



Contents lists available at [SciVerse ScienceDirect](#)

Limnologia

journal homepage: www.elsevier.de/limno



Re-establishment of zooplankton communities in temporary ponds after autumn flooding: Does restoration age matter?

Carla Olmo*, Xavier Armengol, Raquel Ortells

Departament de Microbiologia i Ecologia, Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, E-46100 Burjassot, Spain

ARTICLE INFO

Article history:

Received 17 March 2011

Accepted 8 August 2012

Keywords:

Biodiversity

Dispersal

Egg bank

Mediterranean temporary ponds

Taxon richness

Restoration ecology

Community composition

ABSTRACT

In temporary ponds, reestablishment of zooplankton communities depends on recruitment from the egg bank, the arrival of dispersers from within the region, and on successful establishment of newly arrived species following interaction with local abiotic and biotic factors. When the ponds dry up, zooplankton species may survive as dormant eggs, and since not all eggs hatch in the next season, eggs will accumulate in the sediment over time, representing an archive of the pond's historical biodiversity.

To study the effect of “restoration age” (the time since a water body was restored), we studied groups of ponds that were restored in different years (1998, 2003 and 2007). The restoration process involved extensive dredging of sediments which were used to bury the ponds in the 1960s. Our expectation was that the oldest ponds would have the richest zooplankton community, as they have been accumulating biodiversity over a longer time period. We took weekly quantitative samples of zooplankton during four consecutive weeks after flooding to compare taxon richness and zooplankton community composition between ponds of different restoration age during an early stage of zooplankton community re-establishment.

Taxon richness was high and similar to regional levels in all the ponds under investigation, suggesting restoration success and unlimited dispersal. Although cumulative richness at the end of the period was not significantly different between ponds, we observed temporal changes within the study period and certain age-related trends in relation to differences in zooplankton composition. These results suggest a difference in the succession of zooplankton communities depending on restoration age (which could be due to historical or local factors) and that this effect becomes evident from the beginning of the pond hydroperiod.

© 2012 Elsevier GmbH. All rights reserved.

Introduction

Ponds are exceptionally rich in terms of biodiversity (Williams et al. 2004). They create links between existing aquatic habitats and provide ecosystem services such as water supply, nutrient retention, hydrological regulation, wildlife protection and research (Oertli et al. 2005). Despite their ecological importance, ponds face many threats from a variety of human activities (Álvarez-Cobelas et al. 2005; Biggs et al. 2005). In increasingly degraded aquatic systems (through destruction, pollution and introduction of exotic species) pond restoration may be necessary to maintain biodiversity and function at the landscape scale (Moreno-Mateos and Comín 2010). Restored habitats can provide useful data – on population persistence, recovery from disturbance and the development of aquatic communities – and are therefore valuable for

testing ecological hypotheses, the result of which can be used to develop good conservation strategies and priorities (Beklioglu et al. 2007). Strategic plans that aim to conserve or enhance aquatic biodiversity can only be effective if based on a sound understanding of the factors that affect species diversity and the processes that determine pond community composition (Céréghino et al. 2008). This strong relationship between scientific research and conservation management was a theme picked up at the 4th European Pond Conservation Network (EPCN) Conference and is reflected in the contributions selected for this special issue of Limnologia.

Mediterranean temporary ponds are important biodiversity hotspots with particular characteristics (exposure to unpredictable climatic conditions, species endemism, high species rarity and habitat fragility (Blondel and Aronson 1999). Due to the number of anthropogenic pressures on Mediterranean coastal wetlands, many temporary ponds have been drained or filled for agriculture, recreation or urban projects (Sahuquillo et al. in this issue). They are now included as a Priority Habitat under the EU Habitats Directive (Grillas et al. 2004) and several projects are underway to restore this habitat type.

* Corresponding author at: Departament de Microbiologia i Ecologia, Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, A.O. 46100 Valencia, Spain. Tel.: +34 96 963543405; fax: +34 963544570.

E-mail address: Carla.Olmo@uv.es (C. Olmo).

Typically temporary ponds undergo a recurrent dry phase with different degrees of duration and predictability. At the beginning of the hydroperiod, there is a period of community reassembly, followed by gradual changes in community composition (Boix et al. 2004). In the early stages permanent residents typically appear first through recruitment from the dormant egg bank. The identity and abundance of these early recolonizers will ultimately determine the composition of the community (Brendonck and De Meester 2003; Louette et al. 2008). For this reason, the abundance and diversity of the egg bank may have a considerable impact on the structure and dynamics of pond communities (Marcus et al. 1994; Hairston 1996; Cáceres 1998). Immediately after (if dispersal is high), dispersers arrive from other habitats and may settle successfully depending on their interaction with local abiotic (habitat characteristics including hatching cues for dispersing eggs) and biotic factors (competition, predation and parasitism (Caley and Schluter 1997; Shurin and Allen 2001; Cottenie and De Meester 2004). Over time, recolonization after inundation generally increases taxon richness (Boix et al. 2004) until the number of species in the pond resembles the regional species pool or until the strength of local biotic interactions results in decreased establishment success for immigrants (Louette et al. 2006; Ruhí et al. in this issue).

Arrival in a habitat is determined by a species regional abundance (Louette et al. 2008) and its dispersal ability, which can differ enormously among zooplankton species (Cáceres and Soluk 2002; Badosa et al. 2010) resulting in important differences between pond communities (Jenkins and Buikema 1998). High dispersal rates and rapid colonization have been repeatedly reported in zooplankton (De Meester et al. 2002; Louette and De Meester 2005). However, other studies have reported few species dominating the community during repopulation (Bohonak and Jenkins 2003; Badosa et al. 2010). Moreover, variation in historical colonization processes leading to priority effects (invasion resistance by the resident community) is thought to be a primary mechanism creating variation in community structure (Chase 2003). When early colonists affect the settlement success of subsequent species, initial community differentiation tends to be conserved (De Meester et al. 2002). In this sense, even nearby ponds with similar environmental characteristics may harbor very different communities depending on the first colonists (Jenkins and Buikema 1998; Cottenie et al. 2001; Chase 2003).

Over time, exposure to immigrant arrival may result in additional opportunities for a more diverse array of organisms. Consequently, species richness and/or densities increase over time (Louette and De Meester 2005), local biotic interactions become more important (Wellborn et al. 1996) and the abundance and diversity of species in the dormant egg bank increase (Vandekerckhove et al. 2005). Differences in community structure may increase or decrease depending on whether local factors in the ponds converge to similar environments or diversify into alternative states for factors such as habitat diversity, predation pressure or aquatic vegetation, which will in turn affect the composition of the community and its egg bank. Since not all eggs hatch in the following season, the accumulation of eggs in the sediment increases over time, representing an archive of the pond's historical biodiversity (Hairston 1996; Cáceres 1998). In ponds that have been naturally or artificially buried, the remains of the egg bank become progressively degraded, although some studies suggest that this egg bank can remain active for decades (review in Cáceres 1997; Alekseev et al. 2007).

In this study we analyzed the reassembly of zooplankton communities in nine temporary ponds of different restoration age. The more recently restored ponds were active for two years before this study and the oldest ponds were restored 11 years ago. All ponds had been buried for more than 30 years. The restoration process consisted of dredging sediments and presumably the withdrawal

of all or most of the former egg bank. We expect that restoration age may act as a limiting factor to taxon richness because aging of a habitat results in an increased number of resident species both in the water column and the resting egg bank. This study aimed to identify, differences in community composition in different restoration age categories during the early stages of community re-establishment at the beginning of the pond hydroperiod. Studies on assembly trajectories in aquatic animal populations or communities deal mainly with inter-annual patterns (Louette et al. 2008; Badosa et al. 2010) and few cover several groups of zooplankton (Jenkins and Buikema 1998; Badosa et al. 2010) and zoobenthos taxa (Aguilar-Alberola and Mesquita-Joanes 2011). The added value of this study resides in detailed analyses during the main emergence period (during the first weeks after inundation) on the establishment of the most important zooplankton groups.

