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Luis Valls (Luis.Valls@uv.es)
Juan Rueda (Juan.Rueda@uv.es)
Francesc Mesquita-Joanes (mezquita@uv.es)

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Rice fields as facilitators of freshwater invasions in protected wetlands: the case of Ostracoda (Crustacea) in the Albufera Natural Park (E Spain)

Luis Valls[1*]
[*] Corresponding author
Email: Luis.Valls@uv.es

Juan Rueda[1]
Email: Juan.Rueda@uv.es

Francesc Mesquita-Joanes[1]
Email: mezquita@uv.es

[1] Department of Microbiology and Ecology and Cavanilles Institute of Biodiversity and Evolutionary Biology, University of València, Av. Dr. Moliner, 50, E-46100 Burjassot, Spain

Abstract

Background

Previous studies have identified rice fields in the Mediterranean region as 'hot spots' for the introduction of alien freshwater organisms. Consequently, special attention should be paid when rice fields are located inside or near protected areas for the conservation of native, endangered species. To analyse the relationship between rice field environmental traits and the ecology of aquatic invaders, a study of zoobenthic communities was carried out in July-September 2008 and May-August 2009 in ten rice fields located in the Albufera Natural Park (E Spain), with focus on Ostracoda.

Results

A total of nine ostracod species were found including four considered exotic: *Candonocypris novaezelandiae*, *Stenocypris macedonica*, *Cypris subglobosa* and *Hemicypris barbadensis*. The presence of *H. barbadensis* is remarkable, which is recorded for the first time in Europe and *S. macedonica* in the Iberian Peninsula. A checklist of Ostracoda from Albufera Natural Park is presented, including 11 exotic species, mostly unknown from Holocene sedimentary records. The analysis of ostracod assemblages showed significant relationship between oxygen content and ostracod species associations, suggesting that their abundance are partially controlled by habitat variables in the rice fields. The exotic species *C. novaezelandiae* was more abundantly collected in samples with reduced oxygen concentrations, in contrast to other native species whose abundances were lower in such conditions.

Conclusions

The rice fields in Mediterranean areas present a summer inundation period which is unlikely in natural temporary water bodies in the area and which may facilitate invasion by subtropical species. Lower proportion of exotic to native ostracods is observed in less disturbed areas compared to rice fields with intense human activities. We emphasise the role of anthropogenic effects in the dispersal and colonisation processes of exotic ostracods and their particular strong influence in the protected areas closest to rice fields.

Keywords

Alien species; Paddy fields; Ostracods; *Hemicypris barbadensis*; *Stenocypris macedonica*

Background

Invasion by alien species is considered as a threat to global biodiversity, second only to habitat loss, and has its greatest impact in aquatic ecosystems (Mooney and Cleland 2001). Indeed, in recent decades, a general increase in the number of exotic aquatic invertebrates, ostracods in particular, has been detected in freshwaters (McKenzie and Moroni 1986, Leppäkoski et al. 2002, Rossi et al. 2003).

In the Iberian Peninsula, an increasing number of freshwater ostracods are regarded as exotic species (Baltanás 1992, Baltanás et al. 1996, García-Berthou et al. 2007). Many vectors for the passive dispersal of ostracods have been recognised (Vanschoenwinkel et al. 2008, Sabagh et al. 2011, Aguilar-Alberola et al. 2012), but these do not fully explain their distribution. A vast percentage of these exotic species, mostly with subtropical and tropical origins, are established in the Mediterranean rice fields (Rossi et al. 2003, Escrivà et al. 2012). Among the studied potential vectors, the most important are probably waterbirds and humans (Green and Figuerola 2005, Waterkeyn et al. 2010). In rice fields, evidences point to human activities (e.g. transport of seeds, soil and machinery moving between different areas) as the most important dispersal vector for the introduction of exotic ostracods from distant regions (Fox 1965, McKenzie and Moroni 1986, Rossi et al. 2003, Escrivà et al. 2012).

