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## Seasonal and inter-annual zooplankton dynamics in temporary pools with different hydroperiods

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### Abstract

The results of a research carried out in 2001 on nine temporary mountain pools (Northern Apennines, Italy) underlined a major role of hydroperiod in shaping zooplankton communities of temporary habitats. In 2002, the same pools were studied to assess inter-annual differences in zooplankton seasonal patterns. Data on precipitations (both snow and rainfalls) were collected to evaluate the influence of precipitation regimes on hydroperiod and concurrently on hydrochemical features and zooplankton dynamics.

Mean annual snow and rainfall abundances were highly similar in both years but precipitation patterns were different. Moreover, different air temperatures were measured in the 2 years of study. These factors influenced water persistence and dry and wet cycles in the pools: in 2001, three pools dried out in summer and remained dry until autumn rainfalls (type A pools), in five pools (type B pools) the summer dry period was interrupted by re-filling due to storms in July and only in one pool water did remain for the entire research period (C1). In 2002, type A and B pools underwent only one dry phase (June–July) while C1 showed a hydroperiod similar to the one that occurred in the previous year. Overall, type A and B pools can be classified as ‘seasonal’ and C1 as ‘near-permanent or permanent’.

Principal component analysis and paired *t*-tests did not show significant differences between years in the hydrochemical features of the pools. However, the seasonal pools showed a wide range of variation in their hydrochemical parameters while water features of the permanent pool presented less variability.

Within the pools, divergences in the number and in the type of zooplankton taxa between the 2 years were limited. Rotifer and copepod density of the seasonal pools were comparable over years and only cladocerans exhibited distinct density dynamics. Cladoceran appeared to be associated with ionic content and influenced by the occurrence of ice-melting and by the wet phase length of the pools.

On the contrary, the permanent pool showed diverse zooplankton seasonal patterns in 2001 compared to 2002. Over years, different pH values were measured; pH and conductivity varied with changing water volume, which in turn explained a significant amount of the observed variation in zooplankton densities in 2002.

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**Keywords:** Water permanence; Precipitation pattern; Hydrochemistry; Temperature; Cladocerans

### Introduction

Plankton seasonal succession in permanent habitats has been investigated in several studies, both for

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phytoplankton (e.g., Morabito & Curradi, 1997; Padi-sak et al., 1998; Reynolds, 1984) and zooplankton (e.g., Straile, 2000; Talling, 2003; Wolfinbarger, 1999). The PEG model (Sommer, Gliwicz, Lampert, & Duncan, 1986) is one of the most exhaustive essays to describe and explain seasonal dynamics of planktonic communities in permanent waterbodies. The model clearly illustrates how the interplay between abiotic (physical and chemical requirements of the organisms) and biotic (predation and competition) factors can generate patterns in plankton dynamics that are generally repeated every year. However, the statements reported by Sommer and colleagues (1986) derived from observations of lakes, reservoirs and permanent pools, while no information was collected on temporary habitats at that time.

So far, despite the fact that temporary waters can maintain communities with many rare species (Forró, De Meester, Cottenie, & Dumont, 2003; King, Simovich, & Brusca, 1996), they have drawn little interest compared to permanent waterbodies (both lakes and ponds); only recently limnologists have been paying more attention to the plankton communities of these kind of habitats. In addition, considering zooplankton, very few of these studies were performed in temporary mountain pools (Hamer & Martens, 1998; Jersabek, Brancelj, Stoch, & Schabetsberger, 2001; Rossetti, Tireni, & Tavernini, 2004).

Although seasonal dynamics in deep and permanent biotopes may be disturbed by irregular seasonal events (e.g., changing in mixing depth), in temporary habitats zooplankton succession is, by definition, interrupted by the seasonal absence of water. Drying events also prevent the colonisation of many large predators, such as fish, even if some other predaceous taxa can tolerate desiccation (i.e., turbellarians) or leave the pool when it dries out (i.e., amphibians and insects) (Bohonak & Whiteman, 1999; Hobæk, Manca, & Andersen, 2002; Murdoch, Scott, & Ebsworth, 1984; Spencer, Blaustein, Schwartz, & Cohen, 1999). As in all freshwater habitats, hydrochemical characteristics are supposed to influence the regulation of zooplankton communities in temporary pools as well. Many water features of temporary pools dramatically fluctuate during the diurnal cycle because of the limited depth and water volume (Podrabsky, Hrbek, & Hand, 1998 and reference therein) and large differences in the range of variation of physico-chemical features are measured within pools of same geographic location exhibiting different surface areas (Podrabsky et al., 1998). Furthermore, the greatest changes in hydrochemical parameters are measured during desiccation phase and habitat refilling (Boulton & Brock, 1999). Concurrently, communities of temporary waters are supposed to tolerate a wide range of environmental variables which usually influence physiological processes.

For these reasons, hydroperiod is considered as an important determinant of zooplankton communities in temporary habitats (e.g., Girdner & Larson, 1995; Mahoney, Mort, & Taylor, 1990). The extent of water permanence and the length of the dry phase in temporary waters are usually regulated by snow and rainfall amount (Fischer, Marinane, Fontanarrosa, Nieves, & Schweigmann, 2000; Hanes, Hecht, & Stromberg, 1990). Thus, while the timing of wet and dry periods is the most predictable aspect of the water regime, the irregularity comes from the annual differences in the amount of precipitation and within years in both the pattern and intensity of storms (Goldman, Jackson, & Bursztynsky, 1986). Water losses from different evaporation and evapotranspiration rates have to be considered as well.

In 2001, a limnological research was carried out in nine temporary mountain pools (northern Apennines, Italy) to describe zooplankton seasonal patterns and phenology of these largely unknown habitats (Tavernini, Mura, & Rossetti, 2005). This study showed that water fluctuations affected the hydrochemical features of the pools and suggested that the hydroperiod was a major factor influencing pools colonisation and species richness. In 2002, additional sampling activities were carried out on the same habitats to assess: (i) the effect of precipitations on pools hydroperiod and hydrochemical parameters, and (ii) the role of changing water features on zooplankton communities. (iii) Inter-annual patterns in zooplankton densities and dynamics were also investigated to test if they were repeated every year. Results of this research are reported in the present paper.

