

Crustacean and aquatic insect assemblages in the Mediterranean coastal ecosystems of Empordà wetlands (NE Iberian peninsula)

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ABSTRACT

Crustacean and aquatic insect assemblages in the Mediterranean coastal ecosystems of Empordà wetlands (NE Iberian peninsula)

Coastal wetlands are characterized by high biodiversity, which is one of the main criteria considered when establishing protection policies or when proposing adequate management actions. In this study, the crustacean and aquatic insect composition of the Empordà wetlands is described. These two faunal groups contribute highly to the total biodiversity in these wetlands but are seldom considered when managing natural areas. A selection (84 sampling points) of all water body types present in the Empordà wetlands were sampled monthly (surber and dip net with a 250 µm mesh). Sampling was carried out during 3 surveys (1991-92, 1996-97 and 1999-2000). A rich fauna of 125 crustacean and 295 aquatic insect taxa was identified. We characterized each water body type using the most abundant species and the relative species richness of the taxonomic groups. A classification of the water body types, according to similarity between inventories, groups the brackish and hyperhaline systems in one cluster and the various freshwater systems in another one. Among freshwater systems, lotic waters and freshwater wetlands have a high similarity, whereas rice fields and freshwater springs have a low similarity.

Key words: Mediterranean coastal wetlands, water body types, composition, species richness, crustaceans, aquatic insects.

RESUMEN

Comunidades de crustáceos e insectos acuáticos en los ecosistemas costeros mediterráneos de los Aiguamolls del Empordà (NE de la península Ibérica)

Los humedales costeros se caracterizan por una alta biodiversidad, que es uno de los principales criterios considerados al establecer políticas de protección o al proponer acciones de gestión adecuada. En este estudio se describe la composición de crustáceos e insectos acuáticos de los aiguamolls del Empordà. Estos dos grupos faunísticos contribuyen de forma importante al total de la biodiversidad en los humedales, pero raramente se tienen en consideración al gestionar las áreas naturales. Se muestreó mensualmente una selección (84 puntos de muestreo) de todas las tipologías de masas de agua presentes en los aiguamolls de l'Empordà mediante redes surber y salabres de poro de malla de 250 µm. El muestreo se llevó a cabo durante tres campañas (1991-92, 1996-97 y 1999-2000). Se identificó una riqueza faunística de 125 taxones de crustáceos y 295 taxones de insectos acuáticos. Cada tipología de masa de agua se caracterizó utilizando las especies más abundantes y la riqueza específica de los grupos faunísticos. La clasificación de las tipologías de masas de agua, según la similaridad entre inventarios faunísticos, agrupó los sistemas salobres y hiperhalinos en un grupo. Entre los sistemas de agua dulce, los sistemas lóticos y los humedales de agua dulce presentaron una alta similaridad, mientras que los arrozales y las surgencias de agua dulce mostraron una baja similaridad.

Palabras clave: Humedales costeros mediterráneos, tipología de masas de agua, composición, riqueza específica, crustáceos, insectos acuáticos.

INTRODUCTION

Wetlands, marshes, ponds and other permanent or temporary shallow waters have increasingly attracted conservation biologists during the last years. Several studies underline their ecological importance indicating that they not only contain species or environments that are becoming rarer, but also have a high specific richness (Gudicelli & Thiéry, 1998; Gopal & Junk, 2000; Boix *et al.*, 2001). Despite the fact that their importance has been recognized in the European Directive that considers them as priority habitats (92/43/CEE), these ecosystems are still under the threat of degradation and loss (Tagliapietra *et al.*, 1998; Brown, 1998; Mistri *et al.*, 2000; Gibbs, 2000). Biodiversity is one of the main criteria used when elaborating wetland protection policies (Ramsar Convention Bureau, 1992). Invertebrates are the most important proportion of faunal richness, but the knowledge of wetland aquatic invertebrate species composition is still relatively poor, and most management efforts today are being focused on the conservation of a small number of species, mainly water birds (Britton, 1982; Mocci, 1983).

The aim of this paper is to present current knowledge on the composition of crustaceans and aquatic insects of different water body types in a group of Mediterranean coastal wetlands (Empordà wetlands), located in the NE Iberian Peninsula. Empordà wetlands present a wide range of environmental types, due to the existence of high gradients of salinity, water permanence, and nutrients.

STUDY AREA

The Empordà wetlands are located in the north-eastern part of the Iberian Peninsula. They are situated in a deltaic plain originated by quaternary depositions from the Muga, Fluvia, Ter, and Daró rivers. The Montgrí massif divides the deltaic plain in two halves, which are connected inland (Fig. 1). The wetlands in the northern part of the deltaic plain are larger and protected by the Empordà Wetlands Natural Park (4731 ha).

Conversely, the protection status of the wetlands of the southern part of the plain is weaker, and restricted to the larger lagoons. The hydrology of the littoral wetlands is influenced by the sea, and is characterised by sudden and irregular flooding (caused by sea storms, rainfall and inputs from rivers or channels), followed by dry periods, when most of the basins become isolated and gradually dry out (Bach, 1990; Quintana, 2002). The hydrology of the inland wetlands is influenced by rainfall and river inputs (superficial or groundwater), and marine influence is scarce or nonexistent (Trobajo *et al.*, 2002).

METHODS

Quantitative sampling was carried out monthly during three different surveys (1991-92, 1996-97, 1999-2000), each of them including different water bodies. For detailed information about sampling surveys see Gifre *et al.* (1996), Sala *et al.* (1998) and Quintana *et al.* (2000). Besides these surveys, qualitative samplings have been carried out during the last fifteen years, in order to detect rare species. All sampled water bodies (84 sampling points) are shown in figure 1 Additional qualitative data were obtained from the literature.

Sampling in lentic ecosystems was conducted using a dip-net 20 cm in diameter and 250 µm mesh size. In each water body 20 dip-net sweeps (sweeps were done by pushes in a rapid sequence) per visit were carried out. In lotic ecosystems, sampling was done using the dip-net and a surber net with a 30 × 30 cm opening and 1 mm mesh size.

All water bodies were grouped into the different environmental types found in the study area, following Trobajo *et al.* (2002). This classification is based on the physical, chemical and biological characteristics of 22 water bodies from the study area. Because this classification did not encompass all types of water bodies in the area, we included 4 more types (lotic waters, ephemeral brackish wetlands, ephemeral freshwater wetlands, and rice fields). Some of the physical, chemical, and biological characteristics of each water body type are shown in Table 1.

