

Temporal and spatial variation of an aquatic invertebrate community subjected to avian predation at the Odiel salt pans (SW Spain)

Marta I. Sánchez^{1, 2, 3, *}, Andy J. Green¹ and Eloy M. Castellanos²

With 5 figures and 7 tables

Abstract: We studied the temporal variation in abundance and distribution of invertebrates in the water column in both traditional and industrial salt pans in the Odiel marshes, south-west Spain, in 2001. We selected 12 ponds that were representative of different salinities and stages of salt production. Every two months, invertebrates were sampled within the 0–20 cm depth range used by foraging waders. We identified 40 taxa, including 30 aquatic and eight terrestrial metazoan invertebrates. Aquatic invertebrate taxa richness and diversity decreased significantly with increasing pond salinity, whereas total biomass showed a non-significant increase. Overall, *Artemia parthenogenetica* constituted 67.6 % of invertebrates by number, and 95.5 % of the biomass. The copepod *Cletocamptus retrogressus* represented 31.1 % of invertebrates by number, and 0.6 % of the biomass. Invertebrate biomass and dominance of *A. parthenogenetica* was highest in September and lowest in November. There was significant spatial and temporal variation in abundance for all aquatic taxa, and for a given pond and month, the depth, distance to shoreline and fetch (wind effects) all had important partial effects on invertebrate distribution. Ordination methods showed a strong relationship between community structure and water chemistry (salinity, pH and redox potential), with the salinity gradient being the most important. There was a clear separation between low salinity ponds with fish and submerged macrophytes and other ponds. The more intensively managed industrial salines held lower densities and biomass of invertebrates than traditional salines, perhaps owing to greater protection from wind or greater inputs of detritus. The beetle *Ochthebius corrugatus* was abundant in the tradi-

¹ **Authors' addresses:** Departamento de Biología Aplicada, Estación Biológica de Doñana- CSIC, Avenida de María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain.

² Departamento de Biología Ambiental y Salud Pública, Facultad de Ciencias Experimentales, Universidad de Huelva. Campus de El Carmen. Avda. Fuerzas Armadas s/n 21071 Huelva, Spain.

³ Present address: Génétique et Evolution des Maladies Infectieuses (GEMI), UMR CNRS/IRD 2724, IRD – 911 avenue Agropolis, BP 64501, 34394 Montpellier cedex 5, France.

* Author for correspondence; e-mail: marta.sanchez@ebd.csic.es

tional ponds but absent from the industrial ones. The number of feeding waders using each pond was strongly correlated with the available biomass of invertebrates.

Key words: *Artemia parthenogenetica*, *Cletocamptus retrogressus*, diversity, salt pans, salinity, shorebirds, species richness, Odiel marshes, wind.

Introduction

Salt pans are widespread, artificial hypersaline habitats that are of great importance for migratory waterbirds owing to the high productivity and predictability in time and space, as well as their shallow depth (BRITTON & JOHNSON 1987, WARNOCK et al. 2002). In recent decades, many salt pans have been abandoned or transformed into other uses, leading to the loss of their waterbird and invertebrate populations (MASERO 2003). This has been accompanied by a tendency to convert small salt pans managed with traditional methods to larger, intensive pans where heavy machinery is used to extract salt (SADOUŁ et al. 1998, PÉREZ-HURTADO 2004).

With the exception of the extensive literature on brine shrimps *Artemia* spp. (ABATZOPOULOS et al. 2002), there are few studies of the invertebrate community in salt pans on which waterbirds depend. Only a handful of studies have described temporal and spatial fluctuations in the invertebrate community or attempted to identify determinants of invertebrate abundance (CARPELAN 1957, BRITTON & JOHNSON 1987, WILLIAMS 1998, AMARAL & COSTA 1999). None of these studies have compared the effects of different management practices found within a given salt pan complex. Traditional management maintains a less artificial environment that might be expected to favour biodiversity.

The Odiel salt pans in south-west Spain hold internationally important numbers of migratory waders (SÁNCHEZ et al., in press). In this study we describe the temporal changes in abundance (in terms of numbers and biomass) and distribution of different invertebrate taxa in the water column of salt pans of different salinities during an annual cycle. We analyse the relationship between spatial variation in abundance at a given moment in time and variation in depth, wind effects and water chemistry. We compare the abundance of invertebrate taxa between small, traditional salt pans and larger industrial ones. We consider how fluctuations in space in the available invertebrate biomass affect the abundance of migratory waders. We consider the implications of our results for the conservation of salt pans and the waders and invertebrates that depend on them.

Study area

The Odiel marshes ($37^{\circ} 17' \text{N}$, $06^{\circ} 55' \text{W}$), located in the combined estuaries of the Tinto and Odiel rivers, are tidal marshes with a total surface area of 7,185 ha, including 1,120 ha of industrial and 60 ha of traditional salt pans

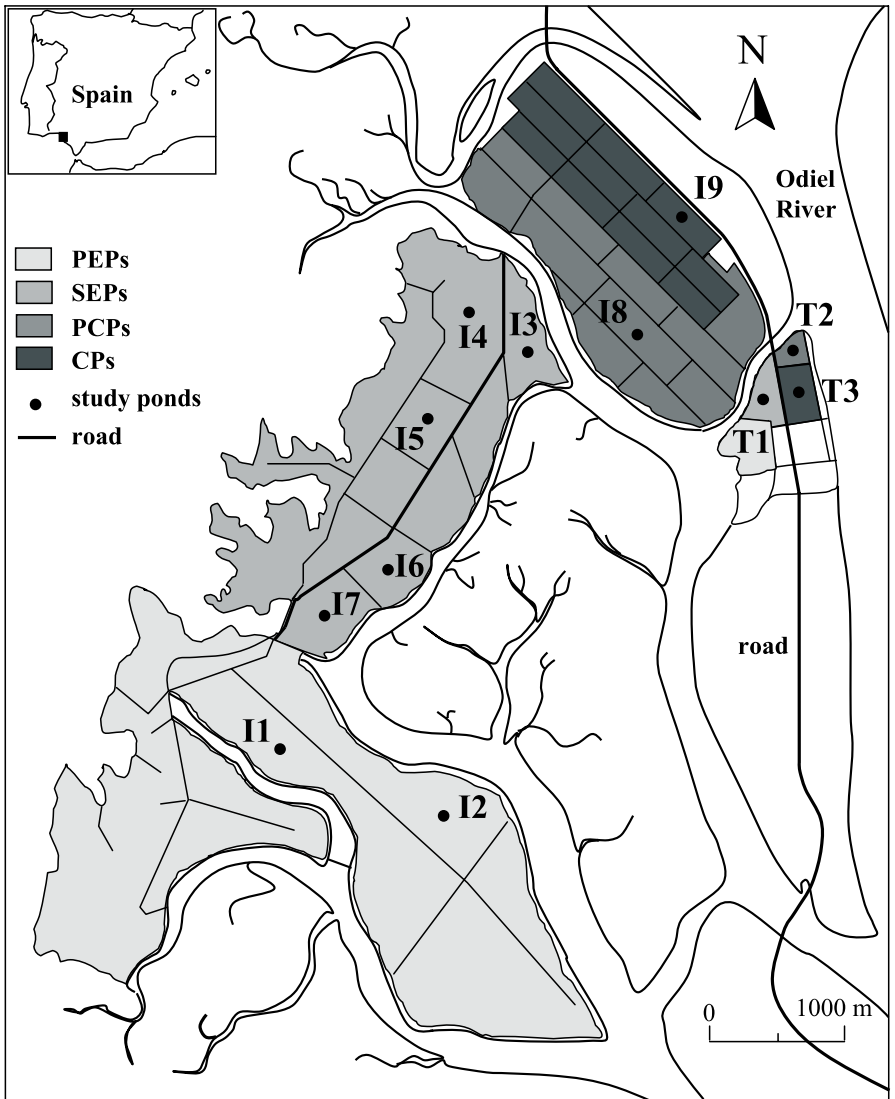


Fig. 1. Location of the Odiel salt pans included in the present study (industrial ponds I1–I9 and traditional ponds T1–T3). PEPs = primary evaporation ponds, SEPs = secondary evaporation ponds, PCPs = pre-crystallization ponds, CPs = crystallization ponds. The Atlantic Ocean lies out of the figure 1.3 km to the south.

(Fig. 1). In the industrial complex (I ponds from hereon), sea water is pumped along a series of ponds and salinity increases via evaporation until the final crystallizing pans are reached. Sea water first circulates through eight primary evaporation ponds, followed by 11 secondary evaporation ponds and 12 pre-crystallization ponds, ending up in 11 crystallization ponds where the salt precipitates (Fig. 1). Annual production is 160,000 tonnes. A single harvest is extracted between early summer and late autumn.

The traditional salt pans (T ponds from hereon) are a circuit of canals following a similar progression of increasing salinity, with approximately 30 % of the surface area being dykes, 30 % primary evaporation ponds, 30 % secondary evaporation ponds and 10 % crystallisers. Water circulates by gravity via sluice gates. Three to five successive harvests are obtained between spring and early autumn.

