



Distribution and ecology of copepods in mountainous regions of the Eastern Alps

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Abstract

Copepod species richness, patterns of distribution and composition of assemblages were evaluated in high-altitude sites in the Eastern Alps. Diverse habitats were sampled in 160 lentic water bodies from different geologic areas, ranging from acid bog ponds to alkaline karst waters and from small temporary puddles to deep lakes. The altitudinal range comprised all mountainous regions from the montane (1290 m a.s.l.) to the alpine (2886 m a.s.l.) zone. Forty-four species were recorded, with the harpacticoids being the richest group. Although most species occupied a wide altitudinal range, some stenotopic mountain forms were restricted to alpine habitats. The most widespread taxa were *Acanthocyclops vernalis*, *Eucyclops serrulatus*, *Bryocamptus rhaeticus*, *Arctodiaptomus alpinus* and *Cyclops abyssorum taticus*. All species found were listed along with notes on their distribution, ecology and patterns of coexistence. There was both a marked change in species composition and a decline in species richness from hardwater habitats in the Limestone Alps to softwater sites in the Central Alps. Copepod taxocoenoses were most diverse in montane limestone lakes and impoverished with increasing altitude. Copepods and sampling sites were ordinated using canonical correspondence analysis (CCA), and copepod assemblages were defined in relation to physical and chemical parameters, habitat type and presence/absence of planktivorous fish. Planktonic species were largely absent from lakes with introduced fish. Although calanoid associations were common, coexisting diaptomids were rare, suggesting a strong interspecific competition between these predominantly filter feeders. Most copepods found are common eurytopic or cold stenothermal, but some exhibit peculiar disjunct patterns of geographical distribution, and others are apparently restricted to the Alps. Some species are discussed in more detail from a zoogeographical point of view. A complete checklist of copepods recorded to date from high-altitude sites in the Eastern Alps is provided.

Introduction

High mountain areas in the Alps are among those zoogeographical regions in which the latest post-glacial colonization events occurred. Most lakes are younger than 10 000 years, and several are still *in statu nascendi*, directly influenced by retreating glaciers. Thus, recent distribution patterns of aquatic organisms are a young post-glacial event, and communities are frequently in an early stage of succession. The Eastern Alps consist of a complex pattern of geological

strata that impose different limnological conditions on aquatic habitats. These are further determined by altitudinal and north-south changes in climate, soils and vegetation. Basically, two major limnological provinces may be distinguished from the different solubilities of bedrocks: lakes on primary rock in the Central Alps tend to have ion-poor, soft water, while lakes in the Limestone Alps and eastern Dolomites are rich in carbonate, and frequently receive a higher amount of allochthonous nutrients from the watershed. Freshwater species assemblages may thus show affin-

ities to different localities, and ecological preferences should be reflected in the species' distributions.

Several studies have been devoted to the distribution of crustaceans in high-altitude areas. They are scattered over diverse regions of the world, including the Rocky Mountains in North America (Reed & Olive, 1958; Patalas, 1964; Anderson, 1971, 1974), tropical mountains in East Africa (Löffler, 1968) and Central America (Löffler, 1972), and the Himalayan region (Manca et al., 1994 and references therein). The earliest compilation of freshwater organisms known from high-altitude lakes in the Alps was made by Zschokke (1900), who listed 26 copepod species. Important early contributions covering the copepod fauna from the Western Alps include those of Pelosse (1934) and Thiebaud (1936). But the number of regional surveys of copepod distribution in the Eastern Alps is still low (e.g. Pesta, 1923, 1935; Tonolli & Tonolli, 1951; Kiefer, 1963; Tilzer, 1968; Reed, 1970; Brancelj, 1988 and references therein), and gaps remain in our knowledge of the geographical distribution and basic ecology of high-altitude species. In sum, while the spectrum of planktonic species inhabiting alpine lakes is relatively well known, poor information is available on littoral and benthic assemblages. However, general features revealed by the aforementioned studies include low faunal similarities between different geographical regions and a negative correlation of species diversity and individual densities with altitude. Following the results of Stemberger (1995) for Pleistocene glaciated mountain regions of the United States, species with effective dispersal mechanisms should predominate at high altitudes, while occurrences of species that rely on passive dispersal in surface waters should be rare.