Inter- and intra-annual variability of environmental conditions may influence colonisation success by exotic organisms (Davis, 2009). In this framework, ecosystems with physical alteration by human activities, such as rice fields, often present alien species (Ehrenfeld 2011). Shurin (2000) demonstrated that both the probability of successful invasion by colonists and the abundance of alien species once established decline with the increasing diversity of native species. Therefore, human impacts in wetlands through rice field culturing and management activities can produce an increase of probability of alien invertebrates (and ostracods in particular) to be established in the study area.

The Albufera Natural Park (Eastern Iberian Peninsula) is mostly made up of a shallow lake surrounded by rice fields and has a large variety of native ostracods species recorded from interdune and spring ponds (Rueda et al. 2006, Rueda et al. 2013), but an impoverished community in the highly impacted lake itself (Poquet et al. 2008). In this way, this protected area can become a hot spot for invasions because of the facilitation role for the entry and establishment of alien species in disturbed aquatic ecosystems. In addition, these invasion

events may increase affected by climate change and globalisation (Walther et al. 2009, McGeoch et al. 2010).

In this study, we aimed at evaluating the importance of exotic species in aquatic invertebrate communities, exemplified by ostracods, in modified and strongly human-managed habitats such as rice fields, in comparison with less impacted environments in the same area and in contrast with paleolimnological evidence of past communities. We also planned to test whether or not environmental factors influenced significantly the structure of ostracod communities in such a highly modified environment as rice fields, subjected to strong human impacts and management.

Methods

Rice fields studied are located in the natural preserve 'Tancat de Zacarés' (UTM: 30S 0729272/4354601), inside the Natural Park Albufera of Valencia (eastern Iberian Peninsula), at the southern border of the lake and covering 25.12 ha (Figure 1). Rice fields and Lake Albufera are connected by a web of irrigation canals. We sampled ten different rice fields, each named with codes 'A' to 'J'. No pesticides were used in the restricted area Tancat de Zacarés during the study period.

Figure 1 Location of sampling sites. (A-J) Rice fields in the Tancat de Zacarés area in the Albufera of Valencia Natural Park (Eastern Iberian Peninsula).

In the field, pH, oxygen content, conductivity, salinity and water temperature were measured with portable probes. At the same time, we collected water samples for laboratory analyses of alkalinity, chloride, phosphate, nitrate, nitrite and ammonium concentration. Benthic samples from each rice field were taken in July and September 2008 and again in May, June, July and August 2009 with a 100-μm mesh size, D-frame hand net over approximate area of 600 cm^2. Sediment obtained was fixed in the field with 30% ethanol. In the laboratory, the samples were washed and sieved through a 250-μm mesh sieve and stored in 70% ethanol. When present, ostracods were hand-picked under a stereomicroscope and stored in 70% ethanol for specific determinations. All complete animals collected alive (i.e. belonging to the biocoenosis) were picked, so as all disarticulated valves and empty shells belonging to the taphocoenosis. Ostracod dissections were prepared following Namiotko et al. (2011), and specimens were determined using the taxonomic publications by Meisch (2000), Broodbakker (1983), Petkovski and Meisch (1996) and Karanovic (2012). We obtained SEM photos of ostracod valves with a Hitachi S-4800 microscope (Hitachi, Chiyoda-ku, Japan) at the University of Valencia. We could not take pictures of *Dolerocypris sinensis* Sars 1903 and *C. subglobosa* Sowerby 1840 because of the poor preservation of their valves.

Species richness and total abundance were calculated for each sample. In addition, community differentiation was quantified with an analysis of similarities (ANOSIM) test to compare the abundance of species between samples collected either in spring (May-June) or summer (July-September). A similarity percentage (SIMPER) analysis was used for identification and quantification of the species contributing most to the observed differences between these groups of samples.

Species-environment relationships were studied using multivariate constrained ordination. Detrended correspondence analysis (DCA) showed a wide environmental gradient (SD > 4),

indicating that some species respond unimodally to underlying ecological gradients (ter Braak and Verdonschot 1995). Consequently, canonical correspondence analysis (CCA) was performed to relate ostracod abundance to their environmental setting and the significance of habitat variables tested with Monte Carlo permutations. The DCA and CCA were performed with CANOCO 5.0 (ter Braak and Šmilauer 2012). ANOSIM, SIMPER and Spearman correlation analyses were carried out with PAST 2.17 (Hammer et al. 2001).