Table 1. Physical, chemical, and biological characteristics of each water body type of the Empordà wetlands. Mean values in bold and coefficients of variation in italics. Legend: HHW: hyperhaline wetlands; BW: brackish wetlands; HTW: hypertrophic freshwater wetlands; MFW: meso-eutrophic freshwater wetlands; FS: freshwater springs; LW: lotic waters; EBW: ephemeral brackish wetlands; EFW: ephemeral freshwater wetlands; RF: rice fields; —: no data available. *Características físicas, químicas y biológicas de las diferentes tipologías de masas de agua de los aiguamolls del Empordà. Valores medios en negrita y coeficientes de variación en cursiva. Leyenda: HHW: humedales hiperhalinos; BW: humedales salobres; HTW: humedales hipertróficos de agua dulce; MFW: humedales meso-eutróficos de agua dulce; FS: surgencias; LW: sistemas lóticos; EBW: humedales salobres efímeros; EFW: humedales de agua dulce efímeros; RF: arrozales; —: datos no disponibles.*

	Waterbody types									
	HHW	BW	HTW	MFW	FS	LW	EBW	EFW	RF	
Approximated hydroperiod length (months·year ⁻¹)	12	7-12	12	7-12	12	12	<2	<2	7	
Conductivity (mS·cm ⁻¹)	49.6 48	18.9 66	1.3 136	3.9 179	1.1 99	0.8 76	6.9 96	1.4 39	1.2 39	
Chlorophyll-a (μg·L ⁻¹)	21.5 186	20.9 183	12.1 107	14.3 150	18.1 143	6.5 103	—	—	—	
Ammonium (μM)	9.1 196	4.3 260	34.1 109	8.6 245	2.6 351	29.8 214	—	—	—	
Nitrite (μM)	0.7 569	0.5 234	6.9 156	2.0 289	5.5 148	10.9 193	—	—	—	
Nitrate (μM)	2.1 253	11.1 312	109.9 58	53.7 151	705.9 25	205.6 100	—	—	—	
Phosphate (μM)	4.3 298	3.7 253	5.8 173	2.9 174	0.93 368	8.5 159	—	—	—	
Total N (μM)	219.3 160	164.8 94	212.7 49	125.0 75	851.9 27	—	—	—	—	
Total P (μM)	10.5 248	9.2 213	11.0 83	6.1 121	2.0 197	—	—	—	—	

RESULTS AND DISCUSSION

Faunal composition of the Empordà wetlands

A remarkable rich fauna including 420 taxa was found in the studied area, 125 of which were crustaceans and 295 aquatic insects (Table 2). Within the crustaceans, Copepoda and Branchiopoda were the best represented classes (41 and 42 taxa respectively), followed by Ostracoda (24 taxa) and Malacostraca (18 taxa). Within the aquatic insects, Coleoptera (129 taxa), Diptera (94 taxa), Odonata (36 taxa), and Heteroptera (25 taxa) were the richest orders, together representing 97 % of the insect taxa

found in the area. Following these orders were Ephemeroptera (7 taxa), Trichoptera (2 taxa), Neuroptera (1 taxon), and Plecoptera (1 taxon). A reverse pattern is observed when abundance is taken into account, crustaceans (mainly Branchiopoda, Copepoda and Ostracoda) being far more abundant than aquatic insects. Within the insects, Diptera and some species of Ephemeroptera and Odonata were the most abundant taxa in the studied area.

Several crustacean species collected in the Empordà wetlands are rare in the Iberian Peninsula. This is the case of the exotic cladoceran *Wlassicsia pannonica*, which has only been captured in the rice fields of Badajoz (M. Alonso,

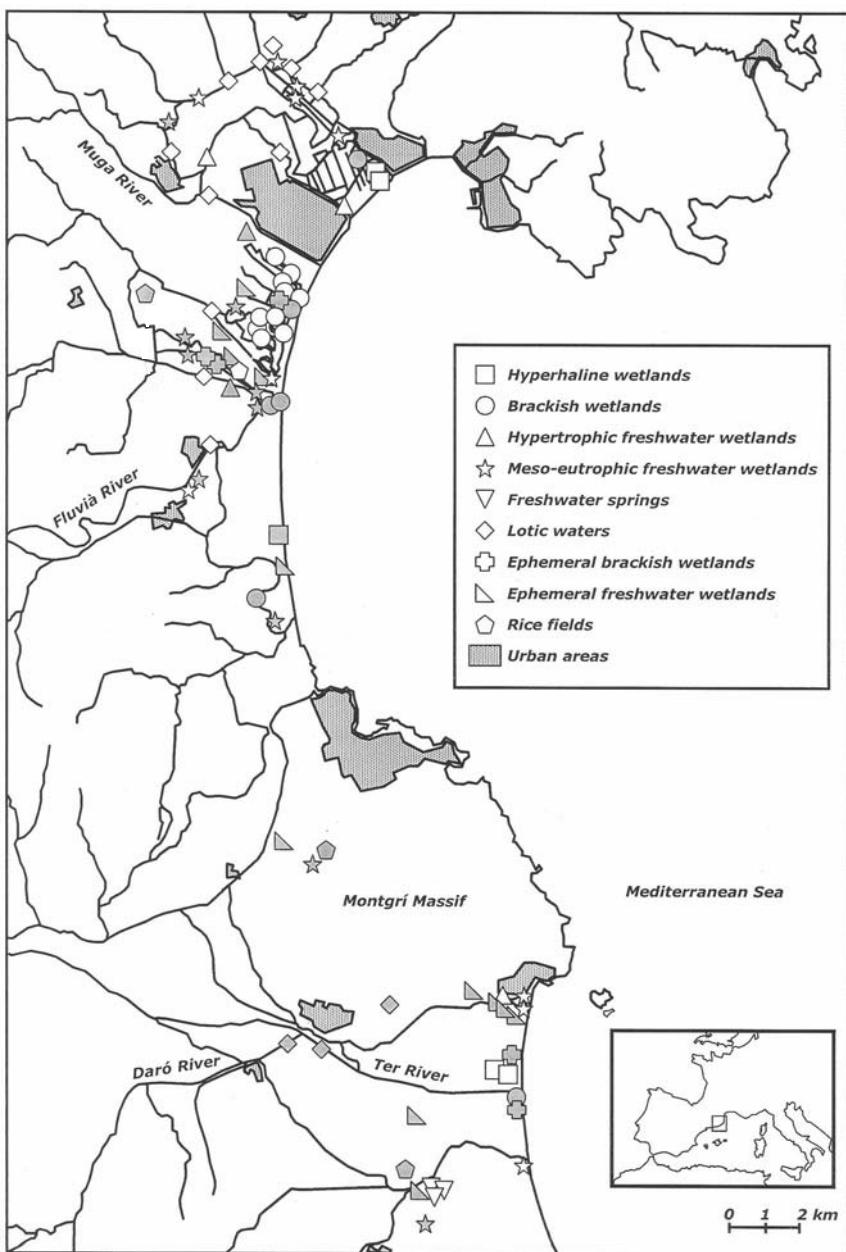


Figure 1. Map of the study with the location of the 84 water bodies studied. Shaded symbols correspond to qualitative samples, whereas open symbols correspond to quantitative samples. *Mapa del área de estudio con la localización de las 84 masas de agua estudiadas. Los símbolos grises corresponden a muestras cualitativas, mientras que los símbolos blancos corresponden a muestras cuantitativas.*

pers. com.). Similarly, several ostracod species such as *Fabaeformiscandona fabaeformis*, *Potamocypris variegata*, *Limnocythere inopinata*, *No-todromas persica*, and *Bradleystrandesia reticu-lata*, are barely known in the Iberian Peninsula

(Baltanás *et al.*, 1996), and are first citations for the region of Catalunya. The calanoid *Eurytemora velox* has its southern limit of distribution in the Empordà wetlands. Among the insects, some coleopteran species have a special inte-

rest, such as *Cyphon laevipennis*, which is cited for the first time in the Iberian Peninsula, although it is abundant in common reeds in the Empordà wetlands. *Ochthebius gr. maculatus* and *Tanysphyrus lemmnae* are first cited for Catalonia. The former species is frequently observed in salt marshes, while the latter one is especially abundant in rice fields. The coleopterans *Georissus* sp., *Megasternum* sp., *Helophorus rufipes*, *Cymbiodita marginella*, and *Cercyon terminatus* are rarely found in the Iberian Peninsula. Other insects found in our study are also rare, such as the heteropterans *Gerris asper* (first citation in Catalonia), *Sigara selecta*, and *Mesovelia vittigera*. The coleopteran *Cercyon* sp.1 seems to be a species not included in the checklist of the Iberian water beetles (Ribera *et al.*, 1998) (C. Hernando, *pers. com.*).

