

# Relation between macroinvertebrate life strategies and habitat traits in Mediterranean salt marsh ponds (Empordà wetlands, NE Iberian Peninsula)

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**Abstract** The influence of water permanence and high intra- and inter-annual hydrological variability on macrobenthos (organisms >1 mm) was studied using a taxonomical and a functional approach. The study was carried out in a Mediterranean salt marsh. Monthly samples of macrobenthic fauna were collected during two consecutive hydroperiods from six ponds with different water permanence (temporary, semi-permanent and permanent waters). Organisms were assigned to five functional response groups based on life-strategies according to their capacity to survive desiccation events, their dispersion capability and the necessity of water for their reproduction. Results from both approaches showed that the benthic community was more related to pond type than to intra- and inter-annual variability. The second aim was to analyse to which extent patterns in functional groups were determined by the existence of succession patterns or to environmental variability. In this sense, a clear succession pattern was not observed. In contrast, in most of the functional groups (4 out of 5), species within each functional group showed similar

responses to water fluctuations. However, species of the fifth functional group, which comprised species without any particular adaptation to desiccation survival or avoidance, showed different responses to water level fluctuations.

**Keywords** Functional group · Water permanence · Hydroperiod · Habitat type · Temporal variability · Generalized Additive Model

## Introduction

The relationship between species and environmental conditions has been traditionally studied using multivariate analyses (e.g. correspondence analysis, canonical analysis, multi-dimensional scaling), usually based on a taxonomical approach (e.g. ter Braak, 1987; Birks et al., 1994). The results of multivariate analyses have also been related to specific concepts of theoretical succession and predictive modelling (Jassby & Powell, 1990; Mesléard et al., 1991; Noest, 1991; Quintana, 2002a; Boix et al., 2004). The development of powerful statistic techniques has led to an expansion of predictive habitat distribution models (Guisan & Zimmermann, 2000). These are used to predict species responses to environmental fluctuations or to find similarities/generalities in these responses. For example, Generalized Additive Models (GAMs) provide an interesting extension to Generalized Linear Models (GLMs), since they allow

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linear and non-linear response shapes, for both continuous and categorical variables, and for a combination of those within a single model (Hastie & Tibshirani, 1990). Recently, several studies have used GAMs to model macroinvertebrate species response to environmental variables (Castella et al., 2001; Horsák, 2006).

Ecosystem level processes are affected by the functional characteristics of the organisms involved, rather than by their taxonomic identity (Hooper et al., 2002). Functional groups have been defined as sets of species showing either similar responses to the environment or similar effects on major ecosystem processes (Gitay & Noble, 1997). Thus, two types of functional groups can be used: (1) functional effect groups, which are used when the goal is to investigate the effects of species on ecosystem properties (e.g. trophic groups); and (2) functional response groups, which are used when the goal is to investigate the response of species to changes in the environment, such as disturbance, resource availability or climate (e.g. life strategies). Studies of macrobenthic fauna based on functional effect groups, mainly covering feeding strategies, are very common from lotic systems (e.g. Goodman et al., 2006; Tomanova et al., 2006), while studies focusing on functional response groups are less abundant (e.g. Wiggins et al., 1980; Usseglio-Polatera et al., 2000). However, in lotic systems, some recent studies have used functional response groups to show community responses to some environmental factors (e.g. salinity; Piscart et al., 2004). On the other hand, studies on functional response groups based on life-strategies in lentic systems have been mainly used to see succession patterns in temporary waters (e.g. Williams, 1985; Bazzanti et al., 1996), and not to study community response to environmental variability.

Environmental variability is especially high in Mediterranean wetlands, where irregularity and unpredictability of hydrological patterns are well known (Quintana et al., 1998a; Álvarez-Cobelas et al., 2005). A flooding and a drying phase are distinguishable at intra-annual level, with significant effects on nutrient concentration, species composition and even in competitive and predatory interactions (Quintana et al., 1998b; Serrano et al., 1999; Boix et al., 2004). Inter-annual variability is also high and some studies have reported a higher variation of zooplankton assemblages at inter-annual than at intra-annual level

(Serrano & Fahd, 2005). Inter-annual changes due to unusual drought events can have drastic effects on temperature, nutrient contents and invertebrate assemblages in Mediterranean wetlands (Angeler et al., 2002; Gascón et al., 2007). Furthermore, habitat type due to differences in water permanence has been shown to determine benthic species composition, and differences in benthos (Gascón et al., 2005) and zooplankton (Brucet et al., 2005; Serrano & Fahd, 2005) assemblages in these Mediterranean environments. Using a taxonomical approach, differences in benthic communities have already been found to be mainly related to water level fluctuations of the ponds (Gascón et al., 2005), but it remains to be established whether these hydrological patterns determine the functional response of the species involved.

Our objectives were to investigate if macrobenthic communities are influenced by pond type (classified according to water permanence), and high inter- and intra-annual hydrological variability, and to compare if observed effects are similar depending on whether a taxonomical or a functional approach is used. Secondly, we will analyse to which extent patterns in functional response groups, related to life-strategies, are determined by the existence of succession patterns or by environmental variability, as a function of water level fluctuations. Water level was chosen as target factor since differences in water level are related to water permanence, and also to (intra- and inter-annual) temporal variability.

