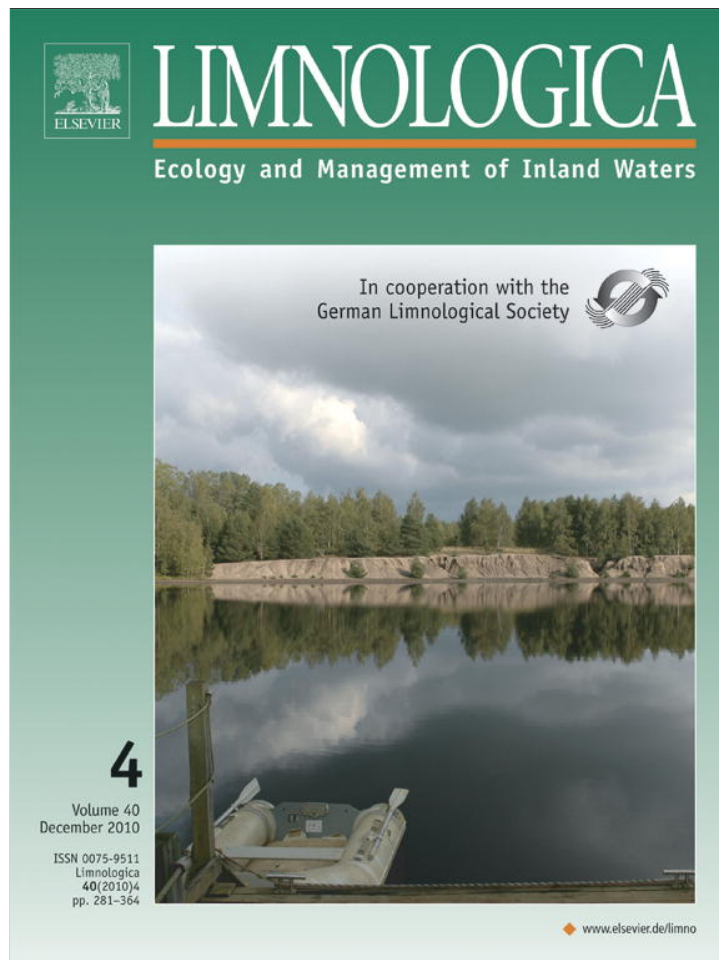


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Microdistribution of macroinvertebrates in a temporary pond of Central Italy: Taxonomic and functional analyses

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ABSTRACT

Spatial distribution of physical and chemical variables and macroinvertebrate composition, structure and functional aspects were investigated in five microhabitats available (*Ranunculus acquatilis*+*Ranunculus sardous*, *Spirogyra* sp., *Juncus effusus*, and unvegetated littoral sediments and central sediments) in a temporary pond near Rome during spring 2004. The central sediments were found to differ greatly from the other substrates. They were characterized by higher nutrient contents (total P, total N), organic matter and organic C, and silt and clay in the sediments, and lower dissolved oxygen content and lower pH in the water. Species richness and densities of total macrofauna showed the lowest values in central sediments and the highest ones in submerged macrophytes (*Ranunculus* spp.) and emergent vegetation (*Juncus effusus*). Oligochaeta Tubificidae, some Nematoda (*Dorylaimus* spp.), and Chironomidae Tanypodinae (*Procladius* sp. and *Psectrotanyptus varius*) and Chironominae (*Chironomus plumosus* group) characterized the central sediments, whereas Ephemeroptera and most of the Odonata and Coleoptera species were commonly found in submerged macrophyte beds. Some species of Coleoptera and Hemiptera (*Hygrobia hermanni*, *Helochaeres lividus*, *Berosus signaticollis* and *Gerris maculatus*) were mainly found in the algal substratum, and some Nematoda species (*Tobrilus* spp. and *Aporcelaimellus obtusicaudatus*), Oligochaeta Enchytraeidae, young larvae of *Sympetrum* and Diptera Ceratopogonidae in littoral sediments. *Juncus effusus* appeared to be mainly colonized by Chironomidae Orthocladiinae (*Psectrocladius sordidellus* group and *Corynoneura scutellata*) and Tanytarsini (*Paratanytarsus* sp.). Central sediments also favoured high abundances of collector-gatherers, burrowers and drought resistant forms with passive dispersal, whereas *Ranunculus* spp. hosted mainly scrapers, shredders, swimmers+divers and active dispersal forms without any resistant stages to desiccation. *Juncus* plants were mostly colonized by collector-filterers and by organisms capable of both active dispersal and surviving desiccation. Littoral sediments and algae showed similar functional organization and intermediate features between central sediments and submerged macrophyte beds. All these results demonstrate that microhabitat characteristics play a crucial role in selecting macroinvertebrate taxa according to their environmental requirement, feeding mechanism, movement and resistance to drought. Moreover, our study confirms the role of submerged and emergent vegetation in maintaining high biodiversity and suggests that all microhabitats should be considered to provide both an exhaustive collection of species for pond management and conservation and basic insights into the functioning of pond communities.

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1. Introduction

The three recent European Pond Workshops, hosted in Geneva (2004), Toulouse (2006) and Valencia (2008), and the European Pond Conservation Network (E.P.C.N., 2007) demonstrated that the importance of pond biota as a biodiversity resource is growing all over Europe. There has been a considerable increase in awareness of the importance of ponds as habitats able to support

a high number of species of which some are rare and threatened, together with a variety of (unique) flora and fauna. Scientific research into these ecosystems is, therefore, of the utmost importance. Ponds are globally recognized as being particularly important for amphibian (Beebe, 1997; Beja and Alcazar, 2003), macroinvertebrate (Collinson et al., 1995; Oertli et al., 2002; Nicolet et al., 2004) and aquatic plant conservation (Grillas and Roché, 1997; Linton and Goulder, 2000), contributing highly to freshwater biodiversity at a regional level.

Ponds, and particularly those of temporary character, are aquatic habitats with multiple constraints relating to their great abiotic variability, but this offers to species with particular

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adaptations many opportunities to succeed (Schwartz and Jenkins, 2000). For organisms inhabiting temporary waters, drought is the principal constraint, which is even greater because of its unpredictability with alternating dry and wet phases, which vary from year to year, especially in the Mediterranean region (Grillas and Roché, 1997). Their survival strategies adopted to cope with fluctuations in environmental conditions involve resistant stages, dormant parts, and life-cycle flexibility (Williams, 1985). These adaptations represent the driving factors in structuring biological assemblages in wetlands with different hydroperiod lengths (Wellborn et al., 1996).

