

Zooplankton community from restored peridunal ponds in the Mediterranean region (L'Albufera Natural Park, Valencia, Spain)

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ABSTRACT

Zooplankton community from restored peridunal ponds in the Mediterranean region (L'Albufera Natural Park, Valencia, Spain)

The zooplankton of eight restored peridunal ponds located in L'Albufera Natural Park (Valencia, Spain) was sampled fortnightly from November 2006 to July 2007 to study the effect of hydroperiod, restoration and other environmental variables in the zooplankton community structure. Ponds with different hydroperiods were selected: two permanent ponds, two temporary ponds with a long hydroperiod (> 6 months a year) and four temporary ponds with short hydroperiod (< 6 months). The time since they were restored was also different: two of them were only modified; some were restored in the 1990s, and others were regenerated in recent years (2004-05). The results showed great heterogeneity in the zooplankton community, most probably due to the strong differences in some limnological variables (mainly conductivity and depth). The dominant group, in terms of density, were the copepods in four ponds, mainly because the high densities of nauplii and copepodites; the rotifers in three; and cladocerans only in one pond. However, the rotifers presented the highest cumulative richness in all the systems. Species richness in the permanent ponds was higher than in the temporary ones. The main environmental variables affecting the community composition were depth, highly related to permanence of water, restoration time and conductivity.

Key words: Hydroperiod, peridunal ponds, species richness, zooplankton.

RESUMEN

Comunidad zooplanctónica en charcas peridunares mediterráneas restauradas (Parc Natural de l'Albufera, Valencia, España)

El zooplancton de ocho charcas peridunares del Parque Natural de L'Albufera (Valencia, España) se siguió quincenalmente desde Noviembre 2006 a Julio 2007 para conocer el efecto del hidropериодо, de la restauración y de otras variables ambientales en la estructura de la comunidad zooplanctónica. Se estudiaron dos charcas permanentes; dos temporales con hidropериодо largo (> 6 meses al año); y cuatro con hidropериодо corto (< 6 meses). También diferían en el año en que fueron restauradas: dos de ellas existían previamente y fueron parcialmente modificadas, algunas fueron restauradas en los 90's, y otras fueron regeneradas más recientemente (2004-05). Los resultados muestran una gran heterogeneidad en la comunidad de zooplancton debido probablemente a las grandes diferencias en las variables limnológicas, principalmente la profundidad y conductividad. El grupo dominante (en densidad) fueron los copépodos en cuatro de los sistemas, debido a la alta densidad de los nauplios y copepoditos, los rotíferos en tres charcas, y los cladóceros solo en una. Pero en todas las charcas, los rotíferos presentaron la mayor riqueza acumulada. Las principales variables ambientales en la composición de la comunidad fueron la profundidad, muy relacionada con la permanencia del agua, la restauración y la conductividad, ya que en las charcas permanentes la riqueza específica fue mayor que en las temporales.

Palabras clave: Hidropериодо, charcas peridunares, rotíferos, riqueza de especies, zooplancton.

INTRODUCTION

In the Mediterranean region, limnological studies have shown the great biodiversity of their aquatic systems (Quintana *et al.*, 2006; Céréghino *et al.*, 2008). The wide array of ecological factors (depth, hydroperiod, macrophytes, productivity and salinity) that can be found in them (Beklioglu *et al.*, 2007) could explain this fact, by promoting a high environmental heterogeneity. In this region, temporary ponds are very important for aquatic organisms, due to the scarcity of permanent water bodies. A relevant factor influencing their aquatic community is the duration of the wet phase (or hydroperiod). Inhabitants of these ponds must have adaptations such as rapid life-cycles, diapausing eggs or resting stages (Wellborn *et al.*, 1996; Williams, 2000) to ensure the survival in the dry phase. The structure of zooplankton communities can be influenced by several biotic and abiotic factors. Different studies have suggested the relative importance of some environmental variables such as: morphometry, flooded surface, duration of hydroperiod, trophic status, salinity and vegetation cover (e.g. Armengol & Miracle, 1999; Boix *et al.*, 2001, Oertli *et al.*, 2002, Eitam *et al.*, 2004, Green *et al.*, 2005, Frisch *et al.*, 2006). Only a few of these studies include rotifers, even though they usually represent the major fraction of zooplankton species ri-

chness (e.g. Fahd *et al.*, 2000; Ortega-Mayagoitia *et al.*, 2000; Serrano & Fahd, 2005).