## Material and methods

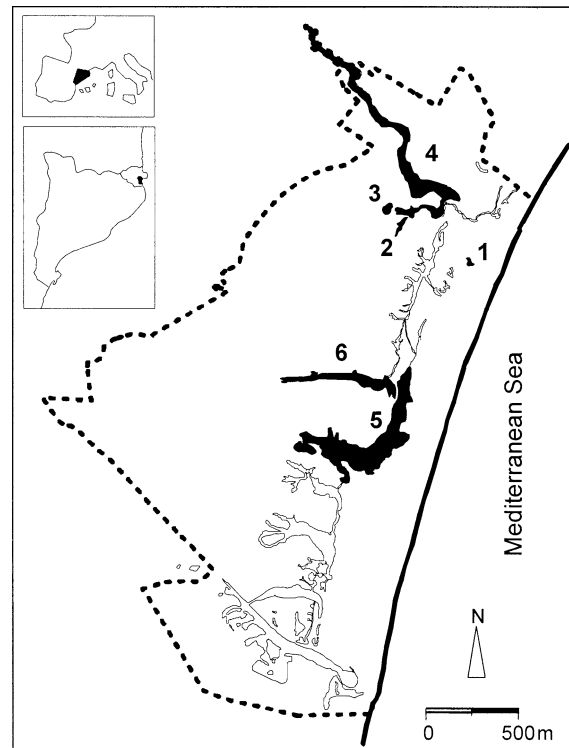
### Study site

Empordà wetlands salt marshes are located close to the Mediterranean Sea, in the northeast of the Iberian Peninsula, and are free from tidal influence. The hydrology is characterized by sudden and irregular flooding (caused by rainfall, inputs from rivers or channels and sea storms), followed by dry periods, when most of the ponds become isolated and gradually dry out (Quintana, 2002b). Thus, two phases can be differentiated: a flooding phase from autumn to winter, and a drying phase from spring to summer. Note that the study site is characterized by a high connectivity, since flooding events usually connect all ponds (Quintana, 2002b).

The ponds under study are depressions occurring between sand bars in salt marshes, where water accumulates. Their depth varies greatly depending on the flooding regime, but they are usually less than 1 m deep. The ponds are flat, not vegetated and they do not communicate directly with the sea. They differ in water permanence, from temporary to permanent ponds. Following the classification of temporary ponds made by Wiggins (1973), the studied ponds which dry out completely are similar to temporary autumnal ponds, since they have a wet phase of approximately 9 months and a dry phase of 3 months, the wet phase starting in autumn (Brucet et al., 2005). However, during the study the wet phase was unusually short, due to intrinsic inter-annual variability of the Mediterranean climate (Table 1).

#### Sampling procedure and processing

The study was undertaken from November 1997 until July 1999 during two hydroperiods (from November 1997 to July 1998, and from November 1998 to July 1999) in six ponds of Empordà wetlands salt marshes (Fig. 1). The ponds were grouped into pond types according to their water permanence, size and landscape variables. To obtain landscape variables (isolation, waterbodies density and predominance of aquatic habitat), freely available aerial photographs were used (DPTOP, 2005; MAPA, 2006). Isolation of the wetlands was calculated as the distance (m) to the nearest pond, the waterbodies density as the number of waterbodies within a radius of 500 m from the



**Fig. 1** Map of the study site, indicating the basins studied in black: 1 and 3 are temporary ponds, 2 and 4 semi-permanent ponds and 5 and 6 permanent ponds. The discontinuous line indicates the limit of the integral reserve of the Empordà Wetlands Natural Park

waterbody and the predominance of aquatic habitat as the proportion of water surface in a square kilometre centred in the waterbody. Ponds which were connected during most of the hydroperiod, were considered in the same pond type. Thus, three pond

**Table 1** Water and landscape characteristics of the ponds during the study (mean; range in brackets and number of samples in italics)

	Temporary ponds	Semi-permanent ponds	Permanent ponds
Pond	1 and 3	2 and 4	5 and 6
Surface (m <sup>2</sup> )	(983–1,649)	(3,236–55,837)	(87,369–19,151)
Isolation (m)	(90–10)	(10–35)	(10–10)
Waterbodies density (n° of waterbodies/500 m radius)	(11–11)	(11–11)	(5–5)
Predominance of aquatic habitat (%)	(5.3–6.3)	(5.9–6.3)	(13.2–15.4)
Hydroperiod mean length (month/year)	7	7	12
Water level (cm)	41.8 (0–108.6), <i>40</i>	45.8 (0–111.8), <i>37</i>	54.3 (21.7–109.4), <i>37</i>
Water temperature (°C)	16.0 (5.9–27.5), <i>38</i>	17.5 (4.9–26.8), <i>35</i>	15.3 (7.2–24.0), <i>36</i>
Water conductivity (mS cm <sup>-1</sup> )	35.3 (20.8–73.2), <i>38</i>	30.3 (13.0–41.3), <i>35</i>	22.1 (14.0–38.8), <i>36</i>

Hydroperiod mean length was observed during the study period

types were differentiated by water permanence, size and landscape variables (Table 1): (1) temporary ponds (T) dry out completely every year, have small sizes and the landscape is characterized by a low predominance of aquatic habitat, and a high waterbodies density (ponds 1 and 3); (2) semi-permanent ponds (SP) do not dry out completely every year, and have similar characteristics of predominance of aquatic habitat and waterbodies density than those observed in temporary ponds, but they have intermediate sizes (ponds 2 and 4); (3) permanent ponds (P) never dry out completely, and in contrast with the rest of the ponds, have bigger sizes, a higher predominance of aquatic habitat and the lowest waterbodies density (ponds 5 and 6). Water level was measured monthly using a graduated gauge firmly fixed on the bottom of the ponds. Water temperature and conductivity were measured monthly in situ.

