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# Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients

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## SUMMARY

1. Temporary aquatic habitats often are inhabited by a unique fauna and flora and contribute significantly to regional diversity. Temporary wetlands around the world are disappearing rapidly. The individual and interacting impacts of factors influencing community structure and dynamics in temporary wetlands are not always well known.
2. Camargue wetlands are mainly characterized by variable salinity and hydroperiod. The individual and combined impacts of these local factors, together with regional variables, on invertebrate communities remain unknown. We therefore characterized and sampled invertebrates in 30 temporary wetlands along salinity and hydroperiod gradients in the Camargue (Southern France) 3, 5 and 7 months after inundation.
3. Over the three sampling occasions, a total of 17 cladoceran species and 49 macroinvertebrate taxa were identified. Hydroperiod and salinity were the most important variables explaining variation in taxonomic composition and can be considered key factors shaping the invertebrate communities in Camargue wetlands. The impact on taxon richness was significantly positive for hydroperiod but significantly negative for salinity. Regional factors had no significant effect on the structure of the studied invertebrate communities, suggesting that dispersal was not limiting and that species sorting was the most important structuring process.
4. The results of this study suggest that the combined and interacting effects of salinization and hydrological modification of Mediterranean temporary wetlands (due to water management, climate change, etc.) can result in reduced diversity in large numbers of Mediterranean wetlands and induce a considerable decline in regional diversity of aquatic invertebrates.

*Keywords*: hydroperiod, invertebrate community structure, Mediterranean wetlands, salinity, temporary wetlands

## Introduction

Temporary aquatic habitats are diverse ecosystems that play important roles in the landscape such as flood control, groundwater recharge, toxicant removal and recycling of nutrients. They are also the main breeding and feeding grounds for many birds and other wildlife (Williams, 2006). These habitats are home to a unique fauna and flora and contribute significantly to regional diversity (Williams *et al.*, 2004; Biggs *et al.*, 2005). Unfortunately, temporary wetlands around the world are declining rapidly (Mura, 1993; Brendonck & Riddoch, 1997; King, 1998;

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Deil, 2005) and their inhabitants are disappearing at a high rate (Grillas *et al.*, 2004; Oertli *et al.*, 2005). Temporary pools are defined as being small (generally <10 ha), shallow wetlands characterized by alternating phases of drought and flooding and whose hydrology is largely autonomous. They occur in depressions that are often endorheic and remain submerged for sufficiently long periods to allow the development of hydromorphic soils, aquatic and semi-aquatic vegetation and specific animal communities (Ramsar, 2002). Some temporary wetlands in the Mediterranean Region are considered as priority habitat under the Habitat Directive according to the Natura 2000 network of the European Union (Natura code 3170, 92/43/CEE, 21 May 1992).

Hydroperiod (length of the inundation period) and salinity (total concentration of ions in the water) are important factors influencing the diversity and the structure of temporary wetland invertebrate communities (Spencer *et al.*, 1999; Bilton, Foggo & Rundle, 2001; Brock, Nielsen & Crosslé, 2005; Gascon *et al.*, 2005). Longer hydroperiods allow organisms with longer aquatic phases to complete their life cycles and provide more time for colonization and succession (Schneider & Frost, 1996; Kiflawi, Eitam & Blaustein, 2003). Salinization, on the other hand, can lead to the disappearance of species and result in dominance of a few tolerant ones (Williams, 1999; Kefford, 2000). Salinity affects the occurrence of species primarily through its link with osmoregulatory physiology (Withers, 1992). The presence of species can also be influenced by other abiotic factors and biotic interactions that covary with salinity (Pinder *et al.*, 2005).

The phenology (hydroperiod, hydroregime) of temporary wetlands depends on local climatic, topographic and hydrological conditions (Bauder, 2005). Due to their often shallow depth and small size, temporary wetlands are vulnerable to land use changes (Nicolet *et al.*, 2004) and they are often regarded as good early warning systems for biological impacts of shifting climate (Pyke, 2005). The salinity of wetlands can be influenced by variation in sea levels through connection with groundwater in coastal regions, freshwater recharge and evaporation (Schallenberg, Hall & Burns, 2003). Both phenology and salinity can be altered by management practices and climate change (Bauder, 2005; Brock *et al.*, 2005; Jeffries, 2005; Gonçalves *et al.*, 2007).

Organisms can respond to environmental changes in different ways: by means of acclimatization, avoidance through dispersal or (rapid) local adaptation (Greenwood & Wood, 2003; James, Cant & Ryan, 2003; Gonçalves *et al.*, 2007). While these processes provide a buffer against the effects of mild salinization or small changes in wetland phenology, they may not be able to buffer against drastic changes. As salinization and hydrological modification of temporary wetlands become more severe and widespread, many species are at risk of local extinction (Williams, 1999). The combined impact of both stressors is not yet known (Brock *et al.*, 2005) and could eventually lead to changes in community composition and wetland functioning and ultimately the extinction of specialized, endangered species.

Many wetlands in Europe and especially in the Camargue have been subject to hydrological modification by drainage, irrigation, changes in catchment hydrology or even conversion to permanent waterbodies (Grillas *et al.*, 2004; Nicolet *et al.*, 2004; Williams, 2006). Other threats such as salinization are often closely linked to hydrological changes (Brock *et al.*, 2005). In the Camargue, the balance between salt and freshwater is very unstable. Therefore modification of any of the driving factors (such as sea level fluctuations, drought, drainage and irrigation) could result in drastic changes in wetland salinity. Invertebrates often constitute 60–70% of the total number of species present over a complete hydrological cycle in Mediterranean temporary wetlands (Grillas *et al.*, 2004) and consequently represent a large part of their biodiversity. It is, however, currently unknown how species composition and diversity patterns are influenced by hydroregime, salinity and the interaction between the two factors.

The objective of this study was to assess the impact of salinity and hydroperiod on invertebrate community structure in relatively pristine Mediterranean wetlands in the Camargue region (southern France). We sampled the invertebrate communities of 30 wetlands three times in one season along hydroperiod and salinity gradients and investigated how local and regional factors affected the communities. Based on the observed patterns, we make predictions about how local communities may respond to expected future changes in hydrology and salinity.

