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An empirical test of the impact of drying events and physical disturbance on wind erosion of zooplankton egg banks in temporary ponds

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Abstract Most temporary pond zooplankton species produce drought-resistant eggs that accumulate in the sediment and form an egg bank. When a pond dries and the egg bank is exposed, wind erodes eggs and wind action has been suggested as an important determinant of population demographics. While field observations suggest that egg bank erosion may be highest shortly after pond drying and physical disturbance of the sediment crust, this remains to be tested empirically. We performed a laboratory wind tunnel experiment to assess the effects of wind speed and sediment characteristics on egg pickup rates over time in a controlled environment. We used sediment samples in which an egg bank of the fairy shrimp *Branchipodopsis wolfi* was embedded and compared the number of eggs that blew away from dry, drying and disturbed egg banks as a function of time. Few eggs were picked up when the egg bank was dry prior to exposure, even at winds of 70 km h^{-1}. Most eggs were eroded when the egg bank was exposed to wind before it dried out, after the last water evaporated. Likewise, physical disturbance resulted in strong erosion fluxes. Overall, our results suggest that the state of the egg bank may be more important for egg bank erosion rates than the prevailing wind speed or the wind exposure time. Also, our findings are worrying in the context of climate change since they imply that predicted increases in drying events and reduced inundation lengths may compromise egg bank persistence in temporary ponds.

Keywords Wetlands · Dispersal · Large branchiopods · Dormancy · Benthic pelagic coupling · Climate change

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Introduction

Temporary freshwater ponds are often inhabited by diverse assemblages of zooplankton. These aquatic organisms typically bridge the dry phases of their habitat by producing drought-resistant life stages (Williams 2006), hereafter referred to as 'eggs.' Following deposition, zooplankton eggs can enter an energetically favorable state of developmental arrest, called dormancy, that can be maintained for at least several years if needed (Hairston et al. 1995). Upon the return of water and suitable conditions for growth and reproduction, eggs can resume development and rapidly initiate an active population. Long-term survival of temporary pond zooplankton populations hinges on the maintenance of a viable egg bank (Pinceel et al. 2016a). Still, resting eggs stored in pond sediment face many threats including predators, energy depletion and erosion by flowing water and wind (Brendonck and De Meester 2003). In particular, erosion of the sediment from pond basins by wind action can rapidly reduce egg bank sizes, as has been observed during field surveys (Graham and Wirth 2008). Although a number of hypotheses have been formulated with regard to potential mediators of egg bank erosion (Vanschoenwinkel et al. 2009; Pinceel et al. 2016b), supporting experimental evidence for these is largely deficient. Field interceptions of eggs can help to reconstruct dispersal fluxes in nature (Graham and Wirth 2008; Vanschoenwinkel et al. 2008; Rivas et al. 2019) but provide little information on the underlying factors that determine whether eggs are picked up or not. In this regard, experimental wind tunnels provide important advantages including the ability to incrementally increase wind speeds to quantify the speed at which propagules are picked up from different types of substrates (Pinceel et al. 2016b).

Typically, zooplankton egg banks in temporary ponds contain large numbers of eggs with densities ranging in the millions per square meter in the upper sediment layers for some species (Brendonck et al. 2017). After deposition, the egg bank needs to be maintained, especially during dry phases when the protecting water layer is removed and the egg bank is exposed to wind (Pietrzak and Slusarczyk 2006; Vanschoenwinkel et al. 2010). Erosion of pond sediment depends on physical properties of the sediment including cohesion of particles, adhesion to the rocky pond basin of particles and particle weight (Gillette 1978). In addition, also the formation of an organic crust during pond drying and the presence of root systems and tubers of (semi)-aquatic vegetation have been suggested to stabilize egg banks (Graham and Wirth 2008; Vanschoenwinkel et al. 2010). It has been repeatedly suggested that physical disturbance of dry egg banks could promote erosion rates. In a field experiment with an experimental vacuum cleaner, Graham and Wirth (2008) showed that more eggs were blown from a dry bank that was physically disturbed. However, it is possible that most of the eggs that were recently produced during the preceding inundation were already blown away at that point given that the pools had already dried. While field observations suggest that egg bank erosion may be highest shortly after pond drying (Vanschoenwinkel et al. 2008), direct empirical support for this hypothesis is lacking.

