Contributions of airborne dispersal and dormant propagule recruitment to the assembly of rotifer and crustacean zooplankton communities in temporary ponds

Journal:	<i>Freshwater Biology</i>
Manuscript ID	FWB-P-Mar-15-0147.R3
Manuscript Type:	Standard Paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Lopes, Paloma; Federal University of Rio de Janeiro, Ecology; Netherlands Institute of Ecology, Aquatic Ecology Bozelli, Reinaldo; Universidade Federal do Rio de Janeiro, Ecology Bini, Luis; Universidade Federal de Goiás, Ecology Santangelo, Jayme; Federal Rural University of Rio de Janeiro, Environmental Sciences Declerck, Steven; Netherlands Institute of Ecology, Department of Aquatic Ecology
Keywords:	Temporary pools < Habitat, Dispersal < Process / Approach / Methods, Zooplankton < Taxonomic Group / Assemblage, Ponds < Habitat, Community < Level of Organisation

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

**Contributions of airborne dispersal and dormant propagule
recruitment to the assembly of rotifer and crustacean zooplankton
communities in temporary ponds**

Paloma M. Lopes^{a, d*}, Reinaldo Bozelli^a, Luis M. Bini^b, Jayme M. Santangelo^c & Steven A.J.
Declerck^d

^a Laboratório de Limnologia, Departamento de Ecologia, Instituto de Biologia, Universidade
Federal do Rio de Janeiro, CCS, Cidade Universitária, Rio de Janeiro, RJ, CEP 21940-590,
Brazil.

^b Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás,
Caixa Postal 131, 74001-900 Goiânia, GO, Brazil.

^c Universidade Federal Rural do Rio de Janeiro, Instituto de Florestas, Departamento de
Ciências Ambientais. Rodovia BR 465 Km 07, 23890-000 - Seropédica, RJ – Brazil.

^d Netherlands Institute of Ecology (NIOO-KNAW), Department of Aquatic Ecology,
Droevendaalsesteeg 10, 6708 PB Wageningen P.O. Box 50, 6700 AB Wageningen, The
Netherlands

***Corresponding author e-mail: paloma.marinho@gmail.com**

Keywords: aerial colonization, metacommunities, passive dispersal, resting egg bank,
zooplankton

SUMMARY

1. Metacommunity theory assumes that communities are not only affected by local processes, but also interact with each other through dispersal. It is generally assumed that zooplankton can quickly recolonize water bodies after droughts, via both dormant egg banks and dispersal of resting eggs. Hitherto, few studies have evaluated the relative importance of resting egg bank recruitment and airborne dispersal in the re-establishment of zooplankton communities.

2. Because zooplankton communities of temporary ponds are frequently confronted by dry phases and have the potential to build up large resting egg banks, we expected the contribution of such resting egg bank to be more important than airborne dispersal for community re-establishment after drought. We also expected that the relative importance of airborne dispersal would be higher for rotifers than for microcrustaceans, as the former group has key traits (e.g. smaller body sizes, shorter generation times and higher reproductive potential) that are thought to enhance the dispersal to and colonization of vacant habitat.

3. We performed an enclosure experiment in the vicinity of seven temporary ponds, simulating the colonization by zooplankton exclusively via the resting egg bank, exclusively via airborne dispersal and via both pathways simultaneously. The enclosures were sampled five times during a period of 53 days.

4. Our results show that zooplankton organisms were able to rapidly colonize the experimental enclosures, either through their resting egg bank or by airborne dispersal of resting eggs. However, microcrustaceans tended to rely more on recolonization from the resting egg banks than rotifers, at least for the spatial and temporal scales considered in our study.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

50 **Introduction**

51 Metacommunity theory states that local community assembly is not only determined by local
52 processes, but also by dispersal (Leibold *et al.*, 2004). Most zooplankton species have the
53 ability to produce resting eggs tolerant to desiccation, permitting organisms to disperse in
54 both time (i.e. from the resting egg bank) and space (i.e. overland) (Bilton, Freeland &
55 Okamura, 2001; Havel & Shurin, 2004; De Meester *et al.*, 2005). Zooplankters are thought to
56 be effective (passive) overland dispersers, especially at small spatial scales (see Havel &
57 Shurin, 2004; Soininen *et al.*, 2007). Many vectors are responsible for the overland transport
58 of zooplankton in its dormant phase, such as invertebrates, birds, mammals and humans
59 (Proctor & Malone, 1965; Brendonck & Riddoch, 1999; Cáceres & Soluk, 2002; Havel &
60 Shurin, 2004; Green & Figuerola, 2005; Vanschoenwinkel *et al.*, 2011), although wind is
61 believed to be the most important (Cáceres & Soluk, 2002; Cohen & Shurin, 2003). However,
62 high genetic divergence among populations (Boileau, Heber & Schwartz, 1992; Campillo *et*
63 *al.*, 2009) and the delay of zooplankton communities in recovering from regional stressors
64 (Gray & Arnott, 2011; Gray & Arnott, 2012) provide evidence that the colonization potential
65 of zooplankton communities has its limitations. Indeed, high dispersal capacity (transport of
66 dormant stages) does not guarantee effective dispersal, which also depends on establishment
67 success. Successful establishment depends on biotic interactions, as well as interactions with
68 the local environment (Shurin, 2000; De Meester *et al.*, 2002).

69 Dispersal in time may be achieved by the accumulation of resting eggs in the sediment
70 and their attachment to plants, with subsequent hatching when suitable conditions are restored
71 (Bilton *et al.*, 2001; Brendonck & De Meester, 2003). Resting eggs can remain viable for
72 decades or longer (Hairston *et al.*, 1995; Hairston, 1996; Cáceres, 1998) and accumulate in
73 high densities in the sediment (Hairston, 1996), playing an important role for the
74 recolonization of temporary aquatic environments (de Stasio, 1989; Hairston, 1996).

Zooplankton populations can quickly recolonize the water column of lacustrine systems after droughts (Brock *et al.*, 2003) and reduce the establishment success of new incoming species via priority effects (De Meester *et al.*, 2002; Havel & Shurin, 2004). Resting egg banks can be impoverished by predation, disease, senescence and dispersal towards other habitats (de Stasio, 1989; Cáceres & Hairston, 1998; Vandekerkhove *et al.*, 2005). Despite their crucial importance to the structure of communities, propagule banks are seldom taken into account in community studies (de Stasio, 1989; Wolf & Carvalho, 1989; Cáceres, 1998; Hairston, Hansen & Schaffner, 2000; Brendonck & De Meester, 2003).

Several studies have tried to infer the importance of overland zooplankton dispersal by observing the colonization process of new habitats (Jenkins & Buikema, 1998; Cáceres & Soluk, 2002; Cohen & Shurin, 2003; Allen, 2007; Louette, De Meester & Declerck, 2008; Vanschoenwinkel *et al.*, 2008a; Juračka *et al.*, in press), the recolonization of restored freshwater systems (Sundermann, Stoll & Haase, 2011; Gray & Arnott, 2012) or by intercepting wind-dispersed dormant propagules (Brendonck, 1999; Vanschoenwinkel *et al.*, 2008b; Vanschoenwinkel *et al.*, 2009). These studies suggested different zooplankton colonization rates depending on factors such as distance and number of source habitats as well as biological interactions. Other studies have mainly documented the importance of resting eggs banks in determining the structure, diversity and dynamics of water-column zooplankton communities (de Stasio, 1989; Cáceres, 1998). Although most studies focusing on colonization through overland dispersal state that overland dispersal is unlikely to be more important for community assembly than resting egg bank recruitment, the relative importance of the both has rarely been investigated simultaneously (but see Gray & Arnott, 2011).