## Methods

### *Study area*

The Rhône delta (Camargue, Southern France) is an alluvial plain that extends over 145 000 hectares, gently sloping from north to south. It was formed by the combined action of the Rhône river and the Mediterranean sea. The climate is typically Mediterranean, with hot, dry summers and an annual evapotranspiration deficit exceeding 600 mm (from March to September). The Mediterranean climate is variable, with a mean annual precipitation of 600 mm, mainly concentrated in autumn.

The Camargue is a vast wetland area of international importance (Ramsar site, Man and Biosphere reserve and 'Parc naturel régional de Camargue') holding many saltpans, lakes, lagoons, saline and freshwater marshes and temporary wetlands. These aquatic systems, naturally characterized by elevated salinity levels due to the proximity of the underlying saline aquifer, are supplied by freshwater through rain and from the Rhône River, from which water is abstracted for agricultural purposes (particularly rice cultivation). The equilibrium between salt and fresh water is very sensitive to anthropogenic impact.

It is difficult to estimate the extent of potential changes in salinity and hydrology in a hydrologically complex area like the Camargue. Depending on the relative contributions of several factors, such as water management schemes (the amount of fresh water imported from the Rhône river, irrigation and drainage) and climate change, different scenarios are possible. Predicted effects of climate change in the Camargue are (i) intensified drought through less evenly spread, but more intense rainfall and reduced summer rains and (ii) sea level rise causing more sea water intrusion and a rise in saline groundwater tables (Deneux, 2002).

### *Study site*

A cluster of 30 temporary wetlands was studied on the biological reserve of Tour du Valat, in the Rhône delta (Camargue) (Fig. 1). The estate of Tour du Valat is located 10 km from the sea and encloses approximately 55 temporary and five semi-permanent wetlands. The wetlands are filled during the wet season (from September to March) and dry up in the dry season (April until the end of August). The dates of both flooding and drying of these wetlands fluctuate considerably between years, depending on rainfall pattern. The wetlands are not subjected to any direct water management and occur on extensive pasture land (for local breeds of horses and cattle). Our selection of wetlands aimed to cover a broad range of hydroperiods and salinities. The most abundant aquatic plant species in the wetlands are *Zannichellia palustris* L. subsp. *pedicellata* (Wahlenberg & Rosén) Archangeli, *Ranunculus peltatus* Schrank and *Callitriche truncata* Guss.

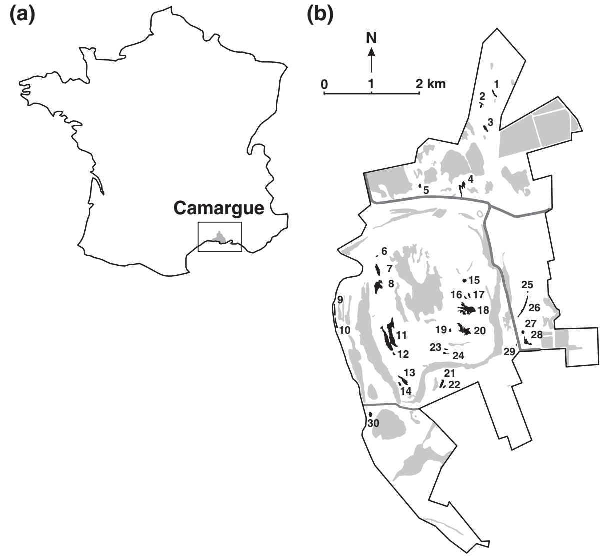

**Fig. 1** (a) Location of the Camargue in France and (b) the locations of the studied temporary wetlands (dark grey) on the study site Tour du Valat (light grey = other semi-permanent and temporary aquatic systems).

### *Assessment of local habitat characteristics*

The study period (wet season of 2005–06) started with a very wet autumn, most of the precipitation being concentrated from September to November (355 mm). The 30 temporary wetlands were monitored 3, 5 and 7 months after inundation (T1 = mid-December, T2 = mid-February and T3 = mid-April). For each wetland, we determined hydroperiod (length of the inundation phase). Ten of the wetlands with the shortest hydroperiods were already dry on T3 and were only sampled twice. At each sampling date, we monitored total flooded surface of each wetland by drawing its shape, measuring length and width and comparing resulting morphologies to known geometrical figures. The maximum depth was measured with a measuring stick. Conductivity (mS $cm^{-1}$), water temperature (°C), pH and oxygen concentration (mg $L^{-1}$) were measured *in situ* using WTW meters (conductivity meter 330i, oxygen meter 315i, pH meter 340). The measured electrical conductivity was used as a proxy for salinity. An integrated sample of 10 L for water quality analyses was prepared by collecting water at four different locations in the wetland using a 5-L beaker. The chlorophyll a concentration (mg $L^{-1}$) was determined using the methanol extraction method (Talling & Driver, 1963). The amount of suspended solids (mg $L^{-1}$) was determined by measuring the dry weight on a Whatman GF/C filter after filtration of a known volume of pool water (dried for 24 h at 105 °C). Nutrient concentrations (nitrate, orthophosphate, ammonia, total nitrogen and total phosphorus) were spectrophotometrically assessed with the Hach DR2400. Nitrate concentration was measured using a cadmium reduction method (low range 0.01–0.50 mg $L^{-1}$ $NO^{3-}$) and orthophosphate concentration using an ascorbic acid (PhosVer 3; Hach Company, Loveland, CO, U.S.A.) method (low range 0.02–2.50 mg $L^{-1}$ $PO_4^{-3}$). We measured total nitrogen concentrations using a persulphate digestion method (low range 0.5–25.0 mg $L^{-1}$ N) and for total phosphorus we used a PhosVer 3 method with acid persulphate digestion (low range 0.02–1.10 mg $L^{-1}$ P). Both digestions were carried out using a COD reactor. For ammonia concentration measurements we used the Nessler method (low range 0.02–2.50 mg $L^{-1}$ $NH_3$). As nitrate concentrations were always below 0.01 mg $L^{-1}$, they were within the measuring error of the instrument and therefore excluded from the analyses. Turbidity was determined using a Snell's tube (cm visibility) (described in Louette & De Meester, 2005). Total percentage vegetation cover (submerged and emergent macrophytes) (%) was estimated and the amount of organic matter (decomposing terrestrial vegetation) and the amount of macroscopic algae were each classified on a scale 0–4 (0 = <5%; 1 = 5–25%; 2 = 25–50%; 3 = 50–75%; 4 = 75–100%). Due to heavy rains in autumn some of the temporary wetlands were temporarily connected with permanent aquatic systems through which fish (mosquito fish *Gambusia affinis* (Baird & Girard, 1853) and stickleback *Gasterosteus aculeatus* Linnaeus 1758) moved into these normally fishless wetlands. The number of fish caught with a 250-$\mu$m net (total net surface area of 500 $cm^2$) during 3 min was therefore used as an extra explanatory variable in the analyses.

