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THE FAUNAL COMPOSITION OF ESPOLLA POND (NE IBERIAN PENINSULA): THE NEGLECTED BIODIVERSITY OF TEMPORARY WATERS

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Abstract: The faunal composition, richness, and their determinant factors were analyzed in a Mediterranean temporary pond located in NE Spain. The aquatic community was sampled weekly over 7 periods of flooding during 4 years (1996–1999). Composition of the pond community was found to be influenced by duration of the hydroperiod and, secondarily, by seasonality. Insects and crustaceans were the most well-represented types of fauna. The small numbers of species captured over all hydroperiods spend the dry periods *in situ* or have an important dispersal capacity. Comparison of the faunal composition of several temporary ponds of temperate latitudes confirms the great diversity of faunal groups found in temporary aquatic environments, and this richness is comparable to that found in permanent water bodies. The richness of these temporary ponds is related to flooded surface and to hydroperiod duration. The peculiarity of the fauna of temporary waters, together the deteriorating condition of those habitats, make it necessary for more active policies of preservation to be pursued.

Key Words: temporary pond, richness, faunal composition, hydroperiod length, flooded surface

INTRODUCTION

The importance of lentic aquatic ecosystems of the Iberian peninsula and their deterioration has given rise to concern (Seminario sobre Bases Científicas para la Protección de los Humedales en España 1986, Proyecto ''Charcas'' 1997). Temporary aquatic environments are those that are in the most precarious situation, as their condition has continued to deteriorate despite, in the case of the temporary Mediterranean ponds, the existence of preservation initiatives (European Directive 92/43/CEE). During last century, there has been a worldwide disappearance or degradation of these environments (Holland et al. 1995, Brown 1998), and the negative effect of intensive agricultural practices on the aquatic temporary fauna is known (Euliss and Mushet 1999). Although certain zoological groups only inhabit temporary basins and ponds (Hartland-Rowe 1972, Giudicelli and Thiéry 1998), there has been a tendency to undervalue the fauna and flora of these waterbodies. The true importance of the flora of Mediterranean temporary aquatic environments has recently been clarified (Boutin et al. 1982, Rita and Bibiloni 1991, Font and Vilar 1998, Quézel 1998, Médail et al. 1998), and the need to protect and create these environments for the conservation of the species that inhabit them has been noted (Jeffries 1991, Baltanás et al. 1992, Valdecasas et al. 1992, Collinson et al. 1995, Hughes 1997). Furthermore, the scientific community has called for a revision of the existing ideas regarding the biodiversity of temporary environments (Williams 2000). Human perceptions, such as the concept that drying-out constrains the fauna of temporary waters, have had a negative influence over the present state of its knowledge (Biggs et al. 1994, Williams 1996). The study of the faunal and floral composition of temporary environments is necessary in order to broaden our knowledge of the biodiversity of these habitats, which is one of the most important factors taken into consideration when establishing preservation criteria (Ramsar Convention Bureau 1992).

In this paper, we present an inventory of the fauna of a temporary pond, highlighting the importance of the different taxonomic groups. We use the faunal composition to classify the different hydroperiods. Finally, we make a comparison with other temporary ponds of temperate latitudes to highlight faunal similarities.

STUDY SITE

Espolla temporary pond (42°9′6″N, 2°46′1″E; surface = 3.1 ha, maximum depth = 4.5 m, mean depth = 1.3 m) is located in the Banyoles karstic area (NE Iberian peninsula). It has the same ground-water supply as that of the lake of Banyoles and the other ponds in the area. Ground water reaches the pond at a high temperature (19° C) and has a low concentration of

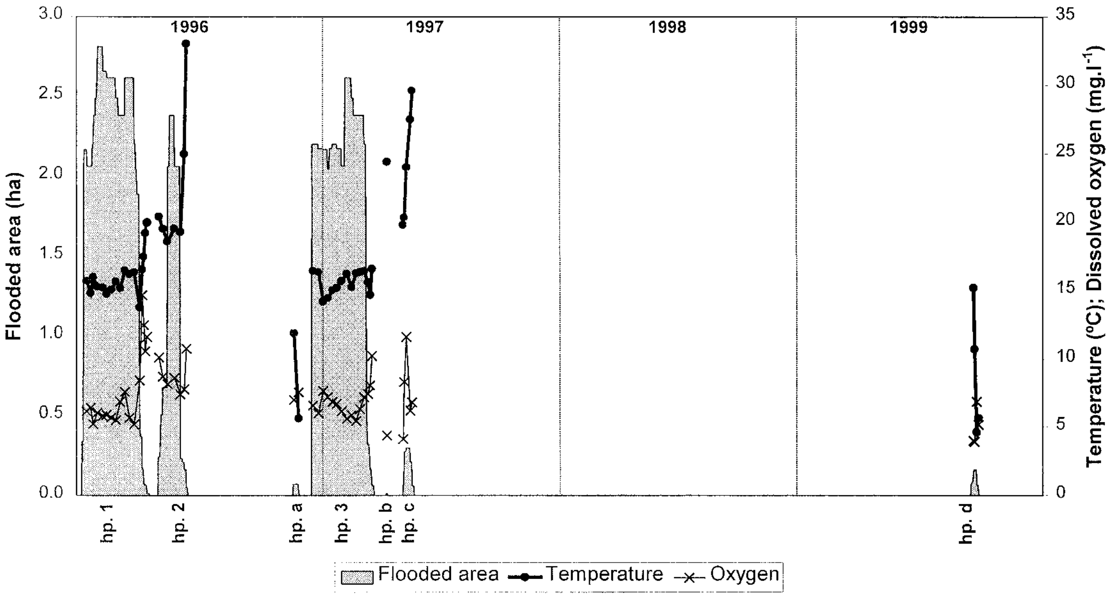

Figure 1. Hydroperiods that occurred in Espolla temporary pond between 1996 and 1999. The figure shows flooded surface, water temperature and dissolved oxygen in the pond.

oxygen (3 $mg \cdot l^{-1}$ approx.), but usual values of the water in the pond are about 15° C and about 6 $mg \cdot l^{-1}$, respectively (Figure 1). The flooding dynamics of this pond are irregular (Figure 1). Some years there are two hydroperiods (autumn and spring) separated by a period of total desiccation. It is not, however, uncommon for there to be years with only one hydroperiod, in late autumn or winter, and occasionally no flooding at all. Some hydrologic and physico-chemical information can be found in Vila et al. (1988) and Costa (1992).