In primary evaporation ponds, the submerged macrophytes *Ruppia cirrhosa* and *Althenia filiformis* were present, as well as *Chaetomorpha* and *Enteromorpha* algae. As salinity increased, the biomass of primary producers became dominated by microalgae. At the highest salinities, the chlorophyte *Dunaliella salina* was dominant.

Methods

Invertebrate sampling

Samples were collected throughout 2001. Nine industrial ponds (I1–I9) were selected, reflecting the whole salinity range (Fig. 1). Three traditional ponds (T1–T3) were selected excluding the primary evaporation ponds which were too deep to be attractive to waders. Every two months (in January, March, May, July, September and November), four points were sampled per pond. At each point, 20 l of water were collected in subsamples of a litre taken from different heights within the water column, and were then filtered throughout a plankton net of 47 µm mesh. The exact points varied each month and were selected randomly from the depth range of 0–20 cm accessible to waders (NTIAMOA-BAIDU et al. 1998). Depth and hence the position of areas sampled varied seasonally. In each pond, we measured the salinity (with a densometer, ° Baumé converted to g l⁻¹), temperature (°C), pH and redox potential (mV) in one point. At all four points we measured the depth (m), distance to the nearest shoreline (m) and fetch (up-wind distance, in metres, to shoreline, according to the prevailing winds), all of them being continuous variables.

The samples were stored in 70 % alcohol and the total sample volume was measured by displacement as an estimate of biomass. The percentage of total volume that was made up by each taxon was estimated visually. Usually a single species made up over 90 % of the sample. Taxa were identified to the lowest possible taxonomic level using GIUSTI & PEZZOLI (1980), RICHOUX (1982), NIESER et al. (1994), ARIAS & DRAKE (1997) and ALONSO (1998). Identification to species level was not always pos-

sible. Numbers of each taxon were counted, and their volume per individual was estimated based on linear measurements of average sized individuals and using the volume for a simple geometric figure. For example, the volume of chironomid larvae was estimated using the formula for a cylinder. By multiplying this individual volume by the number of each taxon in a sample, we obtained a second estimate of the total volume of each taxon in that sample. We used the average of our two measures in our analyses (GREEN & SÁNCHEZ 2003, GREEN et al. 2005).

We included all the invertebrates recorded in our samples in this study, including terrestrial species owing to their value as prey items for waders (SÁNCHEZ et al. 2005). We also included egg stages such as *Artemia parthenogenetica* cysts, which are important food items for waders (SÁNCHEZ et al. 2005).

Wader counts

One day each week, we counted and identified waders feeding and resting in each pond, using a 20–60 × telescope. On each day, we carried out a count of three hours duration around high tide when the densities of waders were highest (SÁNCHEZ et al. 2005). The ponds were always censused at about the same time of day, using the same route between ponds. Waders made few movements between ponds at this time of day, and we are confident that the order with which ponds were counted did not affect our measure of the use of different ponds by waders.

Calculation of the available surface area

In most ponds, only shallow areas of 0–20 cm around the edge and around islands were available to foraging waders. The accessible surface area varied with fluctuations in the overall water level, which were monitored by recording depth at a fixed point in each pond at the time of invertebrate sampling. The depth profile of each pond was established by conducting 20 transects, and the surface area accessible for foraging at the time of survey was estimated via image analysis using Sigma Scanpro 4.0 (Jandel Scientific, San Rafael, CA, USA).

Statistical analysis

We used generalized linear models (GLMs) following GENMOD procedure in SAS (v. 8.2, SAS Institute Inc. 2000) to analyse the spatial and temporal variation in the density and estimated biomass (volume) of those invertebrate taxa present in more than 10% of samples. These were *Artemia parthenogenetica* (diploid strain) and their cysts, *Cletocamptus retrogressus*, other unidentified harpacticoid copepods, adults of the coleopteran *Ochthebius notabilis*, *Ochthebius* spp. larvae, *Chironomus salinarius* larvae and unidentified Turbellaria (see Table 2 for other taxa that could not be analysed). Owing to overdispersion observed in the data, we used a negative binomial error distribution (GRAY 2005), log link function and type III tests to analyse density. To analyse volume we could find no suitable transformation owing to the high proportion of zeros. We thus only analysed non-zero data (\log_{10} transformed to remove heteroscedasticity), with an identity link and normal error distribution.

Pond and month were included as fixed factors in all models. We also included depth, distance to shoreline and fetch as continuous variables. While controlling for pond and month, there were significant partial correlations between fetch and distance ($r = 0.13$, $p = 0.017$, $n = 264$) and also between depth and distance ($r = 0.23$, $p < 0.001$, $n = 264$), but these r values are too low to cause problems of multicollinearity (Graham 2003). GLMs were used instead of ANOVAs because only the former allowed the simultaneous analysis of this many independent variables, and the use of appropriate error distributions such as the negative binomial. Null hypotheses used in our analyses showed that there were no differences between months or ponds in the abundance of invertebrates, and no relationship with depth, fetch or distance to shoreline.

The deviance of each fitted GLM model is analogous to the residual sum of squares in ordinary linear regression. The reduction in deviance compared to the null model is used to assess the contribution of the model to the explanation of the variance in the data set. The significance of the reduction in deviance for the models for density was estimated by comparison with the chi-square distribution, with degrees of freedom (df) equal to the change in df compared to the null model. Significance for the models of volume was derived from F tests (CRAWLEY 1993). Post-hoc least-squares means tests (SAS Institute Inc. 1997) were used to compare taxa density and biomass (volume) between pairs of traditional and industrial ponds with similar salinities (a pair of secondary evaporation ponds, a pair of precrystallization ponds and a pair of crystallization ponds).

In order to test the relationship between different measures of abundance of waders and of their invertebrate prey in different ponds, we calculated Pearson correlation coefficients (after confirming normality using Kolmogorov-Smirnov tests) employing Statistica 5.5 (StatSoft 1999). We related invertebrate abundance and available surface area (i. e. that of 0–20 cm depth) on the days of invertebrate sampling to the data from wader counts carried out on the nearest date (1–2 days before or after sampling). Similarly, we calculated the Pearson correlation coefficient between the salinity of different ponds and overall measures of invertebrate volume, taxa richness and diversity (using the Shannon-Wiener index (KREBS 1989), based on \ln (total numbers) and \ln (total volume) of each taxon (excluding terrestrial invertebrates)). We also calculated the correlation between mean salinity and the Coefficient of Variation of salinity for each pond, since invertebrates may be sensitive to levels of variation in salinity values, as well as mean values. In cases where variables did not meet assumptions of normality, we calculated Spearman correlation coefficients. In order to determine the partial effects of invertebrate volume and the area accessible to waders in each pond on the number of waders, we used a multiple regression with log transformed variables (using SAS Institute Inc. 1997)

We used multivariate ordination methods and cluster analysis to assess the degree of association between ponds in water chemistry, invertebrate community and the interaction between the two. Principal Components Analysis (PCA) was used to plot ponds against chemistry data (log transformed). The affinities between ponds based on the density of different invertebrate taxa were established using MDS (non-metric multidimensional scaling) together with a cluster analysis using the UPGMA (unweighted pair group method using arithmetic averages) method. The significance of the ordination in the MDS was tested using the Kruskal stress coefficient (KRUSKAL & WISH 1978).

We used a Canonical Correspondence Analysis (CCA) to explore the relationship between water chemistry and the invertebrate community. The resulting ordination of the ponds using this method is directly related to the values of the chemistry data (TER BRAAK 1990). Data on the density of invertebrates was square root transformed and the Bray-Curtis similarity index (SÁNCHEZ-MOYANO et al. 2000) was used to establish the similarity between ponds based on their invertebrate fauna. PCA and MDS were carried out using PRIMER (CLARKE & GORLEY 2001) and CCA, using PC-ORD (McCUNE & MEFFORD 1997) software.

Results

Water chemistry varied between ponds (Table 1). Overall, salinity ranged from 21 g l⁻¹ (pond I1 in November) to 231 g l⁻¹ (T3 in May). Temperatures ranged from 8 °C (in November) to 37.5 °C (in May), pH from 7.09 (in May) to 9.49 (in January) and redox potential from -8.46 (in May) to 175.5 (in January). The Coefficient of Variation of salinity was positively correlated with average salinity between ponds ($r = 0.83$, $p = 0.001$, $n = 12$). There was no evidence for a difference in water chemistry between the industrial and traditional salt pan complexes (Table 1).

We identified a total of 40 taxa including 30 aquatic metazoan invertebrates, one foraminiferan, one fish and eight adult terrestrial invertebrates (Table 2). The copepod *Cletocamptus retrogressus* and *Chironomus salinarius* larvae were abundant in the water column, despite being principally benthic. The most diverse group were the insects with representatives of four orders and nine families (excluding terrestrial species, Table 2). The number of aquatic taxa recorded in each pond was negatively correlated with average salinity ($r = -0.78$, $p = 0.003$, $n = 12$), and ranged from four at pond I8 to 27 at pond I1. The Shannon-Wiener diversity index based on numbers of individuals of each taxon showed a negative correlation with the average salinity of each pond ($r = -0.65$, $p = 0.022$, $n = 12$) and ranged from 0.002 (pond I8) to 1.693 (I2). Similarly, an alternative Shannon-Wiener diversity index based on the overall volume of each taxon showed a negative correlation with salinity ($r = -0.70$, $p = 0.01$) and ranged from 0.004 (pond I8) to 1.835 (I1). In the least saline ponds, the fauna included the exotic fish *Fundulus heteroclitus* and Copepoda, Gastropoda, Oligochaeta and Corixidae were abundant. Ponds of intermediate salinity were dominated by *A. parthenogenetica*, *C. salinarius* larvae and *Ochthebius* spp. beetles (Fig. 2). In ponds with highest salinity *A. parthenogenetica* were dominant (Fig. 2). *C. salinarius* larvae, *A. parthenogenetica* and the cystercercoids of their cestode parasite *Flamingolepis liguloides* were the only taxa recorded in all ponds (Table 2). The number of aquatic taxa recorded in a given month ranged from 19 in January to 26 in March.