In the Valencian Community (Eastern Spain) some of the temporary ponds are peridunal ponds located in coastal areas. The coastal temporary ponds are considered ecosystems with high species richness (López *et al.* 1991; Mazuelos *et al.* 1993; Boix *et al.*, 2007), although some of their aquatic fauna is still unknown and poorly studied (Boix *et al.*, 2001). In L'Albufera Natural Park, there are many peridunal ponds, where only few studies have been carried out (Soria & Alfonso 1993; Alfonso, 1996; Rueda-Sevilla *et al.*, 2006). In the 1960s most of these systems were heavily altered by humans, but in the last twenty years some of them have been restored. These ponds are adequate systems to study the influence of natural processes and anthropogenic activities on the zooplankton community. The main aim of this study is to assess the zooplankton community composition in a selected group of these restored peridunal ponds, and to address the main environmental factors which have influenced their community structure.

STUDY AREA

“Malladas” is the local name of the peridunal ponds in L'Albufera Natural Park (Valencia, Spain).

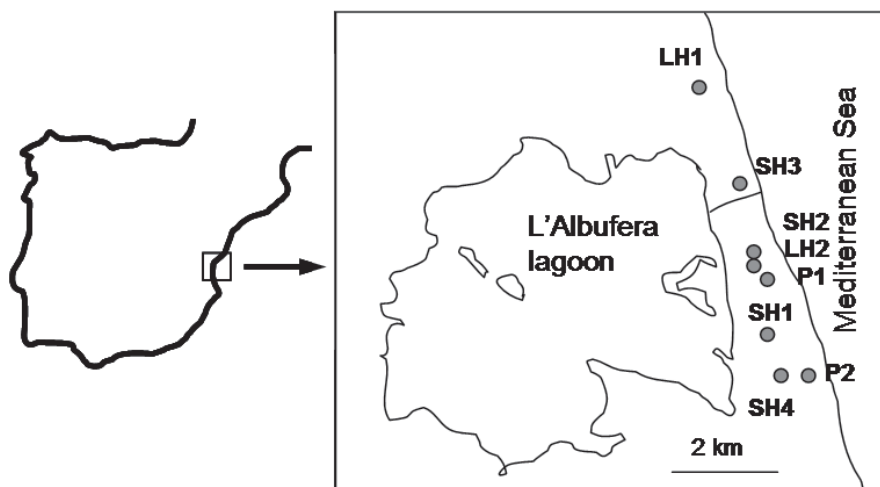


Figure 1. Map of the study site. *Mapa del área de estudio.*

They are located in the sandy stretch that separates l'Albufera, a coastal lagoon, from the Mediterranean Sea. They are filled by rain and ground water.

From the 1960s-1970s most of the ponds and wetlands were silted, but since the late 1980s, several restoration projects have been carried out with the aim of restoring the original habitat. Therefore, the remains of the antique ponds were dug to different depths, to create both temporary and permanent ponds.

A set of eight ponds (Fig. 1) was selected for this study: two permanent and six temporary ones, showing differences in hydroperiod duration. The ponds were quite close, the longest distance among them is eight km (between LH1 and P2). The permanent systems (P1 and P2) have a dense bed of macrophytes in their central areas. They house small fish as *Gambusia holbrooki* and the endemic *Aphanius iberus* (pers. obs.) and amphibians (*Rana perezi*). The pond P1 was specifically restored to be used as a refuge for *A. iberus*, an endangered species. The temporary ponds are fishless systems, but house amphibian populations. In this set of temporary ponds, two of them had water more than 7 months in the studied period, they were labeled as long hydroperiod (LH1 and LH2), and 4 ponds with shorter hydroperiod (SH) had water less than 6 months in the same period. The ponds differed also in the year of restoration: some of them (P2, LH1, SH1, and SH4) were totally restored in the 1990s; and others (P1, LH2, SH2 and SH3) were restored between 2003 and 2004. P1 and SH3 were never completely desiccated and silted, but through the restoration process their depth and water surface increased.

The basic limnological characteristics of some of the ponds were studied in the 1980s, before the restoration project (Soria & Alfonso, 1993; Alfonso, 1996), and recently only a study on large crustaceans (Rueda Sevilla *et al.*, 2006) has been done.

METHODS

The study period started in autumn, when the ponds were filled by rainfall (November 2006). Ponds were sampled fortnightly until they dried

out (or contained less than 5 cm water). For the permanent ones, sampling finished in July 2007.

Several variables were measured *in situ*: conductivity, temperature, pH, dissolved oxygen and maximum depth. One liter water sample was taken at 0.1 m from the surface and filtered for nutrient and chlorophyll *a* analysis in the laboratory. Chlorophyll *a* concentration was determined spectrophotometrically from Whatman GF/F glass fibre filters, after extraction with 90 % acetone, following the method of Jeffrey & Humphrey (1975). Nitrate and phosphate were measured by colorimetry from filtered samples (Golterman *et al.*, 1978; APHA, 1980; Murphey & Riley, 1962). For all these procedures a Hitachi U2001 Spectrophotometer was used.

