

Differential responses of zooplankton assemblages to environmental variation in temporary and permanent ponds

Zooplankton of temporary and permanent ponds

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Abstract Permanent and temporary wetlands in Mediterranean shrublands represent unique repositories of biodiversity, which are increasingly threatened by human-induced habitat loss. The zooplankton of a permanent (P1) and a temporary pond (T35) in the Natural Reserve of Castelporziano, a rare residual stretch of such a shrubland in Central Italy (Latium), was investigated to: (1) expand and deepen knowledge of these endangered freshwater habitats, which represent a crucial component of Mediterranean biodiversity; (2) identify environmental controls regulating the development of zooplankton communities of each environment; and (3) highlight differences in the adaptive responses of the zooplankton community in relation to the different ecological conditions experienced by permanent and temporary habitats. Despite summer desiccation in T35, the two ponds exhibited a relative homogeneity in hydrological and physico-chemical dynamics. Zooplankton assemblages contained 41 total taxa, of which 32 were found in P1 and 28 in T35. Out of the 41 taxa identified, 22 (>50%) were exclusively present in one of the two ponds. On a yearly basis, the community

dynamics of P1 seemed to be conditioned by physical and chemical factors and by hydrological cycle characteristics, while the community of T35 responded to algal blooms, food competition and predator/prey equilibria rather than correlating to abiotic factors. The main differences amongst zooplankton assemblages were observed over short time scales and occurred both within and between seasons, highlighting the role of some structural taxa that dominated the average composition of the community throughout the year, and the importance of “quick-response” taxa in determining the short-term composition and structure variation of pond zooplankton. A year-round cyclic community succession peculiar to each pond is described.

Keywords Zooplankton · Freshwater ponds · Biodiversity · wetlands · Mediterranean ecosystems

Introduction

In recent decades, a large number of salt marshes, coastal lagoons and peatlands have been progressively reclaimed, mostly for agricultural purposes. Meanwhile, both scientists and conservationists have increasingly focused on the qualitative and quantitative impoverishment of these ecosystems and their geographical fragmentation. This has

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led to a widely shared perception of the need for the conservation and restoration of wetlands, considered “hot spots” of plant and animal biodiversity (Williams 1999). Consequently, there is an increasing demand for a better understanding of the ecosystem dynamics of these complex and vulnerable habitats, which provide a valuable opportunity to enhance our comprehension of basic ecological and evolutionary processes in aquatic population dynamics.

In the literature, most aspects of wetlands assessment, classification and management refer to larger water bodies, generally of greater interest to human exploitation (e.g. Whigham et al. 1993; Tiner 1999; Gopal et al. 2000, 2001), whereas only a few studies focus on small biotopes, such as temporary and permanent pools and their communities (Mahoney et al. 1990; Collinson et al. 1995; Watson et al. 1995; Spencer et al. 1999); furthermore, many of these studies focus mainly on single-taxon biology or are part of large scale habitat surveys such as the UK National Pond Survey (Williams et al. 1998). The importance of the limnological and hydrobiological characteristics of small ponds (i.e. hydroperiod, size, water chemistry, macrophytic and microalgal vegetation, etc.) and their consequences on the development, the seasonal evolution and the predictability of their communities, are often neglected, in spite of the large number of taxa surviving and flourishing in these fluctuating environments and the role they play in contributing to the biodiversity of large scale ecosystems such as Mediterranean shrublands (Fahd et al. 2000). In this respect, the zooplankton assemblages of these biotopes attract considerable ecological interest. They tend to be highly diversified and constituted by both rare and very common pioneer species with fast turnover; this guarantees a high adaptive plasticity to cope with environmental fluctuations, allowing the community to survive the drought phase as resistant eggs or cysts, and to resume numerical dominance as soon as the pond enters a new wet phase.

In this paper, we present a comparative study of the zooplankton of a permanent and a temporary pond in Central Italy, with the aim to: (a) explore relationships between community dynamics and habitat parameters, and (b) highlight

adaptive responses of zooplankton to different hydrological patterns. At the regional level, we intend to contribute to a better knowledge and appreciation of these small freshwater biotopes, which represent an endangered component of Mediterranean biodiversity, to which few studies have been devoted thus far (i.e. Crosetti and Margaritora 1987; Mura 1991; Bazzanti et al. 1996; Vagaggini et al. 2002; Marrone et al. 2006). More generally, we show how the occurrence of a one-month dry phase, within a scenario of otherwise identical climatic conditions, leads to marked differences in ecosystem functioning.

Study site

The study was carried out in the Natural Reserve of Castelporziano, which constitutes a rare residue of Mediterranean shrubland situated 20 km SW of Rome along the Latium coast (Italy). The high floristic and faunistic biodiversity which characterises this area has been the subject of several studies during a five-year monitoring project (1994–1998) supported by the General Secretariat of the Italian Presidency and aimed at the development of a geographical information database regarding flora, fauna and environmental characteristics (SITAC, Sistema Informativo Territoriale Ambientale di Castelporziano). The Reserve covers a surface area of about 6,000 ha and is dominated by a Mediterranean climate characterised by dry and hot summers and mild winters, with rainfall concentrated in autumn and spring (mean annual rainfall: 750 mm; Moisélo 1998). The Castelporziano reserve hosts many different habitats with numerous small ponds (>160). These are shallow rain-fed freshwater bodies, which can be permanently, semi-permanently or temporarily inundated. Their depth and surface area vary consistently with the rainfall seasonality and the high evaporation rates, causing wide and sudden variations in abiotic parameters.

For the purpose of this research, started in April 1999, we chose a permanent pond (hereafter named P1) located in the northern zone of the reserve, and a temporary autumnal pond (*sensu* Wiggins et al. 1980, labelled T35) in the southern

zone. While T35, situated 6 km from P1, regularly undergoes a dry phase in August, P1 did not dry out during at least the last 20 years (Margaritora, pers. comm.). The ponds are known to be isolated from groundwater (Fricano et al. 2001) and depend on a precipitation pattern that is relatively consistent over the whole study area.