Table 1. Physico-chemical measurements from different ponds, showing mean \pm se and the range (in parentheses). N = 6 for each pond with data taken from one point every two months. CV = Coefficient of Variation of salinity. Ponds are listed in order of increasing salinity.

Pond	Salinity (g l^{-1})	CV	Temperature $^{\circ}\text{C}$	pH	Redox potential (mV)
I1	25.12 \pm 0.62 (21.19–29.28)	0.12	21.25 \pm 1.56 (13–31)	8.41 \pm 0.03 (8.20–8.64)	82.45 \pm 2.46 (70.90–103.30)
T1	44.10 \pm 3.14 (27.00–67.54)	0.35	19.48 \pm 1.13 (12.8–25)	8.61 \pm 0.06 (8.27–9.01)	70.96 \pm 3.47 (50.30–103.30)
I2	44.64 \pm 1.23 (35.28–54.08)	0.14	19.17 \pm 1.38 (11.5–29.5)	8.79 \pm 0.04 (8.50–9.19)	61.82 \pm 2.49 (53.10–84.30)
I3	66.16 \pm 2.82 (46.41–83.57)	0.21	20.5 \pm 1.23 (15–31.5)	8.22 \pm 0.03 (8.01–8.52)	79.70 \pm 4.09 (51.60–113.50)
I4	66.86 \pm 2.76 (43.45–86.17)	0.20	22.67 \pm 1.00 (17–31)	8.14 \pm 0.10 (7.09–8.63)	85.83 \pm 6.78 (47.10–141.06)
I5	71.22 \pm 2.62 (54.82–86.92)	0.18	23.58 \pm 1.25 (15–30)	8.26 \pm 0.05 (8.01–8.66)	58.16 \pm 2.80 (34.40–73.40)
T2	80.46 \pm 6.45 (47.06–113.50)	0.36	23.57 \pm 2.24 (10–34.4)	8.38 \pm 0.07 (7.97–8.94)	51.12 \pm 6.00 (2.85–73.50)
I6	86.01 \pm 4.65 (58.65–118.93)	0.26	22.5 \pm 1.28 (13–29.5)	8.26 \pm 0.09 (7.69–8.78)	63.56 \pm 4.46 (23.43–89.60)
I7	90.27 \pm 5.28 (58.88–125.26)	0.29	23.75 \pm 1.87 (12–36)	8.35 \pm 0.08 (7.80–8.89)	44.01 \pm 2.06 (31.30–60.80)
I8	103.79 \pm 8.30 (44.18–148.19)	0.39	19.42 \pm 0.94 (12–25.5)	8.57 \pm 0.11 (8.02–9.49)	47.36 \pm 3.15 (29.50–68.60)
I9	117.72 \pm 19.43 (37.43–221.28)	0.66	21.12 \pm 1.46 (15.5–30)	8.00 \pm 0.07 (7.50–8.21)	65.59 \pm 17.96 (–8.46–175.5)
T3	125.77 \pm 22.86 (56.21–231.23)	0.63	20.17 \pm 3.79 (8–37.5)	7.87 \pm 0.12 (7.35–8.27)	38.13 \pm 7.06 (17.70–70.90)

Table 2. Taxa richness per pond considering all sampling occasions. L = Larvae, P = Pupae, A = Adult; I1-I9 = Industrial ponds, T1-T3 = Traditional ponds.

TAXA	Ponds												
	I1	T1	I2	I3	I4	I5	T2	I6	I7	I8	I9	T3	
Foraminiferans													
Granuloreticulosea			x	x									
Aquatic invertebrates													
<i>Plumatella</i> spp. (statoblast)	x							x					
Turbellaria	x	x	x	x	x	x	x	x	x				
<i>Flamingolepis liguloides</i> (cysticercoïds)	x	x	x	x	x	x	x	x	x	x	x	x	x
Nematoda	x		x				x		x				
<i>Hydrobia ulvae</i>	x	x					x						
Other Gastropoda	x												
Oligochaeta	x												
<i>Artemia parthenogenetica</i>	x	x	x	x	x	x	x	x	x	x	x	x	x
Calanoida	x	x	x										
<i>Cletocamptus retrogressus</i>	x	x	x	x	x	x	x	x	x			x	x
Other Harpacticoida	x	x	x	x	x		x		x				x
Ostracoda	x		x		x								
Gammaridae	x												
Other Malacostraca	x	x			x								
<i>Sigara stagnalis</i>	x	x	x				x						
Dytiscidae (L)		x		x		x		x	x				
<i>Berosus spinosus</i> (A)								x					
<i>Paracymus aenas</i> (A)	x	x					x						
<i>Hydrophillus</i> spp. (L)	x	x	x										
<i>Ochthebius notabilis</i> (L, A)	x	x	x	x	x	x	x	x	x	x			x
<i>Ochthebius corrugatus</i> (L, A)		x					x						x
<i>Halocladius</i> spp. (L)	x		x										
<i>Chironomus salinarius</i> (L, P, A)	x	x	x	x	x	x	x	x	x	x	x	x	x
Other Chironomidae (L)		x		x									
<i>Ephydra</i> spp. (L, P)	x	x	x	x	x		x	x				x	
<i>Nemotelus</i> spp. (L)		x	x				x						
Dolychopodidae (L)		x	x			x	x	x					
Syrphidae (L)							x						
Other Diptera (L)	x	x	x	x			x	x	x	x			x
Collembola	x	x					x		x				x
Terrestrial invertebrates													
Hymenoptera		x				x	x		x				
Hemiptera	x	x			x		x	x					
Mallophaga	x	x											
Diptera				x								x	
Coleoptera		x	x										x
Other Insecta		x		x		x	x	x		x	x	x	
Araneida	x	x	x		x			x					x
Acarina	x	x	x	x			x	x	x				x
Vertebrates													
<i>Fundulus heteroclitus</i>	x	x	x										
TOTAL TAXA RICHNESS	28	29	22	15	12	10	22	16	13	6	7	13	

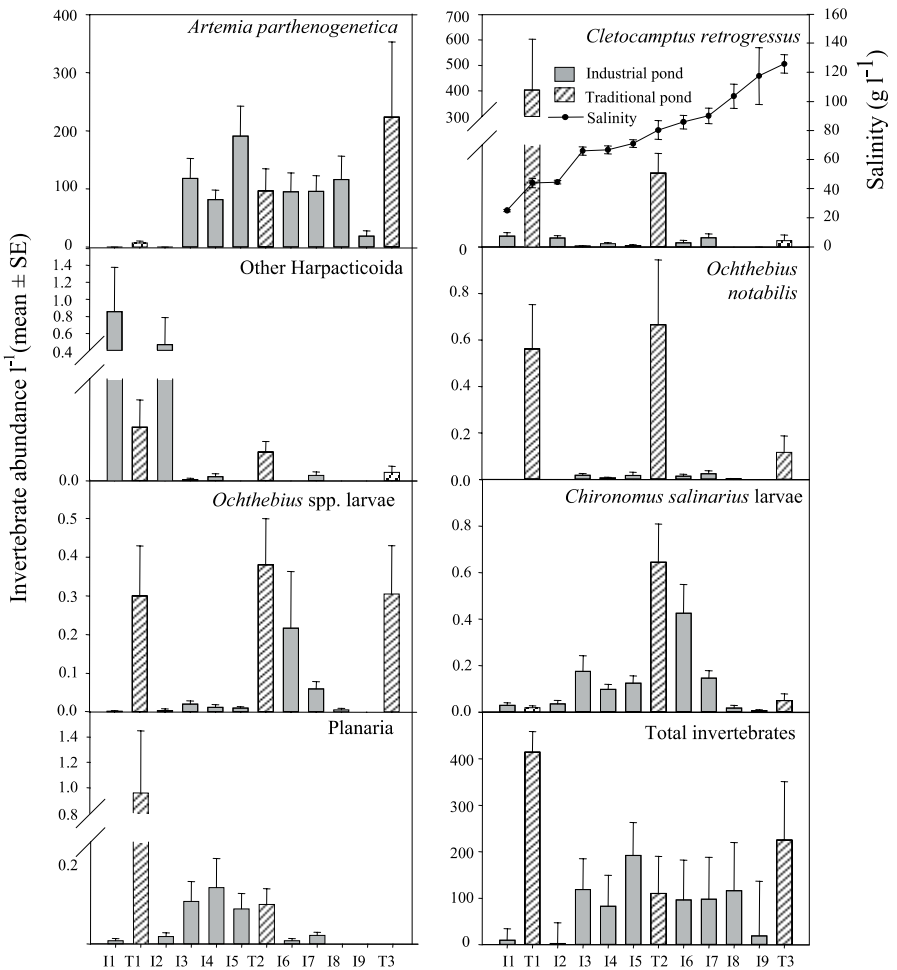


Fig. 2. Density of major invertebrate taxa (numbers per litre, mean±SE) in different ponds in relation to their average salinity, considering all sampling events. Mean salinity in each pond increases from left to right.

