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Mechanistic and evolutionary aspects of light-induced dormancy termination in a temporary pond crustacean

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Abstract. Most freshwater zooplankton species produce dormant eggs or other long-lived resistant life stages to bridge periods that are unsuitable for growth and reproduction. One of the principal cues that determine activation of these dormant stages is light exposure. Contrary to the analogous process of seed germination in plants, relatively little is known about the mechanism of light activation and its potential adaptive value in freshwater zooplankton. We made use of a temporary pool model to investigate the hatching response of resting eggs of the fairy shrimp *Branchipodopsis wolfi* to a specific set of selected light regimes and to evaluate the importance of egg pigmentation for mediating susceptibility to light cues. Our results suggest the presence of a critical light threshold for activation leading to maximal hatching. Moreover, the process of light activation does not appear to be purely cumulative because light administered in a single continuous pulse resulted in much higher hatching than the same amount of light administered in several 2-h pulses. Last, darkly pigmented eggs were less sensitive than lightly pigmented eggs to light exposure, resulting in delayed hatching of darker eggs during an experimental inundation. This result indicates that natural variation in egg pigmentation could be a risk-spreading mechanism that trades off the risks of mortality caused by kin competition during the nutrient-limited conditions that typically prevail early during inundations on one hand and the risk of mortality from premature pond drying on the other hand. Overall, our results indicate that light-energy activation thresholds and variation in pigmentation of the eggshell can be important traits that may contribute to variation in hatching phenology among zooplankton lineages.

Key words: Dormancy, fairy shrimps, light, hatching, resting eggs, risk spreading.

Many freshwater zooplankton groups produce long-lived resting stages that accumulate in pond and lake sediments to form a dormant propagule bank (Brendonck and De Meester 2003). Such a reserve of species and genotypes has important advantages because it allows populations to persist through periods that are unsuitable for growth and reproduction, including episodes of intense fish predation in lakes (Hairston et al. 1983) or dry periods characteristic of temporary aquatic habitats (Gyllström and Hansson 2004). For this mechanism to be effective, the reactivation of propagules and subsequent entry of hatchlings into the water column must be carefully timed. Mortality associated with hatching under bad conditions presumably results in strong selection for mechanisms enabling resting stages to assess the suitability of the outside environment for growth and reproduction (Cáceres 1997). Zooplankton resting stages are known to respond to a variety of environmental cues, such as water presence, temperature, conductivity (Brendonck 1996), and hormones (Beladjal et al. 2007), that reflect the quality of their environment. For instance, in temporary ponds, low conductivity is used as a hatching cue because it is a reliable indicator of larger water volumes that permit longer inundations and, thus, more time for reproduction (Brendonck et al. 1998, Vanschoenwinkel et al. 2010a).

Light is thought to play a particularly essential role in metabolic activation and dormancy termination in both plants and animals. In freshwater crustacean zooplankton, light exposure was identified as one of the prerequisites to initiate hatching in representatives of all major branchiopod crustacean groups, including water fleas (Davison 1969, De Meester and De Jager 1993), clam shrimps (Belk 1972), tadpole shrimps (Takahashi 1977, Horiguchi et al. 2009,

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Kashiyama et al. 2010), and fairy shrimps (Van der Linden et al. 1985, Mitchell 1990, Murugan and Dumont 1995). Branchiopod embryos are activated by a broad spectrum of wavelengths, from ultraviolet (UV; 395 nm) to red (660 nm) (Kashiyama et al. 2010), a finding that suggests the involvement of different optical pigments in photoreception. Thus, light energy is likely to be more important for activation than the wavelength of the light. Indications for specific light-energy thresholds to break dormancy were found in the brine shrimp *Artemia franciscana* Kellog 1906 (Van der Linden et al. 1985) and the fairy shrimp *Thamnocephalus platyurus* Packard 1877 (Murugan and Dumont 1995). The length and sequence of light and dark phases (photoregime) also is likely to be an important determinant of hatching (Vandekerkhove et al. 2005). Earlier work clearly indicates that light plays a crucial role in dormancy termination, but the mechanism and the potential adaptive relevance of metabolic reactivation by light remain largely unexplored (Vanvlasselaer and De Meester 2010). Davison and Stross (1986) found indications for the existence of light-sensitive molecules in branchiopod resting eggs that function in a manner similar to plant phytochromes. The pigment content of the egg shell is thought to influence the sensitivity and the response time of resting eggs to light exposure (Van der Linden et al. 1985) because light must penetrate the protective eggshell to influence the photoreceptive molecules inside the embryo (Van der Linden et al. 1987). Van der Linden et al. (1986) showed that decapsulated brine shrimp eggs responded to a broader array of wavelengths than did intact eggs, thereby demonstrating the presence of light-absorbing pigments in the eggshell. The shell of fairy shrimp eggs, which is of maternal origin, typically contains substantial amounts of pigments, among which haematin is one of the most prevalent (Van der Linden et al. 1986). Thus, analogous to a pair of sunglasses, the degree of eggshell pigmentation is likely to modulate the transmission of light and affect hatching of the embryo.