During 1985–1987 a rich population of mosquitofish (*Gambusia holbrooki*) dwelt in P1, following their introduction as a measure to contrast *Anopheles* mosquitoes, but disappeared in 1988–1998 possibly as a consequence of extreme water level fluctuations (Margaritora et al. 2001). During the investigation period the surface area of P1 at maximum water level was 500 m² while T35 reached 699 m².

Available data of total P and total N in the two ponds come from Fricano et al. (2001), and correspond to the following annual mean values in P1 and T35, respectively: 0.67 mg l⁻¹ and 1.05 mg l⁻¹ for total P, 2.44 mg l⁻¹ and 3.33 mg l⁻¹ for total N.

Another difference between the two ponds relates to the presence of aquatic macrophytes. In spring and early summer, P1 is covered by *Myriophyllum alterniflorum*, *Potamogeton polyg-onifolius*, *P. trichoides* and *Callitriche cophocarpa* (Lattanzi, pers. comm.), up to a seasonal maximum of 95% of the sediment surface area in June, whereas no macrophytes usually grow in T35.

Both study ponds are fishless but are colonised by rich communities of benthic macroinvertebrates (Bazzanti et al. 1996, 2003), by amphibians and reptiles (i.e. *Rana agilis*, *Hyla intermedia*, *Bufo bufo*, *Triturus italicus*, *T. cristatus carnifex*, *Emys orbicularis*, *Natrix natrix*), and intensely frequented, especially P1 in summer, by large terrestrial vertebrates such as wild boar (*Sus scrofa*), fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*).

Materials and methods

Samples were collected fortnightly from April 1999 to April 2000. In both the ponds, zooplankton was sampled quantitatively using a plankton net (opening diameter 25 cm, mesh size 80 µm) attached to a handle. This allowed the net to be

used on one side of the operator, to avoid the samples being affected by bottom sediment disturbance caused by walking, as would probably be the case using a towed net. A preliminary evaluation performed during the high-water period indicated that a 10-m transect corresponded to the sampling effort beyond which no further zooplankton species were likely to be collected. That is, the curve describing the number of species versus the sampling transect length became asymptotic.

Since the distribution of plankton inside the ponds is usually non-homogeneous and depends upon different factors, such an exposure to sunlight, algal blooms, submerged macrophytes growth, canopy fragmentation, wind action, etc., the 10 m sampling transect was broken up into two or more sub-transects, to better characterise pond microhabitats. The data obtained were later pooled. Moreover, depending on the changes in the pond size from maximum filling to drought, the length of the sampling transect was suitably modified. On each sampling date, a further qualitative sample, always much larger than the quantitative one, was collected in order to verify sampling effectiveness, and to facilitate the identification of some taxa by means of in vivo observations (i.e. rotifers).

The zooplankton collected was preserved in 4% formalin to which 40 g l⁻¹ of sucrose had been added, to prevent female cladocerans from losing eggs (Haney and Hall 1973). Samples were allowed to settle and then diluted to a specific volume (250 ml or more), depending on the amount of sedimented zooplankton obtained. Up to ten 1-ml subsamples, depending on zooplankton abundance, were taken from each diluted sample for counts and identification down to the lowest possible taxonomic level. The resulting numbers were then related to the volume unit (as individuals l⁻¹). Pond morphological characteristics were recorded on each sampling occasion (T35 was likened to an ellipse, P1 to a circle). Water temperature, pH, conductivity and dissolved oxygen were measured by means of submersible probes. Rainfall data related to the study period were kindly supplied by the Environment Protection Bureau of the Castelporziano Reserve.

We expressed the zooplankton species richness (R) as number of taxa, and calculated Shannon's H diversity index and J evenness index (Pielou 1969). Paired sampling dates allowed the calculation of Percent Similarity (PSc) and the Jaccard's similarity (J_c) coefficient using Kovach's *MVSP* 3.1 software (1999). Applying both the PSc coefficient (based upon percent densities of species) and the J_c coefficient (which considers only presence–absence and species ubiquity), allowed us to obtain both a quantitative and a qualitative evaluation of zooplankton community similarity. The zooplankton density data matrix was analysed by Canonical Correspondence Analysis (CCA, Ter Brack 1986; *MVSP* 3.1 Kovach's software 1999). Correlation between parameters was tested by means of non-parametric Spearman's r_s , while zooplankton density differences were tested by means of the non-parametric Mann–Whitney U test (Zar 1984) both performed with *Statistics* 5.1 software (1997). In order to simplify graphical representations, in all the figures sampling dates were reported as codes (Table 1).

Table 1 Dates of sampling with the correspondent codes utilised in the graphs

Dates	Codes
26 April 1999	A1
11 May 1999	M1
25 May 1999	M2
8 June 1999	Jn1
21 June 1999	Jn2
6 July 1999	J11
21 July 1999	J12
6 August 1999	Au1
25 August 1999	Au2
9 September 1999	S1
23 September 1999	S2
6 October 1999	O1
19 October 1999	O2
3 November 1999	N1
18 November 1999	N2
2 December 1999	D1
16 December 1999	D2
29 December 1999	D3
11 January 2000	Ja1
24 January 2000	Ja2
7 February 2000	F1
21 February 2000	F2
6 March 2000	Mr1
20 March 2000	Mr2
3 April 2000	A2

Results

The volume of the two ponds (Fig. 1) decreased progressively from spring to summer 1999 along with temperature increase and precipitation decrease. Pond T35 dried up in August, while the volume in P1 reached its minimum yearly level (1.2 m^3). Maximum values were reached in January in both ponds. The maximum depths observed during the time of investigation reached 75.2 cm and 69.0 cm in P1 and in T35, respectively.

During the study period, water temperature (Fig. 1) was similar in both biotopes and the temperature range varied from 29.9°C (August) to 5.8°C (January) in P1 and from 27.2°C (July) to 5.0°C (January) in T35. The shallowness of the basins did not allow any thermal stratification of the water column.

pH values (Fig. 2a) were higher in T35 than in P1. In P1 the range of pH varied from 4.28 to 8.18, with both the minimum and the maximum values reached in July. In T35 the pH was less variable, from 5.70 (September) to 7.42 (February), with the majority of values in the vicinity of the neutral point.

