Knowledge and Management of Aquatic Ecosystems (2014) 412, 09 http://www.kmae-journal.org
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DOI: 10.1051/kmae/2013091

Artificial dam lakes as suitable habitats for exotic invertebrates: Ostracoda ecology and distribution in reservoirs of the Eastern Iberian Peninsula

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Received September 19, 2013
Revised December 4, 2013
Accepted December 5, 2013

ABSTRACT

Key-words:
ostracoda,
exotic species,
reservoirs,
Spain,
benthos

Reservoirs are the most common deep lakes in Spain, as a consequence of water needs and dry climate. Although these aquatic systems can play an important ecological role in such an area with few large natural lakes, they can also provide new habitats for exotic species, which can colonize ecosystems that native species have not explored yet. Here we present our results for a biannual survey of the ostracod fauna from 24 reservoirs in Xúquer River basin. We check which variables affect ostracod presence, test for differences between winter and summer assemblages, and compare our data with previous available ostracod records from the same river drainage network. Our results reveal that ostracod presence is positively related to high diversity of the invertebrate community and reservoir volume, and negatively with phosphorus concentration. Among the 22 species found, it is noteworthy the first Iberian record of *Ilyocypris getica* and the second European record of *Candonocypris novaezelandiae*. Ostracod assemblages significantly vary between summer and winter, and strong differences are found between ostracod communities of reservoirs and those from their connected rivers. Remarkably higher frequency of exotic species in the reservoirs confirms previous findings about the facilitation that artificial ecosystems confer to aquatic invasions.

RÉSUMÉ

Les lacs de barrage comme habitats appropriés pour les invertébrés exotiques : écologie et distribution des ostracodes dans les réservoirs dans l'Est de la péninsule ibérique

Mots-clés :
ostracodes,
espèces exotiques,
réservoirs,
Espagne,
benthos

Les réservoirs sont les plus courants lacs profonds en Espagne, en réponse aux besoins en eau et au climat sec. Bien que ces systèmes aquatiques puissent jouer un rôle écologique important dans une région avec peu de grands lacs naturels, ils peuvent aussi fournir de nouveaux habitats pour les espèces exotiques, qui peuvent coloniser ces écosystèmes que les espèces indigènes n'ont pas encore explorés. Ici, nous présentons les résultats d'un suivi semestriel de la faune d'ostracodes de 24 réservoirs dans le bassin de la rivière Xúquer. Nous recherchons quelles variables affectent la présence des ostracodes, testons les différences entre les assemblages d'hiver et d'été, et comparons nos données avec des données antérieures d'ostracodes disponibles du même bassin versant. Nos résultats révèlent que la présence des ostracodes est positivement liée à la grande diversité

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de la communauté d'invertébrés et au volume du réservoir, et négativement avec la concentration en phosphore. Parmi les 22 espèces présentes, il est à noter le premier enregistrement ibérique de *Ilyocypris getica* et le deuxième d'Europe de *Candonocypris novaezelandiae*. Les assemblages d'ostracodes varient considérablement entre l'été et l'hiver, et de fortes différences sont observées entre les communautés d'ostracodes de réservoirs et celles de leurs rivières tributaires. Une fréquence remarquablement élevée d'espèces exotiques dans les réservoirs confirme des conclusions précédentes sur la facilitation que les écosystèmes artificiels confèrent aux invasions aquatiques.

INTRODUCTION

Reservoirs represent an extreme modification of rivers, changing the hydric regime from lotic to lentic, what implies a deep alteration of their limnological characteristics, which also differ from a natural lake. Dam construction disturbs the previously established flora and fauna, as it usually implies water eutrophication (Moss, 1998). Furthermore, most of the substrate area for the new waterbody has never been linked to the aquatic environment (as usually they are not floodplains, but heavy mountain slopes), and the shore level shifts rapidly not because of the natural water cycle but strongly depending on human demand. All these factors highly affect the reservoirs' ecology, making them unique habitats and, in the case of Spain, what Margalef (1983) described as an "ecological experiment". Indeed, Spain presents a high degree of human-control and channel modifications of rivers due to the Mediterranean climate, which triggers low availability of water for agriculture and human use during long periods (from months to years) (Aupí, 2005).

Biological invasions are frequent in reservoirs, as they are relatively new, disturbed, man-managed habitats (Moss, 1998; Havel *et al.*, 2005). In the Iberian Peninsula, most of known introduced aquatic species are fishes, which arrive to the reservoirs both form accidental and deliberate introductions (Elvira, 1995). Some of these species are able to produce great disturbances and become dominant, like the black bass, *Micropterus salmoides* (Lacépède, 1802) (Elvira, 1995). Aquatic invertebrate invasions, although not as noticeable as vertebrate's, are becoming increasingly common (Gherardi, 2007). In Spain, the zebra mussel *Dreissena polymorpha* (Pallas, 1771) is the best-known case, because of its enormous ecological and economic impact (Durán *et al.*, 2009, 2012). This invasive species is present in the Ebro and Xúquer basins and it is still spreading, mainly because of the fishing-related transport (boats, shoes, car tires), even though several control measures are strict and operative in all the territory where it is found (Durán Lalaguna and Anadón Marco, 2008). Other examples of aquatic invasive invertebrates in the area are the American crayfish *Procambarus clarkii* (Girard, 1852) (which is widespread and not only related to reservoirs but to all kind of water systems) and molluscs such as the snail *Pomacea insularum* (d'Orbigny, 1835), which produces large ecological and agricultural disturbances in the Ebro Delta, or the clam *Corbicula fluminea* (Müller, 1774) (Geiger *et al.* 2005; Pérez-Quintana, 2008; MMAMRM, 2011).