## Materials and methods

### Study area

Nine temporary mountain pools located at an altitude varying between 1595 and 1733 m a.s.l. (above the tree-line), on the northern slope of the Tuscan-Emilian Apennines (Italy) were considered in this study. The pools lie in an area of approximately 4 km<sup>2</sup> and they were chosen to minimise possible variations due to different microclimates. Pools are small (~36–396 m<sup>2</sup> in surface area) and shallow (<120 cm in depth) and precipitation-fed. Pools are normally frozen to the bottom from November to May and first fed up by snow-melting. In 2001, three pools (A1–A3) were filled twice, drying out uninterruptedly from the beginning of June to mid September; in five pools (B1–B5) the summer dry period was interrupted by re-filling due to stormy events in July and the waterbodies filled three different times (May–beginning of June; mid July, mid September–October). Only in one pool (C1) water was

present during the entire research period despite a 2/3 reduction in volume during summer. In 2002, the first two groups of pools underwent only one dry phase (June–July) while C1 was always filled. More detailed information on pool features and hydroperiod length calculation are reported in Tavernini, Mura et al. (2005).

Data on precipitations (both rainfall and snow) and air temperature were collected from the nearest meteorological station located 1 km from the study area, at an altitude of 1343 m a.s.l.

### Water sampling and analytical methods

In 2001, pools were sampled during the ice-free season (May–October), at approximately 2-week intervals from 18 May to 23 October 2001 (13 surveys). The first sampling was carried out 2 days after the last snow fall. In 2002, pools were sampled at approximately 3-week intervals from 21 May to 29 October (9 surveys) and the first sampling was carried out 17 days after the last snow fall.

Water temperature was measured in each pool at each sampling date; water samples were collected from the surface layer with a 1 L polyethylene bottle and analysed within 24 h for pH, conductivity (EC), total alkalinity (TA) (Rodier, 1978), chlorophyll-*a* (Chl-*a*) and soluble reactive phosphorus (SRP), dissolved inorganic nitrogen ( $\text{DIN} = \text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$ ) and dissolved reactive silica (DRSi) (A.P.H.A., 1975; Valderrama, 1981).

### Zooplankton sampling and counting

Given the shallowness of the pools, zooplankton samples were collected by a 15 l bucket from 3 sampling points; the samples were pooled and the 45 l of water were filtered through a 50  $\mu\text{m}$  mesh and immediately fixed and preserved in a 4% buffered formalin solution. Zooplankton density was estimated following Bottrell, Duncan, Gliwicz, Grygierek, and Herzig (1976). When possible, identification was done to species level, except for bdelloid rotifers and harpacticoid copepods. Only adults of copepods were identified to species level, while all juveniles were grouped in two categories (nauplii and copepodites) separately for cyclopoids, calanoids and harpacticoids.

### Statistical analysis

As the normality and homogeneity of the variance were violated for meteorological data (Shapiro–Wilk test and Levene test, respectively) a Wilcoxon test was performed to test for differences in daily precipitations in the study area between 2001 and 2002.

Differences in pool volumes between years within pools were estimated by fitting a linear mixed-effect model (Pinheiro & Bates, 2000) with date of sampling modelled as random effect within pool.

A principal component analysis (PCA) was carried out to assess the main chemical and physical water features of the pools in the studied years. T, pH, EC, TA, Chl-*a*, DIN and DRSi values measured in each pool in each sampling occasion were included in the PCA. SRP values were not considered in the analysis because lower than the detection limit ( $5 \mu\text{g L}^{-1}$ ) in most of the samples. All physico-chemical parameters (except pH) were  $\text{Log}(x+1)$  transformed due to the skewed frequency distributions of the untransformed data.

Paired *t*-tests were performed to detect significant differences between the 2 years in (a) air temperature (mean daily value, after a Celsius to Kelvin conversion), (b) physical and chemical features and (c) zooplankton densities of the pools. Hydrochemical and zooplankton densities data were month-wise pooled to compensate for the different sampling dates and intervals between 2001 and 2002. All data were tested for normality (Shapiro–Wilk test) after log-transformation before being included in the test.

Given the different cladoceran dynamics showed in B pools in 2001 and 2002, correlation analyses (Spearman's correlation) were performed between hydrochemical characteristics and cladoceran densities. The same analyses were performed between hydrochemical features and total zooplankton abundances of C1, which had different zooplankton seasonal patterns in the 2 years. Because of the strong variation in C1 volume in 2001, this latter parameter was also included in the analysis.

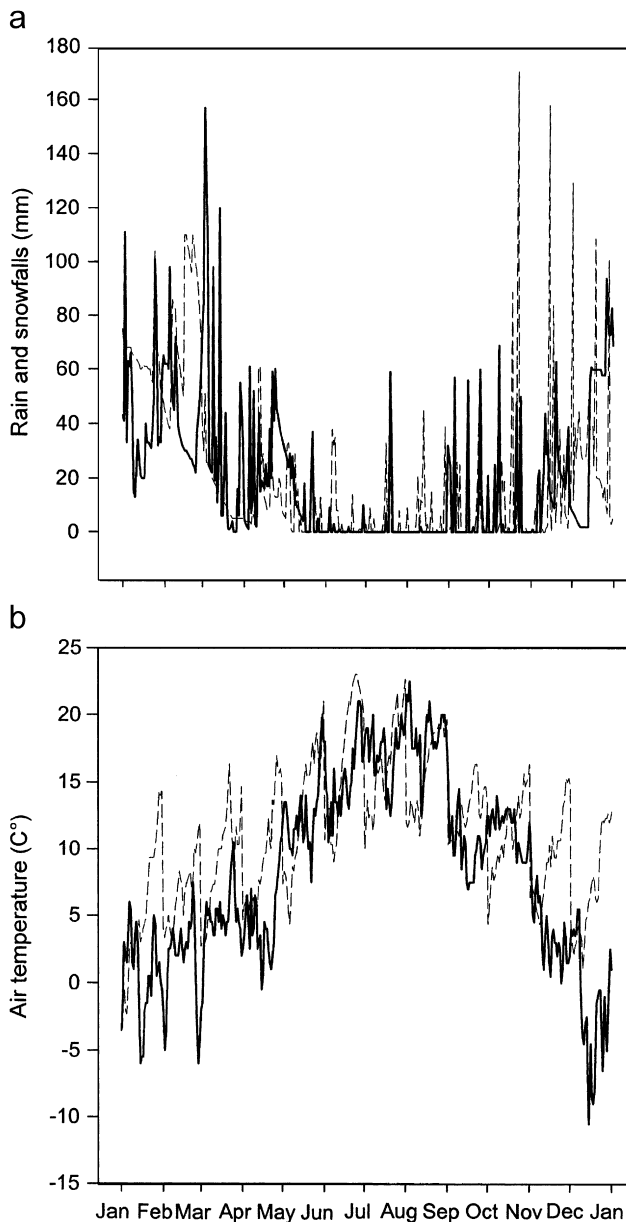
Physical and chemical features considered in the paired *t*-test and in the correlation analysis were the same ones included in the PCA.