Analyses of density

The average annual density (number l⁻¹) of *A. parthenogenetica* and *C. salinarius* larvae reached a maximum in ponds of intermediate salinity (around 70–80 g l⁻¹, Fig. 2). The total density of aquatic invertebrates (excluding eggs) peaked in March (767.7 ± 121.2 individuals l⁻¹, mean ± SE) and was lowest in November (9.1 ± 1.3 individuals l⁻¹). The relative density of the main taxa varied between months (Table 3). *A. parthenogenetica* were numerically dominant in all months except March, when 80% of individuals were *Cletocamptus*

Table 3. Relative abundance (% of individuals and of sample volume) of major invertebrate taxa. L = larvae. Harpacticoida = unidentified harpacticoids (excluding *C. retrogressus*). *Ochthebius* spp. L = larvae of both *O. notabilis* and *O. corrugatus*. Others: Phylactolaemata (Bryozoa), Annelida, Nematoda, Gastropoda, Copepoda, Ostracoda, Malacostraca, Insecta (terrestrial invertebrates are excluded). Total volume is given in cm³.

month	<i>Artemia parthenogenetica</i>		Cysts		<i>Cletocampus retrogressus</i>		Harpacticoida		<i>O. notabilis</i>		<i>Ochthebius</i> spp. L		Chironomus L		Turbellaria		<i>S. stagnalis</i>		Others		Total	
	% ind	% S vol	% ind	% S vol	% ind	% S vol	% ind	% S vol	% ind	% S vol	% ind	% S vol	% ind	% S vol	% ind	% S vol	% ind	% S vol	% ind	% S vol	sum ind	sum vol
January	52.6	72.55	41.1	7.24	2.91	1.5	0	0	0.03	0.41	0.04	0.15	0.02	1.4	0	0	0	0	3.35	16.74	111333	5.16
March	14.9	83.57	3.73	0.56	80.5	7.04	0	0	0	0.04	0.01	0.05	0.07	5.31	0	0	0	0.77	3.43	233502	12.73	
May	76.5	94.34	20.2	0.55	1.23	0.12	0.03	0	0.04	0.1	0.09	0.05	0.12	1.56	0.06	0.02	0	1.75	3.22	161210	48.75	
July	74.5	96.92	23.2	0.38	0.51	0.03	0.28	0.01	0.18	0.27	0.13	0.05	0.1	0.79	0.35	0.07	0.07	1.24	0.72	0.25	131550	65.4
September	63.2	97.78	33	0.6	3.06	0.2	0.1	0	0.12	0.2	0.05	0.02	0.07	0.59	0.04	0.01	0.01	0.3	0.37	0.29	183737	82.06
November	29	49.9	57.6	2.22	8.11	1.1	0.57	0.05	0.22	0.79	0.23	0.19	0.73	13.83	0.04	0.02	0.59	25.14	2.97	6.75	20625	4.37

Table 4. Results of generalized linear models analysing effects of pond, month, depth, distance to shoreline and fetch on the density (numbers per 20 l sample) of aquatic invertebrates. D = percentage of deviance explained by the model in comparison with the null model. k = aggregation parameter of the negative binomial distribution, where the variance of the dependent variable $y = \mu + k*\mu^2$, and μ is the mean of y . Data are used from all sampling occasions (N = 264).

	Effect	DF	Estimate	Chi-Square	P	
<i>A. parthenogenetica</i>	Pond	11		218.58	<0.0001	
	Month	5		81.78	<0.0001	
	D = 8.01	Depth	1	0.01	0.35	0.5514
	$k = 1.27$	Shore distance	1	-0.002	0.2	0.6575
	Fetch	1	-0.0001	0.03	0.8527	
<i>A. parthenogenetica</i> cysts	Pond	11		195.31	<0.0001	
	Month	5		22.66	0.0004	
	D = 9.81	Depth	1	-0.06	6.77	0.0093
	$k = 1.30$	Shore distance	1	-0.01	7.58	0.0059
	Fetch	1	0.002	5.55	0.0184	
<i>C. retrogressus</i>	Pond	11		213.16	<0.0001	
	Month	5		68.17	<0.0001	
	D = 10	Depth	1	-0.04	2.52	0.1124
	$k = 1.03$	Shore distance	1	-0.01	1.79	0.1814
	Fetch	1	-0.0004	0.13	0.7149	
Other Harpacticoida	Pond	11		64.24	<0.0001	
	Month	5		46.56	<0.0001	
	D = 9.50	Depth	1	-0.1	3.12	0.0772
	$k = 0.33$	Shore distance	1	-0.01	0.08	0.7788
	Fetch	1	-0.001	0.31	0.5763	
<i>O. notabilis</i>	Pond	11		84.21	<0.0001	
	Month	5		16.76	0.005	
	D = 3.05	Depth	1	0.04	1.24	0.2661
	$k = 0.51$	Shore distance	1	-0.04	9.61	0.0019
	Fetch	1	-0.003	3.79	0.0515	
<i>Ochthebius</i> spp. larvae	Pond	11		105.51	<0.0001	
	Month	5		34.03	<0.0001	
	D = 2.50	Depth	1	-0.06	3.55	0.0637
	$k = 0.63$	Shore distance	1	-0.02	6.06	0.0138
	Fetch	1	-0.001	0.27	0.6022	
<i>C. salinarius</i> larvae	Pond	11		135.07	<0.0001	
	Month	5		54.24	<0.0001	
	D = 0.04	Depth	1	-0.04	5.58	0.0182
	$k = 0.97$	Shore distance	1	-0.01	3.64	0.0565
	Fetch	1	0.002	8.44	0.0037	
Turbellaria	Pond	11		97.24	<0.0001	
	Month	5		92.85	<0.0001	
	D = 5.06	Depth	1	-0.07	4.49	0.034
	$k = 0.53$	Shore distance	1	0.0001	0	0.9911
	Fetch	1	0.0003	0.1	0.7548	

Table 5. Summary of post-hoc tests of the differences between industrial (I2, I6, I9) and traditional (T1, T2, T3) salt pans of comparable salinities, as calculated from generalized linear models analysing effects of pond, month, depth, distance to shoreline and fetch. These ponds were paired because they had very similar salinities (Table 1). The estimate for the traditional pond was subtracted from that for the industrial pond, thus (-) indicates that numbers or biomass were greater in the traditional pond. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Density (counts)			Biomass (volume)		
	I2-T1	I6-T2	I9-T3	I2-T1	I6-T2	I9-T3
<i>Artemia parthenogenetica</i>	(-) *	(-)	(-) ***	(-)	(-)	(-) **
<i>A. parthenogenetica</i> cysts	(-) ***	(+)	(-) ***	(-) ***	(-)	(-) **
<i>Cletocampius retrogressus</i>	(-) ***	(-) ***	(-) ***	(-) ***	(-) ***	(-)
Other harpacticoida	(+) **	(-)	(-)	(+) *
<i>Ochthebius notabilis</i>	(-)	(-) **	(-)	...	(-)	...
<i>Ochthebius</i> spp. larva	(-) ***	(-)	(-)	(-)	(-)	...
<i>Chironomus salinarius</i> larva	(+)	(-) **	(-)	(-)	(-) **	(-)
Turbellaria	(-) ***	(-) **	(+)	(-) **	(-)	...

retrogressus (Table 3). *A. parthenogenetica* constituted 67.6 % of the total number of aquatic invertebrates sampled (excluding cysts).

There were significant differences between ponds and months in the density of all major taxa (Table 4). Depth had a significant partial effect on *C. salinarius* larvae, *A. parthenogenetica* cysts and Turbellaria, with density increasing at lower depths (Table 4). Distance to shoreline showed a significant negative correlation with density of *A. parthenogenetica* cysts, *Ochthebius* spp. larvae and *O. notabilis* adults (Table 4). Density of *C. salinarius* larvae and *A. parthenogenetica* cysts also showed a significant positive correlation with fetch (Table 4). Post-hoc tests showed that, for all taxa, there were significant differences between at least one of the three pairs of industrial and traditional ponds (Table 5). In 12 of 13 significant differences, invertebrates were more abundant in traditional than in industrial ponds, the exception being for unidentified harpacticoids (Table 5, Fig. 2).

Analyses of volume

There was a marked seasonal pattern in the volume of invertebrates in the water column, with a maximum in September ($0.10 \pm 0.04 \text{ cm}^3$ of invertebrates l^{-1} , mean \pm s. e., $n = 40$) and minimum in November (0.004 ± 0.0009 , $n = 40$). The relative volume of the different taxa varied between seasons (Table 3). *A. parthenogenetica* always constituted over 70 % of invertebrate volume, except in November when corixids and chironomid larvae were particularly important (Table 6). *A. parthenogenetica* constituted 95.5 % of the total volume of aquatic invertebrates (excluding cysts).