Zooplankton samples were taken by filtering, through a 35 µm mesh-size net, a known volume of water taken from different sites in the ponds. We usually filter 10 l except when there were many organisms in the water column, then the filtered volumes were smaller (a minimum of 6 l) to avoid filter clogging. The organisms were stored in 4 % formalin, and identified and counted in the laboratory using an inverted microscope (Olympus CK40). All the organisms in the samples were counted and, when possible, the individuals were identified to species level, according to Koste (1978) for rotifers; Dussart (1967 and 1969) for copepods, and Alonso (1996) for branchiopods. Nauplii, copepodites and other juveniles were assigned to species considering adult species proportions.

Some community structure parameters were calculated: species richness per visit of the three main groups (rotifers, cladocerans and copepods), mean diversity calculated with Shannon-Wiener index, and the evenness. A one-way ANOVA was performed to see the differences in the measures of diversity related with the hydroperiod (in the permanent, the long hydroperiod, and the short hydroperiod ponds) and with the different time of restoration of the ponds (partially restored, restored in the 1990s and recently restored).

For the multivariate analysis, all the environmental variables, except pH, and the species densities were log transformed. Time since restoration was added as a categorical variable in three

Table 1. Mean values and standard deviation (in brackets) of the environmental variables measured during the study period in the different ponds. P: permanent pond; LH: long hydroperiod pond; SH: short hydroperiod pond; Rest: restoration; 1: partially modified; 2: restored in 90s; 3: restored in 2003-2004. *Valor medio y desviación típica (entre paréntesis) de las variables ambientales medidas durante el periodo de estudio en las diferentes charcas. P: charca permanente; LH: charcas de hidroperiodo largo; SH: charcas de hidroperiodo corto; Rest: restauración; 1: parcialmente modificadas; 2: restauradas en los 90; 3: restauradas en 2003-2004.*

	Conductivity mS/cm	Temperature °C	pH	Oxygen mg/L	Depth cm	Chl <i>a</i> mg/L	Nitrate mg/L	Phosphate mg/L	Rest
P1	1.8 (± 0.2)	17.8 (± 5.5)	8.7 (± 0.3)	9.3 (± 2.4)	110 (± 9)	1.80 (± 1.68)	0.98 (± 0.24)	0.03 (± 0.01)	1
P2	4.0 (± 0.4)	16.5 (± 5.5)	8.8 (± 0.4)	8.4 (± 2.4)	114 (± 42)	12.03 (± 16.81)	0.87 (± 0.22)	0.04 (± 0.05)	2
LH1	1.5 (± 0.5)	15.9 (± 4.9)	8.2 (± 0.3)	8.9 (± 2.0)	38 (± 9)	1.40 (± 0.97)	1.30 (± 0.92)	0.03 (± 0.01)	2
LH2	2.8 (± 1.1)	17.3 (± 3.8)	9.1 (± 0.2)	8.9 (± 1.3)	21 (± 6)	7.82 (± 14.06)	1.07 (± 0.16)	0.03 (± 0.01)	3
SH1	1.2 (± 0.3)	16.4 (± 4.6)	8.6 (± 0.3)	8.5 (± 1.4)	11 (± 3)	2.33 (± 1.97)	1.10 (± 0.24)	0.06 (± 0.08)	2
SH2	2.0 (± 0.9)	18.3 (± 4.0)	9.1 (± 0.2)	9.7 (± 0.8)	17 (± 5)	4.14 (± 3.94)	1.11 (± 0.28)	0.04 (± 0.03)	3
SH3	6.3 (± 1.9)	17.4 (± 3.8)	8.9 (± 0.4)	11.6 (± 1.5)	21 (± 5)	4.81 (± 4.14)	1.08 (± 0.22)	0.12 (± 0.27)	1
SH4	0.8 (± 0.3)	13.7 (± 2.7)	8.3 (± 0.2)	9.0 (± 1.5)	14 (± 5)	4.21 (± 2.78)	1.09 (± 0.24)	0.03 (± 0.01)	2

groups: ponds modified; ponds restored in the 1990s and ponds restored recently (between 2003 and 2004). A CCA was carried out using CANOCO to detect the patterns of variation in the species composition and the main relations between the species and each of the environmental variables. Rare species were downweighted and two Monte Carlo tests (499 permutations) were performed to test the significance of the canonical axes.