The evolutionary relevance of responses to light cues is mentioned by different authors (Murugan and Dumont 1995, Cáceres et al. 2007, Kashiyama et al. 2010). However, experimental evidence is scarce, and relatively little is known about how variation in response to light cues contributes to population persistence. We investigated both mechanistic and evolutionary aspects of light-induced dormancy termination in zooplankton resting eggs. As a model organism, we used the fairy shrimp *Branchipodopsis wolfi* Daday 1910, which inhabits clear temporary rock pool habitats in South Africa. By exposing eggs to a carefully selected set of different light regimes, we assessed whether hatching of *B. wolfi* eggs is characterized by a distinct light-energy (= light intensity × exposure time) threshold, corresponding to an all-or-nothing effect, as observed in plant seeds and other invertebrates. By alternating light pulses with periods of darkness, we tested the potential reversibility of light activation, and we discuss the adaptive value of such a mechanism. Last, we assessed whether variation in eggshell pigmentation is reflected in differential hatching behavior, and we discuss the potential adaptive value of the observed patterns in the light of competition avoidance and risk-spreading strategies that might contribute to the survival of fairy shrimps in the variable temporary pool environment.

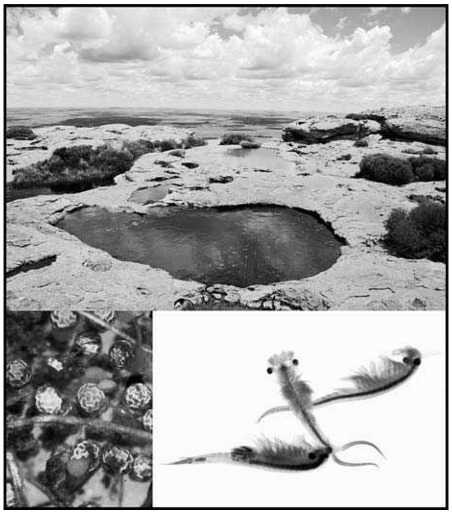

FIG. 1. The rock pool study system along with the fairy shrimp *Branchipodopsis wolfi* and a batch of resting eggs with typical variation in pigmentation (photographs by B. Vanschoenwinkel).

Methods

Study site

We used a population that originated from a temporary rock pool that is part of a pool cluster on the South African Korannaberg mountain (lat 28°51′13″S, long 27°13′51″E; Fig. 1) and has been the subject of intensive recent study (Vanschoenwinkel et al. 2008, 2009, 2010a, b). Variation in environmental conditions, including physicochemical, hydrological, and biotic conditions, in these pools is well known. These pools are generally oligotrophic, clear, and contain variable amounts of sediment ranging from a thin layer of ~2 mm up to sediment banks of >5 cm (Vanschoenwinkel 2009). The timing, frequency, and duration of filling events vary greatly among pools and years. The proportion of these inundations that are long enough to allow reproduction of *B. wolfi* can be quantified with simulations generated by a hydrological model based on climate data and field calibrations (Vanschoenwinkel et al. 2009). Under optimal growth conditions, inundations ≥7 d typically result in successful reproduction (Vanschoenwinkel et al. 2010a).

