Limnetica, 35 (2): 323-336 (2016). DOI: 10.23818/limn.35.26

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Dispersal of zooplankton dormant propagules by wind and rain in two aquatic systems

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Received: 09/01/2015 Accepted: 07/02/2016

ABSTRACT

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Zooplankton dispersal may regulate population dynamics and the structure of aquatic communities. Zooplankton and other aquatic invertebrates, such as freshwater bryozoans, are potentially dispersed overland by abiotic vectors (e.g., wind, rain and water flow) or by organisms (e.g., waterfowl and insects), and although these dispersal vectors have been widely studied, the importance of dispersal by wind remains controversial. In addition, little information is available on passive deposition rates and the differentiation between dry deposition (sedimentation from the air) and wet deposition (from rainfall). In the present study, we quantified zooplankton propagule dispersal by passive deposition from the air and rainfall using deposition collectors designed to gather samples from dry or wet atmospheric deposition. The collectors were located in two regions with distinct limnologic and topographic characteristics: Doñana National Park and Ruidera Natural Park. In Doñana, we also used windsocks to intercept the dormant propagules dispersed by wind, and a larger number were collected in the dry atmospheric deposition collector than in the wet one. Moreover, the deposition of dormant propagules was only related to the meteorological variables, wind direction and temperature, and most of the propagules appeared to arrive in Doñana from the northwest. Our results indicate that overland dispersal by wind and rain is relatively infrequent and probably limited to a few zooplankton species. Despite the few dormant propagules that were collected, they were present in passive deposition collectors and windsocks. Aerial overland dispersal at low rates implies long-term relevance to the genetic structure of zooplankton and their colonization of water bodies.

Key words: Dispersal, zooplankton, wind, rainfall, passive deposition.

RESUMEN

Relevancia de la dispersión de los huevos latentes de zooplancton por el viento y la lluvia en dos sistemas acuáticos

La capacidad de dispersión de las distintas especies de zooplancton parece jugar un importante papel en la regulación de las dinámicas poblacionales y la estructura de las comunidades acuáticas. El zooplancton, al igual que otros invertebrados acuáticos como los briozoos de agua dulce, es potencialmente dispersado entre sistemas acuáticos a través de vectores abióticos como el viento, la lluvia y los flujos de agua, y por medio de organismos tales como aves acuáticas e insectos. Aunque muchos estudios han evaluado los distintos vectores de dispersión, la importancia de la dispersión por el viento sigue siendo objeto de discusión. Desafortunadamente, se conoce muy poco acerca de las tasas de deposición pasiva, tanto seca como húmeda, de las distintas formas de resistencia de invertebrados acuáticos. El presente estudio se ha llevado a cabo en dos localizaciones con diferentes características: el Parque Nacional de Doñana y el Parque Natural de Ruidera, y para su desarrollo hemos usado colectores de deposición atmosférica que nos permitían recoger y discriminar los propágulos latentes sedimentados desde el aire (deposición seca) y aquellos recogidos por el agua de lluvia (deposición húmeda). Además, para contabilizar los propágulos latentes que viajaban por el viento se emplazaron en Doñana unas mangas de viento que permitían interceptar dichos propágulos. Los resultados mostraron diferencias en el número de propágulos recogidos por los colectores en Doñana y Ruidera. Además, el número total de propágulos recogidos en los colectores de deposición atmosférica seca instalados en Doñana fueron mayores que los encontrados en los de deposición atmosférica húmeda. Por otro lado, la deposición de propágulos sólo estuvo relacionada con las variables meteorológicas temperatura y dirección del viento, sugiriendo que la mayoría de los propágulos provenían del noroeste. A pesar de que la cantidad total de propágulos *interceptados por las mangas fue mayor que la recogida por los colectores, la composición de especies fue muy similar a la de los colectores. La mayoría de taxones dispersados estuvieron representados por rotíferos, tanto en los colectores como en las mangas. Aunque nuestros resultados sugieran que la dispersión por el viento es escasa y posiblemente esté limitada a unas pocas especies, la recogida de propágulos tanto en los colectores como en las mangas nos estaría indicando la relevancia de la dispersión por el aire y su posible impacto en la colonización de nuevos cuerpos de agua.*