Table 6. Results of generalized linear models analysing effects of pond, month, depth, distance to shoreline and fetch on the volume (cm^3 of invertebrates per l of water, \log_{10} transformed) of aquatic invertebrates. D = percentage of deviance explained by the model in comparison with the null model. DF_n = DF for numerator, DF_d = DF for denominator.

	Effect	DF _n	DF _d	Estimate	F	P
<i>A. parthenogenetica</i> N = 216 D = 64.05	Pond	11	196		15.54	< 0.0001
	Month	5	196		32.55	< 0.0001
	Depth	1	196	0.03	8.5	0.0036
	Shore distance	1	196	-0.002	1.46	0.2262
	Fetch	1	196	-0.0002	0.34	0.5606
<i>A. parthenogenetica</i> cysts N = 243 D = 47.19	Pond	11	223		14.83	< 0.0001
	Month	5	223		1.98	0.0776
	Depth	1	223	-0.01	0.66	0.4169
	Shore distance	1	223	-0.004	4.11	0.0425
	Fetch	1	223	0.001	3.92	0.0479
<i>C. retrogressus</i> N = 158 D = 55.75	Pond	10	139		11.73	< 0.0001
	Month	5	139		6.48	< 0.0001
	Depth	1	139	-0.03	6.23	0.0126
	Shore distance	1	139	-0.0001	1.76	0.1846
	Fetch	1	139	0.6308	0.07	0.7887
Other Harpacticoida N = 41 D = 51.48	Pond	7	27		2.88	0.0052
	Month	3	27		0.65	0.5831
	Depth	1	27	-0.003	0.1	0.7544
	Shore distance	1	27	-0.001	0.03	0.8601
	Fetch	1	27	0.4751	1.17	0.2785
<i>O. notabilis</i> N = 60 D = 48.37	Pond	8	43		1.1	0.358
	Month	5	43		1.64	0.1464
	Depth	1	43	0.01	0.15	0.6966
	Shore distance	1	43	-0.01	0.36	0.5486
	Fetch	1	43	-0.0003	0.09	0.7648
<i>Ochthebius</i> spp. larvae N = 76 D = 58.10	Pond	10	57		2.45	0.0063
	Month	5	57		1.29	0.2653
	Depth	1	57	-0.03	11.62	0.0007
	Shore distance	1	57	0.005	2.37	0.1238
	Fetch	1	57	-0.0002	0.33	0.5674
<i>C. salinarius</i> larvae N = 131 D = 44.94	Pond	11	111		5.62	< 0.0001
	Month	5	111		3.02	0.0099
	Depth	1	111	-0.02	10.51	0.0012
	Shore distance	1	111	-0.001	1.01	0.3147
	Fetch	1	111	0.001	11.01	0.0009
Turbellaria N = 65 D = 45.07	Pond	8	49		2.62	0.0072
	Month	4	49		4.34	0.0016
	Depth	1	49	-0.02	2.41	0.1203
	Shore distance	1	49	-0.001	0.15	0.6976
	Fetch	1	49	0.0004	0.76	0.3845

Invertebrate volume was highest in high salinity ponds, with a maximum of $0.14 \pm 0.01 \text{ cm}^3$ of invertebrates per litre of water (mean \pm SE, $n = 24$) in I8 where 99.6 % was constituted by *A. parthenogenetica*. The lowest value (0.003 ± 0.0003) was recorded in low salinity I1 where only 0.7% was *A. parthenogenetica*. There was a positive but non-significant correlation between average invertebrate volume per sample and the salinity of each pond ($r = 0.43$, $p = 0.16$, $n = 12$).

There were significant differences between both ponds and months in the volume of *A. parthenogenetica*, *C. retrogressus*, *C. salinarius* larvae and Turbellaria (Table 6). With the exception of *Ochthebius notabilis*, there were significant differences between ponds for the volume of other taxa analysed (Table 6). Depth had a significant partial effect on volume for four taxa, with a positive correlation for *A. parthenogenetica* and a negative one for *C. retrogressus*, *Ochthebius* spp. larvae and *C. salinarius* larvae (Table 6). The volume of *A. parthenogenetica* cysts showed a significant negative correlation with distance to shoreline and positive one with fetch (Table 6). The volume of *C. salinarius* larvae also showed a significant positive correlation with fetch. Post-hoc tests showed that, for six taxa, there were significant differences between at least one of the three pairs of industrial and traditional ponds (Table 5). In seven of eight significant differences, the volume of invertebrates was greater in traditional than in industrial ponds, the exception being for unidentified harpacticoids (Table 5).

Relationship between abundance of invertebrates and waders

The numbers of waders underwent seasonal variation (Fig. 3), with counts for the 12 study ponds at high tide peaking in September (9701 ± 1782 waders per census, mean \pm SE, $n = 4$) with a minimum in March (2338 ± 547 , $n = 4$). There was evidence that birds distributed themselves spatially between ponds in relation to differences in the volume of prey present in the water column. There was a strong relationship between the mean number of feeding waders in a given pond and the total food available (estimated as the mean volume of invertebrates per sample multiplied by the total area in the accessible depth range of 0–20 cm, $r_s = 0.71$, $p = 0.008$, $n = 12$). However, it is the combination of both differences between ponds in the available surface area and in the mean food abundance that appears to cause this relationship. On their own, neither the available surface area ($r_s = 0.52$, $p = 0.08$, $n = 12$) nor food abundance ($r_s = 0.50$, $p = 0.09$) showed a significant correlation with the number of feeding waders in each pond. Similarly, when these two variables were considered together as two predictors in a multiple regression with the number of feeding birds as the dependent variable, each had a positive but non-significant partial effect ($P > 0.06$).

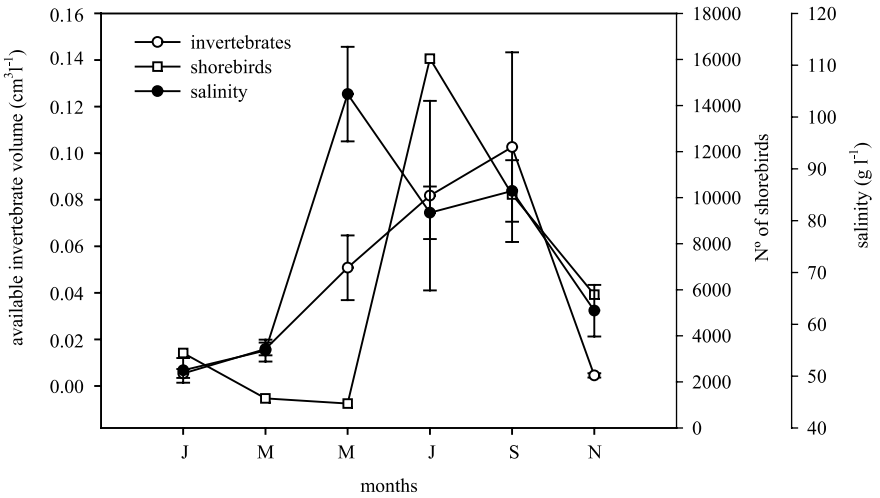


Fig. 3. Seasonal changes in the abundance of waders in our 12 study ponds, in the mean volume (\pm SE) of invertebrates available in the same area, and in mean salinity (\pm SE). N° of waders correspond to the high tide count made closet to the date of invertebrate sampling.

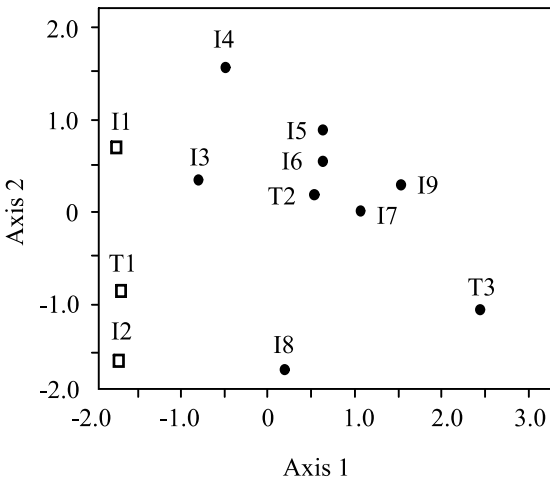


Fig. 4. Principal Components Analysis of the physico-chemical data from each pond. Solid circles represent ponds without and open squares ponds with fish and macrophytes.