The number of first faunal citations obtained in this initial attempt to describe the invertebrate biodiversity of Empordà wetlands, evidences the lack of information regarding invertebrate distribution in the area. This makes the development of conservation strategies to avoid biodiversity loss a difficult task. Although some proposals exist, they consider only a specific group such as coleopterans. In one of these proposals (Ribera, 2000), *Stenelmis consobrina* appears as a species in need of protection, and several other coleopterans (*Chasmogenus livornicus*, *Graphoderus cinereus*, *Hydatinicus seminiger*, *Hygrotus parallelogrammus*, *Ilybius quadriguttatus*, *Helophorus illustris*, *Cymbiodyta marginella* and *Hydrochara caraboides*) are shown as having few known populations in the Iberian Peninsula.

A revision of the material during this study has also detected some misidentifications. This is the case of *Heterocypris barbara*, cited in Gifre *et al.* (2002), which corresponds to juvenile *H. incongruens*. Similarly, *Mesochra rapiens*, cited in Appendix II in Martinoy *et al.* (2004), corresponds to *M. heldti*, whereas *Upogebia tipica* and *Palaemon elegans*, which were cited by Vila *et al.* (1989), correspond to *U. pusilla* and *P. adpersus*, respectively. Finally, *Haliphus ruficollis*, found by Lagar (1968), was attributed to *Haliphus heydeni* by Rico *et al.* (1990).

Invertebrate composition of the different water body types

Hyperhaline wetlands (HHW) were dominated in terms of richness by microcrustacean taxa. The best represented species (higher abundances) were the calanoids *Eurytemora velox* and *Calanipeda aquaedulcis*, while cladocerans were very scarce. Coleoptera and Diptera had also high richness in this water body type. Coleoptera as *Nebrioporus ceresi*, *Ochthebius dentifer*, *Helophorus fulgidicollis*, *Berosus hispanicus*, and the Culicidae *Ochlerotatus detritus* were characteristic of this water body type (Fig. 2 and Table 2).

Brackish wetlands (BW) differ from hyperhaline ones in the higher richness of Malacostreca and Heteroptera found in them (Fig. 2). Opposite to HHW, brackish wetlands had a higher richness of insects due to the appearance of new taxa (such as ephemeropterans, trichopterans, and heteropterans). Moreover, some crustaceans found in the previous wetland type were also found in BW, but their relative importance was different (Table 2). Thus, in this water body type, high abundances of some copepods such as *Acanthocyclops* spp., *Cyclops* sp., *Thermocyclops dybowskii*, and *Cletocamptus confluens*, as well as some ostracods such as *Loxoconcha elliptica* and *Cypridopsis vidua* were characteristic. High abundances of cladocerans such as *Ceriodaphnia dubia* and *Daphnia pulicaria* were found coinciding with lower salinity values.

Basins with freshwater inputs of treated wastewater or agricultural origin (i.e., with high nutrient concentrations) were classified as hypertrophic freshwater wetlands (HTW). This type of wetland is characterised by an irregular water flux conditioned by human management. In such conditions, cladocerans had the highest richness (Fig. 2). As for abundance, some cyclopoids (*Eucyclops serrulatus* and *Macrocylops albidus*) and cladocerans (*Bosmina longirostris*), even benthic ones (*Tretocerphala ambigua*), were dominant. Insects were dominated by Chironomidae larvae (Table 2).

Freshwater wetlands (FW), with a less artificial flooding pattern, encompassed a heterogeneous group of basins (drainage channels, either inland

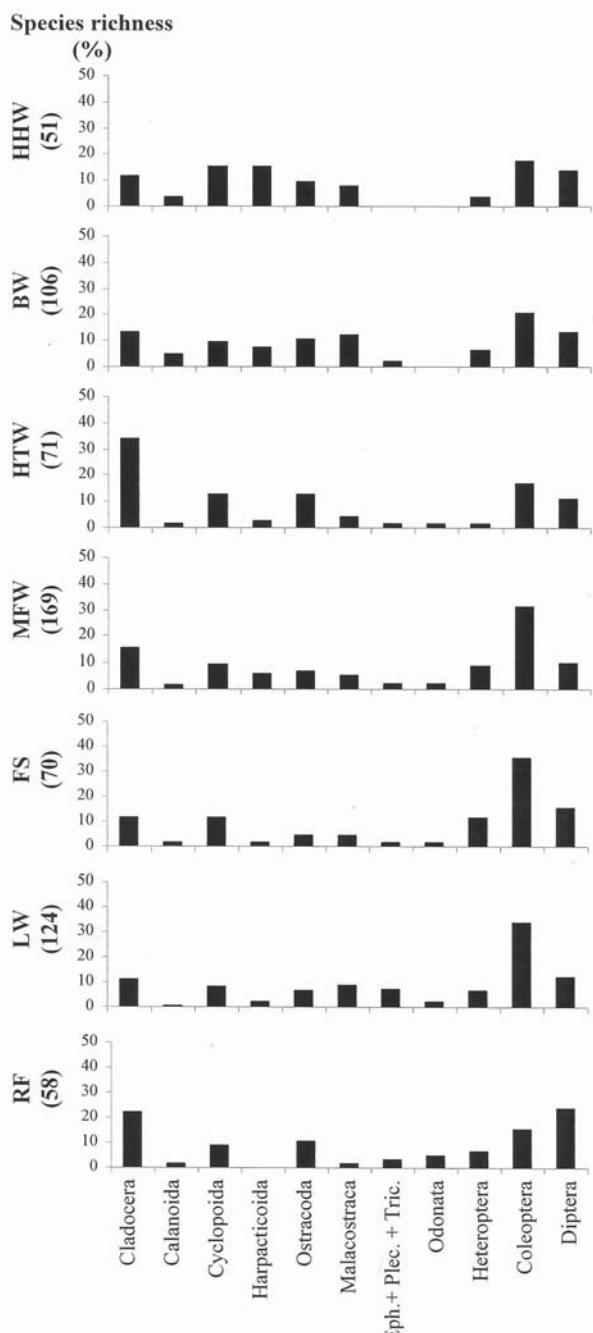


Figure 2. Taxonomic composition of each water body type. The relative species richness of each taxonomic group is shown. The figures in brackets indicate the total richness of each water body type. *Composición taxonómica de cada masa de agua. Se representa la riqueza específica relativa de cada grupo taxonómico. Los números entre paréntesis indican la riqueza total de cada tipo de masa de agua.*

or coastal freshwater basins, and alluvial basins) with some similarities: (1) low salinity values, although subjected to sporadic marine water inputs, and (2) relatively high concentrations of nutrients, but always lower than those reported in the hypertrophic freshwater wetlands. In these environments, the cyclopoid *Acanthocyclops* spp. was dominant during situations with high water turnover rate, while the calanoid *Calanipeda aquaedulcis* was dominant in confinement situations with low water inputs. Coleoptera was the group with the highest specific richness, *Ochthebius dilatatus* being the most abundant species (Fig. 2 and Table 2).