This paper presents data on 44 copepod species sampled in 160 lakes and ponds, and examines relationships between the occurrence of species and environmental factors along an altitudinal gradient of 1600 m. The intention of our work is to assist in revealing whether copepod assemblages typical of high altitudes exist, and to contribute to aspects such as habitat preferences, effects of fish stocking, species coexistence and biogeography.

Study area

About 350 substrate-classified samples were taken from 160 lakes and permanent and temporary ponds between August 1985 and September 1998. Most of

the water basins originate from activities of Pleistocene glaciers and are barrier lakes impounded by moraine dams, fill depressions gouged from solid rock, or karst depressions that were later sealed from the permeable bedrocks. They may be covered by up to 4 m of snow and ice in winter, and ice cover may persist for 7–10 months of the year.

The surveys covered 6 geographically distinct regions in the Eastern Alps: the crystalline Central Alps in Austria (Hohe Tauern; altitudinal range: 1824–2811 m a.s.l.) and Italy (Alpi Venoste, Alpi Aurine, Ortles, Adamello, Presanella; 1449–2886 m), the Northern Limestone Alps (Sengsengebirge, Totes Gebirge, Dachstein, Salzburger Kalkalpen; 1290–1805 m) in Austria, the Southern Limestone Alps in Slovenia (Juliske Alpe; 1325–2150 m) and the Dolomites (1370–2833 m) in Italy. Further samples were taken from ponds in the Pohorje Massif (1430–1612 m) in Slovenia (Fig. 1).

The Northern Limestone Alps are built up by sedimentary and reef limestone, mainly of Triassic, locally also of Jurassic origin. The Julian Alps in the southeastern border of the Alps are formed by sedimentary Upper Triassic/Jurassic limestone. Sampling sites in non-dolomitic areas of the Central Alps were located predominantly on various types of unsoluble variscan granitoids ('Zentralgneise') (various gneisses and granites) in Austria, while in Italy low- and middle-grade alpine metamorphites (phyllites, micaschists and paragneisses) dominate; the waters on these rocks have a low content of electrolytes. The Dolomites in Italy are a complex mosaic structure dominated by Triassic crystalline dolomites and, to a lesser extent, by Jurassic limestones and dolomites; several smaller metamorphic complexes are inserted within larger dolomitic massifs in the same area.

This study focuses on records of copepods at altitudes above 1300 m a.s.l., thus including the upper montane belt (below the upper limit of the closed forest), the subalpine belt (between the montane and alpine belts), the alpine belt (treeless region) and the subnival region (at the edge of glaciers). The lower limit of the subalpine belt is between 1500 and 1700 m (northern/southern slope of the Alps) in the study area, that of the alpine belt between 2000 and 2300 m, and that of the subnival region between 2600 and 2900 m.