Tests were performed by means of the software packages SPSS 13.0 for Windows (Release 13.0.0, © 2004, SPSS, Inc., Chicago, IL, USA), CANOCO version 4.5 (ter Braak & Šmilauer, 2002) and R (R Development Core Team, 2005).  $\alpha$ -level was set at 0.05.

## Results

### Precipitation patterns and hydrological features of pools

Daily precipitation in 2002 were not significantly different from 2001 (Wilcoxon test,  $p > 0.05$ ) but diverse patterns of precipitations characterised the study period (May–October) (Fig. 1). Moreover, air temperatures were different in the 2 years (paired *t*-test,  $p < 0.05$ ) (Fig. 1), determining different dry and wet cycles of the pools. In 2002, both A and B pools filled twice (May–mid June, August–October). Only in A2 and A3 the wet-phase length was shorter than in 2001 (A2: 59 days in 2001 and 37 days in 2002; A3: 74 days in 2001 and 20 days in 2002). On the contrary, A1 (2001: 59



**Fig. 1.** (a) Daily precipitations (snow and rainfalls, in mm) and (b) daily air temperature (mean value, °C) measured in the study area in 2001 (black line) and in 2002 (short dash line).

days; 2002: 101 days) and type B pools (mean wet phase length: 88 days in 2001; 130 days in 2002) had a longer hydroperiod in 2002 than in 2001. C1 never dried out and its volume was always greater than in 2001 (linear mixed-effect model,  $p < 0.05$ ), while no differences between years were noted in the volumes of the other pools.

### Physical and chemical features of the pools

Minimum and maximum value of the physical and chemical characteristics of the pools are reported in

**Table 1.** Type A and B pools generally presented a wide range of variations in their hydrochemical parameters within year for both years. Only C1 (and partially B4) showed more limited fluctuations in water features. Moreover, both in 2001 and 2002, C1 and B4 showed the highest values of TA (up to 186 and 109  $\mu\text{eq L}^{-1}$  in C1 and B4, respectively) while in the other pools TA was generally below 50  $\mu\text{eq L}^{-1}$ . C1 and B4 also presented the highest DRSi concentrations (up to 587 and 932  $\mu\text{g L}^{-1}$ , respectively).

A PCA based on the main water features is shown in Fig. 2; eigenvalues of the first two PCA axes are  $\lambda_1 = 0.480$  and  $\lambda_2 = 0.209$ , respectively; eigenvalues for the third and fourth axes ( $\lambda_3 = 0.186$  and  $\lambda_4 = 0.075$ ) are lower and therefore are not discussed further. On the whole, as seen from the overlap of the points, no clear separation can be noted between samples collected in 2001 and 2002 (Fig. 2). However, along the first axis, according to a gradient of decreasing DRSi and TA concentrations, 13 samples collected in 2001 (mainly in September) and 2 samples collected in 2002 (right quadrants) are separated from the others. In all these samples, DRSi concentrations are always below the detection limit of 20  $\mu\text{g L}^{-1}$ .

In 2002, A2 and A3 contained water only during three and two of the nine surveys, respectively. For this reason, paired  $t$ -test on hydrochemical parameter was performed on A1 data only. In this pool, only Chl-*a* concentration was significantly different between years (paired  $t$ -test,  $p < 0.05$ ). No significant differences were detected in water features of each B pool between 2001 and 2002. In C1, pH was different between years (paired  $t$ -test,  $p < 0.05$ ); DIN ( $p = 0.05$ ) and, to a lesser extent, also EC ( $p = 0.06$ ) and TA ( $p = 0.06$ ), resulted to be slightly different.