Materials and methods

Study system: description of the area and restoration process

The local name of “malladas” is used to refer to small inter-dunar water bodies located in a sand bar 14 km long and 1 km wide between the Albufera Lagoon and the Mediterranean Sea, in Eastern Spain (Fig. 1). This sand bar originated with sediment depositions from two rivers that isolated the lake from the sea (García and Cabrejas 1996). The area is included in the Albufera Natural Park, a wetland area of international relevance with special protection for birds and home to several endangered species of flora and fauna. Despite the current levels of governmental protection, the area has suffered from several anthropogenic impacts which were intensified in the 1960s. Due to an urban development plan, the sea-shore dune front was destroyed and the malladas leveled off with beach sand and other substrates, resulting in drastic alterations or the total destruction of many of them. In the 1980s, ecological movements led to the cessation of the urban plan. Since then, many projects have tried to restore the environment and its high ecological value. The restoration of malladas was included in EU funded projects such as Life Duna (2001–2004) and Life Enebro (2004–2008), and previous projects between 1997 and 1998 aimed to recover their hydrological regime and their ecological and landscape functioning. The restoration plan consisted of extensive and intensive dredging of the former buried wetland by removing sediment down to a gray lime layer approximately 1 m deep. We believe that this limit represents the original impermeable layer but not the sediment of the old water bodies; thus, at this depth it is unlikely that strong evidence of the former sediment egg bank would remain. Nevertheless, it is possible that these ponds include a remnant egg bank, particularly around the shores. Genetic analyses of *Daphnia magna* from recently restored malladas revealed variable levels of genetic diversity, ranging from one to 28 clones during the first growing season right after colonization, (Ortells et al. 2012 and unpubl. data), confirming the possibility of a residual egg bank in some ponds at least for this species.

There are several limnological studies on the malladas (Soria and Alfonso 1993; Alfonso 1996; Rueda et al. 2006; Antón-Pardo and Armengol 2010; Antón-Pardo 2011), providing evidence of substantial spatial and temporal variation in zooplankton communities with relevance to these restoration projects.

For this study, we selected nine ponds restored during three different years: three in 1998 (old: O1, O2 and O3), three in 2003 (intermediate: I1, I2 and I3), and three in 2007 (recent: R1, R2 and R3). The former ponds were buried and have remained inactive for more than 30 years, but since dredging (restoration) and prior to this study they have been functioning for 11, 6 and 2 years (hydrological cycles) respectively. The maximum distance

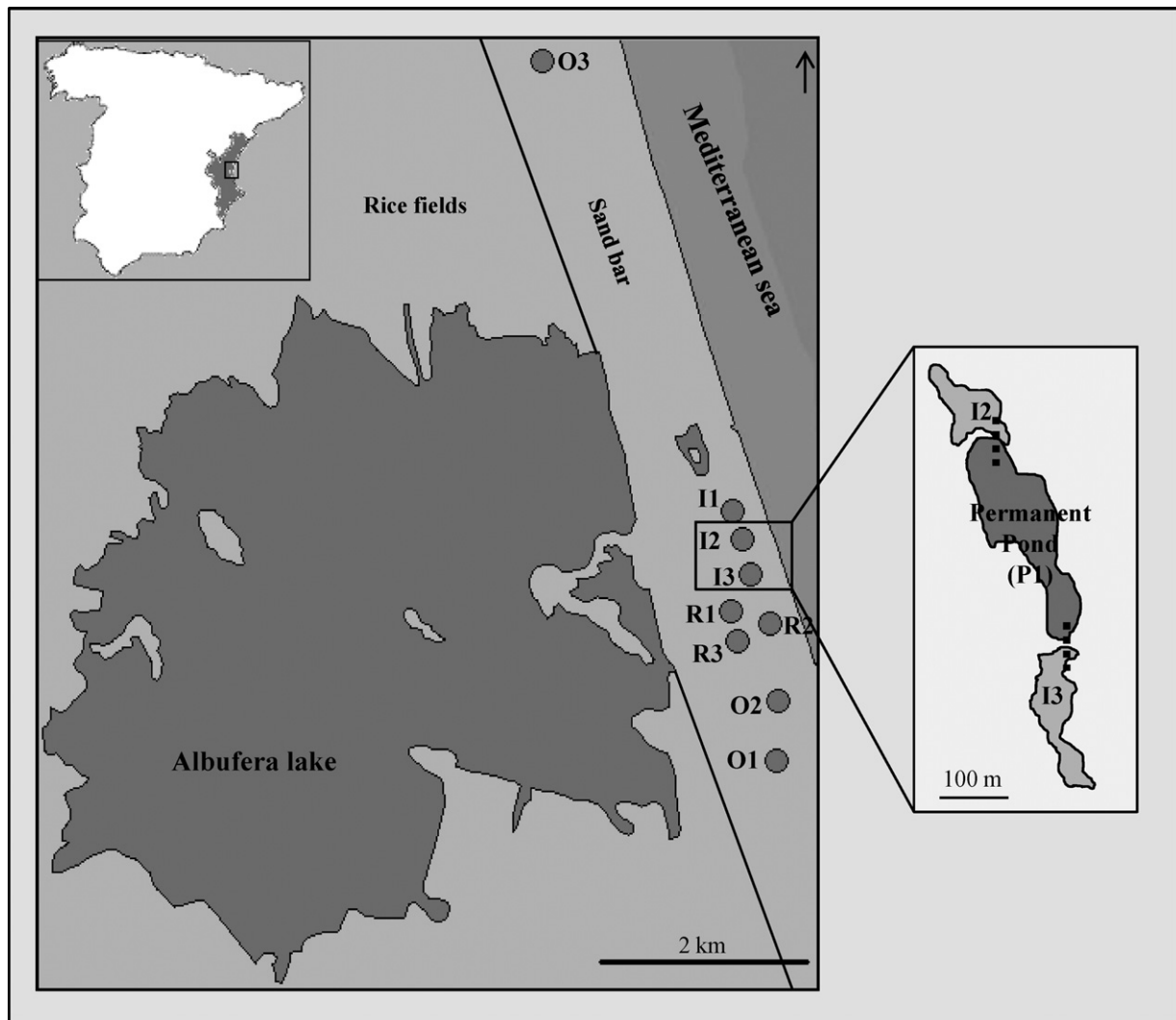


Fig. 1. Map of the study area showing the situation of the 9 ponds analyzed and a detailed augmentation of the intermediate connected ponds with a permanent body water (P1). Dotted lines represent occasional water connection.

between ponds was 7 km. They were all isolated from each other, but I2 and I3 were occasionally connected to an adjacent permanent pond (named P1, see Fig. 1) under strong winds or heavy rains when the water table was high (not observed in our study period). The ponds are endorheic, shallow and temporary. They fill up with rain and ground water, resulting in seasonal hydrological dynamics with important level fluctuations (Antón-Pardo 2011) typical of Mediterranean systems (Blondel and Aronson 1999; Sahuquillo et al. in this issue). Geographical, morphometrical and limnological features are summarized in Table 1. The inundation period normally begins with the autumn rains and lasts until late spring or early summer. The most common aquatic plants observed in the study ponds were Common Reed (*Phragmites australis* (Cav.) Trin. ex Steud) and Spiny Rush (*Juncus acutus* L.). Macrophytes, represented by a few characea stems have only been observed in one of the ponds (R1), but not during our study period. They were therefore considered not relevant. These were fishless ponds, but they may harbor amphibian populations (Iberian Water Frog *Pelophylax perezi* Seoane has been observed on several occasions). Potential predators occasionally found in these ponds belong to the groups Turbellaria, Oligochaeta, Heteroptera, Coleoptera and Odonata; but they were not observed during our study. Ducks find shelter in the malladas during the hunting season (autumn and winter) and they were observed in I2, I3 and R2 during this study. Animals

and wind are probably the most important dispersal vectors in the area.