Microdistribution of macroinvertebrates is well known in rivers and lakes where most results indicate that environmental aspects, including the heterogeneity of habitats, are generally mainly responsible for the spatial distribution of taxa in these waters. Particularly for running waters, stream hydraulics (Statzner and Higlér, 1986; Brooks et al., 2005) and land use (Resh et al., 1988) are the major determinants of benthic invertebrate zonation patterns. On the contrary, composition and abundance of aquatic plants (Waters and San Giovanni, 2002), substrate heterogeneity (Heino, 2000), depth, granulometry composition and oxygen content (Heino, 2000; Brinkhurst, 2002) seem to govern macroinvertebrate distribution in lakes. In contrast, relatively few studies have addressed the spatial distribution of the entire macroinvertebrate communities in ponds and wetlands (Oertli, 1995; De Szalay and Resh, 2000; Van der Meutter et al., 2008), or have been limited to only one taxonomic group (Fairchild et al., 2003; Bazzanti et al., 2008). In particular, three recent studies have dealt with the distribution of macroinvertebrate taxa, their size structure and functional aspects (Della Bella et al., 2005; Solimini et al., 2005; Bazzanti et al., 2009) in different mesohabitats (*sensu* Pardo and Armitage, 1997) of twenty-one temporary and permanent ponds in Central Italy. The results of the above-mentioned literature highlight that, in spite of their small size, ponds cannot be considered as uniform systems with homogeneous environmental and biological characteristics. In fact, they can offer biota a great heterogeneity of micro/mesohabitats. Despite the ubiquity of these temporary environments, much still remains unknown regarding the distribution of invertebrates in different microhabitats of ponds.

During the spring 2004, a study of a temporary pond in a nature reserve near Rome was carried out with the following aims:

- to evaluate the environmental differences of the five available microhabitats;
- to explore the spatial variation of the macroinvertebrate community within the pond and which abiotic variables regulate its composition, structure and functional aspects.

2. Study area and methods

2.1. Study area

The temporary pond studied (coded as T35 and locally named DOGANA) is located (Fig. 1) in the Presidential Nature Reserve of Castelporziano (about 20 km southwest of Rome), which encompasses a relatively undisturbed area of about 6000 ha and contains more than 160 temporary and permanent ponds. The Reserve is dominated by a Mediterranean climate characterised by dry and hot summers and mild winters. For a more detailed description of the study area, see Bazzanti et al. (1996, 2000, 2003). The study pond was of autumnal (fall) origin (autumnal ponds, *sensu* Wiggins et al. 1980) and the length of its

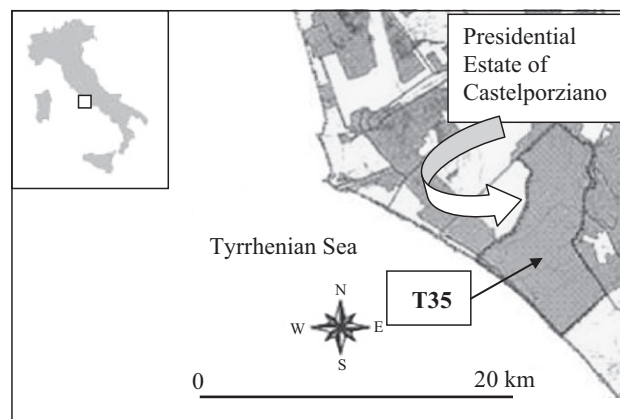


Fig. 1. Map of Castelporziano Presidential Estate with indication of temporary pond T35.

hydroperiod depends on rainfall, which usually peaks in autumn and spring. In the study year (2004), the wet phase of the pond lasted about 310 days. At the time of sampling, the surface area and maximum depth of the pond were about 2600 m² and 72 cm, whereas riparian tree and aquatic vegetation covers were about 1–5% and 30–40% of the pond surface area, respectively.

2.2. Sampling and laboratory methods

At the end of April 2004, we sampled macroinvertebrates using a dip net (opening 25 × 35 cm², mesh size 280 μm) for 1 m sweep in five available microhabitats (*Ranunculus acquatilis*+*R. sardous*, *Spirogyra* sp., *Juncus effusus*, littoral sediments, central sediments, the latter two unvegetated and very homogeneous in appearance). The net was dragged through and pushed into the sediments for about 5 cm in each microhabitat. This dip net samples macroinvertebrates from wetlands efficiently (Cheal et al., 1993) and the results have been also considered for quantitative studies to compare densities from different sites and/or ponds (Batzer et al., 2004; Geoffrey et al., 2003; Della Bella et al., 2005; Bazzanti et al., 2008). Ten replicates were collected in each microhabitat for a total of 50 biological samples. We sampled the macroinvertebrates in a period of the year, which is generally characterized by the highest richness of species (Bazzanti et al., 1996). The material was preserved in 10% formaldehyde solution to which we added Bengal Rose stain to facilitate the identification of organisms. Individuals were identified according to their lowest taxonomic possible level and assigned to different feeding categories and habits following Merritt and Cummins (1996) and Cummins and Wilzbach (1985), and to the four groups according to the different survival strategies of animals to drought reported in Wiggins et al. (1980). Clear explanations of the Wiggins et al. (1980) groups can also be found in Bataille and Baldassarre (1993) and Schneider and Frost (1996). Clingers were not considered because they are typically found in running water or in rocky littoral zones of lakes (Merritt and Cummins, 1996). For an example of functional trait assignment to taxa see Bazzanti et al. (2009).

At about 10–15 cm from the bottom of each microhabitat we registered (10 replicates) some water characteristics (pH, conductivity, dissolved oxygen) by electronic meters. Sediment characteristics, such as organic matter, organic carbon, total phosphorus and total nitrogen contents, and granulometric composition, were also measured by laboratory analysis, according to Cummins (1962), Gaudette et al. (1974), Marengo and Baudo (1988), and Bremner (1965), respectively. Environmental data of the study pond are reported in Table 1.

Table 1
Mean values and range (in parenthesis) of environmental variables (10 replicates) in the five microhabitats of the study pond.