### *Assessment of regional characteristics*

Wetland isolation was assessed as the number of aquatic systems within 100 m and connectivity as the number of connections to other aquatic systems. Additionally, the spatial configuration of the wetlands was integrated in a distance matrix using the nearest edge to edge distances between each wetland pair.

### *Sampling and processing of zooplankton and macroinvertebrates*

On each sampling occasion, zooplankton (Cladocera and Copepoda) was collected quantitatively from the entire vertical water column using a tube-sampler (Ø 7.5 cm; 1 m). A spatially integrated sample of 50–100 L (depending on the density of the zooplankton) was taken by filtering water from eight randomly chosen locations in the wetland and filtering through a mesh of 64 $\mu$m. Non-benthic macroinvertebrates were sampled by sweeping with a 250-$\mu$m net (total net surface area of 500 $cm^2$) through all microhabitats in the wetland for a time period proportional to the structural heterogeneity and surface of the wetland (3–6 min). The zooplankton and macroinvertebrates were kept in ethanol (70%), and counted and identified under a stereo microscope. For zooplankton, subsamples of at least 300 cladocerans were counted. The cladocerans were identified to species level according to Alonso (1996) and Flössner (2000). Copepods were identified to the level of Calanoida or Cyclopoida. Macroinvertebrates were identified according to Tachet *et al.* (2000). Odonata, Gastropoda, Ephemeroptera, Trichoptera, Hemiptera, Coleoptera, Amphipoda and Isopoda were identified to genus level and the Diptera to family level. We also included the taxa Collembola, Hydracarina and Turbellaria. Large branchiopods were identified to species level according to Defaye, Rabet & Thiéry (1998).

### *Data analyses*

To study the relationship between local and regional factors and community structure we used a multivariate approach. We opted for redundancy analyses

(RDA) since detrended canonical correspondence analyses (DCCA) indicated a dominance of linear gradients (CANOCO 4.5) (Lepš & Šmilauer, 2003). The statistical power of all analyses was assessed by Monte Carlo permutation tests ($n = 999$). All analyses were performed separately for each sampling date (T1, T2 and T3) and for zooplankton and macroinvertebrates, whose absolute abundances were quantified differently: zooplankton abundance as number per L and macroinvertebrates as number caught per minute. Rare species that occurred in only one wetland were not taken into account as they may have a disproportional impact on the analyses. Abundance data were logarithmically transformed.

To determine the subset of local habitat characteristics explaining most variation in community structure between wetlands, forward selection was used. To study the importance of hydroperiod and salinity on community structure, the unique and shared explanatory power of both variables were disentangled using variance partitioning (Borcard, Legendre & Drapeau, 1992). To visualize the relations between hydroperiod and salinity (maximum measured conductivity) and community composition (macroinvertebrates and zooplankton), ordination diagrams of correspondence analyses (CA) were edited using cumulative presence–absence data over the three sampling dates. Additionally, the relation between total taxon richness (cumulative over the three samplings) and hydroperiod and salinity (maximum measured conductivity) was investigated through multiple regression models (STATISTICA 7.0; StatSoft Inc., Tulsa, OK, U.S.A.).

To determine whether species-poor wetlands were nested within species-rich wetlands, the matrix temperature was calculated by means of the BINMATNEST algorithm (Rodríguez-Gironés & Santamaría, 2006) as an index of nestedness. The probability of the observed pattern being random was determined by 500 random permutations (null model 3).

To study the impact of regional factors on community structure a community dissimilarity matrix was constructed using the Bray-Curtis dissimilarity index (Legendre & Legendre, 1998) (PRIMER 5). An environmental distance matrix was created using normalized Euclidean distances based on significant local habitat characteristics determined during RDA forward selection procedures (PRIMER 5). The correlation between these two matrices and the distance matrix were analysed using partial Mantel-tests (method of Vanschoenwinkel *et al.*, 2007). Mantel tests were computed using the freeware mantel function mantel.fcn (Reynolds & Bolker, 2001) in S-Plus (Anonymous, 1999). Significance of Mantel correlations was computed through permutations ($n = 1000$). We also investigated the effect of wetland isolation and connectivity on community structure using RDA (CANOCO 4.5). To correct for spatial environmental covariation, significant habitat characteristics from the forward selection procedure were used as covariables.

## Results

Over the three sampling occasions, a total of 19 zooplankton taxa (17 cladoceran species) and 49 macroinvertebrate taxa were identified. The mean taxon richness per wetland was eight zooplankton taxa (six cladoceran species) and 14 macroinvertebrate taxa.

### *Local factors*

The most important habitat characteristics (determined by forward selection RDA; see below) measured in the 30 sampled temporary wetlands are detailed in Table 1. Hydroperiod varied from 5 to 9 months. Salinity ranged from 0.6 mS cm$^{-1}$ to 5.0 mS cm$^{-1}$ after 3 months of inundation and

**Table 1** Average values (and standard deviations) for the most important local habitat characteristics at the different sampling dates

| Habitat characteristics | T1 ($n = 30$) | T2 ($n = 30$) | T3 ($n = 20$) |
|---|---|---|---|
| Conductivity (mS cm$^{-1}$) | 2.8 ± 1.2 | 5.3 ± 3.2 | 12.7 ± 6.8 |
| Flooded surface (m$^2$) | 13562 ± 22627 | 15819 ± 28187 | 5688 ± 7726 |
| Maximum depth (cm) | 43 ± 17 | 45 ± 16 | 28 ± 12 |
| Turbidity (cm) | 22.3 ± 6.8 | 22.7 ± 7.7 | 15.9 ± 6.5 |
| pH | 8.5 ± 0.5 | 8.8 ± 0.3 | 9.3 ± 0.6 |
| Total phosphorus (mg L$^{-1}$) | 0.26 ± 0.08 | 0.29 ± 0.13 | 0.93 ± 0.73 |
| Algae (0–4) | 2.47 ± 0.82 | 2.57 ± 1.19 | 2.05 ± 1.18 |
| Organic matter (0–4) | 2.67 ± 0.71 | 2.53 ± 1.04 | 2.63 ± 1.12 |
| Vegetation cover (%) | 77. 6 ± 31.8 | 38.0 ± 17.0 | 67.3 ± 24.1 |

