories ( $l_{He} = l_{Ha} = l_D = l$ ), which results in

$$Ha/He = h/l$$

$$D/He = d/l$$

$$E = P/l$$

This assumption is valid if egg losses are due to physical processes regardless of egg category (i.e., deep burial, mechanical fragmentation). Predation, which probably occurs more frequently on healthy-looking diapausing eggs than on other egg categories, is not considered here as an egg-loss mechanism but as a deterioration process. Potential predators (i.e., nematodes and tardigrades) do not ingest the eggs but typically puncture cells to extract their contents (Marcus and Boero 1998), so the egg shells are expected to remain in the sediments and could be scored.

Our equations stress the well-known fact that abundance of any single egg category, for instance the abundance of healthy-looking eggs, is affected by several processes. So, inferring the intensity of a given process is difficult when based on the abundance of a single category of egg. Similarly, some ratios between egg categories, as, for instance, the proportion of healthy-looking eggs ( $He : E$ ), have a complex determination (from the equations:  $He/E =$

$l/[h + d + l]$ ) and are consequently less useful to draw conclusions.

Note that, because we modeled three variables and four processes, we cannot estimate the process rates from the egg densities. However, we can formulate expectations on the relative rates of processes in different localities by using the relative values of the egg abundances in those localities.

*Habitat features, diapause processes, and patterns of diapausing egg categories*—The process rates in the model proposed above will be the result of habitat features imposed on the animals and the evolutionary response of the animals to the habitat characteristics. Some of the rates might be either maximized or minimized by natural selection, while others will be optimized. We propose a comparative classification of the habitats (Fig. 2), which relates habitat features, process rates, and diapausing egg categories.

Very many zooplankton populations are temporary (i.e., ephemeral populations, seasonal populations, and populations that cannot persist in the water column during the entire annual cycle a significant proportion of years), even if they inhabit permanent ponds and lakes. Thus, diapausing egg production can be regarded as strongly correlated to local fitness, even if genetic and physiological differences

between eggs exist, and the timing of egg production within a growth season affects egg survival. Therefore, egg production rate ( $P$ ) is expected to be maximized by natural selection (Serra et al. 2005), and constrained only by the water-column quality, a concept that, as used here, incorporates both biotic and abiotic factors. The average number of diapausing eggs produced per growth season depends on (1) the within-growth-season average population density and (2) the time span of activity in the water column, when these are computed over a time scale so that random fluctuations are nullified. Therefore, as shown in Fig. 2, the higher the production of diapausing eggs, the better the water-column quality.

Deterioration rate of diapausing eggs in the sediment ( $d$ ) is expected to be minimized by natural selection. Resistance to deterioration might trade-off diapausing egg production (fewer, more resistant eggs vs. more, less resistant eggs), which we will overlook. Hence, deterioration rate would be assumed to be controlled by the sediment conditions, including biotic (e.g., noningestive predation of diapausing eggs; see above) and abiotic factors (e.g., desiccation, extreme temperatures, toxicity, etc.). In other words, deterioration rate is the demographic effect of sediment adversity.

Hatching rate ( $h$ ) is expected to be under optimizing selection, and water-column and sediment characteristics are involved as selective pressures working on this rate. On the one hand, diapausing eggs will tend to hatch when favorable conditions are likely to occur in the water column. Then, hatching is advantageous because the ultimate fate of diapausing eggs remaining in the sediment is deterioration. Therefore, there is a tendency toward high hatching rates as a way to exploit the productive part of the habitat (i.e., the water column). This tendency will be more intense if deterioration rates in the sediment are high. However, despite the costs of remaining in the sediment, hatching rates are expected to be low when cues for good conditions are not completely correlated with good conditions in the water column, so that hatching is risky (Cohen 1970). That is, low hatching rates will be promoted in habitats with high water-column unpredictability (Fig. 2). Unpredictability refers to the variance with respect to the type of growth season (i.e., growth season in which the probability of producing new diapausing eggs exceeds, or not, the chance of survival in the sediment).