Palabras clave: *Dispersión, zooplancton, viento, lluvia, deposición pasiva.*

INTRODUCTION

The dispersal of freshwater invertebrates is crucial to the development of aquatic communities, and its role in shaping their structure is an important research question for aquatic ecologists. Freshwater organisms have traditionally been considered cosmopolitan due to their wide distribution and their capacity for dispersal between water bodies (Darwin, 1859), although differences in dispersal capacity have been observed among taxa. Zooplankton and freshwater bryozoans produce numerous dormant propagules that resist desiccation and passively disperse overland between water bodies in diapause as resting eggs, cysts, or statoblasts, among other cryptobiotic stages (Hairston, 1996; Brendonck & Riddoch, 1999; Bilton *et al.*, 2001; Panov *et al.*, 2004). These propagules can be dispersed by wind (Jenkins & Underwood, 1998; Brendonck & Riddoch, 1999; Caceres & Soluk, 2002; Cohen & Shurin, 2003; Vanschoenwinkel *et al.*, 2008a; Vanschoenwinkel *et al.*, 2008b), water flow (Michels *et al.*, 2001; Vanschoenwinkel *et al.*, 2008a), and biotic agents (Maguire, 1963; Green *et al.*, 2008; Vanschoenwinkel *et al.*, 2008c). Their dispersal has been quantified and the effectiveness of the dispersal vectors has been evaluated by various means, including the interception of dormant propagules borne overland by wind and rain (Jenkins & Underwood, 1998; Brendonck & Riddoch, 1999; Vanschoenwinkel *et al.*, 2008a); the performance of colonization experiments taking wind, rainfall, and/or animals into account (Caceres & Soluk, 2002; Cohen & Shurin, 2003; Frisch *et al.*, 2012; Sciullo & Kolasa, 2012); and the study of water flows (Allen, 2007; Sciullo & Kolasa, 2012). However, the results of these investigations have been inconsistent.

The low wind dispersal rates found for zooplankton dormant propagules led some researchers to question the importance of this vector (Jenkins, 1995, Jenkins & Underwood, 1998, Brendonck & Riddoch, 1999), and it has been proposed that zooplankton passively dispersed by wind are relatively slow to colonize new habitats (Jenkins & Buikema, 1998; Jenkins & Underwood, 1998; Cohen & Shurin, 2003). However, observations of passive dispersal are influenced by several methodological factors, including the proximity of dispersal collectors (artificial mesocosms, windsocks, or sticky traps) to water bodies with egg bank sources, their elevation, and their orientation relative to the prevailing winds (Cáceres & Soluk, 2002; Vanschoenwinkel *et al.*, 2008a; Vanschoenwinkel *et al.*, 2008b). Higher wind dispersal rates of dormant propagules were observed (using windsocks and sticky traps placed very near sources) in studies of rock pool metacommunities (Vanschoenwinkel *et al.*, 2008a; Vanschoenwinkel *et al.*, 2008b), but the collected samples did not accurately represent the zooplankton community as there was an absence of rotifers (Vanschoenwinkel *et al.*, 2008a; Vanschoenwinkel *et al.*, 2008b; Sciullo & Kolasa, 2012). Overall, the most abundant passive dispersers appear to be monogonont and bdelloid rotifers followed by cladocerans (Cáceres & Soluk, 2002; Cohen & Shurin, 2003). The proximity and exposure of the resting egg bank and the direction rather than speed of the wind may be the most relevant factors in wind dispersal (Vanschoenwinkel *et al*., 2008a). Egg banks may be more exposed to the wind during the dry season in aquatic systems with highly fluctuating water levels (Bilton *et al*., 2001; Vanschoenwinkel *et al*., 2008a; Tuytens *et al*., 2014), so the key dispersal vectors may be wind during dry seasons and water flow during wet seasons (Hulsmans *et al*., 2007). However, only a few studies have taken the passive deposition of resting eggs from the air into account (Jenkins & Underwood 1998; Sciullo & Kolasa, 2012), and these studies did not discriminate between passive wet deposition (due to rainfall) and passive dry deposition (due to sedimentation from the air).

The main objectives of the present study were i) to compare the dispersal of zooplankton, including rotifers and bryozoans, by wind and rainfall between two regions with different limnologic and topographic characteristics (Doñana National Park and Ruidera Natural Park) using automatic atmospheric deposition collectors to examine differences between dry and wet passive deposition; ii) to investigate the relationship between meteorological variables and the passive deposition of propagules in Doñana; and iii) to measure the dormant propagules dispersed by wind in Doñana using two windsocks.

MATERIALS AND METHODS

The dispersal of zooplankton dormant propagules by wind was studied in Ruidera Natural Park and Doñana National Park. Ruidera Park is in central Spain, between the provinces of Albacete and Ciudad Real, and consists of 15 lakes connected in a chain, separated by travertine barriers and fed by groundwater and, when groundwater levels are high, by surface drainage from the upper to the lower lakes. The climate is continental Mediterranean with rainfall mostly in spring and autumn, and the prevailing wind is from the southwest. The lakes that flow from 920 m to 720 m above sea level present different surface areas (from 100 ha to less than 12 ha), and their depths range from 8 m to 19 m. They are warm monomictic, and their trophic state varies from oligotrophic to eutrophic. The zooplankton composition changes seasonally and is mainly represented by rotifers followed by cladoceran and copepods (Bort *et al*., 2005; Álvarez-Cobelas *et al*., 2006; Rojo *et al*., 2007).