Results

The rice fields were flooded from April to August, and rice was sown in May. At the end of June 2008 and 2009, water was drained for fourteen days. The rice was harvested in September 2008 and August 2009. The remaining months of the rice cycle, water was drained, and the field substrate was remixed by tractors.

The rice fields included in this study were located close to each other (Figure 1) but varied notably in their environmental conditions. A summary of the physical and chemical features measured in the ten rice fields studied is shown in Table 1. Electrical conductivity at point G was, on average, higher than 3,300 $\mu S \cdot cm^{-1}$ while sites C, E and H showed values below 2,000 $\mu S \cdot cm^{-1}$. A similar trend was observed for chloride concentration (Spearman rank correlation between conductivity and chloride concentration: $r = 0.988$; $p < 0.01$). High phosphates concentrations (>15 $mg \cdot L^{-1}$) were found in fields F and G, while concentrations at B, C, E and J were below detection level (<0.05 $mg \cdot L^{-1}$). Total nitrite concentration was highest in field C (1.83 $mg \cdot L^{-1}$ on average) and values were lower than 1.0 $mg \cdot L^{-1}$ in the other points. The highest ammonia concentrations (>0.9 $mg \cdot L^{-1}$) were detected in fields F, A and I.

Table 1 Mean and standard deviation values of physical and chemical variables analysed during the study period in Zacarés rice fields

Field	N	n	Cond (μS cm^{-1})	Sal (mg L^{-1})	O$_2$ (%)	WT (°C)	pH	Cl$^-$ (mg L^{-1})	Alk/Cl$^-$	PO$_4^{3-}$ (mg L^{-1})	NO$_3^-$ (mg L^{-1})	NO$_2^-$ (mg L^{-1})	NH$_4^+$ (mg L^{-1})
A	5	3	2,376 ± 34	1.2 ± 0.0	93.5 ± 29.4	25.8 ± 0.6	8.2 ± 0.7	296 ± 33	0.65 ± 0.20	0.06 ± 0.00	31.5 ± 2.8	0.12 ± 0.47	1.70 ± 0.18
B	6	4	2,906 ± 402	1.5 ± 0.2	138.2 ± 23.2	29.8 ± 2.6	8.8 ± 0.5	436 ± 70	0.38 ± 0.15	0.00 ± 0.00	33.7 ± 11.0	0.05 ± 0.04	0.58 ± 0.10
C	4	4	1,980 ± 184	1.0 ± 0.1	94.3 ± 42.1	27.8 ± 3.5	8.3 ± 0.1	209 ± 31	0.82 ± 0.26	0.00 ± 0.00	38.3 ± 12.5	0.71 ± 1.12	0.35 ± 0.13
D	4	4	2,503 ± 749	1.3 ± 0.4	112.5 ± 13.6	30.6 ± 2.3	8.7 ± 0.5	316 ± 70	0.64 ± 0.44	0.10 ± 0.20	33.7 ± 11.0	0.03 ± 0.00	0.35 ± 0.19
E	3	3	1,631 ± 218	0.8 ± 0.1	109.3 ± 50.9	29.8 ± 3.7	8.6 ± 0.2	152 ± 60	0.99 ± 0.02	0.00 ± 0.00	28.3 ± 14.1	0.33 ± 0.27	0.27 ± 1.27
F	4	3	2,610 ± 337	1.3 ± 0.2	128.6 ± 57.2	29.0 ± 1.4	8.5 ± 0.4	331 ± 61	0.48 ± 0.17	0.17 ± 0.14	25.0 ± 8.6	0.11 ± 0.12	0.97 ± 0.90
G	3	2	3,393 ± 1,034	1.8 ± 0.5	89.6 ± 33.5	29.9 ± 2.0	8.2 ± 0.2	448 ± 200	0.47 ± 0.40	0.17 ± 0.00	26.6 ± 11.5	0.19 ± 0.03	0.77 ± 0.12
H	2	1	1,845 ± 50	0.9 ± 0.0	161.0 ± 24.7	29.1 ± 0.1	8.5 ± 0.1	177 ± 3	0.73 ± 0.21	0.07 ± 0.07	30.0 ± 0.0	0.78 ± 0.18	0.05 ± 0.00
I	6	2	2,376 ± 410	1.2 ± 0.2	93.5 ± 23.5	25.8 ± 0.6	8.2 ± 0.3	296 ± 58	0.65 ± 0.19	0.06 ± 0.14	31.5 ± 12.8	0.12 ± 0.04	1.70 ± 0.29
J	4	3	2,506 ± 548	1.2 ± 0.3	83.7 ± 30.6	25.4 ± 1.0	8.3 ± 0.2	344 ± 141	0.53 ± 0.43	0.00 ± 0.00	33.0 ± 4.6	0.03 ± 0.04	0.53 ± 0.40