**Table 2** Results of redundancy analyses using forward selection for each sampling date. Only significant explanatory variables are included

| Invertebrates | Date | Habitat characteristics | Explained var. (%) | *F*-ratio | *P*-value |
|---|---|---|---|---|---|
| Macro invertebrates | T1 | HP, Sal, Surface | 24.4 | 2.795 | 0.001 |
| | T2 | HP, Sal, Depth, Algae | 30.4 | 2.735 | 0.001 |
| | T3 | HP, Sal, Turbidity | 51.5 | 5.319 | 0.001 |
| Zooplankton | T1 | HP, Veg, Org mat, pH, Fish | 45.9 | 4.072 | 0.001 |
| | T2 | HP, Depth, pH, Fish, Algae | 40.2 | 3.232 | 0.001 |
| | T3 | Sal, Surface, Tot P, Org mat | 61.2 | 4.097 | 0.001 |

HP, hydroperiod; Sal, salinity; Org mat, organic matter; Veg, vegetation cover; Tot P, total phosphorus.

increased to a range of 3.0–25.0 mS $cm^{-1}$ near the end of inundation. Twenty-two of the studied wetlands were colonized by fish (catch sizes varied from 1 to 51 fish per wetland).

The most important explanatory habitat characteristics for macroinvertebrates and zooplankton on each sampling date, determined by forward selection, are presented in Table 2. Hydroperiod and salinity were the most frequent explanatory variables of significance and more so for macroinvertebrates (all three dates) than for zooplankton (hydroperiod for first two dates, salinity for T3). Other significant explanatory variables were hydro-morphological variables (surface and maximum depth), the number of fish, vegetation cover, algae, organic matter and water quality variables such as pH and total phosphorus concentration.

When focussing only on the effects of hydroperiod and salinity, there was a significant correlation between the two variables ($P = 0.024$; $R^2 = 0.42$). For macroinvertebrates, cumulative taxon richness was significantly related to hydroperiod ($F = 12.85$; d.f. = 1; $P = 0.001$), salinity ($F = 7.45$; d.f. = 1; $P = 0.011$) and the interaction between the two variables ($F = 8.53$; d.f. = 1; $P = 0.007$) (Fig. 2a). The model explained 37% of variability in taxon richness. Wetlands poor in macroinvertebrates were nested within taxon-rich wetlands (matrix temperature = 29.04; $P < 0.01$). The length of hydroperiod had a significantly positive effect on cumulative zooplankton taxon richness ($F = 8.02$; d.f. = 1; $P = 0.008$), while salinity had a significantly negative effect ($F = 6.01$; d.f. = 1; $P = 0.021$) (Fig. 2b). Both factors together explained 27% of the variability in

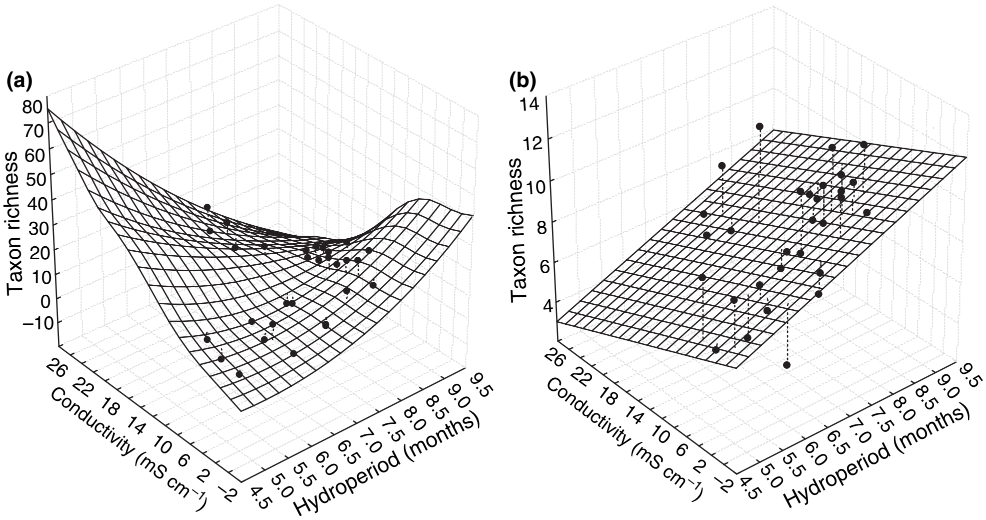

**Fig. 2** Surface plots of cumulative taxon richness versus hydroperiod and salinity for (a) macroinvertebrates (distance weighted least squares fit) and (b) zooplankton (linear fit).

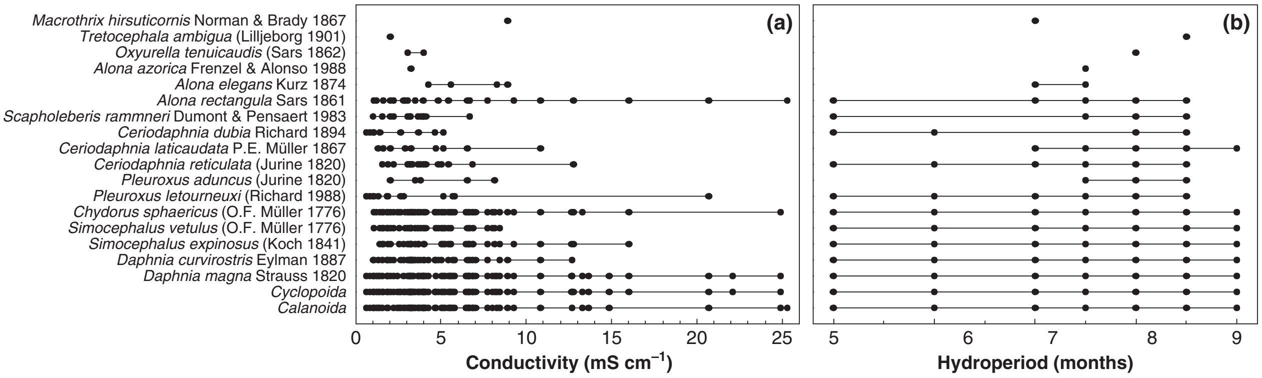

**Fig. 3** (a) Salinity and (b) hydroperiod records for the zooplankton taxa. Dots represent encounters of a taxon at a certain salinity level or hydroperiod; bars represent encounter ranges.