Ordination analyses

The first axis of a PCA (Fig. 4) explained 50.6% of the total variance in chemistry data, and was positively correlated with salinity ($r = 0.66, p < 0.025, n =$

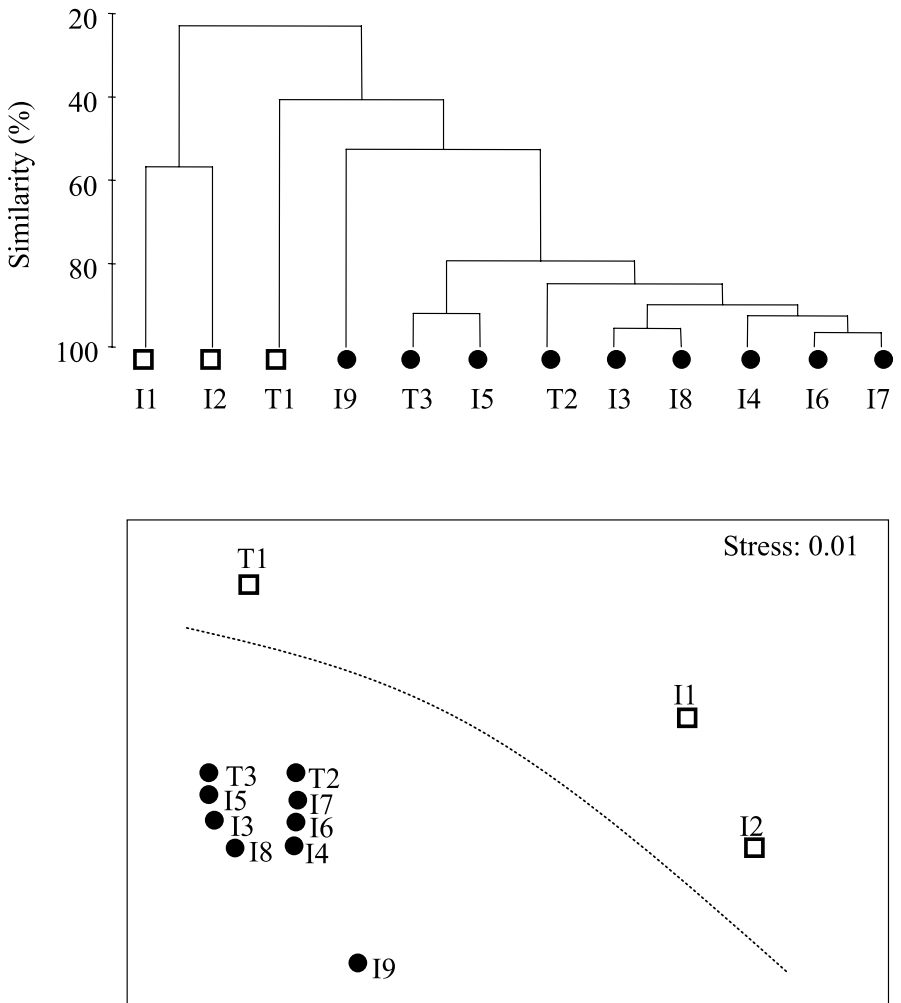


Fig. 5. Cluster analysis (UPGMA method) and MDS ordination of the ponds according to the density of different invertebrate taxa. Solid circles represent ponds without and open squares ponds with fish and submerged macrophytes. The spots line stress the spatial segregation between ponds with fishes and ponds without them.

12) and negatively correlated with pH ($r = -0.52$, $p < 0.05$, $n = 12$). The second axis explained 27.9% of the variance and was positively correlated with temperature ($r = 0.69$, $p < 0.01$, $n = 12$) and redox potential ($r = 0.64$, $p < 0.025$, $n = 12$). The MDS and cluster analyses of the invertebrate community revealed a clear separation of the three ponds of lowest salinity (T1, I1 and I2) from the others (Fig. 5). These ponds were the only ones to have submerged macrophytes and fish. Traditional and industrial ponds were not clustered separately.

Table 7. Results of a Canonical Correspondence Analysis (CCA) between measures of invertebrate density and water chemistry. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

	Axis 1	Axis 2
Species-environment correlation	0.95	0.18
Percentage of species variance	43.4	1.2
Correlation with environmental variables		
Salinity	0.82***	-0.52*
Temperature	0.5	0.41
pH	-0.75**	-0.28
Redox	-0.28	0.53*

The relationship between the invertebrate community and environmental variables was further described by a CCA (Table 7). The first axis indicated a strong correlation between the two classes of variables, and explained 43.4 % of the variance in distribution of invertebrate taxa. This axis had a stronger correlation with salinity than with other environmental variables. Salinity was also the only variable to have a significant correlation with both the first and second axes of the CCA.

Discussion

Ours is the most detailed study to date of spatio-temporal variation in the invertebrate community in active saltworks of the Mediterranean region. We have recorded a marked variation in the composition of the invertebrate community and abundance of different taxa in space and time in the Odiel salt pans. As observed in salt pans in Mediterranean France (BRITTON & JOHNSON 1987) and in Portugal (AMARAL & COSTA 1999), we recorded a drop in taxa richness and diversity as salinity increased between ponds. This suggests that abandonment may increase the diversity of invertebrates in an individual pond if it leads to a decrease in salinity. However, in 9 of 12 ponds (Table 2) we observed more than the eight aquatic taxa recorded in an abandoned Camargue salt pan in which salinity ranged from 96 to 30 g l⁻¹ over a six month period in response to rainfall (THIÉRY & PUENTE 2002). Thus abandonment may lead to the disappearance of taxa, both because of the loss of the spatial salinity gradient between pans and because salinity in each pan becomes more unstable.

Most of the invertebrates we recorded in our study are important prey for waders (KALEJTA 1993, PÉREZ-HURTADO et al. 1997, MASERO 2003, SÁNCHEZ et al. 2005). Even the terrestrial invertebrates detected in our samples are consumed by waders in an opportunistic manner (SÁNCHEZ et al. 2005). The differences in invertebrate community between ponds of different salinities are

likely to benefit the wader community by accommodating species with different dietary preferences, and by ensuring that different ponds do not all peak in their food supply at the same time.

We found salinity to be the most important environmental factor determining the structure of the invertebrate community along a spatial gradient. The ordination of ponds based on the invertebrate community (Fig. 5) is closely related to the first axis of the PCA that is correlated most strongly with salinity, but not with the second axis correlated with temperature and redox potential (Fig. 4). The CCA provided further evidence that the most important environmental gradient is that of salinity. Ponds of higher salinity also had relatively more variation in salinity, and this variation is an additional stressor that may partially determine the structure of the invertebrate community. The strong effect of salinity as a limiting factor on primary producers and invertebrates is well known (HART et al. 1998, LÓPEZ-GONZÁLEZ et al. 1998, THIÉRY & PUENTE 2002, TRIPP & COLLAZO 2003). However, it is often unclear whether the distribution of a given taxon is limited directly by salinity itself, or by its association with other factors such as pH or the influence of salinity on other taxa (especially predators, prey species or food plants, WILLIAMS 1998). Our ordination analyses suggest that the presence of fish and submerged plants in the three ponds of lowest salinity has a major additional influence on invertebrate community structure. These ponds are more clearly separated from the others in the MDS (Fig. 5) than in the PCA (Fig. 4). Submerged macrophytes may be one reason why the invertebrate community in these ponds was more diverse, since they have a profound effect on community structure and provide a substrate for many macroinvertebrates (WOLFRAM et al. 1999, WEATHERHEAD & JAMES 2001).

Fish were also limited to the ponds of lowest salinity, and can have profound effects on invertebrate community composition (JEPPESEN et al. 1997, HART et al. 1998, ZIMMER et al. 2000, MARKLUND et al. 2002). *Fundulus heteroclitus* feeds mainly on invertebrates, and caging experiments showed that it can have a positive indirect effect on some benthic invertebrates by controlling the abundance of intermediate predators (KNEIB & STIVEN 1982, KNEIB 1988). In Odiel, the fish together with other predators (notably corixids and copepods) may be directly responsible for the absence of *A. parthenogenetica* from the ponds of lowest salinity (WILLIAMS 1998). The number of predatory taxa was highest in these ponds, whereas the importance of detritivorous taxa such as *C. salinarius* and *Ochthebius* spp. was highest in ponds of intermediate salinity, in which *A. parthenogenetica* were dominant. In ponds of highest salinity, the food web was at its simplest and *A. parthenogenetica* were highly dominant. Despite the drop in taxa diversity and richness with increasing salinity, total biomass tended to increase. The increase in dominance of *A. parthenogenetica* at higher salinities recorded here, and the negative correlation

amongst ponds between salinity and densities of benthic chironomid larvae (SÁNCHEZ et al., in press) suggest that the relative importance of planktonic food chains compared to benthic ones increases at extreme salinities, at least for the metazoa.

VERKUIL et al. (1993) previously suggested that the density of brine shrimps in lagoons was strongly influenced by wind direction. We found no evidence for that for *A. parthenogenetica* adults, but a strong influence of fetch on the abundance of their cysts and of chironomid larvae, both of which are important food items for waders and other waterbirds using salt pans (GREEN et al. 2002, SÁNCHEZ et al. 2005). Amongst wader species, feeding depth tends to increase with increasing leg length (NTIAMOA-BAIDU et al. 1998, PARACUELLOS et al. 2002). VERKUIL et al. (1993) found that the density of *Artemia* increased with depth and suggested that longer legged wader species were better able to exploit this food resource. We found that the biomass of *A. parthenogenetica* increased with depth, supporting this suggestion. In contrast, we found that the density and/or biomass of *A. parthenogenetica* cysts, chironomid larvae, *C. retrogressus*, *Ochthebius* spp. and Turbellaria is greatest at the shallowest depths over the 0–20 cm range studied, suggesting that shorter legged birds may be better able to feed on these resources. However, the chironomid larvae we have recorded in the water column are less numerous than those remaining in the sediments, and benthic larval density increased with depth in our ponds (authors, unpublished data).