RESULTS

Environmental variables

Conductivity in the temporary ponds (Table 1) ranged from 0.43 mS/cm in SH4 in Decem-

ber, to 10.06 mS/cm in November in SH3. Temporary ponds showed greater temporal variation than permanent ponds. Depth was positively correlated with water permanence ($R^2 = 0.78$; $p < 0.01$) and it was higher in the permanent ponds (P1 and P2). The pH varied from 8.2 to 9.1 and, like the oxygen concentration, which ranged from 9.4 mg/l (P2) to 11.6 mg/l (SH3), did not show a high temporal variation. The nutrient concentrations were low, varying between 0.87 and 1.30 mg/l (nitrate) and between 0.03 and 0.12 mg/l (phosphate), with a maximum value of phosphate of 0.89 mg/l in November in SH3. The chlorophyll *a* concentration was slightly higher in P2 and LH2 (maximum of 50 μ g/l), which had also a higher temporal variation.

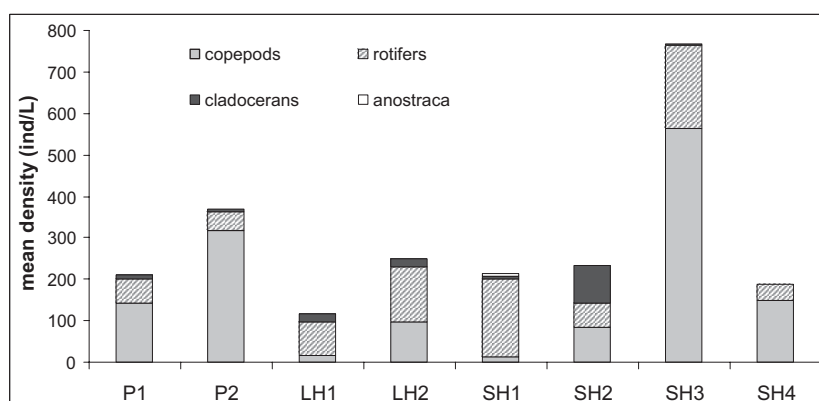


Figure 2. Mean density (ind/l) of the main zooplankton taxa found in each pond: Permanent ponds (P), long hydroperiod ponds (LH) and short hydroperiod ponds (SH). *Densidad media (ind/l) de los principales taxones de zooplancton de cada charca: charcas permanentes (P), con largo hidroperiodo (LH) y con corto hidroperiodo (SH).*

Table 2. List of rotifer, copepod and branchiopod species with an abundance higher than 0.5 % and their presence in the ponds. Other species found with an abundance lower than 0.5 %: *Brachionus angularis*, *B. calyciflorus*, *B. ibericus*, *B. quadridentatus brevispinus*, *B. urceolaris*, *B. variabilis*, *Cephalodella cf cyclops*, *C. cf intuta*, *C. gracilis*, *Cephalodella sp.*, *Collotecha sp.*, *Colurella uncinata*, *Cupelopagis vorax*, *Encentrum cf marinum*, *E. saundersiae*, *Eosphora ehrenbergi*, *Euchlanis meneta*, *Lecane cf abanica*, *L. aculeata*, *L. curvicornis*, *L. decipiens*, *L. grandis*, *L. hamata*, *L. hornemanni*, *L. inermis*, *L. inopinata*, *L. lamellata*, *L. latissima*, *L. luna*, *Lepadella acuminata*, *L. triptera*, *Lophocaris salpina*, *Mytilina ventralis*, *Notholca acuminata*, *Platyas quadricornis*, *Pleurotrocha petromyzon*, *Proales sp.*, *Ptygura sp.*, *P. cf longicornis*, *Squatinella rostrum*, *Testudinella patina*, *Trichocerca rattus*, *T. weberi*, *Trichocerca sp.*, *Tripleuchlanis sp.*, *Horsiella brevicornis*, adult Calanoida, adult Harpacticoida, *Alona rustica*, *Pleuroxus aduncus*, *Daphnia pulicaria*, *Macrothrix laticornis*, *Megafenestra aurita*, *Moina sp.*, *Scapholeberis ramneri* and *Simocephalus vetulus*. Listado de especies de rotíferos, copépodos y branquiópodos con una abundancia mayor de 0.5 % y su presencia en las diferentes charcas. Otras especies encontradas con una abundancia menor a 0.5 % fueron: *Brachionus angularis*, *B. calyciflorus*, *B. ibericus*, *B. quadridentatus brevispinus*, *B. urceolaris*, *B. variabilis*, *Cephalodella cf cyclops*, *C. cf intuta*, *C. gracilis*, *Cephalodella sp.*, *Collotecha sp.*, *Colurella uncinata*, *Cupelopagis vorax*, *Encentrum cf marinum*, *E. saundersiae*, *Eosphora ehrenbergi*, *Euchlanis meneta*, *Lecane cf abanica*, *L. aculeata*, *L. curvicornis*, *L. decipiens*, *L. grandis*, *L. hamata*, *L. hornemanni*, *L. inermis*, *L. inopinata*, *L. lamellata*, *L. latissima*, *L. luna*, *Lepadella acuminata*, *L. triptera*, *Lophocaris salpina*, *Mytilina ventralis*, *Notholca acuminata*, *Platyas quadricornis*, *Pleurotrocha petromyzon*, *Proales sp.*, *Ptygura sp.*, *P. cf longicornis*, *Squatinella rostrum*, *Testudinella patina*, *Trichocerca rattus*, *T. weberi*, *Trichocerca sp.*, *Tripleuchlanis sp.*, *Horsiella brevicornis*, adult Calanoida, adult Harpacticoida, *Alona rustica*, *Pleuroxus aduncus*, *Daphnia pulicaria*, *Macrothrix laticornis*, *Megafenestra aurita*, *Moina sp.*, *Scapholeberis ramneri* y *Simocephalus vetulus*.