Resting egg production

We bred the study population for 2 generations in the laboratory to remove unwanted parental effects before we isolated eggs for experiments. We started the laboratory population by dividing 200 g of dried, field-collected rock-pool sediment containing *B. wolfi* resting eggs among three 2-L plastic containers. We inundated these containers with Environmental Protection Agency (EPA) medium with a conductivity of 50 µS/cm (distilled water with 0.00033 mol/L $NaHCO_3$, 0.000098 mol/L $CaSO_4 \cdot 2H_2O$, 0.00014 mol/L $MgSO_4$, 0.000015 mol/L KCl; Anonymous 1985) and subsequently incubated them under a 12-h light:dark regime at a temperature of 20°C (Vanschoenwinkel 2009). We transferred hatched individuals to clean 2-L plastic containers at densities of 30 animals/2 L under the same optimal conditions and fed them *Scenedesmus obliquus* daily ad libitum (10^6 cells/mL). Following sexual maturation of most of the population (at day 10), we harvested resting eggs on a daily basis and stored them in darkness in a drying oven at 20°C for 2 mo. We repeated this protocol for 2 subsequent generations. We kept the total size of the parental populations contributing to the next generations >90 individuals at any time with an equal proportion of males and females to avoid inbreeding.

Experimental design

In the 1st experiment, we used a variety of light and inundation regimes. First, we investigated the possibility that eggs hatch at night by incubating eggs under total and continuous darkness (CD). We also evaluated hatching of eggs that experienced light only after 4 (4D) or 8 h (8D) of inundation in darkness to assess whether hydration and light activation had to be experienced simultaneously. Second, we investigated whether resting eggs have a critical light-exposure threshold by subjecting resting eggs to 4 (4L) or 8 h (8L) of light followed by darkness. We compared hatching frequencies in 4L and 8L with hatching frequencies in CD and in high- and low-intensity continuous light (CL and LL, respectively). Third, we tested the effect of sequences of 2 (L2) or 4 (L4) 2-h light pulses alternated with 2-h dark periods. We compared hatching frequencies in L2 and L4 with the presumed maximal response in CL to assess whether the effects of light exposure on diapause termination are reversible until a certain light-energy threshold is reached. We exposed all treatments that received light to high-intensity white light (full spectrum, 640 cd, 4000 lx, lamp type: Osram L 8W/640; Osram, Rotterdam, The Netherlands) during incubation except the LL treatment (full spectrum, 288 cd, 1800 lx, lamp type: Osram L 8W/640). We attained the desired LL intensity by partly wrapping the lamps with aluminum foil.

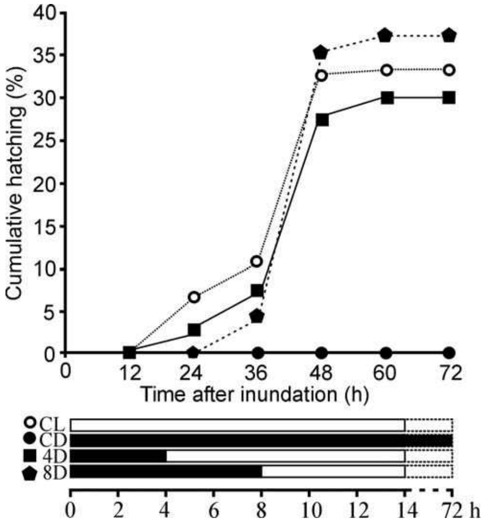

FIG. 2. Cumulative hatching of dormant fairy shrimp eggs exposed to continuous light (CL), continuous darkness (CD), 4 h of darkness followed by continuous light (4D), or 8 h of darkness followed by continuous light (8D) in a 72-h experiment.

In a 2nd experiment, we investigated whether the observed differences in eggshell pigmentation in *B. wolfi* resting eggs led to differences in timing of hatching by incubating eggs in CL. We compared the pigmentation of eggshells among eggs that hatched at different times during the inundation.

Egg hatching procedure

In the 1st experiment, we incubated a total of 1296 *B. wolfi* resting eggs under 9 different light regimes (see *Experimental design* above; Figs 2, 3). To avoid interference by stray light (i.e., unwanted light exposure during manipulation), we evaluated hatching and manipulated eggs under red light (700 nm, 8 cd, 2 lx). We exposed 144 eggs to each treatment. We used a total of six 24-well plates and transferred every egg individually to a well. It was impossible to impose