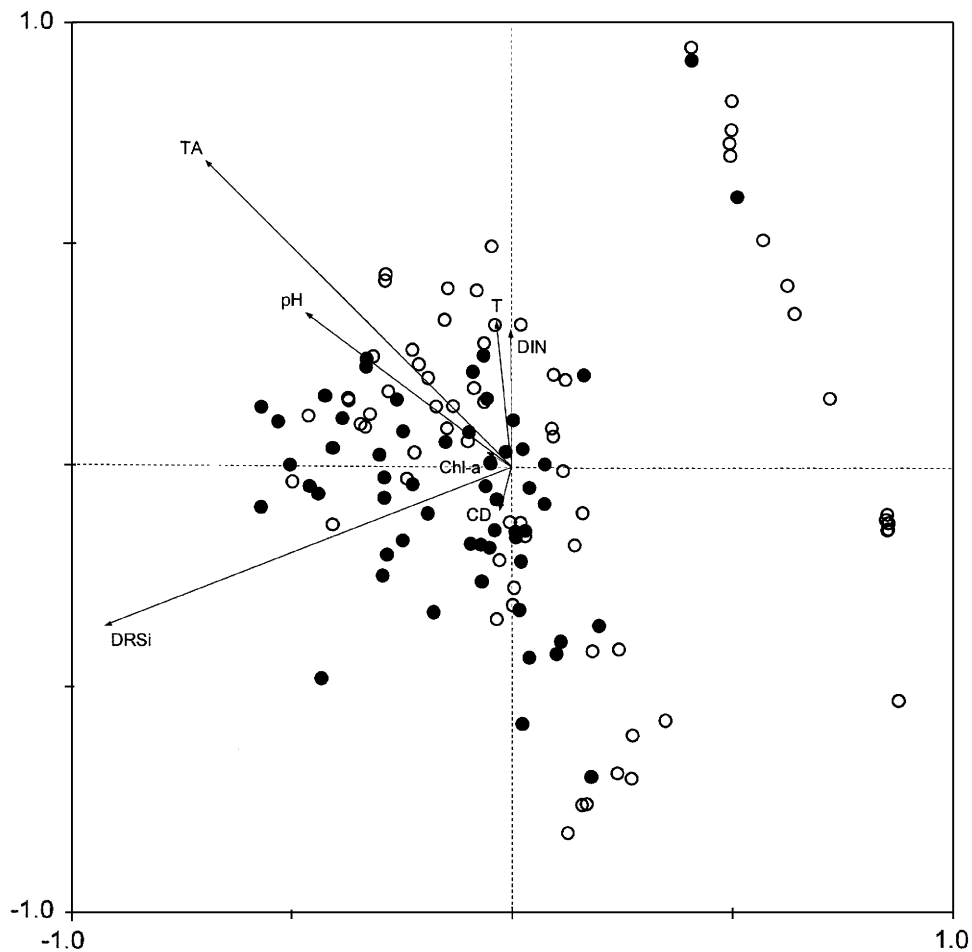
### Zooplankton communities

In 2002, 38 zooplankton taxa were identified: 26 rotifers, 5 cladocerans, 5 copepods and 2 anostracans (Table 2). The most noticeable difference between 2001 and 2002 occurred in the rotifer component: the same 21 taxa were found in both years, 15 taxa were exclusively found in 2001 and 5 taxa exclusively in 2002. Microcrustacean species were the same in 2001 and 2002, except for one species (i.e., *Paracyclops fimbriatus*) found only in 2001 (Table 2).

As in 2001, also in 2002 bdelloids, *Lepadella* sp. and copepod immature stages were the first taxa emerging from dormancy in all the three types of pools. Most of the rotifers were found at least 1 week before in 2002 compared with 2001. Some rotifer species like *Keratella quadrata*, *Colurella uncinata*, *Trichocerca myersi* were only found on the first survey of 2001 while they were not recovered in the remaining sampling dates of 2001

**Table 1.** Range of water temperature (T), pH, conductivity (EC), total alkalinity (TA), dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), dissolved reactive silica (DRSi) and chlorophyll-*a* (Chl-*a*) measured in each pool in 2001 and 2002

Pool	Year	T (°C)	pH	EC ( $\mu\text{S cm}^{-1}$ )	TA ( $\mu\text{eq L}^{-1}$ )	DIN ( $\mu\text{g L}^{-1}$ )	SRP ( $\mu\text{g L}^{-1}$ )	DRSi ( $\mu\text{g L}^{-1}$ )	Chl- <i>a</i> ( $\mu\text{g L}^{-1}$ )
A1	2001	5.8–23.5	5.1–5.7	13–29	<1–93	53–83	4–16	<20–87	0.1–2.1
	2002	6.0–16.5	4.7–5.9	10–16	<1–23	<2–92	<5–8	13–336	0.4–8.7
A2	2001	5.3–20.1	4.9–5.6	5–26	<1–47	41–65	<5–13	<20–133	0.2–2.5
	2002	5.6–14.5	5.3–5.9	10–11	7–35	30–93	<5	<20–91	0.6–8.2
A3	2001	4.3–14.8	5.9–7.2	6–23	8–88	27–308	4–18	<20–387	0–12.7
	2002	4.6–11.5	6.5–6.6	11–14	66–73	<2–66	<5	145–480	0.4–7.0
B1	2001	5.4–27.6	5.0–6.1	8–30	<1–44	46–1030	<5–20	<20–78	0.3–6.4
	2002	4.8–23.8	5.5–6.4	11–16	9–24	41–171	<5–6	31–125	0.5–8.3
B2	2001	5.2–26.6	5.0–7.2	9–26	<1–22	23–1297	<5–18	<20–76	0.1–4.4
	2002	4.7–23.4	5.3–6.6	11–17	9–65	<2–111	<5	28–243	0.3–6.5
B3	2001	5.7–25.4	5.5–6.1	12–26	12–61	47–85	7–12	<20–60	0.3–4.9
	2002	6.2–24.3	5.8–6.3	10–19	17–50	28–115	<5–11	38–165	0.7–7.7
B4	2001	3.4–22.2	6.0–6.9	9–19	35–109	41–1125	<5–12	47–234	0–7.5
	2002	5.6–22.8	6.2–6.6	10–18	40–79	6–189	<5	135–932	0–2.9
B5	2001	5.6–23.9	5.1–5.9	9–22	<1–41	33–197	<5–16	24–111	0–2.8
	2002	6.9–22.8	5.4–6.3	6–17	1–33	6–106	<5–11	45–1037	0–4.5
C1	2001	5.7–20.0	5.9–6.7	4–22	73–141	40–361	<5–15	<20–533	0–25.4
	2002	6.6–21.5	6.4–7.0	12–27	88–186	<2–173	<5	<20–587	1.5–27.5

**Fig. 2.** PCA ordination of the samples collected in the studied pools in 2001 (black plots) and 2002 (white plots) and associated environmental variables (symbols as in the text).