Doñana National Park in southwest Spain is a region with an extremely flat topography and a Mediterranean climate with an Atlantic influence that is characterized by mild winters and hot dry summers and prevailing westerly winds (Bayán,

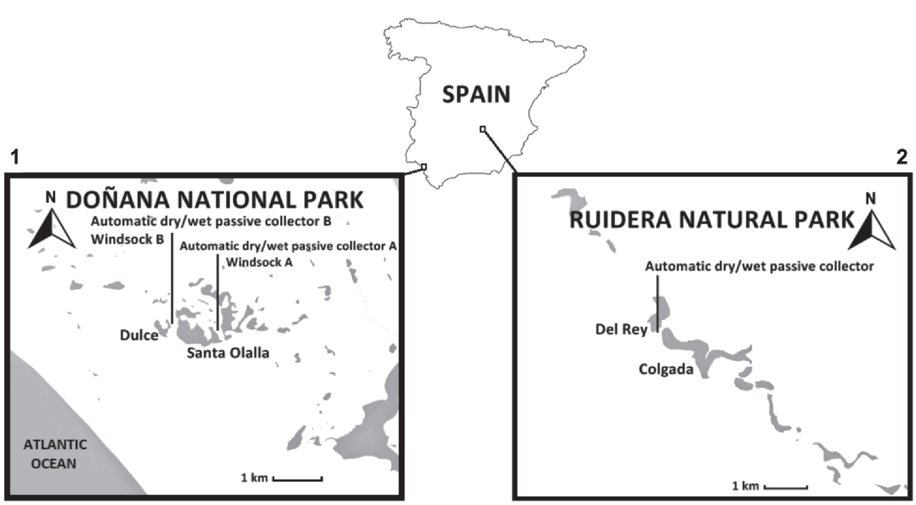

Figure 1. Maps of the study areas and the locations of the automatic dry/wet passive collectors and windsocks in Doñana (1) and the automatic dry/wet passive collector in Ruidera (2). *Mapas de las áreas de estudio y localización de los colectores de deposición pasiva seca/húmeda y mangas de viento en Doñana (1), y colector de deposición pasiva seca/húmeda en Ruidera (2).*

2005; Espinar & Serrano, 2009). The rainfall varies seasonally and interannually, producing drastic fluctuations in water levels and in the physical-chemical and biological processes of freshwater bodies (Serrano *et al.,* 2006; Serrano & Zunzunegui, 2008; Espinar & Serrano, 2009; López-Archilla *et al*., 2012). The zooplankton community varies intraannually and interannually, and rotifers, mostly from the genus *Brachionus* or the species *Keratella tropica*, are particularly predominant, especially during the flooding season followed by cladoceran and copepods (López *et al*., 1991; Serrano & Toja, 1998).

The dispersal of the dormant propagules reaching the lakes by wind and rainfall was measured using MTX®ARS 1010 automatic dry/wet passive collectors (MTX Italia SPA, Modane, Italy) equipped with two polyethylene buckets (surface area of 0.0667 m^2 each) and a hygroscopic sensor cell. This device activated an aluminium lid that covered the dry bucket and uncovered the wet bucket during rainfall and *vice versa* during periods without rain. One collector was located in Ruidera between the *del Rey* (Ciudad Real, Spain) and *Colgada* (Ciudad Real/Albacete, Spain) lakes (38°57′48.70″N, 2°53′15.35″W; elevation 790 m; Ciudad Real, Spain), and two were located in Doñana (Huelva, Spain), one on the east side of *Santa Olalla* lake (Doñana A; 36°58′47.38″N, 6°28′22.40″W; elevation 8 m) and the other between the *Dulce* and *Santa Olalla* lakes (Doñana B; 36°58′43.60″N, 6°28′59.82″W; elevation 6 m), which are two coastal shallow peridune ponds and natural eutrophic to hypereutrophic systems surrounded by a number of temporary ponds (see Fig. 1). The distances of the Doñana A and Doñana B collectors from the nearest water body were 30 m and 100 m, respectively, and the Ruidera collector was located 30 m from the nearest lake. Dry and wet deposition buckets were collected every one to three months during 2008, 2009 and 2010 in Doñana and during 2008 and 2009 in Ruidera. On each sampling date, the dry and wet deposition buckets from the three collectors were replaced and taken to the laboratory. First, the dry deposition was carefully and thoroughly examined to detect and gather any bird faeces or large insects, which were then inspected for the presence of dormant propagules. We also found an important amount of plant seeds, but we did not take them into account. Next, the deposition bucket was rinsed with distilled water, and this solution and the contents of the wet deposition bucket were pre-filtered with a 500-µm nylon mesh. The particles retained in the nylon mesh were examined under a stereoscopic microscope. The pre-filtered water was then filtered through a 10-µm nylon mesh, and the contents were rinsed with distilled water and examined under a stereoscopic microscope to detect dormant propagules.

Because of the consistently higher density of dormant propagules collected in Doñana Park (see Results), the dispersal by wind was also evaluated during the last four months of the study using two windsocks, which were conical, 30-µm plankton nets fitted to a conical metal frame that rotated in the direction of the wind (Vanschoenwinkel *et al*., 2008a). One was placed close to the Doñana A collector (Windsock A) and the other close to the Doñana B collector (Windsock B). They were in place from June to October 2010 and were collected and replaced monthly, except for Windsock B during the last month (due to tearing). Each collected windsock was carefully rinsed with distilled water to obtain all of the intercepted propagules, and the water was then collected in bottles and kept in dark, cold conditions during transport to avoid breaking diapause. Each of the dormant propagules obtained from the collectors and windsocks and identified under the stereoscopic microscope was photographed and then placed in a well of a 96-well polyethylene microplate under a 14 h light/10 h dark-photoperiod and a temperature of 20 °C, which simulated summer conditions for hatching (Jenkins & Underwood, 1998; Vandekerkhove *et al*., 2004).