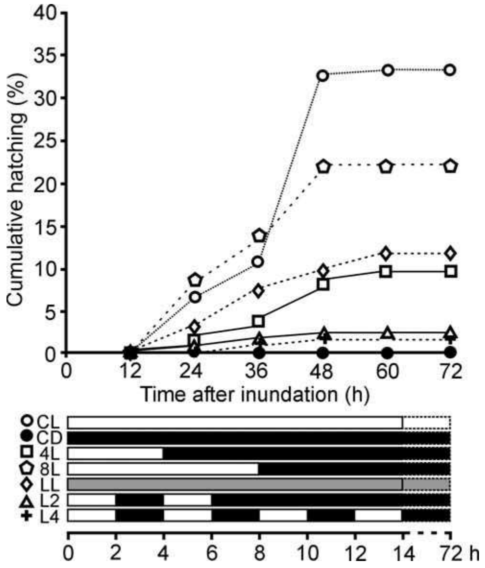

FIG. 3. Cumulative hatching of dormant fairy shrimp eggs exposed to continuous light (CL), continuous darkness (CD), 4 h of light followed by continuous darkness (4L), or 8 h of light followed by continuous darkness (8D), continuous low light intensity (LL), or light provided in two 2-h (L2) or four 2-h (L4) pulses alternating with 2-h periods of darkness and followed by continuous darkness in a 72-h experiment.

different light regimes on eggs in the same plate, so treatments could not be randomized within plates. We accounted for the influence of plate identity by including it as a random blocking factor in our analyses. We filled wells with 2 mL of EPA medium with a conductivity of 50 μS/cm. We positioned plates randomly in a temperature-controlled incubator at 20°C for 72 h. We kept all plates on the same shelf to avoid small differences in temperature and randomized the position of plates every 6 h. We evaluated hatching at 12-h intervals until no additional hatching was observed in any treatment for ≥12 h.

In the 2nd experiment, we incubated 264 *B. wolfi* resting eggs isolated from a 2nd generation laboratory egg stock under the optimal hatching conditions as for experiment 1 and exposed them continuously to white light (full spectrum, 640 cd, 4000 lx). We evaluated hatching every 12 h. We removed eggshells of hatched individuals immediately and mounted them on a slide in a drop of distilled water under a cover glass. We photographed each eggshell 4 times under constant background illumination on an Olympus BX50 microscope (20 × 10× magnification) fitted with an Olympus DP50 photo camera (Olympus, Hamburg, Germany). We assessed the degree of pigmentation by measuring the average gray-scale value in 8 selected polygons covering ~40% of the eggshell using Cell^P software (version 3.3, build 2108; Olympus).

Statistical analyses

We ran all analyses in R (version 2.12.2; R Core Development Team, Vienna, Austria). We tested for differences in hatching (0/1 response) among light-regime treatments after 24 and 60 h with Generalized Linear Models (GLM) with binomial error distributions and a *logit* link function. The experiment lasted 72 h, but we assessed differences in total cumulative hatching after 60 h because no additional hatching was observed between 60 and 72 h in any treatment. We used a sequential Bonferroni correction (Holm 1979) to correct *p*-values for pairwise contrasts. We tested for differences in pigmentation of eggs that hatched 24, 36, 48, and 60 h after inundation with a 1-way analysis of variance (ANOVA) and Tukey post hoc tests.

Results

No hatching was observed in the absence of light. A maximal hatching frequency of ~35% during a single inundation was reached in the CL, 4D, and 8D treatments (Fig. 2, Table 1). After 24 h, hatching was significantly higher in the CL (7%) than in the 8D (0%) treatment. However, this difference disappeared over the subsequent 36 h of incubation. Hatching was initially delayed in the 8D treatment, but a similar fraction of eggs hatched in 8D and in CL and 4D after 60 h (34% in CL, 31% in 4D, 38% in 8D; Fig. 2). After 60 h, hatching was considerably lower in the 4L (9%) than in the 8L (21%) and CL treatments. After 60 h, hatching was significantly lower in the LL (11%) than in the CL and 8L treatments (Fig. 3).

The L2 and L4 treatments were characterized by very low cumulative hatching frequencies of ~2 to 3% (Fig. 3). Hatching frequencies were significantly lower in these treatments than in treatments in which eggs were exposed to the same amount of light energy in 1 continuous pulse (4L and 8L treatments; Fig. 3).

Pigmentation of eggshells was significantly lower for eggs that hatched after 24 h (n = 15) of inundation than eggs that hatched after 36 (n = 37), 48 (n = 16), or 60 h (n = 18) (ANOVA, F_3= 73.56, $p < 0.01$; Tukey post hoc, $p < 0.001$; Fig. 4).

Discussion

We investigated the light-activation process of zooplankton resting eggs using a rock-pool fairy shrimp as a model. We showed that activation of *B. wolfi* eggs entails a relatively simple mechanism

TABLE 1. *p*-values of pairwise comparisons of hatching frequency among different treatments at 24 h (above diagonal) and 60 h (below diagonal) after inundation. See Figs 2, 3 for treatment abbreviations. Bold indicates significant *p*-values.