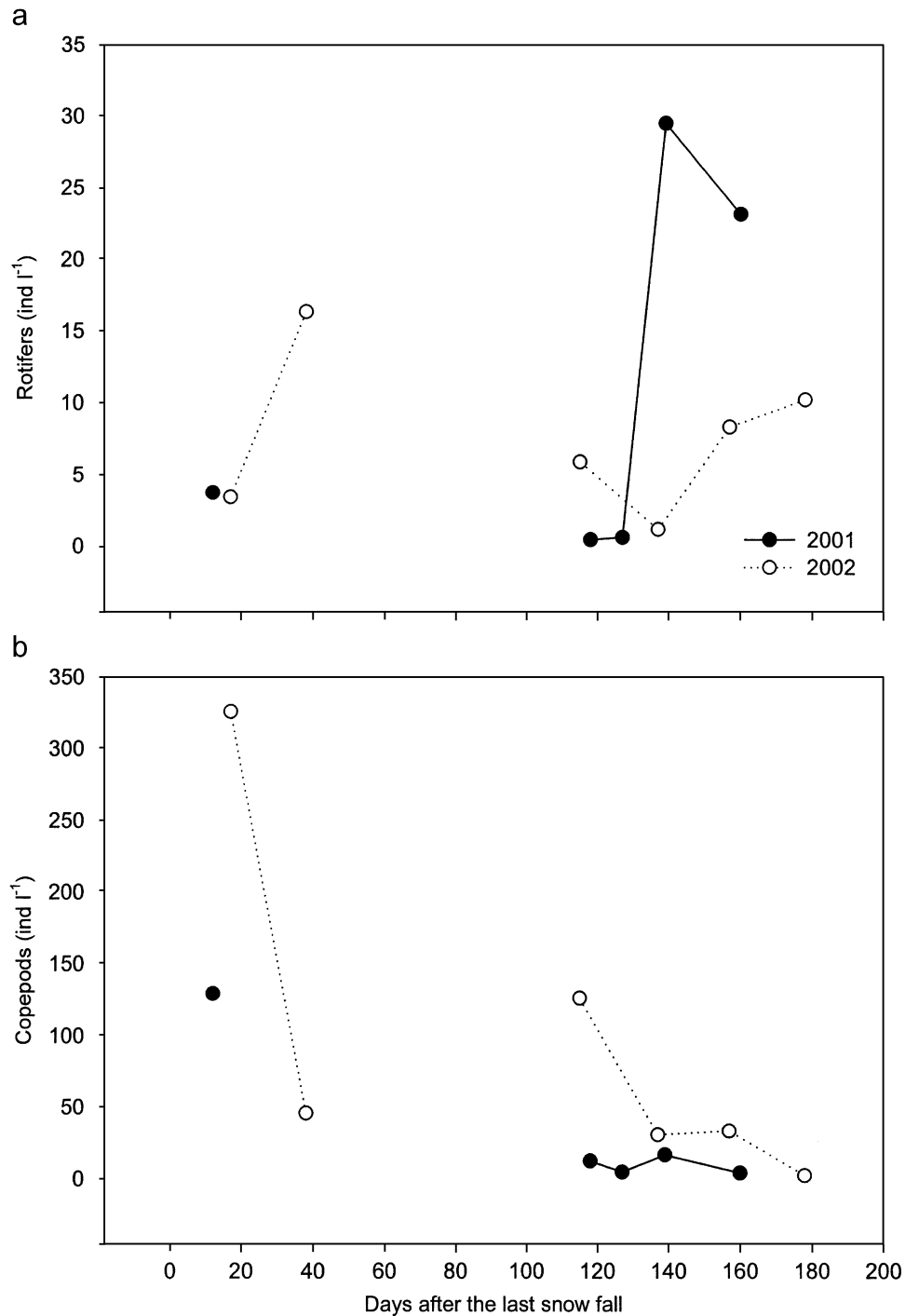
**Table 2.** List of zooplankton taxa found in the studied pools

	2001	2002	Both
<b>Rotifera</b>			
1 <i>Bdelloidea</i>			X
2 <i>Anuraeopsis fissa</i> (Gosse)	X		
3 <i>Ascomorpha ecaudis</i> Perty	X		
4 <i>Ascomorpha saltans</i> Bartsch			X
5 <i>Cephalodella</i> sp.			X
6 <i>Cephalodella gibba</i> Koste			X
7 <i>Cephalodella intuta</i> Myers	X		
8 <i>Collotheca</i> sp.		X	
9 <i>Colurella uncinata</i> O.F. Müller	X		
10 <i>Dicranophorus</i> sp.		X	
11 <i>Encentrum</i> sp.	X		
12 <i>Euchlanis</i> gr. <i>dilatata-parva</i> sensu Ruttner-Kolisko			X
13 <i>Itura</i> sp.	X		
14 <i>Itura aurita</i> (Wulfert)	X		
15 <i>Itura myersi</i> Wulfert		X	
16 <i>Kellicottia longispina</i> (Kellicott)	X		
17 <i>Keratella cochlearis</i> (O.F. Müller)	X		
18 <i>Keratella quadrata</i> (O.F. Müller)	X		
19 <i>Keratella tropica</i> (Apstein)	X		
20 <i>Lecane closterocerca</i> (Schmarda)		X	
21 <i>Lecane flexilis</i> (Gosse)			X
22 <i>Lecane</i> gr. <i>lunaris</i> Pejler			X
23 <i>Lecane luna</i> (O.F. Müller)			X
24 <i>Lepadella</i> sp.			X
25 <i>Notommata</i> sp.			X
26 <i>Proales</i> sp.			X
27 <i>Polyarthra</i> gr. <i>vulgaris-dolichoptera</i> Ruttner-Kolisko			X
28 <i>Resticula gelida</i> Haring & Myers			X
29 <i>Synchaeta</i> gr. <i>stylata-pectinata</i> sensu Ruttner-Kolisko	X		
30 <i>Testudinella caeca</i> (Parsons)			X
31 <i>Testudinella incisa</i> sensu Koste			X
32 <i>Trichocerca</i> sp.	X		
33 <i>Trichocerca bidens</i> (Lucks)		X	
34 <i>Trichocerca cavia</i> (Gosse)			X
35 <i>Trichocerca elongata</i> (Gosse)			X
36 <i>Trichocerca insignis</i> (Herrick)			X
37 <i>Trichocerca longiseta</i> (Schrank)			X
38 <i>Trichocerca myersi</i> (Myersi)	X		
39 <i>Trichocerca pusilla</i> sensu Koste	X		
40 <i>Trichocerca vernalis</i> Hauer			X
41 <i>Trichotria tetractis</i> sensu Koste			X
<b>Cladocera</b>			
42 <i>Alona elegans</i> Kurz			X
43 <i>Alonella nana</i> (Baird)			X
44 <i>Alona affinis</i> (Leydig)			X
45 <i>Chydorus sphaericus</i> O.F. Müller			X
46 <i>Daphnia longispina</i> O.F. Müller			X
<b>Copepoda</b>			
47 <i>Acanthocyclops</i> gr. <i>vernalis-robustus</i> sensu Kiefer			X
48 <i>Diacyclops bisetosus</i> (Rehberg)			X
49 <i>Paracyclops fimbriatus</i> (Fischer)	X		
50 <i>Mixodiaptomus kupelwieseri</i> (Brehm)			X
51 <i>Mixodiaptomus tatricus</i> (Wierzejski)			X
52 Harpacticoida			X
<b>Anostraca</b>			
53 <i>Chirocephalus ruffoi</i> Cottarelli & Mura			X
54 <i>Tanymastix stagnalis</i> (Linnaeus)			X