N, number of samples; n, number of samples with alive ostracods; Cond, conductivity; Sal, salinity; O$_2$, oxygen saturation percentage; WT, water temperature; Alk, alkalinity.

Nine ostracod species were recorded among the zoobenthos assemblages in the rice fields during our sampling period (Table 2). Out of these, seven were found alive in the biocoenoses (Figure 2). The most frequent species was *Heterocypris salina* (Brady 1868), followed by *Candonocypris novaezelandiae* (Baird 1843) (fields A, D, E, F and J) and *Trajancypris clavata* (Baird 1838) (fields A, D, E and F). Other species were found in lower abundance values, including *Ilyocypris gibba* (Ramdohr 1808) (fields B and D), *Hemicypris barbadensis* Broodbakker 1983 (fields B and J) and *Stenocypris macedonica* Petkovski and Meisch 1996 collected only in field B. All of these species were also found in the taphocoenoses. One juvenile of *Fabaeformiscandona* sp. was collected but could not be further identified to species level. Furthermore, *D. sinensis* and *C. subglobosa* were only represented in the taphocoenoses (B and J fields, respectively).

Table 2 List of ostracod species found in the Albufera Natural Park

Species	Lake Holocene	Lake (sub-)recent	Spring ponds	Rice fields	S. Llorenç pond	Interdune ponds	References
Cyprididae Baird 1845							
Bradleystrandesia reticulata (Zaddach 1844)	(1)	0 (1)					5,7
Cypris sp.	(1)		0 (1)				5,7
C. bispinosa Lucas 1849			0 (1)				7
C. subglobosa Sowerby 1840		*0 (1)*	*0 (1)*	*0 (1)*			7,11
Cypridopsis vidua (Müller 1776)	(3)	0 (1)	3 (1)			10 (2)	3,4,5,7,8,9,10
Plesiocypridopsis newtoni (Brady and Robertson 1870)						0 (1)	8
Potamocypris sp.	(1)						3
Sarscypridopsis sp.						*0 (1)*	8
S. aculeata (Costa 1847)	(1)	0 (1)	0 (1)			16 (6)	5,7,8,10
S. lanzarotensis (Mallwitz 1984)			*1*				9
Hemicypris sp.	(1)						4
H. barbadensis Broodbakker 1983				*2 (1)*			11
Heterocypris sp.	(1)		0 (1)			5 (2)	5,7,8
H. incongruens (Ramdohr 1808)		0 (1)	1			2 (1)	7,8,9
H. cf. *rotundata* (Bronshtein 1928)			0 (1)				7
H. salina (Brady 1868)	(1)	0 (1)	1(1)	9 (10)	2	25 (12)	4,6,7,8,9,10,11
D. sinensis Sars 1903				*0(1)*			11
Eucypris pigra (Fisher 1851)						0 (1)	8
E. virens (Jurine 1820)		0 (1)				31 (5)	7,8,10
T. clavata (Baird 1838)				6 (4)			11
C. novaezelandiae (Baird 1843)				*5 (2)*		*3(2)*	10,11
Herpetocypris sp.	(1)						3
H. cf. *chevreuxi* (Sars 1896)	(2)	0 (1)					5,7
S. macedonica Petkovski and Meisch 1996				*1*			11
Stenocypris major (Brady 1868)			*1 (1)*				7,9
Isocypris beauchampi (Paris 1920)		*0 (1)*	*2*				7,9
Candonidae Kaufmann 1990							
Candona sp.	(1)						3
C. angulata G. W. Müller 1900	(3)	0 (1)	0 (1)				3,4,5,7
C. neglecta Sars 1887			0 (1)				7