Here, we investigated the relative contributions of resting egg bank recruitment (dispersal in time) and airborne dispersal to the short-term re-establishment of zooplankton communities of temporary ponds. For this, we conducted an enclosure experiment simulating

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

the colonization by zooplankton exclusively via the resting egg bank, exclusively via airborne dispersal and via both pathways simultaneously. Because zooplankton communities of temporary ponds are frequently confronted by dry phases and have the potential to build up large resting egg banks, we expected the contribution of such egg bank to be more important than airborne dispersal for community re-establishment. We also expected that re-establishment of the rotifer communities would rely less on existing resting egg banks than that of microcrustaceans, as the former group is characterized by traits (e.g. larger populations, higher production capacity of smaller dispersal propagules, higher population growth rates and reproductive output) that are expected to be associated with high dispersal and colonization capacities.

Methods

Study Area

We performed an enclosure experiment in March 2010 in the vicinity of seven fishless temporary ponds in the Restinga de Jurubatiba National Park (Northern Rio de Janeiro State in the Southeast of Brazil). The region has a great variety and number of water bodies, such as coastal lakes, coastal lagoons and ponds. The studied ponds are humic, small (maximum surface area of 60 m²), shallow (between 0.1 and 0.5 m), colonized by aquatic macrophytes and hydrologically isolated from other waterbodies. The ponds are surrounded by a *restinga* vegetation and have high dissolved organic carbon concentrations (10-160 mg C L⁻¹), mainly composed of humic substances, due to high leaching of allochthonous DOC from the permeable, sandy soil (Farjalla *et al.*, 2009). These ponds dry out several times a year, resulting in hydroperiods of about five months. At the beginning of this experiment, all ponds had been recently filled by rain.

125

126 *Experimental Design*

127 We used a randomized complete block design, simulating three scenarios of colonization by
128 zooplankton: via the resting egg bank only (EB), via airborne dispersal only (DISP) and via
129 both pathways simultaneously (EB+DISP). Each of the three experimental groups was
130 randomly assigned to one of three enclosures placed at each of the seven ponds (blocks),
131 totalling 21 enclosures. We conducted the experiments in 100 litres plastic enclosures
132 (diameter: 0.73 m; depth: 0.41 m). Each enclosure was thoroughly scrubbed and washed prior
133 to the beginning of the experiment in order to eliminate any resting egg. The enclosures were
134 positioned next to each temporary pond under study (three metres apart approximately). To
135 avoid unnaturally large temperature variations, we buried them but with the top of the
136 enclosures protruding at a height of approximately 20 cm above the ground. We filled the
137 enclosures by pumping pond water first through a 50 μm mesh-size and then through a 10 μm
138 mesh-size plankton net, with the aim to remove all resident zooplankton and their resting
139 eggs. A pilot sampling, where the water of several ponds was filtered following this
140 procedure, showed this method to be 100% efficient (i.e. neither individuals nor resting eggs
141 were found in the samples). Since every pond was inhabited with aquatic macrophytes, we
142 introduced thoroughly rinsed artificial plants.

143 Before filling the enclosures with water, we added three centimetres of sediment from
144 the nearby pond to all enclosures, in order to create a resting egg bank, similarly to Waterkeyn
145 *et al.* (2010). Resting eggs in a sediment layer of this thickness likely form an 'active' egg
146 bank, because they are able to receive hatching cues (Cáceres & Hairston, 1998). The
147 sediment was collected from different parts of the pond (up to a depth of 10 cm), thoroughly
148 mixed and divided in three equal parts. Prior to addition to the enclosures, the sediments of
149 the DISP group were frozen for 48 hours, thawed and refrozen (Emmerson *et al.*, 2001) and

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

150 then autoclaved with the aim to kill all zooplankton resting eggs. Previous tests showed this
151 procedure to be 100% efficient, with no hatchlings being observed for a period of two months.
152 For the experimental group EB, a 10 μm mesh was placed over the enclosures to avoid
153 colonization of zooplankton by airborne dispersal while still allowing for gas exchange. The
154 effectiveness of the 10 μm mesh in preventing zooplankton airborne colonization was tested
155 by us prior to the experiment and by Langley *et al.* (2001). Specifically, after examining the
156 entire sample (100 L of water filtered through a 10 μm mesh-size plankton net) of three 100 L
157 enclosures covered by the 10 μm mesh, no individuals were found. For the experimental
158 groups with dispersal (DISP and EB+DISP), a 1 mm mesh covered the enclosures in order to
159 prevent colonization by invertebrate predators (e.g. insect larvae), while allowing only
160 airborne colonization by zooplankton (i.e. excluding animal vectors).

161 Abiotic and biotic interactions are likely to have an important influence on the
162 establishment success of the zooplankters in our enclosures. Therefore, it is important to point
163 out that the DISP and EB+DISP treatments in our experiment allows evaluation of the
164 combination of effective dispersal with colonization, i.e. transport of resting eggs followed by
165 establishment success, rather than the mere transport of propagules. Similarly, in the
166 experimental groups with resting egg banks (EB and EB+DISP) the establishment of
167 individuals after hatching from the sediment may also be determined by the outcome of
168 ecological interactions.

169 The enclosures were sampled for zooplankton and water quality five times during a
170 time span of 53 days (at days 5, 15, 22, 38 and 53). The choice of the duration of the
171 experiment was based on a pilot experiment specifically designed to assess the time needed
172 for airborne colonization by rotifers and microcrustaceans to take place (see Fig. S1). At each
173 sampling occasion, we collected zooplankton by filtering 4 L of water through a 50 μm mesh-
174 size plankton net. We also took zooplankton samples from the seven ponds on the first day of

1
2
3 175 the experiment by filtering 100 L of water (collected with a bucket in different parts of each
4
5 176 pond) through a 50 µm mesh-size plankton net. Samples were immediately fixed with 4%
6
7 177 formaldehyde buffered with calcium carbonate. Different nets and buckets were used for each
8
9
10 178 experimental group and rinsed thoroughly between each sampling event to avoid
11
12 179 contamination.