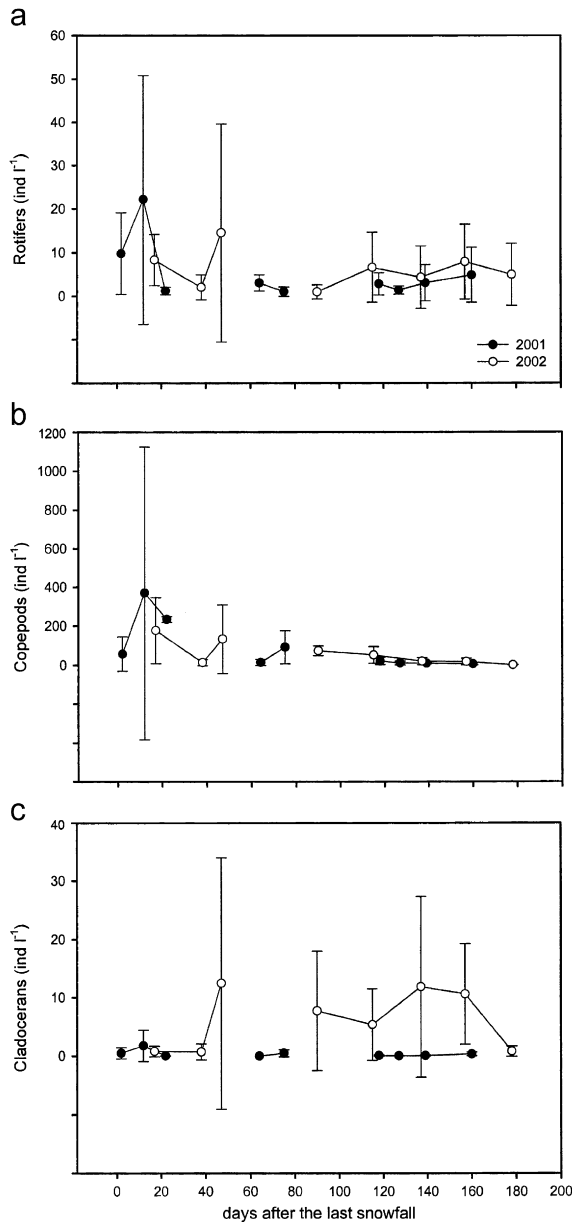
and 2002. Adults of copepods, cladocerans and anostracans appeared earlier in 2002 than in 2001, except for *Daphnia longispina* and *Biapertura affinis* which in C1 developed 1 month later in 2002 than in 2001. Nauplii and copepodites were present throughout all the sampling seasons, even if the highest abundances were measured at pool filling.

No similarities or dissimilarities of development patterns can be assessed in type A pools because of

the short water permanence in A2 and A3 in 2002. Only in A1 water was present on six of the nine sampling dates and zooplankton abundances (both rotifers and copepods) showed no significant differences (paired  $t$ -test, both  $p > 0.05$ ) between years. Zooplankton abundance patterns at the beginning of the sampling seasons are difficult to compare due to the different occurrence of the last snow fall (LSF) and concurrently of the complete snow melting in the 2 years. Indeed,



**Fig. 3.** Densities of rotifers (a) and copepods (b) in A1 in 2001 (black plots) and 2002 (white plots).



**Fig. 4.** Densities (mean  $\pm$  SD) of rotifers (a), copepods (b) and cladocerans (c) in B pools in 2001 (black plots) and 2002 (white plots).

after summer drying, rotifers generally increased in both years, from less than 1 ind L<sup>-1</sup> (September 11, 118 days after the LSF) to 23 ind L<sup>-1</sup> (October 23, 160 days after the LSF) in 2001 and from 6 ind L<sup>-1</sup> (August 27, 115 days after the LSF) to 10 ind L<sup>-1</sup> (October 29, 178 days after the LSF) in 2002 (Fig. 3a). On the contrary, copepods abundances were higher at pond refilling, followed by gradual decrease until the onset of late autumn pool freezing (Fig. 3b).

Similarly, also in type B pools the abundance of rotifers and copepods did not significantly differ in 2001 and 2002 (paired *t*-test, both  $p > 0.05$ ). From the late summer pond refilling to the end of the sampling period rotifers showed a general linear increase in 2001, while the pattern was less clear in 2002 (Fig. 4a). In the same period, copepod abundances showed a slight decrease (Fig. 4b). The main diversities were noted in cladoceran assemblages, which present the highest densities in 2002 (paired *t*-test,  $p < 0.05$ ) (Fig. 4c). More specifically, in 2001 cladocerans were generally  $< 1$  ind L<sup>-1</sup>, and in B3 and B4 they were only found on one sampling date (July 30). In 2002, cladocerans were not found in B3 at all and the lowest densities ( $< 4$  ind L<sup>-1</sup>) were measured in B4. In the remainder of the pools, the highest abundances were measured at the beginning of the sampling season in B5 (37 ind L<sup>-1</sup>) and on September 18 in B1 (32 ind L<sup>-1</sup>) and in B2 (25 ind L<sup>-1</sup>) (data not shown).

In 2001, cladoceran abundances were related to Chl-*a* in B5 and to Chl-*a*, pH and EC in B2. In 2002, cladocerans were correlated with Chl-*a* in B1, pH in B2 and EC, TA and DRSi in B4 (Spearman correlation analysis, Table 3). No other significant relationships were noted between hydrochemical features of B pools and their cladoceran assemblages.

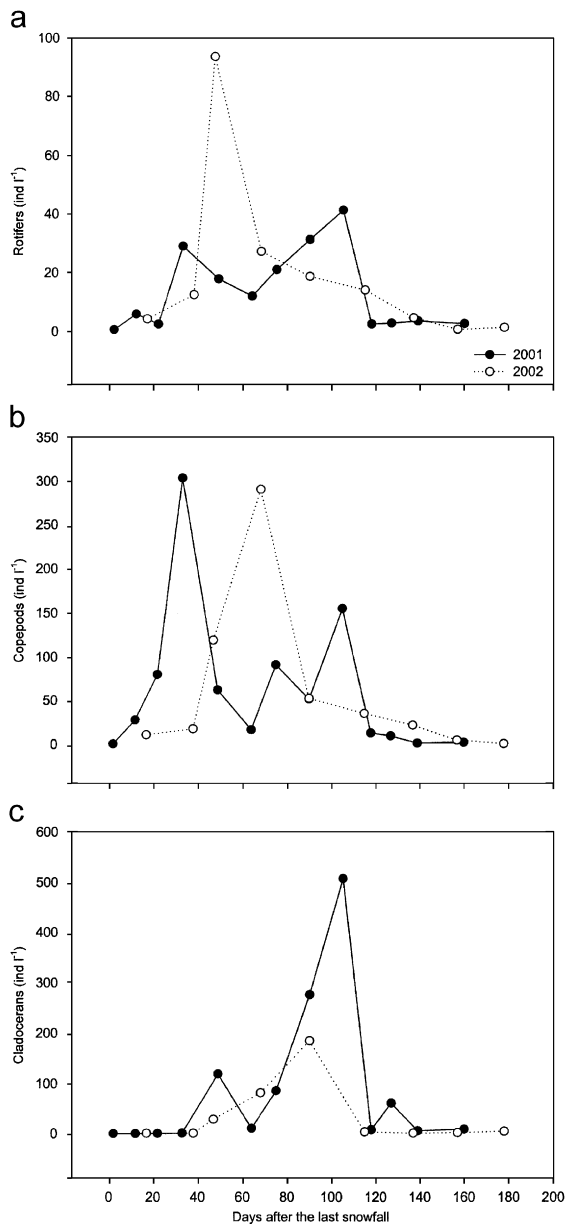
Total zooplankton density did not significantly differ between the two years (paired *t*-test,  $p > 0.05$ ) in C1, even if rotifers, cladocerans and copepods were considered separately. However, seasonal dynamics were diverse (Fig. 5). In 2001, rotifers (Fig. 5a) and copepods (Fig. 5b) showed two abundance peaks on June 18 (33 days after the LSF) and August 29 (105 days after the LSF), respectively, while cladocerans had their