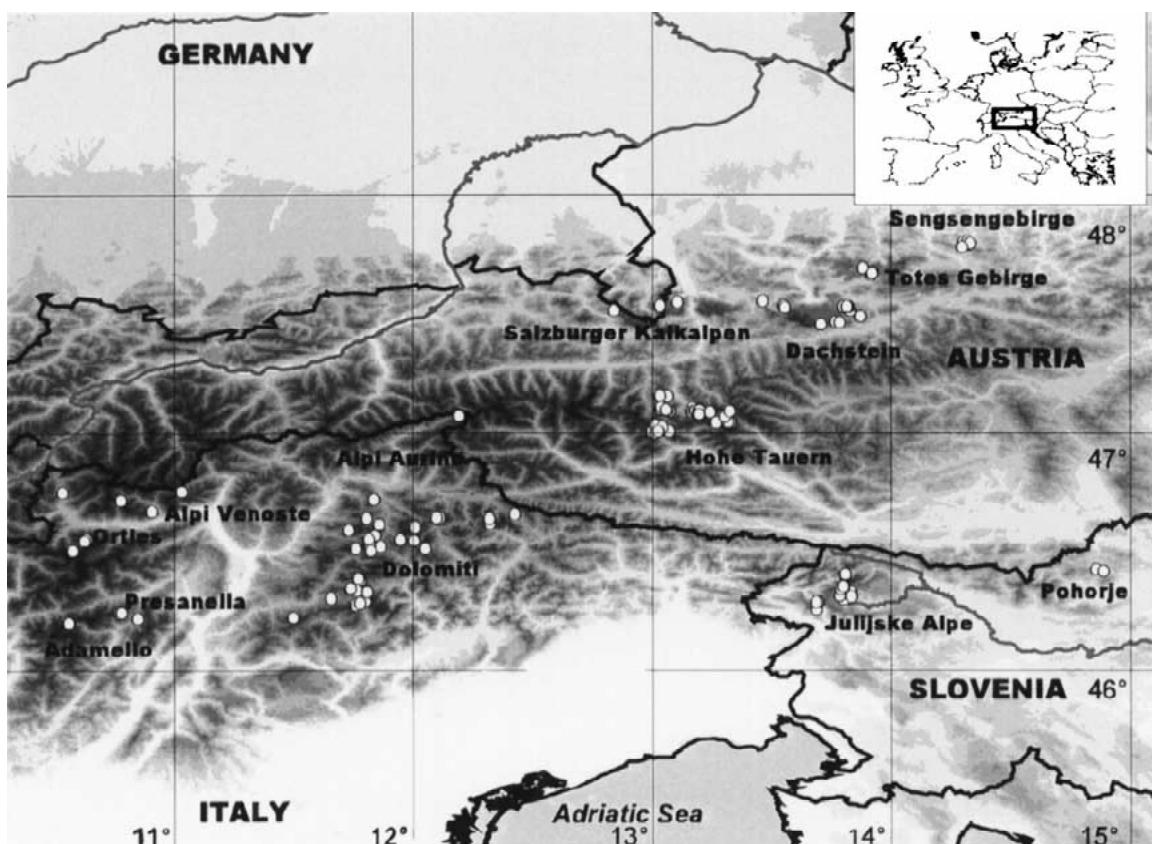


Figure 1. Distribution of sampling sites in the study area. One symbol may represent more than a single site.

Methods

Habitat-specific samples were taken using plankton nets (mesh size 30–100 µm) to collect copepods in the open water, generally including the whole water column. To collect the bottom dwelling fauna either 60 µm-mesh handnets were used and periphyton was brushed off from benthic substrates, or sediments were sucked up with a wide-pore pipette. Waterplants were squeezed or collected together with the surrounding water. Benthos samples from greater depths were obtained by scraping a net along the sediment (usually collecting several dm²), or occasionally by diving. These normally included the deepest part of the basin, but were restricted to deeper littoral regions in some more extensive lakes. Nets were washed thoroughly before and after sampling to prevent contamination by other samples. All samples were taken in summer/early autumn between August and September, and most sites were visited only once. In one lake (Dvojno Jezero), introduction of fish during the study resulted in a marked change in the zooplankton com-

position which was, therefore, considered as having two distinct assemblages.

Temperature, pH and electrical conductivity (E.C. 25 °C) were measured in the field using WTW-electrodes. Smaller water bodies were measured and sounded for their dimensions and maximum depth. Waters exceeding a surface area of 0.5 ha and a depth of 2 m were arbitrarily designated as lakes, smaller or shallower ones as ponds or pools. Generally, the trophic conditions of a site were estimated from substrate composition (organic vs. inorganic) and amount of submersed vegetation, hence mostly 'visual parameters' were used to assess productive features of a water body. In each lake, the presence/absence of fish was recorded by direct observation in the field and by inspecting records of stocking activities. Stock sizes of introduced fish (charr, trout, minnows) were generally large relative to the lake size.

Samples were preserved in 4% formaldehyde solution. In the laboratory, samples were examined in a Petri dish using 40–100 × magnification. In gen-

eral, successive aliquots were checked for copepods until the total amount of material in each sample was inspected. For species identification a compound microscope was used to study details at 1000 \times magnification; most specimens were preserved in 70% alcohol or mounted on slides in glycerine, gelatine-glycerine, or Faure's medium, and deposited in the authors' collections.

Data management and data analysis

By recording the presence/absence of each species for each sampling site, a database was compiled for statistical analysis. Ten localities that contained only immature developmental stages were not included in further analyses. Sites from which only plankton samples were available were excluded from ordination analysis. Some rare species, showing a strong preference for interstitial waters (*Diacyclops* sp., *Bryocamptus* (L.) *dacicus*, *Moraria alpina*, *Pseudomoraria triglavensis*) were excluded from the analyses as well.

Ordination was carried out using canonical correspondence analysis (CCA) (Ter Braak, 1986). This procedure allows the calculation of linear combinations of the environmental variables with the species data. The Multivariate Statistical Package MVSP 3.0 (Kovach, 1998) was used.