Monthly samples of macroinvertebrates (organisms >1 mm) were obtained using an Ekman grab (225 cm<sup>2</sup>), taking two replicates for the smallest ponds (1 and 3) and four replicates for the bigger ponds (2, 4, 5 and 6). Sampling was carried out until the sampling site dried out. In the case of permanent ponds, sampling sites were located at levels which also dried out due to high water level fluctuation. Organisms were separated alive from the sediment using a 1 mm mesh-size sieve and preserved in 4% formalin until taxonomic identification. All individuals were identified to species whenever it was possible. Abundances were estimated by counting all individuals retained on the sieve. Following Wiggins et al.'s (1980) classification and according to the literature (Wiggins et al., 1980; Takeda & Nagata, 1998; Herbst, 1999; Tachet et al., 2002), taxa were grouped in four life strategies. A new group different from those established was added, comprising species without any particular adaptation to avoid or survive desiccation (Table 2).

## Statistical analyses

### *Environmental data*

Differences in water level, temperature and conductivity among different pond types (temporary, semi-permanent and permanent ponds), between phases (flooding vs. drying phases) and hydroperiods

**Table 2** Characteristics of each life-strategy group

	Type of dispersion	Need of water to reproduce	Can survive desiccation in the basin
G1	Passive	Yes	Yes
G2	Active	Yes	Yes
G3	Active	No	Yes
G4	Active	Yes	No
G5	Passive	Yes	No

Groups 1, 2, 3 and 4 correspond to the classification made by Wiggins et al. (1980); group 5 was created to include organisms with passive dispersion and without adaptations to desiccation

(1997–1998 vs. 1998–1999) were analysed using a multivariate analysis of variance (MANOVA). To ensure homogeneity of the variances, water level was log transformed [ $\log(\text{variable} + 1)$ ]. Initially, MANOVA was run with the most complex model, introducing all possible interactions. Then, to increase statistical power, the model was simplified by removing non-significant interactions, identified using Pillai's statistic ( $P > 0.05$ ). The relationship between species richness and hydroperiod length was calculated using Spearman's correlation. Species richness values were obtained for each hydroperiod and pond, and were related to the number of weeks in which ponds remained flooded for each hydroperiod. The relationship between species richness and pond surface was analysed using Pearson's correlation after log transforming all variables [ $\log(\text{variable} + 1)$ ]. Species richness values corresponded to accumulative richness from this study and were related to the surface of each pond. All statistical analyses were performed using SPSS 11.5.1 for Windows.

### *Pond type and temporal variability*

For the taxonomical approach, a canonical correspondence analysis (CCA) using CANOCO 4.5 (ter Braak & Šmilauer, 2002) was performed to study temporal variability (between phases and hydroperiods) and pond type (water permanence) influence on macrobenthic community. Water permanence has been chosen to summarize pond type characteristics, since all the variables that describe pond types are

highly related. The rest of pond type descriptors have been included as supplementary variables. Only taxa which appeared in more than one sample were considered in the analysis (Table 3). The species-abundance matrix was squareroot transformed. Following ter Braak & Šmilauer (2002), we downweighted rare species to reduce their influence in the analysis. Forward-selection procedure available in CANOCO 4.5 was used to obtain the conditional effect for each variable, and the significance of the explanatory effect for each variable was

evaluated using a Monte Carlo permutation test (ter Braak & Šmilauer, 2002).

For the functional approach, pond type and temporal (phases and hydroperiods) variability for each functional group were analysed using generalized linear models (GLMs), instead of ANOVA, which it is not appropriate for count data. GLM were calculated for each functional group using a Poisson distribution as error and the log link function, which ensures that all the fitted values are positive. The significance of the different explanatory variables

**Table 3** Abundance (ind · 10 cm<sup>-2</sup>) of the 21 most frequent taxa (occurrence higher than 1%)

Taxa	Life strategy group	Temporary ponds	Semi-permanent ponds	Permanent ponds
<b>Gastropoda</b>				
<i>Hydrobia acuta</i> (Draparnaud, 1805)	5	0.01 (0.00–0.06)	0.01 (0.00–0.10)	<0.01 (0.00–0.03)
<b>Polychaeta</b>				
<i>Nereis diversicolor</i> Müller, 1776	5	0.24 (0.00–2.46)	0.11 (0.00–0.80)	0.20 (0.00–1.36)
<i>Streblospio shrubsolii</i> (Buchanan, 1890)	5	–	–	0.05 (0.00–0.22)
<b>Oligochaeta</b>				
<i>Paranais</i> sp.	1 <sup>a</sup>	–	<0.01 (0.00–0.02)	0.01 (0.00–0.17)
<i>Nais</i> sp.	1 <sup>a</sup>	–	–	<0.01 (0.00–0.03)
Tubificidae undet.	1 <sup>a</sup>	<0.01 (0.00–0.09)	<0.01 (0.00–0.02)	<0.01 (0.00–0.01)
<b>Malacostraca</b>				
<i>Leptocheirus pilosus</i> Zaddach, 1844	5	–	–	<0.01 (0.00–0.02)
<i>Corophium orientale</i> Schellenberg, 1928	5	–	<0.01 (0.00–0.01)	0.63 (0.00–7.34)
<i>Gammarus aequicauda</i> (Martynov, 1931)	5	0.01 (0.00–0.29)	0.09 (0.00–1.56)	<0.01 (0.00–0.03)
<i>Orchestia</i> sp.	5	<0.01 (0.00–0.02)	<0.01 (0.00–0.01)	–
<i>Lekanesphaera hookeri</i> (Leach, 1814)	5	–	<0.01 (0.00–0.02)	0.01 (0.00–0.06)
<b>Coleoptera</b>				
<i>Hydroporus planus</i> (Fabricius, 1781)	2 <sup>a</sup>	0.01 (0.00–0.11)	<0.01 (0.00–0.02)	–
<i>Enochrus bicolor</i> (Fabricius, 1792)	4 <sup>a</sup>	<0.01 (0.00–0.06)	–	–
<b>Diptera</b>				
<i>Culicoides</i> sp.	2 <sup>a</sup>	<0.01 (0.00–0.06)	<0.01 (0.00–0.02)	<0.01 (0.00–0.04)
<i>Halocladus varians</i> (Staeger, 1839)	2 <sup>a</sup>	0.13 (0.00–2.70)	0.01 (0.00–0.15)	<0.01 (0.00–0.05)
<i>Chironomus gr. salinarius</i> Kieffer, 1915	2 <sup>a</sup>	2.29 (0.00–8.62)	0.35 (0.00–1.82)	0.05 (0.00–0.82)
Dolichopodidae undet.	3 <sup>b</sup>	<0.01 (0.00–0.02)	<0.01 (0.00–0.02)	<0.01 (0.00–0.04)
Chloropidae undet.	3 <sup>c</sup>	–	<0.01 (0.00–0.04)	<0.01 (0.00–0.02)
<i>Ephydra</i> sp.	4 <sup>d</sup>	0.04 (0.00–0.86)	<0.01 (0.00–0.04)	–
<i>Scatella</i> sp1	4 <sup>d</sup>	<0.01 (0.00–0.06)	–	0.01 (0.00–0.20)
<i>Scatella</i> sp2	4 <sup>d</sup>	–	–	<0.01 (0.00–0.02)
Richness without rare taxa		13	15	17
Total richness		(18)	(17)	(21)