Light treatment	CL	CD	4L	8L	4D	8D	L2	L4	LL
CL	–	**0.0002**	0.0139	0.6571	0.0950	**0.0002**	0.0029	**0.0002**	0.0950
CD	**<0.0001**	–	0.0951	**<0.0001**	0.0179	1.00000	**<0.0001**	1	0.0179
4L	**<0.0001**	**<0.0001**	–	0.0040	0.4049	0.0951	0.5579	0.0950	0.4049
8L	0.0166	**<0.0001**	**0.0045**	–	0.0355	**<0.0001**	**0.0007**	**<0.0001**	0.0355
4D	0.6132	**<0.0001**	**<0.0001**	0.0584	–	0.0179	0.1616	0.0179	1
8D	0.3893	**<0.0001**	**<0.0001**	**0.0012**	0.1720	–	0.2384	1	0.0179
L2	**<0.0001**	0.0407	0.0077	**<0.0001**	**<0.0001**	**<0.0001**	–	0.2384	0.1616
L4	**<0.0001**	0.2384	0.0004	**<0.0001**	**<0.0001**	**<0.0001**	0.3031	–	0.0179
LL	**<0.0001**	**<0.0001**	0.5566	0.0234	**<0.0001**	**<0.0001**	**0.0013**	**<0.0001**	–

involving a light-energy threshold. Our results also illustrated the potential adaptive value of light activation and the possible role of variation in eggshell pigmentation as a risk-spreading strategy.

The adaptive origin of developmental (re-)activation by light

Like other branchiopod crustacean eggs (Brendonck and De Meester 2003) and seeds of certain plants (Milberg et al. 2000), *B. wolfi* eggs do not hatch in darkness. However, once exposed to light, eggs inundated for 4 (4D) or 8 (8D) h in the dark had a similar cumulative hatching fraction as eggs inundated in CL, a result illustrating that hydration of resting eggs can precede light activation without loss of hatching capacity. Light could be a necessary prerequisite for hatching for purely biochemical reasons if it serves as a crucial trigger in the biochemical pathway that initiates hatching (Vanvlasselaer and De Meester 2010). However, observations in plant species with seeds that readily germinate in the dark suggest other possible explanations. Unlike the seedlings of many plants (Milberg et al. 2000), zooplankton hatchlings are very fragile and probably are too weak to emerge if they hatch while buried under sediment. Therefore, responding to light cues is probably adaptive. The temporal advantage that could be gained by hatching at night probably does not outweigh the costs of hatching while covered by sediment. Even under optimal (CL) hatching conditions only ~35% of the *B. wolfi* resting eggs in our experiment hatched. This feature is typical of fairy shrimp eggs and presumably evolved as part of an evolutionary risk-spreading strategy buffering against the unpredictable nature of the inundations of their habitats (bet hedging; Simovich and Hathaway 1997). Staggered recruitment from the egg bank, with only a fraction of eggs hatching during a single inundation, is likely to promote population continuity in the variable temporary pool habitat in which many inundations are too short to allow reproduction (Van Dooren and Brendonck 1998, Philippi et al. 2001).

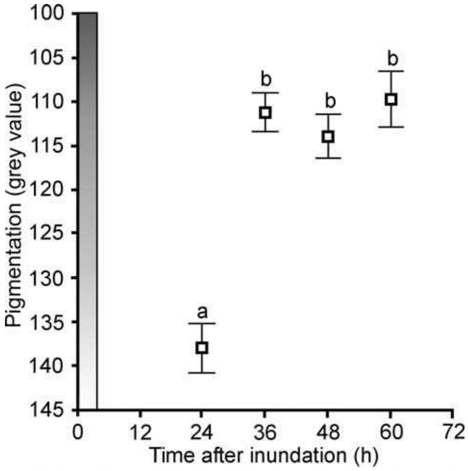

FIG. 4. Mean (±1 SE) degree of eggshell pigmentation of eggs that hatched after 24, 36, 48, or 60 h of continuous exposure to light after inundation. Points with the same letter are not significantly different.