Although riverine ostracods in eastern Spain have been studied before (Mezquita *et al.*, 1999, 2001), there is not any comprehensive survey of this widespread crustacean group in Iberian or European reservoirs hitherto. In our broad survey, we aimed at contributing to the knowledge of exotic ostracod species, which have been poorly reported from Spanish freshwater ecosystems (Forés *et al.*, 1986, Escrivà *et al.*, 2012). Despite reservoirs are physically connected to their associated rivers, they should be considered disparate ecosystems, and therefore we expected to found wide differences in ostracod assemblages between them. In this framework, one of our main scopes was to test the hypothesis that ostracod communities would differ between reservoirs and rivers, and a higher number of exotic species is expected in the artificial impoundment lakes, as they have been described as "stepping stones" for invasive species (Havel *et al.*, 2005).

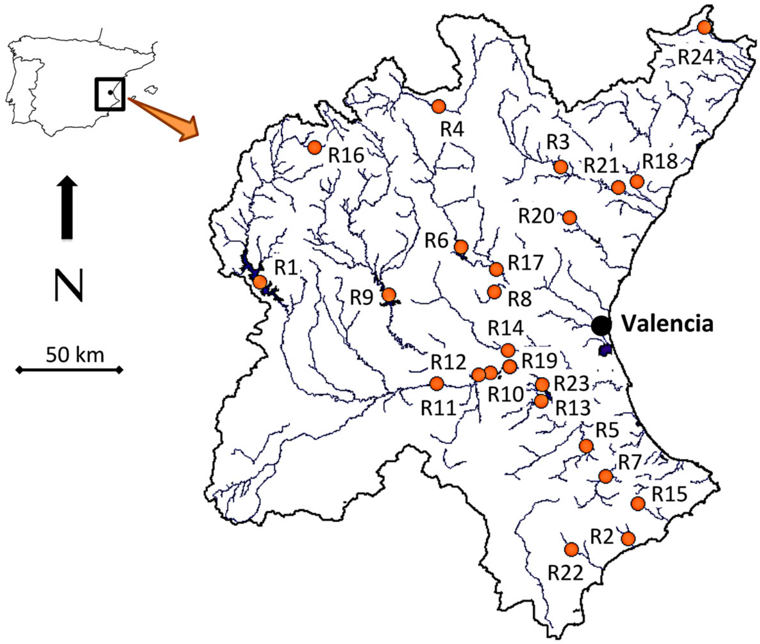

Figure 1
Map of the study area showing sampling locations. Codes for reservoirs are the same as in Table II.

MATERIALS AND METHODS

We analysed the ostracod communities of 24 reservoirs (Figure 1) managed by the Xúquer River Basin Hydrological Administration (CHJ, Confederación Hidrográfica del Júcar). This management unit covers 48832 km^2 on the central slope of the Eastern Iberian Peninsula, encompassing Xúquer (=Júcar) and Túria rivers as the two largest basins in this unit. The geography of the area consists mainly of an extensive Quaternary alluvial plain surrounded by limestone massifs reaching almost 2000 m a.s.l. The climate is mainly Mediterranean, with rainfall concentrated in spring and autumn, and summer drought affecting almost all the rivers and generating a considerable ecological stress to the riparian vegetation and fauna inhabiting the banks and riverbeds (Aupí, 2005)

All reservoirs were sampled on 4 occasions: summer 2006, winter 2006/2007, summer 2007 and winter 2007/2008, with the only exception of Guadalest (R15) that was not sampled in winter 2007/2008. All of the acquired samples (95) were collected using an Ekman dredge (0.0225 m^2 sampled once), from a boat located in the central area of the reservoir, but always at depths ranging between 3 and 5 m to avoid hypoxic layers. The samples were preserved with dilute formaldehyde (4%) in the field, and then washed (mesh size = 200 μm) and preserved in ethanol (70%) in the laboratory. Macroinvertebrates and ostracods were identified with a stereomicroscope and light microscopy using Meisch (2000) for Ostracoda and Tachet *et al.* (2000) for macroinvertebrates. Pictures of ostracod valves and carapaces were taken with a Philips XL30 scanning electron microscope (SEM) at the University of Valencia, after their coating with Au-Pd.