Infraestructura Científica y Tecnológica Singular (ICTS; http://icts.ebd.csic.es) provided daily meteorological data including wind speed and direction, precipitation (mm), and air temperature (°C) from the *Control* RM1 Station (37°1′21″N, 6°33′19″W; elevation 6 m), which was located 8 km from the Doñana B collector and 8.70 km from Doñana A. ICTS also provided accumulated evaporation (mm) and temperature (°C) data from the *Cancela Millan* RMN2 Station (37°1′9″N, 6°21′55″W; elevation 2 m), which was located 10.50 km from Doñana A and 11.40 km from Doñana B. Meteorological data were not gathered in Ruidera Park because of the small number of dormant propagules collected (see Results).

Statistical analysis

Statistical analyses were performed using program R 2.14.0 (R Foundation for Statistical Computing). For these analyses, we used the number of dormant propagules collected per day, accounting for the total number of days that the automatic dry/wet passive collectors were working, and the average values of the meteorological variables (wind direction, wind speed, precipitation and temperature) between sampling days. The meteorological variables related to the number of dormant propagules were selected by model selection, which was based on the second-order Akaike information criterion (AIC_c) because of the small sample sizes (Burnham & Anderson, 2002). The AIC_c values were compared following the convention that if the ΔAIC_c (differences in AIC_c between each model and the model with the minimum AIC_c) is less than 2, the two models have relatively equal support. Otherwise, the model with the lowest AIC_c value was considered to be the most plausible model (Burnham & Anderson, 2002). As we have no previous information about the possible models to explain propagule deposition, we include all of the possible models with the independent variables as well as the null model with only an intercept term. The normality of the residuals of the selected models was tested with the Shapiro test. Additionally, the Akaike weights were summed (cumulative AIC_c weights) over all possible models containing a given variable to measure the relative importance of each independent variable (Burnham & Anderson, 2002; Burnham & Anderson, 2004). The larger the cumulative AIC_c weight, the more important the variable is relative to the other variables. Barbieri and Berger (2004) suggest that variables with a cumulative weight ≥ 0.5 show strong evidence of inducing a response in the dependent variable. All of the meteorological variables were previously log-transformed because, in all cases, the models showed a higher explanatory power (higher R^2). Model selection was conducted using the AIC cmodavg package (Mazerolle, 2015).

Additional correlation analyses were used to explore the relationships between some meteorological variables and for studying the propagules collected in windsocks because of the few data available. The non-parametric Spearman's test was used when the normality assumption was

Table 1. Zooplankton dormant propagules collected in the automatic dry/wet passive collectors located in Doñana and Ruidera and in the windsocks located in Doñana. *Propágulos latentes de zooplancton recogidos en los colectores de deposición pasiva seca/húmeda en Doñana y Ruidera, y en las mangas de viento localizadas en Doñana.*

	Brachionus spp	*Hexarthra spp*	*Keratella spp*	Bdelloids	*Plumatella spp statoblast*	Cladoceran ephippia	Ostracods	Total
Doñana A Wet	1				1			2
Doñana A Dry					3	1		4
Doñana B Wet		2						2
Doñana B Dry	3	2			4	1		10
DoñanaWindsock A	2	6	3		3	1	3	18
DoñanaWindsock B	1	2			2	1	2	8
RuideraWet				2				2
RuideraDry	1							1
Total								47

violated, and the Oriana program (Kovach Computing Services) was applied to obtain the vector-averaged wind direction for each period and a circular histogram. The circular wind direction covariate was accommodated by including the sine and cosine of the wind direction rather than the wind direction itself during model selection (Johnson & Wehrly, 1978; Mardia & Jupp, 2000; Jammalamadaka & Lund, 2006). STATISTICA (Statsoft) was used for the remaining histograms and graphs.