Conductivity (Fig. 2b) in the spring summer period displayed a quite different pattern in the two ponds: in T35 it constantly increased until it reached a maximum value ($389.0 \mu\text{S cm}^{-1}$) in

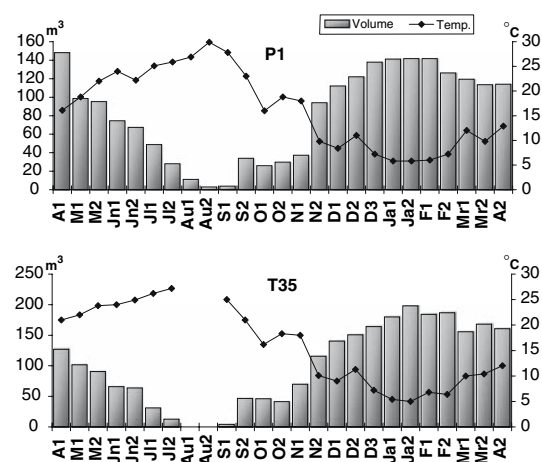


Fig. 1 Water temperature and volume variations in P1 and T35 during the period of investigation. Codes of sampling dates as in Table 1

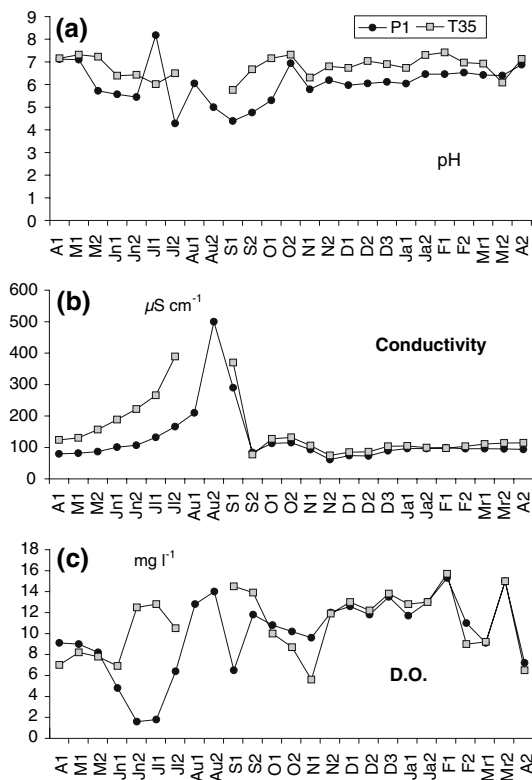


Fig. 2 Variations of pH, conductivity and dissolved oxygen values in P1 and T35 during the period of investigation. Codes of sampling dates as in Table 1

summer (July), whereas in P1 the values remained consistently low, and then increased to a maximum value ($500.0 \mu\text{S cm}^{-1}$) in August. The lowest values were reached in November for both ponds ($74.4 \mu\text{S cm}^{-1}$ and $61.3 \mu\text{S cm}^{-1}$ for T35 and P1, respectively), corresponding to the peak rainfall season.

In both ponds dissolved oxygen levels fluctuated widely over short time intervals (Fig. 2c). In P1 the minimum value (1.6 mg l^{-1}) was recorded in June, while the maximum value was reached in February (15.3 mg l^{-1}). In T35 the minimum value occurred in November (5.6 mg l^{-1}) and the maximum in February (15.7 mg l^{-1}).

The zooplankton community in P1 was comprised of 32 taxa: 17 rotifers, 9 cladocerans and 6 copepods (Table 2). All taxa identified in the qualitative hauls were always found also in the quantitative samples, confirming sampling representativity. The seasonal dynamics of the three groups are shown in Fig. 3. In P1, rotifers

Table 2 List of taxa collected in the ponds studied, with respective presence notation (+)

	P1	T35
Rotatoria		
<i>Epiphanes brachionus</i> v. <i>spinosus</i> (Rousselet)	+	
<i>Brachionus patulus</i> (O.F.M.)	+	
<i>Brachionus angularis</i> Gosse		+
<i>Brachionus quadridentatus</i> Hermann	+	+
<i>Brachionus urceolaris</i> (O.F.M.)	+	+
<i>Platylas quadricornis</i> (Ehrenberg)	+	
<i>Keratella tropica</i> (Apstein)	+	
<i>Keratella quadrata</i> (O.F.M.)	+	+
<i>Keratella cochlearis</i> gr. Ruttner & Kolisko	+	+
<i>Kellicottia longispina</i> (Kellicott)	+	+
<i>Euchlanis dilatata</i> Ehrenberg		+
<i>Mytilina ventralis</i> (Ehrenberg)	+	
<i>Lecane luna</i> (O.F.M.)	+	+
<i>Trichocerca</i> sp.		+
<i>Synchaeta</i> sp.	+	
<i>Polyarthra vulgaris dolichoptera</i> gr. (Carlin)	+	+
<i>Asplanchna girodi</i> De Guerne	+	
<i>Asplanchna sieboldi</i> (Leydig)		+
<i>Filinia terminalis</i> (Plate)	+	+
<i>Hexarthra mira</i> (Hudson)	+	+
<i>Sinantharina socialis</i> (L.)	+	+
Cladocera		
<i>Ceriodaphnia reticulata</i> (Jurine)	+	
<i>Ceriodaphnia laticaudata</i> P.E. Müller		+
<i>Scapholeberis rammneri</i> (Dumont & Pensaert)	+	
<i>Simocephalus vetulus</i> (O.F.M.)	+	+
<i>Daphnia chevreuxi</i> Richard		+
<i>Daphnia obtusa</i> Kurz	+	+
<i>Moina micrura</i> Kurz	+	+
<i>Macrothrix hirsuticornis</i> Norman & Brady	+	+
<i>Chydorus sphaericus</i> (O.F.M.)	+	+
<i>Leydigia leydigi</i> (Schoedler)	+	+
<i>Alona rectangula</i> G.O. Sars	+	
<i>Alona nuragica</i> Margaritora		+
Copepoda		
<i>Eudiaptomus padanus etruscus</i> (Losito)	+	+
<i>Mixodiaptomus kupelwieseri</i> (Brehm)		+
<i>Cyclops abyssorum</i> G.O. Sars	+	+
<i>Megacyclops viridis</i> (Jurine)	+	
<i>Acanthocyclops robustus</i> (Sars)		+
<i>Microcyclops</i> sp.	+	
<i>Microcyclops varicans</i> (Gurney)	+	
<i>Harpacticoida</i> undet.	+	+