Richness without rare taxa (occurrence <1%) and, in brackets, total richness are also shown. References are indicated by superscript: (a) Wiggins et al., 1980; (b) Tachet et al., 2002; (c) Takeda & Nagata, 1998 and (d) Herbst, 1999

was checked through comparisons of changes in deviance and degrees of freedom with a Chi-square distribution (Crawley, 2002). GLM analyses were carried out with S-PLUS 2000.

### Species responses

Generalized Additive Models (GAMs) were used to analyse to which extent patterns in functional response groups were determined by the existence of succession patterns related to life-strategies (functional response groups), or to environmental variability summarized by water level fluctuations. We used the log link function and Poisson distribution as error. Two degrees of freedom were specified to obtain a low complexity model (i.e. a more general pattern). A stepwise selection using the Akaike Information Criterion (AIC) was used to select the best model with increasing complexity (degrees of freedom equal to 1 and 2). GAM analyses were performed with CANOCO 4.5 (ter Braak & Šmilauer, 2002).

## Results

### Environmental variability

During the study, semi-permanent ponds dried out completely (Fig. 2). Thus, temporary and semi-permanent ponds had similar hydroperiod length. There were no significant differences in water level ( $F_{2,100} = 1.04$ ;  $P = 0.357$ ) and temperature values

( $F_{2,100} = 7.06$ ;  $P = 0.407$ ) among different pond types. In contrast, significant differences were found in conductivity values ( $F_{2,100} = 18.27$ ;  $P < 0.001$ ): temporary ponds had higher values than semi-permanent ponds, and semi-permanent ponds had higher values than permanent ponds (Table 1, Fig. 3).

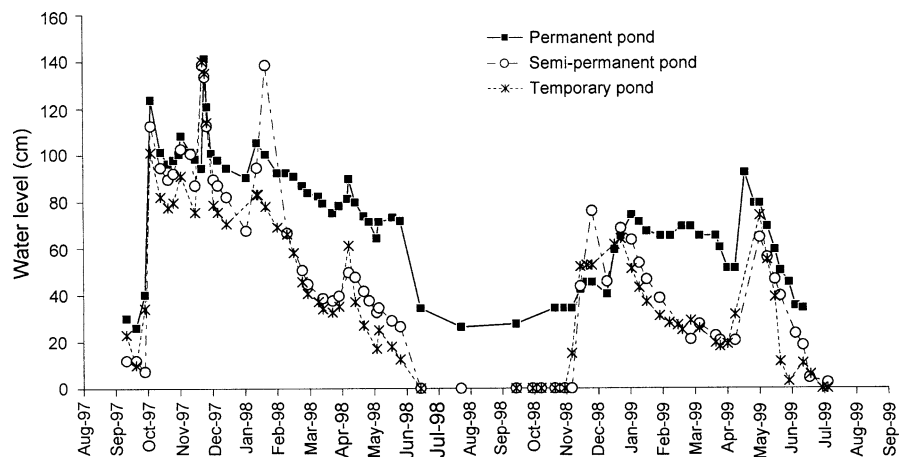
Significant temporal variability was detected for water level, conductivity and temperature values. At intra-annual level (between phases), significant lower water level ( $F_{1,100} = 8.78$ ;  $P < 0.05$ ) and higher temperature values ( $F_{1,100} = 172.92$ ;  $P < 0.001$ ) were observed during the drying phase (Fig. 3). At inter-annual level (between hydroperiods), significant differences were also found. Water level values ( $F_{1,100} = 14.79$ ;  $P < 0.001$ ) and temperature values ( $F_{1,100} = 16.19$ ;  $P < 0.05$ ) were significantly higher during the first hydroperiod. However, the temporal variability of conductivity values was more complex, due to the significant interactions found between phases and hydroperiods ( $F_{1,100} = 18.46$ ;  $P < 0.001$ ). Thus, while conductivity values remained similar during the flooding phases for both hydroperiods, an increase in conductivity values was observed during the drying phase only in the second hydroperiod (Fig. 3).