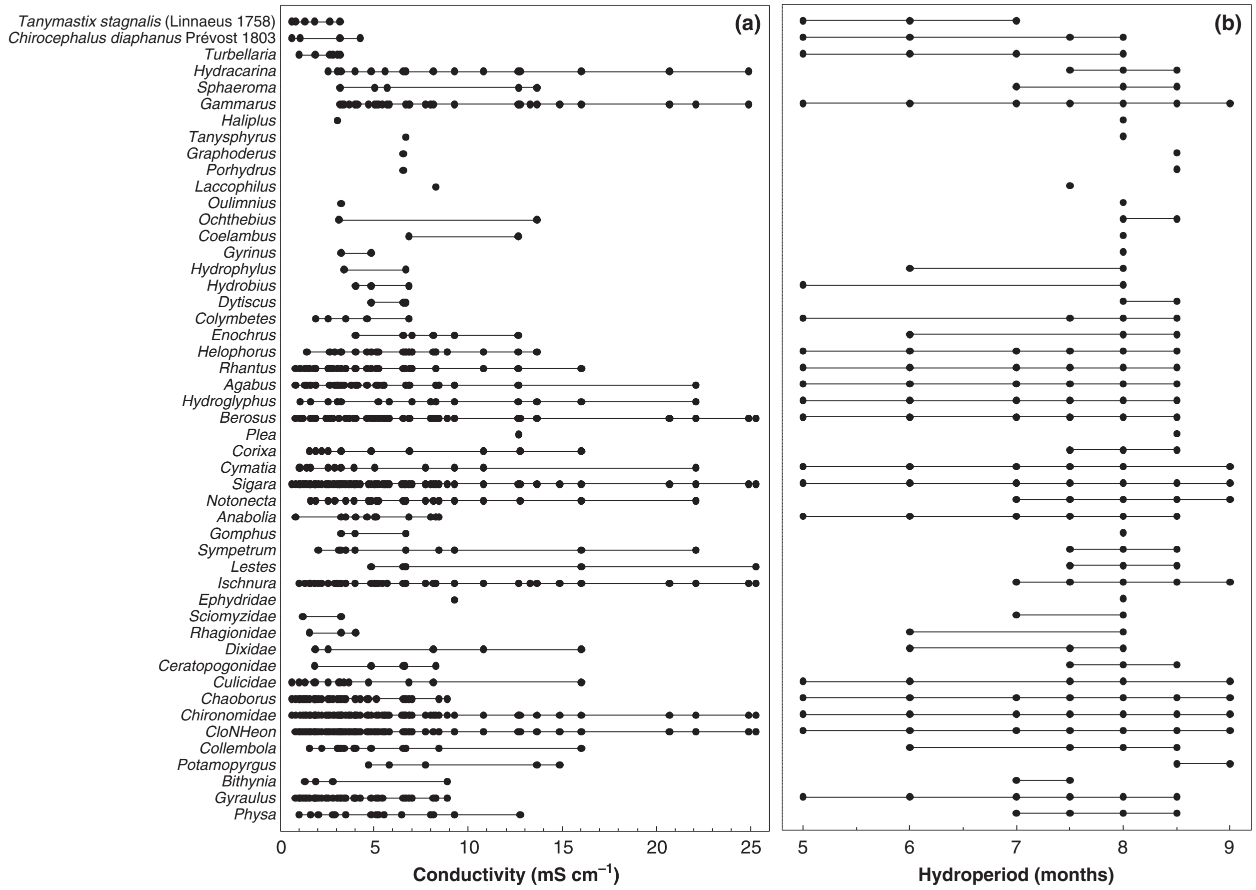

**Fig. 4** (a) Salinity and (b) hydroperiod records for the macroinvertebrate taxa. Dots represent encounters of a taxon at a certain salinity level or hydroperiod; bars represent encounter ranges.

taxon richness. Zooplankton taxon-poor wetlands were significantly nested within taxon-rich wetlands (matrix temperature = 18.79; $P < 0.01$).

Most rare species (species encountered less than three times) occurred where conductivity was low and hydroperiod was long (Figs 3 & 4). Most taxa occurred in wetlands with conductivity values below 10 mS cm$^{-1}$ (19 cladoceran species and 48 macroinvertebrate taxa). At conductivities >10 mS cm$^{-1}$, 26 macroinvertebrate taxa (of 49) and 10 zooplankton

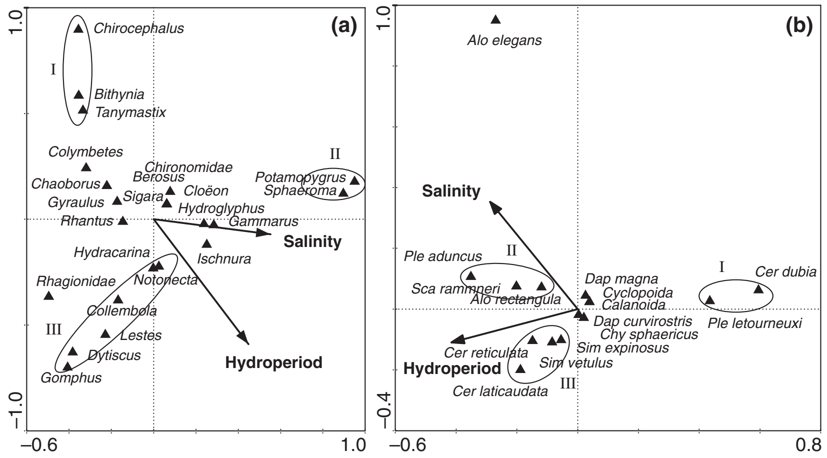

**Fig. 5** Ordination diagrams from correspondence analyses (CA) illustrating the relations between invertebrate community composition and the hydroperiod and salinity of the wetlands plotted as supplementary variables. (a) The macroinvertebrate community (only taxa where more than 21% of the variation is explained by the explanatory variables are visualized). (b) The zooplankton community.

taxa (of 19) were counted. At conductivities >20 mS cm$^{-1}$ only 13 macroinvertebrate taxa and six zooplankton taxa occurred.