(Fig. 3a) reached their highest densities during summer (maximum in September: $447 \text{ individuals l}^{-1}$), with *Hexarthra mira*, *Polyarthra vulgaris dolichoptera* gr. and especially *Brachionus urceolaris* being the most abundant. In winter, abundance decreased to a minimum of $0.7 \text{ individuals l}^{-1}$ (early December). Rotifer abundance did not correlate with any environmental variable.

The cladoceran seasonal dynamic (Fig. 3b) in P1 was characterised by relatively high spring densities in April (27 individuals l^{-1}), built up by *Ceriodaphnia reticulata* and *Simocephalus vetulus*, the only species which occurred during this period. In early summer the abundance of the group decreased, and there were no cladocerans in late August and September. After the autumn recolonisation, the group remained numerically stable; *Daphnia obtusa* and *Chydorus sphaericus* became dominant. Variations in cladoceran density correlated significantly with water volume ($r = 0.63$, $P < 0.01$) and conductivity ($r = -0.61$, $P < 0.01$). Correlation coefficients indicated a significant inverse relationship between rotifer and cladoceran densities ($r_s = -0.58$, $P < 0.005$). In P1 copepods were the most abundant group (Fig. 3c). The dominant species was *Eudiaptomus padanus etruscus*, while *Megacyclops viridis* and

Microcyclops varicans were exclusive to the spring period of 1999. In summer, we observed a progressive decline in copepods, followed by a new colonisation and a maximum group density in mid October (203 individuals l^{-1}). No significant correlation between copepod density and any environmental variable was found.

Pond T35 exhibited up to 10 times greater zooplankton densities than the permanent pond, while the total number of species was similar to P1 with 28 taxa collected consisting of 14 rotifers, nine cladocerans and five copepods (Table 2). The seasonal dynamics of the three groups are shown in Fig. 4. In the first samples, rotifers exhibited high-density fluctuations with a peak of 1,185 individuals l^{-1} in late June, just before summer drought (Fig. 4a); the commonest species were *Filinia terminalis* and *Brachionus urceolaris*. In September, T35 was recolonised by *Brachionus*

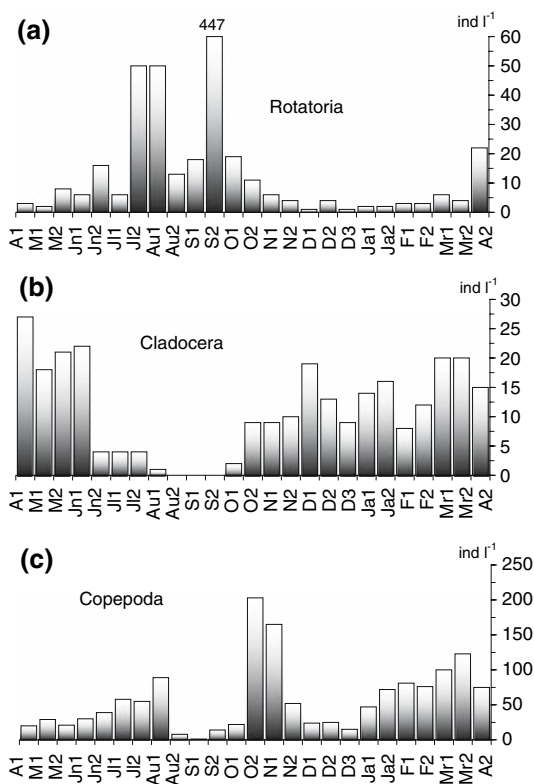


Fig. 3 Density variations of the three major zooplanktonic groups in P1 during the period of investigation. Codes of sampling dates as in Table 1. Please note the different unit scales

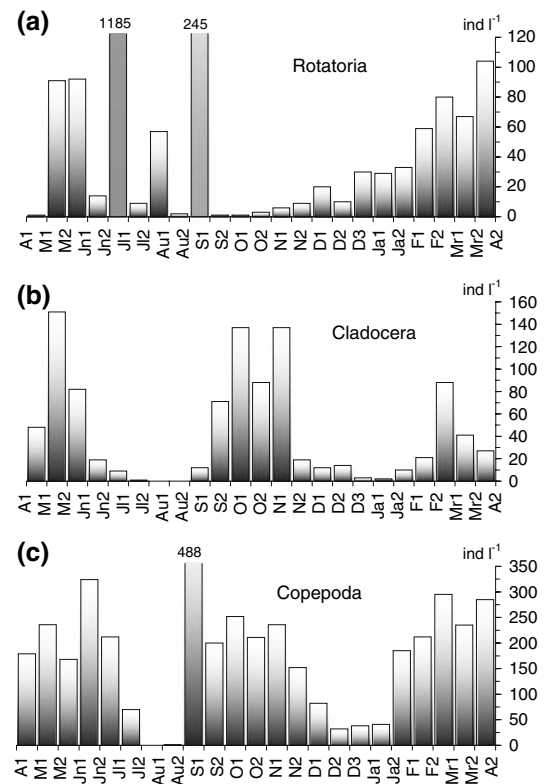


Fig. 4 Density variations of the three major zooplanktonic groups in T35 during the period of investigation. Codes of sampling dates as in Table 1. Please note the different unit scales