Not all zooplankton eggs that are eroded necessarily perish. Egg bank erosion can result in wind-mediated dispersal (Caceres and Soluk 2002; Horváth et al. 2016). Besides being able to withstand extended periods of harsh environmental conditions, the tough protective integument and long viability of the embryo inside ensure that these dormant eggs are effective dispersal propagules (Brendonck and De Meester 2003). Although most eggs do not end up in another suitable habitat, their ability to survive long periods in the absence of water ensures that at least some reach a new pond before they expire. Therefore, especially when ponds occur in clusters, wind can be an important vector for dispersal and wind-mediated dispersal could potentially even be a driver of metapopulation dynamics at the local scale (Altermatt et al. 2008; Vanschoenwinkel et al. 2008).

We performed a laboratory wind tunnel experiment to assess the effects of wind velocity, exposure time and sediment characteristics on propagule pickup rates from a reconstituted egg bank. To compile the egg bank samples, we used eggs of the fairy shrimp *Branchipodopsis wolfi* Sars 1898, a species which inhabits different types of temporary ponds across Southern Africa. During the wind tunnel trials, we compared the number of eggs that was blown away between dry egg banks, drying egg banks and disturbed egg banks as a function of exposure time. To assess the impact of wind velocity on the erosion process, we performed the trials at a moderate and high wind velocity of 32.5 km h^{-1} and 70 km h^{-1}, respectively. First of all, we hypothesized that egg erosion would drastically increase when egg banks were disturbed physically. Second, we expected that egg bank erosion would be much lower if the egg bank was allowed to dry before being exposed to wind than when the moist egg bank was subjected to wind. Finally, we expected that eggs that were picked up by wind would be mostly picked up during the first 30 min of wind exposure and that erosion rates would drastically decrease with time.

Methods

Egg bank samples

We used field-collected sediment samples from natural temporary pond systems in which the fairy shrimp model species is one of the dominant competitors. A mixed sediment sample of 1000 g was compiled by collecting 100 g of sediment from ten different rock pool basins on top of Korannaberg Mountain (Eastern Free State, South Africa). The samples were collected when the temporary rock pools were dry. All sediment was transferred to a plastic ziplock bag and transported to the laboratory at KU Leuven for further experiments. Sediment was first sieved over a 120-µm sieve to remove zooplankton eggs, coarse organic material and rocks and subsequently autoclaved for 15 min at 121 °C.

Sixty polystyrene petri dishes, with a diameter of 3.5 cm and a height of 0.5 cm, were filled with 3 mL of the sterilized sediment. Sediment samples were wetted with 2 mL of aged tap water (conductivity 600 µs cm^{-1}). Subsequently, eggs of a laboratory population of the fairy shrimp *B. wolfi* were added to each sediment sample. The laboratory population originated from the same ten temporary rock pools on top of Korannaberg that served as sources for the sediment. The mixed population was reared for three generations under optimal conditions in the laboratory. To compile the egg banks, eggs were suspended in aged tap water and 100 eggs were divided in a homogenous way across each plate using a 20-µL micro-pipette. Plates were kept open for 21 days in a temperature-controlled incubator at 20 °C and a 12-h light: 12-h dark cycle to allow the egg banks to dry completely. After 21 days, each plate was weighed up to the nearest milligram using a microbalance.

Each of the 60 prepared 'egg banks' was randomly assigned to one of the six experimental conditions. The conditions varied in the state of the egg bank ('dry egg bank,' 'drying egg bank' and 'disturbed egg bank') and the wind velocity to which the egg bank was exposed (32 km h^{-1} or 70 km h^{-1}). The chosen wind velocities correspond to moderate and high velocities on Korannaberg. In the 'dry egg bank' conditions, egg banks were kept dry and intact. To each plate of the 'drying egg bank' condition, 2 mL of aged tap water (conductivity 600 µs cm^{-1}) was added 2 h before the wind tunnel trial to simulate a drying egg bank, at the interface of the wet and dry phase. This amount of water sufficed to completely saturate the sediment and to create a thin water film of < 1 mm on top of the sediment. Much like under natural conditions (Pinceel et al. 2013), part of the eggs floated on top of the water while the rest remained in the sediment. In the 'disturbed egg bank' condition, physical disturbance of the egg bank was simulated by scratching two orthogonal, radial lines in the dried egg bank with a preparation needle (Fig. 1).