13
14 180 Zooplankton individuals were identified to the lowest possible taxonomic unit.
15
16 181 Triplicate aliquots of zooplankton samples were counted in either a Sedgewick-Rafter cell
17
18 182 under a microscope (for rotifers and nauplii) or in open chambers under a stereomicroscope
19
20 183 (for microcrustaceans). At least 200 individuals per aliquot were counted. In addition, we
21
22 184 screened the entire sample aiming also to detect and enumerate rare species. In each enclosure
23
24 185 and pond, we measured pH (Analion PM 608), dissolved oxygen (YSI 95 probe), temperature,
25
26 186 salinity and conductivity (YSI 30 multifunctional probe) and chlorophyll-*a* content
27
28 187 (AquaFluor™ Handheld Fluorometer/Turbidimeter).
29
30
31
32 188

33 34 189 *Statistical Analyses*

35
36 190 We applied repeated measures ANOVA (RM-ANOVA) to test for effects of experimental
37
38 191 group (EB, DISP and EB+DISP) and ponds (block) on square-root-transformed species
39
40 192 richness and on the environmental variables temperature, conductivity, salinity, pH, dissolved
41
42 193 oxygen and chlorophyll-*a*, with the time of sampling as the repeated factor.
43
44

45 194 Differences in community composition among the experimental groups were
46
47 195 investigated through a permutational multivariate analysis of variance (PerMANOVA;
48
49 196 Anderson, 2001) for each sampling date separately, with block as a random effect and
50
51 197 experimental group as a fixed effect. The analyses were based on square-root transformed
52
53 198 abundance data using Bray-Curtis distances and significances were tested with 4999
54
55 199 permutations. These were followed by pairwise comparisons of experimental groups when
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

significant effects were detected. Plots from canonical analysis of principal coordinates (CAP, Anderson & Willis, 2003) were used to visualize Bray–Curtis dissimilarity patterns among zooplankton communities. One of the enclosures turned anoxic during the experiment; therefore this pond was not included in the analyses.

All statistical analyses were carried out in R 2.13.0 (R Development Core Team 2011) using the *aov* function and the *adonis* and *capscale* functions available in the *vegan* package (Oksanen *et al.*, 2011). Separate analyses were performed on data for each group of organisms (rotifers and microcrustaceans).

Results

Environmental conditions varied among enclosures, but in general, they did not differ among experimental groups (except conductivity and temperature; see Table 1) and remained constant during the sampling period (except temperature and oxygen, where the latter increased over time for almost every enclosure; mean coefficient of variation = 0.17; Table 1). Differences in temperature and conductivity between experimental groups were probably due to the presence of the 10 µm mesh on the EB enclosures that slightly increased the temperature of the water (mean difference of 0.4°C between EB and the experimental groups DISP and EB + DISP) and decreased the conductivity (mean difference of 21.2 µScm⁻² between EB and DISP and of 17.7 µScm⁻² between EB and EB + DISP). The decrease in conductivity in the enclosures with the 10 µm mesh may be associated to lower evaporation. Despite being statistically significant, the differences in conductivity between the experimental groups were small, especially for these coastal aquatic systems that experience high variation in the values of conductivity throughout time, and had most probably no effect on zooplankton community responses to the experimental groups. Over the study period, the temperature of the enclosures ranged from 21.3 to 34°C (mean = 26.2°C ± 2.9), conductivity

225 ranged from 50 to 665 μScm^{-2} (mean = $233 \mu\text{Scm}^{-2} \pm 180$), salinity ranged from 0 to 0.3
 226 (mean = 0.1 ± 0.1), pH ranged from 3.2 to 5.6 (mean = 4.1 ± 0.5), dissolved oxygen ranged
 227 from 1.3 to 8.4 mg L^{-1} (mean = $5.3 \text{ mg L}^{-1} \pm 1.7$) and chlorophyll-*a* ranged from 2.3 to 20.4
 228 $\mu\text{g L}^{-1}$ (mean = $9.7 \mu\text{g L}^{-1} \pm 4.4$). The pH of the temporary (natural) ponds ranged from 3.2 to
 229 4.2, salinity ranged from 0 to 0.3, dissolved oxygen ranged from 1.1 to 4.7 mg L^{-1} and
 230 chlorophyll-*a* ranged from 4.5 to 22 $\mu\text{g L}^{-1}$.

231 We identified a total of 51 rotifers and 25 microcrustacean species during the
 232 experiment (see Table S1). In the natural ponds, we detected a total of 34 rotifer (mean local
 233 richness: 11; range: 8 - 17) and 30 microcrustacean species (mean local richness: 11; range: 6
 234 - 17) and most of these species were also found in the enclosures (Table S1).

235 For both groups of organisms, total species richness was higher for enclosures with a
 236 resting egg bank (EB+DISP and EB) than those receiving airborne dispersers only (DISP; Fig.
 237 1a). Of the 51 species of rotifers, 14 were uniquely observed in enclosures exclusively
 238 allowing resting egg bank recruitment (EB) and seven species were uniquely recorded in
 239 enclosures allowing dispersal only (DISP) (Fig. 1b). However, the majority of the species of
 240 rotifers (27) were observed at least once in both experimental groups. Of the 25 species of
 241 microcrustaceans, 12 were uniquely found in enclosures exclusively allowing resting egg
 242 bank recruitment (EB), whereas only five species were uniquely found in enclosures allowing
 243 only the entrance of airborne dispersers (DISP) (Fig. 1b). For rotifers, a majority of species
 244 was able to colonize enclosures both by hatching from the resting egg bank and through
 245 airborne dispersal (~55 % of the species). On the other hand, only 24 % of the species of
 246 microcrustaceans were able to colonize the enclosures via both pathways (Table S1).

247 The proportion of species that were locally present (observed in EB group or in the
 248 pond community) but missing in the dispersal group (DISP) was considerably higher for
 249 microcrustaceans (60%; range: 38-78%) than rotifers (28%; range: 0-46%) (Fig. 2).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Nevertheless, the contribution of species that were solely detected in the DISP enclosures and not in the corresponding pond or EB enclosures equalled 18% (range: 6-38%) for rotifers and 14% (range: 0-38%) for microcrustaceans, suggesting that the assemblages in the DISP enclosures may also have been enriched by species from the regional species pool (Fig. 2).

Species richness of both rotifers and microcrustaceans increased with time in all groups. Rotifer species richness tended to level off after 20 days with averages well within the range of values observed for the ponds (mean: 11; range: 8-17). Microcrustacean species richness showed a much weaker tendency to level off only towards the end of the experiment (> 40 days) and stayed well below the species numbers observed in ponds (mean: 11; range: 6-17). Rotifer species richness did not differ significantly among experimental groups (Table 2). Conversely, microcrustacean species richness in groups with a resting egg bank (EB and EB+DISP) increased more rapidly and reached maxima about twice as high than in the group with only airborne dispersal (DISP) (Fig. 3 & Table 2). On average, most microcrustacean species (60%) that hatched from the resting egg bank appeared in the first 15 days, whereas only 18% of the species that arrived through dispersal were detected in the same period.

Rotifers and microcrustacean zooplankton also showed different patterns of community differentiation in species composition among experimental groups during the course of time. For rotifers, initial differences between enclosures with egg banks (EB and EB+DISP) and enclosures with airborne dispersal only (DISP) diminished with time (Fig. 4, Table 3 & Table S2). Experimental groups differed only significantly at days 15 and 22 (Table 3). We found no significant differences among experimental groups for microcrustacean composition during the first two sampling dates (Fig. 5, Table 3 & Table S2). The rest of the experiment, however, was characterized by a tendency of the DISP group to differ from the EB and EB+DISP enclosures (Fig. 5, Table 3 & Table S2).

Discussion

We found that zooplankton organisms were able to rapidly colonize the experimental enclosures, either through their resting egg bank or by airborne dispersal. We, nevertheless, observed some marked differences in this colonization process between rotifers and microcrustaceans. Rotifer communities showed a rapid accumulation of species in both experimental groups with a resting egg bank and with only airborne dispersal, reaching species numbers similar to the levels of natural ponds already a few weeks after the start of the experiment. Community build-up of microcrustaceans, on the other hand, was markedly slower and average species richness stayed lower than natural pond levels throughout the experiment. Moreover, microcrustacean species richness increased more rapidly in enclosures with a resting egg bank than in enclosures with airborne dispersal only. Finally, compositional differences of rotifer communities between enclosures with only airborne dispersal and enclosures with resting egg banks converged with time, whereas the respective microcrustacean communities diverged with time.