The whole basin is a grassland of *Agrostis stolonifera* L. with *Rorippa sylvestris* L., *Potentilla reptans* L., and *Ranunculus repens* (L.). Terrestrial vegetation dominates the plant community during the whole hydroperiod when the pond is flooded. Several hygrophilous species (*Mentha cervina* L., *Galium palustre* L., *Gratiola officinalis* L., *Juncus articulatus* L., and *Eleocharis palustris* L.) develop during the aquatic phase, and only one floating aquatic plant is present, *Ranunculus trichophyllus* Chaix. The filamentous algae *Oedogonium* sp. and several epiphytic diatoms bloom one month after the pond fills. Additional information about the vegetation can be found in Vila et al. (1990).

Previous studies of the fauna of this pond have focused on the biology of the *Triops cancriformis* (Lamarck) and *Heterocypris incongruens* (Ramdohr) crustaceans (Margalef 1951a, 1951b, López 1979, Ribes 1979, Pla 1980, Vila and Abellà 1990, Zandonati 1998). Attention has also been paid to the conservation of the amphibians: 8 anurans and 3 urodeles (Massip 1994, Boix 1999, Boix et al. 2000).

The ecological value of this ecosystem has been officially recognized since 1992 (Government of Catalunya, Decree 328/1992 of 14 December, by means of which approval is given to the Areas of Natural Interest Plan). Despite this decree, measures for its protection have still not been introduced.

METHODS

Sampling was carried out during all hydroperiods occurring between 1996 and 1999 (Table 1). It should be noted that the pond was dry between August 1997 and November 1999. We have distinguished complete flooding events (hydroperiods 1, 2, and 3, in which almost the whole surface of the pond was flooded) from those periods in which only the lower parts of the basin were flooded (hydroperiods a, b, c, and d). With the exception of hydroperiod 1, all flooding events began with the pond completely dry. A complete flooding event previous to hydroperiod 1 began on 16 December 1995, and the pond was drying on 10 January 1996 (flooded surface was reduced to 7% of the total). The pond filled rapidly on 11 January 1996, and this date is taken as the beginning of the hydroperiod 1.

Sampling was conducted weekly, except at the end of each hydroperiod, when the sampling frequency was increased. The pond was divided into seven areas by bathymetry, hydrology, and vegetation. A modified Elster beam trawl (Schwoerbel 1966) was pulled along a 20-m transect in each area. Due to low water levels in hydroperiods b and d, some samples were taken with a dip net. Both sampling devices had a mesh size of 250 μm. Samples were preserved *in situ* with 4% formalin. During dry periods, the pond was visited af-

Table 1. Details of the hydroperiods sampled at the Espolla temporary pond.

Hydroperiod	Start	End	Duration of Inundation (days)	Number of Sampling Days	Maximum Flooded Surface (m^2)	Number of species
1	11-01-1996	19-04-1996	100	17	28131	67
2	02-05-1996	16-06-1996	46	7	23825	54
a	21-11-1996	30-11-1996	10	2	719	11
3	09-12-1996	14-03-1997	96	15	26175	73
b	06-06-1997	08-06-1997	3	1	125	7
c	04-07-1997	21-07-1997	18	5	2969	34
d	13-11-1999	26-11-1999	14	4	1638	18

ter rains, and we observed that holes and depressions on calcareous stones held water for only a few days. Sample results from these small ''rock pools'' (maximum size 380 cm^2) are presented, but they are not used in the dendrogram.

Comparison of the different hydroperiods was carried out using a hierarchical classification (analysis of clusters, UPGMA algorithm) dependent on the similarities of the different inventories. The Sørensen index (community coefficient) was used as a measurement of similarity using the presence or absence of taxa, given that it is less sensitive to species richness than other qualitative indices (Jongman et al. 1987).

The following observations need to be made with regards to the taxonomic classification:

a) In the case of neorhabdocoele turbellarians, classification of individuals captured was complicated by the fact that 4% formalin is not suitable for their preservation. We have only been able, by the position and shape of the pharynx and by the shape of the body, to distinguish two groups of individuals; some belong to the Typhloplanidae family, but it has not been possible to assign the others to a specific Neorhabdocoela family.

b) The only earthworm species identified in the adult stage is *Allolobophora caliginosa* (Savigny). The prostomium and the arrangement of setae of the immature earthworms were the same as in individuals classed as *A. caliginosa*, so immature stages have been attributed to this species for the analysis of clusters.

c) Similarly, the only tubificid species identified in the adult stage was *Tubifex tubifex* (Müller). The distribution and form of the setae, and the presence of hair setae, were features that coincided with the immature tubificids and adult specimens classified as *T. tubifex*, so immature stages have been attributed to this species for the analysis of clusters.

d) Heteropteran nymphs have been identified at the fifth stage, and in some cases, it has been possible to identify species in the third and fourth stages through patterns observed in adults and fifth instar nymphs.

e) Little-developed larvae of urodeles were not classified. These individuals were attributed to *Triturus marmoratus* (Latreille) for the analysis of clusters, as all larvae sufficiently developed for their identification were of this species. The temporal pattern of their presence also supported this conclusion.

f) It has not been possible to classify the larvae of anurans in stages prior to 25 of the Gosner classification (Gosner 1960).

We compared the faunal composition of the Espolla pond with other similar temperate latitude systems (30°–60° north or south). We chose those studies that have included sampling over at least one year and were carried out at intervals not greater than once per month (Kenk 1949, Barclay 1966, Terzian 1979, Boutin et al. 1982, Williams 1983, Metge 1986, Lake et al. 1989, Bazzanti et al. 1996). Pools have not been included nor temporary waters that have high levels of salinity, given that the faunal composition of these waters is heavily determined by their special characteristics. The size of the geographical area taken into consideration in this study, and the wide range of zoogeographical regions, only allows for comparison of taxonomic groups that are superior to species level.