quadridentatus (205 individuals l^{-1}), but shortly afterwards rotifer densities collapsed (minimum value: 0.1 individuals l^{-1} in early October), to build slowly up again over winter with *Sinanthrerina socialis*, *Polyarthra vulgaris dolichopectera* gr. and *Keratella tropica*. No significant correlation of rotifers with any environmental variable was found. In T35, cladocerans (Fig. 4b) reached peak densities in spring (151 individuals l^{-1} , May) with *Daphnia obtusa* being the dominant species followed by *Moina micrura*, and then in October, but collapsed during winter down to 2.1 individuals l^{-1} (January). Cladocerans were not found to be significantly correlated with any of the abiotic environmental variables. As in P1, copepods were the most abundant group in T35 as well (Fig. 4c). Copepods (mainly *Acanthocyclops robustus*) appeared in all samples with huge densities. In summer and autumn this species accounted for the entire copepod community (maximum: 488 individuals l^{-1} , September), while in spring it co-occurred with *Eudiaptomus padanus etruscus* and in winter with *Cyclops abyssorum*; their minimum density occurred in December (32 individuals l^{-1}). In T35, no significant correlation was found between any zooplankton group and environmental variables.

The seasonal dynamics of the zooplankton communities in the studied ponds can be interpreted by observing the seasonal evolution of species richness (R) and the Shannon diversity index (H) and by the application of Canonical Correspondence Analysis to biological and environmental data. In P1 (Fig. 5), the highest values of R and H were recorded in spring 1999 (R maximum: 18 taxa, May; H : 2.9, June) and the lowest values in summer (minimum R in September: 2 taxa and H : 0.2). In autumn, species richness increased again, but the Shannon index did not, due to over-dominance by *Eudiaptomus padanus etruscus*. In pond T35 species richness and Shannon index values followed a similar pattern to what we observed in P1 (Fig. 5), but in this pond diversity values maintained more uniform levels over the whole year (R maximum: 13, February and maximum H : 2.03, December). The PSc and Jc similarity coefficients, calculated for paired sampling dates of P1 and T35, evidenced low values (Table 3), never exceeding 35% (PSc)

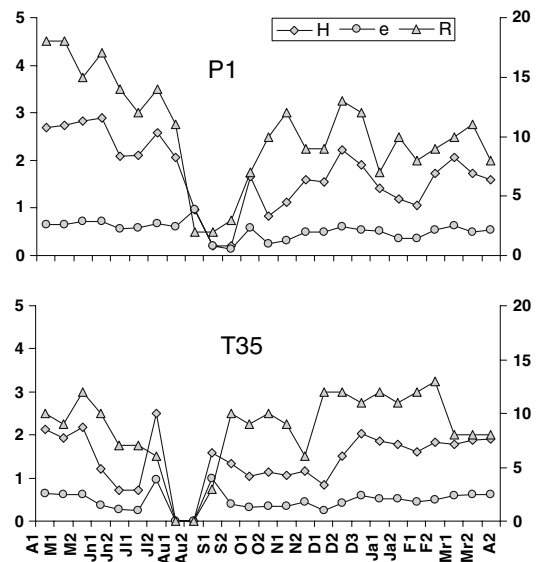


Fig. 5 Trend of number of taxa (R), diversity (H) and evenness (e) indices values in P1 and T35 during the period of investigation. Codes of sampling dates as in Table 1

or 0.538 (Jc) of similarity. Generally, PSc indicated higher similarity during the winter–spring period, while the Jc coefficient showed greater similarity in the winter samples alone.

The plot of the first two axes of the CCA performed on P1 environmental and biological data (Fig. 6a) shows two main clusters segregated along CC1 (34.56% of explained variance), which is positively correlated with temperature and negatively correlated with dissolved oxygen. A positive correlation is also observed for CC2 (12.2% of explained variance) and conductivity, while a similar but inverse correlation exists for the latter axis with pH and with pond size variables. The left hand-side group of clusters relates to the November–March samples with the addition of A2, while the right hand-side group relates to the April–July samples. Samples collected at the height of summer appear scattered between the two groups in a circular shape.

The first two axes of CCA plotted for T35 (Fig. 6b) show a tight, collapsed grouping of the winter–spring data and, unlike P1, no other distinct cluster, but a scattered distribution of data relative to the April–October period. CC1 (27.5% of explained variance) is positively

Table 3 Values of PSc and Jaccard's coefficients calculated for paired sampling dates of P1 and T35. The August samples were neglected in the calculation

Dates	PSc	Jaccard
A1	12.821	0.12
M1	7.939	0.286
M2	7.067	0.286
Jn1	3.465	0.174
Jn2	1.123	0.105
Jl1	0.262	0.056
Jl2	5.013	0.053
Au1	–	–
Au2	–	–
S1	0	0
S2	3.041	0.182
O1	0.16	0.231
O2	0.312	0.25
N1	1.836	0.167
N2	4.049	0.154
D1	7.697	0.4
D2	10.395	0.471
D3	26.299	0.438
Ja1	3.901	0.462
Ja2	5.728	0.4
F1	8.074	0.538
F2	21.165	0.375
Mr1	16.632	0.2
Mr2	34.794	0.267
A2	6.64	0.333

correlated with temperature and conductivity, and negatively correlated with pond size variables; conversely CC2 (15.13% of explained variance) does not significantly correlate with any environmental parameter.

Discussion and conclusions

As already observed in previous studies on the ecology and hydrology of the Castelporziano shallow waterbodies (Bazzanti et al. 1996; Fricano et al. 2001; Vagaggini et al. 2002), the annual rainfall and temperature regime cause profound changes to: water levels and volumes, conductivity, and to a lesser extent to: pH values, nutrient availability and oxygen concentrations. This confirmed the true surface nature of these ponds, which are known to be unrelated even to the upper layers of groundwater catchments (Fricano et al. 2001).