	P1	P2	LH1	LH2	SH1	SH2	SH3	SH4
ROTIFERA								
<i>Anuraeopsis fissa</i> (Gosse, 1851)	0.6	0.3	0.1	0.1				0.1
Bdelloidea	0.7	1.6	0.3	0.7	0.9	5.2	0.1	0.1
<i>Brachionus plicatilis</i> (Müller, 1786)	0.2	1.7	0.3	0.1			4.5	
<i>Cephalodella catellina</i> (Müller, 1786)	0.0			1.3	0.0	0.4	0.1	0.1
<i>Cephalodella gibba</i> (Ehrenberg, 1832)	0.1	0.1	0.4		0.3	0.3		3.6
<i>Colurella adriatica</i> (Ehrenberg, 1831)	0.5	0.2	0.1	0.1			0.1	
<i>Colurella colurus</i> (Ehrenberg, 1830)			0.1	0.1	0.1	0.5	0.1	0.7
<i>Eosphora najas</i> (Ehrenberg, 1830)	0.7							
<i>Hexarthra fennica</i> (Levander, 1892)		0.1	11.4	26.4	77.6	11.1	4.8	0.1
<i>Hexarthra oxyuris</i> (Sernov, 1903)	4.0							
<i>Keratella tropica</i> (Apstein, 1907)	1.1		0.2	0.1	0.1	0.1	7.5	0.1
<i>Lecane bulla</i> (Gosse, 1851)	0.5	0.1	0.3	0.1				
<i>Lecane closteroerca</i> (Schmarda, 1859)	0.2	1.8	0.4					0.1
<i>Lecane furcata</i> (Murray, 1913)	1.5		0.3					
<i>Lecane nana</i> (Murray, 1913)	0.1	0.1			0.1	0.2		1.5
<i>Lecane punctata</i> (Murray, 1913)	5.7	0.9						
<i>Lecane pyriformis</i> (Daday, 1905)	0.1	0.1	0.1					0.6
<i>Lecane quadridentata</i> (Ehrenberg, 1832)	2.5							
<i>Lepadella patella</i> (Müller, 1786)	0.2	0.3	6.8	0.1	0.1	2.4		2.0
<i>Lindia torulosa</i> (Dujardin, 1841)	0.1			0.1	0.8	1.5	0.1	0.1
<i>Notholca squamula</i> (Müller, 1786)	0.1	0.2	0.1		0.5		0.1	0.1
<i>Polyarthra dolichoptera</i> (Idelson, 1925)	11.3	2.8	29.4	0.1			0.1	0.1
<i>Synchaeta oblonga</i> (Ehrenberg, 1832)	0.1	0.5	5.5					
<i>Synchaeta pectinata</i> (Ehrenberg, 1832)	3.4		0.1					
<i>Trichocerca cf elongata</i> (Gosse, 1886)	0.1		0.7	0.1				
<i>Trichocerca pusilla</i> (Lauterborn, 1898)	0.1	0.5						0.1
COPEPODA								
<i>Tropocyclops prasinus</i> (Fischer, 1860)	34.2			0.6				3.9
<i>Acanthocyclops americanus</i> (Marsh, 1892)	21.1	86.0		56.2	0.4	34.0	26.6	0.2
<i>Eucyclops serrulatus</i> (Fischer, 1851)	3.0			0.9	6.2			
<i>Eucyclops speratus</i> (Lilljeborg, 1901)			2.2			8.0		
<i>Diacyclops bisetosus</i> (Rehberg, 1880)			15.0	9.1		4.5	55.2	6.0
<i>Diacyclops bicuspidatus</i> (Claus, 1857)			4.4		0.4		0.1	80.6
<i>Metacyclops minutus</i> (Claus, 1863)			6.7		0.4			
cf <i>Speocyclops</i>					2.9			

Cont.

Table 2. (cont.)