RESULTS AND DISCUSSION

The Faunal Composition of the Pond

A rich fauna of 113 taxa was found in our temporary pond, although 64 taxa had an occurrence less than 10% of the sampling days. Thirty percent of these taxa are characteristic of temporary environments. Insects (82 taxa) clearly dominated the faunal composition (Table 2). Two species were abundant in most samples (larvae of *Agabus nebulosus* Forster and adult *Berosus signaticollis* (Charpentier)), and three other species

Table 2. Faunal inventory for each hydroperiod sampled in Espolla temporary pond. Legend: + = presence; l = larva; n = nymph; p = pupa; a = adult; c = colony; s = statoblast.

Taxa	Hydroperiod							Rock Pools
	1	2	a	3	b	c	d	
Ph. Plathelminthes								
Neorhabdocoela undet.	+			+				
Typhloplanidae undet.				+				
Rhynchodemus cf. *sylvaticus* (Leidy)				+			+	
Ph. Nematoda								
Rhabditida undet.	+							
Tobrilus gracilis (Bastian)	+							
Cl. Oligochaeta								
Enchytraeidae undet.	+	+		+				
Tubifex tubifex (Müller)	+		+	+				
Tubificidae immature with hair setae	+	+	+	+	+	+	+	
Allolobophora caliginosa (Savigny)				+				
Lumbricidae immature undet.	+	+		+				
Cl. Crustacea								
SCl. Branchiopoda								
Chirocephalus diaphanus Desmarest				+				
Triops cancrifromis (Lamarck)	+	+	+	+	+	+	+	
Daphnia pulicaria Forbes	+	+	+	+		+		
Simocephalus vetulus (Müller)	+	+		+				
Moina brachiata (Jurine)	+	+		+		+		
Alona elegans Kurz	+			+				
Tretocephala ambigua (Lilljeborg)	+			+				
SCl. Ostracoda								
Heterocypris incongruens (Ramdohr)	+	+	+	+		+	+	
Eucypris virens (Jurine)	+	+		+		+		
Cyprididae immature undet.	+	+		+		+		
Hyocypris gibba (Ramdohr)	+							
SCl. Copepoda								
Megacyclops viridis Jurine	+	+	+	+	+	+	+	
Cyclops sp.	+	+		+				
SCl. Malacostraca								
Stenasellus cf. *buili* Remy	+							
Niphargus cf. *delamarei* Ruffo	+			+				
Cl. Insecta								
O. Ephemeroptera								
Cloeon inscriptum Bentgsson		n				n		
O. Odonata								
Lestes viridis (Vander Linden)		n						
Anax imperator Leach						n		
O. Heteroptera								
Aquarius paludum Frabricius		n, a						
Micronecta cf. *scholtzi* (Fieber)						a		
Cymatia rogenhoferi (Fieber)						a		
Corixa affinis Leach	a	a		n				
Corixa panzeri (Fieber)	n, a	a		n, a				
Corixa punctata (Illiger)	n, a	a	a	n			a	
Hesperocorixa moesta (Fieber)				a				
Heliocorisa vermiculata (Puton)						n, a		

Table 2. Continued.

Taxa	Hydroperiod 1	2	a	3	b	c	d	Rock Pools
Paracorixa concinna (Fieber)	n, a	n, a		n, a		a		
Sigara dorsalis (Leach)	n, a		a	n, a			a	
Sigara falleni (Fieber)	n, a						a	
Sigara lateralis (Leach)	n, a	n, a	a	a		n, a	a	
Sigara limitata (Fieber)							a	
Corixidae nymphs undet.	n	n		n				
Anisops sardea Herrich-Schäffer		a				a		
Notonecta viridis Delcourt				a				
Notonecta glauca L.	a						a	
Notonectidae nymphs undet.	n	n		n		n		
Plea minutissima Leach						a		
O. Coleoptera								
Haliplus lineatocollis (Marsham)	l			l, a		a		
Hygrobia hermanni (Fabricius)	l	a						
Gyrinus caspius Ménétries				a				
Hydroporus tessellatus Drapiez							a	
Hydroporus sp.	l			l				
Laccophilus sp.		l						
Copelatus haemorrhoidalis (Fabricius)	l, a	a		l				
Agabus didymus (Olivier)	l, a	l		l, a				
Agabus nebulosus Forster	l	l, a		l, a			a	
Agabus bipustulatus (L.)	l			l				
Ilybius sp.	l			l		l		
Colymbetes fuscus (L.)	l			l				
Meladema coriacea Castelnau	l	l		l		l		
Eretes sticticus (L.)		l, a				l		
Dytiscus circumflexus Fabricius				a				
Dytiscus sp.	l			l				
Berosus signaticollis (Charpentier)	a	a	a	a	a	a		
Berosus sp.	l	l		l		l		
Dryops algiricus (Lucas)	a	a		a				
Dryops sp.	l	l		l				
Oulimnius rivularis (Rosenhauer)						a		
Helophorus brevipalpis Bedel		a						
Helophorus gr. *maritimus*		l, a					a	
Helophorus obscurus Mulsant							a	a
Helophorus cf. *asturiensis* Kuwert				a				
Alleculidae undet.	l	l		l			l	
O. Trichoptera								
Limnephilus cf. *decipiens* (Kolenati)				l				
Melampophylax mucoreus (Hagen)				l				
Stenophylax sp.				l				
Micropterna sp.				l				
Mesophylax aspersus (Rambur)	l							
Mesophylax impunctatus McLachlan	l			l				
O. Diptera								
Tipula sp. 1				l				
Tipula sp. 2			l					
Dolichopeza sp.				l				
Limonia sp.				l				
Psychoda sp.							l	
Chaoborus flavicans (Meigen)		l, p				l, p		

Table 2. Continued.