The high colonization rates of rotifers in enclosures allowing for dispersal only and the absence of systematic differences between this group and the egg bank derived communities are remarkable. These results suggest a high potential of rotifers to colonize new habitat patches through airborne dispersal in a very short time span. In contrast, colonization of crustacean zooplankton was considerably slower. This may, at least partly, have been due to the lower development rates of crustacean zooplankton compared to rotifers, resulting in a longer time span between the arrivals of species through airborne dispersal, the hatching of their resting eggs and the detection of their populations in the samples. Nevertheless, our results are also consistent with the idea of a stronger dispersal limitation of microcrustaceans compared to rotifers and, therefore, a higher dependency of resting egg banks for their community establishment. The latter interpretation is supported by the observation that the

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

proportion of microcrustacean species that were locally present at sites (egg bank experimental group + pond) but found to be missing in the dispersal experimental group was considerably higher for cladocerans (60%) than rotifers (28%) (Fig. 2). These results are consistent with experimental field studies that reported rotifers rather than microcrustaceans to be among the first colonizers in enclosures or newly created artificial ponds (see Jenkins & Buikema, 1998; Cáceres & Soluk, 2002; Frisch & Green, 2007; Frisch *et al.*, 2012). It is also consistent with the data obtained by Gray & Arnott (2011; 2012) whom emphasized that dispersal limitation may be an important impediment for recovery of microcrustacean communities damaged by acidification. Jenkins & Underwood (1998) studied wind dispersal in zooplankton using windsocks and rain samplers and only collected rotifers in their samples. Cohen & Shurin (2003), on the other hand, found that dispersal abilities varied substantially among species, independently of the group of organisms. Our results are also in agreement with those of field surveys that suggest weaker spatial patterning in metacommunities of rotifers than microcrustaceans after taking into account the effects of environmental gradients (De Bie *et al.*, 2012; Frisch *et al.*, 2012).

There are several potential explanations why rotifer populations may be faster colonizers of vacant habitats than microcrustacean populations. First, due to their smaller size, rotifers produce smaller propagules than microcrustaceans, which require less energy to be transported to another location (De Bie *et al.*, 2012). This may be especially relevant in the case of airborne dispersal (Finlay, 2002; Shurin, Cottenie & Hillebrand, 2009; Farjalla *et al.*, 2012). Second, rotifers have shorter generation times and can reach higher population densities than cladocerans (Finlay, 2002; Cohen & Shurin, 2003; Rundle, Bilton & Foggo, 2007). This also results in a higher potential of propagule production and, therefore, a larger pool of propagules that can be exchanged among patches of available habitat at the regional scale. Indeed, former studies with estimates of egg bank sizes indicate that densities of rotifer

resting eggs in lake or pond sediments are usually much higher than those of microcrustaceans (Hairston, 1996; Maia-Barbosa *et al.*, 2003; García-Roger, Carmona & Serra, 2006; Santangelo *et al.*, 2015). Third, in contrast to rotifers, microcrustaceans such as copepods are only able to reproduce sexually. Together with their longer generation times and lower production of propagules, sexual zooplankton species can be more susceptible to Allee effects than cyclic parthenogens, reducing the chance of successful population establishment (Gray & Arnott, 2012). In our study, this may be exemplified by the case of the Calanoida species *Diaptomus azureus*. This taxon was found frequently in enclosures with resting egg banks but was never found in enclosures with airborne dispersal only. On the other hand, all Cyclopoida species were found in enclosures allowing airborne dispersal. Although they reproduce sexually and undergo diapause as copepodites and adults (including fertilized female adults; Gyllstrom & Hansson, 2004), they are considered to be good colonizers (Cáceres & Soluk, 2002; Frisch & Green, 2007). Their colonization success has been related to a fast development and the ability to store sperm that allows fertilization of multiple clutches in a single mating (Frisch & Green, 2007). Finally, propagules of several microcrustaceans (e.g. Chydoridae, Macrothricidae and a few Sididae) have specific traits, such as sticky envelopes or hooks, that render them more likely to become firmly attached to the vegetation (Fryer, 1996; Korovchinsky & Boikova, 1996; Brendonck & De Meester, 2003), and may effectively reduce their potential for aerial dispersal (Fryer, 1972; Fryer, 1996).

The colonization rates observed in enclosures with only airborne dispersal were high compared with other studies. While the majority of rotifer and microcrustacean species that colonized our enclosures throughout the experiment did so in approximately 20 and 40 days, respectively, most other studies have reported longer times, ranging from three to 12 months (Holland & Jenkins, 1998; Jenkins & Buikema, 1998; Cáceres & Soluk, 2002; Louette & De

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Meester, 2005; Louette *et al.*, 2008; Frisch *et al.*, 2012; Taylor & Duggan, 2012). One important reason for these fast colonization rates undoubtedly is the close proximity of our enclosures to the source ponds. Nevertheless, the average percentage of species that were solely detected in the dispersal only experimental groups and not in the corresponding pond or enclosures with resting egg banks equalled 18% (range: 6-38%) for rotifers and 14% for microcrustacean species (range: 0-38%). Thus, a substantial proportion of species may have come from ponds other than the ones used in the experiments. Some features of the study area may have facilitated the arrival of species from the regional species pool. The area is a coastal region that is characterized by the occurrence of quasi-permanent winds that can often be very strong. The region contains hundreds of temporary pond systems. Airborne dispersal of zooplankton is most likely facilitated by the exposure of dry pond sediments to strong winds during droughts (Vanschoenwinkel *et al.*, 2008b). A period of rains had begun when we started the experiment, but because it was not enough to fully fill the ponds large areas of their sediments were still exposed to wind actions throughout the duration of the experiment. In summary, the fact that the enclosures were placed at a short distance from sources of colonizers (an average of three meters) and in a windy region has likely increased the importance of airborne dispersal relative to the resting egg bank. It is therefore likely that this contribution would have been lower if distances between ponds and experimental enclosures had been larger. Our findings nevertheless indicate that at the small spatial and temporal scales of our experiment rotifers are able to more rapidly colonize temporary ponds than cladocerans.

Our results suggest that after a disturbance (e.g. drought, acidification, eutrophication), in the absence of a resting egg bank, the recovery of microcrustacean communities may be delayed by dispersal limitation, especially if surrounding aquatic ecosystems are also impacted or isolated. As egg banks can be potentially depleted by impacts such as prolonged

drought (Brendonck & Riddoch, 2000; Jenkins & Boulton, 2007), acidification (Arnott & Yan, 2002) and farming practices (Frisch, Arechederra & Green, 2009), lack of connectivity may lead to local extinction of microcrustacean species (Lake, 2011). For example, in lakes recovering from acidification it has been observed that the re-establishment of microcrustaceans was low for species dependent on overland dispersal (Gray & Arnott, 2011; Gray & Arnott, 2012).

In conclusion, we observed that the recolonization of temporary environments seems to be influenced by both the resting egg bank and airborne dispersal, but their relative importance depends on the zooplankton group. Small organisms, such as rotifers, are capable of rapidly recolonizing these habitats via both pathways over short spatial and temporal scales. On the other hand, the relative importance of the resting egg bank for community reestablishment increases substantially when organisms are large and with lower dispersal abilities (cladocerans).

