

Exploring species distribution of spring meiofauna (Annelida, Acari, Crustacea) in the south-eastern Alps

Fabio STOCH*, Reinhard GERECKE¹⁾, Valentina PIERI²⁾, Giampaolo ROSSETTI³⁾ and Beatrice SAMBUGAR⁴⁾

Dipartimento di Scienze Ambientali, University of L'Aquila, Via Vetoio, Coppito, I- 67100 L'Aquila, Italy

¹⁾Biesingerstr. 11, D-72070 Tübingen, Germany

²⁾Dipartimento di Scienze Chimiche e Tecnologie, University of Udine, Via Cotonificio 108, I-33100 Udine, Italy

³⁾Dipartimento di Scienze Ambientali, University of Parma, Viale G.P. Usberti 33A, I-43100 Parma, Italy

⁴⁾Museo Civico di Storia Naturale, Lungadige Porta Vittoria 9, I-37100, Verona, Italy

*e-mail corresponding author: fstoch@faunaitalia.it

ABSTRACT

The distribution patterns of Alpine crenic meiofauna were studied using a standardised sampling procedure at 110 springs, evenly distributed across both carbonate and siliceous rocks in Trentino (northern Italy). Spring altitude ranges between 170 and 2800 m a.s.l. One hundred and thirty-eight taxa (mainly identified at species level), belonging to the Annelida (39), freshwater Acari (57), Copepoda (24), and Ostracoda (18) were found in springs of the investigated area. Using Canonical Correspondence Analysis, spatial patterns of meiofaunal assemblages at the regional scale were best explained by altitude, water chemistry (mainly related to geology) and water-flow regime; the role of microhabitat structure and anthropogenic disturbance as environmental descriptors was of minor importance.

Key words: springs, meiofauna, Alps

1. INTRODUCTION

Mountain areas in the Alps are one of the zoogeographical regions that were affected by the latest post-glacial colonization events. Most water bodies are less than 10,000 years old and originated after the retreat of ice-sheets after the Last Glacial Maximum (~21,000 BP). Therefore, distribution patterns of aquatic organisms reflect recent post-glacial events and their determinants are mainly ecological (Stoch 2007).

Several studies have been devoted to the ecology and distribution of spring fauna in Europe (Botosaneanu 1998), but information is still sparse on crenic meiofauna (Särkkä *et al.* 1997; Notenboom *et al.* 1999; D'Ambrosio *et al.* 2003; Fiasca *et al.* 2004; Di Lorenzo *et al.* 2005; Gerecke *et al.* 2005). Most recent faunistic inventories of freshwater organisms from springs in the Alps were assembled from their northern slopes, in Switzerland, Austria, and Germany (see for example Gerecke *et al.* 1998; Gerecke & Franz 2006; Staudacher & Füreder 2007; Fumetti *et al.* 2006). Only more recent contributions (see Crema *et al.* 1996; Stoch 1998b, 2003; Sambugar *et al.* 2006 and references therein) have been devoted to the Alpine and pre-Alpine crenic meiofauna on the southern slopes of the Alps, and have revealed the presence of rare or new species. In the meantime, several studies have produced evidence that the meiofauna plays an outstanding role in the invertebrate communities of freshwater habitats (Rundle *et al.* 2000), not only in terms of species diversity, but also with respect to their high population densities (Stoch

2003) and their role within the food webs (Schmid-Araya & Schmid 2000). However, the number of regional surveys of crenic meiofauna distribution in the Alps remains limited, and gaps remain in our knowledge of the geographical distribution and basic ecology of meiofaunal species.

This paper presents data on meiofauna sampled from 110 Alpine springs in Trentino (south-eastern Alps) within the CRENODAT project (Laveder 2007). The main focus is on the Annelida, freshwater mites (Hydrachnidia and Halacaridae), and microcrustaceans (Ostracoda and Copepoda). The aims of this paper are (i) to assess species richness and composition of meiofaunal assemblages in a large Alpine region; ii) to examine the relationship between the occurrence of meiofaunal species and environmental descriptors at a regional scale along an altitudinal gradient of over 2600 metres; (iii) to compare the role of the measured environmental variables for the different taxonomic groups.

2. MATERIALS AND METHODS

2.1. Study area

The south-eastern Alps form a complex pattern of geological strata that offers different hydrological conditions to the aquatic biota. Basically, two major hydrobiological provinces can be distinguished on the basis of the different solubility of the bedrock: springs on primary rocks in the Alps tend to have ion-poor softwater, while springs in the limestone Alps and Dolomites are rich in carbonate (Cantonati *et al.* 2007 and references therein).

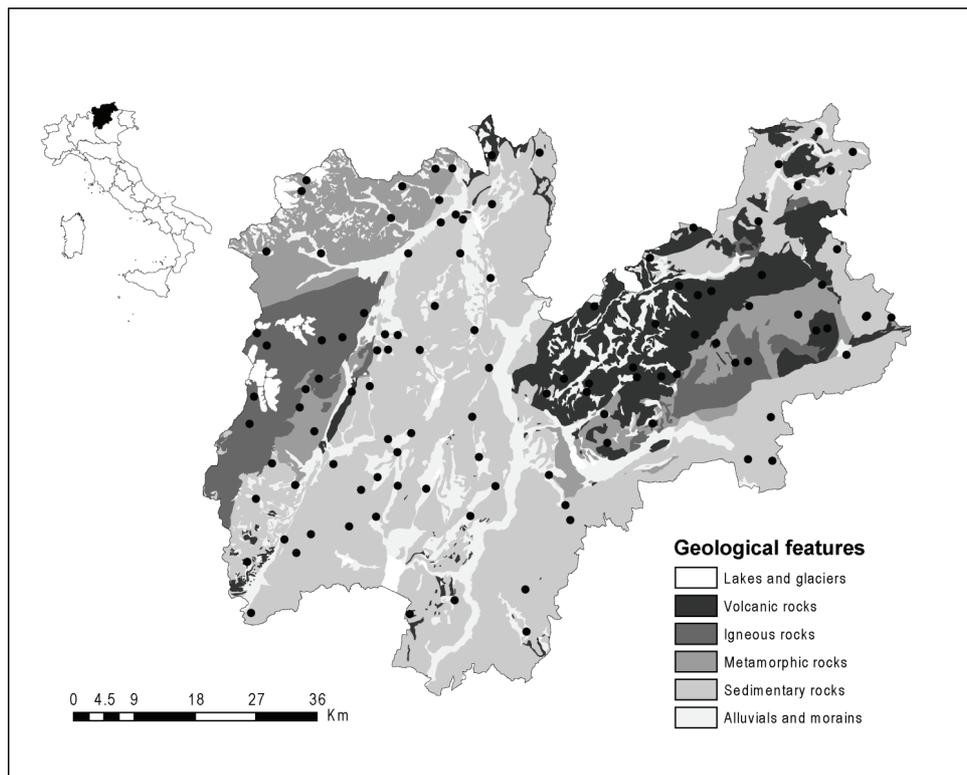


Fig. 1. Map of the springs sampled in Trentino, superimposed on the geological features of this geographic area.