Taxa	Hydroperiod 1	2	a	3	b	c	d	Rock Pools
Culex hortensis Ficalbi		l						
Aedes vexans (Meigen)					l	l		
Atrichopogon sp.				l				
Dasyhelea sp.	l, p							l
Procladius choreus (Meigen)	p	l, p		p		l		
Zavrelimyia sp.	l	l, p		l				
Macropelopia nebulosa (Meigen)				p				
Potthastia gr. *gaedii*	l			l				
Corynoneura sp.		l						
Cricotopus bicinctus (Meigen)	l, p			l, p				
Cricotopus sylvestris (Fabricius)	l	l, p		l		l		
Gymnometriocnemus sp.	l		l	l				
Hydrobaenus sp.				l, p				
Metriocnemus sp.				l				
Orthocladius thienemanni Kieffer				p				
Orthocladius oblidens (Walker)	p			p				
Psectrocladius gr. *sordidellus*	l, p	l, p		l, p		l		
Thienemannia sp.	l							
Chironomus riparius Meigen	l	l		l, p		l	l	
Microtendipes gr. *pedellus*	p			l				
Parachironomus gr. *arcuatus*						l		
Micropsectra sp.	p	l		l				
Tanytarsus sp.						l, p		
Virgatanytarsus sp.		l						
Chloropidae undet.		l						
Ephydra sp.		l						
Hydrellia sp.	l	l, p		l				
Setacera sp.	l							
Ph. Bryozoa								
Plumatella repens (L.)	c, s	c, s	s	c, s	s	c, s		
Cl. Gastropoda								
Fossaria truncatula (Müller)	+	+		+	+	+		
Physella acuta (Draparnaud)	+	+		+				
Cl. Amphibia								
Triturus marmoratus (Latreille)	l, a			l				
larvae of urodeles undet.	l			l				
Discoglossus pictus (Otth)	l	l		l				
Hyla meridionalis (Boettger)	l	l				l		
Pelobates cultripes (Cuvier)	l, a	l		l				
Pelodytes punctatus (Daudin)	l	l		l				
Bufo calamita (Laurenti)	l	l				l		
larvae of anurans undet.	l	l		l				

were remarkably abundant at certain times (larvae of *Psectrocladius* gr. *sordidellus*, *Cricotopus bicinctus* (Meigen), and *Cloeon inscriptum* Bentgsson). The pond was particularly rich in dipterans and especially chironomids, with one of the highest number of species that has been observed in a temporary pond (Table 3). The crustaceans were the second richest group, of which the branchipods and particularly the cladocerans, were the most well-represented. Unlike the insects, crustacean species had great abundances, with the exception of *Chirocephalus diaphanus* Desmarest, *Alona elegans* Kurz, *Tretocephala ambigua* (Lilljeborg), *Ilyocypris gibba* (Ramdohr), *Stenasellus* cf. *buili* Remy, and *Niphargus* cf. *delamarei* Ruffo.

Only three species were present during all hydroperiods: *Tubifex tubifex*, *Triops cancriformis*, and *Megacyclops viridis* Jurine. Three other species were found in six of the seven hydroperiods: *Heterocypris* *incongruens*, *Sigara lateralis* (Leach), and *Berosus signaticollis*. All six are pioneer species that have adaptations that permit their appearance soon after inundation or, in the case of the tubificids, have the ability to inhabit all types of aquatic environments. *Triops cancriformis* leaves diapause and reaches the fifth larval stage in 43 hours (Fryer 1988) and is capabile of carrying out the first oviposition less than 20 days after eclosion (Takahashi et al. 1980). *Megacyclops viridis* has a diapause in the fourth copepodite stage (Einsle 1996), which explains our finding of adult specimens a few hours after inundation. Similarly, *Heterocypris incongruens* produces diapausing eggs and develops very quickly, completing three initial larval stages in four days (Szczechura 1971). *Berosus signaticollis*, similar to other species of the genus, remains embedded (both larvae and adults) in the sediment, where it is able to finish its metamorphosis (Thiéry 1979, Barbero et al. 1982). In the Espolla pond, *B. signaticollis* adults were found embedded in the sediment three months after the complete drying of the pond. *Sigara lateralis* does not remain in the pond during the dry phase but has a marked dispersal capacity, even for a corixid (Brown 1951, Fernando 1959). *Tubifex tubifex* is found in a wide range of aquatic environments, from running waters (large rivers and small streams) to stagnant waters (lakes and mountain pools). *Tubifex tubifex* and *Limnodrilus hoffmeisteri* Claparède are the only two species of oligochaetes found frequently in small pools (Brinkhurst and Jamieson 1971). Some authors consider tubificids to be typical of permanent environments (Wiggins et al. 1980), whereas others have found them in temporary waters (Kenk 1949, Barclay 1966, Bevercombe et al. 1973, Bazzanti et al. 1996). The absence of *Heterocypris incongruens* and *Sigara lateralis* in hydroperiod b could be attributed to its short length, while the absence of *Berosus signaticollis* in hydroperiod d could be explained by the long dry period prior to flooding.

The two taxa captured in the rock pools have different biologies, but their strategies allow them to live in these temporary environments. *Dasyhelea* is widely found in rain-filled rock pools round the world (Williams 1987), and its larvae have the ability to withstand desiccation (McLachlan and Cantrell 1980, Dodson 1987). The widely-distributed species of the genus *Helophorus* are very mobile insects and able to colonize new habitats quite rapidly (Fernando 1958, Fernando and Galbraith 1973). *Helophorus obscurus* Mulsant shows a preference for sites that dry up rapidly (Eyre et al. 1992).

The finding of rare species in Espolla pond indicates that species rarity is a factor to be considered in temporary ecosystems (Collinson et al. 1995). The terrestrial planarian, *Rhynchodemus* cf. *sylvaticus* (Leidy), is the first reference for the Iberian peninsula. Two species of corixids, *Sigara falleni* (Fieber) and *Sigara limitata* (Fieber), and two limnephilids, *Mesophylax impunctatus* McLachlan and *Limnephilus* cf. *decipiens* (Kolenati), have not been previously reported in the autonomous region of Catalunya (NE Iberian Peninsula). Three species of corixids (*Cymatia rogenhoferi* (Fieber), *Hesperocorixa moesta* (Fieber), and *Heliocorisa vermiculata* (Puton)) and two genera of chironomids, *Gymnometriocnemus* sp. and *Hydrobaenus* sp. are rare in the Iberian peninsula. Few individuals of two species of hypogeal crustaceans, *Niphargus* cf. *delamarei* and *Stenasellus* cf. *buili*, were captured. Their presence is related to the fact that the waters that feed the pond are subterranean. Given the importance of the findings of *Niphargus* cf. *delamarei* and *Stenasellus* cf. *buili*, the validation of the species will be left for a detailed later study of the morphology of the specimens. *Niphargus* cf. *delamarei* had been previously reported only at the Cova de la Mosquera at Beuda in Catalunya (Ginet 1977, Karaman 1986) and at different sites in the south of France (Ruffo 1953), although indeterminate individuals of the genus *Niphargus* have been reported in different sites in Catalunya (Notenboom 1990, Pretus and Sabater 1990). *Stenasellus* cf. *buili* was found for the first time at the Grotte de la Giraudasso at Les Corbières in France (Remy 1949), and it was initially thought to have a very limited distribution. Subsequent reports (the Hérault gorges, oriental Corbières, and the NE of Carcassonne) indicate that it has a more widespread distribution (Magniez 1976), and its presence in Espolla pond, beyond the limits of the Pyrenees, supports this hypothesis.