Microhabitat environmental variable	LS	CS	A	SM	J
Conductivity ($\mu\text{s cm}^{-1}$)	87.2 (82.7–90.4)	90.1 (89.9–90.5)	81.1 (72.1–92.4)	89.6 (88.4–90.8)	92.6 (91.7–93.5)
Dissolved oxygen (mg L^{-1})	7.6 (7.2–8.7)	6.6 (6.0–7.7)	9.5 (8.1–10.9)	7.8 (7.0–9.4)	6.3 (5.7–6.9)
pH	8.1 (6.8–8.9)	7.6 (7.5–7.9)	9.3 (8.2–10.2)	9.1 (8.7–9.5)	8.7 (8.3–9.2)
Organic C (%)	0.39 (0.24–0.55)	1.24 (0.46–1.73)	0.35 (0.15–0.68)	0.25 (0.18–0.61)	0.36 (0.13–0.53)
Total N (%)	0.06 (0.04–0.10)	0.18 (0.12–0.29)	0.06 (0.03–0.10)	0.05 (0.03–0.09)	0.05 (0.03–0.07)
Total P (g Kg^{-1})	0.15 (0.11–0.20)	0.61 (0.28–0.87)	0.22 (0.13–0.89)	0.17 (0.10–0.32)	0.24 (0.11–0.29)
Organic matter (%)	3.1 (2.0–4.4)	10.5 (3.5–13.4)	4.1 (2.9–6.6)	2.0 (1.0–4.0)	3.5 (2.1–4.6)
Sand (%)	80.9 (73.0–87.8)	27.9 (11.2–74.4)	73.1 (57.9–84.8)	85.7 (74.2–92.2)	79.2 (71.0–92.2)
Silt (%)	9.3 (6.2–11.3)	28.5 (11.6–36.8)	13.7 (7.6–22.1)	7.1 (3.8–13.8)	10.6 (4.0–17.0)
Clay (%)	9.8 (6.1–16.2)	43.6 (14.0–56.1)	14.0 (10.2–22.1)	7.3 (4.5–12.1)	10.1 (4.0–15.2)

LS=Littoral sediments, CS=Central sediments, A=Algae (*Spirogyra* sp.), SM=Submerged macrophytes (*Ranunculus* spp.), J=*Juncus effusus*. Sampling was carried out at the end of April 2004.

2.3. Statistical treatment of data

Differences between microhabitat characteristics were estimated by one-way ANOVA and the *post hoc* Tukey test. The Spearman rank coefficient of correlation (r_s) was adopted to discover relationships among variables. Non-Metric Multidimensional Scaling (N-MDS) was performed on the similarity matrix based on the Bray-Curtis similarity coefficient (Clarke and Warwick, 1994) in order to summarize variations among sites and to elucidate environmental gradients taking environmental variables into account. Canonical Correspondence Analysis (CCA) was adopted to correlate abiotic characteristics and taxa (or functional group) abundances of the different microhabitats. Taxa present only in a replicate of a microhabitat and in very low densities (1 individual) were considered rare and excluded from the counts. Before the analyses, absolute data were $\log(x+1)$ transformed, while relative data were $\arcsin\sqrt{p}$ transformed, in order to stabilize the variance (Sokal and Rohlf, 1973). We performed our statistical analyses with Statistica (version 5), PRIMER 5 (version 5.2.0) and CANOCO 4.0 for Windows (ter Braak and Smilauer, 1998) software.

3. Results

3.1. Microhabitat environmental variables

Non-Metric Multidimensional Scaling (N-MDS) performed on physical and chemical data (Fig. 2) showed a clear separation of the central sediments from other substrates according to a gradient of decreasing total P and N, organic matter and C, silt and clay contents and increasing of the sand component. Along this gradient dissolved oxygen and pH in the water also increased. A second separation can be observed between algae and other substrates according to higher pH, and silt+clay and dissolved oxygen contents in the former microhabitat.

3.2. Macroinvertebrate–microhabitat associations

A total of 11,554 individuals belonging to 9 high zoological groups and to 63 lower taxa (mostly genera/species) of macroinvertebrates were recorded during the study (Table 2). The number of taxa was significantly lower in central sediments than in other substrates (ANOVA: $F_{4,45}=30.4$; $p < 0.001$; Tukey test: at least $p < 0.05$ for all comparisons). Densities of total fauna (Fig. 3) showed lower values in central sediments and algae and higher densities in submerged macrophytes and *Juncus* (ANOVA: $F_{4,45}=19.7$; $p < 0.001$; Tukey test: at least $p < 0.05$).

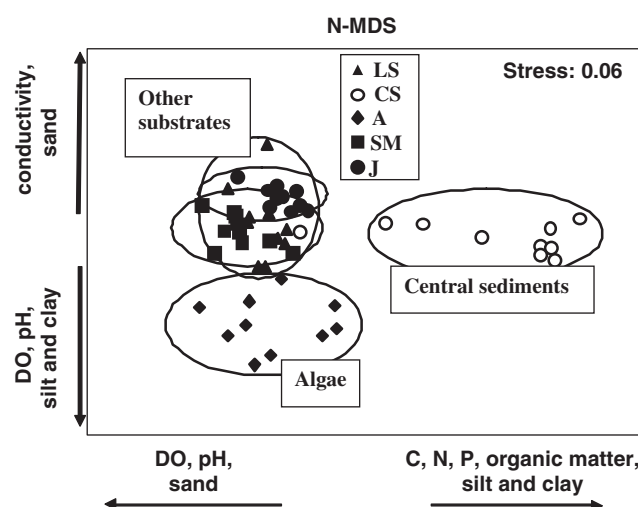


Fig. 2. Non Metric Multidimensional Scaling (NMDS) performed on the physical and chemical data of the different microhabitats (sampling was carried out at the end of April 2004) of the temporary pond T35. Arrows indicate environmental gradients according to r_s between site scores and abiotic variables (significance at least of $p < 0.05$). DO=dissolved oxygen. LS=Littoral sediments, CS=Central sediments, A=Algae (*Spirogyra* sp.), SM=Submerged macrophytes (*Ranunculus* spp.), J=*Juncus effusus*.