*Discussion*—Abundance patterns in zooplankton diapausing egg banks can be effectively interpreted on the basis of verbal arguments or conceptual, nonformal models (De Stasio 1989; Cáceres 1998). However, new insights can be achieved by using explicit formal models. Here we provide a simple model that allows a clear interpretation of diapausing egg abundances when several ponds or lakes are compared. Our model clarifies the relationships between processes acting on diapausing stages and observable abundances of types of eggs or their remains. It identifies what quantities (abundances and abundance ratios) are relevant and under what conditions they are informative. The model makes explicit the assumptions needed to draw

our conclusions, while the assumptions in verbal models are usually much less explicit.

Our model stresses that it is difficult to point out what processes affect egg-bank features when only healthy-looking (or viable) egg abundances are quantified. Several authors, being aware of this difficulty, have measured directly some of the rates involved in diapausing egg dynamics (i.e., production and hatching rates; Wolf and Carvalho 1989; Cáceres 1998; Hairston et al. 2000). However, the direct estimation of the rates is technically difficult and might be biased by the measurement method. Our model shows how the relative importance of these rates can be assessed by estimating abundances of different categories of diapausing eggs in the sediment. The relevant question remaining is how feasible it is to determine the abundance of healthy-looking, hatched, and deteriorated eggs from different zooplankton taxa in sediment samples. These egg categories can be estimated from sediment samples of rotifer populations of the genus *Brachionus* (Arndt 1991; García-Roger et al. 2005) and *Hexarthra* (E. M. García-Roger, pers. observ.). Many other rotifer genuses (i.e., *Notholca*, *Filinia*, *Conochilus*) also open their diapausing eggs via opercula or suture lines (Gilbert 1974), which likely makes the identification of hatched eggs feasible. In the copepod *Hesperodiaptomus*, hatching of diapausing eggs results in two hemispherical shells, which have been used to infer the historical presence and hatching of copepods in paleolimnological studies (Parker et al. 1996; Knapp et al. 2001). Diapausing eggs in cladocerans of the genus *Daphnia* open through a less chitinous area that leaves two hemispherical shells after breaking (R. Ortells pers. comm.). This evidence, although scarce, is promising, given the little research effort allocated in this topic. On the other hand, it is noteworthy that our model clearly points out what are the consequences of being unable to quantify hatched eggs. Thus, by only using the abundance of healthy-looking and deteriorated eggs, the predictions on the processes affecting sediment egg-bank dynamics will be poor.

Our model provides a rationale for a habitat classification based on the demographic features of zooplankton populations. Such a classification focuses on the coupling between active and dormant subpopulations and takes into account both water-column and sediment properties. General theory of life-history evolution is often qualitatively assessed by testing the expectation on how trait values (e.g., reproductive allocation) should be ranked when different habitats are compared (Begon et al. 1996). The classical r-K theory is an example of such an analysis, where habitats are classified by their effects on body size, longevity, and reproduction. Here we propose a similar approach to test predictions about diapause. We identify three important habitat features (water-column quality, water-column predictability, and sediment adversity), as well as three major processes (diapausing egg production, egg deterioration, and hatching). While our model is quantitative, we expect it to be used for qualitative comparisons. As in other life-history analyses, parameters in our model are related to fitness, and so educated conjectures on their evolution are possible. While diapausing egg production and deterioration are quite



directly associated with habitat features, at least in temporary populations, hatching rate is expected to be the result of the balance between the quality of the sediment as a refuge and the uncertainty associated with hatching (Cohen 1966, 1970).

Our classification provides clear and testable predictions when the composition of the diapausing egg bank of different habitats are compared (Fig. 2). Thus, we can infer the processes dominating egg-bank dynamics by simply comparing abundances of total diapausing eggs and ratios among diapausing egg types. For instance, high numbers of diapausing eggs are indicative of high water-column quality (e.g., long-lasting conditions for population growth, high levels of resources, low predation, etc.). Conditions in the sediment can be also inferred from the composition of the diapausing egg bank. For instance, a higher  $D : He$  ratio is expected to be found in habitats where sediment adversity is higher. The monogonont rotifer *Brachionus plicatilis* is, as far as we know, the only case where the abundance of deteriorated eggs has been estimated in several habitats (García-Roger et al. unpubl.). It has been observed that the sediments of a wide set of shallow and brackish ponds from eastern Spain contain high percentages of deteriorated to total diapausing eggs ( $85.7\% \pm 8.7\%$ ). This finding points out the fact that the sediment refuge in these kinds of ponds is not as safe as previously thought (García-Roger et al. unpubl.), and suggests that sediment adversity can work as a selective pressure on diapause patterns, whose effects cannot be neglected.