Wind tunnel setup

The open wind tunnel was modified from Pinceel et al. (Pinceel et al. 2016a, b) and constructed at KU Leuven (Leuven, Belgium) (Fig. 2). The tunnel is powered by a fan (ID: D2E146-HT67-02, ebm-papst Mulfingen, Germany), mounted in a wooden frame and positioned at a 22° angle toward the presentation platform. Generated wind velocities can be regulated with an accuracy of up to 0.1 km h^{-1} using an in-line speed controller (ID: REE 50, ebm-papst Mulfingen, Germany). The wind flow is directed through a Perspex tube with a diameter of 9 cm and a length of 21 cm. The presentation platform has a circle-shaped depression with a diameter of 3.5 cm and depth of 0.6 cm to hold a polystyrene petri dish in which the egg bank sample is prepared. A wind sock (64 µm mesh size), holding a collection jar at its far end with a mesh (120 µm) bottom, is placed behind the wind tunnel outlet to collect any eroded eggs. The setup to capture eggs was duplicated to always have a ready-to-use setup at hand and to be able to rapidly switch at the designated points in time.

Wind tunnel trials

All wind tunnel trials were conducted at 20 °C (± 0.5 °C). Two wind velocities were implemented: a moderate wind velocity of 32.5 km h^{-1} and a high velocity of 70 km h^{-1}. During the wind tunnel trials, a

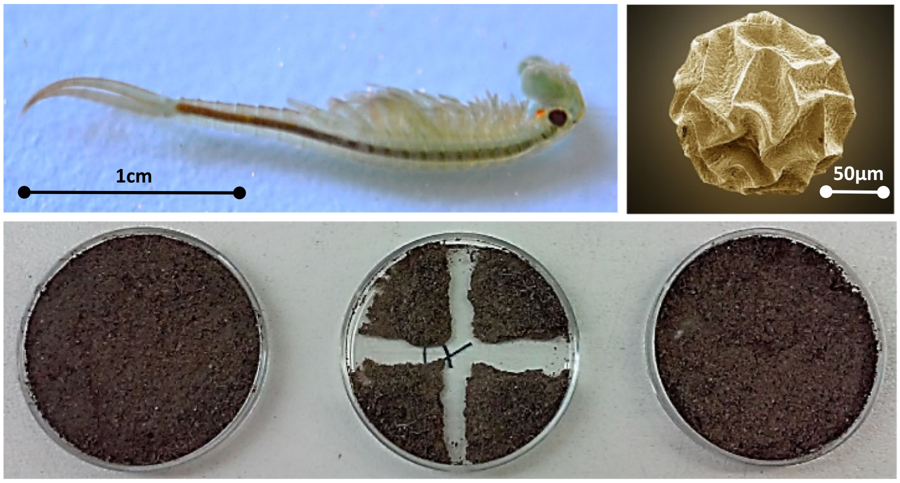

Fig. 1 Egg banks of the fairy shrimp *B. wolfi* (top left) were compiled by randomly positioning 100 dormant eggs (top right) in 3 mL of sterilized sediment in a petri dish (bottom). Three egg bank types were exposed to moderate (32.5 km h^{-1}) or high (70 km h^{-1}) wind velocities in wind tunnel trials, yielding a total of six treatments. These pictures represent a 'dry egg bank' (left), a 'disturbed egg bank' and a 'drying egg bank' after 210 min of exposure to 32.5 km h^{-1}. The diameter of the petri dishes is 3.5 cm

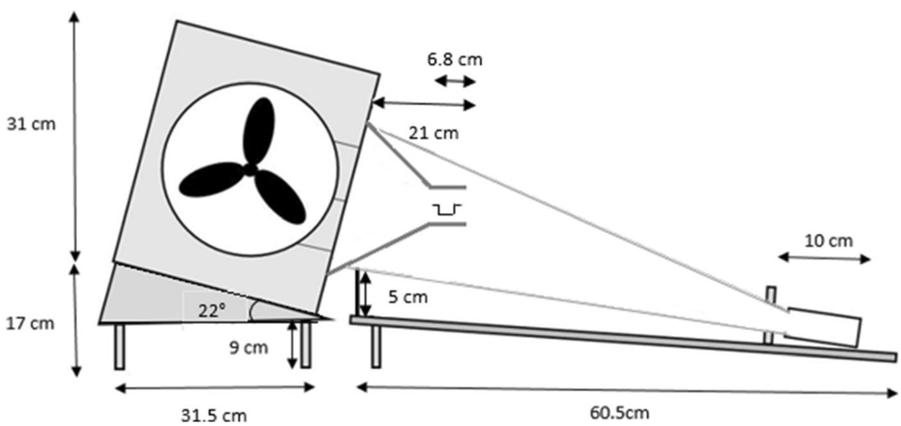

Fig. 2 An open wind tunnel was constructed at the Animal Ecology, Global Change and Sustainable Development laboratory (KU Leuven). Wind tunnel trials ran at 32.5 km h^{-1} and 70 km h^{-1} (± 0.1 km h^{-1}) in the moderate and high wind velocity conditions, respectively. At the start of each trial, a reconstituted *B. wolfi* egg bank with 100 eggs was positioned in the presentation platform. Eggs were captured in a vial at the extremity of a modified zooplankton egg (mesh size 64 µm), and vials were changed after 10, 20, 30 and 210 min to determine eroded egg fractions at each of these moments