Freshwater springs (FS) were characterised by groundwater circulation with low phosphate concentrations, and small temperature and salinity oscillations. They also presented high densities of submerged macrophytes. As in the previous water body type (FW), Coleoptera was the richest taxonomic group (Fig. 2), *Hydroglyphus geminus* being the most abundant (Table 2). The lower taxonomic resolution used for non-biting midges (Chironomidae) in this water body type could explain, almost partially, the lower value of dipteran richness obtained. Regarding abundance, the microcrustacean assemblage was characterised by the cyclopoid *Eucyclops serrulatus* and the cladoceran *Chydorus sphaericus* (Table 2). Additionally, species generally associated with macrophytes were also found to be abundant (*Cypridopsis vidua* and *Pleuroxus aduncus*; Alonso, 1996; Meisch, 2000). The high abundance of some insects that were scarcer in other lentic systems, such as *Cloeon inscriptum*, *Naufragus maculatus* and *Anopheles atroparvus*, was also characteristic of this water body type.

Lotic waters (LW), included all types of running waters present in the study area, from channels, fluvial sites, and river mouths (which are characterized by an estuarine behaviour with slow water circulation) to temporary streams. Coleopterans had the highest richness in this water body type (Fig. 2), but the most abundant organisms were the cladoceran *Chydorus sphaericus*, followed by the copepod *Eucyclops serrulatus* and the non-biting midge *Polypedilum* sp. (Table 2).

No quantitative data were available for ephemeral wetlands, either brackish (EBW) or freshwater (EFW), and qualitative data were not obtained for all taxonomic groups, so their faunal composition cannot be correctly assessed. However, the presence of large branchiopods (*Branchipus schaefferi* and *Triops cancriformis*), both in fresh and brackish waters, was characteristic of these habitats. The other large branchiopod present in the studied area, *Chirocephalus diaphanus*, was only found in ephemeral freshwater wetlands. Note that mosquitoes had a high number of species in these water body types (Table 2). *Ochlerotatus caspius* and *Ochlerotatus detritus* were characteristic of brackish waters, while the remaining species were found in fresh waters.

In rice fields (RF) the most abundant taxa were cladocerans, *Moina macrocopus*, *Chydorus sphaericus* and the exotic *Wlassicsia pannonica* being particularly relevant (Table 2). Among the insects, two ephemeropteran species (*Caenis luctuosa* and *Cloeon inscriptum*) and

the biting midges (Ceratopogonidae) had high abundances. Species richness was dominated by cladocerans and dipterans (together representing approximately 50 % of total richness; Fig. 2).

Comparison of the assemblages observed in each water body type (Fig. 3) identifies salinity as the most important factor regulating species composition, as has been previously stated in several studies (Britton & Johnson, 1987; Timms, 1993; Cognetti & Maltagliati, 2000). Thus, the two water body types with higher salinities, brackish wetlands and hyperhaline wetlands, appear clearly separated from the rest of the water body types (Fig. 3). Among freshwater water body types, three of them (freshwater wetlands, lotic waters, and hypertrophic freshwater wetlands) show a high similarity, while freshwater springs and rice fields show a different composition. According to the position of the freshwater body types in the cluster, hypertrophy and water flux seem to be less important for assemblage composition than artificial water regimes and oligo-

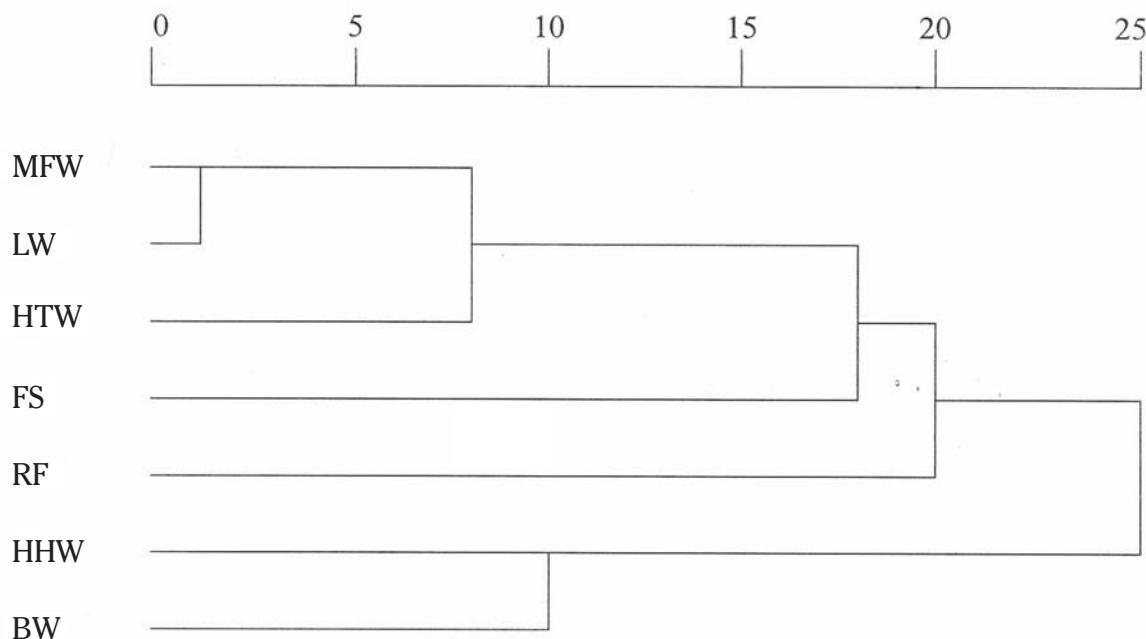


Figure 3. Dendrogram showing the classification of water body types by the similarity of their faunal inventories. Presence/Absence data, average linkage as a cluster method, and Dice measurement as similarity distance were used. *Dendrograma mostrando la clasificación de las tipologías de masas de agua según la similaridad de los inventarios faunísticos. Se utilizaron datos de presencia/ausencia, la vinculación inter-grupos como método de conglomeración, y la medida de Dice como distancia de similaridad.*

Table 2. Composition of crustaceans and aquatic insects in each water body type of the Empordà wetlands. Mean and, in brackets, maximum values of abundances (CPUE: individuals in one sweep). Legend: HHW: hyperhaline wetlands; BW: brackish wetlands; HTW: hypertrophic freshwater wetlands; MFW: meso-eutrophic freshwater wetlands; FS: freshwater springs; LW: lotic waters; EBW: ephemeral brackish wetlands; EFW: ephemeral freshwater wetlands; RF: rice fields; +: presence; (1): riparian pools; (2): coastal rock pools; (3): fluvial pools; (4): tree holes; (5): artificial pools; (6): captured by light tramp; A: Cuní, 1885; B: Lagar, 1968; C: Petitpierre, 1983; D: Sabater, 1986; E: Vila *et al.*, 1989; F: Jäch, 1993; G: Comín *et al.*, 1994; H: Marquès *et al.*, 1994; I: Rosales & Lafuente, 1993; J: Rosales, 1996; K: Ribera *et al.*, 1997; L: Fery & Brancucci, 1997; M: Pibernat & Abós, 2000; N: Garrigós, 2004. *Composición de crustáceos e insectos acuáticos en las diferentes tipologías de masas de agua de los aiguamolls del Empordà. Media y, entre paréntesis, máximos de abundancias (CPUE: individuos por barrido de salabre). Leyenda: HHW: humedales hiperhalinos; BW: humedales salobres; HTW: humedales hipertróficos de agua dulce; MFW: humedales meso-eutróficos de agua dulce; FS: surgencias; LW: sistemas lóticos; EBW: humedales salobres efímeros; EFW: humedales de agua dulce efímeros; RF: arrozales; +: presencia; (1): humedales riparios; (2): charcos supralitorales; (3): charcas aluviales; (4): agujeros de árboles; (5): charcas artificiales; (6): capturados con trampas de luz; A: Cuní, 1885; B: Lagar, 1968; C: Petitpierre, 1983; D: Sabater, 1986; E: Vila *et al.*, 1989; F: Jäch, 1993; G: Comín *et al.*, 1994; H: Marquès *et al.*, 1994; I: Rosales & Lafuente, 1993; J: Rosales, 1996; K: Ribera *et al.*, 1997; L: Fery & Brancucci, 1997; M: Pibernat & Abós, 2000; N: Garrigós, 2004.*