A first group of invertebrates (I in Fig. 5a,b), containing the anostracans *Chirocephalus diaphanus* and *Tanymastix stagnalis*, the gastropod *Bithynia* and the cladocerans *Ceriodaphnia dubia* and *Pleuroxus letourneuxi*, was typical of wetlands with short hydroperiods and low salinities. The second group (II), with the gastropod *Potamopygrus*, the isopod *Spaeroma* and the cladocerans *P. aduncus*, *Scapholeberis rammneri* and *Alona rectangula*, was typical of long-lived, saline wetlands. The third group (III), containing all odonate genera, *Dytiscus*, *Notonecta*, *Hydracarina* and the cladocerans *C. reticulata*, *C. laticaudata*, *Simocephalus vetulus* and *S. expinosus*, was typical of wetlands with long hydroperiods and medium salinities. The cladoceran *A. elegans* was only found in wetlands of intermediate hydroperiods and salinities.

Variance partitioning revealed that hydroperiod and salinity had significant unique effects on the macroinvertebrate community on the three sampling dates (Table 3). The amount of variation explained by the two variables increased towards the end of inundation. Compared with the amount of variation explained by the models obtained through forward selection (Table 2), hydroperiod and salinity alone already explained a substantial part of the variation (for macroinvertebrates: 18.5% on T1; 16.1% on T2 and 31.5% on T3; for zooplankton: 17.7% on T1; 14.4% on T2 and 28.2% on T3) (Table 3, Fig. 6). Salinity only played a significant role for the zooplankton community at the end of the hydroperiod, while pond duration was more important at the beginning (Table 2). On all sampling dates the shared variation explained by hydroperiod and salinity was very small (maximum 1.6%), both for the macroinvertebrate and the zooplankton community

**Table 3** Results of variance partitioning of hydroperiod (HP) and salinity (Sal) for each sampling date

| Invertebrates | Date | Explanatory variables | Explained var. (%) | *F*-ratio | *P*-value |
|---|---|---|---|---|---|
| Macro invertebrates | T1 | HP-Sal | 6.5 | 2.143 | **0.026** |
| | | Sal-HP | 10.4 | 3.449 | **0.003** |
| | | HP∩Sal | 1.6 | | |
| | | HP*Sal | 3.2 | 1.077 | 0.397 |
| | T2 | HP-Sal | 6.3 | 2.028 | **0.055** |
| | | Sal-HP | 8.1 | 2.615 | **0.017** |
| | | HP∩Sal | 1.7 | | |
| | | HP*Sal | 7.6 | 2.596 | **0.016** |
| | T3 | HP-Sal | 17.7 | 4.138 | **0.002** |
| | | Sal-HP | 16.1 | 3.753 | **0.008** |
| | | HP∩Sal | 0.0 | | |
| | | HP*Sal | 13.0 | 3.501 | **0.005** |
| Zooplankton | T1 | HP-Sal | 12.8 | 4.186 | **0.001** |
| | | Sal-HP | 4.0 | 1.319 | 0.262 |
| | | HP∩Sal | 0.0 | | |
| | | HP*Sal | 1.7 | 0.548 | 0.793 |
| | T2 | HP-Sal | 10.0 | 3.147 | **0.020** |
| | | Sal-HP | 6.3 | 1.975 | 0.126 |
| | | HP∩Sal | 0.0 | | |
| | | HP*Sal | 3.7 | 1.183 | 0.293 |
| | T3 | HP-Sal | 8.4 | 1.879 | 0.097 |
| | | Sal-HP | 24.7 | 5.498 | **0.001** |
| | | HP∩Sal | 0.0 | | |
| | | HP*Sal | 2.6 | 0.569 | 0.744 |

HP-Sal = unique variation explained by the hydroperiod, Sal-HP = unique variation explained by the salinity, HP∩Sal = variation shared by hydroperiod and salinity, HP*Sal = Variation explained by the interaction between the hydroperiod and salinity.
Significant P-values are represented in bold.

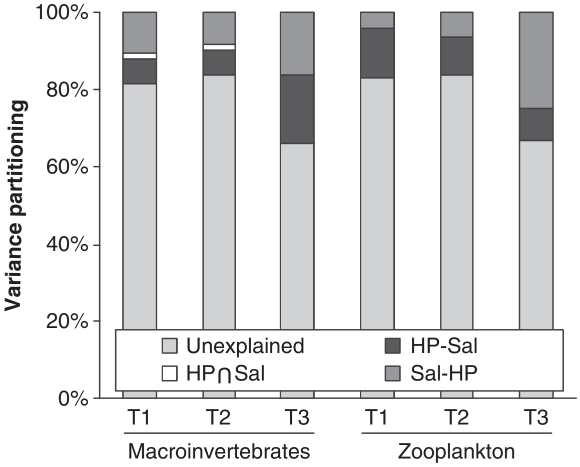

**Fig. 6** Variance partitioning of the macroinvertebrate and zooplankton data matrix for hydroperiod (HP) and salinity (Sal) on each sampling date. Four components are distinguished: unique variation explained by the hydroperiod (HP-Sal), unique variation explained by the salinity (Sal-HP), variation shared by hydroperiod and salinity (HP∩Sal) and the remaining unexplained variation.

(Table 3, Fig. 6). The interaction term between hydroperiod and salinity explained a significant amount of variation (7.6% on T2 and 13.0% on T3) in community composition of macroinvertebrates, but not of zooplankton (Table 3).

### *Regional factors*

Both for macroinvertebrates and zooplankton, neither the number of aquatic systems within a 100 m range nor connectivity had a significant effect on community structure (using RDA; $P > 0.05$). Using partial mantel tests we found a significant correlation between community dissimilarity and geographic distance between wetlands for zooplankton on T1 ($r_M = 0.162$; $P = 0.04$), but not on T2 ($r_M = -0.015$; $P = 0.577$) or T3 ($r_M = -0.071$; $P = 0.695$). For the macroinvertebrates, no significant relationship was found for T1 ($r_M = -0.089$; $P = 0.807$), while a marginally significant relationship was established at T2 ($r_M = 0.017$; $P = 0.061$) and T3 ($r_M = 0.217$; $P = 0.064$).