CCA, performed on high zoological group densities and environmental characteristics (Fig. 4 and Table 3), indicated an environmental gradient determined by nutrients and granulometry composition of the sediments along the first axis, and a second one along the second axis in relation to conductivity and oxygen content in the water. The plot give an immediate idea concerning the preferences of Oligochaeta and Nematoda for central sediments, whereas Odonata, Ephemeroptera and Coleoptera were commonly found in submerged macrophytes, Diptera Chironomidae in *Juncus*, Hemiptera in littoral sediments and algal substratum, and Diptera Ceratopogonidae in both littoral and central sediments. The results of this analysis on the high taxonomic groups appeared to be strongly affected by which substratum their higher densities occurred in and give only a preliminary description of the relationships between fauna and environmental variables. To obtain a more precise picture on this relationships a detailed analysis on lower taxa was therefore necessary.

CCA (Fig. 5 and Table 3) performed on lower taxa densities shows the same environmental gradients and gives a more detailed description of the relationships between taxa, microhabitats and environmental variables. Taxa characterizing less oxygenated, silty, and nutrient rich central sediments were the chironomids *Chironomus plumosus* group, *Psectrotanytus*

Table 2
List and presence (+) of macroinvertebrate taxa collected in the five microhabitats of the study pond T35.

TAXA	Code	LS	CS	A	SM	J
Turbellaria						
<i>Rhabdocoela</i> undet.	Rha	+	+	+	+	+
Nematoda						
<i>Aporcelaimellus obtusicaudatus</i> (Bastian)	Aobt	+	+	+	+	
<i>Dorylaimida</i> undet.	Dor	+	+	+	+	+
<i>Dorylaimus stagnalis</i> (Dujardin)	Dsta	+	+	+	+	+
<i>Mononchus</i> sp.	Mon	+	+	+	+	+
<i>Tobrilus diversipapillatus</i> (Daday)	Tdiv	+	+	+		
<i>T. stefansky</i> (Micoletzky)	Tste	+	+	+		
<i>Tobrilus</i> sp.	Tob	+	+	+		+
Oligochaeta						
Naididae undet.	Nai	+	+	+	+	+
Tubificidae undet.	Tub	+	+	+	+	+
Enchytraeidae undet.	Enc	+	+	+	+	
Lumbricidae undet.	Lum		+			
Hydracarina						
<i>Eylais tantilla</i> Koen					+	
<i>Hydracna skorikowi</i> Piersig					+	
Ephemeroptera						
<i>Cloeon dipterum</i> (Linnaeus)	Cdip	+		+	+	+
Odonata						
<i>Ischnura elegans</i> (Van der Linden)					+	
<i>Lestes barbarus</i> (Fabricius)	Lbar	+	+	+	+	+
<i>Sympetrum fonscolombei</i> (Sélys)	Sfos			+	+	
<i>S. sanguineum</i> (Muller)	Ssan			+	+	+
<i>Sympetrum</i> sp.	Sym	+				
Hemiptera						
<i>Corixa punctata</i> (Illiger)	Cpun	+	+	+	+	+
<i>Sigara lateralis</i> (Leach)	Slat		+	+	+	
<i>Notonecta</i> sp.	Not					+
<i>Anisops sardeus</i> Herrich-Schaeffer						+
<i>Gerris maculatus</i> Tamanini	Gmac			+	+	
<i>Plea minutissima</i> Leach	Pmin	+			+	+
Coleoptera						
<i>Brychius</i> sp.	Bry			+	+	+
<i>Peltodytes</i> sp.				+	+	
<i>Hygrobia hermanni</i> (Herbst)	Hher	+	+	+	+	+
<i>Agabus bipustulatus</i> (Linnaeus)	Abip	+	+	+	+	
<i>Agabus nebulosus</i> (Forster)	Aneb	+	+	+	+	
<i>Coelambus confluens</i> (Fabricius)		+				
<i>Laccophilus minutus</i> (Linnaeus)	Lmin	+	+	+	+	
<i>Hydroglyphus pusillus</i> (Fabricius)	Hpus	+				
<i>Hydroporus pubescens</i> (Gyllenhal)	Hpub	+		+	+	
<i>Hyphydrus aubei</i> Ganglbauer	Haub	+		+	+	
<i>Berosus signaticollis</i> (Charpentier)	Bsig	+		+	+	
<i>Helochaeres lividus</i> (Forster)	Hliv	+		+	+	
<i>Coelostoma</i> sp.	Coe	+		+	+	
Diptera						
<i>Anopheles maculupennis</i> Meigen				+	+	+
<i>Culex martinii</i> Medschid		+				
<i>Monopelopia</i> sp.						+
<i>Labrundinia longipalpis</i> (Gtgh)						+
<i>Zavrelimyia</i> sp.	Zav	+		+		
<i>Macropelopia</i> sp.	Mac	+		+	+	
<i>Procladius</i> sp.	Pro	+	+	+	+	
<i>Psectrotanyptus varius</i> (Fabricius)	Pvar		+	+	+	
<i>Corynoneura scutellata</i> (Winnertz)	Cscu	+		+	+	
<i>Isocladius sylvestris</i> (Fabricius)	Isyl	+		+	+	
<i>Limnophyes</i> sp.	Lim	+		+	+	
<i>Psectrocladius sordidellus</i> gr.	Psor	+		+	+	
Orthoclaadiinae sp. 1			+			
Orthoclaadiinae sp. 2					+	
Orthoclaadiinae sp. 3	Ort				+	+
Orthoclaadiinae sp. 4						+
<i>Micropsectra</i> sp.	Mic	+		+		
<i>Paratanytarsus</i> sp.	Par	+		+	+	
<i>Chironomus plumosus</i> gr.	Cpl		+			
<i>Microtendipes pedellus</i> gr.				+		
<i>Dicrotendipes lobiger</i> gr.						+
<i>Polypedilum nubifer</i> (Skuse)						+
Ceratopogonidae undet.	Cer	+	+	+	+	+
Diptera alia	Alia	+		+	+	+
Number of taxa		38	16	37	42	36

Microhabitat codes are reported as in Table 1. Taxon codes are reported only for taxa used in Fig. 5.

varius and *Procladius* sp., Oligochaeta Tubificidae and the nematode *Dorylaimus* spp. The submerged vegetated area, in which pH and oxygen content showed intermediate values