	HHW	BW	HTW	Waterbody types				RF
				MFW	FS	LW	EBW	
Copepoda								
<i>Ergasilus</i> sp.		+						
<i>Calanipeda aquaedulcis</i>	19.0 (387)	100.9 (2326)	0.0 (0.7)	23.6 (1325)		0.8 (18)	+	0.1 (2.1)
<i>Acartia bifilosa</i>		+						
<i>Acartia clausi</i>		+						
<i>Acartia margalefi</i> ^G								
<i>Eurytemora velox</i>	47.6 (1356)	39.6 (1098)		0.001 (0.1)	0.1 (3.7)		+	
<i>Mixodiaptomus kupelwieseri</i>		2.1 (104)		0.004 (0.3)				
<i>Halicyclops magniceps</i>	0.001 (0.001)	+						
<i>Halicyclops rotundipes</i>	0.5 (15)	0.1 (2.0)		0.01 (0.9)		0.0 (0.2)		
<i>Macrocyclops albidus</i>			6.6 (221)	0.2 (8.9)	2.4 (21)	0.3 (12)		0.2 (7.4)
<i>Eucyclops serrulatus</i>	0.0 (0.2)	0.6 (29)	13.8 (479)	0.6 (14)	22.2 (339)	1.9 (44)		
<i>Tropocyclops prasinus</i>			0.0 (0.5)	0.006 (0.4)	0.6 (8.2)	0.0 (0.8)		0.3 (7.0)
<i>Paracyclops affinis</i>	0.0 (0.1)				0.6 (16)			
<i>Paracyclops fimbriatus</i>			0.01 (0.2)	0.01 (1.1)	0.0 (1.4)	0.1 (3.2)		
<i>Ectocyclops phaleratus</i>			0.01 (0.1)	0.01 (0.6)		0.004 (0.1)		
<i>Cyclops</i> sp.	0.1 (1.9)	7.0 (100)		1.5 (84)		0.1 (2.4)		
<i>Megacyclops viridis</i>		0.0 (2.3)		0.02 (2.0)	7.1 (97)			
<i>Megacyclops gigas</i>				0.001 (0.1)				
<i>Acanthocyclops</i> spp.	0.1 (1.3)	41.4 (1677)	10.7 (103)	15.6 (451)	1.5 (32)	0.7 (6.7)		10.9 (84)
<i>Diacyclops bicuspidatus</i>	0.01 (0.4)	0.6 (51)		0.2 (15)		0.001 (0.1)	+	
<i>D. bicuspidatus odessanus</i>	2.3 (51)	41.4 (821)	0.003 (0.1)	0.6 (29)		0.002 (0.1)	+	
<i>Diacyclops bisetosus</i>		0.5 (20)		0.5 (28)			+	
<i>Microcyclops varicans</i>			0.01 (0.4)	0.02 (3.5)				0.02 (1.6)
<i>Microcyclops rubellus</i>				0.1 (8.3)	0.9 (24)			
<i>Thermocyclops dybowskii</i>		1.0 (51)	0.2 (7.7)	0.2 (24)				0.7 (24)
<i>Canuella perplexa</i>	1.8 (30)	0.4 (23)		0.004 (0.4)				
<i>Phyllognathopuss viguieri</i>				0.002 (0.3)				
<i>Harpacticus littoralis</i>	0.1 (1.4)			0.001 (0.1)		0.001 (0.1)		
<i>Tigriopus fulvus</i>	0.1 (2.9)			0.001 (0.2)				
<i>Tisbe longicornis</i>	0.4 (14)			0.001 (0.1)			+	
<i>Nitokra lacustris</i>	0.1 (2.4)	0.02 (1.5)		0.02 (2.6)				
<i>Nitokra spinipes</i>	0.1 (2.4)	0.001 (0.1)		0.02 (3.1)			+	
<i>Bryocamptus minutus</i>		+						
<i>Bryocamptus pygmaeus</i> ^D				0.002 (0.3)				
<i>Canthocamptus staphylinus</i>			0.003 (0.1)	0.03 (2.4)	1.8 (28)	0.02 (0.4)		
<i>Mesochra lilljeborgi</i>	+	+					+	
<i>Mesochra heldti</i>	1.5 (21)	+	0.5 (6.0)	0.1 (5.4)		0.05 (1.1)		
<i>Cletocamptus confluens</i>	0.002 (0.1)	0.5 (15)						
<i>Onychocamptus mohammed</i>								
<i>Paronychocamptus nanus</i>		+						
<i>Paraleptastacus spinicauda</i> ^D								
<i>Parastenocaris</i> sp. ^D								
Ostracoda								
<i>Cyprieis torosa</i>	1.4 (37)	0.8 (23)		0.02 (2.0)		0.01 (0.4)		
<i>Limnocythere inopinata</i>						0.005 (0.3)		
<i>Loxoconcha elliptica</i>	0.003 (0.2)	0.5 (34)						
<i>Ilyocypris gibba</i>		0.2 (20)						+
<i>Fabaeformiscandona fabaeformis</i>			0.003 (0.1)					
<i>Cypris ophtalmica</i>		0.002 (0.2)		0.001 (0.2)	0.8 (22)			
<i>Notodromas monacha</i>				0.001 (0.2)				
<i>Notodromas persica</i>		0.1 (6.8)						
<i>Heterocypris incongruens</i>	0.1 (2.7)	0.2 (8.8)	0.003 (0.2)				+	+
<i>Heterocypris salina</i>	0.01 (0.7)	+	+				+	+
<i>Eucypris virens</i>	0.004 (0.3)	0.4 (11)		1.1 (75)		0.5 (17)		
<i>Bradleystrandesia reticulata</i>	0.02 (1.3)			0.01 (1.3)				
<i>Isocypris beauchampi</i>					0.002 (0.1)			
<i>Herpetocypris brevicaudata</i>				0.8 (11)				