Physical and chemical data from reservoirs, collected at the same time than the biological samples, were downloaded from the Spanish Ministry of Agriculture, Food and Environment, through its CHJ webpage (www.chj.es). These variables included altitude (m), depth (m) and volume (hm^3); water temperature (°C), conductivity (μS·cm^{-1}), pH, oxygen content (mg·L^{-1}) and saturation percentage and turbidity (NTU), measured *in situ* with portable probes as an average of the water column; Secchi disc depth (m); chlorophyll *a* (μg·L^{-1}), nitrite, nitrate, ammonia, total nitrogen, ortophosphate and total phosphorus concentrations (mg·L^{-1}) and algal biovolume (mm^3·L^{-1}) measured in the lab from water samples collected at 2 m depth.

Macroinvertebrate Shannon diversity index (H, with log base 2) was calculated from the identified taxa obtained with the dredge. From the same samples, presence, absence and abundances of ostracod taxa were obtained. For statistical comparisons, ostracod data from associated rivers was acquired from the only comprehensive work published on the ostracod fauna of the basins sampled in the present survey (Mezquita *et al.*, 1999).

In order to check for environmental effects on the presence of living ostracods we performed a binary multivariate logistic regression (LR) with stepwise forward selection of variables, using the software SPPS v19.0 (SPPS Inc., 2010). In LR we introduced the above mentioned predictor variables. With the exceptions of temperature, diversity, altitude, depth, Secchi Disc and oxygen saturation percentage, the rest of variables were $\log_{10}$-transformed because they presented a right-skewed distribution.

We performed Analyses of Similarities (ANOSIM) and Similarity Percentage (SIMPER) analyses (Clarke and Warwick, 2001) to compare the ostracod communities (presence-absence data) between winter and summer seasons and between reservoirs and rivers. Both were carried out using the Jaccard index in PAST software (Hammer *et al.*, 2001). The relationship between ostracod assemblages (presence-absence) and environmental data was studied using CANOCO for Windows (ter Braak and Šmilauer, 2002). We performed a DCCA in order to evaluate the length of the gradient; as we obtained a value higher than 4, we decided to use a CCA unimodal analysis (with downweighting of rare species) following Lepš and Šmilauer (2003). The forward selection of variables (FSV) with 999 permutations was used to select the most relevant parameters explaining ostracod species distribution.

RESULTS

In the 95 samples from 24 reservoirs we found a total of 351 individuals accounting for 22 species of ostracods (Table I). The most common species were *Ilyocypris gibba* and *Darwinula stevensoni*. *Ilyocypris getica* was here found for the first time on the Iberian Peninsula and the presence of two exotic species (*Fabaeformiscandona subacuta* and *Candonocypris novaezelandiae*) was also remarkable. SEM photographs of selected species are shown in Figure 2.

A total number of 43 taxa of macroinvertebrates were found. These data were used to calculate Shannon diversity as a proxy for reservoirs' ecological state (shown in Table II) , taking into account that increasing stress in reservoirs through level variations and eutrophic conditions reduces benthic diversity (Margalef, 1983). Two exotic species were detected: the zebra mussel *Dreissena polymorpha*, found abundantly in one reservoir (R21), and the crayfish *Procambarus clarkii,* that was found in reservoirs R11 and R19. Further detailed discussion of the invertebrate data will be published elsewhere.

As can be seen in Table II, the studied reservoirs have a broad range of physical, chemical and biological conditions. Altitude ranges between 106 and 1156 m a.s.l., and volume between 4 and 1118 hm^3. Conductivity varies an order of magnitude, from a minimum measured value of 308 to a maximum of 3228 $\mu\text{S}\cdot\text{cm}^{-1}$; the macroinvertebrate Shannon diversity index ranged from a minimum observed value of 0 (no taxa found) to a maximum value of 2.99 $\text{bits}\cdot\text{ind.}^{-1}$.

According to logistic regression analysis, the presence of living ostracods (found in 40 out of 95 samples) is positively related to macroinvertebrate diversity and reservoir volume, and negatively to total phosphorus concentration. The final model with these three variables included was significant ($p < 0.001$; $R^2 = 0.29$) and allowed a correct classification of 74% of samples according to the presence or absence of living ostracods.

An ANOSIM analysis was performed comparing the ostracod fauna (occurrence data) between reservoirs and rivers. Here, dead specimens (*i.e.* valves and other remaining parts of ostracod individuals) were considered as "presence" to account for inter-annual variability in ostracod assemblages. This analysis shows that these two habitats can be clearly separated because of their ostracod fauna ($R = 0.3764$, $p = 0.0001$). A SIMPER analyses was performed to identify the main species that differed between each habitat. The mean rank

Table I

List of ostracod species found in reservoirs of the Eastern Iberian Peninsula. N = number of individuals found in this survey (number of alive specimens between brackets). Sample codes in roman type correspond to samples with the presence of living individuals, those in italics correspond to samples with only ostracod remains (shells or valves). Sample codes are composed of reservoir code (first 2–3 digits as in Table II) plus two last digits indicating sampling year and season (11 = summer 2006; 12 = winter 2006–2007; 21 = summer 2007; 22 = winter 2007–2008).