Indications for an adaptive light-energy threshold

We found evidence that a critical amount of light energy had to be administered in a single dose to achieve maximal hatching. When we applied the same light dose as multiple pulses alternated by darkness, hatching was lower, a result suggesting that light activation was, to some extent, reversible in the dark. Such a mechanism could be analogous to phytochrome functioning in plant seeds (Chory et al. 1996). Light-energy thresholds probably evolved to prevent eggs from hatching when they are covered by sediment or obstacles. Results of other studies indicate these thresholds could be lower in turbid habitats where less light penetrates. Compared to *B. wolfi*, which inhabits clear rock pools (Vanschoenwinkel et al. 2009), light energy thresholds appear to be much lower in the turbid-water species *T. platyurus* (Murugan and Dumont 1995). The same may be true for species with resting banks in deep lakes where little light can penetrate, but this possibility remains to be investigated.

The observation that maximal hatching under CL was reached after an exposure of ~8 h, whereas similar hatching rates were never obtained in LL (288 cd), regardless of the exposure time, further suggests that light activation is not an entirely cumulative process. Only a fraction of eggs seemed to respond to LL, and others never reacted, regardless of the exposure time. Therefore, hatching in *B. wolfi* is probably regulated by both light energy and intensity thresholds that could be genetically determined. We think it likely that variation in eggshell pigmentation modulates the amount of light experienced by an embryo, regulating its responsiveness to light, and consequently, its hatching behavior.

The role of pigmentation

The shell of crustacean zooplankton resting eggs contains the light-absorbing haemopigment, haematin (Van der Linden et al. 1986, 1987). Some authors have hypothesized that this pigment protects the embryo against harmful mutagenic UV radiation (Hobaek and Wolf 1991, Dumont and Negrea 2002).

We showed that, within a batch of newly produced eggs, variation in pigmentation results in differences in the timing of hatching within a single inundation. Lightly pigmented eggs hatch earlier than more darkly pigmented ones. Variation in pigmentation could be an innate trait but also could result from environmental influences. For instance, in the brine shrimp *Artemia*, oxidation leads to bleaching of the eggshells over time (Van der Linden et al. 1986), which ultimately may result in eggs with different pigment intensities in the egg bank. Declining pigment concentrations over time would promote light sensitivity and could explain why resting eggs of several branchiopod species display higher hatching frequencies with increasing age (Brendonck 1996, Abatzopoulos et al. 2002).

Differential pigmentation exists within populations and within single broods (TP, personal observation). Good reasons exist to think that variation in egg pigmentation could be adaptive. First, early hatching can be advantageous when inundations are short because it helps ensure that individuals can reproduce before the habitat dries. Second, different fairy shrimp larval stages (nauplius, metanauplius) feed on different resources (Eriksen and Belk 1999, Abatzopoulos et al. 2002, Dumont and Negrea 2002), so hatching later could reduce kin competition (Allan 1976). Moreover, given that inundations are long enough, gradually increasing algal concentrations during the first days after inundation (Williams 2006) may ensure lower larval mortality (Belk 1977). Thus, hatching early carries both advantages and costs that probably depend on the relative frequency of both strategies in the population (cf. evolutionary game theory; Smith 1973). As such, both early and late hatching strategies could be maintained as a genetic polymorphism within populations when temporal variation in the length of inundations prevents fixation or when maternal genotypes produce phenotypically different eggs as part of an evolutionary bet-hedging strategy (Philippi and Seger 1989).

General implications

Besides the general implications for diapause ecology of fairy shrimps, our results might shed some light on similar processes occurring in other plankton species in larger, more complex systems, such as ponds and lakes. For example, the typical hatching peak of zooplankton in permanent lakes or estuaries in response to increasing day length (Vandekerkhove et al. 2005) could result from a similar light-energy threshold. Our results also generate novel testable predictions. For instance, several zooplankton species have floating eggs (Brendonck and Riddoch 2000, Cáceres et al. 2007), and floating eggs are likely to be less responsive to light cues than eggs deposited in the sediment of deep lakes where little light can permeate. We also found good indications that variation in pigmentation could result in short-term within-inundation risk spreading, but its potential role in spreading hatching over different inundations remains unknown. Therefore, tests are needed to assess whether degradation of pigments over time (Van der Linden et al. 1986) may be an adaptive mechanism that prevents resting eggs from becoming locked in diapause. Last, given the similarities in observed responses to light activation in both crustacean resting eggs and plant seeds, parallel patterns in these taxonomically distant groups might possibly reflect an old evolutionary mechanism tapping the same biochemical pathways, but this hypothesis also remains to be confirmed.

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