RESULTS

A total of 47 zooplankton and bryozoan dormant propagules were collected in the passive automatic deposition collectors and windsocks (Table 1). Considering the number of days that the collectors were working, an average of 0.076 dormant propagules/day/m^2 (per collector bucket) were passively deposited in Doñana, and 0.040 dormant propagules/day/m^2 (per collector bucket) were passively deposited in Ruidera. In the windsocks, an average of 0.163 dormant propagules/day per windsock were intercepted in Doñana. The propagules collected in the Doñana passive collectors were gathered between June and November in 2008 and between June and September in 2010, while those in the Ruidera collectors were gathered between July and September in 2008 and in January and February in 2009. The most abundant zooplankton dormant propagules were rotifers followed by ostracods and cladocerans. Dormant propagules of rotifers of the genus *Brachionus* were found in the Doñana A wet, Doñana B dry, and Ruidera dry collectors and those of the genus *Hexarthra* in the Doñana B wet and dry collectors. Cladocera ephippia of *Daphnia magna* were collected in Doñana, and bryozoans were represented by *Plumatella* statoblasts collected in both collectors and windsocks. Finally, two live bdelloids were found in the Ruidera wet collector. A larger amount of propagules was collected in the collectors in Doñana than in Ruidera (Fig. 2), and the maximum detection rate was 0.548 dormant propagules/day/m^2 in the Doñana collectors *versus* 0.713 dormant propagules/day/m^2 in the Ruidera passive collector, corresponding to the sampling in October 2008 and January 2009, respectively. The two windsocks deployed in Doñana collected a higher density of propagules with greater taxonomic richness over a shorter time period in comparison with the passive deposition collectors (Table 1). Rotifers from the genus *Brachionus* and resting eggs from two different *Hexarthra* species were intercepted in both windsocks, and one resting *Keratella tropica* egg was found in Doñana windsock A, which had a healthy appearance and was the only dormant propagule hatched under the present study conditions. Ostracod dormant propagules were

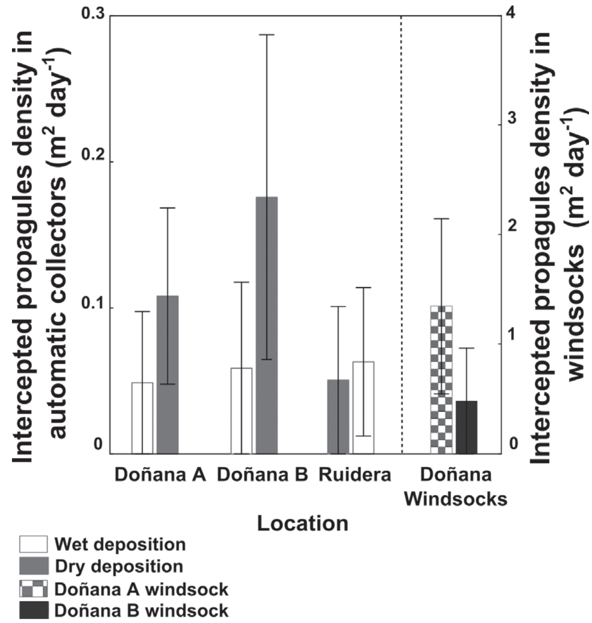

Figure 2. Dispersal rates of zooplankton dormant propagules intercepted by the automatic dry/wet passive collectors located in Doñana and Ruidera (left side of the figure) and the windsocks located in Doñana (right side of the figure). Error bars correspond to standard errors. Distances of collectors and windsocks from the main sources of dormant propagules: 30 m to Doñana A and Windsock A, 100 m to Doñana B and Windsock B and 30 m to Ruidera. *Tasas de dispersión de los propágulos latentes de zooplancton recogidos en los colectores de deposición pasiva seca/húmeda en Doñana y Ruidera (parte izquierda de la figura), y las mangas de viento localizadas en Doñana (parte derecha de la figura). Las barras de error se corresponden a los errores estándar. Distancias de los colectores y las mangas de viento a las principales fuentes de propágulos latentes: Doñana A y Manga de viento A 30 m, Doñana B y Manga de viento B 100 m y Ruidera 30 m.*

collected in both windsocks, and cladocerans were represented by a *Daphnia longispina* ephippium. The most abundant species in the windsocks were the same as in the atmospheric deposition samplers.

According to the AIC_c, the best model to explain the dry deposition of propagules is the model using the cosine of wind direction and temperature as independent variables (see Table S1, available at www.limnetica.com). However, other models are also plausible candidates, and even the null model was selected, especially for the total propagule deposition (see Table S1). However, when we analysed the relative importance of each independent variable, we found that the temperature and the cosine of wind direction are more important than the other variables according to their Akaike weights (Table 2). As a consequence, in our study, propagule deposition in the dry deposition containers seems to be mainly related to temperature and wind direction, although the results were unclear when considering total deposition (including wet containers) (Table 2). Similar results were observed for zooplankton dormant propagules alone (ostracods, cladocerans, and rotifers) and for rotifer resting eggs alone (Table 2). As shown in Figure 3, wind speeds ranged from 2.3 m/s to 3.1 m/s in Doñana, and the prevailing wind was from the west. However, wind speed seems to not be relevant in our study. The accumulated evaporation was significantly correlated with temperature (Spearman's nonparametric correlation, rho = 0.5408, n = 220, p < 0.0001) and wind speed (Spearman's nonparametric correlation, rho = 0.2204, n = 220, p = 0.0008). No

Table 2. Relative importance of meteorological variables in predicting the abundance of collected propagules. For each variable, we report the sum of AIC_c weights for all models in which the variable occurred. cosw: cosine of wind direction, sinw: sine of wind direction, tem: temperature (log-transformed), wspeed: wind speed (log-transformed), rain: rainfall (log-transformed). *Importancia relativa de las variables meteorológicas como predictoras de la abundancia de los propágulos recogidos. Para cada variable mostramos la suma de la relevancia AIC_c para todos los modelos en los que la variable aparece. cosw: coseno de la dirección del viento, sinw: seno de la dirección del viento, tem: temperatura (log-transformada), wspeed: velocidad del viento (log-transformada), rain: precipitación (log-transformada).*