Species	Code	*N*	Samples
***Darwinula stevensoni* (Brady and Robertson, 1870)**	DWS	126 (30)	R911 R1011 R1212 R1221 R1222 R1311 R1312 R1911 R1921 R2112 R2311 R2322 *R1211 R1322 R2321*
***Fabaeformiscandona subacuta* (Yang, 1982)**	FSU	18 (7)	R1311 R1911 R1921 R2012 R2321 R2422 *R722 R1312 R1322 R2112 R2122*
***Pseudocandona albicans* (Brady, 1864)**	PSA	6 (3)	R322 R421 R2422 *R1011 R1512 R2112*
***Pseudocandona rostrata* (Brady and Norman, 1889)**	PRO	1 (1)	*R2412*
***Cryptocandona* sp.**	CRC	2 (0)	R2311
***Ilyocypris gibba* (Ramdohr, 1808)**	ILG	79 (44)	R111 R112 R121 R122 R311 R421 R911 R912 R922 R1122 R1222 R1312 R1322 R1622 R1712 R2112 R2311 R2322 *R1011 R1111 R1121 R1212 R1522 R1611 R1722 R1821 R2321*
***Ilyocypris bradyi* Sars, 1890**	ILB	2 (1)	R111 *R1311*
***Ilyocypris getica* Masi, 1906**	IGE	15 (13)	R311 R611 *R612 R1521*
***Ilyocypris inermis* Kaufmann, 1900**	ILI	10 (5)	R112 R1312 *R911*
***Eucypris virens* (Jurine, 1820)**	EVI	1 (0)	R2312
***Herpetocypris brevicaudata* Kaufmann, 1900**	HBR	6 (6)	*R221 R1011 R1911 R2322*
***Herpetocypris helenae* G. W. Müller, 1908**	HHE	11 (2)	R2311 *R911 R2321*
***Candonocypris novaezelandiae* (Baird, 1843)**	CNZ	5 (4)	R1121 *R1111 R1122*
***Heterocypris salina* (Brady, 1868)**	HSA	3 (3)	*R511 R512 R2012*
***Isocypris beauchampi* (Paris, 1920)**	ISB	28 (0)	R112 R121 R122 R422 R612 R1212 R1222 R1521 R1712 R1722 R2311
***Cypridopsis vidua* (O.F. Müller, 1776)**	CVI	21 (14)	R221 R222 R421 R2421 *R311 R422 R511 R611 R612 R722 R1312 R2112*
***Potamocypris variegata* (Brady and Norman, 1889)**	PVA	2 (2)	*R2322*
***Potamocypris arcuata* (Sars, 1903)**	PAR	2 (1)	R722 *R511*
Cyprididae juv. indet.	CYJ	1 (1)	*R712*
***Limnocythere inopinata* (Baird, 1843)**	LIN	10 (6)	R722 R1011 R1611 R1712 R2122 *R422 R611 R2112 R2312*
***Paralimnocythere messanai* Martens, 1992**	PAM	1 (0)	R2112
***Cyprideis torosa* (Jones, 1850)**	CYT	1 (1)	*R711*