ANOSTRACEA								
<i>Tanymastix stagnalis</i> (Linnaeus, 1758)								1.6
CLADOCERA								
<i>Alona rectangula</i> (Sars, 1862)	0.2	1.3						0.1
<i>Chydorus sphaericus</i> (Müller, 1776)	0.6	0.2	4.5	0.1			0.2	
<i>Ceriodaphnia quadrangula</i> (Müller, 1785)	3.2							
<i>Ceriodaphnia reticulata</i> (Jurine, 1820)	0.7		2.8	0.1				
<i>Daphnia curvirostris</i> (Eylmann, 1887)		0.1	4.8					0.2
<i>Daphnia magna</i> (Straus, 1820)	2.1			4.3	4.2	31	0.1	0.1
<i>Moina macrocopus</i> (Straus, 1820)								1.4

Zooplankton community structure

Across the study a total of 100 species were found: 71 rotifers, 15 cladocerans, 13 copepods and one anostracan. In the permanent ponds a higher number of species appeared (Tables 2 and 3). The most common species were bdelloid rotifers which were present in all studied ponds and *Acanthocyclops americanus*, *Hexarthra fennica*, *Keratella tropica* and *Lepadella patella* which were recorded in seven of the eight ponds.

The highest average zooplankton density (Fig. 2) was found in SH3, (767.8 ind/l), and the lowest in LH1 (116.8 ind/l) (Fig. 2). The dominant group varied among the ponds: in the permanent ponds (P1 and P2), and two of the short period temporary ones (SH3 and SH4), the copepods (mainly larval and juvenile stages) dominated. The short hydroperiod pond SH2 was the only one dominated by cladocerans (*Daphnia magna*). Rotifers were the most abundant group

in the rest of the ponds: planktonic species, such as *Polyarthra dolichoptera* and *H. fennica*, were dominant. The only anostracan species found, *Tanymastix stagnalis*, occurred in SH1 with a mean density of 6.2 ind/l, mostly in the juvenile stage.

Rotifers were the group with the highest number of species in all the ponds, with a maximum value of 47 species in P1, and a minimum of 12 species in SH1. Overall, between three and six copepod species were recorded per pond, while for the cladocerans, between three (temporary ponds) and 11 species (permanent pond, P1) were encountered.

The highest copepod, rotifer and total richness per visit was obtained in P1 (Table 3), which also showed a wide range of variation (represented by the high standard deviation). The highest cladoceran richness was found in LH1. In the group of ponds with short hydroperiod, SH4 had the highest copepod, rotifer and total richness. Diversity calculated with the Shannon-Wiener index ranged from 0.7 bits ind⁻¹ (SH3) to

Table 3. Values of species richness per visit of the main groups of zooplankton, mean diversity (calculated using Shannon-Wiener index) and mean evenness in the ponds. *Valores de riqueza por visita de los principales grupos zooplanctónicos, diversidad promedio (calculada usando el índice de Shannon-Wiener) y equitatividad promedio en las lagunas.*

Pond	Species richness per visit			Mean Diversity (bits ind ⁻¹)	Evenness
	cladocerans	copepods	rotifers		
P1	2.7 (± 1.3)	2.1 (± 0.8)	11.9 (± 5.6)	1.3 (± 0.4)	0.3 (± 0.1)
P2	0.4 (± 0.6)	0.6 (± 0.6)	11.4 (± 4.8)	1.0 (± 0.6)	0.3 (± 0.2)
LH1	3.5 (± 0.9)	1.2 (± 0.8)	10.2 (± 3.2)	1.4 (± 0.6)	0.3 (± 0.3)
LH2	1.4 (± 0.8)	1.3 (± 0.8)	4.0 (± 1.9)	0.8 (± 0.4)	0.4 (± 0.2)
SH1	0.7 (± 1.1)	1.3 (± 1.0)	5.9 (± 2.6)	1.3 (± 0.7)	0.5 (± 0.2)
SH2	0.9 (± 0.6)	0.8 (± 0.9)	5.5 (± 2.3)	1.0 (± 0.3)	0.4 (± 0.1)
SH3	0.9 (± 0.6)	1.0 (± 0.7)	5.4 (± 1.9)	0.7 (± 0.4)	0.3 (± 0.1)
SH4	0.7 (± 0.8)	2.0 (± 0.6)	9.7 (± 1.2)	1.0 (± 0.6)	0.3 (± 0.2)

1.4 bits ind⁻¹ (LH1). Evenness was low and quite homogeneous ranging from 0.3 to 0.5.