		Variable AIC_c weights				
Collectors	Response variable	tem	cosw	sinw	wspeed	rain
Doñana B dry	Zooplankton propagules + bryozoan statoblasts	**0.71**	**0.66**	0.15	0.18	0.25
	Zooplankton propagules	**0.72**	**0.59**	0.19	0.18	0.33
	Rotifer resting eggs	**0.68**	**0.53**	0.25	0.21	0.32
Total dry (collectors A and B)	Zooplankton propagules + bryozoan statoblasts	0.48	0.33	0.16	0.18	0.31
	Zooplankton propagules	**0.86**	**0.81**	0.12	0.14	0.27
	Rotifer resting eggs	**0.68**	**0.54**	0.24	0.21	0.31
Total Donaña B (dry and wet)	Zooplankton propagules + bryozoan statoblasts	0.46	0.28	0.27	0.26	0.15
	Zooplankton propagules	0.46	0.17	0.31	0.21	0.15
	Rotifer resting eggs	0.44	0.17	0.34	0.22	0.15
Total Doñana A-B (dry and wet)	Zooplankton propagules + bryozoan statoblasts	0.41	0.26	0.23	0.23	0.17
	Zooplankton propagules	0.50	0.23	0.32	0.26	0.14
	Rotifer resting eggs	0.42	0.17	0.35	0.25	0.14

Bold type indicates that the variable was in the top model based on AIC_c (see Table S1, which is available at www.limnetica.com). *En negrita: la variable estaba incluida en el modelo superior basado en el AIC_c (Tabla S1, disponible en www.limnetica.com).*

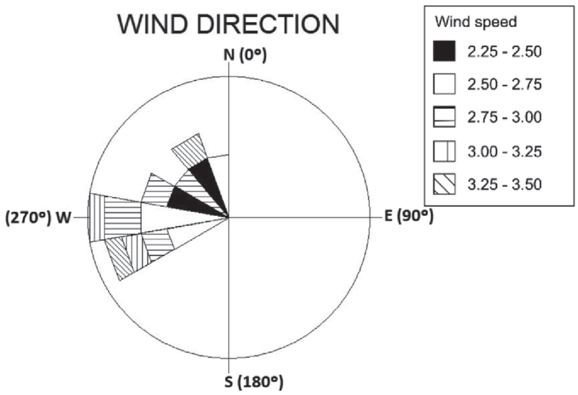

Figure 3. Raw wind direction and speed data throughout the study period (15 intervals from 26 May, 2008 to 23 October, 2010). *Datos brutos de la dirección y velocidad del viento durante el periodo de estudio (15 intervalos) (desde el 26 de mayo de 2008 al 23 de octubre de 2010).*

analyses were performed on the data for dormant propagules collected in Ruidera because of their scarcity (Table 1).

The relationship between the time of year and the amount of dormant propagules collected was analysed by converting the day of the year into a circular variable (Jammalamadaka & SenGupta, 2001), which was excluded from the previous model selection to avoid redundancy with other variables. The sine and cosine of the day were used in a circular-linear correlation analysis of the total number of dormant propagules gathered in each collector. The day of the year was only significantly related to the total number of dormant propagules collected in the Doñana B dry deposition container ($r = 0.522$, $p < 0.05$) and to the mean number in the Doñana A and B dry deposition containers ($r = 0.516$, $p < 0.05$).

DISCUSSION

This is the first study to use automated wet/dry collectors in combination with windsocks to collect dormant zooplankton propagules. The total number of resting propagules gathered per collector was higher in Doñana than in Ruidera, although the difference was not statistically significant due to the small sample size in Ruidera. The advantage of using the automated wet/dry collectors is that they allowed for discrimination between dry and wet atmospheric deposition. According to this we collected more dormant propagules in the dry deposition buckets than in the wet deposition buckets (0.119 dormant propagules per day/m^2 and 0.034 dormant propagules per day/m^2, respectively) in Doñana. In Ruidera, the wet deposition buckets collected more propagules (0.054 dormant propagules per day/m^2 in the wet deposition buckets and 0.027 dormant propagules per day/m^2 in the dry deposition buckets).These differences in the number of dormant propagules collected in each deposition bucket, the proximity of the collectors to water bodies (30 or 100 m), and the scarceness of dormant propagules collected during our study period support the idea that overland dispersal by wind and rain is infrequent and operates as a regional-scale process (Jenkins & Underwood, 1998; Brendonck & Riddoch, 1999). Although the total number of dormant propagules collected was very low in both systems, wind and rain could be relevant dispersal vectors that play a key role in community assembly in new aquatic systems if we consider wind dispersal to be a stochastic process and that a single or a few individuals may colonize new water bodies (Ortells *et al.*, 2014).