The Effect of Hydroperiod Duration and Season

Recent studies have indicated that hydroperiod duration is the main factor in determining the faunal composition and the structure of temporary aquatic communities (McLachlan 1985, Jeffries 1994, Schneider and Frost 1996, Wellborn et al. 1996, Schneider 1999). Our results support this idea, as the classification of the hydroperiods (Table 4 and Figure 2) follows a grouping that depends on the duration of the hydroperiod. The main division of the dendrogram separates the cluster [1-3-2-c] from the [a-d-b]. This latter element includes the shorter hydroperiods, where the faunal composition is limited to pioneer species, with fast growth and development, resistance structures (eggs, cocoons), lifestages embedded in the sediment, or highly migrating species (corixids). The duration of these hydroperiods is too short for community structuring to take place.

Seasonal factors also influence community composition, but this is difficult to establish in our case be-

Table 3. Number of species of each taxon captured at different temporary ponds. Legend: * estimated from bibliographical data; + present but number of species unknown; − organisms ignored; ? family data was not given.

Reference	This study	Terzian (1979)	Terzian (1979)	Bazzanti et al. (1996)	Metge (1986)	Metge (1986)
Pond	*Espolla*	*Crau*	*Catchéou 2*	*T19*	*daya 1*	*daya 4*
Geographical location	Catalunya Spain	Provence France	Provence France	Lazio Italy	Sidi Bettache Morocco	Ben Slimane Morocco
Max. flooded area (m^2)	28131	3850*	300*	1080	2537	31337
Max. depth (m)	3.9	0.8	0.7	0.5	0.25	0.4
Max. hydroperiod length (days)	100	240*	300*	302	77	225*
Porifera	0	0	0	0	0	0
Turbellaria	3	+	+	1	0	0
Nematoda	2	+	0	4	−	−
Nematomorpha	0	0	0	0	0	0
Rotifera	−	−	−	−	−	−
Anellida	3	5	2	9	0	0
Oligochaeta	3	4	2	7	0	0
Hirudinea	0	1	0	2	0	0
Crustacea	14	19	17	≥3	24	37
Anostraca	1	2	0	2	1	3
Conchostraca	0	1	0	0	1	1
Notostraca	1	1	0	1	1	1
Cladocera	5	6	6	−	9	16
Ostracoda	3	2	6	−	5	6
Copepoda	2	7	5	−	7	10
Isopoda	1	0	0	0	0	0
Amphipoda	1	0	0	0	0	0
Decapoda	0	0	0	0	0	0
Aracnida	0	2	3	1	2	2
Araneae	0	0	0	0	0	0
Acari	0	2	3	1	2	2
Insecta	82	90	85	67	39	53
Collembola	0	1	1	0	0	0
Ephemeroptera	1	1	2	1	1	1
Plecoptera	0	0	0	0	0	0
Odonata	2	8	13	4	3	3
Heteroptera	17	17	20	8	8	10
Corixidae	12	8	8	4	2	2
Notonectidae	3	2	4	3	3	4
other families	2	7	8	1	3	4
Coleoptera	22	45	33	32	15	24
Dytiscidae	11	19	15	19	6	10
Hydrophilidae	1	9	7	7	3	5
other families	10	17	11	6	6	9
Trichoptera	6	1	3	0	0	0
Limnephilidae	6	1	1	0	0	0
other families	0	0	2	0	0	0
Lepidoptera	0	0	0	0	0	0
Diptera	34	17	13	22	12	15
Tipulidae	4	1	1	1	0	1
Culicidae	2	3	2	1	6	6
Ceratopogonidae	2	0	0	3	0	1
Chironomidae	20	8	3	15	5	4

Table 3. Extended.

Boutin et al. (1982)	Lake et al. (1989)	Barclay (1966)	Kenk (1949)	Kenk (1949)	Williams (1983)
daya 3	*East Pomborneit*	*Ardmore*	*pond 1*	*pond 2*	*Sunfish*
Marrakech Morocco	Victoria Australia	Auckland New Zealand	Michigan USA	Michigan USA	Ontario Canada
1600	370	1210*	500*	1600*	2830*
0.3	0.9	1.1	0.5	0.6	0.8
75*	211	224*	190*	230*	100*
0	1	0	0	0	0
0	0	3	5	5	1
+	0	0	+	+	1
0	1	0	0	0	0
1	–	–	–	–	–
1	2	1	3	11	4
1	0	1	3	5	3
0	2	0	0	6	1
11	33	9	25	24	9
1	0	0	1	1	1
1	1	0	1	1	1
1	1	0	0	0	0
3	14	2	3	8	2
3	5	6	9	4	2
2	11	1	7	7	3
0	0	0	1	1	0
0	1	0	2	1	0
0	0	0	1	1	0
0	5	2	12	17	6
0	0	0	2	2	0
0	5	2	10	15	6
≥21	71	16	56	60	61
0	0	0	0	1	2
1	2	0	0	1	3
0	1	0	0	0	0
1	6	2	3	4	2
4	11	4	6	8	5
3	1	1	1	1	1
1	5	1	1	1	1
0	5	2	4	6	3
11	29	5	21	21	23
7	9	4	9	13	11
1	10	1	3	3	3
3	10	0	9	5	9
0	0	2	1	4	3
0	0	0	1	2	3
0	0	2	0	2	0
0	2	0	1	1	0
≥4	20	3	24	20	23
1	0	0	1	1	2
2	7	1	4	2	3
0	1	0	3	2	0
≥1	10	1	8	12	12

Table 3. Continued.