Sampling and data analysis

Between 22 and 27 September 2009 the autumn rains (more than 100 L m^{-2}) immediately flooded the ponds to a water level 40–50 cm deep. The nine ponds were studied during four consecutive weeks starting 15 days after this inundation (the first sampling corresponds to the third week after flooding). On every sampling date limnological parameters were measure in situ – conductivity, pH, temperature (HI 98129, Hanna Instruments) and oxygen saturation (Oxi 340i, WTW).

Water samples were collected with a 1.5 L plastic bottle and filtered for nutrient and Chlorophyll *a* analysis in the laboratory. Chlorophyll *a* concentration was measured spectrophotometrically from Whatman GF/F glass fiber filters after extraction with 90% acetone following Jeffrey and Humphrey (1975). Nitrate and Phosphate concentrations were analyzed by colourimetry from filtered water (APHA 1980). Zooplankton samples were obtained by filtering 20 L of water (when possible) through a mesh size of $35 \mu\text{m}$ from different sites of the pond to include all possible microhabitats. Samples were immediately fixed with 4% formaldehyde. Emergent vegetation was estimated at each pool as percentage cover. The

Table 1
Geographical, morphometrical and environmental features of each pond. For each limnological variable, the mean and the standard deviation (sd) are shown. SRP: soluble reactive phosphate.

Pond name	Age category	Location	Area (ha)	Perimeter (m)	Maximum depth (cm)	Vegetation cover (%)	Conductivity (mS/cm)	pH	Oxygen saturation (%)	Chlorophyll <i>a</i> (µg L ⁻¹)	Nitrate (mg L ⁻¹)	SRP (mg L ⁻¹)
R1	Recent	39°20'17.80"N	0°18'38.23"W	0.66	725	31	10	2.1 ± 0.4	8.7 ± 0.1	107.4 ± 8.5	1.1 ± 0.5	0.04 ± 0.02
R2	Recent	39°20'7.11"N	0°18'27.68"W	0.47	310	22	10	1.6 ± 0.4	8.9 ± 0.1	86.6 ± 8.5	1.2 ± 0.2	0.04 ± 0.01
R3	Recent	39°20'3.36"N	0°18'32.07"W	0.36	421	25	5	2.8 ± 0.7	8.6 ± 0.2	89.1 ± 11.4	1.1 ± 0.2	0.03 ± 0.03
I1	Intermediate	39°20'34.77"N	0°18'39.08"W	0.49	300	31	70	1.4 ± 0.3	8.3 ± 0.2	80.5 ± 16.5	1.1 ± 0.1	0.04 ± 0.01
I2	Intermediate	39°20'30.91"N	0°18'38.01"W	0.29	280	29	65	1.5 ± 0.4	8.7 ± 0.3	114.0 ± 24.2	1.1 ± 0.2	0.03 ± 0.02
I3	Intermediate	39°20'24.38"N	0°18'34.92"W	0.43	428	18	50	1.2 ± 0.3	8.5 ± 0.3	100.7 ± 32.8	1.1 ± 0.1	0.04 ± 0.01
O1	Old	39°19'37.57"N	0°18'19.92"W	0.81	540	38	75	0.5 ± 0.1	7.8 ± 0.2	62.3 ± 6.7	1.2 ± 0.2	0.04 ± 0.02
O2	Old	39°19'23.34"N	0°18'23.34"W	1.23	708	30	85	0.9 ± 0.2	8.1 ± 0.2	77.7 ± 13.8	1.3 ± 0.2	0.04 ± 0.02
O3	Old	39°23'5.37"N	0°19'34.91"W	3.59	1361	50	80	1.2 ± 0.3	7.6 ± 0.1	34.0 ± 14.3	1.5 ± 0.3	0.03 ± 0.02

observation of macroinvertebrates was null in the recently restored ponds and anecdotic in the older ponds and was therefore not taken into account.

Once in the laboratory, zooplankton was counted under an inverted Olympus CK40 microscope at 10×. All cladocerans, adult copepods and minoritarian rotifer species were counted from the total sample volume, whereas abundant rotifers and immature copepod densities were estimated from an aliquot (5 mL out of 20 mL). Taxonomic identification followed Koste (1978) and Segers (1995) for rotifers, Alonso (1996) and Amorós (1984) for cladocerans and Dussart (1967, 1969) for copepods. When possible, identification was to species level except for immature copepod stages, bdelloids and ostracods. Although not identified, these groups were included for group proportion and total density estimations, but were excluded in the multivariate analysis. To calculate taxon richness (per visit and cumulative) we included rotifers (with bdelloids as a single species), cladocerans, ostracods and adult copepods. The list of species detected was compared to the literature and to species occurring in a permanent “mallada” in the area (P1, see Fig. 1).

In order to detect differences in limnological variables in ponds of different age categories at different sampling times, repeated measures ANOVA was performed with week (repeated factor) and age categories as independent variables (PASW version 17.0 SPSS Statistics). Limnological variables included pH, conductivity, oxygen concentration, Chlorophyll *a*, and nitrate and phosphorus concentration. Log (10) transformations were used in some cases in order to reach normality. Each pool within a category was treated as a replicate. Post hoc comparisons were obtained with Tukey's HSD test under the assumption of equal variance. The same analysis was performed for taxon richness at the community-level (number of species per visit), and for each zooplankton group separately (rotifers, copepods and cladocerans).

Cumulative taxon richness and other variables that were constant through our study period (area, maximum depth, perimeter and vegetation cover) were included in a multivariate ANOVA using ponds as replicates and age as a fixed factor. Analysis was followed by a Tukey's HSD posthoc test.

A redundancy analysis (RDA, Canoco for windows 4.5; ter Braak and Šmilauer 2002) was used to test for changes in species composition with time. This linear method was chosen because the length of the gradients as estimated with a detrended correspondence analysis was lower than 3 SD (Lepš and Šmilauer 2003). We used centered and standardized species density data (logarithmically transformed). Only those species that appeared in more than one pool and more than one sampling event were included, and in any case, species representing less than 5% of the total density of species in their respective zooplankton group (rotifers, copepods and cladocerans) were excluded from the analysis. The significance of the models was tested using Monte Carlo permutations ($n = 999$), performed by a split-plot design, with whole plots (ponds) permuted at random and split plots (temporal samples) permuted using cyclic shifts. Forward manual selection was used to identify explanatory variables significantly related to zooplankton community composition. Explanatory variables included the nominal variable age, age × time interaction, and the limnological measurements previously detailed.

Results

A total of 63 zooplankton species – 43 rotifers, 12 cladocerans, 7 copepods and 1 anostracan – were found during the study (Table 2). All the species found had been previously recorded in the area (Alfonso 1996; Rueda et al. 2006; Antón-Pardo and Armengol 2010; Antón-Pardo 2011). In a preceding study performed between

Table 2
Species list with high occurrence (more than 5% of density for each sampling date and zooplankton group).