**Table 3.** Spearman correlation coefficients for associations between cladoceran density in B pools and pH, conductivity (EC), total alkalinity (TA), dissolved inorganic nitrogen (DIN), dissolved reactive silica (DRSi), chlorophyll-*a* (Chl-*a*) and temperature (T) in 2001 and 2002

Pool	pH	EC	TA	DIN	DRSi	Chl- <i>a</i>	T
B1 (2002)	ns	ns	ns	ns	ns	0.886*	ns
B2 (2001)	0.747**	-0.735*	ns	ns	ns	-0.778*	ns
B2 (2002)	-0.873*	ns	ns	ns	ns	ns	ns
B4 (2002)	ns	0.855**	0.778*	ns	0.778*	ns	ns
B5 (2001)	ns	ns	ns	ns	ns	0.775*	ns

Only pools with significant relationships between cladoceran densities and hydrochemical parameters are reported. ns =  $p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ .





**Fig. 5.** Densities of rotifers (a), copepods (b) and cladocerans (c) in C1 in 2001 (black plots) and 2002 (white plots).

**Table 4.** Spearman rank correlation coefficients for associations between zooplankton density (Zoo) and volume (V), pH, conductivity (EC), total alkalinity (TA), dissolved inorganic nitrogen (DIN), dissolved reactive silica (DRSi), chlorophyll-*a* (Chl-*a*) and temperature (T) in C1 in 2001

	V	pH	EC	TA	DIN	DRSi	Chl- <i>a</i>	T
Zoo	ns	-0.602**	-0.509*	ns	ns	-0.709**	0.622*	0.680**
V		ns	ns	ns	ns	0.712**	-0.520*	ns
pH			0.652**	ns	ns	0.535	-0.605*	-0.544*
EC				ns	ns	0.578	-0.712**	-0.534*
TA					ns	ns	ns	ns
DIN						ns	ns	ns
DRSi							-0.711**	ns
Chl- <i>a</i>								ns

ns =  $p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ .

maximum at the end of August (Fig. 5c) and two isolated peaks were also measured on July 4 and September 20. The following year, only one peak was recorded for rotifers (June 20, 47 days after the LSF), copepods (July 11, 68 days after the LSF) and cladocerans (August 2, 90 days after the LSF) (Fig. 5).

A Spearman rank correlation analysis evidenced that zooplankton density in 2001 was significantly negatively correlated with pH, EC and DRSi and positively with Chl-*a* and T (Table 4). In 2002, zooplankton abundance was correlated only with T and DRSi (Table 5).

## Discussion

According to the classification proposed by Boulton and Brock (1999), type A and B pools can be classified as 'seasonal', i.e. pools that usually fill during the wet season and dry out annually (and predictably); on the other hand C1, which is normally filled but may dry out or strongly reduce its volume during extreme drought, can be considered as a 'permanent' (or 'near permanent') pool.

Precipitation abundance in the study area did not significantly differ in 2001 and 2002, but the pattern and the intensity of rainfall and snow events were different in the 2 years and daily air temperatures were generally higher in 2002. Moreover, despite being located in a quite restricted area, due to their topographic position the studied pools are exposed to the action of sun and wind to a different degree. In addition, the pools have different sediment type (bare or vegetated) and macrophytes are present only in C1 (Tavernini, Bartoli, & Rossetti, 2005). All these factors clearly determine diverse evaporation rates in each pool, inducing different responses to rainfall extent and pattern which lead ultimately to different intra and inter-annual hydroperiods.

No significant differences in hydrochemical features were found between 2001 and 2002 in the seasonal pools, even if each pool showed a wide range of annual

**Table 5.** Spearman rank correlation coefficients for associations between zooplankton density (Zoo) and volume (V), pH, conductivity (EC), total alkalinity (TA), dissolved inorganic nitrogen (DIN), dissolved reactive silica (DRSi), chlorophyll-*a* (Chl-*a*) and temperature (T) in C1 in 2002

	V	pH	EC	TA	DIN	DRSi	Chl- <i>a</i>	T
Zoo	ns	ns	ns	ns	ns	−0.800**	ns	0.720*
V		0.776**	ns	−0.675*	ns	0.804**	ns	ns
pH			0.722*	0.975**	−0.630*	0.647*	ns	ns
EC				0.812**	−0.678*	ns	ns	ns
TA					−0.633*	ns	ns	ns
DIN						ns	ns	ns
DRSi							ns	ns
Chl- <i>a</i>								ns

ns =  $p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ .

variability in water features. Only B4, which presents the highest surface area and volume (Tavernini, Mura et al., 2005), together with C1, underwent a less pronounced annual variation (Table 1). C1 also showed significant differences in pH values between 2001 and 2002.

A total of 54 zooplankton taxa were found in the 2 years. Given the high number of taxa inhabiting the studied pools, and considering that temporary habitats can provide habitat for important assemblages of rare and/or endangered species (Collinson et al., 1995) and support assemblages that clearly differed from those of permanent waterbodies (Brönmark & Hansson, 1998), it is clear the importance of temporary sites as biodiversity hotspots.