Fabaeformiscandona cf. *brevicornis* (Klie 1940)			0 (1)				7
F. cf. *latens* (Klie 1940)		0 (1)				0 (1)	7,8
F. subacuta (Yang 1982)		*0 (1)*	*1 (1)*	*2*		*2 (1)*	2,7,8,9,10,11
Pseudocandona cf. *albicans* (Brady 1864)			1		(1)		6,9
P. cf. *marchica* (Hartwig 1889)		0 (1)	1 (1)				7,9
P. pratensis (Hartwig 1901)						6 (4)	8
Candonopsis kingsleii (Brady and Robertson 1870)			2 (1)				7,9
C. scourfieldi Brady 1910			1 (1)				7
Cypria sp.	(1)						5
C. ophtalmica (Jurine 1820)	(1)	0 (1)	3 (1)				3,7,9
C. cf. *subsalsa* Redeke 1936			0 (1)				7
Ilyocyprididae Kaufmann 1900							
I. gibba (Ramdohr 1808)	(3)	0 (1)	4 (1)	2 (4)		5 (3)	3,4,5,7,8,9,10,11
Ilyocypris monstrifica (Norman 1862)		0 (1)					7
Darwinulidae Brady and Robertson 1885							
Darwinula stevensoni (Brady and Robertson 1870)	(3)	0 (1)	3 (1)		2	1 (1)	3,4,5,6,7,8,9
Vestalenula sp.		0 (1)					7
Cushmanideidae Puri 1973							
Pontocythere cf. *rubra* Müller 1894						0 (1)	10
P. cf. *turbida* Müller 1894	(1)						4
Cytherideidae *Kollmann* 1960							
Cyprideis torosa (Jones 1850)	(3)	0 (1)	3 (1)		1	14 (13)	3,4,5,6,7,8,9,10
Entocytheridae Hoff 1942							
Ankylocythere sinuosa (Rioja 1942)						*1*	1
Hemicytheridae Puri 1953							
Aurila arborescens (Brady 1865)	(2)						3,4
Leptocytheridae Sars 1925							
Leptocythere sp.	(1)	0 (1)					3,7
L. cf. *porcellanea* (Brady, 1869)	(1)						5
Limnocytheridae Klie 1938							
Limnocythere inopinata (Baird 1843)	(2)	0 (1)	2			2 (2)	3,5,7,8,9
L. stationis Vavra 1891	(2)		1		0 (1)		3,5,6
Paralimnocythere psammophila (Flössner 1965)	(2)	0 (1)	0 (1)				3,5,7
Loxoconchidae Sars 1925							

Loxoconcha elliptica Brady 1868	(3)	0 (1)	0 (1)				3,4,5,7
L. rhomboidea (Fischer 1855)	(2)					0 (1)	3,4,8
Paradoxostomatidae Brady and Norman 1889							
Cytherois sp.	(1)						5
C. cf. *stephanidesi* Kile 1983	(1)						3
Xestoleberidae Sars 1866							
Xestoleberis nitida (Liljeborg 1853)	(3)	0 (1)					3,4,5,7
Total number of exotics/natives	**0/29**	**3/20**	**5/24**	**6/3**	**0/5**	**4/16**	

Number of samples where alive specimens (without parentheses) or only shell remains (in parentheses) were found are indicated for each type of environment or period (sedimentary Holocene records as Holocene; (sub-)recent samples for the rest). Numbers of samples for species considered (putatively) exotic are shown in italics. Numbers of exotic and native species are shown in bold. References: 1: Aguilar-Alberola et al. 2012; 2: Escrivà et al. 2012; 3: Marco-Barba 2010; 4: Marco-Barba et al. 2013a; 5: Marco-Barba et al. 2013b; 6: Mezquita et al. 2005; 7: Poquet et al. 2008; 8: Rueda et al. 2006; 9: Rueda et al. 2013; 10: Valls et al. 2013; 11: This study.