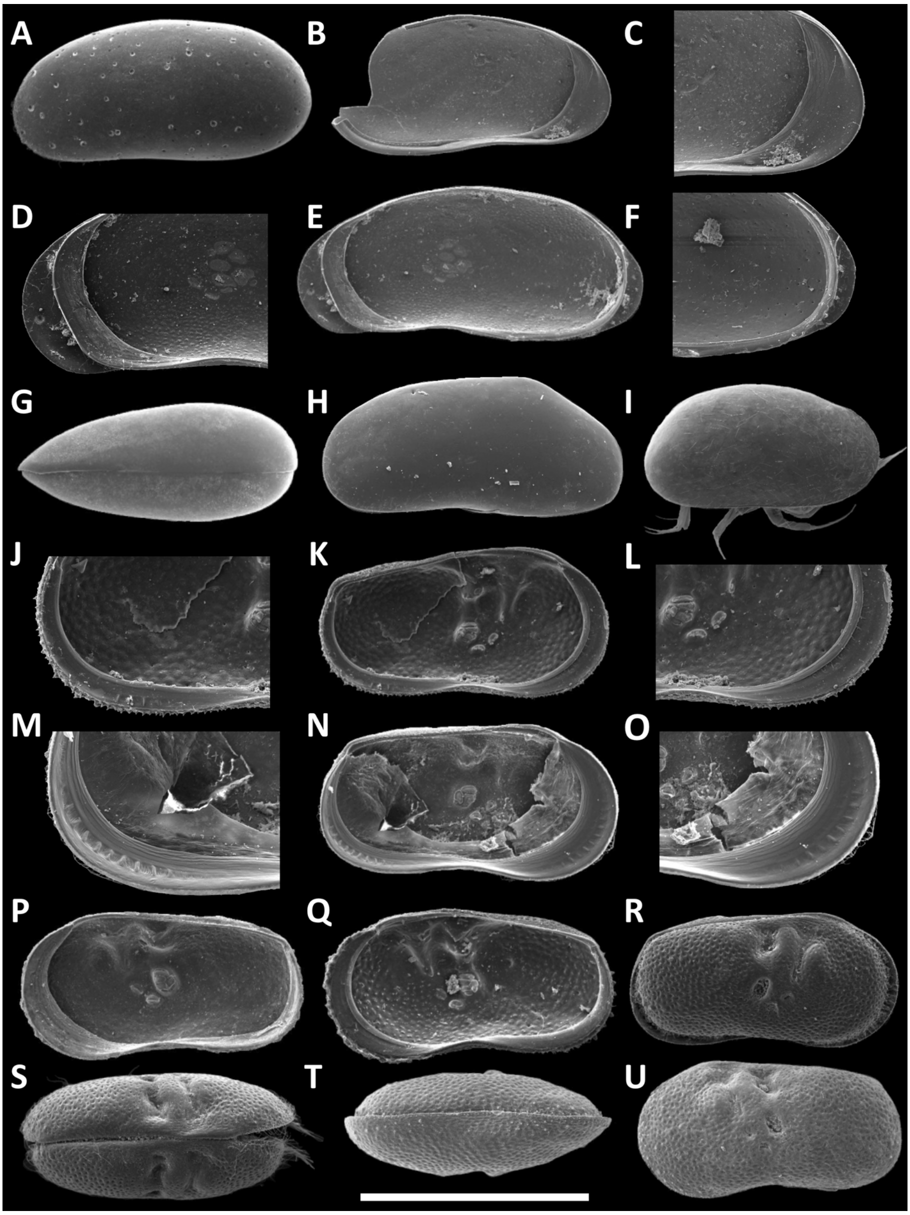

Figure 2

SEM photographs of Candonocypris novaezelandiae (A–F), Darwinula stevensoni (G), Fabaeformiscandona subacuta (H), Isocypris beauchampi (I), Ilyocypris gibba (J–L, Q), and Ilyocypris getica (M–P, R–U). A, C. novaezelandiae, female, carapace, left view (bar = 1221 μm); B, C. novaezelandiae, female, left valve inner view (bar = 1244 μm); C, C. novaezelandiae, female, detail of left valve, anterior inner view (bar = 840 μm); D, C. novaezelandiae, female, detail of right valve, anterior inner view (bar = 833 μm); E, C. novaezelandiae, female, right valve inner view (bar = 1120 μm); F, C. novaezelandiae, female, detail of right valve, posterior inner view (bar = 861 μm); G, D. stevensoni, female, carapace, dorsal view (bar = 544 μm); H, F. subacuta, female, carapace, left view (bar = 640 μm); I, I. beauchampi, female, carapace, right view (bar = 1208 μm); J, Ilyocypris gibba, female, detail of left valve, posterior inner view (bar = 426 μm); K, Ilyocypris gibba, female, left valve inner view (bar = 652 μm); L, Ilyocypris gibba, female, detail of left valve, anterior inner view (bar = 438 μm); M, Ilyocypris getica, female, detail of left valve, posterior inner view (bar = 438 μm); N, Ilyocypris getica, female, left valve inner view (bar = 828 μm); O, Ilyocypris getica, female, detail of left valve, anterior inner view (bar = 557 μm); P, Ilyocypris getica, female, right valve inner view (bar = 789 μm); Q, Ilyocypris gibba, female, right valve inner view (bar = 629 μm); R, Ilyocypris getica, female, carapace, right view (bar = 841 μm); S, Ilyocypris getica, female, carapace, dorsal view (bar = 895 μm); T, Ilyocypris getica, female, carapace, ventral view (bar = 725 μm); U, Ilyocypris getica, female, carapace, left view (bar = 789 μm).

Table II
Geographical location, physical, chemical and biological data of sampling sites. Average and standard deviation values are indicated for variables measured through the four sampling campaigns. H refers to macroinvertebrate Shannon diversity.