The selection of springs throughout the Trentino area (6207 km²) was based on the following attributes: perennial flow regime, no water exploitation, free surface flow of the emerging water without anthropogenic disturbance, and an even altitudinal distribution, including high altitude springs (Laveder 2007). The location of the springs sampled during CRENODAT project is reported in figure 1, superimposed on a simplified geological map. The sampled springs were located over a wide altitudinal range (from 170 to 2792 m a.s.l.), and a variety of geological substrata: from sedimentary (mainly limestone and dolomites) to siliceous rocks (metamorphic, microcrystalline, crystalline). A more detailed description of the whole environmental dataset can be found in Cantonati *et al.* (2011, submitted).

2.2. Sampling methods

The crenal area *sensu stricto* (eucrenal) was selected for sampling, limiting this area to the spring mouth, as well as to smaller rivulets before they merge in a single channel (the so-called hypocrenal: Gerecke *et al.* 1998). Sampling methods for meiofauna used in the CRENODAT project, as well as preparation and study methods for individual meiofaunal groups are described elsewhere [Sambugar (2007) for Annelida, Gerecke & Di Sabatino (2007) for Acari, Stoch (2007) for Copepoda, Rossetti (2007) for Ostracoda]. Individual microhabitats were sampled at each spring and the sampling

techniques were calibrated to obtain quantitative results comparable to a small Surber-like sampler (Gerecke *et al.* 2007). Three distinct microhabitats were retained in this study: a) stones, pebbles, and rocky surfaces; b) bryophytes; c) sediments (sand and debris). Samples were filtered through a sieve (mesh size 100 µm). More details are reported in Gerecke *et al.* (2011).

Species abundances used in the statistical analyses were obtained, combining the values of every microhabitat for each spring, weighting each microhabitat by its coverage of the crenic habitat.

2.3. Measurement of environmental variables

Eighteen environmental variables were chosen as environmental descriptors of species distribution in the region and measured at each site: (1) altitude, determined with a Geographic Positioning System (GPS III Plus™) and verified on topographic maps; (2) specific conductivity at 25 °C, measured using Hydrolab multiprobes (H20 and Quanta); (3) average discharge, measured using a graduated bucket; (4) average current velocity, measured with an OTT propeller-flow meter; (5) pH, (6) alkalinity, (7) dissolved organic carbon (DOC), and concentrations of (8) calcium, (9) magnesium, (10) nitrates, (11) phosphates, (12) silica, (13) sulphates, (14) chloride, (15) sodium, and (16) potassium, measured using standard methods after the American Public Health Association (APHA 2000); (17) spring typology (limnocrenic, helocrenic, and

rheocrenic); (18) impact index (a visual index ranging from 0 = no anthropogenic pressure to 4 = high anthropogenic pressure). Additional morphological variables measured in the field were coverage of bryophytes (20), sediments (sand and gravel) (21), and pebbles, boulders and rocks (22). More details can be found in Cantonati *et al.* (2007). Due to the observed collinearity among some measured environmental variables, average discharge and average current velocity were combined, together with spring typology, in a single variable (flow velocity condition, coded as "flow") and scored (1-5) following Cantonati *et al.* (2007).

2.4. Statistical analysis of data

In order to assess relationships between the distribution of meiofauna and environmental variables, a Canonical Correspondence Analysis (CCA) was performed using the statistical package CANOCO version 4.5 (ter Braak & Šmilauer 2002). CCA was based on the environmental matrix of measured physical and chemical water variables and species abundance data. Species abundances were $\log(x+1)$ transformed to reduce the effect of the most abundant species on the ordination. Due to the tendency of rare species to distort the analyses, species with a single record or springs with a single species were excluded from the ordination, and rare species were down-weighted. The Monte Carlo permutation test (999 permutations) was used to assess the significance of the canonical axes.

3. RESULTS

3.1. Meiofaunal species richness

One hundred and thirty-eight taxa (mainly identified at species level), belonging to the Annelida (39), freshwater Acari (57), Copepoda (24), and Ostracoda (18), were found in the Trentino springs (Tab. 1). The freshwater Acari (41% of total species richness) were the most species-rich group, followed by the Annelida (28%), Copepoda (18%), and Ostracoda (13%). However, by considering taxon abundance in terms of number of individuals for each group, the composition of crenic assemblages is dominated by Crustacea (Copepoda, 39% and Ostracoda, 32%), followed by Acari (21%), while the abundance of Annelida was very low (8%).

Distributional rarity was high: no meiofaunal species were found in seven sites (6% of all sites) and 47 species (34% of all species) occurred in one site only. The most common species belong to the Copepoda; five out of 24 species were present in more than 20% of the springs, *Bryocamptus echinatus* being present in 60 springs (43%). Only three of 57 species of Acari (*Soldanellonyx chappuisi*, *Partnunia steinmanni* and *Atractides panniculatus*), one species of Annelida (*Nais communis*) and two species of Ostracoda (*Psychrodromus fontinalis* and *Potamocypris pallida*) were recorded in more than 20%

of the springs, and never more than in 28 springs (*Psychrodromus fontinalis*).

The mean number of species per spring was 9.4 ± 6.0 (mean \pm standard deviation), slightly higher in siliceous than in carbonate springs (Tab. 2). The Acari have the highest local diversity (3.6 ± 3.8), followed by Copepoda (3.3 ± 1.9), Annelida (1.3 ± 1.8) and Ostracoda (1.2 ± 1.1).

3.2. Environmental gradients

The summary of environmental variable values (mean \pm standard deviation) is shown in table 3. In the same table summaries are given for carbonate and siliceous springs. Siliceous springs have a lower specific conductivity and alkalinity, lower pH values, as well as a lower value for all chemical variables except silica. The coverage of bryophytes, pebbles and stones, and fine sediments show wide variation (Tab. 3). Bryophytes (especially liverworts) are more frequent in siliceous springs, where there is a lower amount of fine sediments. However, the differences were not statistically significant, probably linked more to altitude and flow velocity than to lithology.