The results of CCA are presented as biplots on which species scores and environmental loadings on the two major axes are graphed together. Arrows represent environmental variables and thus indicate the direction of maximum change of that variable across the diagram. The length of an arrow can be taken as a measure of the relative importance of the respective variable, while the position of a species score in relation to the arrows indicates the environmental preferences of that species (Ter Braak, 1986).

Results

Faunal composition

Forty-four species of copepods (7 Calanoida, 17 Cyclopoida, 20 Harpacticoida) were found in lentic waters of the investigated area (Table 1). Of these, 16 species were found only once. Some of them occurred accidentally, as they either prefer lotic or groundwater environments (*Bryocamptus alpestris*, *B. dacicus*, *Moraria alpina*, *Pseudomoraria triglavensis*), or have a higher frequency of occurrence in warmer waters at

lower altitudes (*Acanthocyclops robustus*, *Cyclops vernalis*, *Mesocyclops leuckarti*). In ultraoligotrophic environments beyond 2500 m a.s.l., low population densities may have camouflaged a wider distribution of some further species (*Maraenobiotus vejvodskyi truncatus*, *Hypocamptus paradoxus*). About half of these species regularly occur in subalpine and/or alpine regions, although several may be widely distributed at lower altitudes as well (Table 1). These are generally species of wide ecological plasticity (*Acanthocyclops vernalis*, *Eucyclops serrulatus*, *Paracyclops fimbriatus*, *Bryocamptus minutus*, *Bryocamptus pygmaeus*, *Canthocamptus staphylinus*).

Although calanoid species most frequently occurred alone, almost every possible combination of coexistence, with up to four coexisting species, was recorded. Syntopic calanoid populations were restricted to montane ($n=8$) and subalpine ($n=4$) waters, and no coexisting calanoids were recorded at higher altitudes. The most frequently encountered association was one temorid species (*Heteropeope saliens*) together with one diaptomid species. Syntopic diaptomids were found in only 5 lakes with a high input of allochthonous nutrients in the Limestone Alps, while a number of single species occurrences, mainly of *Arctodiaptomus alpinus* and *Mixodiaptomus tetricus*, was confined to oligotrophic alpine lakes or small pools and puddles, respectively. The most frequent species combinations were *E. serrulatus* with *A. vernalis* (24), *Bryocamptus rhaeticus* (24), *A. alpinus* (17) and *Cyclops abyssorum tetricus* (17) as well as *A. vernalis* with *B. rhaeticus* (17) (Fig. 2).

A complete list of Copepoda so far recorded from high-altitude sites in the Eastern Alps is compiled in Table 2.

Altitudinal occurrence

Four calanoid species are typical of alpine waters, with *A. alpinus* showing the strongest preference for high altitudes above 2000 m, and *Acanthodiaptomus denticornis*, *M. tetricus* and *H. saliens* being most frequently encountered in upper montane and subalpine waters (1500–2000 m). With the exception of *H. saliens*, which is also a rare species in lowland lakes, these calanoids are true 'mountain species', although for each of them exceptional records from lower altitudes exist (Table 1). *Mixodiaptomus laciniatus* serves as an example of a stenothermic coldwater species that in Northern and Southern Europe inhabits ponds and small mountain lakes, respectively, but

Table 1. Altitudinal occurrence in the Alps, ecology and biogeography of recorded copepods. *Altitudinal distribution* (vegetation zones): c: col-line (<600/800 m northern/southern slope; not included in this study), m: montane (600/800–1500/1700 m), s: subalpine (1500/1700–2000/2300 m), a: alpine (> 2000/2300 m). Thick bars indicate highest frequency of occurrence, broken lines exceptional encounters. Stippled areas indicate altitudinal belts in which a species was found in this study. *Habitat types*: Pp: permanent ponds; Pt: temporary ponds; L: lakes; Mo: bog ponds, moor lakes; B: brooks, rivers; S: springs, wells; Gw: groundwater, subterranean habitats. Preferred habitat types are printed in bold, uncertain or exceptional records in brackets. Letters printed in italics indicate habitat types in which a species was found in this study. Values of pH, conductivity and temperature are ranges measured in this study. Biogeographical realms: aus: Australian; eth: Ethiopian; hol: Holarctic; neo: Neotropics; orient: Oriental; pal.: Palaearctic; cosm: cosmopolite