Reservoir	Code	Latitude (°)	Longitude (°)	Volume (hm^3)	Depth (m)	Conductivity ($\mu S \cdot cm^{-1}$)	Altitude (m)	O_2 (%)	Chlorophyll *a* ($\mu g \cdot L^{-1}$)	H ($bits \cdot ind^{-1}$)
Alarcón	R1	39.64864	–2.21396	1118	**16.0 ± 1.8**	768 ± 87	477	**91 ± 19**	2.65 ± 1.25	1.62 ± 0.65
Amadorio	R2	38.54322	–0.26072	16	**25.8 ± 6.4**	1109 ± 271	108	**93 ± 20**	1.07 ± 0.62	0.97 ± 0.76
Arenós	R3	40.10545	–0.56679	136	**38.3 ± 17.9**	762 ± 97	600	**95 ± 20**	1.57 ± 1.41	1.26 ± 1.13
Arquillo S. Blas	R4	40.37289	–1.22785	21	**28.5 ± 3.1**	661 ± 58	974	**86 ± 17**	0.83 ± 0.24	2.16 ± 0.68
Bellús	R5	38.93493	–0.47334	69	**15.3 ± 4.6**	1027 ± 172	160	**88 ± 28**	23.00 ± 20.22	0.55 ± 0.70
Benagéber	R6	39.78351	–1.12101	221	**41.8 ± 3.9**	1234 ± 122	527	**92 ± 24**	1.32 ± 0.61	1.70 ± 0.49
Beniarrés	R7	38.80436	–0.37461	27	**15.3 ± 2.6**	1255 ± 284	285	**105 ± 23**	35.35 ± 41.08	0.63 ± 0.96
Buseo	R8	39.59061	–0.94382	8	**6.3 ± 1.0**	357 ± 23	240	**103 ± 10**	2.84 ± 1.38	1.07 ± 0.97
Contreras	R9	39.58790	–1.51692	852	**26.8 ± 3.3**	1070 ± 194	640	**91 ± 19**	0.88 ± 0.10	1.58 ± 0.80
Cortes II	R10	39.25145	–0.97398	117	**76.3 ± 11.6**	1070 ± 128	326	**100 ± 11**	0.89 ± 0.10	1.36 ± 1.08
El Molinar	R11	39.21109	–1.26593	4	**6.5 ± 1.9**	794 ± 107	476	**106 ± 7**	2.15 ± 1.99	1.10 ± 0.73
Embarcaderos	R12	39.24307	–1.04093	11	**2.8 ± 0.5**	1065 ± 196	315	**101 ± 10**	1.11 ± 0.62	1.89 ± 0.32
Escalona	R13	39.12763	–0.70947	99	**15.0 ± 2.2**	1742 ± 310	143	**104 ± 12**	0.99 ± 0.26	1.36 ± 0.43
Forata	R14	39.34305	–0.87954	37	**11.8 ± 1.3**	1069 ± 85	380	**79 ± 27**	2.50 ± 1.00	0.08 ± 0.16
Guadalest	R15	38.68713	–0.20418	13	**29.3 ± 8.3**	344 ± 34	380	**107 ± 10**	0.91 ± 0.18	1.98 ± 0.75
La Toba	R16	40.20981	–1.91078	10	**8.5 ± 1.3**	602 ± 69	832	**92 ± 12**	1.33 ± 0.62	0.68 ± 0.60
Loriguilla	R17	39.68443	–0.93252	73	**18.8 ± 1.5**	1176 ± 81	1156	**104 ± 11**	1.07 ± 0.54	1.49 ± 0.22
María Cristina	R18	40.03439	–0.15732	18	**5.3 ± 1.7**	645 ± 165	320	**93 ± 17**	3.77 ± 2.94	0.83 ± 0.63
Naranjero	R19	39.27323	–0.85265	29	**41.5 ± 12.7**	1092 ± 98	116	**97 ± 17**	0.83 ± 0.06	1.75 ± 0.64
Regajo	R20	39.89486	–0.52624	6	**11.8 ± 1.3**	627 ± 85	240	**106 ± 24**	3.35 ± 2.69	1.83 ± 0.95
Sitjar	R21	40.01588	–0.25711	49	**22.5 ± 5.8**	865 ± 119	405	**100 ± 13**	1.09 ± 0.63	2.02 ± 0.74
Tibi	R22	38.50445	–0.56555	4	**10.5 ± 0.6**	2918 ± 237	164	**121 ± 31**	23.70 ± 25.48	0.65 ± 1.29
Tous	R23	39.19592	–0.69865	378	**24.5 ± 7.0**	1038 ± 74	300	**92 ± 21**	0.74 ± 0.13	0.98 ± 0.69
Ulldecona	R24	40.68350	0.23109	11	**35.3 ± 5.0**	396 ± 50	130	**94 ± 21**	0.83 ± 0.13	1.56 ± 0.77