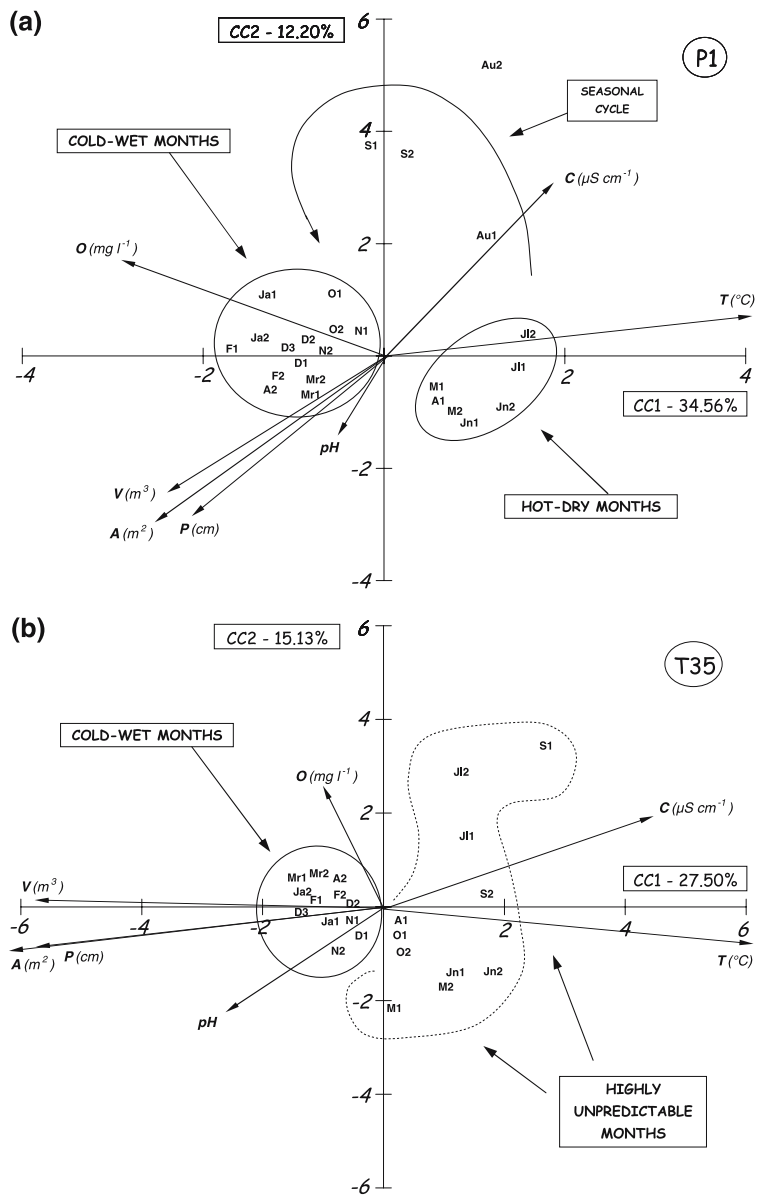
Both ponds had similar hydrological cycles and temperature fluctuations, except that pond T35

became desiccated in August 1999, whereas P1 remained wet. Especially in P1, pH and conductivity showed a high variation range, while oxygen concentrations varied widely over short time scales in both ponds, with minima occurring at different times. Pond T35 exhibited a three-times higher nutrient concentration, probably due to the more effective mineralisation of organic matter, which occurs in drying biotopes; this created conditions for recurrent algal blooms, which determined the fluctuation of the above-mentioned parameters. As known for some other astatic pools (Lopez et al. 1991; Toja et al. 1991), in P1 nutrient availability remained under the control of macrophytes and no algal blooms occurred. Different macrophyte taxa (i.e. *Potamogeton* sp. and *Callitriche* sp.) affected conductivity and pH to a different extent, producing more or less alkaline microhabitats by means of their photosynthetic activity (Riis et al. 2000). Macrophytes with floating leaves are known to prevent oxygen exchange at the water/air interface, in direct proportion to surface coverage (Gee et al. 1997). Such physiological controls explain the relative independence from the hydrological cycle observed in P1; rather than following the cycle, physico-chemical parameters were under the influence of biotic mechanisms regulating nutrient utilisation, oxygen production/consumption and pH.

The two study ponds contained similar numbers of rotifer, cladoceran and copepod taxa. Nineteen taxa were common and ubiquitous, while 13 were exclusive of P1 and 9 of T35; amongst these, 8 taxa occurred only in one or two sampling dates. The high percentage of exclusive taxa observed in these two small ecosystems (37.5% in P1 and 32.1% in T35) indicates that several small ponds are likely to support a higher global biodiversity than a single large wetland of equivalent surface, as already observed by Gee et al. (1997).

Unlike the former ones, the occurrence of rare and occasional taxa showed no relation with the hydrological cycle, as shown by Fahd et al. (2000). In each pond, a group of eurytopic taxa dominated the planktonic community throughout different seasonal phases; however, the assemblage of species was markedly different for the two ponds.

Fig. 6 Plot of first two axes of the CCA performed on P1 and T35 abiotic parameters and density data of zooplankton. Codes of sampling dates as in Table 1



The presence of a restricted number of species could be attributed to main habitat characteristics. *Daphnia chevreuxi* and *Alona nuragica* are considered to be typical of temporary ponds (Stella and Margaritora 1968). *Simocephalus vetulus*, present only from April to July in P1, is closely linked to the presence of the aquatic macrophytes amongst which it feeds (Corigliano and de Bernardi 1978; de Bernardi et al. 1978); consequently it was unable to colonise pond T35

(it was found in T35 only once, with few individuals). *Ceriodaphnia reticulata* appeared in P1 during the period of macrophyte cover and, at the same time, low density of *Daphnia obtusa*. The cladoceran succession appears to be partly driven by changes in vegetation cover as observed in the littoral zone of lakes (Paterson 1993) and in prairie coastal wetlands (Hann and Zrum 1997). The absence of macrophyte canopy in T35, and the higher availability of phytoplankton, seems to

favour the succession of free-swimming species such as *Daphnia obtusa* and *Eudiaptomus padanus etruscus*.