Species	Altitudinal distribution	Habitat type	pH	Cond. (20°C)	T(°C)	Biogeography
Calanoida	c m s a					
<i>Acanthodiaptomus denticornis</i> (Wierzejski, 1887)	Aden	Pt Pp L Mo	7.2 - 8.6	127 - 330	11.6 - 18.3	hol
<i>Arctodiaptomus (A.) laticeps</i> (Sars, 1863)	Alat	Pt Pp L	7.2 - 7.3	203	7.9 - 16.2	pal (Europe, disjunct N/S)
<i>Arctodiaptomus (R.) alpinus</i> (Imhof, 1885)	Aalp	Pt Pp L	6.7 - 9.3	7 - 230	3.5 - 22.5	pal (Europe)
<i>Eudiaptomus hadzici</i> (Brehm, 1939)	Ehad	Pt Pp L	7.2 - 7.3	203	7.9 - 16.2	pal (Balkan, Alps)
<i>Heteropeope saliens</i> (Lilljeborg, 1863)	Hsal	Pt Pp L	6.6 - 8.3	7 - 203	4.5 - 27.1	pal (Europe)
<i>Mixodiaptomus laciniatus</i> (Lilljeborg, 1889)	Mlac	Pp L	7.5 - 8.4	110 - 170	3.0 - 14.0	pal (Europe, Caucasus, Morocco)
<i>Mixodiaptomus tetricus</i> (Wierzejski, 1883)	Mtat	Pt Pp (L) Mo	5.6 - 10.3	10 - 204	12.7 - 25.4	pal (E-, C-Europe)
Cyclopoida						
<i>Acanthocyclops robustus</i> (Sars, 1863)	Arob	P L B	8.0	80	17.9	hol neo aus
<i>Acanthocyclops vernalis</i> (Fischer, 1853)	Aver	Pt Pp L Mo Gw	4.3 - 10.3	5 - 530	3.8 - 27.8	hol?
<i>Cryptocyclops bicolor</i> (Sars, 1863)	Cbic	Pp L Mo	7.2 - 8.4	203 - 530	7.9 - 20.4	hol eth orient
<i>Cyclops abyssorum tetricus</i> (Kozminski, 1927)	Ctat	Pp L	6.1 - 8.6	6 - 160	3.5 - 24.3	pal (European Mountains)
<i>Cyclops vicinus Ulljanin</i> , 1875	Cvic	Pp L	7.7 - 8.3	171	7.2 - 14.5	hol
<i>Diacyclops longidorsus</i> (Sars, 1863)	Dlan	Pt Pp L Mo Gw	7.0 - 8.0	83 - 530	4.8 - 20.4	hol orient
<i>Diacyclops longidorsoides</i> s.l. (Lilljeborg, 1901)	Dlao	L Mo Gw B	7.7 - 8.0	60 - 136	4.5 - 11.6	hol
<i>Ectocyclops phaleratus</i> (Koch, 1838)	Epha	(Pt) Pp L B	8.4	390	14.8	cosm
<i>Eucyclops macruroides</i> (Lilljeborg, 1901)	Emao	Pp L (Gw)	7.2 - 8.6	160 - 203	7.9 - 16.2	pal eth
<i>Eucyclops macrurus</i> (Sars, 1863)	Emac	Pp L (Gw)	7.2 - 7.3	203	7.9 - 16.2	hol
<i>Eucyclops serrulatus</i> (Fischer, 1851)	Eser	eurytopic	4.7 - 9.3	6 - 400	3.5 - 25.2	cosm
<i>Macrocylops albifidus</i> (Jurine, 1820)	Malb	(Pt) Pp L B (Gw)	7.2 - 8.5	30 - 203	7.9 - 18.3	cosm
<i>Macrocylops fuscus</i> (Jurine, 1820)	Mfus	(Pt) Pp L (Gw)	7.7 - 8.5	127 - 390	7.7 - 14.8	hol neo
<i>Megacyclops viridis</i> (Jurine, 1820)	Mvir	Pt Pp L (Gw) B	5.6 - 8.5	11 - 390	3.7 - 24.2	hol neo eth orient
<i>Mesocyclops leuckarti</i> (Claus, 1857)	Mleu	Pp L (Mo)	7.8	170	6.0	pal (Europe)
<i>Microcyclops varicans</i> (Sars, 1863)	Mvar	Pp L (Mo)	7.5 - 8.3	171 - 530	7.2 - 20.4	cosm