Differences in the number and in the type of taxa found in the two years of study were limited and mainly evident in the rotifer component. In particular, some rotifer species (i.e., *Keratella quadrata*, *Colurella uncinata*, *Trichocerca myersi*) were exclusively found in 2001 during the first survey when some pools were partially or totally covered by snow (Tavernini, Mura et al., 2005). In mountain waterbodies, the starting condition for the spring plankton succession at the beginning of the open water season depends on the length of the ice cover period since ice affects light and temperature gradient in the water column (Adrian, Waltz, Hintze, Hoeg, & Rusche, 1999). Therefore, zooplankton groups developing earlier are affected by ice melting while the overall successional pattern remains basically the same. Actually, in the studied pool zooplankton appearance order was similar in the 2 years: filter and detritus feeders (mainly rotifers and copepod immature stages) appeared first, parallel to the abundant supply of phytoplankton and organic matter which accompanies pools filling, while predators (cyclopoids) arrived later to outnumber prey species. Thus, discrepancies in zooplankton occurrence data are likely to be due to the effect of different environmental conditions (i.e. lower temperature at the ice melting) together with a different sampling effort, more frequent

in 2001 than in 2002. To this end, it cannot be excluded that in both years the sampling interval was too long in relation with the short life cycles of rotifers, leading to an underestimation of their occurrence in the studied pools.

Rotifers and copepods of the seasonal pools showed similar density patterns and only cladocerans followed different dynamics of successional development. Cladocerans were found in A1 only in 2002, while they were not found in A2 and A3 at all. Mahoney et al. (1990) reported that cladoceran species richness increases with size and hydroperiod. Since cladocerans are present in the smallest pools B1 (36 m<sup>2</sup>) and A1 (53 m<sup>2</sup>), their absence in A2 and A3, which present the shortest hydroperiod among the studied sites, is probably related to the high degree of ephemerality of these latter pools. This finding is in agreement with that of Frisch, Moreno-Ostos, and Green (2006) who reported that the absence of cladocerans from temporary pools in Spain was due to the short wet phase. In the remainder of the pools, the lowest cladoceran abundances were measured in 2001 (often < 1 ind L<sup>−1</sup>). Moreover, cladocerans were present at the first sampling date of 2001 only in B1, while in 2002 they were present in all the pools (except for B4) at the first survey. Differently from copepods, particularly cyclopoids, which overwinter as immature copepodite stages, cladocerans survive as resting eggs during winter and consequently have a later appearance (Pennak, 1978). As also reported by Taylor and Mahoney (1990), a few species became active immediately after the pool fills up, but most appeared after the pool held water for weeks or months. For this reason, it is reasonable that the short wet phase (ca. 18 days) which occurred before the summer drying in 2001 did not allow most of the cladocerans to hatch in B pools. Moreover, the longest water permanence after the summer dry phase in 2002, together with high temperatures and long photoperiod, had probably provided the proper hatching and growing cues for cladocerans determining the highest densities measured in B pools from August to October 2002 (Fig. 4c).

Only in C1, where water persisted throughout the entire sampling season both in 2001 and 2002, zooplankton seasonal patterns differed among years (Fig. 5). In 2001, after an explosive growth at the beginning of the open water season, the abundance of the whole zooplankton community decreased during the period of lower precipitation (mid June–mid July), while the highest densities were measured immediately after the complete pool refilling as a result of the storm events at the end of July (Fig. 1). On the contrary, in 2002, when C1 volume was constant throughout the studied period, a single density peak was noted in mid summer. Only in September and October, when the lowest zooplankton abundances were measured, zooplankton of C1 showed similar dynamics in both 2001 and 2002. Significant relationships between zooplankton densities and temperature were found in the two studied years (Tables 4 and 5). As also shown by Watson and Smallman (1971), the worsening of environmental conditions (i.e. lowest temperature) in the last part of the sampling season had probably determined a decrease in zooplankton growth rates. A similar pattern in zooplankton development was also observed in the seasonal pools.

Considering the above-mentioned role of temperature in structuring zooplankton communities, and the immediate effect of weather on water features of temporary sites because of their low heat storage capacity (Boulton & Brock, 1999), it appears clear that climate change is expected to alter pool hydrology, and in turn zooplankton dynamics of temporary pools much more than in other larger and permanent habitats.

Zooplankton of C1 was related to pH and EC in 2001 (Table 4). The lowest pH values were measured soon after complete refilling at the end of July and when the water volume of C1 was strongly reduced (i.e. August 29). An increasing trend of conductivity was noted from September onwards, when the pool was filled to capacity, probably due to a slow diffusion of ions from sediments to water. A similar conductivity pattern was noted two months earlier in 2002, from July onwards (Tavernini, Bartoli et al., 2005). The effects of different mineralisation gradients on zooplankton distribution, in particular microcrustaceans, have been previously assessed by several authors (e.g., Boronat, Miracle, & Armengol, 2001; Frisch et al., 2006; Hann & Turner, 2000). Different water ionic content in C1 in the two studied years can explain the different zooplankton seasonal dynamics of 2001 and 2002. pH, EC and TA appear to control cladoceran abundances also in B2 and B4 (Table 3). Moreover, the negative correlation between Chl-*a*, pH and EC (Table 4) may indicate that pH and EC are among the main factors controlling also phytoplankton dynamics in C1. In particular, the influence of pH on phytoplankton community of C1 is confirmed by the dominance of Conjugatophyceae

(Tavernini, unpublished data) which are typical of water bodies characterised by low pH values (Bold & Wynne, 1978).

The continuous presence of water in C1 favoured the appearance of predators, like the newt *Triturus alpestris* Laurenti and macroinvertebrates such as Dytiscidae, Hydrophilidae and Odonata (Tavernini, Mura et al., 2005) in both years. Predation is known to regulate the presence of species in permanent pools (Bohonak & Whiteman, 1999; Schneider & Frost, 1996; Wellborn, Skelly, & Werner, 1996) while in temporary pools the dry period generally precludes the colonisation of these habitats by predators (i.e. fish) and prevents competitive exclusion by reducing the growing season (Dodson, 1975). Unfortunately, no detailed information on the presence and the behaviour of predators in the studied habitats is available.

On the whole, differently from animals living in A and B pools, the community of C1 has been probably less exposed to different dry and wet cycles and concurrently to changing water characteristics. As such, the animals may have not evolved the capacity to withstand frequent changes in environmental features.

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