Rotifera	Pond	Recent												Intermediate												Old											
		R1				R2				R3				I1				I2				I3				O1				O2				O3			
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	Abbrev.																																				
Zooplankton group																																					
<i>Brachionus angularis</i> (Gosse, 1981)	Bang																																				
<i>Brachionus urceolaris</i> (Müller, 1773)	Burc																																				
<i>Cephalodella gibba</i> (Ehrenberg, 1832)	Cgib																																				
<i>Eosiphora nanjus</i> (Ehrenberg, 1830)	Enan																																				
<i>Euchlanis dilatata</i> (Ehrenberg, 1832)	Edil																																				
<i>Hexarthra fennica</i> (Levander, 1892)	Hfen																																				
<i>Lecane bulla</i> (Gosse, 1851)	Lbul																																				
<i>Lecane closterocerca</i> (Schmarda, 1859)	Lclo																																				
<i>Lecane flexilis</i> (Gosse, 1886)	Lfle																																				
<i>Lecane pyriformis</i> (Daday, 1905)	Lpyr																																				
<i>Lepadella patella</i> (Müller, 1786)	Lpat																																				
<i>Polyarthra dolichoptera</i> (Idelson, 1925)	Pdol																																				
<i>Squatinella rostrum</i> (Milne, 1886)	Sros																																				
<i>Trichocerca cf pusilla</i> (Lauterborn, 1898)	Tpus																																				
<i>Trichocerca rattus</i> (Ehrb., 1830)	Trat																																				
<i>Trichocerca cf dixon – nutalli</i> (Jennings, 1903)	Tdxn																																				
Copepoda																																					
Nauplii (Cyclopoid)	Nci																																				
<i>Acanthocyclops americanus</i> (Marsh, 1893)	Aame																																				
<i>Diacyclops bicuspidatus</i> (Claus, 1857)	Dbic																																				
<i>Diacyclops bisetosus</i> (Rehberg, 1880)	Dbis																																				
<i>Metacyclops minutus</i> (Claus, 1863)	Mmin																																				
<i>Microcyclops</i> sp Claus, 1893	Micr																																				
<i>Tropocyclops prasinus</i> (Fischer, 1860)	Tpra																																				
Nauplii (<i>Mixodiaptomus kupelwieseri</i>)	Nca																																				
<i>Mixodiaptomus kupelwieseri</i> (Brehm, 1907)	Mkup																																				
Cladocera																																					
<i>Ceriodaphnia reticulata</i> (Jurine, 1820)	Cret																																				
<i>Chydorus sphaericus</i> (Müller, 1776)	Csph																																				
<i>Daphnia magna</i> (Straus, 1820)	Dmag																																				
<i>Daphnia cf pulicaria</i> Straus, 1820 (Forbes, 1893)	Dpul																																				
<i>Megafenestra aurita</i> (S. Fischer, 1849)	Maur																																				
<i>Moina micrura</i> Kurz, 1875	Mmic																																				
<i>Scapholeberis rammeri</i> (Dumont and Pensacert, 1983)	Sram																																				
<i>Simocephalus</i> sp Schödler, 1858	Simo																																				
Ostracoda																																					
	Ost																																				
Anostraca																																					
<i>Tanytastix stagnalis</i> (Linnaeus, 1758)	Tsta																																				

Rare species (not included): Rotifers: *Anuraeopsis fissa*, Bdelloid, *Cephalodella catellina*, *Cephalodella cf intuta*, *Cephalodella* sp 3, *Cephalodella* sp 4, *Collotheca* sp, *Colurella adriatica*, *Colurella uncinata*, *Keratella tropica*, *Lecane hamata*, *Lecane hornemanni*, *Lecane latissima*, *Lecane luna*, *Lecane nana*, *Lepadella triptera*, *Lindia torulosa*, *Lophocaris salpina*, *Mytilina ventralis*, *Notholca squamula*, *Ptygura* sp, *Rotifer non identified*, *Synchaeta pectinata*, *Testudinella patina*, *Trichocerca cf capucina*, *Trichocerca elongata*, *Trichocerca* sp 2; Cladocers: *Alona* sp, *Macrothrix cf rosea*, *Pleoroxus aduncus*, *Pleoroxus cf uncinatus*.

2006 and 2009 on the permanent pond (P1) occasionally connected to I2 and I3 (but not during our study), Antón-Pardo (2011) found 76% of the species encountered here, and 84.8% of the species found in I2 and I3 during our study had been described in this pond.

The three age categories shared 15 species (12 rotifera, 2 cladocera, 1 copepoda). Only one species (copepoda) was found in both recent and old ponds, whereas 7 species were detected in recent and intermediate ponds (7 rotifera, 3 cladocera, 1 copepod), and 18 species appeared in both intermediate and old ponds. In the recent ponds 5 unique species (rotifera) were detected, while the intermediate ponds had 11 (7 rotifera, 3 cladocera and 1 copepoda) and the old ponds had 9 (5 rotifera, 2 cladocera, 1 copepoda, 1 anostracan). Only three rotifer species (*Hexarthra fennica*, *Lecane closterocerca* and *Lepadella patella*) were found in all ponds, while two copepod, 12 rotifer, four cladoceran and one anostracan species was found

exclusively in one pond. In one of the old ponds (O3) calanoid copepods were exclusive and *Daphnia magna* was not detected, despite being present in the rest of the ponds regardless of age. On the other hand, 31 species were considered rare (less than 5% density). The highest number (21 rare species) was found in the intermediate ponds that occasionally connect to a permanent pond (I2 and I3), 12 species in the old ponds and nine in the recently restored ponds. Additionally, ostracods were observed throughout the study period in all ponds. Table 2 represents graphically the densities of those species with an occurrence greater than 5% of their own group species density on a sampling event.

Table 1 summarizes the environmental characteristics of the ponds during the study. Although the ponds were located close to each other and shared many ecological conditions (climate, substrate), some differences in limnological variables were detected.

Significant temporal changes (i.e., week effect) were found for pH (intra-subject comparison: $F=9.912$; $p<0.001$), conductivity ($F=53.733$; $p<0.001$) and oxygen concentration ($F=7.859$; $p=0.001$). Time \times age interaction was not significant for any variable (multivariate contrast: $F=1.368$; $p=0.107$). There was no significant temporal change in richness for either the whole zooplankton community ($F=1.531$, $p=0.241$) or for each main zooplanktonic group (copepods: $F=1.438$; $p=0.265$; rotifers: $F=0.539$, $p=0.662$; cladocerans: $F=1.139$, $p=0.360$).

Between age categories, differences were significant for pH (inter-subject: $F=12.252$; $p=0.008$), conductivity ($F=9.116$; $p=0.015$), oxygen concentration ($F=6.272$; $p=0.034$) and nitrate concentration ($F=6.232$; $p=0.034$). Pairwise comparisons detected differences in pH and in oxygen concentration between the old ponds and the rest (Tukey's HSD: $p<0.05$ for both pairwise tests), in conductivity between the old ponds and the recently restored ones ($p=0.012$) and in nitrate concentration between the old ponds and the intermediate ones ($p=0.041$). Taxon richness at community level was marginally significant between age categories ($F=4.768$; $p=0.058$). When analyzing zooplankton groups separately, these differences in taxon richness were highly significant for cladocerans ($F=40.791$, $p<0.001$) due to differences between the recently restored ponds and the rest (Tukey's HSD: $p<0.001$ for both pairwise comparisons).

Despite the differences in the unique species described above, there were no significant differences in cumulative taxon richness between ponds from different restoration age categories (multivariate ANOVA $F=3.083$; $p=0.120$). Among all variables tested (depth, area, perimeter and vegetation cover), only the latter was significantly different ($F=88.059$; $p<0.001$) and tended to increase with restoration age: the recently restored ponds had less vegetation cover than the intermediate and the old ponds ($p<0.001$ for both pair-wise comparisons) and the intermediate ponds less than the old ponds ($p=0.039$).

Cumulative richness and temporal changes in average richness per visit in each age category can be observed in Fig. 2. Due to the sporadic connection of two of the intermediate ponds with an adjacent permanent water body before our study (P1, see Fig. 1) we split this age category in two subgroups for graphical visualization: one intermediate isolated (Ii: I1) and two intermediate connected ponds (Ic: I2 and I3). Concordant with cumulative richness, average richness along the four weeks was always highest in the latter (Ic), followed by the old ponds (O), intermediate isolated (Ii) and recently-restored ponds (R). These differences became more evident from the second week onwards, as the species cumulative richness in old and intermediate connected ponds continued increasing and the recently-restored and intermediate isolated ponds increased more slowly. Additionally, recently-restored and intermediate isolated ponds had a peak richness during the first week, whereas in old and intermediate connected ponds this peak was observed during the second week. Rotifers were the main contributors to specific richness per visit.