Water-column predictability is related to the ratio  $Ha : He$  rather than to the density of a single type of egg. If water-column predictability is low, as, for example, if an ephemeral pond is compared with a permanent pond, a lower  $Ha : He$  ratio should be expected (Cohen 1966; Ellner et al. 1998). According to our analysis, the  $Ha : He$  ratio is also affected by sediment conditions that would reinforce the tendency of diapausing eggs to hatch, if the sediment is adverse, or to remain in the sediment refuge, if adversity is low. When water-column predictability and sediment adversity have opposing expected effects on hatching rates, we expect that water-column predictability will have a dominant effect. We conclude this because, if, on average, the water column is a worse habitat than the sediment (where diapausing egg survival is lower than 1), the population cannot survive at this location. Gilbert and Schröder (2004) suggested that hatching rates of diapausing eggs are expected to be higher in shallow than in deep lakes. The reason would be that conditions in deep-lake sediment (low temperature, anoxia, and darkness) favor preservation and inhibit hatching. As a result, more healthy-looking eggs would be found in deep rather than shallow lakes. Although sediment conditions could impose constraints on the optimization of hatching rates (e.g., absence of hatching cues, physicochemical conditions preventing embryo development), the classification arising from our model suggests an alternative explanation for such observation based on a larger diapausing egg production and a lower sediment adversity.

In our model, it is assumed that all healthy-looking diapausing eggs are viable. However, some healthy-looking

eggs might lose their viability without any detectable signs. There is evidence suggesting that older eggs lose their ability to respond to hatching cues even though they still look healthy (Cousyn and De Meester 1998; Garcia-Roger et al. unpubl.). If so, the ratios  $D : He$  and  $Ha : He$  would respectively overestimate the rate ratios  $d : l$  and  $h : l$  (see equations). Even if this bias affects the data, the comparative habitat scheme depicted in Fig. 2 should still be useful if the correlation between healthy-looking eggs and actually viable eggs is not habitat dependent.

A more serious difficulty to interpret egg-bank features arises when sedimentation rate varies significantly between habitats. For instance, if the same depths are explored in two habitats with different sedimentation rates, then the loss rate, as implemented in the model, would be higher in the habitat with higher sedimentation rate, because eggs are quickly buried into deeper, unexplored layers. Because differences in loss rate are neglected in the Fig. 2 scheme, the actual production (water-column quality) would be underestimated by  $E$ . It should be noted that deterioration ( $D : He$ ) and hatching rates ( $Ha : He$ ) would also, respectively, underestimate the rate ratios  $d : l$  and  $h : l$ . The complication arises because high sedimentation rates should select for high hatching rates, as it occurs when sediment adversity is high. This complication may make restricting the analysis to habitats with similar sedimentation rates advisable. Alternatively, the measurement of high sedimentation rate in a habitat, or indirect evidence for this (e.g., high population density in the water column associated with low total egg abundance in the sediment) would suggest that diapausing egg production, deterioration, and hatching rates have been underestimated. Thus, the proper prediction would be that this habitat has a higher water-column quality and a higher sediment adversity than that expected from the observed egg abundances and ratios.

Our model has several simplifying assumptions needed in order to interpret it. However, by making assumptions explicit, the model makes the detection of anomalies in the habitat classification predictions easy, and thus provides alternative explanations for observed patterns, which is, in turn, a virtue of this model. Finally, we stress that our habitat classification can also be used to compare populations of different species inhabiting the same habitat. In such a case, fewer assumptions are required because all populations share the same sediment conditions.

We propose that the abundances of healthy-looking, hatched, and deteriorated diapausing eggs in the sediment are the result of a coupling between the sediment and the water column. Egg-bank phenology in temporary habitats is the result of selective forces operating in both the water column and the sediment. Therefore, the abundance of the different types of diapausing eggs in the sediment provides insights on those selective forces.

Eduardo M. García-Roger<sup>1</sup>

María José Carmona

Manuel Serra

<sup>1</sup> Corresponding author (e-mail: eduardo.garcia@uv.es).

Institut Cavanilles de Biodiversitat i Biologia Evolutiva  
 Universitat de València, A.O. 22085  
 València 46071, Spain

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