Figure 2 SEM and stereomicroscope pictures of ostracod species found in Zacarés. (A-F): *H. barbadensis* Broodbakker 1983. (A) External view of the right valve (RV), (B) carapace in anterior view, (C) carapace in posterior view, (D) carapace in dorsal view, (E) detail of the antero-dorsal view and (F) detail of the postero-dorsal view. **(G-H)** *C. novaezelandiae* (Baird, 1843). (G) Inner view of the RV and (H) detail inner list of the left valve (LV). **(I)** *S. macedonica* Petkovski and Meisch 1996, external view of the RV. **(J)** *T. clavata* (Baird 1838), inner view of the RV. **(K)** *I. gibba* (Ramdohr, 1808), external view of the RV. **(L)** *H. salina* (Brady, 1868), external view of the LV.

The majority of the species found in this study can be considered non-indigenous species in Europe (see e.g. Griffiths 1995, Meisch 2000). One of the most singular exotic species collected is *H. barbadensis* (Figure 2A, B, C, D, E, F), as this is the first citation of the species for Europe. Moreover, this is the first time that *S. macedonica* (Figure 2I) is detected in the Iberian Peninsula. The other exotic species collected alive in the Zacarés rice fields are also rare in the Europe. This is the case of the exotic ostracod *C. novaezelandiae* (Figure 2G, H) that has been only recorded in nearby areas (Valls et al. 2013). Pustules located in the posteroventral inner list of the left valve of *C. novaezelandiae* (Figure 2H), a trait previously recognised in individuals from a nearby population in Racó de l'Olla (Valls et al. 2013), were observed again and seem to account for a morphological trait of the species that was previously unnoticed.

In order to compare the studied rice fields with other nearby habitats, we built a checklist of ostracods from the Albufera Natural Park, shown in Table 2. In all, 59 ostracod species have been recorded in the area; 27 of them were found alive and 32 were represented only in taphocoenoses. Some species present in Zacarés rice fields were never found in paleolimnologic studies carried out in the Lake Albufera (Santisteban et al. 2009, Marco-Barba et al. 2013a, 2013b). This confirms that *H. barbadensis, C. novaezelandiae, S. macedonica, C. subglobosa* and *D. sinensis* could be considered exotic species in this protected area. However, it should be noticed that *Hemicypris* sp. found in earlier Holocene records could have probably colonised the area through bird dispersion from Africa, where this genus is widely distributed (Martens 1984). A similar process could be related to *Sarscypridopsis lanzarotensis* (Mallwitz 1984), common in the Canary Islands (Malmqvist et al. 1997), and perhaps in northern Africa as well. The species identified as *Stenocypris major* (Brady 1868) by Poquet et al. (2008) should be taken with caution, as these authors did not take into account the review of the genus by Petkovski and Meisch (1996).

Figure 3 shows the mean abundance of three species common to the studied Zacarés rice fields, two species common in Mediterranean temporary habitats (*H. salina* and *T. clavata*) and one alien species (*C. novaezelandiae*). High abundance of native species and the lowest of the alien species were found in May and June. On the other hand, in July and August, abundance of native species decreased and *C. novaezelandiae* abundance increased. The results of ANOSIM indicated significant differences ($p = 0.013$) in community structure between sampling periods. According to posterior SIMPER analysis, samples collected in May-June were dominated by *H. salina* and *T. clavata*, while those collected later in summer (July-September) were dominated by *C. novaezelandiae*. These three species together accumulated 84% of the differences between these sampling periods.