Ninety-five species and 96 springs were retained for Canonical Correspondence Analysis. As a first step, CCA was performed including all environmental variables. The contribution of substratum structure (expressed as coverage of the three main substratum types) to CCA axes was weak. Variance partitioning (following Borcard *et al.* 1992) between substrata and chemico-physical variables demonstrated that substratum structure accounted for 3.2% of overall variation, while the contribution of the other variables was high (27.2%), and, together with joint variation with substratum (1.4%), explained approximately one third of the total variation in the species abundance matrix. After excluding substratum structure, the first two CCA axes (Fig. 2) accounted for 43.4% (28.3% the first axis, 15.1% the second axis) of the cumulative variation of the species-environment relationship (Tab. 4). Species-environment correlations were high (0.87 for axis 1 and 0.81 for axis 2), suggesting a strong influence of environmental gradients on the composition of the meiofaunal assemblages. The Monte Carlo permutation test showed that both canonical axes were significant ($P < 0.001$).

Altitude, together with specific conductivity, alkalinity, calcium, magnesium and chloride had the strongest correlations with the first axis (Tab. 4), defining an altitudinal gradient. Along this main gradient the ionic content of crenic waters decreased with increasing altitude, in relation to the geological substratum. Silica and sodium have a strong, negative correlation with the second axis, while pH, calcium and magnesium have a positive correlation, clearly separating springs on carbonate rocks from those on siliceous (Fig. 2a), including volcanic, rocks mostly defined by sodium content.

Tab. 1. List of meiofaunal species collected from spring waters in Trentino. Identification codes used for CCA. Frequencies calculated on 110 springs.

Taxonomic group	Species	ID Code	No. springs	Frequency
ANNELIDA				
POLYCHAETA				
Family Aelosomatidae	<i>Aeolosoma</i> sp.	Aeo	6	5.5%
Family Parergodrilidae	<i>Parergodrilus</i> sp.		1	0.9%
OLIGOCHAETA				
Family Enchytraeidae	<i>Achaeta affinis</i> Nielsen & Christensen, 1959		1	0.9%
	<i>Buchholzia appendiculata</i> (Buchholz, 1862)	Bap	3	2.7%
	<i>Buchholzia simplex</i> (Nielsen & Christensen, 1963)		1	0.9%
	<i>Cernosvitoviella aggtelekiensis</i> Dózsa-Farkas, 1970		1	0.9%
	<i>Cernosvitoviella atrata</i> (Bretscher, 1903)	Cat	8	7.3%
	<i>Cernosvitoviella goodhui</i> Healy, 1975	Cgo	2	1.8%
	<i>Cernosvitoviella minor</i> Dózsa-Farkas, 1990	Cmi	13	11.8%
	<i>Cernosvitoviella palustris</i> Healy, 1979	Cpa	2	1.8%
	<i>Cernosvitoviella parviseta</i> Gadzinska, 1974	Cpv	7	6.4%
	<i>Cernosvitoviella</i> sp. 1 group <i>parviseta</i>	Cp1	3	2.7%
	<i>Cernosvitoviella pusilla</i> Nurminen, 1973	Cpu	2	1.8%
	<i>Cernosvitoviella tatrensis</i> (Kowalewski, 1916)	Cta	3	2.7%
	<i>Cognettia cognettii</i> (Issel, 1905)		1	0.9%
	<i>Enchytraeus</i> sp. group <i>buchholzi</i> Vejdovsky, 1879	Ebu	3	2.7%
	<i>Fridericia alata</i> Nielsen & Christensen, 1959		1	0.9%
	<i>Fridericia perrieri</i> (Vejdovský 1878)		1	0.9%
	<i>Henlea perpusilla</i> Friend, 1911	Hpe	3	2.7%
	<i>Marionina argentea</i> (Michaelsen, 1889)	Mar	16	14.5%
	<i>Marionina</i> cfr. <i>spicula</i> (Leuckart, 1847)	Msp	3	2.7%
	<i>Marionina</i> sp. prope <i>charlottensis</i> Coates, 1980		1	0.9%
	<i>Marionina</i> sp. prope <i>hoffbaueri</i> Möller, 1971		1	0.9%
	<i>Mesenchytraeus armatus</i> Levinsen, 1884	Msa	6	5.5%
	<i>Timmodrilus</i> sp.		1	0.9%
Family Naididae	<i>Bothrioneurum</i> sp.		1	0.9%
	<i>Chaetogaster diastrophus</i> (Gruithuisen, 1828)	Cdi	4	3.6%
	<i>Chaetogaster langi</i> Bretscher, 1896	Cla	4	3.6%
	<i>Nais bretscheri</i> Michaelsen, 1899	Nbr	2	1.8%
	<i>Nais communis</i> Piguet, 1906	Nco	29	26.4%
	<i>Nais pardalis</i> Piguet, 1906		1	0.9%
	<i>Nais variabilis</i> Piguet, 1906	Nva	4	3.6%
	<i>Pristina rosea</i> (Piguet, 1906)		1	0.9%
	<i>Rhyacodrilus falciformis</i> Bretscher, 1901	Rfa	5	4.5%
	<i>Tubifex tubifex</i> (Müller, 1774)	Ttu	3	2.7%
	Tubificinae gen. sp. 1		1	0.9%
Family Lumbriculidae	<i>Lumbriculus</i> sp.		1	0.9%
	<i>Stylodrilus</i> cfr. <i>lemanii</i> (Grube, 1879)		1	0.9%
	<i>Stylodrilus</i> sp. 1		1	0.9%
ACARI				
HALACAROIDEA				
Family Halacaridae	<i>Lobohalacarus weberi</i> (Romijn & Viets, 1924)	Lwe	2	1.8%
	<i>Soldanellonyx chappuisi</i> Walter, 1917	Sch	27	24.5%
HYDRACHNIDIA				
Family Aturidae	<i>Aturus crinitus</i> Thor, 1902		1	0.9%
	<i>Aturus fontinalis</i> Lundblad, 1920	Afo	2	1.8%
	<i>Aturus serratus</i> K. Viets, 1922		1	0.9%
	<i>Ljania bipapillata</i> Thor, 1898	Lbi	8	7.3%
Family Feltriidae	<i>Feltria</i> cf. <i>armata</i> Koenike, 1902		1	0.9%
	<i>Feltria cornuta</i> Walter, 1927	Fco	6	5.5%
	<i>Feltria minuta</i> Koenike, 1892	Fmi	12	10.9%
	<i>Feltria setigera</i> Koenike, 1896	Fse	12	10.9%
	<i>Feltria zschokkei</i> Koenike, 1896	Fzs	5	4.5%
Family Hydrovolziidae	<i>Hydrovolzia placophora</i> (Monti, 1905)	Hpl	22	20.0%
Family Hydryphantidae	<i>Parathyas palustris</i> (Koenike, 1912)		1	0.9%
	<i>Panisellus thienemanni</i> (K. Viets, 1920)	Pth	4	3.6%
	<i>Panisopsis curvifrons</i> (Walter, 1907)	Pcu	4	3.6%
	<i>Panisopsis setipes</i> (K. Viets, 1911)		1	0.9%
	<i>Panisus michaeli</i> Koenike, 1896	Pmi	5	4.5%
	<i>Partnumia steinmanni</i> Walter, 1906	Pst	26	23.6%

(continued)

Tab. 1. Continuation.