The results of the ANOVA showed significant differences in the species richness between the permanent and the temporary ponds ($p < 0.05$ between permanent and long hydroperiod ponds; and $p < 0.01$ between permanent and short hydroperiod ponds) and it was higher in the permanent ponds. To reduce the effect of the different sampling effort in the permanent and the temporary ponds, only the dates when all the ponds were filled were compared. The differences in the species richness remained significant. With regard to the differences in the time since restoration, the species richness in the ponds recently restored was significantly lower than in the other two groups ($p < 0.01$ in both analysis), also if only the dates when all the ponds had water were compared ($p < 0.05$ between modified and recently restored ponds, and $p < 0.01$ between restored in the 90s and recently restored).

Relationships between zooplankton and environmental variables

A total of six environmental variables (depth, conductivity, time since restoration, chlorophyll *a* and oxygen) as well as 25 zooplankton species were retained to perform the CCA. The first two axes extracted from the CCA accounted for 19 % of variance (10.2 % of variance the first axis and 8.8 % the second one) and both Monte Carlo tests were significant ($p < 0.01$). The first axis (Fig. 3a) was highly correlated with depth, and separated the deeper and permanent ponds from most of the temporary (shallower) ones. The second axis showed higher correlation with conductivity, chlorophyll *a* and oxygen; thus in the positive region of this axis were located the systems with higher values of these variables, in particular conductivity and chlorophyll *a* (SH3, P2 and LH2).

The species distribution agrees with this ordination (Fig. 3b); a group of species tolerant to higher salinity levels, including *A. americanus*, *Brachionus plicatilis* or *C. adriatica*; appeared in the positive region of the second axis where the ponds with higher conductivity were distributed. The species associated with the permanent

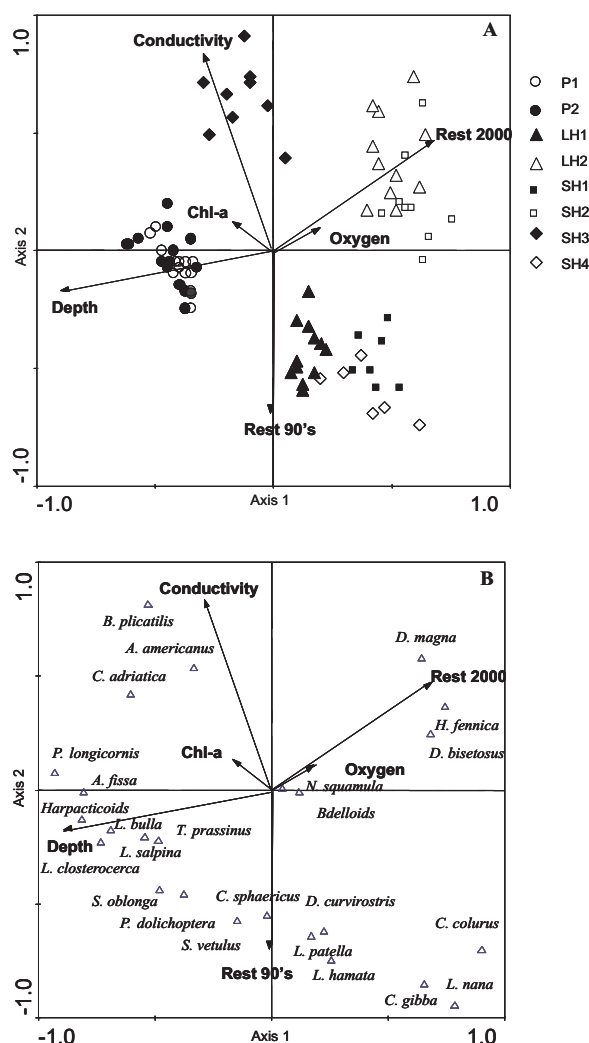


Figure 3. CCA ordination diagram showing the distribution of samples (3a, upper graph) and species position (3b, lower graph) in relation to environmental variables in the space represented by the two first axes. *Diagrama de ordenación del CCA mostrando la distribución de las muestras (3a, gráfica superior) y la posición de las especies (3b, gráfica inferior) en relación con las variables ambientales en el espacio representado por los dos primeros ejes.*

ponds (negative part of the first axis), are not only characteristic of open waters (such as the rotifers *P. dolichoptera*, *Anuraeopsis fissa* and *Synchaeta oblonga* or the copepod *T. prasinus*) but are also species associated to macrophytes (such as the rotifers *Lophocaris salpina* and *L. bulla* or the cladoceran *S. vetulus*). Taxa that appeared in most of the lakes (such as bdelloid rotifers

fers or *N. squamula*) appeared in the centre of the figure. Several littoral species (such as the rotifers *L. patella*, *L. nana*, *C. colurus* or the cladocerans *D. curvirostris* and *C. sphaericus*) were found associated with the shallowest ponds with the shortest hydroperiods.