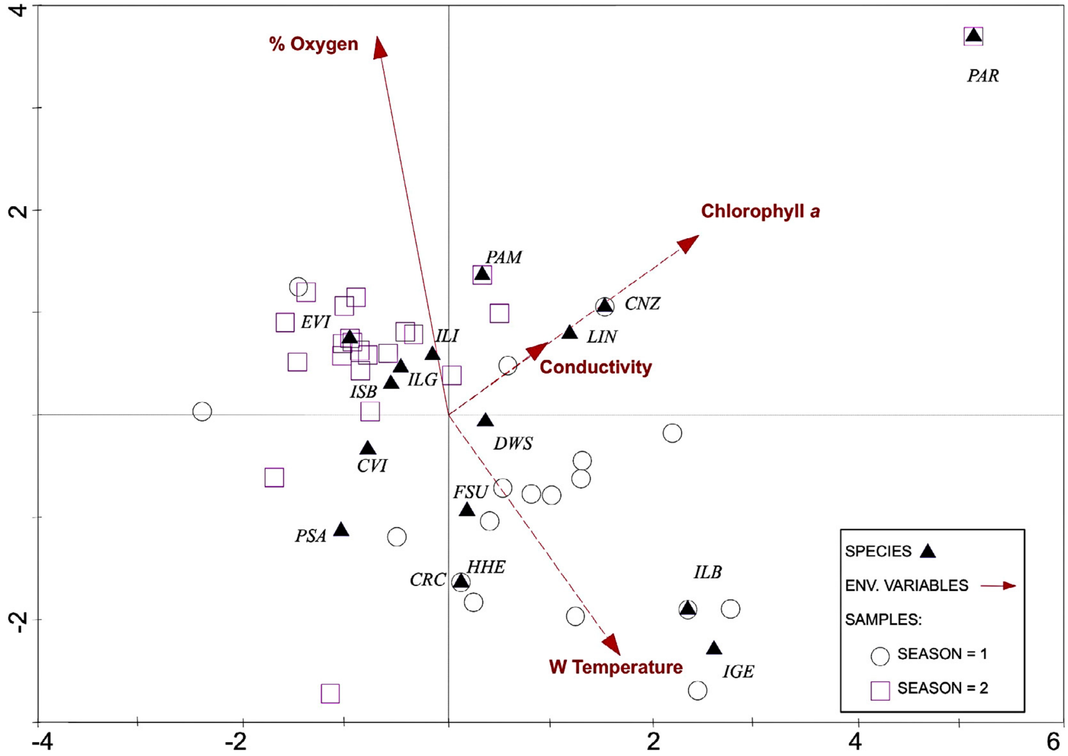

Figure 3
Canonical Correspondence Analysis (CCA) ordination diagram (first two axes) of ostracod species and reservoir samples in relation to the four most relevant variables according to the Forward Selection of Variables (FSV) permutation test. Species codes as in Table I. Arrows with solid line indicate significant variables, those with dashed line correspond to non significant variables ($p > 0.05$) according to FSV test. Season 1 = summer; Season 2 = winter.

value of dissimilarities within groups was 1000, being 1455 between groups (9999 permutations). The main seven species that together contributed to nearly 60% of the differences found are (in order of contribution) *Herpetocypris brevicaudata*, *I. gibba*, *Cypridopsis vidua*, *Limnocythere inopinata*, *Ilyocypris inermis*, *Isocypris beauchampi* and *D. stevensoni*. The last two species, together with *I. gibba* are more frequently found in reservoirs, in comparison to the others.

Further tests were performed in order to reveal the influence of sampling season (winter vs. summer). ANOSIM results show that there is a significant difference between the ostracod communities present in both seasons ($R = 0.013$, $p = 0.028$), but only when taking into account alive specimens (*i.e.* excluding ostracod remains). When adding the valves and carapaces to this analysis no difference is found. According to SIMPER analysis, the mean rank value of dissimilarities within groups was 2265, being 2295 between groups (9999 permutations). Four species contributed to 61% of the differences between seasons. The species *I. gibba* and *I. beauchampi* were more frequent in winter while *D. stevensoni* and *F. subacuta* were more commonly found in summer.

CCA analyses resulted in a low relative amount of species data explained (first axis 5.0%, second axis 4.4%, and total inertia equal to 8.5), but high species-environment correlations (axis 1: 0.74, axis 2: 0.70). The only significant variable selected by FSV was oxygen saturation percentage. Figure 3 shows the ordination of the species and samples in relation to the four most relevant variables to allow an easier interpretation of the CCA results. To allow a better understanding of limnological variation in the reservoirs in relation to ostracod fauna, in addition to oxygen we added to the graph the variables temperature, conductivity and chlorophyll *a* concentration, which had the highest contribution (although not significant) according to FSV.

Samples with highest oxygen saturation and lowest temperature, mainly corresponding to winter months, are dominated by the species *I. gibba* and *I. beauchampi*. On the other side of the diagram, *D. stevensoni* and *F. subacuta* are the most common species found in summer samples, characterised by highest temperatures and lowest oxygen. On the intermediate range of this gradient we found *C. vidua* and *Pseudocandona albicans* related to lower chlorophyll *a* values, while *L. inopinata* related to more eutrophic conditions.

DISCUSSION

In this paper we present the first comprehensive account of ostracods from reservoirs. Our results are remarkable in finding several species not previously recorded in the studied area; this confirms the first European records for *C. novaezelandiae* by Valls *et al.* (2013) and Escrivà (2011) (as "Cypridinae sp1"), which were found in coastal areas of Spain. The results of the present survey notably expand its known distribution to inland water bodies in the Iberian Peninsula. As discussed in Valls *et al.* (2013), the species was previously found in Eastern Africa, Eastern Asia, Australia and New Zealand, but not in Europe. These findings suggest that this exotic species is expanding in the eastern Iberian Peninsula, in a similar way as another potential invader of Asian origin, *F. subacuta* (Escrivà *et al.*, 2012), which has been found several times in the studied reservoirs. *Ilyocypris getica* is here reported for the first time in the Iberian Peninsula (see Baltanás *et al.*, 1996 for a review of ostracod species in the area). The species is widely distributed in Northern Africa and European Mediterranean countries, although it has also been found as north as Germany (Meisch *et al.*, 1996). These authors hypothesize that the presence of this species in Central Europe is attributable to passive transport by migratory birds. Notably, another common species in our survey, *I. beauchampi*, is also considered of African origin (Meisch, 2000; García-Berthou *et. al.,* 2007). It can be argued that the on-going global warming could facilitate colonization of northern habitats by non-indigenous species coming mainly from Africa, through migratory birds stopping at the Iberian Peninsula in their routes. Among the most common ostracods in the studied reservoirs, we found *D. stevensoni*, a species with cosmopolitan distribution (Sohn, 1987; Karanovic, 2012), but see Schön *et al.* (2012) for a discussion of Darwinulidae cryptic species.