Some temporal changes in zooplankton species composition could be highlighted (Fig. 3). In the first week of the study, rotifers were dominant in the recently-restored ponds, the intermediate ponds and in one of the old ponds (O3). The intermediate isolated pond (I1) was dominated by rotifers (54%) but presented a high proportion of ostracods (28%). The other two old ponds were dominated by young copepods. Throughout the four weeks studied there was a general increase in crustaceans. In the fourth week (sixth week after flooding) cladocerans had eventually become dominant in two old ponds (O2 and O3) and in a recently-restored pond (R1). Young copepods were more abundant in the other six ponds. Regarding total density, a decline in density was detected over the four weeks in 7 of the 9 ponds, which was particularly strong in R2 and I2 on the sixth week after flooding. Only two ponds

experienced a slight increase in density at the end of the study period (R3 and I3). After six weeks of flooding, zooplankton densities and composition among the ponds were apparently more similar than it was three weeks after flooding. The main patterns observed in the ponds throughout the study were a general reduction in total density and a reduction in the proportion of rotifers together with an increase in crustaceans and a tendency to acquire an equal proportion of zooplankton groups. We also observed changes from one week to the next, drastically modifying the composition and densities of some ponds (i.e. R2, I2 and O3 between 3rd and 4th week or R1, I1 and O2 between the 5th and 6th week).

The RDA analysis revealed significant differences in the zooplankton community according to pond age ($F=5.242$; $p=0.001$), pH ($F=3.669$; $p=0.001$), oxygen concentration ($F=6.908$; $p=0.002$) and conductivity ($F=2.938$; $p=0.014$). Up to 41.2% of the total variation of the species data was explained by the predictor variables. The first RDA axis alone accounted for 24.6% of the variability whereas the second one explained 11.8% (Fig. 4). All canonical axes were significant (Trace=0.577; $F=3.407$, $p=0.001$). The first RDA axis was positively related to restoration age ($r=0.716$) while negatively to oxygen concentration ($r=-0.658$), pH ($r=-0.572$) and conductivity ($r=-0.307$). It separated the old ponds from the rest. Thus, pH, oxygen and conductivity decreased with restoration age. Oxygen concentration was the variable most related with the second axis ($r=-0.658$). This axis separated one of the old ponds (O3) from the other two (O1 and O2) which were drawn closer to the intermediate connected ponds, and plotted the new ponds together with the intermediate isolated pond. Restoration age was also an important variable in explaining the variation observed in species distribution; species including the copepods *T. prasinus*, *M. minutus* and *D. bicuspidatus*, the cladocerans *C. sphaericus*, *C. reticulata* and *D. pulicaria* and the rotifers *L. closterocerca*, *P. dolichoptera* and *L. patella* were associated to the older ponds. Two copepod species, *A. americanus* and *D. bisetosus* and the cladoceran *D. magna* were more closely associated with intermediate ponds and the rotifer *H. fennica* was represented closer to the recently restored ponds.

Discussion

Zooplankton communities provide an excellent model for understanding restoration and community ecology (Louette et al. 2009; Badosa et al. 2010). Major differences in zooplankton communities (taxon richness, composition and their densities) may be due to regional abundance (Chase 2003), dispersal (Jenkins and Buikema 1998) local environmental characteristics (Chase 2003), biotic interactions (Cottenie and De Meester 2004) and density and species richness in the egg bank (García-Roger et al. 2006), which are at the same time affected by historical processes such as priority effects (Louette and De Meester 2006) or the age of the egg bank (Hairston et al. 1995). Normally, all these factors are jointly responsible for structuring zooplankton assemblages but the relative role of each factor is difficult to determine (Caley and Schluter 1997; Shurin 2000; Chase 2003).

Taxon richness in our system was similar to that found in the region. All taxa recorded had been previously recorded in the surrounding area (Alfonso 1996; Rueda et al. 2006; Antón-Pardo and Armengol 2010). According to Shurin (2000), when dispersal and posterior establishment is high, local taxon richness should be representative of the regional species pool. From this result we can attempt several conclusions. First, dispersal is unlikely to be a limiting factor due to the proximity of a large lake, other ponds and rice fields. Zooplankters are passive dispersers and the effectiveness of connectivity, wind, waterfowl, macroinvertebrates, amphibians and mammals as agents of passive dispersal has been largely evidenced (Bohonak and Whiteman 1999; Michels et al. 2001; Cáceres

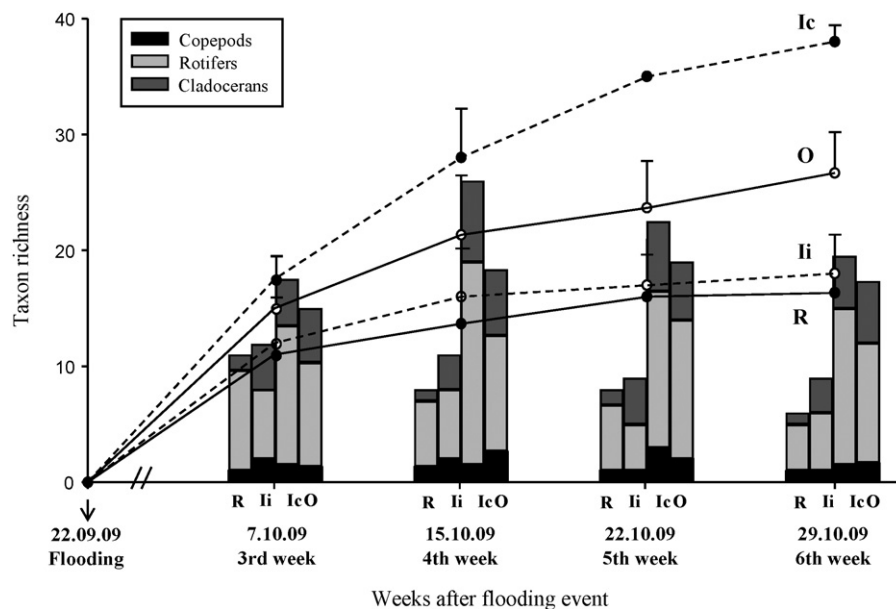


Fig. 2. Average taxon richness per visit and cumulative richness of the main zooplankton taxa found in each age category. R: recently restored; li: intermediate isolated; Ic: intermediate connected; O: old. Nauplii and copepodite stages are not included.

and Soluk 2002; Figuerola and Green 2002; Charalambidou et al. 2003; Cottenie and De Meester 2004; Van de Meutter et al. 2008; Vanschoenwinkel et al. 2008). Sometimes overlooked, humans and the vectors associated with them (pets, vehicles and clothes) can also have a strong impact on the dispersal of zooplankton in high traffic areas (Waterkeyn et al. 2010) such as ours. Second, the fact that in only one month of inundation we detected a high variety of species similar to that obtained after sampling during the whole inundation period or over the years (Antón-Pardo 2011) suggests that the initial period we covered represents the moment when most species hatch in this type of system. Third, similar to previous studies (Louette et al. 2006; Badosa et al. 2010), we can hypothesize that the recovery of zooplankton communities in areas of high dispersal can be achieved in restored ponds within a short time period. Two years after restoration (those of the recently restored ponds) is probably enough time for a pond to amass a high number of species, encouraged by high dispersal rates and recruitment from the egg bank. Due to the restoration process in our system, exhaustive excavation, the influence of a former egg bank was difficult to quantify. Contrary to normal restoration actions, attempts to conserve the initial egg bank were not among the objectives of the restoration project in the malladas. In this sense, right after restoration, our ponds could be comparable to new ponds. However, the possibility of dormant eggs accelerating the colonization process should be taken into consideration.