Acknowledgments

Our research was financed by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). P.M.L is grateful to CAPES, CNPq and FAPERJ Institutions for post-graduate scholarships. We are also indebted to the staff of the Núcleo de Desenvolvimento Sócio-Ambiental de Macaé (NUPEM/UFRJ) and to Instituto Chico Mendes for logistical assistantship and permission for sampling the ponds at the Restinga de Jurubatiba National Park, respectively. We thank Dr. Vinicius F. Farjalla (Universidade Federal do Rio de Janeiro) for critical comments on our manuscript.

References

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

399 Allen M.R. (2007) Measuring and modeling dispersal of adult zooplankton. *Oecologia*, **153**,
400 135-143.

401 Anderson M.J. (2001) A new method for non-parametric multivariate analysis of variance.
402 *Austral Ecology*, **26**, 32-46.

403 Anderson M.J. & Willis T.J. (2003) Canonical analysis of principal coordinates: A useful
404 method of constrained ordination for ecology. *Ecology*, **84**, 511-525.

405 Arnott S.E. & Yan N.Y. (2002) The influence of drought and re-acidification on zooplankton
406 emergence from resting stages *Ecological Applications*, **12**, 138-153.

407 Bilton D.T., Freeland J.R. & Okamura B. (2001) Dispersal in freshwater invertebrates. *Annual*
408 *Review of Ecology and Systematics*, **32**, 159-181.

409 Boileau M.G., Heber P.D.N. & Schwartz S.S. (1992) Non-equilibrium gene frequency
410 divergence: persistent founder effects in natural populations. *Journal of Evolutionary*
411 *Biology*, **5**, 25-39.

412 Brendonck L. & Riddoch B.J. (1999) Wind-borne short-range egg dispersal in anostracans
413 (Crustacea : Branchiopoda). *Biological Journal of the Linnean Society*, **67**, 87-95.

414 Brendonck L. (1999) Wind-borne short-range egg dispersal in anostracans (Crustacea:
415 Branchiopoda). *Biological Journal of the Linnean Society*, **67**, 87-95.

416 Brendonck L. & Riddoch B.J. (2000) Egg bank dynamics in anostracan desert rock pool
417 populations (Crustacea: Branchiopoda). *Archiv Fur Hydrobiologie*, **148**, 71-84.

418 Brendonck L. & De Meester L. (2003) Egg banks in freshwater zooplankton: evolutionary
419 and ecological archives in the sediment. *Hydrobiologia*, **491**, 65-84.

420 Brock M.A., Nielsen D.L., Shiel R.J., Green J.D. & Langley J.D. (2003) Drought and aquatic
421 community resilience: the role of eggs and seeds in sediments of temporary wetlands.
422 *Freshwater Biology*, **48**, 1207-1218.

- 423 Cáceres C.E. (1998) Interspecific variation in the abundance, production, and emergence of
424 *Daphnia* diapausing eggs. *Ecology*, **79**, 1699-1710.
- 425 Cáceres C.E. & Hairston N.G. (1998) Benthic-pelagic coupling in planktonic crustaceans: the
426 role of the benthos. *Archiv für Hydrobiologie Special Issues Advancing Limnology*,
427 **52**, 163-174.
- 428 Cáceres C.E. & Soluk D.A. (2002) Blowing in the wind a field test of overland dispersal and
429 colonization by aquatic invertebrates. *Oecologia*, **131**, 402-408.
- 430 Campillo S., Garcia-Roger E.M., Carmona M.J., Gomez A. & Serra M. (2009) Selection on
431 life-history traits and genetic population divergence in rotifers. *Journal of*
432 *Evolutionary Biology*, **22**, 2542-2553.
- 433 Cohen G.M. & Shurin J.B. (2003) Scale-dependence and mechanisms of dispersal in
434 freshwater zooplankton. *Oikos*, **103**, 603-617.
- 435 De Bie T., De Meester L., Brendonck L., Martens K., Goddeeris B., Ercken D., Hampel H.,
436 Denys L., Vanhecke L., Van Der Gucht K. *et al.* (2012) Body size and dispersal mode
437 as key traits determining metacommunity structure of aquatic organisms. *Ecology*
438 *Letters*, **15**, 740-747.
- 439 De Meester L., Gomez A., Okamura B. & Schwenk K. (2002) The Monopolization
440 Hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta*
441 *Oecologica-International Journal of Ecology*, **23**, 121-135.
- 442 De Meester L., Declerck S., Stoks R., Louette G., Van De Meutter F., De Bie T., Michels E.
443 & Brendonck L. (2005) Ponds and pools as model systems in conservation biology,
444 ecology and evolutionary biology. *Aquatic Conservation-Marine and Freshwater*
445 *Ecosystems*, **15**, 715-725.
- 446 De Stasio B.T., Jr. (1989) The seed bank of a freshwater crustacean: copepodology for the
447 plant ecologist. *Ecology*, **70**, 1377-1389.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

448 Emmerson M.C., Solan M., Emes C., Paterson D.M. & Raffaelli D. (2001) Consistent
449 patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature*,
450 **411**, 73-77.

451 Farjalla V.F., Amado A.M., Suhett A.L. & Meirelles-Pereira F. (2009) DOC removal
452 paradigms in highly humic aquatic ecosystems. *Environmental Science & Pollution*
453 *Research*, **16**, 531-538.

454 Farjalla V.F., Srivastava D.S., Marino N.A.C., Azevedo F.D., Dib V., Lopes P.M., Rosado
455 A.S., Bozelli R.L. & Esteves F.A. (2012) Ecological determinism increases with
456 organism size. *Ecology*, **93**, 1752-1759.

457 Finlay B.J. (2002) Global dispersal of free-living microbial eukaryote species. *Science*, **296**,
458 1061-1063.

459 Frisch D. & Green A.J. (2007) Copepods come in first: rapid colonization of new temporary
460 ponds. *Fundamental and Applied Limnology*, **168**, 289-297.

461 Frisch D., Arechederra A. & Green A.J. (2009) Recolonisation potential of zooplankton
462 propagule banks in natural and agriculturally modified sections of a semiarid
463 temporary stream (Doñana, Southwest Spain). *Hydrobiologia*, **624**.

464 Frisch D., Cottenie K., Badosa A. & Green A.J. (2012) Strong spatial influence on
465 colonization rates in a pioneer zooplankton metacommunity. *Plos One*, **7**, e40205.

466 Fryer G. (1972) Observations on the ephippiaof certain macrothricid cladocerans. *Zoological*
467 *Journal of the Linnean Society*, **51**, 79-96.

468 Fryer G. (1996) Diapause, a potent force in the evolution of freshwater crustaceans.
469 *Hydrobiologia*, **320**, 1-14.

470 García-Roger E.M., Carmona M.J. & Serra M. (2006) Patterns in rotifer diapausing egg
471 banks: Density and viability. *Journal of Experimental Marine Biology and Ecology*,
472 **336**, 198-210.