Taxonomic group	Species	ID Code	No. springs	Frequency	
Family Hygrobatidae	<i>Protzia brevipalpis</i> Maglio, 1909	Pbr	2	1.8%	
	<i>Protzia distincta</i> Walter, 1922	Pdi	17	15.5%	
	<i>Protzia eximia</i> (Protz, 1896)		1	0.9%	
	<i>Protzia squamosa</i> Walter, 1908	Psq	2	1.8%	
	<i>Wandesia thori</i> Schechtel, 1912		1	0.9%	
	<i>Atractides (Atractides)</i> sp. [" <i>coriaceus</i> (K. Viets, 1925)"]		12	0.9%	
	<i>Atractides (Atractides) adnatus</i> (Lundblad, 1956)	Aad	1	10.9%	
	<i>Atractides (Atractides) macrolaminatus</i> Láska, 1956	Ama	2	1.8%	
	<i>Atractides (Atractides) nodipalpis</i> Thor, 1899		1	0.9%	
	<i>Atractides (Atractides) panniculatus</i> (K.Viets, 1925)	Apn	24	21.8%	
	<i>Atractides (Atractides) protendens</i> K.O. Viets, 1955		1	0.9%	
	<i>Atractides (Atractides) vaginalis</i> (Koenike, 1905)	Ava	5	4.5%	
	<i>Atractides (Atractides) walteri</i> (K. Viets, 1925)	Awa	18	16.4%	
	Family Lebertiidae	<i>Atractides (Polymegapus) polyporus</i> (K.Viets, 1922)	Apo	3	2.7%
<i>Hygrobates (Hygrobates) calliger</i> (Piersig, 1896)		Hca	2	1.8%	
<i>Hygrobates (Hygrobates) fluvialtilis</i> (Ström, 1768)		Hfl	2	1.8%	
<i>Hygrobates (Rivobates) norvegicus</i> (Thor, 1897)		Hno	13	11.8%	
<i>Lebertia (Brentalebertia) hygropetrica</i> Gerecke, 2008			1	0.9%	
<i>Lebertia (Lebertia) fimbriata</i> Thor, 1901			1	0.9%	
<i>Lebertia (Lebertia) maculosa</i> Koenike, 1908		Lma	10	9.1%	
<i>Lebertia (Lebertia) reticulata</i> Koenike, 1919		Lre	3	2.7%	
<i>Lebertia (Lebertia) schechteli</i> Thor, 1913		Lsc	15	13.6%	
<i>Lebertia (Mixolebertia) bracteata</i> K. Viets, 1925		Lbr	2	1.8%	
<i>Lebertia (Mixolebertia) cuneifera</i> Walter, 1922		Lcu	2	1.8%	
<i>Lebertia (Mixolebertia) giardinai</i> Maglio, 1908		Lgi	7	6.4%	
<i>Lebertia (Mixolebertia) holsatica</i> K.Viets, 1920		Lho	6	5.5%	
<i>Lebertia (Mixolebertia) macilentia</i> K. Viets, 1922			1	0.9%	
Family Momoniidae	<i>Lebertia (Mixolebertia) sefvei</i> Walter, 1911	Lse	5	4.5%	
	<i>Lebertia (Mixolebertia) stigmatifera</i> Thor, 1900		1	0.9%	
Family Momoniidae	<i>Momonium falcipalpis</i> Halbert, 1906		1	0.9%	
Family Pionidae	<i>Pseudofeltria scourfieldi</i> Soar, 1904	Psc	6	5.5%	
Family Sperchontidae	<i>Sperchon (Hispidosperchon)</i> sp. group <i>denticulatus</i>		1	0.9%	
	<i>Sperchon (Hispidosperchon) violaceus</i> Walter, 1944	Svi	8	7.3%	
	<i>Sperchon (Sperchon) brevirostris</i> Koenike, 1895	Sbr	2	1.8%	
	<i>Sperchon (Sperchon) mutilus</i> Koenike, 1895	Smu	8	7.3%	
	<i>Sperchon (Sperchon) resupinus</i> K.Viets, 1922	Sre	3	2.7%	
	<i>Sperchon (Sperchon) squamosus</i> Kramer, 1879	Ssq	8	7.3%	
	<i>Sperchon (Sperchon) thienemanni</i> Koenike, 1907	Sth	18	16.4%	
	<i>Sperchonopsis verrucosa</i> (Protz, 1896)	Sve	12	10.9%	
	<i>Torrenticola elliptica</i> Maglio, 1909	Tel	2	1.8%	
	Family Torrenticolidae				
COPEPODA					
HARPACTICOIDA					
Family Canthocamptidae	<i>Attheyella (Attheyella) crassa</i> (Sars, 1863)	Acr	4	3.6%	
	<i>Attheyella (Attheyella) wierzejskii</i> (Mrázek, 1893)	Awi	28	25.5%	
	<i>Maraenobiotus zschokkei</i> Kreis, 1920		1	0.9%	
	<i>Bryocamptus (Rheocamptus) zschokkei</i> (Schmeil, 1893)	Bzs	61	55.5%	
	<i>Bryocamptus (Rheocamptus) tatrensis</i> Minkiewicz, 1916	Bta	36	32.7%	
	<i>Bryocamptus (Rheocamptus) pygmaeus</i> (Sars, 1863)	Bpy	26	23.6%	
	<i>Bryocamptus (Arcticocamptus) alpestris</i> (Vogt, 1845)	Bal	3	2.7%	
	<i>Bryocamptus (Arcticocamptus) cuspidatus</i> (Schmeil, 1893)	Bcu	22	20.0%	
	<i>Bryocamptus (Arcticocamptus) rhaeticus</i> (Schmeil, 1893)	Brh	20	18.2%	
	<i>Bryocamptus (Arcticocamptus) vandouwei</i> (Kessler, 1914)		1	0.9%	
	<i>Bryocamptus (Arcticocamptus) abnobensis</i> (Kiefer, 1929)	Bab	2	1.8%	
	<i>Bryocamptus (Echinocamptus) echinatus</i> (Mrázek, 1893)	Bec	47	42.7%	
	<i>Pilocamptus pilosus</i> (Van Douwe, 1915)		1	0.9%	
	<i>Epactophanes richardi</i> Mrázek, 1893	Eri	2	1.8%	
	<i>Moraria (Moraria) alpina</i> Stoch, 1998	Mal	29	26.4%	
	<i>Moraria (Moraria) poppei</i> (Mrázek, 1893)	Mpo	2	1.8%	
	<i>Moraria (Moraria) sp.</i>	Ms1	2	1.8%	
	Family Cyclopidae	<i>Eucyclops serrulatus</i> (Fischer, 1851)	Ese	12	10.9%
		<i>Paracyclops imminutus</i> Kiefer, 1929	Pim	21	19.1%
		<i>Acanthocyclops vernalis</i> (Fischer, 1853)	Ave	3	2.7%
	<i>Diacyclops hypnicola</i> (Gurney, 1927)		1	0.9%	

(continued)

Tab. 1. Continuation.