total of ten petri dishes of each of the three egg bank types were exposed to a wind velocity of 32.5 km h^{-1} and ten petri dishes of each egg bank type to 70 km h^{-1}. At the start of each trial, a petri dish was positioned in the depression of the presentation platform and the wind sock, to capture eroded eggs, was put into position. Subsequently, the wind tunnel was started and its velocity set to the desired setting (32.5 km h^{-1} or 70 km h^{-1}). Realized wind speeds were verified at the position of the presentation platform with an AN200 anemometer with a circular vane probe (AN200, EXTECH instruments, Nashua, USA) of the same diameter as the Perspex tube. Each trial ran for a total of 210 min. Eggs were collected after 10 min, 20 min, 30 min and 210 min, and at each of these time points the state of the drying egg bank (i.e., wet or dry) was re-evaluated. Plates with different egg bank states were randomly alternated in the wind tunnel trials to avoid any potential time related bias in the results.

Eggs that blew away during each of the time intervals were counted. This was done by transferring the content of each sampling jar, which captured the eggs at the extremity of the wind sock and was renewed at each sampling interval, to a polystyrene petri dish. Eggs were counted using a stereo microscope. At the end of each wind tunnel trial, all egg bank samples were again transferred to a temperature-controlled incubator in which they were kept open for 21 days at a temperature of 20 °C and 12-h light: 12-h dark cycle to dry. Subsequently, the difference in mass of each egg bank compared to before its exposure in the wind tunnel trial was determined by weighing it again on a microbalance.

Statistical analyses

All analyses were performed in R studio 3.2.2 (R Core Development Team) using the packages lme4 (linear mixed models), car (companion to applied regression) and multcomp (simultaneous inference in general parametric models). We calculated Spearman rank correlations to assess the relation between the total amount of sediment and the number of eggs that eroded from the egg banks. We constructed a linear mixed effects model (lme) to investigate egg bank erosion (log-transformed number of wind dispersed eggs) in relation to the state of the egg bank and exposure time to wind. In this model, we included state of the egg bank (dry, drying or disturbed), time interval (10, 20, 30 or 210 min) and wind velocity (32.5 km h^{-1} or 70 km h^{-1}) as fixed predictors and also their interactions were explored. As random factor, 'plate ID nested in time' was included to account for the fact that four repeated measures were performed on each plate (i.e., at the four time intervals). Assumptions of linearity/additivity, statistical independence, homoscedasticity and normality were taken into consideration where applicable.

Results

Overall, our results show a strong positive correlation between the amount of eroded sediment and the number of eroded *B. wolfi* eggs (Spearman *R* 0.87, $p < 0.001$). When exposed to 32.5 km h^{-1}, wind action eroded on average 0.03 g (SD: ± 0.09 g) of the mass of the dry egg bank samples (i.e., eggs and sediment), 0.01 g (SD: ± 0.01 g) of the drying egg banks and 0.70 g (SD: ± 0.15 g) of the disturbed egg banks after 210 min. Wind action eroded 0.02 g (SD: ± 0.01 g) of the dry egg banks, 0.80 g (SD: ± 0.60 g) of the drying egg banks and 1.17 g (SD: ± 0.31 g) of the disturbed egg banks after 210 min of exposure to winds of 70 km h^{-1}.

In all conditions, with the exception of the drying egg bank condition, most eggs were picked up within the first 10 min of exposure (Fig. 3). In the drying egg bank conditions, most eggs eroded in the interval during which the egg bank dried out, after 30–210 and 20–30 min under a wind velocity of 32.5 km h^{-1} and 70 km h^{-1}, respectively. Depending on the state of the egg bank and the wind velocity, between 0 and 60 eggs were eroded during the 210 min of exposure. On average, wind action eroded 1.5% (SD: ± 1.4%) of the dry egg banks, 2.1% (SD: ± 1.6%) of the drying egg banks and 13.7% (SD: ± 3.4%) of the disturbed egg banks after 210 min of exposure to a wind velocity of 32.5 km h^{-1}. When exposed to 70 km h^{-1} for 210 min, erosion rates increased to 4.3% (SD: ± 2.3%) for dry egg banks, 30.6% (SD: ± 16.8%) for drying egg banks and 22.7% (SD: ± 8.79%) for disturbed egg banks (Fig. 3).