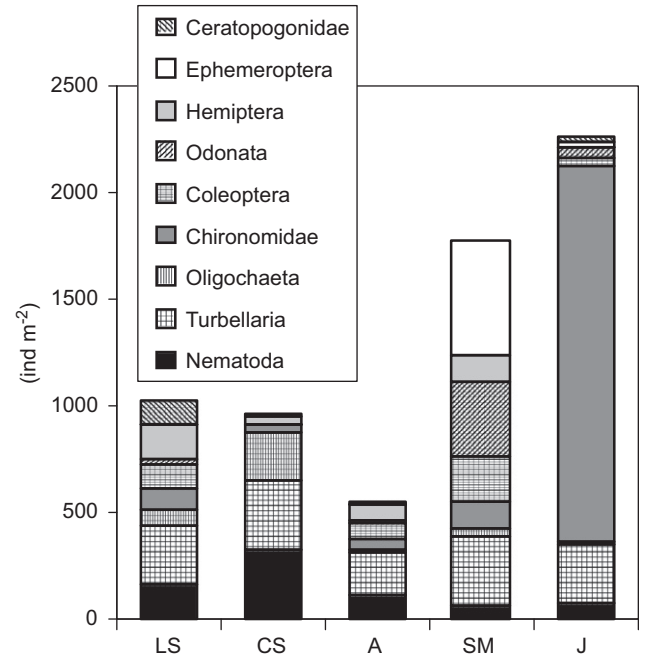


Fig. 3. Mean densities (ind m⁻²) of zoological groups in the studied microhabitats of the temporary pond T35. Microhabitat codes are reported as in Fig. 2. The group "Alia" (Hydracarina and Diptera alia) was not represented because of its very low densities in all microhabitats.

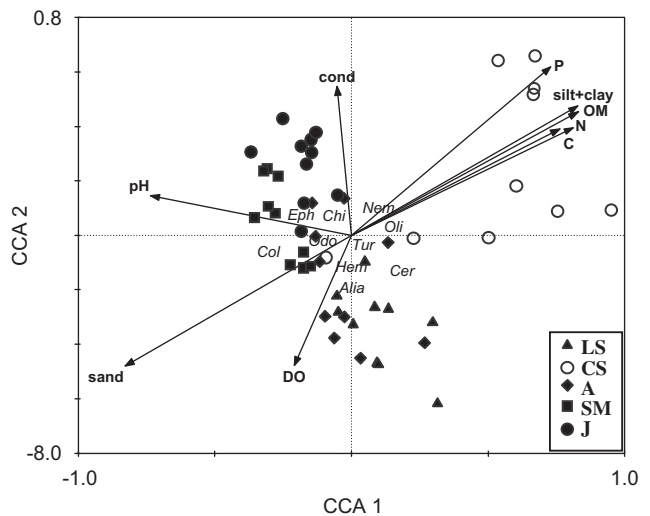


Fig. 4. Canonical Correspondence Analysis (CCA) biplot of environmental-high zoological group relationships of the temporary pond T35. DO=dissolved oxygen, cond=conductivity, OM=organic matter, N, P and C=total nitrogen, total phosphorus and organic carbon contents, respectively. *Tur*=Turbellaria, *Nem*=Nematoda, *Oli*=Oligochaeta, *Eph*=Ephemeroptera, *Odo*=Odonata, *Hem*=Hemiptera, *Col*=Coleoptera, *Chi*=Chironomidae, *Cer*=Ceratopogonidae, *Alia*=Hydracarina, Diptera alia. Microhabitat codes are reported as in Fig. 2.

between algal sites and central sediments, hosted mostly some chironomid Orthoclaadiinae (especially *Psectrocladius sordidellus* group), the odonates *Lestes barbarus*, *Sympetrum fonscolombei*, the heteropteran *Plea minutissima*, the coleopterans *Agabus bipustulatus*, *Hyphydrus aubei*, Oligochaeta Naididae, and the ephemeropteran *Cloeon dipterum*. The heteropteran *Notonecta* sp., the coleopteran *Brychius* sp., and especially the chironomids *Corynoneura scutellata*, *Iocladius sylvestris*, *Psectrocladius sordidellus* group and *Paratanytarsus* sp. characterized in high abundances the *Juncus* stand in which higher conductivity and

Table 3

Summary of Canonical Correspondence Analyses (CCA) performed on high zoological group, low taxa and functional group abundances and environmental variables of the temporary pond T35.

CCA (high zoological groups)				
Axes	1	2	3	4
Eigenvalues	0.106	0.028	0.012	0.007
Zoological group–environment correlations	0.874	0.756	0.607	0.432
Cumulative percentage variance				
number of zoological group data	32.9	41.6	45.3	47.5
number of zoological group–environment relation	65.3	82.6	89.9	94.3
CCA (low taxa)				
Axes	1	2	3	4
Eigenvalues	0.283	0.210	0.087	0.062
Taxa–environment correlations	0.925	0.891	0.787	0.757
Cumulative % variance				
number of taxa data	14.1	24.6	28.9	32.0
number of taxa–environment relation	37.1	64.6	76.0	84.2
CCA (functional groups)				
Axes	1	2	3	4
Eigenvalues	0.069	0.020	0.008	0.004
Functional group–environment correlations	0.836	0.701	0.563	0.559
Cumulative % variance				
number of functional group data	33.2	42.9	46.5	48.3
number of functional group–environment relation	65.0	83.9	91.0	94.5

For all three analyses: overall CCA was significant at $p=0.001$, CCA axis 1 at $p=0.001$ (Monte Carlo test).