With regards to quantitative aspects, the difference between the two ponds was remarkable; population densities in T35 rose up to 10-fold the density levels observed in P1, partly depending on sudden blooms of a small number of species. The ability of such taxa (i.e. *Brachionus urceolaris*, *Daphnia obtusa*) to invade the environment in huge numbers over very short time intervals is often linked to fluctuations of resource availability, predation intensity (Williamson 1983; Stenberger 1985) and food competition. The relative contribution of biotic and abiotic factors in determining changes in the communities remains a challenging question. Sudden changes in temperature and oxygen concentrations occurring during the critical switch from late spring to summer predictably affected the turnover of specific cladoceran taxa, which have well known physiological limits of tolerance to hot and anoxic conditions (Roman et al. 1993; Bertilsson et al. 1995; Davidson et al. 1998). These same changes affected species as *Brachionus urceolaris*, which is able to exploit algal blooms and is adapted to higher temperatures (Xi and Huang 2000). More difficult is to explain possible effects of abrupt variation of pH values occurring in P1 in July (see Fig. 2a), probably due to the peak in photosynthetic activity followed by a bulk of decaying plant matter. Even if the inhibitory consequences of long-lasting acid conditions on entomostracan are well known, there is no literature dealing with the effects of variation occurring over such a short period.

As portrayed in Fig. 5, Shannon diversity (H) followed similar seasonal dynamics in the two ponds, despite their different species composition. Species richness resulted a little higher and much more variable in P1; this could be related to the presence of macrophytes and the microhabitats that they contribute to establish (Van der Brink et al. 1994; Serrano and Toja 1998).

Pond T35 was characterised by a less uniform distribution of individuals amongst the species, an instability which could not be specifically or exclusively related to hydrological cycle characteristics. Differences between the two ponds were

highest in spring, corresponding to the period of macrophyte growth. Consistently, PSc and Jc similarity coefficients (Table 3), show higher levels during the colder months, when abiotic factors such as temperature, dissolved oxygen and water volume, tend to produce uniform conditions in the two ponds.

The variability of environmental factors is clearly reflected in the CCA distribution of sample points along the first axis, which corresponds with the main community changes.

“Cold month” samples formed a quite uniform group in respect of a more scattered “warm month” group of samples characterised by unstable oscillating changes which took place primarily between July and October. Conductivity, pond size, and to a lesser extent pH, assume extreme values in warmer months; during these periods within the ponds, zooplankton populations struggle to find their own equilibrium. A cyclical pattern is recognisable in the anticlockwise returning of the autumnal sample-points to the “colder months” structure.

In the CCA plot of T35, CC1 is positively correlated with temperature and negatively with depth, area and volume. It is along this axis that the main differentiation is observed: not a clustering, but rather a “collapsed versus scattered” structure, with cold months (high water volume) virtually undifferentiated and warmer months all chaotically scattered. The community appeared to be quite unaffected by oxygen concentrations, but it seemed to respond to changes in basin size. Stability was higher during the colder season while unpredictable blooms occur in the warmer season, accompanied by the development of “quick-response” taxa. During summer, unpredictable fluctuations of taxa prevent any cyclical pattern of sample-points to be recognised. A stable “cold month” structure is resumed as soon as the water volume rises again.

The dynamics of zooplankton communities in P1 and T35 appear to be quite different. The permanent pond follows a predictable pattern, defined by the cyclic return of similar environmental conditions, regulated by hydrological, physical and chemical cycles. In the temporary pond, only the colder months follow this path; during the remaining period, the community has

to face harsh and sudden biotic events, which favour particularly adapted taxa often exclusive of temporary waters.