The ordination analyses indicate that the community structure and its relationship with the salinity gradient was generally similar in the traditional and industrial salt pans. However, *O. corrugatus* was absent in the industrial ponds but abundant in traditional ponds. *O. notabilis* was also much more abundant in traditional ponds (Fig. 2). Invertebrate abundance was generally higher in the traditional ponds, and the reasons for this are unclear. The smaller pond size (Fig. 1) and greater relative surface area of dykes in traditional ponds may be important. The dykes provide greater protection from wind and, unlike in industrial ponds, are covered in natural vegetation in traditional ponds, so providing more detritus and potentially boosting productivity. Traditional ponds are used by lower densities of feeding waders than industrial ponds (SÁNCHEZ et al., in press). Thus, reduced predation of invertebrates in traditional ponds may be another factor contributing to our results (SÁNCHEZ et al. 2006). Most waterbirds tend to avoid smaller wetlands surrounded by steep banks making it harder for them to detect predators (GREEN 1998). Although traditional salt pans are not especially important for waders, they provide a better habitat for invertebrates as well as plants and some passerines.

A. parthenogenetica is the most important prey in the water column of salt pans for waders at Odiel (SÁNCHEZ et al. 2005) and elsewhere (MASERO & PÉREZ-HURTADO 2001). We observed a crash in their abundance during winter

months, and AMAT et al. (1991) and THIÉRY & PUENTE (2002) reported the disappearance of *Artemia* adults in winter and their persistence as resistant cysts. In the Camargue, waterbirds moved into areas of lower salinity in winter to look for alternative prey when *Artemia* populations in high salinity ponds collapsed (BRITTON & JOHNSON 1987). In Odiel, waders do not show such a switch to low salinity ponds in winter. Instead, they increase their dependence on benthic chironomids and on invertebrates from adjacent tidal areas (MASERO et al. 2000, SÁNCHEZ et al. 2005).

The energetic value of *Artemia* collected in Spanish salt pans is similar to or even higher than in other prey (MASERO 2003). However, some wader species (notably Red-necked Phalaropes *Phalaropus lobatus* and Broad-billed Sandpiper *Limicola falcinellus*) appear unable to retain their body weight when fed exclusively on *Artemia* (RUBEGA & INOUE 1994, VERKUIL et al. 2003). In contrast, *Artemia* have been shown to be profitable prey for Dunlin *Calidris alpina* and Curlew Sandpipers *C. ferruginea* (VERKUIL et al. 2003). At Odiel, Black-tailed Godwit *Limosa limosa* are major predators of *Artemia*. Of 42 droppings collected in August 2001, in 38 *A. parthenogenetica* represented over 90% of sample volume (authors, unpublished data).

We have found evidence that the distribution of feeding birds between different ponds at a given time is positively related to both the size of the shallow area of 0–20 cm where prey are accessible, and to the density of prey in that area. Our failure to find stronger evidence is probably related to the error in our measurements of abundance of such patchily distributed invertebrate prey, to the importance of benthic prey considered elsewhere (SÁNCHEZ et al., in press) and to our collective analysis of different wader species varying in dietary preferences. Use of different ponds is likely to be related to other factors such as pond shape and size, levels of disturbance (CAYFORD 1993) and distance to alternative habitats (e. g. tidal areas used for foraging at low tide, MASERO et al. 2000, LUÍS et al. 2002). Waders may also take into account the high osmoregulatory costs of feeding in the most saline ponds (WOLLHEIM & LOVVORN 1995, MASERO 2002) when making decisions about pond use. We would need to study a much larger number of ponds to tease apart the importance of all these variables.

It has previously been argued that the maintenance of active salt pans in the Mediterranean region is vital to provide alternative habitats for wader populations and to ensure their conservation (MASERO 2003). Our results show that abandonment of salt production and the resulting loss of the managed salinity gradient will lead to a loss of invertebrate diversity in space and time at the scale of a salt pan complex (although perhaps not at the scale of an individual pond), owing to the presence of species adapted to different salinities. It is thus important to maintain this gradient for the effective conservation of invertebrates and their waterbird predators. The abandonment of salt pans is also

leading to the loss of genetic diversity in native *Artemia* populations (MUÑOZ, A. J. GREEN, J. FIGUEROLA, F. AMAT & C. RICO, unpublished data).

Across the Mediterranean region, remaining salt pans are being transformed into large pans facilitating industrialised harvest methods (SADOUL et al. 1998). Where possible, traditional salt pan management should be retained as this increases the abundance and diversity of invertebrates, as well as providing benefits for terrestrial plants and passerines.

Acknowledgements

The first author was supported by a PhD grant from the Ministerio de Ciencia y Tecnología and an I3P postgraduate grant from the Consejo Superior de Investigaciones Científicas. The Consejería de Medio Ambiente, Junta de Andalucía and Aragonesas Industrias y Energía S. A. provided permission for the fieldwork in the salt pans. JUAN CARLOS RUBIO, Director of the Odiel Marshes Natural Park, provided logistical support and advice. JOSÉ MANUEL GUERRA helped with statistical analysis. CLAUDINE DE LE COURT, JORDI FIGUEROLA, JOSÉ MANUEL SAYAGO and ENRIQUE URBINA also provided helpful advice. FRANCISCO AMAT, DAGMAR FRISCH and CARMEN ELISA SAINZ helped to identify invertebrate taxa. RAQUEL ALEJANDRE and CARLOS ROLDÁN helped with field work.

References

- ABATZOPOULOS, T. J., BEARDMORE, J. A., CLEGG, J. S. & SORGELOOS, P. (2002): *Artemia*: Basic and Applied Biology. – Kluwer Academic.
- ALONSO, M. (1998): CRUSTACEA (BRANCHIOPODA). – In: Fauna Ibérica, Vol 7. Museo Nacional de Ciencias Naturales y Consejo Superior de Investigaciones Científicas, Madrid.
- AMARAL, M. J. & COSTA, M. H. (1999): Macrobenthic communities of salt pans from Sado estuary (Portugal). – *Acta Oecologica* **20**: 327–332.
- AMAT, F., HONTORIA, F., NAVARRO, J. C., GOZALBO, A. & VARÓ, I. (1991): Bioecología de *Artemia* (Crustacea, Branchiopoda) en la Laguna de la Mata, Torre Vieja, Alicante. – Instituto de Acuicultura de Torre de la Sal (CSIC).
- ARIAS, A. M. & DRAKE, P. (1997): Fauna acuática de las salinas del Parque Natural Bahía de Cádiz. – EGMASA. – Consejería de Medio ambiente. Junta de Andalucía.
- BRITTON, R. H. & JOHNSON A. R. (1987): An ecological account of a Mediterranean salina: the Salin de Giraud, Camargue (S. France). – *Biol. Conserv.* **42**: 185–230.
- CARPELAN, L. H. (1957): Hydrobiology of the Alviso SALT ponds. – *Ecology* **38**: 382–385.
- CAYFORD, J. (1993): Wader disturbance: a theoretical overview. – *Wader Study Group Bull.* **68**: 3–5.
- CLARKE, K. R. & GORLEY, R. N. (2001): Primer (Plymouth Routines In Multivariate Ecological Research). Vol 5: User Manual/Tutorial. PRIMER-E Ltd., Plymouth.
- CRAWLEY M. J. (1993): GLIM for Ecologists. – Blackwell Scientific Publications, Cambridge.