Given that almost all of the dormant propagules were collected between June and November in the passive deposition collectors in Doñana, our results may also be related to the exposure of egg banks to wind during the dry season. During the study period, the depth of the lakes in Doñana was reduced by 45-75% in the summer months (high temperatures and virtually no rainfall) with a major reduction in their surface area, although they did not become completely dry. Therefore, the egg banks in the dried areas were potentially exposed to the action of the wind (Galindo *et al.*, 1994), but in contrast, the water levels and the surface areas of the *del Rey* and *Colgada* lakes in Ruidera, which are permanent water bodies with an average depth of 20 and 16 m, respectively, fluctuated less. Our observation of a significant relationship between higher temperatures and a larger number of collected propagules supports the influence of the dry season in these dispersal events. However, the long dry phase and the desiccation of egg banks exposed to the sun may also increase the mortality of diapausing eggs in temporary compared to permanent water bodies, which may reduce viable dispersal (Bohonak & Jenkins, 2003).

Jenkins and Underwood (1998) observed low wind dispersal rates for zooplankton propagules and collected only rotifer species (bdelloids) in their windsocks, which were deployed in sites distant from as well as near to potential sources of zooplankton propagules (400 m and 150 m, respectively). Higher dispersal rates and a greater variety of taxa were collected in our windsocks in Doñana, although the results were considerably lower than those reported by Vanschoenwinkel and co-workers in collectors adjacent to rock pool metacommunities (Vanschoenwinkel *et al*., 2008a; Vanschoenwinkel *et al*., 2009). Previous authors collected from several hundred to thousand wind-dispersed dormant propagules on sticky traps in only one month, a larger amount than we collected in the wet/dry atmospheric deposition collectors in Doñana over approximately three years and in the windsocks over four months. This difference may be because the rock pools in the previous studies become totally dry during the summer season (Vanschoenwinkel *et al*., 2008a; Altermatt & Ebert, 2008; Pellowe-Wagstaff & Simonis, 2014), and their substrate may favour the lifting and subsequent movement of the dormant propagules relative to the muddy lake sediments. Additionally, sticky traps were located very close to sources of dormant propagules and at ground level in a flat open area, where they could receive heavier propagules that arrive by rolling and saltational movements (Vanschoenwinkel *et al*., 2009).

Several studies have demonstrated similarities between established zooplankton communities and dispersing organisms, suggesting that the relative abundance of the species in the local community is reflected in the dispersing community (Jenkins & Buikema, 1998; Ives *et al*., 2004; Sciullo & Kolasa, 2012). Although the dispersed propagules did not represent all of the taxa in the Doñana lakes, the most abundant genera were also those observed with the greatest frequency in the water column (Conde-Porcuna *et al*., 2009). The composition of the species collected in the atmospheric deposition collectors and the windsocks was similar, suggesting that the propagules passively deposited in the collectors adequately reflect the species dispersed by the wind with the exception of ostracods, which were only observed in the windsocks. Rotifers were the most abundant taxa in all the collector systems, while cladocerans were only collected in the dry deposition collector. Rotifers are often prominent among the early colonists of experimental water bodies (Jenkins & Buikema, 1998; Cáceres & Soluk, 2002; Badosa *et al.,* 2010; Frisch *et al*., 2012), so the size of the propagules and their dispersal ability may play a key role in the colonization processes.

Wind speed seems to be irrelevant in the deposition of propagules in Doñana, although other studies found a significant relationship between wind speed and propagule dispersal (Vanschoenwinkel *et al*., 2008a, Parekh *et al*., 2014). During our study period, the minimum wind speed in Doñana was approximately 5 km/h (1.3 m/s), and the average wind speed was two-fold higher, suggesting than eggs could readily be lifted and dispersed by the wind (Parekh *et al*., 2014). Thus, the majority of dormant propagules collected in the present study were small, zooplankton resting eggs (rotifers and ostracods) and bryozoan statoblasts, with a lesser proportion of cladoceran ephippia, which are generally heavier. Wind speed influenced the aerial transportation of propagules but appeared to have no effect on their passive deposition in the present study, although this might be due to the relatively small sample size.

Wind direction seems to play a greater role than wind speed. We observed that the cosine of wind direction and temperature were the most relevant variables in relation to the propagules collected in the dry containers, but the relative importance of both variables, especially the cosine of wind direction, was clearly lower when including both dry and wet collectors (Table 2). This suggests that wind direction could be more relevant to dry deposition than to wet deposition.