DISCUSSION

This studied group of peridunal ponds, all located in the same area (maximum distance among them is less than 8 km), share some basic characteristics in terms of climate and substrate. Nevertheless, a marked temporal and spatial heterogeneity was found, particularly for limnological variables such as conductivity, trophic level and duration of the inundation period. Thus, we have found a wide range of variation in the ponds which favours the diversity of zooplankton species. Some ponds were restored at different time, although this is not clear in the limnological variables, it seems to have a notorious effect on zooplankton community.

Values of specific richness per visit, diversity and evenness are low, compared with other studies in similar ecosystems (e.g. Galindo *et al.*, 1994; Armengol & Miracle, 1999; Rodrigo *et al.*, 2001). This could be related with the restoration and subsequent colonization process. Rotifers contributed greatly to the community structure in these ponds. Although this group has been often neglected in zooplankton studies, they were the most diverse group and the most abundant in some ponds. This was also the case in most studies in similar dune ponds, such as the ones carried out by Galindo *et al.* (1994), Fahd *et al.* (2000) and Serrano & Fahd (2005). With regard to the crustaceans, it is remarkable the presence of the anostracean *T. stagnalis*. It was found in only one of the systems, a temporary pond with short hydroperiod (SH1). This large species can outcompete filter feeder cladocerans and rotifers, but it is very sensitive to predation (Bohonak & Whiteman, 1999). Thus, living in temporary ponds, where larger predators are frequently absent (Schneider & Frost, 1996), can reduce their risk of predation.

The results of CCA suggest the relevance of conductivity and depth, but they have also indicated the importance that the restoration processes could have on these communities. Nevertheless these results should be taken with caution, due to the low number of ponds studied. The results obtained agree with other studies, where the duration of the hydroperiod (here closely related to depth) could be the main factor determining the structure and composition of the community in aquatic systems (e.g. Wellborn *et al.*, 1996; Boix *et al.*, 2001; Eitam *et al.*, 2004). Generally, the species richness is higher in permanent ponds (e.g. Collison *et al.*, 1995; Alonso, 1998; Spencer *et al.*, 1999) or in the temporary ponds with longer hydroperiods (e.g. Boix *et al.*, 2001; Fahd *et al.*, 2000). The comparison between permanent and temporary water bodies is difficult. Obviously the sampling effort (a longer sampling period in permanent ponds) would increase the cumulative specific richness. Nevertheless, as stated previously, significant differences are still found when only the period with water in all the ponds was compared.

In this study, permanent ponds recorded the highest number of species which is probably related to several factors: (i) greater habitat heterogeneity, due to the abundance of macrophytes and to the greater depth of these ponds (Crosetti & Margaritora, 1987), (ii) more time to complete life cycles, community development and colonization, (iii) larger diversity of conditions which could enable the hatching of more species diapausing eggs (iv) abundance of waterfowl, an important vector for the dispersal of zooplankton in resting stages (e.g. Figuerola & Green, 2002), and finally, (v) permanent ponds harbour fish populations and more macroinvertebrate predators (dragonflies, damselflies, water beetles, etc.), so they have stronger predation pressure, preventing the dominance of a few species (Spencer *et al.*, 1999). This can also affect positively small-sized zooplankton species (rotifers and juvenile copepods), which can better support the predatory pressure of fish (Herzig, 1994), and are inferior competitors to large-sized species (e.g. Gilbert, 1988; MacIsaac & Gilbert, 1991). Following hydroperiod-depth, conductivity seems to

be the second factor affecting the zooplankton community. The role of salinity in influencing the community structure in ponds has been largely studied (Williams, 1999; Brock *et al.*, 2005; Toumi *et al.*, 2005; Waterkeyn *et al.*, 2008). In this study, salinity (~ conductivity) negatively affected the species richness, in accordance to other studies (e.g. Boronat *et al.*, 2001; Frisch *et al.*, 2006; Martinoy *et al.*, 2006; Waterkeyn *et al.*, 2008).

In our study, the time since the ponds were restored is also a very important factor to explain the ordination of samples. Badosa *et al.* (2006) found a lower biodiversity in old lagoons. In general terms, the opposite was found, because the ponds which were restored recently had lower species richness. The restoration is very important in terms of community succession and colonization processes, since older ponds frequently have dense egg banks and, therefore greater opportunities for hatching.

In conclusion, in our study ponds, the depth, highly related with the permanence of water, had a positive effect on the diversity of aquatic organisms, especially in the permanent ponds, where the highest number of zooplankton species was recorded, particularly of rotifers. Other factors, such as salinity and the time since the ponds were restored, which involve processes such as the tolerance to high salinity levels or the dispersal and colonization processes, also help to better explain the community structure of these peridunal ponds. The results obtained here highlighted the importance of the restoration processes to recover the biodiversity of aquatic systems, particularly in places heavily affected by human activities.

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