- 473 Gray D.K. & Arnott S.E. (2011) Does dispersal limitation impact the recovery of zooplankton
474 communities damaged by a regional stressor? *Ecological Applications*, **21**, 1241-1256.
- 475 Gray D.K. & Arnott S.E. (2012) The role of dispersal levels, Allee effects and community
476 resistance as zooplankton communities respond to environmental change. *Journal of*
477 *Applied Ecology*, **49**, 1216-1224.
- 478 Green A.J. & Figuerola J. (2005) Recent advances in the study of long-distance dispersal of
479 aquatic invertebrates via birds. *Diversity and Distributions*, **11**, 149-156.
- 480 Gyllstrom M. & Hansson L.A. (2004) Dormancy in freshwater zooplankton: Induction,
481 termination and the importance of benthic-pelagic coupling. *Aquatic Sciences*, **66**,
482 274-295.
- 483 Hairston N.G., Vanbrunt R.A., Kearns C.M. & Engstrom D.R. (1995) Age and survivorship
484 of diapausing eggs in a sediment egg bank *Ecology*, **76**, 1706-1711.
- 485 Hairston N.G. (1996) Zooplankton egg banks as biotic reservoirs in changing environments.
486 *Limnology and Oceanography*, **41**, 1087-1092.
- 487 Hairston N.G., Hansen A.M. & Schaffner W.R. (2000) The effect of diapause emergence on
488 the seasonal dynamics of a zooplankton assemblage. *Freshwater Biology*, **45**, 133-
489 145.
- 490 Havel J.E. & Shurin J.B. (2004) Mechanisms, effects, and scales of dispersal in freshwater
491 zooplankton. *Limnology and Oceanography*, **49**, 1229-1238.
- 492 Holland T.A. & Jenkins D.G. (1998) Comparison of processes regulating zooplankton
493 assemblages in new freshwater pools. *Hydrobiologia*, **387/388**, 207-214.
- 494 Jenkins D.G. & Buikema A.L. (1998) Do similar communities develop in similar sites? A test
495 with zooplankton structure and function. *Ecological Monographs*, **68**, 421-443.
- 496 Jenkins D.G. & Underwood M.O. (1998) Zooplankton may not disperse readily in wind, rain,
497 or waterfowl. *Hydrobiologia*, **387**, 15-21.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Jenkins K.M. & Boulton A.J. (2007) Detecting impacts and setting restoration targets in arid-zone rivers: aquatic micro-invertebrate responses to reduced floodplain inundation. *Journal of Applied Ecology*, **44**, 833-842.

Juračka P.J., Declerck S.A.J., Vondrák D., Beran L., Černý M. & Petrusek A. (in press) Naturally heterogeneous landscape can effectively slow down dispersal of aquatic microcrustaceans. *Oecologia*, in press.

Korovchinsky N.M. & Boikova O.S. (1996) The resting eggs of the Ctenopoda (Crustacea: Branchiopoda): a review. *Hydrobiologia*, **320**, 131-140.

Lake P.S. (2011) *Drought and aquatic ecosystems: Effects and responses*, Wiley-Blackwell, West Sussex, UK.

Langley J.M., Shiel R.J., Nielsen D.L. & Green J.D. (2001) Hatching from the sediment egg-bank, or aerial dispersing? - the use of mesocosms in assessing rotifer biodiversity. *Hydrobiologia*, **446/447**, 203-211.

Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F., Holt R.D., Shurin J.B., Law R., Tilman D. *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601-613.

Louette G. & De Meester L. (2005) High dispersal capacity of cladoceran zooplankton in newly founded communities. *Ecology*, **86**, 353-359.

Louette G., De Meester L. & Declerck S. (2008) Assembly of zooplankton communities in newly created ponds. *Freshwater Biology*, **53**, 2309-2320.

Maia-Barbosa P.M., Eskinazi-Sant'anna E.M., Valadares C.F. & Pessoa G.C.D. (2003) The resting eggs of zooplankton from a tropical, eutrophic reservoir (Pampulha Reservoir, south-east Brazil). *Lakes & Reservoirs: Research and Management*, **8**, 269-275.

- Oksanen J., Blanchet F.G., Kindt R., Legendre P., O'hara R.B., Simpson G.L., Solymos P.,
Stevens M.H.H. & Wagner H. (2011) Vegan: Community Ecology Package. *R*
package version 1.17-11. <http://CRAN.R-project.org/package=vegan>.
- Proctor V.W. & Malone C.R. (1965) Further evidence of the passive dispersal of small
aquatic organisms via the intestinal-tract of birds. *Ecology*, **46**, 728-729.
- Rundle S.D., Bilton D.T. & Foggo A. (2007) By wind, wings or water: body size, dispersal
and range size in aquatic invertebrates. In: *Body Size: The Structure and Function of*
Aquatic Ecosystems. (Eds A.G. Hildrew & D.G. Raffaelli & R. Edmunds-Brown), pp.
186-209. Cambridge University Press, Cambridge.
- Santangelo J.M., Lopes P.M., Nascimento M.O., Fernandes A.P.C., Bartole S., Figueiredo-
Barros M.P., Leal J.J.F., Esteves F.A., Bonecker C.C. & Bozelli R.L. (2015)
Community structure of resting egg banks and concordance patterns between dormant
and active zooplankters in tropical lakes. *Hydrobiologia*, **758**, 183-195.
- Shurin J.B. (2000) Dispersal limitation, invasion resistance, and the structure of pond
zooplankton communities. *Ecology*, **81**, 3074-3086.
- Shurin J.B., Cottenie K. & Hillebrand H. (2009) Spatial autocorrelation and dispersal
limitation in freshwater organisms. *Oecologia*, **159**, 151-159.
- Soininen J., Kokocinski M., Estlander S., Kotanen J. & Heino J. (2007) Neutrality, niches,
and determinants of plankton metacommunity structure across boreal wetland ponds.
Ecoscience, **14**, 146-154.
- Sundermann A., Stoll S. & Haase P. (2011) River restoration success depends on the species
pool of the immediate surroundings. *Ecological Applications*, **21**, 1962-1971.
- Taylor C.M. & Duggan I.C. (2012) Can biotic resistance be utilized to reduce establishment
rates of non-indigenous species in constructed waters? *Biological Invasions*, **14**, 307-
322.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

546 Vandekerkhove J., Louette G., Brendonck L. & De Meester L. (2005) Development of
547 cladoceran egg banks in new and isolated pools. *Archiv Fur Hydrobiologie*, **162**, 339-
548 347.

549 Vanschoenwinkel B., Gielen S., Vandewaerde H., Seaman M. & Brendonck L. (2008a)
550 Relative importance of different dispersal vectors for small aquatic invertebrates in a
551 rock pool metacommunity. *Ecography*, **31**, 567-577.

552 Vanschoenwinkel B., Gielen S., Seaman M. & Brendonck L. (2008b) Any way the wind
553 blows - frequent wind dispersal drives species sorting in ephemeral aquatic
554 communities. *Oikos*, **117**, 125-134.

555 Vanschoenwinkel B., Gielen S., Seaman M. & Brendonck L. (2009) Wind mediated dispersal
556 of freshwater invertebrates in a rock pool metacommunity: differences in dispersal
557 capacities and modes. *Hydrobiologia*, **635**, 363-372.

558 Vanschoenwinkel B., Waterkeyn A., Nhiwatiwa T., Pinceel T., Spooren E., Geerts A., Clegg
559 B. & Brendonck L. (2011) Passive external transport of freshwater invertebrates by
560 elephant and other mud-wallowing mammals in an African savannah habitat.
561 *Freshwater Biology*, **56**, 1606-1619.