## Discussion

### *Species richness*

The studied temporary wetlands in the Camargue support an invertebrate diversity of 17 cladoceran species, calanoid and cyclopoid copepods and 49 macroinvertebrate taxa (with an average of six cladoceran species and 14 macroinvertebrate taxa per wetland). This cladoceran species richness is comparable to other studies on temporary wetlands (King, Simovich & Brusc, 1996; Fahd *et al.*, 2000; Mura & Brecciaroli, 2003; Frisch, Moreno-Osts & Green, 2006), but is relatively limited compared with permanent waters. Dumont & Segers (1996), for example, estimated the presence of about 50 cladoceran species in permanent lakes. Furthermore, Collinson *et al.* (1995) and Della Bella, Bazzanti & Chiarotti (2005) found that macroinvertebrate species richness was much higher in permanent ponds compared to temporary ones (respectively 35 versus 17 and 87 versus 38). Differences in taxon richness in permanent versus temporary aquatic systems can be explained by the ephemeral character, small dimensions and variable environment of temporary waters, requiring specific adaptations of the (especially permanent) inhabitants (e.g. life history, production of resting stages, dispersal capacity) (Mura & Brecciaroli, 2003). Although usually lower than in large and long lived systems, the diversity in small temporary waters is often considered surprisingly high. Reasons suggested for this are rich food resources, reduced stress from biotic factors, patchiness, isolation and egg banks that promote coexistence (Wiggins, Mackay & Smith, 1980; Brendonck & Williams, 2000).

### *Local factors*

*Hydroperiod and salinity.* Hydroperiod and salinity were key factors shaping the invertebrate communities in the Camargue wetlands. The importance of these variables has been stressed before (e.g. Bilton *et al.* (2001) and Rundle *et al.* (2002) for hydroperiod and Grillet, Legendre & Borcard (2002), Gascon *et al.* (2005) and Frisch *et al.* (2006) for salinity). The combined and individual effects of hydroperiod and salinity on community structure, however, have never been analysed together. Both variables combined accounted for roughly half of the variation explained by the forward selection models on taxon composition of macroinvertebrates (on average 22% compared to 35%) and zooplankton (on average 20% compared to 49%). Salinity was slightly less important for zooplankton than for macroinvertebrates. The importance of salinity and hydroperiod increased towards the end of inundation, when the wetlands became smaller and more saline through evaporation.

In the case of taxon richness, we found a positive relationship with hydroperiod, for both macroinvertebrates and zooplankton. This has also been demonstrated by Eitam *et al.* (2004a), Serrano & Fahd (2005) and Tavernini, Mura & Rossetti (2005) for zooplankton and Brooks (2000), Bilton *et al.* (2001) and Baber, Fleishman & Babbitt (2004) for macroinvertebrates. In wetlands with longer hydroperiods, more time is available for completing life cycles, colonization and community development (Schneider & Frost, 1996; Kiflawi *et al.*, 2003). Because the longer-lived systems in this study often had larger surface areas ($P < 0.01$; $R^2 = 0.58$) and more developed aquatic vegetation ($P < 0.01$; $R^2 = 0.15$), increased habitat size and/or habitat heterogeneity could also have enhanced taxon richness. Additionally, larger pools may reduce the chance of local extinction by supporting larger populations and providing more stable physicochemical conditions than smaller pools (Kiflawi *et al.*, 2003). A positive relationship between species richness and surface area in temporary wetlands was also found by, for example, Spencer *et al.* (1999), Boix, Sala & Moreno-Amich (2001), Eitam, Norena & Blaustein (2004b) and Rundle *et al.* (2004).

There was a negative relationship between invertebrate taxon richness and salinity, as also found by Nielsen *et al.* (2003) and Brock *et al.* (2005) for zooplankton and Kefford, Pappas & Nugegoda (2003), Piscart, Moreteau & Beisel (2005) for macroinvertebrates and Pinder *et al.* (2005) for both. While 52% of all taxa were encountered above a 10 mS cm$^{-1}$ limit, only 29% occurred above a 20 mS cm$^{-1}$ limit. Additionally, most rare species occurred in the less saline part of the gradient. Consequently, our results support the hypothesis that rare freshwater species are more sensitive to disturbances than abundant species (Cao & Williams, 1999). We should, however, be careful in deducing tolerance limits from occurrence patterns as the absence of species outside a salinity range may also result from a response to other abiotic factors or biotic interactions that vary together with salinity (Kefford *et al.*, 2004; Pinder *et al.*, 2005).

The long history of natural salinity of the Camargue, due to the proximity of the sea and the underlying saline aquifer, has probably contributed to the wide tolerance of, what are usually considered, freshwater species. For example, large branchiopods in France are generally considered to be restricted to salinities below 0.8 mS cm$^{-1}$ (Defaye *et al.*, 1998). However, in this study, although they were generally found in the most diluted wetlands, they still occurred in wetlands with salinities up to 4.0 mS cm$^{-1}$. For Cladocera, Hart *et al.* (1991) claimed that most species are restricted to aquatic environments with salinities lower than 1.5 mS cm$^{-1}$. Several studies have investigated the distribution of cladocerans in different waterbodies along salinity gradients and found that 2% (Pinder *et al.*, 2005), 19% (Bos, Cumming & Smol, 1999), 24% (Boronat, Miracle & Armengol, 2001) or 29% (Frey, 1993) of cladoceran species were tolerant to field salinities above a 15 mS cm$^{-1}$ threshold. In the Camargue wetlands, 29% of cladoceran species were still encountered above 15 mS cm$^{-1}$. According to Hart *et al.* (1991) and Pinder *et al.* (2005) most dragonflies occur in field salinities of less than 0.8 mS cm$^{-1}$ or 15 mS cm$^{-1}$ respectively. However, in Western Europe, certain odonates are capable of reproducing in brackish environments as long as the salinity does not exceed 23.5 mS cm$^{-1}$ (Grand & Boudot, 2006). In our study systems, most odonates indeed occurred in salinities up to 22–25 mS cm$^{-1}$ (except *Gomphus*). On the other hand, taxa such as Copepoda, some Cladocera (such as *P. letourneuxi* and *D. magna*), Amphipoda (such as *Gammarus*), Diptera, some Coleoptera (such as *Rhantus*) and some Hemiptera (such as *Sigara*) are known to be salinity tolerant (Hart *et al.*, 1991; Kefford, 2000; Boronat *et al.*, 2001; Pinder *et al.*, 2005), which is reflected in our study.