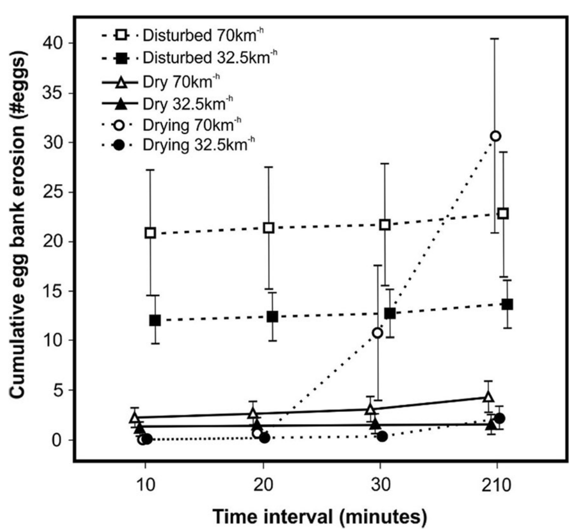

Fig. 3 Three egg bank types were exposed for a total of 210 min under a moderate (32.5 km h^{-1}) and high (70 km h^{-1}) wind velocity in wind tunnel trials. Egg bank erosion was highest in the disturbed and drying egg bank conditions. Most eggs that were picked up by wind eroded within the first 10 min of exposure in all conditions except for the drying egg banks. Error bars indicate standard errors

The linear mixed model describing egg bank erosion, under moderate and high wind speeds, in relation to the state of the egg bank and exposure time to wind identified a significant effect of the state of the egg bank ($F_{2,56}$ 6.39, $p = 0.003$), exposure time ($F_{3,171}$ 53.22, $p < 0.001$) and wind velocity ($F_{1,56}$ 22.17, $p < 0.001$). In addition, we also found a significant 'state of the egg bank x exposure time' interaction ($F_{6,171}$ 41.67, $p < 0.001$). Tukey's post hoc pairwise comparisons showed that, corrected for wind speed, significantly more eggs eroded from disturbed than from dry (Est = 0.82, $z = 7.78$, $p < 0.001$) or drying (Est = − 1.19, $z = -11.33$, $p < 0.001$) egg banks and more eggs eroded from drying than from dry egg banks (Est = − 0.37, $z = -3.54$, $p = 0.001$). Post hoc analyses also showed that, corrected for state of the egg bank, significantly more eggs were eroded under 70 km h^{-1} than under 32.5 km h^{-1} (Est = − 0.25, $z = -4.71$, $p < 0.001$).

Discussion

We performed a laboratory wind tunnel experiment to study the impact of wind velocity, pond drying and physical disturbance on wind erosion rates of the egg bank of a zooplankton model species as a function of exposure time to wind. Our results show that drying events and physical disturbance result in strong erosion fluxes while wind velocity and exposure time contribute only marginally to erosion, at least over the short time scale of the experiment. Our results are of particular relevance in the light of climate change since they imply that increased numbers of short inundations and drying events, as expected under climate change (Moss 2012; Tuytens et al. 2014), will likely be accompanied by increased egg bank erosion rates.

Dry and intact egg banks were relatively resistant to wind erosion in our experiments. Typically < 5% of the egg bank was eroded over the exposure period of 210 min, even under high wind velocities of 70 km h^{-1}. The limited number of eggs that did blow away did so mostly during the first 10 min of exposure, which implies that they were not fixed within the dried sediment crust. Still, field observations indicate that the egg bank size of temporary pond populations can fluctuate extensively among growing seasons (Brendonck et al. 2017) and wind erosion has been suggested as an important underlying process (Tuytens et al. 2014). For instance, > 80% of fairy shrimp eggs can be lost from temporary rock pool basins during a single dry season (Brendonck and Riddoch 2000). The threshold wind velocity that is needed to pick up sediment from temporary pond basins has been shown to depend on sediment characteristics including adhesion among particles, particle sizes and whether or not a crust formed (Gillette 1978; Graham and Wirth 2008). In a field study, Graham and Wirth (2008) used a modified vacuum cleaner to demonstrate that sediment erosion can be caused by wind action after physical disturbance of the sediment crust, in their case by a passing 4 × 4 vehicle. Our results are consistent with this notion. Upon mechanical disturbance of the egg bank, the crust is broken and adhesion among sediment particles and zooplankton eggs is probably strongly reduced. Furthermore, physical disturbance may also directly increase the surface of wind-exposed sediment which, in turn, could also contribute to higher egg erosion rates. When the dried sediment holding the *B. wolfi* egg bank was disturbed, on average 12% and 21% of the egg bank was lost after just 10 min of exposure to moderate and high winds, respectively. Further exposure for 200 min to moderate and high wind velocities resulted in only a 1.7% and 1.8% increase in erosion, respectively.