- GIUSTI, F. & PEZZOLI, E. (1980): Gasteropodi, 2 (Gastropoda: Prosobranchia: Hydrobioidea, Pyrguloidea). – In: Guide per il riconoscimento delle specie animali delle acque interne italiane, Vol 8. Consiglio Nazionale delle Ricerche, Verona.
- GRAHAM, M. H. (2003): Confronting multicollinearity in ecological multiple regression. – *Ecology* **84**: 2809–2815.
- GRAY, B. R. (2005): Selecting a distributional assumption for modelling relative densities of benthic macroinvertebrates. – *Ecological Modelling* **185**: 1–12.
- GREEN, A. J. (1998): Habitat selection by the Marbled Teal *Marmaronetta angustirostris*, Ferruginous Duck *Aythya nyroca* and other ducks in the Göksu Delta, Turkey in late summer. – *Revue d'Ecologie, Terre et Vie* **53**: 225–243.
- GREEN, A. J., FIGUEROLA, J. & SÁNCHEZ, M. I. (2002): Implications of waterbird ecology for the dispersal of aquatic organisms. – *Acta Oecologica* **23**: 177–189.
- GREEN, A. J., FUENTES, C., MORENO-OSTOS, E. & DA SILVA, S. L. R. (2005): Factors influencing cladoceran abundance and species richness in brackish lakes in Eastern Spain. – *Annales De Limnologie – Internat. J. Limnol.* **41**: 73–81.
- GREEN, A. J. & SÁNCHEZ, M. I. (2003): Spatial and temporal variation in the diet of Marbled Teal *Marmaronetta angustirostris* in the western Mediterranean. – *Bird Study* **50**: 153–160.
- HART, C. M., GONZÁLEZ, M. R., SIMPSON, E. P. & HURLBERT, S. H. (1998): Salinity and fish effects on Salton Sea microecosystems: zooplankton and nekton. – *Hydrobiologia* **381**: 129–152.
- JEPPESEN, E., LAURIDSEN, T., MITCHELL, S. & BURNS, C. W. (1997): Do planktivorous fish structure the zooplankton communities in New Zealand lakes? – *N. Z. J. Mar. Freshwat. Res.* **31**: 163–173.
- KALEJTA, B. (1993): Diets of shorebirds at the Berg River Estuary, South Africa: spatial and temporal variation. – *Ostrich* **64**: 123–133.
- KNEIB, R. T. (1988): Testing for indirect effects of predation on an intertidal soft-bottom community. – *Ecology* **69**: 1795–1805.
- KNEIB, R. T. & STIVEN, A. E. (1982): Benthic invertebrate responses to size and density manipulation of the Common mummichog, *Fundulus heteroclitus*, in an intertidal marsh. – *Ecology* **63**: 1518–1532.
- KREBS, C. J. (1989): *Ecological methodology*. – Harper and Row, New York.
- KRUSKAL, J. B. & WISH, M. (1978): *Multidimensional Scaling*. – Sage Publications, Beverly Hills, CA.
- LÓPEZ-GONZÁLEZ, P. J., GUERRERO, F. & CASTRO, M. M. (1998): Seasonal fluctuations in the plankton community in a hypersaline temporary lake (Honda, southern Spain). – *Internat. J. Salt Lake Res.* **6**: 353–371.
- LUÍF, A., GOSS-CUSTARD, J. D. & MOREIRA, M. H. (2002): The feeding strategy of the dunlin (*Calidris alpina*, L.) in artificial and non-artificial habitats in Ria de Aveiro, Portugal. – *Hydrobiologia* **475/476**: 335–343.
- MARKLUND, O., SANDSTEN, H., HANSSON, L. & BLINDOW, I. (2002): Effect of waterfowl and fish on submerged vegetation and macroinvertebrates. – *Freshwat. Biol.* **47**: 2049–2059.
- MASERO, J. A. (2002): Why don't knots *Calidris canutus* feed extensively on the crustacean *Artemia*? – *Bird Study* **49**: 304–306.
- (2003): Assessing alternative anthropogenic habitat for conserving waterbirds: salinas as buffer areas against the impact of natural habitat loss for shorebirds. – *Biodivers. Conserv.* **12**: 1157–1173.

- MASERO, J. A. & PÉREZ-HURTADO, A. (2001): Importance of the supratidal habitats for maintaining overwintering shorebirds populations: how redshank use tidal mudflats and adjacent saltworks in southern Europe. – *The Condor* **103**: 21–30.
- MASERO, J. A., PÉREZ-HURTADO, A., CASTRO, M. & ARROYO, G. M. (2000): Complementary use of intertidal mudflats and adjacent salinas by foraging waders. – *Ardea* **88**: 177–191.
- MCCUNE, B. & MEFFORD, M. J. (1997): PC-ORD. Multivariate Analysis of Ecological Data. – MjM Software design, Gleneden Beach.
- NIESER, N., BAENA, M., MARTINEZ-AVILES, J. & MILLAN, A. (1994): Claves para la identificación de los heterópteros acuáticos (nepomorpha & gerromorpha) de la Península Ibérica. – Asociación Española de Limnología, Publicación No. **5**, Madrid.
- NTIAMOA-BAIDU, Y., PIERSMA, T., WIERSMA, P., POOT, M., BATTLE, P. & GORDON, C. (1998): Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. – *Ibis* **140**: 89–103.
- PARACUELLOS, M., CASTRO, H., NEVADO, J. C., OÑA, J. A., MATAMALA, J. J., GARCÍA, L. & SALAS, G. (2002): Repercussions of the abandonment of Mediterranean salt-pans on waterbird communities. – *Waterbirds* **25**: 492–498.
- PÉREZ-HURTADO, A., (ed.) (2004): Salinas de Andalucía. Consejería de Medio Ambiente, Sevilla.
- PÉREZ-HURTADO, A., GOSS-CUSTARD, J. D. & GARCÍA, F. (1997): The diet of wintering waders in Cádiz Bay, southwest Spain. – *Bird Study* **44**: 45–52.
- RICHOUX, P. (1982): Coléoptères aquatiques. – In: Introduction pratique à la systématique des organismes des eaux continentales françaises, Vol **2**. Association Française de Limnologie, Paris.
- RUBEGA, M. A. & INOUE, C. (1994): Prey switching in Red necked Phalaropes *Phalaropus lobatus*: feeding limitations, the functional response and water management at Mono Lake, California, USA. – *Biol. Conserv.* **70**: 205–210.
- SADOU, N., WALMSLEY, J. & CHARPENTIER, B. (1998): Salinas and nature conservation. Conservation of Mediterranean Wetlands N° **9**. – Tour du Valat. Arles. France.
- SÁNCHEZ, M. I., GREEN, A. J. & ALEJANDRE, R. (2006): Shorebird predation affects abundance and size distribution of benthic chironomids in salt-pans: an enclosure experiment. – *J. N. Amer. Benthol. Soc.* **25**: 9–18.
- SÁNCHEZ, M. I., GREEN, A. J. & CASTELLANOS, E. M. (2005): Seasonal variation in the diet of the Redshank *Tringa totanus* in the Odiel Marshes, south-west Spain: a comparison of faecal and pellet analysis. – *Bird Study* **52**: 210–216.
- SÁNCHEZ, M. I., GREEN, A. J. & CASTELLANOS, E. M. (in press): Spatial and temporal fluctuations in use by shorebirds and in availability of chironomid prey in the Odiel salt-pans, south-west Spain. – *Hydrobiologia*.
- SÁNCHEZ-MOYANO, J. E., ESTACIO, F. J., GARCÍA-ADIEGO, E. M. & GARCÍA GÓMEZ, J. C. (2000): The molluscan epifauna of the alga *Halopteris scoparia* in Southern Spain as a bioindicator of coastal environmental conditions. – *J. Molluscan Studies* **66**: 431–448.
- SAS INSTITUTE INC. (1997): SAS/STAT® Software, changes and enhancements through Release 6.12. Cary, NC.
- (2000): SAS/STAT [] software, User's Guide. Cary, NC.
- StatSoft (1999): Statistica 5.5. – StatSoft Inc., Tulsa, OK.

- TER BRAAK, C. J. F. (1990): Interpreting canonical correlation analysis through biplots of structure correlations and weights. – *Psychometrika* **55**: 519–531.
- THIÉRY, A. & PUENTE, L. (2002): Crustacean assemblage and environmental characteristics of a man-made solar saltwork in southern France, with emphasis on anost-racan (Branchiopoda) population dynamics. – *Hydrobiologia* **486**: 191–200.
- TRIPP, K. J. & COLLAZO, J. A. (2003): Density and distribution of water boatmen and brine shrimp at a major shorebird wintering area in Puerto Rico. – *Wetland Ecol. Manage.* **11**: 331–341.
- VERKUIL, Y., KOOLHAAS, A. & WINDEN, J. V. D. (1993): Wind effects on prey availability: how northward migrating waders use brackish and hypersaline lagoons in the Sivash, Ukraine. – *Netherl. J. Sea Res.* **31**: 359–374.
- VERKUIL, Y., VAN DER HAVE, T. M., VAN DER WINDEN, J. & CHERNICHKO, I. I. (2003): Habitat use and diet selection of northward migrating waders in the Sivash (Ukraine): the use of Brine shrimp *Artemia salina* in a variable saline lagoon complex. – *Ardea* **91**: 71–83.
- WARNOCK, N., PAGE, G. W., RUHLEN, T. D., NUR, N., TAKEKAWA, J. Y. & HANSON, J. T. (2002): Management and conservation of San Francisco Bay salt ponds: effects of pond salinity, area, tide, and season on Pacific Fly-way waterbirds. – *Waterbirds* **25**: 79–92.
- WEATHERHEAD, M. A. & JAMES, M. R. (2001): Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. – *Hydrobiologia* **462**: 115–129.
- WILLIAMS, W. D. (1998): Salinity as a determinant of the structure of biological communities in salt lakes. – *Hydrobiologia* **381**: 191–201.
- WOLFRAM, G., DONABAUM, K., SCHAGERL, M. & KOWARK, V. A. (1999): The zoobenthic community of shallow salt pans in Austria – preliminary results on phenology and the impact of salinity on benthic invertebrates. – *Hydrobiologia* **408/409**: 193–202.
- WOLLHEIM, W. M. & LOVVORN, J. R. (1995): Salinity effects on macroinvertebrate assemblages and waterbird food webs in shallow lakes of the Wyoming High Plains. – *Hydrobiologia* **310**: 207–223.
- ZIMMER, K. D., HANSON, M. A. & BUTLER, M. G. (2000): Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. – *Can. J. Fish. Aquat. Sci.* **57**: 76–85.

Submitted: 26 August 2005; accepted: 27 January 2006.