Reference	This study	Terzian (1979)	Terzian (1979)	Bazzanti et al. (1996)	Metge (1986)	Metge (1986)
Ephydridae	3	1	1	0	0	0
other families	3	4	6	2	1	3
Bryozoa	1	0	0	0	0	0
Mollusca	2	2	3	2	1	2
Gastropoda	2	2	3	2	1	2
Bivalvia	0	0	0	0	0	0
Amphibia	6	5	–	–	1	2
Caudata	1	2	–	–	0	1
Anura	5	3	–	–	1	1
MICROCRUST.	**10**	**15**	**17**	–	**21**	**32**
MACROINV. (without Nematoda)	**95**	**107**	**98**	**82**	**45**	**62**

cause of the confusion between the effect of the season and the duration of the hydroperiod. In cluster [1-3-2-c], the longest hydroperiods take place in the winter (1 and 3), followed by hydroperiod 2 in the spring and hydroperiod c, which corresponds to the summer. The same problem is found in cluster [a-d-b]. Nevertheless, in cluster [1-3-2-c] a seasonal effect is detected indirectly by the presence of certain specific species. There are 16 species present only in the long winter hydroperiods (1 and 3), of which *Alona elegans*, *Tretocephala ambigua*, *Sigara dorsalis* (Leach), *Hydroporus* sp., *Cricotopus bicinctus*, *Potthastia* gr. *gaedii*, *Agabus bipustulatus* (L.), and *Triturus marmoratus* are particularly abundant. Trichopteran and turbellarian species have only been captured during these periods. With regard to the spring and summer hydroperiods, there are four species, *Cloeon inscriptum*, *Anisops sardea* Herrich-Schäffer, *Eretes sticticus* (L.), and *Chaoborus flavicans* (Meigen), that have only been detected during these periods. Odonates have also appeared only in the spring/summer hydroperiods: *Lestes viridis* (Vander Linden) in hydroperiod 2 and *Anax imperator* Leach in hydroperiod c. Some species have been more abundant in spring hydroperiods than winter and vice versa; *Moina brachiata* (Jurine), *Cricotopus sylvestris* (Fabricius), and *Bufo calamita* (Laurenti) have been abundant in spring hydroperiods and *Cyclops* sp., *Agabus nebulosus* Forster, and *Discoglossus pictus* (Otth) in winter hydroperiods.

Faunal Composition of the Temporary Aquatic Ecosystems of Temperate Regions

When comparing faunal inventories of different temporary ponds across the temperate region (Table 3), we found that insects and crustaceans are, respectively, the most well-represented groups. These are typically followed in richness, although not in all ponds, by annelids, arachnids, and molluscs. Turbellarians are present in most ponds but with a low number of species. On the other hand, sponges, cnidarians, decapods, and plecopterans are very rare, having only been found in one or two ponds and represented by one single species in each case. Within the insects, dipterans and coleopterans had the greatest number of species, and within each of these orders, in almost all cases, one single family (Chironomidae and Dytiscidae, respectively) was found to represent more than half the richness of the order. Some interesting differences were also found. Lake et al. (1989) and Bazzanti et al. (1996) found large numbers of hydrophilids, and we found large numbers of corixid and limnephilid species at Espolla. Cladocerans, copepods, and ostracods are the most well-represented crustaceans over all of the ponds that we compared, and no one of these three groups was regularly observed as dominating. Large numbers of crustaceans (>20 species) were recorded in the inventories of Kenk (1949), Metge (1986), and Lake et al. (1989). Amphibians were present, normally with a few species, in all of the ponds. At Espolla, the number of amphibian species is greater than at other ponds, and it is possible that the number may in fact be underestimated, as two other species of urodeles have been reported in earlier studies (*Salamandra salamandra* (L.) and *Triturus helveticus* (Razoumowsky)), and three other species of anurans (*Alytes obstetricans* (Laurenti), *Rana perezi* Seoane and *Bufo bufo* (L.)) were not captured in this study.

Several genera are coincidently present in lentic temporary habitats in temperate latitudes between 30° and 60° north and south (Mozley 1932, Kenk 1949, Kramer 1964, Stout 1964, Barclay 1966, Sublette and

Table 3. Continued. Extended.

Boutin et al. (1982)	Lake et al. (1989)	Barclay (1966)	Kenk (1949)	Kenk (1949)	Williams (1983)
0	0	0	1	1	2
0	2	1	7	2	4
0	0	1	0	0	0
0	4	2	9	6	6
0	4	2	6	5	4
0	0	0	3	1	2
1	4	1	3	4	2
0	0	0	1	0	1
1	4	1	2	4	1
10	**30**	**9**	**19**	**19**	**7**
25	**87**	**25**	**91**	**104**	**77**

Sublette 1967, Williams 1968, Bevercombe et al. 1973, Bishop 1974, Williams 1975, Terzian 1979, Wiggins et al. 1980, Bayly 1982, Boutin et al. 1982, Williams 1983, Metge 1986, Lake et al. 1989, Gladden and Smock 1990, Bazzanti et al. 1996, Schneider and Frost 1996, Moorhead et al. 1998). *Mesostoma*, *Bothromesostoma*, *Dorylaimus*, *Triops*, *Lepidurus*, *Cyzicus*, *Daphnia*, *Simocephalus*, *Ceriodaphnia*, *Chydorus*, *Alona*, *Acanthocyclops*, *Eucypris*, *Prionocypris*, *Herpetocypris*, *Cypris*, *Eylais*, *Hydrachna*, *Arrenurus*, *Hydrometra*, *Mesovelia*, *Microvelia*, *Sigara*, *Plea*, *Haliplus*, *Copelatus*, *Rhantus*, *Eretes*, *Hydrochus*, *Berosus*, *Enochrus*, *Ochthebius*, *Aedes*, *Culex*, *Procladius*, *Cricotopus*, *Chironomus*, *Dicrotendipes*, *Parachironomus*, and *Tanytarsus* are found in temporary waters of the Palearctic, Nearctic, and Australian regions. Genera present in the two regions of the northern hemisphere that most frequently appear in temporary ponds include *Lumbriculus*, *Eiseniella*, *Helobdella*, *Erpobdella*, *Scapholeberis*, *Moina*, *Diaptomus*, *Canthocamptus*, *Cyclops*, *Megacyclops*, *Candona*, *Cypridopsis*, *Crangonyx*, *Hydryphantes*, *Thyas*, *Piona*, *Cloeon*, *Lestes*, *Anax*, *Libellula*, *Sympetrum*, *Gerris*, *Callicorixa*, *Hesperocorixa*, *Notonecta*, *Peltodytes*, *Gyrinus*, *Hydroporus*, *Laccophilus*, *Agabus*, *Ilybius*, *Colymbetes*, *Acilius*, *Dytiscus*, *Cybister*, *Helophorus*, *Anacaena*, *Hydrobius*, *Hydrophilus*, *Limnephilus*, *Tipula*, *Chaoborus*, *Tanypus*, *Ablabesmyia*, *Corynoneura*, *Psectrocladius*, *Polypedilum*, *Micropsectra*, *Tabanus*, *Lymnaea*, *Fossaria*, *Physella*, *Aplexa*, *Pisidium*, *Hyla*, and *Rana*. In addition, Enchytraeidae have often been detected in temporary environments of the northern hemisphere, and Plumatellidae bryozoans have been collected of aquatic temporary ecosystems of both hemispheres. It is worth pointing out that previous comparisons of the faunas of temporary ponds in different regions of the world reported considerable similarities (Williams 1987, 1997).