Taxonomic group	Species	ID Code	No. springs	Frequency
	<i>Diacyclops italianus</i> (Kiefer, 1931)	Dit	2	1.8%
	<i>Diacyclops</i> sp. gr. <i>languidus</i>	Dla	3	2.7%
	<i>Speocyclops cerberus</i> (Chappuis, 1934)		1	0.9%
OSTRACODA				
Family Candonidae	<i>Candona candida</i> (O. F. Müller, 1776)	Cca	2	1.8%
	<i>Candona</i> sp. group <i>neglecta</i>	Cne	5	4.5%
	<i>Candona neglecta</i> Sars, 1887		1	0.9%
	<i>Candona</i> cfr. <i>lindneri</i> Petkovski, 1969		1	0.9%
	<i>Fabaeformiscandona</i> cfr. <i>breuili</i> (Paris, 1920)		1	0.9%
	<i>Cryptocandona vavrai</i> Kaufmann, 1900	Cva	2	1.8%
	<i>Cypria ophthalmica</i> (Jurine, 1820)	Cop	6	5.5%
	<i>Cyclocypris ovum</i> (Jurine, 1820)		1	0.9%
Family Cyprididae	<i>Eucypris pigra</i> (Fischer, 1851)	Epi	11	10.0%
	<i>Bradleystrandesia</i> sp.		1	0.9%
	<i>Psychrodromus</i> cfr. <i>olivaceus</i> (Brady & Norman, 1889)		1	0.9%
	<i>Psychrodromus fontinalis</i> (Wolf, 1920)	Pfo	30	27.3%
	<i>Psychrodromus</i> cfr. <i>betharrami</i> Baltanás et al. 1993	Pbe	7	6.4%
	<i>Scottia pseudobrowniana</i> Kempf, 1971	Sps	3	2.7%
	<i>Cavernocypris subterranea</i> (Wolf, 1920)	Csu	4	3.6%
	<i>Potamocypris fulva</i> (Brady, 1868)		1	0.9%
	<i>Potamocypris pallida</i> Alm, 1914	Ppa	28	25.5%
	<i>Potamocypris zschokkei</i> (Kaufmann, 1900)	Pzs	16	14.5%
	<i>Potamocypris fallax</i> Fox, 1967	Pfa	7	6.4%
	<i>Potamocypris villosa</i> (Jurine, 1820)		1	0.9%

Tab. 2. Summary of species richness (mean \pm SD) in springs in Trentino.

No. sites	Region 96	Carbonate 58	Siliceous 38
All taxa	9.4 \pm 6.0	8.0 \pm 4.9	11.5 \pm 6.8
Annelida	1.3 \pm 1.8	0.9 \pm 1.2	2.0 \pm 2.3
Acari	3.6 \pm 3.8	3.0 \pm 3.4	4.4 \pm 4.2
Copepoda	3.3 \pm 1.9	3.0 \pm 1.8	3.8 \pm 1.9
Ostracoda	1.2 \pm 1.1	1.1 \pm 1.0	1.3 \pm 1.2

Tab 3. Summary of environmental variables (mean \pm SD) in springs in Trentino.

No. sites		Region 96	Carbonate springs 58	Siliceous springs 38
Altitude	(m a.s.l.)	1277.7 \pm 565.3	994.0 \pm 455.8	1710.6 \pm 426.6
Specific conductivity	(μ S cm ⁻¹)	199.2 \pm 152.9	297.4 \pm 115.0	49.3 \pm 38.8
pH		7.0 \pm 0.6	7.9 \pm 0.2	6.6 \pm 0.5
Alkalinity	(mg L ⁻¹)	103.2 \pm 85.6	160.0 \pm 61.6	16.5 \pm 13.9
N-NO ₃ ⁻	(μ g L ⁻¹)	750.3 \pm 886.4	972.9 \pm 1058.9	410.6 \pm 306.3
P-PO ₄ ³⁻	(μ g L ⁻¹)	4.2 \pm 5.7	5.0 \pm 7.1	3.0 \pm 2.2
SiO ₂	(mg L ⁻¹)	5.0 \pm 2.8	4.3 \pm 2.9	6.1 \pm 2.4
SO ₄ ²⁻	(mg L ⁻¹)	9.5 \pm 17.5	11.4 \pm 20.7	6.7 \pm 10.7
Cl ⁻	(mg L ⁻¹)	13.1 \pm 27.7	19.3 \pm 34.3	3.6 \pm 3.8
Ca ²⁺	(mg L ⁻¹)	32.5 \pm 25.6	49.1 \pm 18.8	7.2 \pm 6.8
Mg ²⁺	(mg L ⁻¹)	7.5 \pm 8.4	11.9 \pm 8.3	0.9 \pm 1.0
Na ⁺	(mg L ⁻¹)	1.7 \pm 1.8	1.9 \pm 2.2	1.4 \pm 0.9
K ⁺	(mg L ⁻¹)	0.6 \pm 0.6	0.7 \pm 0.7	0.5 \pm 0.3
DOC	(mg L ⁻¹)	1.5 \pm 1.4	1.6 \pm 1.4	1.5 \pm 1.4
Impact index		0.6 \pm 0.8	0.7 \pm 0.9	0.5 \pm 0.6
Flow index		3.9 \pm 1.3	4.0 \pm 1.2	3.8 \pm 1.4
Mosses	%	29.6 \pm 25.1	25.6 \pm 23.5	35.7 \pm 26.5
Sediments	%	23.7 \pm 22.0	27.2 \pm 23.5	18.3 \pm 18.6
Stones	%	27.4 \pm 23.6	29.0 \pm 24.1	24.9 \pm 22.8