	HHW	BW	HTW	MFW	FS	LW	EBW	EFW	RF
<i>Enallagma cyathigerum</i> ^N									
<i>Ischnura</i> sp. (nymph)			0.01 (0.3)	0.04 (2.0)			+	4.5 (31)	
<i>Ischnura pumilio</i> ^N									
<i>Ischnura elegans</i> ^M									
<i>Ischnura graellsii</i> ^M									
<i>Ceriagrion tenellum</i> ^M									
<i>Aeshna mixta</i> ^N									
<i>Aeshna cyanea</i> ^M									
<i>Anax imperator</i>								0.04 (1.5)	
<i>Anax parthenope</i> ^M									
<i>Hemianax ephippiger</i> ^N									
<i>Onychogomphus forcipatus</i>							+		
<i>Orthetrum cancellatum</i> ^M									
<i>Orthetrum brunneum</i> ^M									
<i>Orthetrum coerulescens</i> ^M									
<i>Crocothemis erythrea</i> ^M									
<i>Sympetrum striolatum</i> ^N									
<i>Sympetrum vulgatum</i> ^M									
<i>Sympetrum meridionale</i> ^M									
<i>Sympetrum fonscolombii</i>				0.01 (0.2)				0.5 (1.3)	
<i>Sympetrum flaveolum</i> ^M									
<i>Sympetrum sanguineum</i> ^M									
<i>Trithemis annulata</i> ^N									
Heteroptera									
<i>Hebrus pusillus</i>				+	+	+	+	+	+
<i>Mesovelia vittigera</i>									+
<i>Hydrometra stagnorum</i>				+		+			+
<i>Microvelia pygmaea</i>							+		+
<i>Velia</i> sp.				+	+				
<i>Aquarius paludum</i>	+			+					
<i>Gerris thoracicus</i>							+		
<i>Gerris asper</i>				+					
<i>Gerris argentatus</i>				+					
<i>Nepa cinerea</i>				0.001 (0.1)					
<i>Naucoris maculatus</i>	0.002 (0.1)				0.1 (0.7)				
<i>Notonecta maculata</i>					0.01 (0.2)				
<i>Notonecta viridis</i>	0.003 (0.2)			0.001 (0.1)					
<i>Anisops sardea</i>				0.014 (1.7)	0.006 (0.1)				+
<i>Plea minutissima</i>						0.001 (0.1)			
<i>Helicorisa vermiculata</i>				0.004 (0.4)	0.003 (0.1)	0.003 (0.2)			+
<i>Corixa punctata</i>					0.032 (1.0)				
<i>Corixa affinis</i>	0.001 (0.1)								+
<i>Hesperocorixa linnaei</i>	0.001 (0.1)			0.001 (0.1)					
<i>Sigara selecta</i>	+								
<i>Sigara stagnalis</i>		+		+			+		+
<i>Sigara dorsalis</i>	0.002 (0.2)			0.002 (0.2)	0.002 (0.1)	0.002 (0.1)			
<i>Sigara lateralis</i>	0.003 (0.1)			0.005 (0.6)		0.001 (0.1)		+	
<i>Micronecta scholtzi</i>			0.02 (0.6)	0.2 (19)		0.028 (1.0)			
<i>Micronecta poweri</i>						+			
Neuroptera									
<i>Sisyra</i> sp.					+				
Coleoptera									
<i>Gyrinus caspius</i>							+		
<i>Gyrinus dejeani</i>		+					+		

	HHW	BW	HTW	MFW	Waterbody types			RF
					FS	LW	EBW	
<i>Gyrinus substriatus</i>		+					+	
<i>Gyrinus urinator</i>				+		0.001 (0.1)	+	
<i>Haliphus lineatocollis</i>						+		
<i>Haliphus heydeni</i> ^B								
<i>Noterus clavicornis</i>		+		0.002 (0.2)	+		+	0.01 (0.2)
<i>Noterus laevis</i>				+				
<i>Copelatus haemorrhoidalis</i>				+		+	+	
<i>Laccophilus hyalinus</i>		+		+	0.01 (0.2)		+	0.01 (0.2)
<i>Laccophilus minutus</i>				+			+	
<i>Laccophilus poecilus</i>					0.001 (0.1)			+
<i>Hyphydrus aubei</i> ^I								
<i>Hydrovatus cuspidatus</i>					+			
<i>Yola bicarinata</i> ^I								
<i>Bidessus goudotii</i> ^I								
<i>Bidessus minutissimus</i>						+		
<i>Bidessus pumilus</i> ^I								
<i>Hydroglyphus geminus</i>		+	+	+	0.04 (0.4)	0.002 (0.2)	+	0.001 (0.1)
<i>Hygrotus confluens</i> ^I				+			+	
<i>Hygrotus impressopunctatus</i>				+			+	
<i>Hygrotus inaequalis</i>				+		+		
<i>Hygrotus parallelogrammus</i>								+
<i>Hydroporus normandi</i> ⁽¹⁾				+		+		
<i>Hydroporus planus</i>	0.002 (0.1)	0.01 (0.3)		+	+		+	+
<i>Hydroporus pubescens</i>	+	+		+	+		+	+
<i>Hydroporus tessellatus</i>						+		
<i>Hydroporus vagepictus</i>					+	+		
<i>Graptodytes flavipes</i> ^I								
<i>Graptodytes ignotus</i>						+		
<i>Graptodytes varius</i> ^I								
<i>Graptodytes bilineatus</i>						+		
<i>Metaporus meridionalis</i>		0.01 (0.2)		0.002 (0.1)	+		+	+
<i>Deronectes hispanicus</i> ^L								
<i>Deronectes opatriinus</i> ^L								
<i>Stictotarsus duodecimpustulatus</i> ^I								
<i>Nebrioporus canaliculatus</i>						+		
<i>Nebrioporus ceresi</i>	+	+					+	
<i>Agabus biguttatus</i> ^I								
<i>Agabus bipustulatus</i>				+	+	+		+
<i>Agabus conspersus</i>				+				
<i>Agabus didymus</i>						+		
<i>Agabus nebulosus</i>					+		+	
<i>Ilybius montanus</i>				+			+	
<i>Ilybius quadriguttatus</i>				+			+	
<i>Rhantus suturalis</i>	+	+	+	0.002 (0.1)	+	+	+	0.004 (0.1)
<i>Colymbetes fuscus</i>				+				
<i>Meladema coriacea</i>						+		
<i>Eretes sticticus</i>							+	
<i>Hydaticus leander</i>	+			+	+		+	0.001 (0.1)
<i>Hydaticus seminiger</i>				+			+	
<i>Graphoderus cinereus</i>				+				
<i>Cybister lateralimarginalis</i>				+				
<i>Helophorus rufipes</i>	+							
<i>Helophorus alternans</i>				0.001 (0.1)	0.002 (0.1)	0.001 (0.1)	+	+
<i>Helophorus aequalis</i> ^J								
<i>Helophorus maritimus</i>				+			+	
<i>Helophorus brevipalpis</i>				0.001 (0.1)	0.005 (0.2)	0.001 (0.1)	+	+