Despite we found a relative high number of species in the studied reservoirs, it must be noticed that about half of the samples did not contain living specimens. According to the LR analysis, it is more probable to find alive ostracods in large, low nutrient content reservoirs, with high diversity of benthic invertebrates. This is in agreement with general aspects of reservoir limnology, in which anoxic conditions are common in the hypolimnion, affecting negatively the proliferation of benthic fauna, particularly in small and highly fluctuating dam lakes (Margalef, 1983).

Although the majority of these reservoirs were built during the 20th century, and are connected to natural rivers, their associated benthic fauna is markedly different from these streams, as we have shown for the particular group of Ostracoda, and as expected from previous findings on zooplankton in other areas (*e.g.* Akopian *et al.*, 1999). Notwithstanding the potential changes in riverine communities that may have occurred taking into account the temporal gap between river (Mezquita *et al.*, 1999) and reservoir sampling campaigns compared in the present work, we would expect certain resilience of the ostracod assemblages for such a period of ten years, particularly when these basins have experienced no major impacts during this time interval. Consequently, we could conclude that the type of habitat, *i.e.* lotic *vs.* lentic has a strong influence on the community composition of limnetic ostracods, as already observed in previous works (Carbonel, 1988; Smith and Delorme, 2009; Mesquita-Joanes *et al.*, 2012).

Seasonality in Mediterranean aquatic habitats has been characterised as one of the main driving factors related to community changes through the year (Florencio *et al.*, 2009). Although reservoirs are non-natural environments managed depending on human needs, they also suffer strong level fluctuations as a result of river input changes related to the seasonality of the Mediterranean climate, which are exacerbated by human consumption of water during summer. In addition to these level changes of natural origin, human management trying to keep water level constant and as high as possible, also affect the ostracod communities of the reservoirs. These fluctuations lead to the summer dominance of species tolerant to low oxygen and high temperature and trophic state, such as *D. stevensoni* (Rossi *et al.*, 2002) and *F. subacuta* (Escrivà *et al.*, 2012), rather than species colonizing from upstream rivers. This duality, functioning both as deep permanent lakes in the centre and temporary habitats at littoral areas, allows the presence of ostracod species such as *Eucypris virens* or *I. gibba* during wet periods (from fall to spring), which show more preferences for temporary waters (Meisch, 2000; Martins *et al*., 2009).

Reservoirs in Mediterranean areas are likely to play the role of stepping-stones for exotic ostracod species, due to their completely different environmental parameters in relation to the river to which they are connected. As the Iberian Peninsula has a very low number of natural inland large permanent lakes, reservoirs can facilitate the colonization of the area by species typical of such habitats, originating from other European areas, Africa or other regions. Previous studies have shown how, despite holding a low number of species due to their disturbed state and dynamics (Prat *et al*., 1992), reservoirs allow the colonization of the Iberian Peninsula by previously unrecorded species of crustaceans (Riera *et al*., 1992).

The colonization of reservoirs by invertebrates, beside river connections, can be driven among other vectors, by humans and aquatic birds (Bilton *et al.*, 2001), that can feed, rest and nest in a diversity of waterbodies, including coastal wetlands, ricefields and nearby reservoirs. Birds are well-known dispersal agents of aquatic invertebrates: they have the ability to transport propagules and living adults, either as mud adhered to their legs and or in their faeces (Figuerola and Green, 2002; Frisch *et al.*, 2007). Birds should therefore be regarded as possible dispersal vectors for exotic species present in reservoirs, which can be coming from the nearby ricefields, a type of habitat that has been recognised as specially suitable for exotic ostracods (Forés *et al.*, 1986; McKenzie and Moroni, 1986; Escrivà *et al.*, 2012).

In this study we have shown how reservoirs can be a new and suitable habitat for the colonization of exotic species of ostracods in the frame of the Mediterranean area. Alien species originating in warmer areas (tropical Asia or Northern Africa) could spread more rapidly in Southern Europe due mainly to the influence of global warming and helped by transport vectors such as birds or humans. Further research is needed in reservoirs of the Iberian Peninsula and other European regions to check whether the common presence of exotic ostracods is also found in different climate and limnological conditions.

ACKNOWLEDGEMENTS

The authors would like to thank the microscope unit of the SCSIE-University of Valencia for their support with ostracod SEM pictures. This work was partially funded by the Spanish Ministry of Science and Innovation project ECOINVADER (CGL2008–01296/BOS) and the University of Valencia (“V-Segles” predoctoral grant to A. Escrivà). We would like to thank C. Rojo (Univ. Valencia) and the CHJ for help in organising the collection of samples and environmental data, and two anonymous referees that suggested helpful improvements to an earlier version of the manuscript.

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