562 Waterkeyn A., Vanschoenwinkel B., Grillas P. & Brendonck L. (2010) Effect of salinity on
563 seasonal community patterns of Mediterranean temporary wetland crustaceans: A
564 mesocosm study. *Limnology and Oceanography*, **55**, 1712-1722.

565 Wolf H.G. & Carvalho G.R. (1989) Resting eggs of lake-*Daphnia* II. *In situ* observations on
566 the hatching of eggs and their contribution to population and community structure
567 *Freshwater Biology*, **22**, 471-478.

Table 1. Summary of results from RM-ANOVA for environmental variables testing the effects of experimental groups and sampling time. Bolded *F*-values indicate statistically significant effects ($P < 0.05$). *df*, degrees of freedom.

Variables	Source	<i>df</i>	<i>F</i>	<i>P</i>
Temperature	Group (G)	2	6.35	0.017
	Block	5	137.9	
	Residual	10		
	Time (T)	4	30.92	<0.001
	(G) x (T)	8	0.13	0.997
Salinity	Group (G)	2	2.38	0.142
	Block	5	73.64	
	Residual	10		
	Time (T)	4	0.45	0.776
	(G) x (T)	8	0.27	0.973
Conductivity	Group (G)	2	10.74	0.003
	Block	5	402.5	
	Residual	10		
	Time (T)	4	0.47	0.760
	(G) x (T)	8	0.08	0.999
pH	Group (G)	2	2.50	0.132

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

	Block	5	19.50	
	Residual	10		
	Time (T)	4	1.03	0.399
	(G) x (T)	8	0.58	0.790
Dissolved oxygen	Group (G)	2	2.16	0.167
	Block	5	9.81	
	Residual	10		
	Time (T)	4	24.42	<0.001
	(G) x (T)	8	1.84	0.088
Chlorophyll <i>a</i>	Group (G)	2	1.84	0.209
	Block	5	32.14	
	Residual	10		
	Time (T)	4	0.71	0.412
	(G) x (T)	8	0.07	0.929

573

574

Table 2. Results from RM-ANOVA for the species richness of rotifers and microcrustaceans as response variables and experimental groups and time as explanatory variables. Bolded *F*-values indicate statistically significant effects ($P < 0.05$). *df*: degrees of freedom.

Variables	Source	<i>df</i>	<i>F</i>	<i>P</i>
Rotifers	Group (G)	2	2.16	0.1658
	Block	5	2.58	
	Residual	10		
	Time (T)	4	29.34	<0.001
	(G) x (T)	8	1.28	0.2699
Microcrustaceans	Group (G)	2	17.42	<0.001
	Block	5	6.63	
	Residual	10		
	Time (T)	4	35.01	<0.001
	(G) x (T)	8	0.89	0.5267

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table 3. Results of PerMANOVA tests for differences among experimental groups for rotifers and microcrustaceans performed on Bray–Curtis dissimilarity matrix. Bolded *F*-values indicate statistically significant effects ($P < 0.05$). In all of the cases, tests were based on 2 and 15 degrees of freedom.

	Rotifers			Microcrustaceans		
	R^2	F	P	R^2	F	P
5 days	0.18	0.96	0.160	0.09	0.41	1
15 days	0.18	1.69	0.005	0.16	0.97	0.625
22 days	0.22	2.11	0.007	0.18	1.40	0.008
38 days	0.12	1.02	0.076	0.17	1.42	0.027
53 days	0.10	0.83	0.295	0.17	1.39	0.008

583

Figure legends

Figure 1. (A) Number of species of rotifers and microcrustaceans identified during the experiment in each of the experimental groups (all experimental blocks and sampling dates combined; DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal). (B) Number of species of rotifers and microcrustaceans observed uniquely in enclosures allowing dispersal only (Dispersal only), of species observed uniquely in enclosures exclusively allowing resting egg bank recruitment (Resting egg bank only) and of species observed in both enclosures allowing egg bank recruitment and airborne dispersal (belonging to EB and DISP; Both).

Figure 2. Percentage of species of rotifers and microcrustaceans found to be present locally (observations in the corresponding pond or EB) but absent in the dispersal only group (EB + Pond), percentage of species exclusively found in DISP (from elsewhere; Dispersal) and percentage of species found locally and in DISP (EB + Pond + DISP) for each experimental block.

Figure 3. Mean ($\pm$ standard error) species richness of rotifers (top) and microcrustaceans (bottom) in each experimental group during the course of time. Results were based on the actual species richness found in the enclosures in a given time. DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal.

Figure 4. Ordination plots of sample scores from a Canonical Analysis of Principal Coordinates (CAP) performed on the Bray–Curtis dissimilarity matrices of rotiferan communities for each of the sampling events. DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal. Data from the first

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

609 sampling date (i.e. after 5 days) were not analysed because most of the enclosures were not
610 colonized at that time.
611
612 **Figure 5.** Ordination plots of sample scores from a Canonical Analysis of Principal
613 Coordinates (CAP) performed on the Bray–Curtis dissimilarity matrices of microcrustacean
614 communities for each of the sampling events. DISP, airborne dispersal only; EB, resting egg
615 bank only; EB+DISP, resting egg bank combined with airborne dispersal. Data from the first
616 sampling date (i.e. after 5 days) were not analysed because most of the enclosures were not
617 colonized at that time. There are missing data for DISP for the sampling dates 15 and 22 days
618 due to the absence of species in the samples.

(A) Number of species of rotifers and microcrustaceans identified during the experiment in each of the experimental groups (all experimental blocks and sampling dates combined; DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal). (B) Number of species of rotifers and microcrustaceans observed uniquely in enclosures allowing dispersal only (Dispersal only), of species observed uniquely in enclosures exclusively allowing resting egg bank recruitment (Resting egg bank only) and of species observed in both enclosures allowing egg bank recruitment and airborne dispersal (belonging to EB and DISP; Both).

99x129mm (300 x 300 DPI)

Percentage of species of rotifers and microcrustaceans found to be present locally (observations in the corresponding pond or EB) but absent in the dispersal only group (EB + Pond), percentage of species exclusively found in DISP (from elsewhere; Dispersal) and percentage of species found locally and in DISP (EB + Pond+ DISP) for each experimental block.
80x133mm (300 x 300 DPI)

Mean ($\pm$ standard error) species richness of rotifers (top) and microcrustaceans (bottom) in each experimental group during the course of time. Results were based on the actual species richness found in the enclosures in a given time. DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal.

224x323mm (300 x 300 DPI)

Ordination plots of sample scores from a Canonical Analysis of Principal Coordinates (CAP) performed on the Bray-Curtis dissimilarity matrices of rotiferan communities for each of the sampling events. DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal. Data from the first sampling date (i.e., after 5 days) were not analyzed because most of the enclosures were not colonized at that time.
99x74mm (300 x 300 DPI)

Ordination plots of sample scores from a Canonical Analysis of Principal Coordinates (CAP) performed on the Bray–Curtis dissimilarity matrices of microcrustacean communities for each of the sampling events. DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal. Data from the first sampling date (i.e., after 5 days) were not analyzed because most of the enclosures were not colonized at that time. There are missing data for DISP for the sampling dates 15 and 22 days due to the absence of species in the samples.