### Pond type and temporal variability

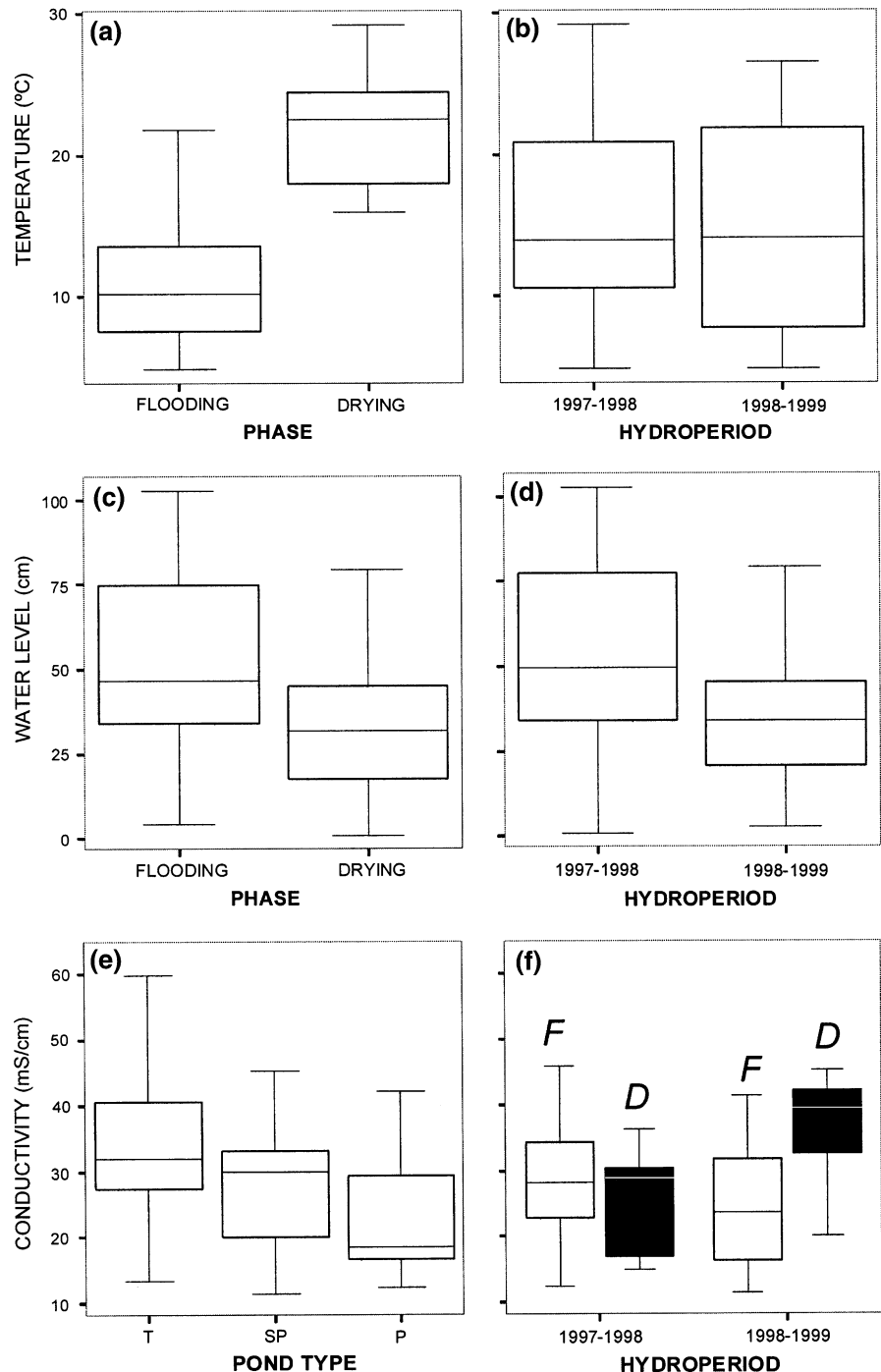
#### Taxonomic approach

Eight of the 21 most frequent taxa (occurrence  $>1$ ) were found in all pond types (Table 3). In contrast,

**Fig. 2** Water level fluctuation (cm) in the three pond types. The values correspond to examples of each pond type: pond 1 for temporary, pond 4 for semi-permanent and pond 5 for permanent pond



**Fig. 3** Box plots showing significant differences of environmental variables among factors after a MANOVA. (a) Temperature vs. phases, (b) Temperature vs. hydroperiod, (c) Water level vs. phases, (d) Water level vs. hydroperiod, (e) Conductivity vs. pond type (T—temporary, SP—semi-permanent, P—permanent waters) and (f) Conductivity vs. phases (*F*—flooding, *D*—drying) within each hydroperiod



only 5 taxa were exclusive of one pond type: 1 taxa was exclusive of temporary ponds (the coleopteran *Enochrus bicolor*), and the other 4 taxa were exclusive of permanent ponds (the polychaeta *Streblospio shrubsolii*, the oligochaeta *Nais* sp., the amphipod

*Leptocheirus pilosus* and the dipteran *Scatella* sp2). No taxon was found to be exclusive of semi-permanent ponds. Species richness was similar among pond types, for both frequent and all taxa (Table 3). Additionally, no significant relationship was found

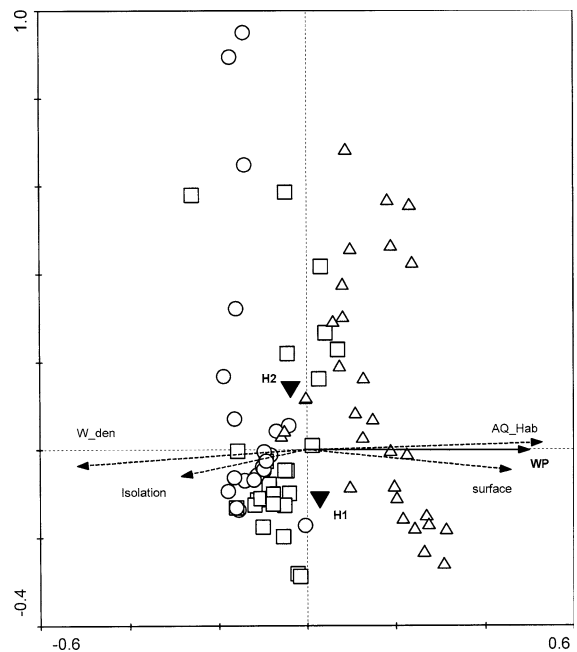
between hydroperiod length and species richness. Similarly, no significant relationship was found between pond surface and species richness.