The recently restored ponds presented the lowest richness. Only few species were found exclusively and rare species were not frequent. This may reflect a lower amount and diversity in the egg bank due to limited time for colonization and establishment (Vandekerckhove et al. 2005). Similarly, it may have been enhanced by environmental homogeneity. The intermediate ponds showed the highest taxon richness, most likely due to the sporadic connection of two of them to a permanent water body before our study. Permanent ponds can harbor high species richness (Collison et al. 1995) and P1 presented the highest species richness for this type of system in the area (Antón-Pardo and Armengol 2010). Given that connectivity is an important means of zooplankton dispersal (Cottenie et al. 2001; Michels et al. 2001; Brendonck et al. 2010) we believe that an extensive egg bank, assembled with inputs from the permanent pond via water connection or animal vectors is the most

likely explanation for the highest richness in the intermediate connected ponds. On the other hand, some species were absent from the old ponds supporting the fact that despite high dispersal capacity, establishment success may be also constrained by the local environment. Establishment success is expected to decrease with increasing diversity due to fewer opportunities to occupy empty niches (Louette et al. 2006), although the reverse pattern has also been observed and related to habitat type, availability of resources, and species-specific interactions (Levine 2000). In our study, vegetation cover increased with age and consequently niche availability for all organisms, including predators.

We detected differences in some environmental variables both within age categories and among all ponds, making it difficult to disentangle any clear effect of increased environmental heterogeneity with time. Nevertheless, we believe that environmental differences are less probable to explain community differences for several reasons. First, although some significant differences in limnological parameters existed between age categories (O_2 , pH, conductivity), the environmental ranges for such variables are unlikely to be limiting zooplankton, which in our area were characterized by euryhaline species. Second, these variables are highly related to the age of the sediment. Following extraction of the old sediment, helophytes, which are tolerant to dry periods, begin to grow. These plants, mostly reeds and rushes enrich the sediment with organic matter, thus decreasing oxygen and altering the pH through decomposition. Rain then washes salt from the pond's sandy sediments slightly diminishing conductivity. Recent, intermediate and old ponds aligned well with respect to these variables. Recently restored ponds had the highest conductivity, oxygen and pH, whilst the old ponds were those with the lowest levels. Third, abiotic variables were found to have less weight in intermediate connected ponds. As their environmental characteristics represent an intermediate position, the same could be expected for taxon richness. However, they showed the highest taxon richness of all ponds. For all these reasons we believe that the differences in community composition related to restoration age may be well explained by the presence of dormant eggs that reflect assemblages of previously established species. The extent and maturity of the sediment egg bank has been described as a function of pond age (Vandekerckhove et al. 2005). Although we hypothesize that

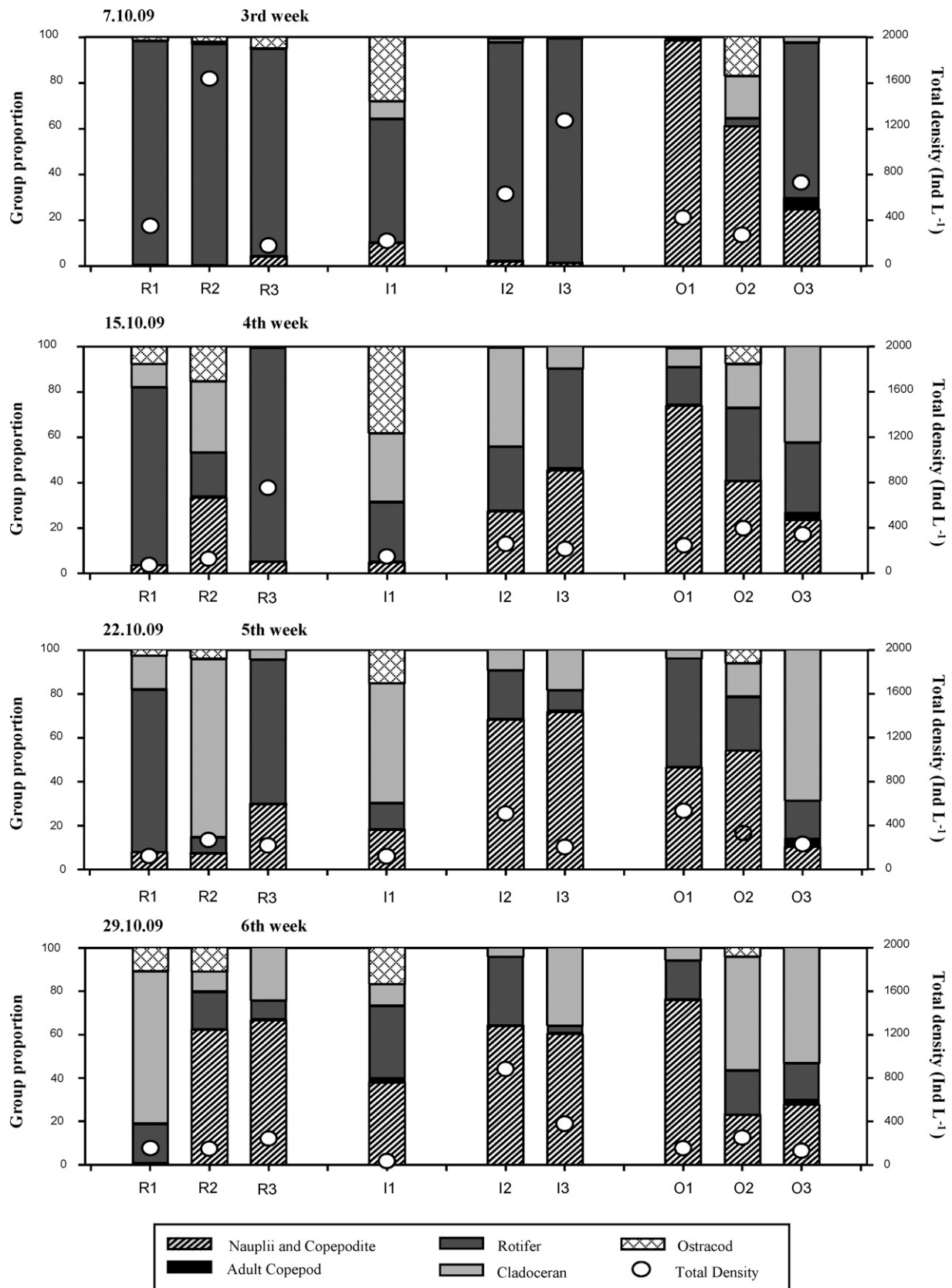


Fig. 3. Group proportion and total density (Ind L⁻¹) of different zooplankton groups in each sampling date for the 9 ponds analyzed. Copepods were separated into adults and immature stages, as the latest were not identified to species level.