The invertebrate taxa in taxon-poor wetlands were nested in the assemblages of taxon-rich wetlands. As hydroperiod and salinity were significantly related to taxon richness, it is possible that these factors were partly responsible for this pattern. Nestedness of communities of shorter-lived wetlands within those of longer-lived wetlands was also reported by Baber *et al.* (2004). The high degree of nestedness in our study implies that protection of wetlands with long hydroperiods or low salinities may be more important than protection of species-poor wetlands with short hydroperiods or high salinities. However, the latter can still act as stepping stones between larger wetlands, maintaining metacommunity dynamics and stability (Baber *et al.*, 2004; Holyoak & Leibold, 2005). Additionally, smaller wetlands may contain certain peculiar species that only occur in high densities in such habitats. For example, the large branchiopod species, such as *C. diaphanus* and *T. stagnalis*, were typical of short-lived freshwater wetlands, while taxa like *Gammarus*, *Sphaeroma, Potamopygrus* and *A. elegans* were characteristic of more saline ones.

The measured impact of hydrology and salinity on biological communities in the Camargue wetlands has implications for conservation. Secondary salinization of aquatic systems through, for example irrigation, drainage, massive clearing of vegetation and climate change (e.g. sea level rise) constitutes an important threat not only for Mediterranean wetlands (Berger *et al.*, 1979; Grillas, 1990), but for wetland communities all over the world (Hart *et al.*, 1991; Williams, 1999; Van Zandt *et al.*, 2003; Kefford *et al.*, 2004). Many wetlands in the Camargue and also in Europe are, moreover, subjected to hydrological modification due to water management, changes in catchment hydrology or climate change (Grillas *et al.*, 2004; Nicolet *et al.*, 2004; Williams, 2006). As also confirmed in other studies, changes in hydrology impose a great risk for invertebrate communities (Bauder, 2005; Brock *et al.*, 2005; Pyke, 2005). In our study we found not only unique effects of hydroperiod and salinity, but the interaction between the two factors also had a significant effect on taxon richness and community composition of macroinvertebrates, indicating a different response to salinity depending on wetland hydroperiod. In long-lived wetlands, saline conditions were associated with lower macroinvertebrate richness, while this was not the case in wetlands with short hydroperiods. This observation may be explained by the fact that wetlands with long inundations are exposed to higher temperatures later in the season, resulting in lower oxygen concentrations. Combined with the high salinities, this may have resulted in a lower diversity in long-lived saline wetlands. On the other hand, the pattern may be related to the presence of fish that more frequently occurred in long-lived wetlands. The fishless environment in the short-lived wetlands may have promoted macroinvertebrate diversity. The significant interaction indicates that the combined effect of the two stressors (hydroperiod and salinity) is non-additive and, in this case, smaller than the response predicted by single effects (antagonism). When designing conservation measures, both stressors should therefore be considered.

*Other local factors.* Apart from hydroperiod and salinity, other local factors, such as the number of fish, water quality (pH and Tot P) and the amount of algae and organic matter also influenced the invertebrate communities. The normally fishless temporary wetlands became connected to the permanent systems during the heavy autumn rains, facilitating fish dispersal to the temporary wetlands. This is not an unusual event for the Camargue as, in the past, such flooding has occurred at least four times in the last 20 years. The invertebrate community was significantly affected by the number of fish (*Gambusia affinis* and *Gasterosteus aculeatus*, with *G. affinis* being much more abundant than *G. aculeatus*). The mosquito fish *G. affinis* has been introduced to waters worldwide for mosquito control. The introduction of fish in previously fishless habitats can cause major changes in the community by substantially reducing the density of some species, sometimes to the point of local extinction (Wellborn, Skelly & Werner, 1996) and is considered a significant threat to, for example, anostracan populations (Leyse, Lawler & Strange, 2004). This probably explains their limited presence during our survey. Additionally, both fish are important predators of large-bodied zooplankton, such as copepods and *Daphnia* and *Simocephalus* species, but also of small or juvenile macroinvertebrate species (Pont, Crivelli & Guillot, 1991; Swanson, Cech & Piedrahita, 1996). Aquatic vegetation cover was also an important factor influencing invertebrate community structure, presumably because the vegetation creates structural heterogeneity and can provide refuges and food resources (Taniguchi, Nakano & Tokeshi, 2003). The factor 'organic matter' is a measure of the amount of vegetation during the previous dry period, which starts to decompose during the wet phase. This resource can then be used by the aquatic community during the following inundation (Williams, 2006).

### Regional factors

Isolation and connectivity had no significant effect on the structure of the invertebrate communities. These results suggest that dispersal is not limited and species sorting probably is the most important structuring process in our study systems. Similar conclusions have been drawn in other studies on permanent ponds (Cottenie, Nuytten & Michels, 2003) and temporary rockpools (Vanschoenwinkel *et al.*, 2007). Wind, water-ways and animals are generally considered to be the most important vectors for passive dispersal of pool invertebrates (reviewed in Bilton *et al.*, 2001). In the studied cluster of wetlands, distances between them were relatively short (inter-wetland distances between 5 m and 8 km). The strong wind (mistral), occasional connections among wetlands during flooding, and the presence of large numbers of water birds and large mammals (cows, horses and wild boars) probably mediate relatively frequent and successful dispersal.

Regional effects, however, cannot be entirely excluded because the more sensitive partial mantel tests revealed a marginally significant correlation between community dissimilarity and geographic distance. For zooplankton this pattern was established early in the season, probably due to the presence of temporary connections between neighbouring wetlands. For the macroinvertebrates, this pattern occurred in the middle and at the end of the inundation; this is probably related to the increased influx of macroinvertebrates in temporary wetlands at that time. Here, inter-pool differences in proximity of permanent source populations might explain the observed isolation by distance pattern in community dissimilarity.

### *Temporary wetlands as early warning systems*

The results of this study suggest that the combined and interacting influences of salinization and hydrological modification of Mediterranean temporary wetlands can result in reduced invertebrate diversity in large numbers of Mediterranean wetlands and consequently induce a considerable decline in regional diversity of aquatic invertebrates. The extent of these modifications is, however, difficult to estimate because future changes in salinity and hydrology in a hydrologically complex area like the Camargue are unclear. Depending on the relative contributions of several factors, such as water management schemes and climate change, different scenarios are possible. Further research is needed to predict the impact of these scenarios on the invertebrate communities of temporary wetlands, which are considered reliable early warning systems for biological impacts of shifting climate.

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