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References

- Bazzanti M, Baldoni S, Seminara M (1996) Invertebrate macrofauna of a temporary pond in Central Italy: composition, community parameters and temporal succession. *Archiv Für Hydrobiol* 137:77–94
- Bazzanti M, Della Bella V, Seminara M (2003) Factors affecting macroinvertebrate communities in astatic ponds in Central Italy. *J Freshwater Ecol* 18:537–548
- Bertilsson J, Bęrzziński B, Pejler B (1995) Occurrence of limnic micro-crustaceans in relation to temperature and oxygen. *Hydrobiologia* 299:163–167
- Collinson NH, Biggs J, Corfield A, Hodson MJ, Walker D, Whitfield M, Williams PJ (1995) Temporary and permanent ponds: an assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. *Biol Conserv* 74:125–133
- Corigliano MC, de Bernardi R (1978) Experimental population dynamics and competition in *Daphnia obtusa* Kurz and *Simocephalus vetulus* (O.F. Müller) (Crustacea, Cladocera). *Memorie dell'Istituto Italiano di Idrobiologia* 36:65–83
- Crosetti D, Margaritora FG (1987) Distribution and life cycle of cladocerans in temporary pools from central Italy. *Freshwater Biol* 18:165–175
- Davidson NL Jr, Kelso WE, Rutherford DA (1998) Relationships between environmental variables and the abundance of cladocerans and copepods in the Atchafalaya River Basin. *Hydrobiologia* 379:175–181
- de Bernardi R, Lacqua P, Soldavini E (1978) Effects of temperature and food on developmental times and growth in *Daphnia obtusa* Kurz and *Simocephalus vetulus* (O.F. Müller) (Crustacea, Cladocera). *Memorie dell'Istituto Italiano di Idrobiologia* 36:171–191
- Fahd K, Serrano L, Toja J (2000) Crustacean and rotifer composition of temporary ponds in the Doñana National Park (SW Spain) during floods. *Hydrobiologia* 436:41–49
- Fricano F, Neri U, Scandella P, Di Blasi N, Mecella G (2001) Studio del sistema di alimentazione di invasi naturali in un particolare ambiente umido costiero mediterraneo. *Accad Naz delle Scienze Scritti e Documenti XXVI*:99–109
- Gee JHR, Smith BD, Lee KM, Griffiths SW (1997) The ecological basis of freshwater pond management for biodiversity. *Aquat Conserv Marine Freshwater Ecosyst* 7:91–109
- Gopal B, Junk WJ, Davis JA (eds) (2000) Biodiversity in wetlands: assessment, function and conservation, vol I. Backhuys Publishers, Leiden, The Netherlands, 354 pp
- Gopal B, Junk WJ, Davis JA (eds) (2001) Biodiversity in wetlands: assessment, function and conservation, vol II. Backhuys Publishers, Leiden, The Netherlands, 311 pp
- Haney JF, Hall DJ (1973) Sugar-coated *Daphnia*: a preservation technique for Cladocerans. *Limnol Oceanogr* 18:331–333
- Hann BJ, Zrum L (1997) Littoral microcrustaceans (Cladocera, Copepoda) in a prairie coastal wetland: seasonal abundance and community structure. *Hydrobiologia* 357:37–52
- Kovach WL (1999) MVSP – a multivariate statistical package for windows, ver. 3.1. Kovach Computing Services: Pentraeth, Wales, UK
- López T, Toja J, Gabellone N (1991) Limnological comparison of two peridunar ponds in Doñana National Park (Spain). *Archiv Für Hydrobiol* 120:357–378
- Mahoney DL, Mort MA, Taylor BE (1990) Species richness of calanoid copepods, cladocerans and other branchiopods in Carolina Bay temporary ponds. *Am Midl Nat* 123:244–258
- Margaritora FG, Ferrara O, Vagaggini D (2001) Predatory impact of the mosquitofish (*Gambusia holbrooki* Girard) on zooplanktonic populations in a pond at Tenuta di Castelporziano (Rome, Central Italy). *J Limnol* 60(2):189–193
- Marrone F, Barone L, Naselli-Flores L (2006) Cladocera (Branchiopoda: Anomopoda, Ctenopoda, and Onychopoda) from Sicilian inland waters: an updated inventory. *Crustaceana* 78(9):1025–1039
- Moisello U (1998) *Idrologia tecnica*. La Goliardica Pavese: Pavia, Italy, 824 pp
- Mura G (1991) Life history and interspecies relationships of *Chirocephalus diaphanus* Prevost and *Tanymastix stagnalis* (L.), (Crustacea, Anostraca) inhabiting a group of mountain ponds in Latium, Italy. *Hydrobiologia* 212:45–59
- Paterson M (1993) The distribution of microcrustacea in the littoral zone of a freshwater lake. *Hydrobiologia* 263:173–183
- Pielou EC (1969) *An introduction to mathematical ecology*. John Wiley, New York, 286 pp
- Riis T, Sand-Jensen K, Vestergaard O (2000) Plant communities in lowland Danish streams: species composition and environmental factors. *Aquat Bot* 66:255–272
- Roman MR, Gauzens AL, Rhinehart WK, White JR (1993) Effects of low oxygen waters on Chesapeake Bay zooplankton. *Limnol Oceanogr* 38:1603–1614
- Serrano L, Toja J (1998) Interannual variability in zooplankton community of a shallow temporary pond. *Verh Internat Verein Limnol* 26:1575–1581
- Spencer M, Blaustein L, Schwartz SS, Cohen JE (1999) Species richness and the proportion of predatory animal species in temporary freshwater pools: rela-

- tionships with habitat size and permanence. *Ecol Lett* 2:157–166
- Stella E, Margaritora FG (1968) La fauna ad Entomostraci di acque astatiche del Lazio. *Ricerche ecologiche e biologiche. Rend Acc Naz XL* 18:3–60
- Stenberger RS (1985) Prey selection by the copepod *Diacyclops thomasi*. *Oecologia* 65:492–497
- Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67(5):1167–1179
- Tiner RW (1999) Wetland indicators. A guide to wetland identification, delineation, classification, and mapping. Lewis Publishers, Boca Raton, FL, USA, 392 pp
- Toja J, López T, Gabellone N (1991) Successional changes in two dune ponds (Doñana National Park). *Verh Internat Verein Limnol* 24:1556–1559
- Vagaggini D, Ulisse G, Seminara M, Margaritora FG (2002) Zooplankton communities in two astatic basins in the natural reserve of Castelporziano (Central Italy): composition and temporal succession. *J Freshwater Ecol* 17:27–36
- Van der Brink FWB, Van Katwijk MM, Van der Velde G (1994) Impact of hydrology on phyto- and zooplankton community composition in foodplain lakes among the Lower Rhine and Meuse. *J Plankton Res* 16:351–353
- Watson GF, Davies M, Tyler MJ (1995) Observations on temporary waters in Northwestern Australia. *Hydrobiologia* 299:53–73
- Whigham DF, Dykyjová D, Hejný S (eds) (1993) *Wetland of the world I: inventory, ecology and management*. Kluwer Acad. Publishers, Dordrecht, The Netherlands, 768 pp
- Wiggins GB, Mackay RJ, Smith IM (1980) Evolutionary and ecological strategies of animals in annual temporary pools. *Archiv Für Hydrobiol Suppl* 58:97–206
- Williams DD (1999) Conservation of wetlands in drylands: a key global issue. *Aquat Conserv Marine Freshwater Ecosyst* 9:517–522
- Williams P, Biggs J, Cummings CP, Gillespie MK, Rich TCG, Baker A, Baker J, Beesley J, Corfield A, Dobson D, Culling AS, Fox J, Howard DC, Luursema K, Rich M, Samson D, Scott WA, White R, Whitfield M (1998) Lowland pond survey 1996. Department of Environment, Transport and The Regions, London
- Williamson CE (1983) Invertebrate predation on planktonic rotifers. *Hydrobiologia* 104:385–396
- Xi Y, Huang X (2000) Effect of temperature on the experimental population dynamics of *Brachionus urceolaris*. *Oceanol Limnol Sin/Haiyang Yu Huzhao* 31:23–28
- Zar HJ (1984) *Biostatistical analysis*, 2nd edn. Englewood Cliffs, New Jersey, 718 pp