Twenty-one taxa (those with occurrence >1) were used in the CCA. The first two axes of the CCA explained 16.2% of the total variability observed in the species dataset. The first axis explained 12.4% of the total variance, while the second axis explained 3.8% of the total variance. The explanatory variable which fitted best the species variability was the water permanence which is a characteristic of the different pond types (conditional effect = 0.46;  $F = 11.94$ ;  $P = 0.001$ ). Hydroperiod was the second variable which also significantly fitted the variability observed in the species data set (conditional effect = 0.14;  $F = 3.68$ ;  $P = 0.001$ ), whereas phases did not improve significantly the explanation of the species variability, as it is shown by the non-significant result of the permutation test (conditional effect = 0.04;  $F = 1.05$ ;  $P = 0.407$ ). Samples of permanent ponds were mostly found in positive coordinates of the first axis, while samples of temporary and semi-permanent ponds were found in negative coordinates (Fig. 4). The relation among landscape variables and water permanence is also shown in Fig. 4. Differences between hydroperiods (inter-annual variability) were related to the second canonical axis. Thus, the centroid for the second hydroperiod is found in positive coordinates of this axis, while the centroid for the first hydroperiod is found in negative coordinates (Fig. 4).

#### Functional approach

Species of the five functional groups were observed during the study, but some groups were better represented than others. Groups 2 and 5 had higher abundances (mean  $\pm$  standard deviation:  $0.904 \pm 1.899$  and  $0.464 \pm 1.045$  ind  $\cdot 10$  cm<sup>-2</sup>, respectively), and different species richness, with higher values in group 5 (4 and 8 taxa, respectively). Groups 1 and 4 had lower abundances (mean  $\pm$  standard deviation:  $0.007 \pm 0.032$  and  $0.018 \pm 0.101$  ind  $\cdot 10$  cm<sup>-2</sup>, respectively), and similar richness (3 and 4 taxa, respectively). Finally, group 3 had the lowest abundance (mean  $\pm$  standard deviation:  $0.003 \pm 0.008$  ind  $\cdot 10$  cm<sup>-2</sup>) and richness (2 taxa).

Significant differences among functional groups, and pond type and temporal (phase and hydroperiod)



**Fig. 4** Weighted average scores of the samples for the different pond types (up-triangles stand for permanent ponds; squares for semi-permanent ponds and circles for temporary ponds) in the first two canonical axes. Only variables with significant relation to species dataset are shown in bold: down-triangles showed centroid position for the hydroperiods (H1: 1997–1998; H2: 1998–1999), solid arrow indicates water permanence (WP). Dashed arrows indicate the position of landscape variables included as supplementary variables: isolation (isolation), Waterbodies density (W\_den), surface (surface), predominance of aquatic habitat (AQ\_Hab)

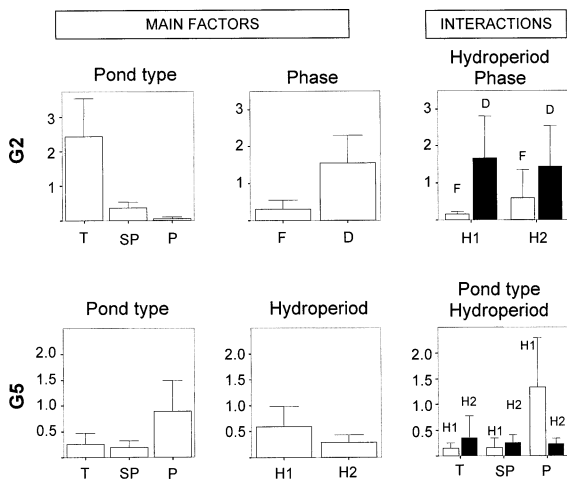
factors were only found for those groups that had higher abundances (Table 4). Pond type explained the highest proportion of variation in both groups (48.8% and 17.4% for group 2 and 5, respectively). However, they showed a different pattern: while group 2 had higher abundances in temporary ponds, group 5 had higher abundances in permanent ponds (Fig. 5). Differences in temporal variability were also found, but they were less important (less proportion of variation). Group 2 showed significant differences between phases (accounting for 9.5% of the variation), and group 5 had significant differences between hydroperiods (accounting for 4.5% of the variation; Table 4). Group 2 had higher abundances during the drying phase than the flooding one, and group 5 had higher abundances during the first hydroperiod (Fig. 5). Significant interactions were found between phase and hydroperiod (accounting for 6% of the variation) for group 2, and between hydroperiod and



**Table 4** Results of the GLM on the influence of phase (flooding, drying), hydroperiod (1997–1998, 1998–1999) and pond type (temporary, semi-permanent, permanent ponds) in the abundance of each life-strategy group studied