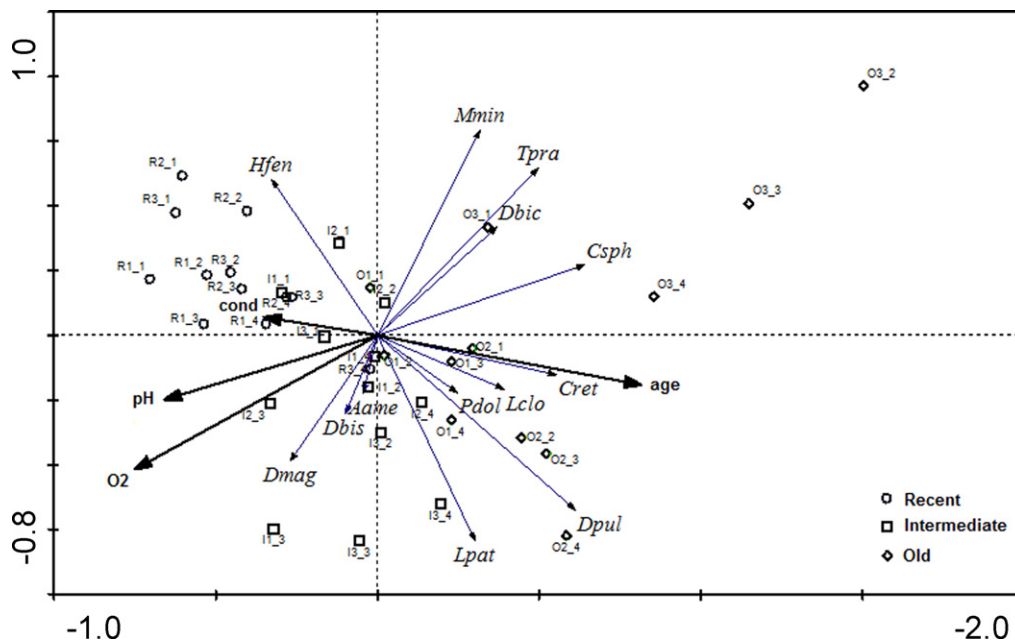


Fig. 4. Triplot of common species, explanatory variables and samples in a redundancy analysis (RDA) illustrating the relationships among communities in pools of different age category. Copepod species: *Dbic*: *Diatylops bicuspidatus*; *Dbis*: *Diatylops bisetosus*; *Mmin*: *Metacyclops minutus*; *Tpra*: *Tropocyclops prasinus*. Cladoceran species: *Cret*: *Ceriodaphnia reticulata*; *Csp*: *Chydorus sphaericus*; *Dmag*: *Daphnia magna*; *Dpul*: *Daphnia pulicaria*. Rotifer species: *Hfen*: *Hexarthra fennica*; *Lc*: *Lecane closterocerca*; *Lpat*: *Lepadella patella*; *Pdol*: *Polyarthra dolichoptera*. Species data were logarithmically transformed densities.

accumulation of dormant eggs in sediments should increase with restoration age, densities of eggs in the sediment were not quantified. We realize this is an important drawback in our study, but the identification of every egg from each taxonomic group was unrealistic. We can only speculate on the assumption of a constant deposition of eggs from an increasing number of species over time.

Our study covered a narrow time frame after flooding. A detailed weekly study of the ponds revealed large changes in community composition during the first month after flooding. This highlights the importance of studying the stages of repopulation in detail, as the high frequency of sampling over a short time period allowed for the detection of important changes in the community (density and proportions) that otherwise would have gone unnoticed. The first weeks after flooding are a very important period in temporary ponds. During this time, resting eggs start to hatch in order to develop viable populations to colonize the water column. Species with high propagule density in the sediment egg bank and with rapid development traits take advantage and monopolize aquatic resources (De Meester et al. 2002). Nevertheless some taxa, especially rotifers, possess very fast life cycles and their dominance is usually ephemeral. This was the case in most of our studied ponds, where rotifers dominated 7 out of 9 ponds on the third week after flooding. Specifically populations of *Hexarthra fennica* reached densities above 100 ind L⁻¹. The initial high abundance of *Hexarthra* may be associated with a lower abundance and later arrival and/or later hatching of cladocerans and copepods, which are known to have a negative effect on rotifers due to competition (Fussmann 1996). In the early stages of community composition predators may be scarce and populations of large zooplankters, which are considered better competitors (Kreutzer and Lampert 1999), may not be fully developed. Over time, interactions are likely to exert stronger effects on community structure (Wellborn et al. 1996). At the end of our study period, zooplankton communities notably changed; total density decreased and the ponds showed more environmentally heterogeneous communities dominated by different species of crustacean zooplankters.

In summary, we observed changes in zooplankton composition during the initial stages of population reassembly. These changes were highly related to restoration age, although local and historical factors were difficult to disentangle in our system due to the close relationship between the two. Diversification of local factors in recently restored ponds and the accumulation of resting eggs from each successive community are likely to increase variation in zooplankton communities in the future.

Acknowledgements

We acknowledge F. Mezquita and M. Serra for statistical advice and two anonymous reviewers for improving the manuscript. We are grateful to the Albufera Natural Park and Valencia City Hall technical office for their permission to sample. This study was funded by the Spanish Ministry of Science and Innovation (Project CGL2008-03760). C. Olmo has a FPI grant from the Spanish Ministry of Science and Innovation. We thank Vicent Pérez, Joan Rodrigo, Cristina Alacreu, Susana Romo and Samuel Rodríguez for their assistance during sampling.

References

- Aguilar-Alberola, J., Mesquita-Joanes, F., 2011. Population dynamics and tolerance to desiccation in a crustacean ostracod adapted to life in small ephemeral water bodies. *Limnologia* 41, 348–355.
- Alekseev, V., De Stasio, B., Gilbert, J.J., 2007. Diapause in Aquatic Invertebrates. Theory and Human Use. *Monographiae Biologicae*, vol. 84. Springer, Dordrecht.
- Alfonso, M.T., 1996. Estudio de las comunidades zooplancónicas de los ecosistemas acuáticos del Parque natural de La Albufera de Valencia. PhD Thesis. University of Valencia, Valencia.
- Alonso, M., 1996. Fauna Ibérica. Vol. 7. Crustacea. Branquiopoda. Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid.
- Álvarez-Cobelas, M., Rojo, C., Angeler, D.G., 2005. Mediterranean limnology: current status, gaps and the future. *J. Limnol.* 64, 13–29.
- Amorós, C., 1984. Introduction pratique à la systématique des organismes des eaux continentales françaises: Crustacés Cladocères. In: *Extrait du Bulletin mensuel de la Société Linnéenne de Lyon*.
- Antón-Pardo, 2011. Influencia de factores bióticos y abióticos sobre el zooplankton de dos zonas litorales sometidas a importantes efectos antrópicos. PhD Thesis. University of Valencia, Valencia.