Figure 3 Temporal dynamics of ostracod species abundance. Abundance ($\log_{10}$ number of individuals + 0.1), mean and standard deviation values for the most common ostracods in Zacarés rice fields in different sampling months. *H. salina*, dark green; *T. clavata*, light green and *C. novaezelandiae*, orange.

CCA was carried out after applying DCA, which indicated a gradient length of 4.49 SD. In CCA, Monte Carlo permutation tests in a forward selection analysis indicated that only oxygen content was significant (p = 0.007) in explaining ostracod community composition with the set of variables used, whereas alkalinity and NH_4^+ were the next variables in order of contribution but were not significant (p = 0.09 and p = 0.12, respectively) (Figure 4). Axis 1 accounted for 14.83% of the explained variance, and axis 2 for 5.11%. Exotic species *C. novaezelandiae* and *H. barbadensis* were ordered in relation to low oxygen concentrations. A temporal gradient in the oxygen content was noticed: higher levels corresponded to May and June months and, by the end of summer (July-September), rice fields presented low oxygen concentration and high relative bicarbonate and ammonia concentrations.

Figure 4 Canonical correspondence analysis (CCA). Triplot graph of CCA showing ordination of species, samples and environmental variables from Zacarés rice fields in the first two axes. Blue triangles, species scores; red circles, samples taken in May-June; green squares, samples collected in July-September; solid line arrow, significance (p < 0.05); dashed line arrows, not significant ($0.2 > p > 0.05$). See text for further explanation.

Discussion

Williamson (1996) proposed three main stages in biological invasion processes, i.e. arrival, establishment and spread. As Blackburn et al. (2011) pointed out, each stage can be delimited by a particular type of barrier. Understanding these barriers and factors that influence invasion success are essential to determine the role of alien species in ecosystems. In this frame, we focused on how physical and chemical aspects and dispersal mechanisms could affect the processes of aquatic invasion by exotic Ostracoda in the study area.

In the colonisation stage, physiological problems are considered the most important barrier for the establishment of alien species (Lomolino et al. 2010). In this sense, rice field ecosystems in the Mediterranean may be particularly fitted for alien species of tropical origin compared to native species (Martens and Toguebaye 1985, Forès 1988). These are temporary water bodies filled in hot, summer periods. Such combination of habitat conditions are extremely rare, if present at all, around the Mediterranean, where summers are extremely dry and temporary water bodies are filled usually in the colder months of autumn, winter or spring, but hardly ever in summer. Conversely, many tropical temporary waters experience high temperatures, and species adapted to such conditions, including ostracods such as *C. novaezelandiae*, *S. macedonica* and *H. barbadensis* may find an empty niche in Mediterranean areas. The world distribution of these and other exotic ostracods shows that they are successful colonizers of rice fields worldwide, but particularly in (sub-)tropical areas. *H. barbadensis* was reported in the Barbados and Japanese rice fields (Broodbakker 1983; Okubo 1990), and from a permanent lake in Jamaica (Holmes 1997). *C. novaezelandiae* has indeed a wider distribution area, as it is present in lakes and ponds in Australia, New Zealand, New Caledonia islands, China, Spain and South Africa (Sars 1924, De Deckker 1981, De Deckker 1983, Martens 1984, Eagar 1994, Martens et al. 1998, Yu et al. 2010, Valls et al. 2013), in the river Nile (Ebtesam 2010) and in fishponds in Japan

(Okubo 1975). Also, *C. subglobosa* has been commonly cited in worldwide tropical wetlands, usually including rice fields, from Africa, America, Asia and Europe (Martens and Toguebaye 1985). These authors remark on the tropical-like functioning of rice field ecosystems in temperate areas.