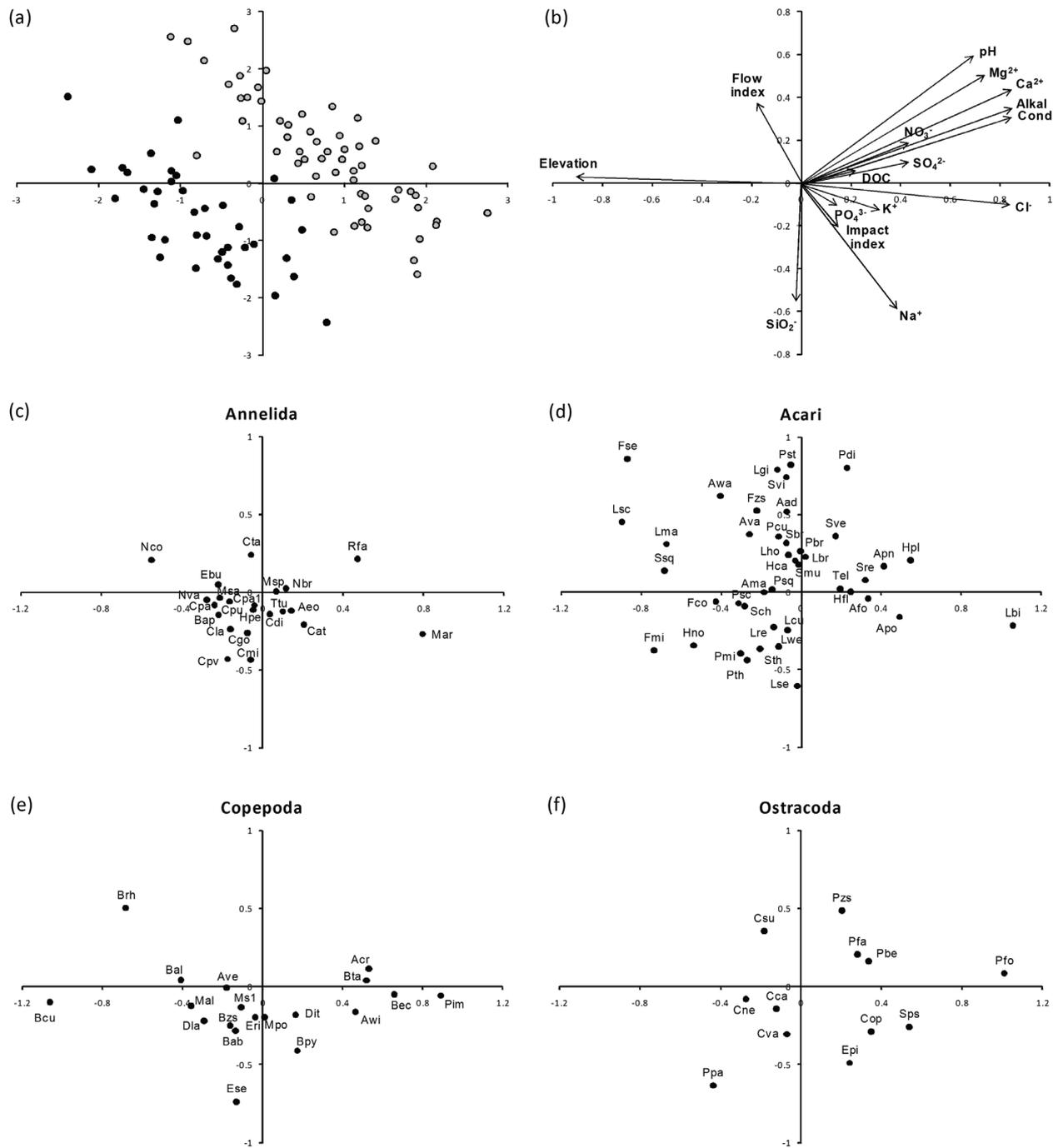


Fig. 2. CCA ordination of sampling sites, environmental variables and meiofaunal species (horizontal axis = first axis, explaining 28.3% of the cumulative variation of the species-environment relationship; vertical axis = second axis, explaining 15.1% of the variation). (a) Sampling sites: black circles = springs occurring in massifs of sedimentary (mainly carbonate) rocks; grey circles = springs occurring in massifs of crystalline (mainly siliceous) rocks. (b) Environmental variables (indicated by arrows). (c), (d), (e), (f) Species (see Tab. 1 for species identification codes).

Tab. 4. Results of Canonical Correspondence Analysis. The intraset correlations between each environmental variable and axes 1 and 2 extracted by CCA are reported (n = 96 sites).

	Axis 1	Axis 2
Explained variation (%)	28.3	15.1
Species-env correlation	0.870	0.813
Altitude	-0.905	0.032
Specific conductivity	0.859	0.318
pH	0.692	0.585
Alkalinity	0.850	0.331
NO ₃ ⁻	0.419	0.179
PO ₄ ³⁻	0.146	-0.097
SiO ₂	-0.018	-0.550
SO ₄ ²⁻	0.430	0.096
Cl ⁻	0.820	-0.087
Ca ²⁺	0.846	0.437
Mg ²⁺	0.731	0.504
Na ⁺	0.312	-0.127
K ⁺	0.389	-0.593
DOC	0.222	0.055
Impact index	0.140	-0.213
Flow index	-0.177	0.378

The two groups of springs were arranged along the altitudinal gradient and along a flow velocity gradient (indicated by the corresponding arrow in Fig. 2b), suggesting that both groups include fast-flowing rheocrenic springs, mainly located at high altitudes, and slow-flowing helocrenic springs at mid-low altitudes. However, most of the low altitude springs are on carbonate substratum (Fig. 2a). As well as the impact index, phosphates show a weak correlation with both axes (Tab. 4 and Fig. 2b), suggesting that their effect on meiofaunal assemblage structure is negligible; nitrates increase slightly at lower altitudes, following alkalinity, calcium and magnesium.

3.3. Species-environment relationships

In the CCA ordination plot (Fig. 2c-f), some species were restricted to high altitude sites, such as the Acari, *Feltria setigera*, *Lebertia schechteli*, *Lebertia maculosa*, and the Harpacticoida, *Bryocamptus cuspidatus* and *Bryocamptus rhaeticus*. *Feltria setigera* and *Bryocamptus rhaeticus* were restricted to fast-flowing, rheocrenic springs. Species showing a preference for low altitude sites were the oligochaete *Marionina argentea*, the mite *Ljania bipapillata*, the cyclopoid *Paracyclops imminutus*, the ostracod *Psychrodromus fontinalis* and, to a lesser extent, the oligochaete *Rhyacodrilus falciformis*, the mite *Hydrovolzia placophora* and the harpacticoids *Bryocamptus echinatus* and *Attheyella crassa*. The remaining copepods and water mites were evenly spaced along the altitudinal gradient, while most annelid species were positioned close to the origin of the axes, indicating wide ecological tolerance to environmental variation. Ostracods showed a preference for low altitude sites.