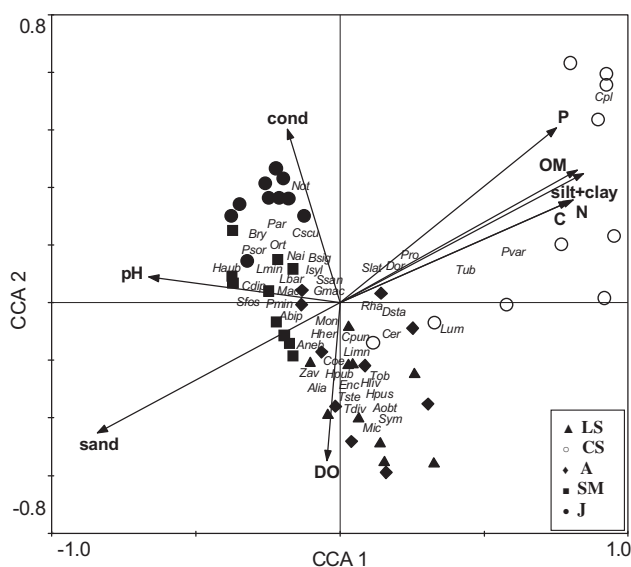


Fig. 5. Canonical Correspondence Analysis (CCA) biplot of environmental–low taxa relationships of the temporary pond T35. DO=dissolved oxygen, cond=conductivity, OM=organic matter, N, P and C=total nitrogen, total phosphorus and organic carbon contents, respectively. Taxon codes are reported as in Table 2, microhabitat codes as in Fig. 2.

lower oxygen content were found. Finally, littoral sediments and algal sites appeared to partially overlap the CCA graphic because of their reciprocal closeness along the pond perimeter. The plot of axes 1–3 of the same CCA (the figure is not reported here) allows, however, to distinguish the littoral sediments characterized by lower pH and oxygen content from the well oxygenated algal sites. The first microhabitat hosted the exclusive presence of the chironomid *Limnophyes* sp. and the coleopteran *Hydroglyphus pusillus*, and higher densities of the nematodes *Tobrilus* spp. and *Aporcelainellus obtusicaudatus*, Oligochaeta Enchytraeidae, young odonate larvae belonging to *Sympetrum* sp. and Diptera Ceratopogonidae, whereas algal mats were mostly colonized by the hemipterans *G. maculatus* and the coleopterans *Hygrobia hermanni*, *Helochares lividus* and *Berosus signaticollis*.

3.3. Functional organization–microhabitat associations

Also the abundances of functional groups showed substantial differences among the study microhabitats, which seemed to contain one or two dominant functional groups (Fig. 6). In almost all the microhabitats, predators, sprawlers+climbers and Groups 1 and 4 of Wiggins et al. (1980) were found to be the most abundant groups. CCA (Fig. 7 and Table 3), performed on percentage data of functional feeding groups, habits and Wiggins et al. (1980) groups considered together, showed that environmental characteristics of central sediments favoured collector-gatherers, burrowers and Group 1 of Wiggins et al. (1980), whereas *Ranunculus* spp. hosted high percentages of scrapers, swimmers+divers and Groups 3 and 4 of Wiggins et al. (1980). *Juncus* was mostly colonized by collector-filterers, whereas littoral sediments showed higher proportion of Group 2 of Wiggins et al. (1980). Littoral sediments and algae showed intermediate functional features between central sediments and submerged macrophyte beds.

4. Discussion

4.1. Environmental features of the five microhabitats

To date, the research of the abiotic characteristics of temporary ponds has been generally limited to few works (Zacharias et al., 2007). As regards their temporal variations, Arle (2002) and Angélibert et al. (2004) reported that in temporary ponds most physical and chemical features widely fluctuate both seasonally and diurnally. Podrabsky et al. (1998) recorded a high degree of variation of abiotic factors among interpool habitats. Moreover, Kłosowski and Jabłońska (2009) recorded significant physical and chemical differences in both water and sediments between several types of phytocoenoses in widely fluctuating water bodies. Finally, Magnusson and Williams (2006) found that spatial and temporal variations were of greater importance than biological factors (including food-web manipulations) for shaping the environmental characteristics of these intermittent ponds. Our study indicates that great physical and chemical differences occurred also within the same pond. These differences were

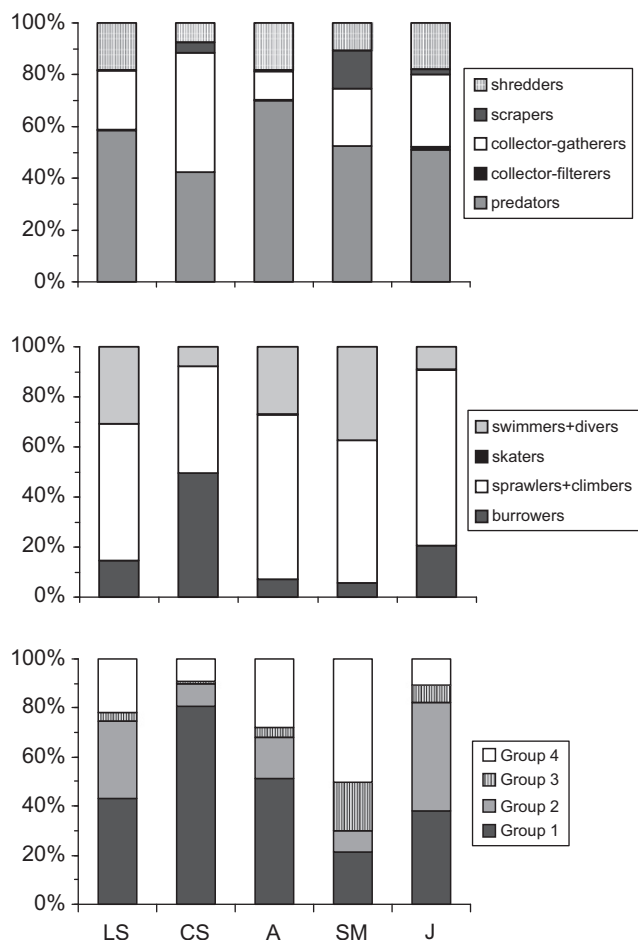


Fig. 6. Mean percentage composition (calculated from number of individuals) of functional groups (functional feeding groups in upper panel, habits in middle panel and Wiggins groups in lower panel) in the different microhabitats of the study pond T35. Microhabitat codes are reported as in Fig. 2.