In spite of this facilitation to exotic ostracod species to colonise the Albufera Natural Park, particularly in rice fields and surroundings (Table 2), most of these are not usually found outside this type of environments. However, some exotic species seem to be pre-adapted to tolerate the conditions of other temperate water bodies. This might be the case of *C. novaezelandiae*, which is not only found in paddy fields in the newly colonised continent (e.g. Valls et al. 2013), but is also able to jump to other type of (disturbed) water bodies such as reservoirs (Escrivà et al. 2014). A similar case is exemplified by *F. subacuta*, an exotic ostracod of Asian origin in the Iberian Peninsula, which apparently dispersed from rice fields to the Albufera Natural Park and other inland areas (Escrivà et al. 2012). This species is widely distributed, and its invasion history reflects the potential problem that we discuss in the present survey. In fact, the presence of *F. subacuta* in Iberian reservoirs could be related to low oxygen concentration (Escrivà et al. 2014), similarly as to the relationship found in this survey of rice fields where the exotic *H. barbadensis* and *C. novaezelandiae* related to the more reduced environments, with low oxygen content in the negative side of the CCA ordination axis (Figure 4). *C. novaezelandiae* and *H. barbadensis* were found only in summer (July and August) (Figure 3) when oxygen presented low values (Figure 4), but alkalinity and ammonium increased. Hence, these conditions where exotic species were present correspond to highly eutrophicated and disturbed environments, with strong dominance of respiration processes related to organic matter decomposition. However, these findings still need corroboration because oxygen content can be highly variable in rice fields and other aquatic systems (Quesada et al. 1997), and we did not measure daily variability to ascertain that our measures taking during the day correlated with night oxygen content values (expected to be much lower). Anyway, under some circumstances in which water bodies are closer to their pristine state, the high diversity of native ostracods might hinder the invasion by exotic species, i.e. the diversity-invasibility hypothesis (but see Davis, 2009). The relatively high ostracod diversity in this natural park (Table 2) could therefore reduce the possibility of further colonisation by alien species, which seem to be more successful in the disturbed rice field areas.

Other studies about ostracod diversity in rice fields in Japan (Okubo 1990), Italy (Fox 1965, Rossi et al. 2003) and Spain (Forès 1988) also show high levels of xenodiversity. This suggests that dispersal and colonisation abilities of exotic ostracods in dynamic and anthropized environments could be higher than in more preserved habitat types. *F. subacuta* was most probably transported to the Iberian Peninsula by human activities. Rice trading might have been the vector accounting for such long-distance ostracod dispersal, as discussed by McKenzie and Moroni (1986) and others (Fox 1965, Forès 1988, Rossi et al. 2003). Devising measures to prevent these dispersal events by human activities is therefore imperative (McGeoch et al. 2010).

Conclusions

The ostracod assemblages analysed in Zacarés rice fields reveal significant relationship between species composition and environmental conditions, in particular reduced oxygen content in summer compared to spring samples, suggesting species sorting effects in the structuring processes of these communities in the area. Among the species found, the high proportion of exotic species with (sub-)tropical origin is remarkable, including *H. barbadensis*, which is recorded for the first time in Europe, *S. macedonica* and *C. novaezelandiae*. A higher ratio of native to exotic species is found in rice fields compared to other environments of the Albufera Natural Park, suggesting these habitats function as facilitators for the establishment of alien species. Rice fields are probably the only temporary environments that follow the opposite trend to most other temporary Mediterranean water bodies, being flooded during the warmest and driest summer months. This human-managed artificial hydroperiod allows the colonisation of the area by exotic ostracods from other continents, some of which might invade other habitat types, with unknown consequences for the native fauna.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

JR and FM conceived the research and performed the analysis. JR collected the specimens and field data. JR and LV performed the laboratory work. LV wrote the first version of the manuscript with help from JR with the figures. JR and FM made modifications to the manuscript. All authors read and approved the final manuscript.

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Albufera lagoon

Ricefields

N

250 m

A

E

C

B

D

Tancat de Zacarés

I

F

J

G

H

Ricefields

Ricefields

Canal

A

B

A–L

Mean abundance ($\log_{10}$ number of individuals + 0.1)

Legend:
- *Heterocypris salina*
- *Trajancypris clavata*
- *Candonocypris novaezelandiae*

May   June   July   August   September

Fabaeformiscandona sp.

S. macedonica

H. barbadensis

H. salina

C. novaezelandiae

T. clavata

I. gibba

Alkalinity

Oxygen

NH_4^+

CCA Axis 1

CCA Axis 2