The altitudinal range for the most frequent meiofaunal species (defined as present in more than 20% of the springs) is shown in figure 3. All these species had their optimum at a certain point along the gradient, as already shown by CCA analysis. Nevertheless, they had a wide tolerance towards altitude and the measured hydrochemical variables, which define the gradient, suggesting that the commonest crenic species are generalists.

Most Oligochaeta (Fig. 2c), especially the Naididae, were linked to siliceous springs located at mid-altitudes, with a low flow index, while the few Enchytraeidae showed a slight preference for carbonate springs. The Acari (Fig. 2d) were more widely scattered on the CCA graph, the species being evenly spaced along both gra-

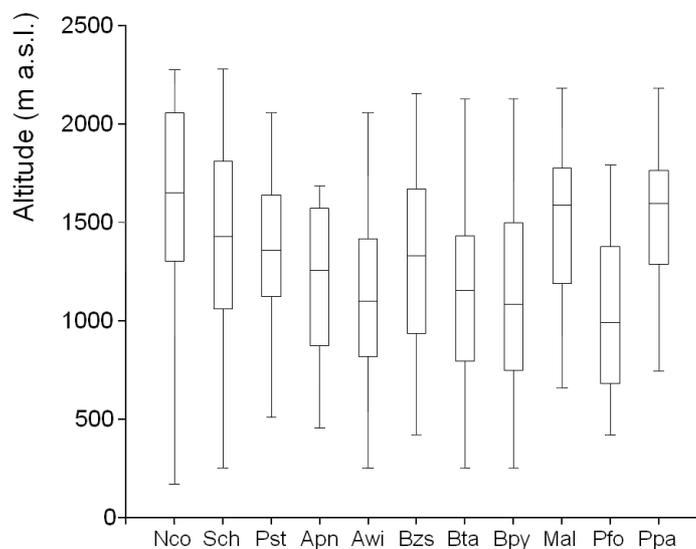


Fig. 3. Box plots showing the altitudinal range for the most frequent meiofaunal species (recorded in more than 20% of the springs; see Tab. 1 for species identification codes).

dients, demonstrating a narrower habitat preference than the other taxa. However, most of the species were collected from siliceous springs. Among the Copepoda (Fig. 2e), only a few species displayed a statistically significant correlation with siliceous springs with moderate current velocity, like the cyclopoid *Eucyclops ser-rulatus*. Finally, among the ostracod species (Fig. 2f), *Psychrodromus fontinalis*, *Potamocypris fallax*, *P. zschokkei*, and *Psychrodromus betharrami* showed a statistically significant preference for carbonate springs, while *Potamocypris pallida* was mainly collected from siliceous springs. All ostracod species avoided fast-flowing springs.

4. DISCUSSION

4.1. Composition of meiofaunal assemblages

The diversity of the meiofaunal assemblages (138 species) is high and supports the statements of some authors (Cantonati *et al.* 2006; Staudacher & Füreder 2007) who considered springs as hotspots of aquatic biodiversity. However, the most frequent species are usually generalists with a high degree of habitat tolerance and a wide altitudinal distribution (see Fig. 3).

The most consistent set of annelid assemblages is given by a group of ubiquitous species (*Nais communis*, *N. variabilis*, *N. pardalis*, *Chaetogaster langi*, *C. diastrophus*, *Enchytraeus buchholzi*, *Mesenchytraeus armatus*). *Nais communis* is the most widespread species. Within the Annelida, few or no species seem to be exclusively linked to crenic habitats. Apart from the above-mentioned, ubiquitous Naididae, the Enchytraeidae include mainly terrestrial and semi-aquatic species that have also proved to be quite common in subterranean aquatic environments (Giani *et al.* 2001). The only genus with exclusively aquatic species, *Cernosvitoviella*, is represented by an unusually high abundance and diversity (nine species, one new to science).

Seven of the ten species present in more than 20 springs belong to the Copepoda. None of them is exclusive to crenic habitats, although *Attheyella wierzejskii* has so far mainly been collected from Alpine and Apenninic rheocrenic springs in Italy (Stoch 2007). Four of the most common copepod species belong to the genus *Bryocamptus* (*B. zschokkei*, *B. tatrensis*, *B. pygmaeus*, *B. echinatus*). They are reported from other habitats, including interstitial habitats, caves, lake shores, and, for *B. pygmaeus*, semi-terrestrial habitats (Janetzky *et al.* 1996). *Paracyclops imminutus* is a rheophilic species, widely distributed in the Palaearctic region in several kinds of surface and in subterranean waters (Karaytug 1999), while *Moraria alpina* is distributed in springs, bogs and interstitial waters in the Alps (Stoch 1998a), as well as in central Europe (Gerecke *et al.* 2005). Ostracods are never as common as copepods. The most frequent species, *Psychrodromus fontinalis*, usually occurs in springs and mountain brooks, but is also found in karstic ground water, mainly

in ecotones between surface and groundwater environments (Baltanás *et al.* 1993). *Potamocypris pallida* was by far the most abundant ostracod species, accounting for 69.7% of the total ostracod specimens. This species is known to inhabit springs, cold streams flowing from springs, and spring-fed ponds (Meisch 1984; Stoch 1998b).

Conversely, some of the crustacean species, recorded from one site only, are interesting from a faunistic and biogeographic point of view. Within copepods, two of these rare species are stygobionts: *Speocyclops cerberus*, formerly known from a single cave in Austria (Gaviria 1998) and new to the Italian fauna, and *Diacyclops* sp. of the *languidus* - group, new to science. *Bryocamptus abnobensis*, previously recorded from central Europe (Janetzky *et al.* 1996), is reported for the first time from Italy, while *Maraenobiotus zschokkei* is a rare Alpine species known from a few springs in Italy (Berera *et al.* 2006) and Switzerland. Among the ostracods, *Potamocypris villosa* was first recorded in an Italian Alpine spring during the present study.

Copepods found in springs are usually not true crenobionts (Stoch 1998b, 2007; Galassi *et al.* 2002). Most of the crenic species also occur in the epirhithral, in the littoral zone of lakes, in semi-terrestrial habitats (e.g., wet bryophytes and moist soil), or in ground water (Gerecke *et al.* 1998; Jersabek *et al.* 2001; Galassi *et al.* 2002; Stoch 1998b, 2003). The same holds true for ostracods too; very few species found in springs seem to be true crenobionts or specifically associated with waters connected to springs (for example, *Cycloocypris helocrenica*, *Psychrodromus olivaceus*, *Potamocypris fallax*). Most ostracods are habitat generalists and occur in other surface aquatic systems, or in interstitial and groundwater environments as well (e.g., several representatives of the subfamily Candoninae after Gidó, 2005).