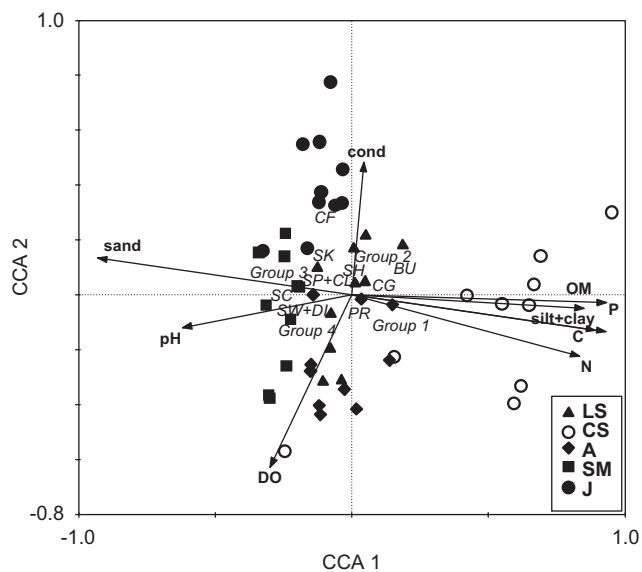


Fig. 7. Canonical Correspondence Analysis (CCA) biplot of environmental-functional group relationships of the temporary pond T35. DO=dissolved oxygen, cond=conductivity, OM=organic matter, N, P and C=total nitrogen, total phosphorus and organic carbon contents, respectively. CF=Collector-filterers, CG=Collector-gatherers, SH=Shredders, SC=Scrapers, PR=Predators. SK=Skaters, SP+CL=Sprawlers + Climbers, SW+DJ=Swimmers + Divers, BU=Burrowers. Groups 1–4=Groups of Wiggins et al. (1980). Microhabitat codes are reported as in Fig. 2.

related to photosynthetic activity of vegetation, granulometric composition of the sediments, rate of sedimentation and decomposition of organic matter within the pond. As regards the granulometric composition, central sediments showed higher abundances of silt and clay, whereas the other substrates were found to mostly have a sandy texture. Temporary ponds are subject to a complete drying out of the soil, which means they are exposed to air for one or more times in a year. This process can cause a faster mineralization of organic matter and a marked fractioning of the coarse component of the soil (Bazzanti et al., 2000; Tavernini et al., 2005), which associated to the concave morphology of the basin, favours fine-sediment accumulation in the centre of the pond.

4.2. Macroinvertebrate–microhabitat associations

The lowest taxonomic richness and abundances of the macroinvertebrate community were registered in a unvegetated central zone and these results are consistent with those of other authors (Schramm and Jirka, 1989; Beckett et al., 1992; Olson et al., 1995) for shallow lakes. Therefore, in this microhabitat very fine sediments, higher values of nutrients, and lower oxygen content tend to reduce faunal diversification and abundance compared to the other substrates. These abiotic characteristics well reflect the ecological requirements of some Nematoda (*Dorylaimus* spp.), Oligochaeta Tubificidae, and chironomid larvae belonging to *C. plumosus* group, *P. varius* and *Procladius* sp. (Wiederholm, 1980; Fittkau and Roback, 1983; Pinder and Reiss, 1983; Abebe et al., 2006).

Compared to central sediments, the littoral unvegetated zone seems to offer better conditions for organisms showing amphibian or semiaquatic conditions of life, such as Oligochaeta Enchytraeidae (Brinkhurst, 1963) and the chironomid *Limnophyes* sp. (Cranston et al., 1983). This substrate seems also to favour invertebrates living in sandy texture of sediments, such as the nematodes *Tobrilus* spp. and *A. obtusicaudatus* (Abebe et al., 2006) or some insects needing to reach the littoral in order to become adults through pupation of mature larvae, such as the dipteran Ceratopogonidae (V.M. Glukhova, Zoological Institute of St. Petersburg, pers. comm.). In a study on three vegetation types, Oertli (1995) found a high density of Ceratopogonidae larvae on *Thypha latifolia* stems, but his study excluded unvegetated sediments. Only a taxonomic identification to genera or species level could explain the different preferences of this dipteran family for some microhabitats.

Larval and adult insects belonging to several orders and families, however, mostly dominated the two vegetated substrates, which showed distinct differences between them. In general, the influence of macrophytes on the composition and abundance of macroinvertebrate taxa of lentic environments is well known and several authors (Beckett et al., 1992; Harper et al., 1997; Waters and San Giovanni, 2002) have highlighted the determinant role of the vascular macrophytes in providing many benefits, such as good oxygenation and greater stability of sediments, a more diversified environment, abundant food coming from senescent plants and algal periphyton development. Van der Meutter et al. (2008), exploring differences in some macroinvertebrate families living in three vegetation types in ponds, recorded a preference of Baetidae and Coenagrionidae larvae for submersed macrophytes. We obtained similar results in our pond, where Odonata, and particularly *L. barbarus* and *S. fonscolombei*, appeared to be strictly associated to the two *Ranunculus* species. According to some authors (Osborne and Samways, 1996; Foote and Rice Hornung, 2005), these insects seem to select ponds where they can lay their eggs according to

the availability of sunny shores and to the high morphological habitat complexity provided by the presence of abundant vegetation, in which larvae can avoid predation and find abundant prey. Also the ephemeropteran *C. dipterum* seemed to be strongly dependent on submerged vegetation where this species is favoured by the availability of food in the form of senescent vegetation and/or algal periphyton (see discussion on feeding functional groups). In spite of their wide distribution in the study pond, some hemipteran and coleopteran species also seemed to prefer submerged macrophytes (Williams and Feltmate, 1992; Fairchild et al., 2003) where they could find prey and good oxygen conditions in order to lay their eggs (Merritt and Cummins, 1996). Finally, some Oligochaeta Naididae appeared associated to this vegetated substrate where they benefit from lower risk of predation and higher food resources represented by algal periphyton (Dvořák and Best, 1982).

As regards the emergent vegetation, our finding that chironomid larvae numerically dominated in *Juncus* is an interesting record, which has already been reported by Benke et al. (1999) for *Juncus* and Van der Meutter et al. (2008) for *Phragmites* and *Thypha*. In particular, in our samples, Orthoclaadiinae (*P. sordidellus* group and *C. scutellata*) and Tanytarsini (*Paratanytarsus*) were greatly abundant in *Juncus effusus* where they act as miners (Coffman and Ferrington, 1996), finding vascular tissues of plants as food and refuge from predation (Nocentini, 1985; Wrubleski, 1999). Moreover, *Juncus* plants possess tissues with greater structural stability, allowing some macroinvertebrates to climb on them, and providing a great quantity of organic matter, which accumulates and serves as a food source (Dvořák and Best, 1982; Parsons and Matthews, 1995; Varga, 2001). In particular, *P. sordidellus* seems to have more advantages than other chironomid taxa because it better resists drops in water levels (Evans et al., 1999) typical of the littoral zones where *Juncus* is abundant. Finally, we found the exclusive presence of the two hemipterans *Notonecta* sp. and *A. sardeus* in *Juncus* plants because they can simultaneously find protection against predators (i.e. aquatic birds) and act as predators on small invertebrates (Williams and Feltmate, 1992). In synthesis, the wide range of food resources and the better environmental conditions, such as greater habitat stability, good refuge from predation, high quantity of organic matter coming from both emergent and submerged macrophytes, are the major driving factors behind the increase in species richness and densities of macroinvertebrate communities in ponds.