Factor	df	G1	G2	G3	G4	G5
Phase (P)	1	0.2	<b>9.5***</b>	4.4	6.8	0.7
Hydroperiod (H)	1	8.7	0.4	0.1	11.6	<b>4.5*</b>
Pond type (Pt)	2	6.7	<b>48.8***</b>	6.3	16.5	<b>17.4**</b>
P × H	1	1.2	<b>6.0**</b>	1.4	0.0	1.5
P × Pt	2	0.0	1.3	5.8	18.3	1.7
H × Pt	2	10.1	2.9	2.4	2.5	<b>8.3*</b>
P × H × Pt	2	1.5	0.9	9.3	0.0	2.3
Error	74					
Total % deviance		28.4	69.7	29.6	55.8	36.4
Dispersion parameter		0.001	0.833	0.010	0.058	0.800

Values are the percentage of the total deviance explained by each factor. Significant results appear in bold. Asterisks show the significance level (\* $P < 0.05$ , \*\* $P < 0.001$ , \*\*\* $P < 0.0001$ )



**Fig. 5** Abundances of life-strategy groups 2 and 5 related to their significant factors after a GLM analysis: pond types (T: temporary, SP: semi-permanent and P: permanent ponds), hydroperiod phases (F: flooding and D: drying phases) and hydroperiod (H1: 1997–1998 and H2: 1998–1999). Significant interactions are also shown: in group 2, white bars correspond to flooding phase and black bars correspond to drying phase; in group 5, white bars correspond to the first hydroperiod (1997–1998) and black bars correspond to the second hydroperiod (1998–1999)

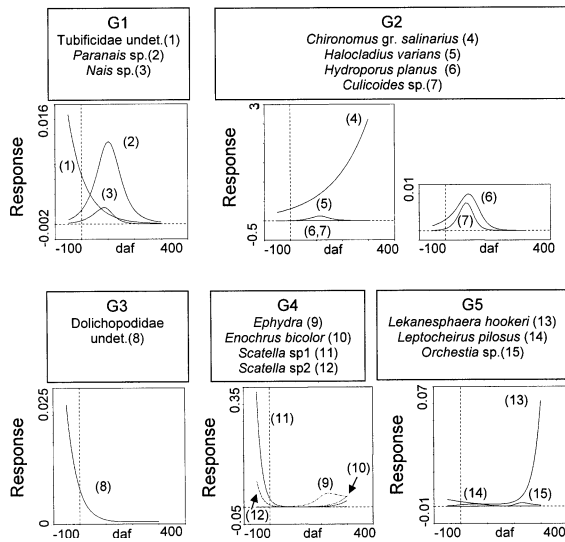
pond type (accounting for 8.3% of the variation) for group 5. In this sense, the differences observed between the two phases during the second hydroperiod in the abundances of group 2 were lower than between the two phases of the first hydroperiod (Fig. 5). Group 5 showed differences between hydroperiods among pond types: for more temporary

waters (temporary and semi-permanent ponds), group 5 was more abundant during the second hydroperiod, while the opposite pattern was observed in permanent ponds, where it was more abundant during the first hydroperiod (Fig. 5).

### Species responses

All functional groups had species that presented a significant response to the GAMs (Figs. 6, 7). The species responses to time (days after flooding) were not similar within each functional group (Fig. 6). Thus, there was not a similar succession pattern for taxa within the same functional group.

In contrast, the GAM results for the first four functional groups showed that species of the same functional group had similar responses to water level variation (Fig. 7). Therefore, taxa from group 1 had a unimodal response to water level variation, and their maximum abundances were expected at high water level values. Taxa of group 2 had their maximum abundances in low water level values, but not as low as those observed to be expected for taxa of groups 3 and 4. Finally, different taxa in group 5 had differing response curves. For example, the snail *Hydrobia acuta* showed a unimodal response with higher abundances at intermediate values of water level, while the amphipod *Corophium orientale* reached its maximum abundance at the highest water level values.

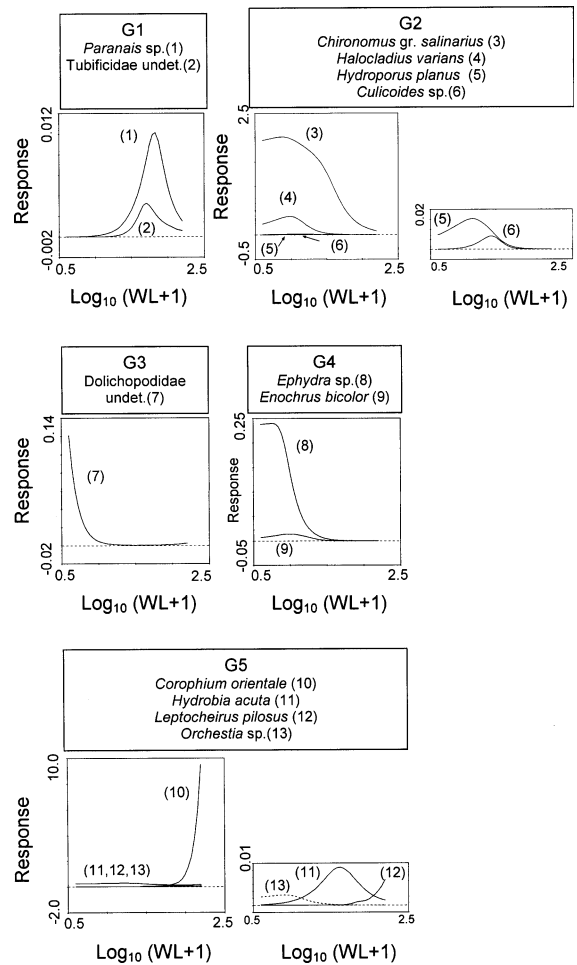


**Fig. 6** Species responses to time (days after flooding (daf)) fitted with the Generalized Additive Model

## Discussion

The functional and the taxonomical approaches showed similar results in relation to pond types, showing that permanent ponds had a different benthic composition than more temporary ones. Previous studies developed in the Empordà salt marshes already noted the importance of water permanence for benthic assemblages (Gascón et al., 2005). Similarly, it has been shown that water permanence also plays an important role in the structure and composition of benthic assemblages in other aquatic systems (Schneider, 1999; Schwartz & Jenkins, 2000). However, as water permanence covaried with other pond characteristics, it is not possible to ascertain that water permanence was only responsible to the observed differences.