99x75mm (300 x 300 DPI)

Supporting Information

Figure S1: Species accumulation curve as observed in a pilot experiment for rotifers and microcrustaceans during the course of time (days 15, 30, 60 and 90) for each enclosure. The pilot experiment consisted of three replicates of the experimental group DISP that were placed next to one pond (approximately four meters) and sampled 4 times over 3 months. We observed that after one month, species accumulation leveled off for both rotifers and microcrustaceans.

Table S1: Occurrence of rotifer and microcrustacean species identified during the experiment in each of the experimental groups (DISP, overland dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with overland dispersal) and in the ponds.

Species	DISP	EB	EB + DISP	Ponds
ROTIFERA				
<i>Anuraeopsis fissa</i>		X		
<i>Ascomorpha ecaudis</i>				X
<i>Beauchampiella eudactylota</i>		X	X	X
<i>Brachionus plicatilis</i>		X		
<i>Cephalodella gibba</i>	X	X	X	X
<i>Collotheca</i> sp.	X	X	X	
<i>Colurella</i> sp.	X		X	
<i>Conochilus</i> sp.			X	
<i>Dicranophorus</i> sp.	X	X	X	
<i>Dipleuchlanis propatula</i>	X	X	X	X
<i>Dissotrocha aculeata</i>		X	X	
<i>Euchlanis dilatata</i>	X			
<i>Gastropus</i> sp.	X	X	X	
<i>Lecane aculeata</i>				X
<i>Lecane boettgeri</i>		X		X
<i>Lecane bulla</i>	X	X	X	X
<i>Lecane clara</i>	X			
<i>Lecane closterocerca</i>	X	X	X	X
<i>Lecane cornuta</i>	X	X	X	X
<i>Lecane curvicornis</i>			X	
<i>Lecane deridderae</i>		X	X	X
<i>Lecane dumonti</i>				X
<i>Lecane elegans</i>	X	X	X	
<i>Lecane elongata</i>	X	X	X	
<i>Lecane eutarsa</i>	X	X	X	X
<i>Lecane furcata</i>	X	X	X	X
<i>Lecane hamata</i>	X	X	X	X
<i>Lecane hornemanni</i>	X	X	X	X
<i>Lecane inermis</i>	X	X	X	X
<i>Lecane leontina</i>	X	X	X	X
<i>Lecane ludwigii</i>	X	X	X	X
<i>Lecane lunaris</i>	X	X	X	X
<i>Lecane papuana</i>				X
<i>Lecane pyriformis</i>			X	

Species	DISP	EB	EB + DISP	Ponds
<i>Lecane quadridentata</i>	X	X	X	X
<i>Lecane signifera</i>	X	X	X	X
<i>Lecane subtilis</i>	X	X	X	
<i>Lecane tenuiseta</i>	X			
<i>Lecane unguolata</i>	X	X	X	
<i>Lepadella acuminata</i>		X		
<i>Lepadella patella</i>	X	X	X	X
<i>Lepadella quinquecostata</i>		X	X	
<i>Monommata</i> sp.	X	X	X	X
<i>Notommata copeus</i>		X	X	
<i>Notommata</i> sp.	X	X	X	
<i>Platyias quadricornis</i>		X		X
<i>Ploesoma truncatum</i>			X	X
<i>Polyarthra dolichoptera</i>		X	X	X
<i>Sinantharina</i> sp.	X			
<i>Squatinella longispinata</i>		X		
<i>Synchaeta</i> sp.		X	X	
<i>Testudinella ohlei</i>				X
<i>Testudinella patina</i>		X		
<i>Trichocerca bicristata</i>				X
<i>Trichocerca bidens</i>	X	X	X	X
<i>Trichocerca insignis</i>	X	X	X	X
<i>Trichocerca montana</i>				X
<i>Trichocerca pusilla</i>	X	X	X	X
CLADOCERA				
<i>Alona dentifera</i>		X	X	X
<i>Alonella dadayi</i>				X
<i>Anthalona verrucosa</i>		X	X	
<i>Camptocercus australis</i>			X	X
<i>Ceriodaphnia cornuta</i>		X	X	X
<i>Chydorus nitidulus</i>				X
<i>Chydorus pubescens</i>				X
<i>Coronatella monacantha</i>		X	X	X
<i>Dadaya macrops</i>		X	X	X
<i>Diaphanosoma birgei</i>		X	X	X
<i>Disparalona leptorhyncha</i>		X		X
<i>Dunhevedia americana</i>	X	X	X	X
<i>Ephemeroporus barroisi</i>	X	X	X	X
<i>Ephemeroporus hybridus</i>		X	X	
<i>Graptoleberis occidentalis</i>				X
<i>Grimaldina brazzai</i>		X		X
<i>Guernella raphaelis</i>				

Species	DISP	EB	EB + DISP	Ponds
<i>Ilyocryptus spinifer</i>	X		X	X
<i>Karualona muelleri</i>		X	X	X
<i>Kurzia polyspina</i>	X	X	X	X
<i>Latonopsis australis</i>	X	X	X	
<i>Macrothrix elegans</i>		X	X	X
<i>Moinodaphnia macleayi</i>				X
<i>Notoalona sculpta</i>	X	X	X	X
<i>Pseudosida ramosa</i>	X		X	X
<i>Scapholeberis armata</i>	X		X	X
COPEPODA				
<i>Diaptomus azureus</i>		X	X	X
<i>Ectocyclops</i> sp.				X
<i>Mesocyclops longisetus</i>	X	X	X	X
<i>Microcyclops alius</i>				X
<i>Microcyclops anceps</i>	X	X	X	X
<i>Microcyclops ceibaensis</i>	X		X	X
<i>Paracyclops</i> sp.	X			
Nauplii	X	X	X	X
Cyclopoida Copepodite	X	X	X	X
Calanoida Copepodite		X	X	X

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table S2: PerMANOVA pairwise comparisons for rotifers and microcrustaceans. Bolded *F*-values indicate statistically significant effects (*P*< 0.05). All tests were based on 1 and 12 degrees of freedom. Pairwise comparisons of experimental groups were only performed when significant effects were detected in the global PerMANOVA.

	Rotifers				Microcrustaceans			
	SS	R ²	<i>F</i>	<i>P</i>	SS	R ²	<i>F</i>	<i>P</i>
15 days								
EB vs EB+DISP	0.21	0.07	0.73	0.32				
DISP vs EB+DISP	0.75	0.21	2.70	0.03				
EB vs DISP	0.53	0.14	1.69	0.09				
22 days								
EB vs EB+DISP	0.18	0.06	0.67	0.12	0.35	0.09	0.96	0.14
DISP vs EB+DISP	0.76	0.25	3.30	0.03	0.74	0.19	1.92	0.06
EB vs DISP	0.77	0.20	2.51	0.06	0.57	0.20	1.53	0.26
38 days								
EB vs EB+DISP	0.11	0.03	0.36	0.66	0.23	0.06	0.68	0.32
DISP vs EB+DISP	0.35	0.11	1.21	0.16	0.67	0.16	1.73	0.10
EB vs DISP	0.46	0.13	1.50	0.13	0.64	0.17	1.82	0.06
53 days								
EB vs EB+DISP					0.20	0.07	0.70	0.06
DISP vs EB+DISP					0.61	0.15	1.65	0.04
EB vs DISP					0.54	0.13	1.48	0.06