	HHW	BW	HTW	Waterbody types				EBW	EFW	RF
				MFW	FS	LW				
<i>Helophorus fulgidicollis</i>	0.01 (0.5)	0.04 (0.6)	+	0.002 (0.2)	0.002 (0.1)	0.006 (0.2)	+	+		
<i>Helophorus illustris</i>				0.001 (0.2)			+	+		
<i>Helophorus minutus</i> ^J						+				
<i>Helophorus obscurus</i>										
<i>Georissus</i> sp.1									+	
<i>Georissus</i> sp.2									+	
<i>Hydrochus flavigaster</i>					+		+			
<i>Hydrochus smaragdineus</i>						+				
<i>Berosus affinis</i>		0.001 (0.1)	+					+		
<i>Berosus hispanicus</i>	0.009 (0.4)	0.001 (0.1)		0.001 (0.1)				+		
<i>Berosus signaticollis</i>		0.001 (0.1)		+				+	+	
<i>Chaetarthria similis</i>										+
<i>Paracymus aeneus</i>	0.002 (0.1)	0.001 (0.1)								
<i>Anacaena bipustulata</i>				+		+				
<i>Anacaena globulus</i>						+				
<i>Anacaena lutescens</i> ^J									+	
<i>Laccobius femoralis</i>										+
<i>Laccobius gracilis</i>										+
<i>Laccobius ytenensis</i>				+	+	+	+	+		
<i>Laccobius striatulus</i>						+				
<i>Helochares lividus</i>			+	+	0.002 (0.1)	+	+	+	+	+
<i>Chasmogenus livornicus</i> ^K										
<i>Enochrus bicolor</i>	0.003 (0.1)	0.002 (0.1)		+	0.004 (0.1)			+	+	
<i>Enochrus quadripunctatus</i>			+	+				+	+	0.01 (0.2)
<i>Enochrus testaceus</i>									+	
<i>Cymbiodyta marginella</i>					+				+	
<i>Hydrobius fuscipes</i>									+	
<i>Limnoxenus niger</i>	+			+	+			+	+	
<i>Hydrochara caraboides</i>									+	
<i>Hydrophilus pistaceus</i>	+			+			+		+	+
<i>Coelostoma hispanicum</i>							+			
<i>Coelostoma orbiculare</i>					0.002 (0.1)		+			
<i>Cercyon subsulcatus</i> ^K										
<i>Cercyon terminatus</i>				+	+					
<i>Cercyon laminatus</i> ⁽⁶⁾				+					+	
<i>Cercyon</i> sp.1								+	+	
<i>Sphaeridium scarabaeoides</i> ^A										
<i>Megasternum</i> sp.									+	
<i>Dactylosternum abdominalis</i> ⁽⁶⁾				+					+	
<i>Hydraena atrata</i>				+		+				
<i>Hydraena testacea</i>						+				
<i>Limnebius furcatus</i> ^F							+			
<i>Limnebius nitidus</i>										
<i>Aulacochthebius exaratus</i>				+		+				
<i>Ochthebius quadricollis</i> ⁽²⁾										
<i>Ochthebius aeneus</i>					+		0.001 (0.1)			+
<i>Ochthebius dilatatus</i>		0.002 (0.1)	0.001 (0.1)	0.003 (0.4)	0.01 (0.1)	0.004 (0.2)	+	+		
<i>Ochthebius gr. maculatus</i>	+	+						+		
<i>Ochthebius subinteger</i> ⁽²⁾										
<i>Ochthebius dentifer</i>	0.03 (1.8)	0.003 (0.2)						+		
<i>Ochthebius marinus</i> ^J										
<i>Ochthebius punctatus</i>		0.001 (0.1)		+	+					
<i>Ochthebius quadrifoveolatus</i>						+				
<i>Ochthebius subpictus</i>		+		+			0.001 (0.1)	+		
<i>Ochthebius viridis</i> sp.2 sensu Jäch, 1992				+						
<i>Cyphon laevipennis</i>			+	+	+			+	+	
<i>Cyphon sulcicollis</i>								+		
<i>Stenelmis canaliculata</i>							+			

	HHW	BW	HTW	Waterbody types				EBW	EFW	RF
				MFW	FS	LW				
<i>Stenelmis consobrina</i> ^J										
<i>Esolus parallelepipedus</i>							+			
<i>Oulinnius rivularis</i>				0.001 (0.1)			0.001 (0.1)			
<i>Dryops algiricus</i>		+		+						
<i>Dryops gracilis</i>		+		+			+	+	+	
<i>Dryops luridus</i>							+			
<i>Dryops nitidulus</i>							+			
<i>Dryops sulcipennis</i>							+			
<i>Botriophorus atomus</i>		+						+		
<i>Heterocerus fenestratus</i>									+	
<i>Heterocerus flexuosus</i>				+				+		
<i>Plateumaris sericea</i> ^C										
<i>Tanysphyrus lemnae</i>										+
Trichoptera										
<i>Limnephilus</i> sp.	0.003 (0.1)			0.001 (0.3)			0.026 (1.5)	+		
<i>Hydropsyche</i> sp.				0.001 (0.2)			0.005 (0.2)			
Diptera										
Tipulidae undet.						0.01 (0.2)				
Limoniidae undet.		+								0.002 (0.1)
Psychodidae undet.				0.1 (18)	0.01 (0.2)	0.007 (0.3)				0.012 (0.2)
Dixidae undet.	0.02 (0.5)	0.01 (0.1)	0.03 (2.4)	0.2 (5.0)	0.005 (0.2)		+			0.1 (1.9)
<i>Dixella autumnalis</i>	+	+	+							
<i>Chaoborus crystallinus</i>					0.3 (8.2)					
<i>Anopheles atroparvus</i>		+			4.5 (129)		+	+	+	1.7 (15)
<i>Anopheles petragnani</i> ⁽³⁾				+						
<i>Anopheles plumbeus</i> ⁽⁴⁾										
<i>Aedes vexans</i>				+						
<i>Aedes vittatus</i> ^H										
<i>Ochlerotatus geniculatus</i> ⁽⁴⁾										
<i>Ochlerotatus caspius</i>	+	+		+			+	+	+	
<i>Ochlerotatus detritus</i>	0.004 (0.2)	0.2 (4.7)		+			+	+	+	
<i>Ochlerotatus mariae</i> ⁽²⁾										
<i>Ochlerotatus rusticus</i> ^H										
<i>Culex hortensis</i> ^H										
<i>Culex impudicus</i>				+			+	+	+	0.001 (0.1)
<i>Culex modestus</i> ^H										
<i>Culex pipiens</i>			0.03 (0.6)	0.002 (0.2)	+	0.001 (0.1)	+	+	+	+
<i>Culex theileri</i>				+	+	+	+	+	+	0.1 (0.5)
<i>Culiseta annulata</i>							+	+	+	
<i>Culiseta longiaerolata</i> ⁽⁵⁾										
<i>Culiseta litorea</i>							+	+	+	
<i>Culiseta subochrea</i>				+			+	+	+	
<i>Coquillettidia buxtoni</i> ^H										
<i>Coquillettidia richiardii</i> ^H										
Simuliidae undet.			0.01 (0.1)	0.001 (0.1)				0.6 (26)		
<i>Simulium ornatum</i>							+			
<i>Simulium velutinum</i>							+			
Ceratopogonidae undet.	0.002 (0.1)	0.02 (0.6)		0.01 (0.8)	0.1 (2.2)	0.005 (0.1)		+		7.7 (244)
<i>Culicoides</i> sp.		+								
Chironomidae undet.	0.3 (3.5)				5.1 (19)			+		
<i>Monopelopia</i> sp.									0.7 (5.5)	
<i>Procladius</i> sp.		+							0.2 (3.4)	
<i>Tanyptus</i> sp.		+								
<i>Rheopelopia</i> sp.						0.04 (2.6)				
<i>Telmatopelopia</i> sp.						0.002 (0.1)				
<i>Xenopelopia</i> sp.									0.001 (0.1)	
<i>Pothastia</i> gr. <i>gaedii</i>				0.001 (0.1)			0.3 (14)			