Finally, in our pond filamentous algal mats showed high taxonomic richness but low densities of macroinvertebrates. In spite of the fact that algae generally constitute a good source of food for macroinvertebrates (Hart and Lovvorn, 2003), their lower densities compared to those observed in macrophytes can be probably attributed to the production by algae of substances, which can reduce growth determining even the death of some invertebrates (Porter, 1973) and to the higher availability of food (algal periphyton, senescent and living tissues) in macrophyte beds rather than in filamentous algae. However, the limited published data concerning this matter makes it difficult for us to formulate further hypothesis regarding the preference of macroinvertebrates for this substrate.

4.3. Functional group–microhabitat associations

The functional aspects have generally been little investigated in aquatic lentic systems (i.e., Dvořák and Best, 1982; Heino, 2000), and very few data are available for ponds, especially in the Mediterranean area. These data generally deal with the phenological sequences (Bazzanti et al., 1996; Culioli et al., 2006), differences between temporary and permanent ponds (Bazzanti and Della Bella, 2004), relationships with wet phase duration (Gascon et al., 2008)

and vegetation cover (Céréghino et al., 2008), and distributional organization in mesohabitats (Bazzanti et al., 2009).

As regards the distribution of functional feeding groups in our pond, shredders (taxa belonging to several taxonomic groups) and predators (i.e. some species of Coleoptera and Hemiptera and all Odonata) showed similar abundances everywhere, with the exception of central sediments where they occurred in lower percentages, probably due to the low availability of coarse particulate organic matter (CPOM) and available prey therein. Differently, collector-gatherers, such as *Chironomus* larvae, Nematoda and Oligochaeta Tubificidae, dominated in central sediments where they can find great quantities of small-sized organic matter (FPOM) as food (Merritt and Cummins, 1996; Heino 2000). On the contrary, scrapers (i.e. *C. dipterum*, some Naididae and chironomid species) were found to be dominant in submerged macrophytes which, as already mentioned, provide abundant growth of algal periphyton which live on them (Brittain, 1982; Merritt and Cummins, 1996). Finally, collector-filterers (i.e. the chironomids *Paratanytarsus* sp., *Microtendipes* sp. and *Dicortendipes* sp., and all Culicidae) were mostly associated to *Juncus* plants where the higher conductivity probably produces high quantities of algal seston on which they fed (Bazzanti and Della Bella, 2004).

As regards the habit traits, submerged macrophytes, algae and littoral zone hosted mostly swimmers+divers (i.e. some Hemiptera and Coleoptera taxa), which generally swim among plants and algae (Merritt and Cummins, 1996), whereas spawlers+climbers (i.e. Ephemeroptera and Odonata) were found mostly on submerged macrophytes, *Juncus*, and algae in which they are well adapted to moving on the three-dimensional-shaped vegetation (Crowder and Cooper, 1982; Hargeby, 1990). Differently, burrowers (Oligochaeta Tubificidae, Nematoda and sedentary Chironomidae) were typically found in soft central sediments (Minshall, 1984; Beckett et al., 1992).

The distribution of Wiggins et al. (1980) groups in the five studied microhabitats seems to be particularly interesting because no data exist on this matter, except for a recent work on mesohabitats in ponds (Bazzanti et al., 2009). Resident (or passive colonizers) organisms (mostly Oligochaeta and Nematoda), belonging to Group 1, are commonly found in central sediments, where they are well adapted to resisting desiccation through eggs, larvae and adults (entire or pieces) (Wiggins et al., 1980; Williams, 1985; Williams, 1987). Group 2, which contains active dispersal animals with oviposition dependent on water and can resist desiccation through eggs, larvae and adults (i.e. some coleopterans and chironomid Orthoclaadiinae), seems to colonize mostly littoral sediments and *Juncus* probably because they need living near the pond margins and on emergent plants in order to lay their eggs. On the contrary, Group 3 (i.e. part of Odonata species), which needs no water for oviposition and can resist desiccation and Group 4 (such as larvae and adults of Coleoptera and Hemiptera, larvae of Ephemeroptera and most of the chironomids) represented by mobile elements, which possess no way of resisting desiccation, are mostly hosted in submerged vegetation. The elements of this group are considered as cyclic colonizers (Williams, 1987) living in temporary ponds during the water phase where they prey and migrate as adults in permanent habitats to avoid desiccation.

5. Concluding remarks

Our study demonstrates that microhabitats play a driving role in the spatial distribution of macroinvertebrate assemblages and their functional groups in ponds, and more particularly our data show:

- substantial differences between the five microhabitats studied indicating that they can provide to macroinvertebrates different resources related to physical and chemical characteristics, food types and feeding mechanisms, type of movements and resistance to drought;
- the higher number of macroinvertebrate taxa and their densities occurring in the macrophyte beds confirm the role of submerged and emergent vegetation in maintaining high biodiversity compared to the other substrate types;
- the presence of some taxa, which appeared to be exclusively related to a specific microhabitat or which were more abundant in some microhabitats than in others, suggests that all microhabitats present in a pond have to be sampled for an exhaustive collection of macroinvertebrates and highlights the importance of the knowledge of species microdistribution in pond management and conservation because a high microhabitat diversity can support a high faunal diversity.

Data on microdistribution of macroinvertebrate taxonomic and functional organization are therefore not only vital for biodiversity conservation purposes and for monitoring water quality in ponds but also for providing a basic ecological understanding of pond functioning. These points constitute a fundamental step in conservation management of ponds, which can be considered as “reservoirs” of species, which tend to favour the (re-)colonization of neighbouring water bodies more or less affected by anthropogenic pressure.

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