The true water mites included one recently described species for which a new subgenus was created, *Lebertia* (*Brentalebertia*) *hygropetrica* Gerecke, 2008, and nine other species new to the Italian fauna (*Panisellus thienemanni*, *Lebertia bracteata*, *L. macilenta*, *L. reticulata*, *Atractides adnatus*, *A. macrolaminatus*, *Feltria cornuta*, *Aturus serratus* and *A. fontinalis*). Moreover, the Acari included 121 (semi-)terrestrial taxa, including nine species new to the Italian fauna (Gerecke *et al.* 2009). For two of the three most abundant Acari, *Soldanellonyx chappuisi* and *Partnunia steinmanni*, other contributions (Gerecke *et al.* 2005, Gerecke & Martin 2006) confirm a rather wide altitudinal range, with *S. chappuisi* also able to colonize extreme habitats at high altitudes, which are potentially subject to drying or freezing, including pools, lake shores and subterranean waters. On the other hand, *Hydrovolzia placophora*, also widely distributed in Central Europe, is a strict crenobiont and depends on continuous year-round flow (Gerecke *et al.* 2007).

Among the meiofaunal groups, the Acari represent a particular case; they include a high number of true crenobionts (Gerecke *et al.* 1998; Gerecke & Di Sabatino 2007) and show a discrepancy between species richness and abundance. While halacarids have a rather simple life cycle, with a larva and three nymphal stages gradually approaching the adult morphology, true freshwater mites (Hydrachnidia) display a particularly complex change in morphology and feeding behaviour during their development. Larvae are obligate parasites of freshwater insects, often with high selectivity for hosts, i.e. to a particular order or family. Active post-larval stages of the Hydrachnidia, deutonymphs and adults, feed as predators, mostly on eggs and early larval stages of insects, but also on other invertebrates (Martin 2005). This feeding habit may explain the discrepancy between the high species richness and the low individual abundance in the Alpine springs. In natural ecosystems, predators are necessarily less abundant than their prey (Schmid-Araya & Schmid 2000). Moreover, the complex interactions between the Hydrachnidia and their insect hosts and prey (Gerecke & Di Sabatino 2007) offer large numbers of niches for exploitation, and may explain the co-existence of several species in microhabitats where representatives of other meiofaunal groups, mainly feeding on organic matter and the associated microbial biofilm, microfauna and microflora (Dole-Olivier *et al.* 2000), display lower species richness. Finally, life style may explain the unusual crenobiosis showed by this taxon (Gerecke *et al.* 1998; Gerecke & Di Sabatino 2000, 2007).

4.2. Meiofaunal diversity patterns and their ecological determinants

Based on the CCA results, at the regional scale in Trentino, crenic meiofaunal assemblages are distributed along a gradient from high altitude, slightly acidic and poorly mineralized springs, to low altitude, alkaline waters, of high ionic content. A second gradient, mainly defined by silica and sodium concentration, separates those springs on siliceous (crystalline, metamorphic, and volcanic) bedrocks from those on carbonate massifs, mainly formed of limestone and dolomite. Finally, both siliceous and carbonate springs also follow a hydraulic gradient, defined by the flow index, and correlated with the altitudinal gradient. Therefore, the main environmental descriptors of meiofaunal distribution patterns in Trentino are altitude, water chemistry, and water flow. This is in agreement with the main results obtained for macroinvertebrates by Lindegaard *et al.* (1998) and several other authors who stated that altitude (Barquín & Death 2006), flow regime (Gooch & Glazier 1991; Smith & Wood 2002; Smith *et al.* 2001, 2003; Ilmonen *et al.* 2009; Fumetti *et al.* 2006), and water chemistry (Barquín & Death 2009; Glazier 1991) are the main determinants of macrozoobenthic assemblages in springs.

The anthropogenic disturbance detected (summarized by the impact index), as well as the environmental parameters linked to human activities, such as phosphate concentration, are not important in the ordination of sites by CCA. The contribution of nitrates is also weak, albeit statistically significant, due to the low anthropogenic pressure in the area (Laveder 2007). Conversely however, when present anthropogenic disturbance can be the most important environmental descriptor of meiofaunal assemblage structure and distribution, as demonstrated for Finnish springs (Särkka *et al.* 1997), where it obscured the effects of the other factors.

Finally, the contribution of substratum composition to the CCA axes was low. This suggests that this variable, advocated as a major determinant of macrozoobenthic abundance and distribution in springs (Glazier & Gooch 1987; Hahn 2000; Dumnicka *et al.* 2007), plays only a minor role in defining environmental gradients of Alpine crenic habitats in Trentino. This agrees with the results obtained by Lindegaard *et al.* (1998) for macroinvertebrates in Danish springs and by Schröder *et al.* (2006) for selected invertebrates in springs of the north-eastern Alps. The high substratum heterogeneity within local crenic habitats may be responsible for the observed low influence on meiofaunal distribution patterns at the regional scale.

However, notwithstanding the high species-environment correlations revealed by CCA, about half the total variation is undetermined. There are at least two possible reasons for the high proportion of unaccounted variation, i.e. other spatially or non-spatially structured biological or environmental factors that were not measured in the field, or stochastic variation.

Spatial structures are of paramount importance in ecological studies because their presence indicates that some process has been at work to create them (Borcard *et al.* 1992, 2004; Dray *et al.* 2006). Apart from environmental factors, these processes include dispersal limitation and spatially constrained biotic interactions. Both abiotic and biotic processes are likely to operate on crenic meiofauna at different spatial scales, and for this reason variation partitioning (Borcard *et al.* 1992) between environmental, biotic and spatial components is under development and will be referred to in another paper. As suggested by Schmid-Araya & Schmid (2000), it would be particularly interesting to explore the interaction between meiofaunal and macroinvertebrate assemblages; meiofaunal distribution patterns may be linked to those of macroinvertebrates. Macroinvertebrates may interact with the meiofauna as predators or competitors in exploiting resources and occupying physical niches during the first larval stages (Schmid-Araya & Schmid 2000), as well as through the complex interactions with the water mites which parasitize them (Martin & Stur 2006, Gerecke & Di Sabatino 2007).

Finally, it is possible that stochastic processes (neutral theory of macroecology: Hubbel 2001), like the dynamics of populations which are partly driven by dispersal and may not be habitat-dependent, may also explain the unaccounted variation. This remains to be tested, but may be particularly important for water mites.

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