Besides disturbed egg banks, also drying egg banks were subject to strongly elevated wind erosion rates in our wind tunnel trials. The highest erosion fluxes were associated with the interval during which the water evaporated, when the protecting surface tension of the water was removed. This notion had been suggested earlier, based on measured fluxes of wind dispersal in a cluster of temporary ponds (Vanschoenwinkel et al. 2008), but until now could not be supported by a solid empirical test. In their study, Vanschoenwinkel and colleagues (2008) captured zooplankton eggs with wind socks in a cluster of temporary rock pools and showed that most eggs were air-borne just after pool drying. Likely, a significant fraction of these eggs consists of eggs that were produced during the previous inundation and were not yet embedded in the sediment. In our experiment, evaporation rates were highest under high wind velocities and egg erosion peaked during the 20–30-min interval in the high wind treatments while it only peaked after 30–210 min under moderate winds. Despite the fact that our wind tunnel trials only ran for 210 min, this period sufficed to erode up to 30% of the egg bank. Analogous to erosion of the disturbed egg banks, most of the eggs that were blown away were picked up almost immediately after they were exposed, when the water had evaporated. Subsequently, erosion rates were negligible. These results are also consistent with observations by Altermatt et al. (2008) who found that Daphnia colonization rates in temporary pools were higher in dry years when presumably more pools dried, providing sources of colonists. Even when evaporation rates are high, crust formation after drying takes a number of minutes. Erosion is highest when the water is removed but before the protective crust, which increases adhesion among sediment particles and eggs, forms. Our findings suggest that it could be highly relevant to take frequency of drying events and prevailing winds during drying into account when studying egg bank erosion.

Long-term survival of zooplankton populations in temporary ponds is highly dependent on the maintenance of a viable egg bank over extended time periods and multiple potential growing seasons (Evans and Dennehy 2005; Pinceel et al. 2018). Climate scenarios predict an overall decrease in favorable inundations for temporary pond zooplankton and increased frequencies of unpredictable early pond drying (Moss 2012; Stoks et al. 2014; Tuytens et al. 2014). Under these conditions, the importance of the egg bank as a buffer against reproductive catastrophes is predicted to increase further (Pinceel et al. 2016a, 2018). Our results are worrying in light of this since they imply that increased numbers of short inundations and drying events will likely be accompanied by increased egg bank erosion rates.

In addition to the condition of the egg bank, also other factors are known to determine egg pickup rates by wind. For instance, the dimensions, shape and external ornamentation of eggs have been shown to impact their propensity to be picked up by wind (Pinceel et al. 2016b). Specific egg shapes, such as the tetrahedral eggs of certain fairy shrimp species, have even been suggested to have evolved as anti-dispersal traits (Brendonck 1996). The same could be true for the many fairy shrimp and clam shrimp eggs that have spiny structures or the extremities of the ephippia of certain water fleas such as *Daphnia magna*. Such structures have typically been hypothesized to facilitate zoochory (Bilton et al. 2001). However, it is arguable that such structures could also serve to improve adhesion to debris in a pool basin and be effective anti-erosional traits. It should be noted that we used only eggs of a single fairy shrimp species in our experiments. *Branchipodopsis wolfi* eggs are globular in shape, typically have a diameter of 200 µm and display ridges and valleys at their surface. Still, it is reasonable to assume that eggs of other zooplankton species would respond in a similar way to egg bank disturbance and subsequent wind action. Although previous studies have shown that eggs of different shapes and sizes are picked up at different wind velocities (Pinceel et al. 2016b), strong winds, as used in this experiment, would most likely pick up dislodged eggs of any shape, as is supported by field observations (Vanschoenwinkel et al. 2008).

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Author contributions TP, BV and LB designed the study. TP and MW performed the experiments, analyzed the data and drafted the manuscript with subsequent feedback from BV and LB.

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