Life histories of species have been frequently related to environmental characteristics in both lentic and lotic systems (e.g. Williams, 1985; Richards et al., 1997). In Empordà salt marshes, life history traits determine species preferences for ponds with a certain water permanence. Thus, organisms adapted to avoid desiccation, with active dispersion and needing water for reproduction (group 2), seemed to select temporary ponds, since they always present higher abundances in these environments. In contrast, taxa which are less adapted to desiccation (group 5), without active dispersion and lacking strategies to



**Fig. 7** Species responses to water level (WL) fitted with the Generalized Additive Model

endure dry periods, select permanent ponds to ensure their survival. In this sense, Wiggins et al. (1980) described that taxa belonging to group 2 (mainly chironomids, which were the most abundant taxa of this group in our study site) can successfully inhabit ponds which start their inundation in autumn and remain with water until summer, since these organisms spend the winter under water, and hence the winter stress is reduced. Wiggins et al. (1980) also described that in fluctuating waters which never dry out, species of all functional response groups are expected to be found. However, in Empordà salt marshes group 5 species were the dominant taxa in permanent water ponds.

The lack of differences between semi-permanent and temporary waters could be explained by the fact

that during the study these ponds had a similar hydroperiod length. This is in accordance with other studies, which have shown that wetland hydroperiod length influences invertebrate community composition and structure (e.g. Schneider & Frost, 1996; Wellborn et al., 1996). Other authors pointed out the effects of hydroperiod length on species richness (e.g. Brooks, 2000; Tarr et al., 2005), but our study showed no such relation. Furthermore, the lack of a species richness-area relationship could be explained by the dry out constraint, since in our study site, short hydroperiod length also occurred in large ponds (e.g. basin 4). This is in agreement with other studies where water permanence has been shown to be more important for species richness than pond surface area (e.g. Schneider & Frost, 1996; Della Bella et al., 2005), although results stating otherwise also exist (March & Bass, 1995).

Inter-annual variability was observed using both approaches. However, only one functional group, comprising organisms without any particular adaptation to survive or avoid desiccation (group 5), presented significant differences between hydroperiods. This was even clearer in permanent ponds, which have a characteristic benthic community not found in more stressed environmental conditions (Gascón et al., 2005). Group 5 had lower abundance during the second hydroperiod which was characterized by more extreme environmental conditions (the temperature during the flooding phase was significantly cooler; and water level values were significantly lower during the second hydroperiod, indicating less water inputs). Thus, the decrease in abundance of group 5 may respond to the higher environmental stress occurring during the second hydroperiod.

Non-taxonomic aggregations based on life history are a better approach to determine seasonal variability, since seasonal patterns of occurrence and abundance in invertebrates depend on their life history and behavioural characteristics (Wolda, 1988; Bêche et al., 2006). Supporting this idea, we observed intra-annual variability using functional groups, whereas differences were not observed using a taxonomical approach. However, this temporal pattern seems to be more related to water level fluctuations than to a succession pattern. Bazzanti et al. (1996) found the highest importance of group 2 taxa at lower water level values. Similarly, during our study group 2 taxa had significantly higher

abundances during the drying phase, which was characterized by significantly lower water level values.

Macroinvertebrate assemblages in Empordà wetlands were highly dominated by few species, which is a typical situation in Mediterranean salt marshes due to their marked daily and seasonal variations in physical and chemical parameters (Guelorget & Perthuisot, 1983; Victor & Victor, 1997; Mistri et al., 2001; Reizopoulou & Nicolaidou, 2004; Álvarez-Cobelas et al., 2005). Thus, our results might be conditioned by particular life history traits of the dominant species. This possible artefact may be easily discarded, since similar response patterns of species within each functional group were observed in four of the five life-strategy groups studied. Only group 5 presented different responses for each species. This group is composed of species with a complete dependence on water permanence. Thus, their different responses could be explained by their preference for other factors which covary with water level, such as water conductivity (Pearson correlation;  $r = -0.249$ ,  $P < 0.05$ ) or by a different degree of desiccation tolerance.

On the other hand, the functional response groups 1, 2, 3 and 4 described by Wiggins et al. (1980) were created to group organisms with similar life history traits, but all share some independence of water presence, as they are adapted to avoid or survive desiccation. Hence, the response curves indicate their preference for a specific water level. In this sense, groups with active dispersion colonize faster new ponds and can remain in the pond until the end of the wet phase (Barnes, 1983; Ribera et al., 1994). Our results support this idea, since all groups with active dispersion are expected to be abundant with low water levels, and these levels occurred at the start and end of the hydroperiods. Moreover, our study revealed that organisms adapted to avoid desiccation, with active dispersion and needing water for reproduction (group 2) preferred temporary ponds, since they always presented higher abundances in this environment.

In summary, the abundance of species with a particular life-strategy was influenced by environmental variability such as water fluctuations. Moreover, species without any adaptation to survive or avoid desiccation did not show similar responses to water fluctuations. Thus, the inter-annual differences

observed in this functional response group are more determined by the life-strategy of the dominant taxon (the amphipod *Corophium orientale*) than by a general functional pattern extended to the rest of the species of this group.

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