Little is known about the average number of propagules deposited by rainfall during a given time period in a region (Vanschoenwinkel *et al.*, 2008b). The passive wet deposition rate was lower (0.029 dormant propagules per day/m^2) than the passive dry deposition rate (0.112 dormant propagules per day/m^2) in Doñana, but the wet deposition rate was higher (0.053 dormant propagules per day/m^2) than the passive dry deposition rate (0.026 dormant propagules per day/m^2) in Ruidera. Our results support the conclusion that overland zooplankton dispersal by wind and rainfall is infrequent and occurs in a few species (Jenkins & Underwood, 1998), at least in the aquatic systems of Doñana and Ruidera. Extrapolating from the passive deposition rate of dormant propagules in the Doñana A collector (0.051 dormant propagules per day/m^2), the nearest lake to the west, *Santa Olalla* with an area of 32.7 ha, could potentially receive 16 415 dormant propagules per day. Based on the rate in the Doñana B collector (0.1002 dormant propagules per day/m^2), the neighbouring *Dulce* Lake, with an area of 6.3 ha, might receive 6325 dormant propagules per day. The automated wet/dry collector from Ruidera was located between the *del Rey* and *Colgada* lakes with surface areas of 38 and 100 ha, respectively, so the extrapolated passive deposition rate of dormant propagules in both lakes might be 15 086 and 39 700 dormant propagules per day, respectively. Although this type of extrapolation is contentious and might ignore distance decay and the viability of dormant propagules, it suggests that a large number of propagules can be dispersed by the wind and reach the lake surface, highlighting the potential of resting eggs and desiccated bdelloids dispersed by wind to be colonizers (Frisch *et al.*, 2012; Ortells *et al.*, 2014). The study of the dispersal of dormant propagules by wind with windsocks is useful, but the impact of propagule dispersal on aquatic systems depends on their passive deposition. In contrast, wind direction played a significant role in their deposition, and based on the positive relationships obtained (with the coefficient of the cosine term and the cosine of angles in quadrants between 0° −90° and 270° −360°; see Table 3) and the absence of winds from the northeast in Doñana during the study period, a larger number of dormant propagules appear to be carried by winds from the northwest (between 270° and 360°) than from the southwest (wind directions between 180° and 270°). This is consistent with the predominant wind direction observed in Doñana and the greater number of temporary ponds in the northwest direction.

Table 3. Signs of the sine and cosine functions for the four quadrants of a circle. *Signos del seno y coseno de los cuatro cuadrantes de un círculo.*

Quadrant/Angle	Sine of wind direction	Cosine of wind direction
1º Quadrant: 0°-90° (0 to $\pi/2$)	+	+
2º Quadrant: 90°-180° ($\pi/2$ to π)	+	−
3º Quadrant: 180°-270° (π to $3\pi/2$)	−	−
4º Quadrant: 270°-360° ($3\pi/2$ to 2π)	−	+

Evidence of the viability of dormant propagules transported by wind, rain, birds or other animals has been published (Jenkins & Underwood, 1998; Bohonak & Whiteman, 1999; Figuerola & Green, 2002; Vanschoenwinkel *et al.*, 2008b). Jenkins & Underwood (1998) incubated particles collected with windsocks and rain samplers, hatching only bdelloid rotifers from the wind samples and monogonont rotifers from the rain samples over one year. Although our study design was not appropriate to determine propagule viability because of the long periods between sampling days, the collected dormant propagules were individually isolated and tested under hatching conditions. The scarceness of viable dormant propagules in the automatic wet/dry collectors could be related to the long and harsh environmental conditions suffered by the dormant propagules passively deposited between each sampling date (Moghraby, 1977; Raikow *et al.*, 2007; Branstrator *et al.*, 2013). Despite this, we collected one viable resting rotifer egg in the windsocks and two viable bdelloids in the Ruidera wet collector. If dormant propagules had reached a water body, they might survive for subsequent hatching, but further research on the hatching rates of dispersed dormant propagules is required with shorter intervals between samplings to establish the colonization potential of zooplankton dormant propagules transported through the air.

In summary, this is the first study of the aerial dispersal of zooplankton and bryozoan dormant propagules to differentiate between dry and wet deposition using automated wet/dry collectors. In Doñana, more dormant propagules were collected in dry than in wet atmospheric deposition collectors, which might be related to the difference in the number of days that each wet and dry sampler was opened, and more dormant propagules were intercepted by windsocks than by passive deposition in the collectors. The composition of the propagules collected in the windsocks and those in the atmospheric deposition collectors was similar, suggesting that zooplankton dispersal may be effectively studied with windsocks alone, although some taxonomical groups may not be detected. Most of the collected propagules were resting rotifer eggs, and we also provided limited evidence of their viability following overland dispersal, including the hatched egg in Doñana and the live bdelloids found in Ruidera. Based on these findings, overland movement of zooplankton dormant propagules by wind appears to be infrequent but may influence colonization over long time intervals.

ACKNOWLEDGEMENTS

This study formed part of Emilio Moreno's Ph.D. project CGL2007-65784/BOS, which was funded by the Inter-ministerial Commission of Science and Technology of Spain. The authors are grateful to the Doñana Biological Station and the Ruidera Natural Park and their park rangers, especially Manuel López Sánchez (Ruidera Natural Park), for their support. Meteorological data were provided by the ICTS Doñana Scientific Reserve (ICTS-2009-39), Spanish Ministry of Science and Innovation.

The authors are grateful to Mr. Richard Davies for linguistic improvements to the text, and we also thank two anonymous reviewers for their valuable comments on earlier drafts of this manuscript.

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