Table 4. Similarities (Sørensen's index) of the seven faunal inventories of the hydroperiods of Espolla temporary pond.

Hydro-period	1	2	a	3	b	c	d
1		0.66	0.26	0.77	0.16	0.38	0.31
2			0.25	0.58	0.20	0.48	0.31
a				0.24	0.44	0.31	0.48
3					0.15	0.32	0.26
b						0.29	0.24
c							0.23
d							

Species Richness of Temporary Environments

The faunal richness in temporary environments has been related to flooded surface (Boutin et al. 1982, King et al. 1996, Findlay and Houlahan 1997, Giudicelli and Thiéry 1998) and to hydroperiod length (Stout 1964, Driver 1977, Ebert and Balko 1987, Baz-

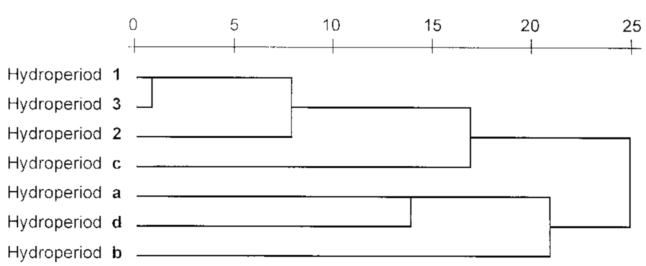

Figure 2. Dendrogram showing the classification of the hydroperiods in Espolla temporary pond by similarity of their faunal inventories (Sørensen's index).

zanti et al. 1996, Schneider 1999), although in some studies, there seems to be no link between flooded surface and community richness (Aubin and Leblanc 1986) nor with microcrustacean richness (Galindo et al. 1994) nor the richness of certain macrofaunal groups such as coleopterans, heteropterans, odonates, water mites, or amphibians (Valdecasas et al. 1984, Richter and Azous 1995).

Schneider and Frost (1996) hold that duration is more important than flooded surface in determining richness on the grounds that composition patterns differ from the model based on chance colonization and extinction, which would be predicted by MacArthur and Wilson's (1967) theory of island biogeography. In contrast, March and Bass' study (1995) of temporary ponds concludes that MacArthur and Wilson's model does explain the richness observed in these environments. It is worth pointing out that, in studies where the duration of natural flooding was artificially extended for several months during a 2-year experiment, observed richness was no greater than in other areas under natural conditions (Neckles et al. 1990). In adjacent ponds sharing environmental characteristics, larger ponds showed greater richness in macroinvertebrates (Kenk 1949, Terzian 1979, Boutin et al. 1982, Metge 1986), although there were exceptions (Leslie et al. 1997). Regarding the duration of the hydroperiod, when permanent and temporary waters were compared, it was the temporary ones that were richer, due perhaps to the trophic state of the pond, a factor associated with water permanence (Balla and Davis 1995). It was also observed (Hershey et al. 1999) that the richness of some taxonomic groups was unrelated to the length of the hydroperiod (e.g., molluscs), while for other groups (e.g., insects) shorter duration was associated with reduced richness.

In Espolla pond, where flooded surface and duration are linked, taxonomic richness is related to both variables (Table 5). In addition, based on this study and on a selection of literature describing other communities of temperate temporary ponds and pools in sufficient taxonomic resolution and sampling frequency (Kenk 1949, Barclay 1966, Williams 1975, Terzian 1979, Boutin et al. 1982, Williams 1983, Metge 1986, Lake et al. 1989, Bazzanti et al. 1996, Leslie et al. 1997), significant correlation (Table 5) was observed between flooded surface and the richness of macroinvertebrates and microcrustaceans (on a double logarithmic scale). Significant correlation was also observed between the length of the hydroperiod in these environments and richness of macroinvertebrates, although not with that of microcrustaceans (Table 5).

The richness of macroinvertebrates found in Espolla is comparable to the maxima in Mediterranean ponds: Crau and Catchéou in France or T19 in Italy. Nevertheless, where microcrustaceans are concerned, the number of species captured at Espolla is lower than in other Mediterranean temporary environments (Terzian 1979, Metge 1986). It is worth pointing out that while the flooded surface of Espolla is much larger than these others Mediterranean temporary waters, the maximum duration of the hydroperiod is among the shortest. The richness in Mediterranean environments (Terzian 1979, Boutin et al 1982, Metge 1986, Bazzanti et al. 1996) is comparable to that in other temporary ponds (Kenk 1949, Barclay 1966, Sublette and Sublette 1967, Williams 1975, Williams 1983, Lake et al. 1989, Leslie et al. 1997) and even to other kinds of temporary environments (Sklar 1985, White 1985, Duffy and LaBar 1994). The number of species for some alluvial plains (Gladden and Smock 1990), however, is much greater, while some episodic salt lakes (Williams and Kokkinn 1988) are much lower (Figure 3). The richness in macroinvertebrates in temporary waters can be considered similar to that found in natural (Kenk 1949) and artificial (Barnes 1983, Friday 1987, Jeffries 1991) permanent ponds, billabong (Hillman 1986), or lacustrine benthos (Rieradevall 1991, Lindegaard 1992, Petridis 1993). Other permanent systems, such as mountain peatlands (Erman and Erman 1975), show lower values, while streams in tropical regions (Pearson et al. 1986) are richer (Figure 3).