	HHW	BW	HTW	MFW	Waterbody types FS	LW	EBW	EFW	RF
<i>Chaetocadius</i> sp.		0.001 (0.1)	0.04 (0.6)	0.03 (1.9)					
<i>Corynoneura</i> sp.		0.001 (0.1)	0.003 (0.1)	0.1 (1.9)		0.1 (1.6)			0.1 (3.4)
<i>Cricotopus</i> gr. <i>bicinctus</i>			0.03 (0.2)	0.03 (0.7)		0.03 (0.6)			
<i>Cricotopus</i> gr. <i>isocladius</i>			0.003 (0.1)						
<i>Cricotopus</i> gr. <i>nostocladius</i>						0.002 (0.1)			
<i>Cricotopus</i> gr. <i>sylvestris</i>		0.01 (0.3)	0.04 (0.3)	0.1 (1.0)		0.01 (0.1)			2.2 (20)
<i>Cricotopus</i> sp.			0.01 (0.1)	0.01 (0.1)		0.002 (0.1)			
<i>Eukiefferiella</i> sp.						0.02 (1.6)			
<i>Halocladius varians</i>		+							
<i>Hydrobaenus</i> sp.				0.01 (0.2)		0.1 (4.5)			
<i>Limnophyes</i> sp.				0.001 (0.1)					
<i>Mesocricotopus</i> sp.				0.001 (0.1)					
<i>Nanocladius</i> gr. <i>bicolor</i>			0.01 (0.1)			0.01 (0.5)			
<i>Nanocladius</i> sp.			0.01 (0.1)	0.002 (0.2)					
<i>Orthocladius</i> gr. <i>eudactylocladius</i>				0.01 (0.7)					
<i>Orthocladius</i> gr. <i>eurthocladius</i>				0.001 (0.1)		0.004 (0.2)			
<i>Orthocladius</i> sp.		0.04 (1.1)	0.04 (0.2)	0.1 (1.5)		0.1 (1.4)			
<i>Parakiefferiella</i> sp.		0.001 (0.1)		0.001 (0.1)					
<i>Parametriocnemus</i> sp.				0.003 (0.1)		0.002 (0.1)			
<i>Paratrichocladius</i> sp.			0.004 (0.1)			0.002 (0.1)			
<i>Psectrocladius</i> sp.		0.01 (0.2)		0.001 (0.1)					1.4 (10)
<i>Rheocricotopus</i> sp.				0.001 (0.1)		0.02 (0.5)			
<i>Synorthocladius</i> sp.				0.001 (0.1)		0.005 (2.6)			
<i>Thienemannia</i> sp.		0.001 (0.1)	0.1 (1.1)	0.1 (3.6)		0.3 (12)			
<i>Thienemanniella</i> sp.			0.1 (0.9)	0.01 (0.6)		0.007 (0.2)			
<i>Chironomus</i> sp.		0.01 (0.1)	0.01 (0.1)	0.002 (0.1)		0.005 (0.2)			
<i>Chironomus</i> gr. <i>halophilus</i>		+							
<i>Chironomus</i> gr. <i>plumosus</i>		+							
<i>Chironomus</i> gr. <i>semireductus</i>		+							
<i>Chironomus</i> gr. <i>thummi</i>		+							
<i>Chironomus</i> <i>salinarius</i>		+							
<i>Dicrotendipes</i> gr. <i>notatus</i>				0.003 (0.1)		0.005 (0.3)			
<i>Dicrotendipes</i> sp.				0.01 (0.3)		0.001 (0.1)			
<i>Einfeldia</i> sp.									0.001 (0.1)
<i>Endochironomus</i> sp.						0.004 (0.2)			
<i>Kiefferulus</i> <i>tendipediformis</i>				0.01 (0.5)					
<i>Micropsectra</i> sp.		+	0.2 (2.3)	0.03 (2.2)		0.008 (0.4)			
<i>Microtendipes</i> gr. <i>pedellus</i>				0.001 (0.1)					
<i>Parapsectra</i> sp.			0.003 (0.1)						
<i>Paratanytarsus</i> sp.		+	0.02 (0.4)	0.03 (0.4)		0.05 (2.6)			0.05 (0.8)
<i>Phaenopsectra</i> sp.				0.002 (0.1)		0.04 (2.6)			
<i>Polypedilum</i> sp.		+	0.1 (1.0)	0.02 (0.5)		0.01 (0.4)			0.02 (1.3)
<i>Polypedilum</i> gr. <i>nubeculosum</i>			0.02 (0.5)	0.01 (0.4)		0.4 (29)			
<i>Polypedilum</i> gr. <i>pedestre</i>						0.04 (2.6)			
<i>Polypedilum</i> gr. <i>scalaenum</i>						0.003 (0.2)			
<i>Rheotanytarsus</i> sp.			0.01 (0.1)	0.01 (0.4)		0.001 (0.1)			
<i>Tanytarsus</i> sp.			0.003 (0.1)			0.002 (0.2)			0.1 (2.1)
Tabanidae undet.		+				0.01 (1.0)			0.001 (0.1)
Stratiomyidae undet.	0.003 (0.2)			0.001 (0.1)	0.001 (0.1)	0.01 (0.1)	0.02 (1.0)	+	0.03 (0.4)
Empididae undet.		0.001 (0.1)	0.001 (0.1)	0.001 (0.1)		0.002 (0.1)			
Dolichopodidae undet.		+	0.001 (0.1)					+	0.1 (7.5)
Syrphidae undet.	+	+							
Sciomyzidae undet.				0.001 (0.1)					0.01 (0.4)
Ephydriidae undet.	0.01 (0.2)	0.004 (0.2)	0.001 (0.1)	0.002 (0.2)	0.1 (0.5)	0.004 (0.1)	+		0.2 (3.7)
<i>Ephydra macellaria</i>			+					+	
<i>Scatella</i> sp.			+						
Chloropidae undet.			+						

trophy. Artificial water regimes, which characterize rice fields, are known to affect community structure (e.g. Gascón *et al.*, 2005). However, the effect of insecticides used to control rice pests, cannot be ruled out as affecting the composition of this type of water body. On the other hand, freshwater springs contrast with the other freshwater bodies studied because they are more oligotrophic (Trobajo *et al.*, 2002). Invertebrate assemblages of this water body type in other Mediterranean wetlands are also characterized by a singular composition (Alfonso & Miracle, 1987).

The faunal composition of the Empordà wetlands is dominated by taxonomic groups described as characteristic of stagnant waters, such as planktonic crustaceans or, among insects, Coleoptera, Heteroptera, and Odonata, whereas the groups typical of running waters, such as Ephemeroptera, Plecoptera, or Trichoptera are poorly represented (Merritt & Cummins, 1996, Tachet *et al.*, 2000). Lentic species are abundant even in lotic environments, since most of these lotic habitats belong to estuarine zones of rivers or water channels with reduced water flow. The importance of invertebrate contributions to biodiversity in shallow lentic ecosystems is often neglected, in spite of the high number of species found. Factors determining the ecology and distribution of invertebrates are still not well known, opposite to other organisms, such as birds or plants, which are especially well known in protected areas. The high species richness found in these ecosystems seems to be a consequence of the high spatial and temporal variability. The heterogeneity of hydrological interactions among rivers, sea, and groundwater facilitate the existence of gradients and contribute to spatial patchiness, increasing the landscape and environmental diversity and, consequently, their ecological interest (Britton & Podlejski, 1981; Trobajo *et al.*, 2002; Williams *et al.*, 2003). The hydrological temporal irregularity and flooding unpredictability characteristic of the Mediterranean climate causes high temporal variability on water composition, to which invertebrates are adapted (Britton & Crivelli, 1993), facilitating invertebrate temporal variability in these ecosystems.

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