- Antón-Pardo, M., Armengol, X., 2010. Zooplankton community from restored peridunar ponds in the Mediterranean region (L'Albufera Natural Park, Valencia, Spain). *Limnologia* 29, 133–143.
- APHA, 1980. Standard Methods for the examination of water and wastewater. American Public Health Association, Washington, DC.
- Badosa, A., Frisch, D., Arechederra, A., Serrano, L., Green, A.J., 2010. Recovery of zooplankton diversity in a restored Mediterranean temporary marsh in Doñana National Park (SW, Spain). *Hydrobiologia* 654, 67–82.
- Beklioglu, M., Romo, S., Kagalou, I., Quintana, X., Becarés, E., 2007. State of the art in the functioning of shallow Mediterranean lakes: workshop conclusions. *Hydrobiologia* 584, 317–326.
- Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Weatherby, A., 2005. 15 Years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 15, 693–714.
- Blondel, J., Aronson, J., 1999. *Biology and Wildlife of the Mediterranean Region*. Oxford University Press, New York.
- Bohonak, A.J., Jenkins, D.G., 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecol. Lett.* 6, 783–796.
- Bohonak, A.J., Whiteman, H.H., 1999. Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. *Limnol. Oceanogr.* 44, 487–493.
- Boix, D., Sala, J., Quintana, X.D., Moreno-Amich, R., 2004. Succession of the animal community in a Mediterranean temporary pond. *J. N. Am. Benthol. Soc.* 23, 29–49.
- Brendonck, L., De Meester, L., 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia* 491, 65–84.
- Brendonck, L., Jocke, M., Hulsmans, A., Vanschoenwinkel, B., 2010. Pools “on the rocks”: freshwater rock pools as model system in ecological and evolutionary research. *Limnologia* 29, 25–40.
- Cáceres, C.E., 1997. Dormancy in invertebrates. *Invertebr. Biol.* 116, 371–383.
- Cáceres, C.E., 1998. Interspecific variation in the abundance, production and emergence of *Daphnia* diapausing eggs. *Ecology* 79, 1699–1710.
- Cáceres, C.E., Soluk, D.A., 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* 131, 402–408.
- Caley, M.J., Schluter, D., 1997. The relationship between local and regional diversity. *Ecology* 78, 70–80.
- Céréghino, R., Biggs, J., Oertli, B., Declerck, S., 2008. The ecology of European ponds: defining the characteristics of a neglected freshwater habitat. *Hydrobiologia* 597, 1–6.
- Charalambidou, I., Ketelaars, H.A.M., Santamaría, L., 2003. Endozoochory by ducks: influence of developmental stage of *Bythotrephes* diapause eggs on dispersal probability. *Divers. Distrib.* 9, 367–374.
- Chase, J.M., 2003. Community assembly: when should history matter? *Oecologia* 136, 489–498.
- Collison, N.H., Biggs, J., Corfield, A., Hodson, M.J., Walker, D., Whitfield, M., Williams, P.J., 1995. Temporary and permanent ponds: an assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. *Biol. Conserv.* 74, 125–133.
- Cottenie, K., De Meester, L., 2004. Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. *Ecology* 85, 114–119.
- Cottenie, K., Nuytten, N., Michels, E., De Meester, L., 2001. Zooplankton community structure and environmental conditions in a set of interconnected ponds. *Hydrobiologia* 442, 339–350.
- De Meester, L., Gómez, A., Okamura, B., Schwenk, K., 2002. The Monopolization Hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecol.* 23, 121–135.
- Dussart, B., 1967. Les copépodes des eaux continentales d'Europe occidentale. Tome I: Calanoides et Hapacticoides. Boubee & Cie, Paris.
- Dussart, B., 1969. Les copépodes des eaux continentales d'Europe occidentale. Tome II: Cyclopoides et Biologie. Boubee & Cie, Paris.
- Figueroa, J., Green, A.J., 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biol.* 47, 483–494.
- Fussmann, G., 1996. The importance of crustacean zooplankton in structuring rotifer and phytoplankton communities: an enclosure study. *J. Plankton Res.* 18, 1897–1915.
- García, E., Cabrejas, M., 1996. Medio ambiente y conflicto social: el caso de la Albufera de Valencia. *Política y Sociedad*, vol. 23. Universitat de València, Madrid, pp. 75–97.
- García-Roger, E.M., Carmona, M.J., Serra, M., 2006. Patterns in rotifer diapausing egg banks: density and viability. *J. Exp. Mar. Biol. Ecol.* 336, 198–210.
- Grillas, P., Gauthier, P., Yavercovski, N., Perennou, C., 2004. *Mediterranean Temporary Pools*, Vol. 1: Issues Relating to Conservation, Functioning and Management. Station biologique de la Tour du Valat, Arles.
- Hairston, N.G., Van Brunt, R.A., Kearns, C.M., 1995. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 76, 1706–1711.
- Hairston, N.G., 1996. Zooplankton egg banks as biotic reservoirs in changing environments. *Limnol. Oceanogr.* 41, 1087–1092.
- Jeffrey, E., Humphrey, G.F., 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanzen* 167, 91–194.
- Jenkins, D.G., Buikema, A.L., 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecol. Monogr.* 68, 421–443.
- Koste, W., 1978. *Rotatoria die rädertiere mitteleuropas*. Monogonta. Gerbrüder Brontraeger, Berlin.
- Kreutzer, C., Lampert, W., 1999. Exploitative competition in differently sized *Daphnia* species: a mechanistic explanation. *Ecology* 80, 2348–2357.
- Lepš, J., Šmilauer, T., 2003. *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge.
- Levine, J.M., 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288, 852–854.
- 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., 2006. Predation and priority effects in experimental zooplankton communities. *Oikos* 116, 419–426.
- Louette, G., De Meester, L., Declerck, S., 2008. Assembly of zooplankton communities in newly created ponds. *Freshwater Biol.* 53, 2309–2320.
- Louette, G., Declerck, S., Vandekerckhove, J., De Meester, L., 2009. Evaluation of restoration measures in a shallow lake through a comparison of present day zooplankton communities with historical samples. *Restor. Ecol.* 17, 629–640.
- Louette, G., Elst, M.V., De Meester, L., 2006. Establishment success in young cladocerans communities: an experimental test. *Limnol. Oceanogr.* 51, 1021–1030.
- Marcus, N.H., Lutz, R., Burnett, W., Cable, P., 1994. Age, viability, and vertical distribution of zooplankton resting eggs from an anoxic basin: evidence of an egg bank. *Limnol. Oceanogr.* 39, 154–158.
- Michels, E., Cottenie, K., Neys, L., De Meester, L., 2001. Zooplankton on the move: first results on the quantification of dispersal of zooplankton in a set of interconnected ponds. *Hydrobiologia* 442, 117–126.
- Moreno-Mateos, D., Comín, F.A., 2010. Integrating objectives and scales for planning and implementing wetland restoration and creation in agricultural landscapes. *J. Environ. Manage.* 91, 2087–2095.
- Oertli, B., Biggs, J., Céréghino, R., Grillas, P., Joly, P., Lachavanne, J.B., 2005. Conservation and monitoring of pond biodiversity: introduction. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 15, 535–540.
- Ortells, R., Olmo, C., Armengol, X., 2012. Colonization in action: genetic characteristics of *Daphnia magna* Strauss (Crustacea, Anomopoda) in two recently restored ponds. *Hydrobiologia* 689, 37–49.
- Rueda, J., Aguilar-Alberola, J.A., Mezquita-Juanes, F., 2006. Contribución al conocimiento de los crustáceos (Arthropoda, Crustacea) de las Malladas de la Devesa del Parque Natural de la Albufera (Valencia). *Bol. Asoc. Esp. Entomol.* 30, 9–29.
- Ruhí, A., Herrmann, J., Gascón, S., Sala, J., Boix, D. How do early successional patterns in made-made wetlands differ between cold temperate and Mediterranean regions? *Limnologia*, in this issue.
- Sahuquillo, M., Miracle, M.R., Morata, S.M., Vicente, E. Nutrient dynamics in water and sediment of Mediterranean ponds across a wide hydroperiod gradient. *Limnologia*, in this issue.
- Segers, H., 1995. *Rotifera: The Lecanidae (Monogononta)*, vol. 2. SPB Academic Publishing, The Hague.
- Shurin, J.B., 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81, 3074–3086.
- Shurin, J.B., Allen, E.G., 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. *Am. Nat.* 158, 624–637.
- Soria, J.M., Alfonso, M.T., 1993. Relations between physico-chemical and biological characteristics in some coastal intradune ponds near Valencia (Spain). *Verh. Internat. Verein Limnol.* 25, 1009–1013.
- ter Braak, C.J.F., Šmilauer, P., 2002. *CANOCO for Windows*. Biometrics-Plant Research International, Wageningen.
- Van de Meutter, F., Stocks, R., De Meester, L., 2008. Size-selective dispersal of *Daphnia* resting eggs by backswimmers (*Notonecta maculata*). *Biol. Lett.* 4, 494–496.
- Vandekerckhove, J., Louette, G., Brendonck, L., De Meester, L., 2005. Development of cladoceran egg banks in new and isolated pools. *Arch. Hydrobiol.* 162, 339–347.
- Vanschoenwinkel, B., Waterkeyn, A., Vandecaetsbeek, T., Pineau, O., Grillas, P., Brendonck, L., 2008. Dispersal of freshwater invertebrates by large terrestrial mammals: a case study with wild boar (*Sus scrofa*) in Mediterranean wetlands. *Freshwater Biol.* 53, 2264–2273.
- Waterkeyn, A., Vanschoenwinkel, B., Elsen, S., Antón-Pardo, M., Grillas, P., Brendonck, L., 2010. Unintentional dispersal of aquatic invertebrates via footwear and motor vehicles in a Mediterranean wetland area. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 20, 580–587.
- Wellborn, G.A., Skelly, D.K., Werner, E.E., 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.* 27, 337–363.
- Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., Sear, D., 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biol. Conserv.* 115, 329–341.