Table 5. Pearson correlation coefficients between richness and flooded surface or hydroperiod length in Espolla temporary pond and other temporary ponds. Legend: ** $p < 0.01$, * $p < 0.05$, ns $p > 0.05$.

Variables	r (Pearson)	n
Espolla hydroperiods		
log (richness)/log (flooded surface)	0.982**	7
richness/hydroperiod length	0.947**	7
Temporary ponds (macroinvertebrates)		
log (richness)/log (flooded surface)	0.781**	29
richness/hydroperiod length	0.461*	29
Temporary ponds (microcrustaceans)		
log (richness)/log (flooded surface)	0.742**	25
richness/hydroperiod length	0.344 ns	25

In conclusion, the faunal composition of temperate temporary aquatic ecosystems includes a remarkable number of (1) uncommon species, (2) species associated with permanent environments and (3) species that frequently or exclusively inhabit these environments due to their biological adaptations. This composition is typified as much by the presence of families with a large number of species (e.g., Dytiscidae or Chironomidae) as by the existence of common genera in wide biogeographical areas, but also by a wide variety of

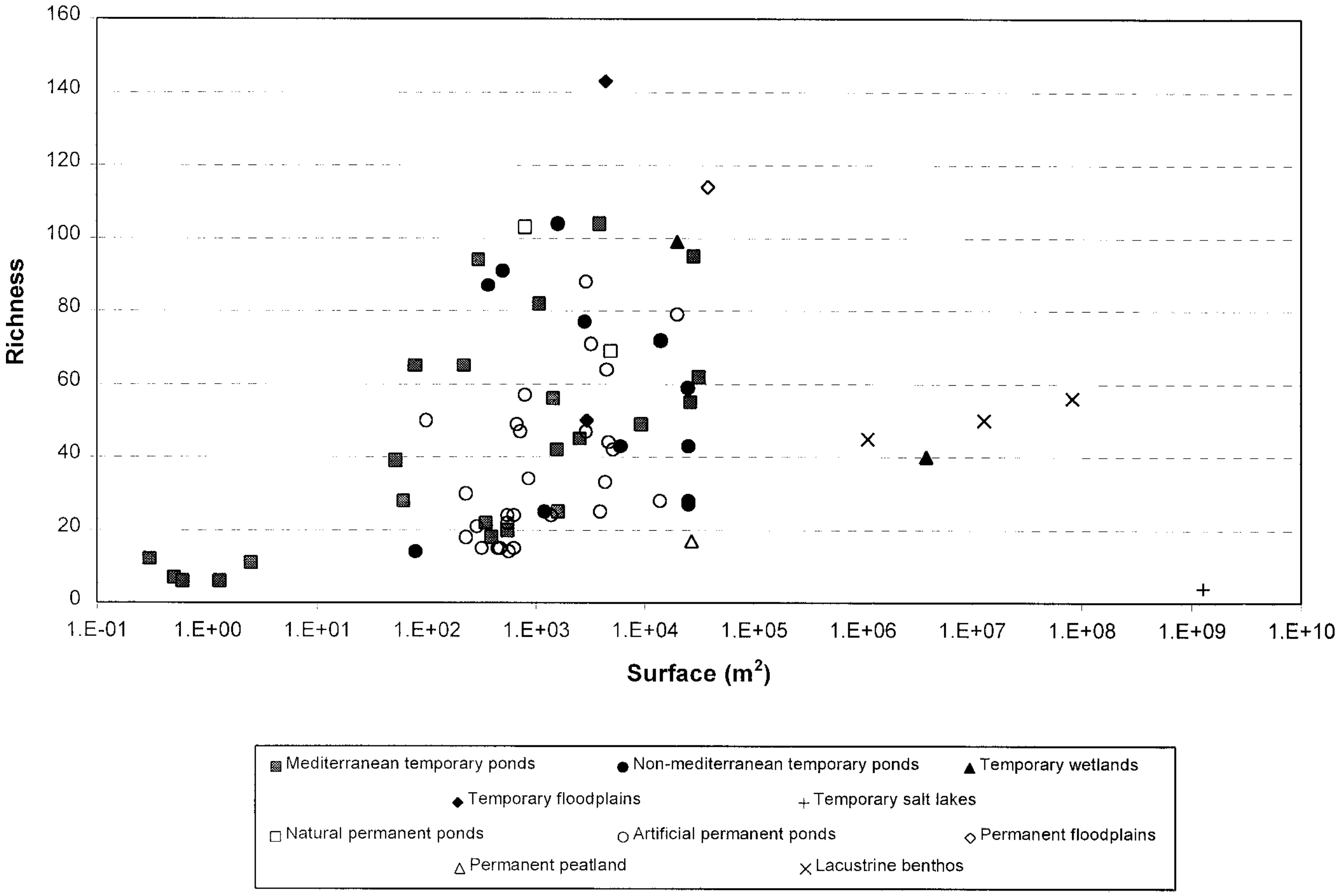

Figure 3. Relation between the surface of several waterbodies and macroinvertebrate richness.

faunal groups, contrary to the current point of view. Hydroperiod length and seasonality are the factors that mainly determine the composition of these environments. The richness of temporary environments does not seem to be smaller than that of permanent ones, without taking into account the richness of terrestrial fauna during the dry phase. In the context of temporary environments, the Mediterranean sites have a similar richness to other temperate areas, and apart from some environments with extreme richness, the majority have a richness determined by flooded surface and hydroperiod length. The composition and richness of temporary waters is at odds with a vision of highly constrained environments, perhaps because the importance of other factors that prevail here has been underestimated: high production and low predation. Thus, the importance of temporary waterbodies in an area for metapopulation dynamics (such as for amphibians or corixids) is explained by high production and low predation, particularly in the Mediterranean, where temporary waterbodies are more common than in other climatic regions. In spite of their biodiversity, temporary ecosystems have long been undervalued and their conservation neglected (Collinson et al. 1995). An effective implementation of strong policies for the conservation of these habitats can no longer be delayed.

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