<i>Paracyclops limnifatus</i> s.l. (Fischer, 1853)	Pflm	Pp L S B Gw Mo	7.2 - 9.0	8 - 290	3.7 - 17.9	pal
Harpacticoida						
<i>Alttheyella (A.) crassa</i> (Sars, 1862)	Aora	Pt Pp L Gw B	7.2 - 8.8	122 - 203	6.1 - 16.2	pal
<i>Bryocamptus (A.) alpestris</i> (Vogt, 1845)	Balp	P L Gw S	8.3	91	6.0	pal (Alpe, Tatra Mts.)
<i>Bryocamptus (A.) cuspisatus</i> (Schmeil, 1893)	Bous	P L (Mo) Gw S B	6.0 - 8.9	8 - 91	8.3 - 17.9	hol (Europe, N-America)
<i>Bryocamptus (A.) rhaeticus</i> (Schmeil, 1893)	Bhra	Pt Pp L Gw S B	5.0 - 9.3	6 - 230	3.2 - 27.8	pal (C-, W-Europe)
<i>Bryocamptus (A.) vandouwei</i> (Kessler, 1914)	Bvan	P L Gw	7.9 - 9.3	9 - 27	16.1 - 16.3	pal (European Mountains, Iceland)
<i>Bryocamptus (B.) minutus</i> (Claus, 1863)	Bmin	eurytopic	5.3 - 8.8	14 - 160	10.0 - 17.9	hol
<i>Bryocamptus (B.) vejvodskyi</i> (Mrázek, 1893)	Bvej	Pt Pp L Mo B	7.5 - 7.9	7 - 390	12.8 - 27.2	pal
<i>Bryocamptus (L.) daucus</i> (Chappuis, 1923)	Bdac	(L) Gw S (dam)	7.5 - 7.6	116	4.4 - 5.5	pal (E-Europe)
<i>Bryocamptus (L.) echinatus</i> (Mrázek, 1893)	Bech	L Gw S B	8.3	30	14.3	pal (Europe, Iran)
<i>Bryocamptus (R.) pygmaeus</i> (Sars, 1862)	Bpyg	eurytopic	7.5 - 8.0	80 - 320	12.8 - 17.9	hol
<i>Canthocamptus staphylinus</i> (Jurine, 1820)	Csta	Pp L S B GW Mo	7.4 - 7.8	126 - 127	4.5 - 11.6	pal (hol? orient?)
<i>Elaphoidella gracilis</i> (Sars, 1862)	Egra	Pp L Mo (Gw)	4.3 - 8.4	5 - 390	7.9 - 18.7	pal (Europe)
<i>Epactophanes richardii</i> Mrázek, 1893	Eric	eurytopic	8.0	80	17.9	cosm
<i>Hypocamptus</i> sp. aff. <i>brehmi</i> (Douve, 1922)	Hbre	L Gw S B		90	10.8	pal (European Mountains)
<i>Hypocamptus paradoxus</i> (Kreis, 1926)	Hpar	Pt Pp	8.9	20	0.3	pal (Alps)
<i>Maraenobiotus insignipes</i> (Lilljeborg, 1902)	Mins	Pp L S	6.7 - 9.3	7 - 164	6.7 - 22.5	hol (Eurasia, Greenland)
<i>Maraenobiotus vejvodskyi truncatus</i> Gurney, 1932	Mtru	Pp	7.6	7	13.1	pal (C-Europe, Great Britain)
<i>Moraria alpina</i> Stoch, 1998	Malp	S Gw Mo	7.9	60	9.6	pal (Alps)
<i>Paracamptus schmeili</i> (Mrázek, 1893)	Psch	Pp L Mo (Gw) B	6.9 - 8.6	11 - 230	3.7 - 16.2	pal (Europe)
<i>Pseudomoraria triglavensis</i> Brancelj, 1994	Ptri	S (dam)	7.5 - 7.6	116	4.4 - 4.5	pal (Slovenia)

is almost restricted to large lowland lakes around the Alps in Central Europe. Altitudinal ranges of the more commonly encountered species are given in Figure 3.

In alpine cyclopoid assemblages, *A. vernalis*, *E. serrulatus* and *C. a. tetricus* predominated. Each of these species is widespread in all mountainous re-

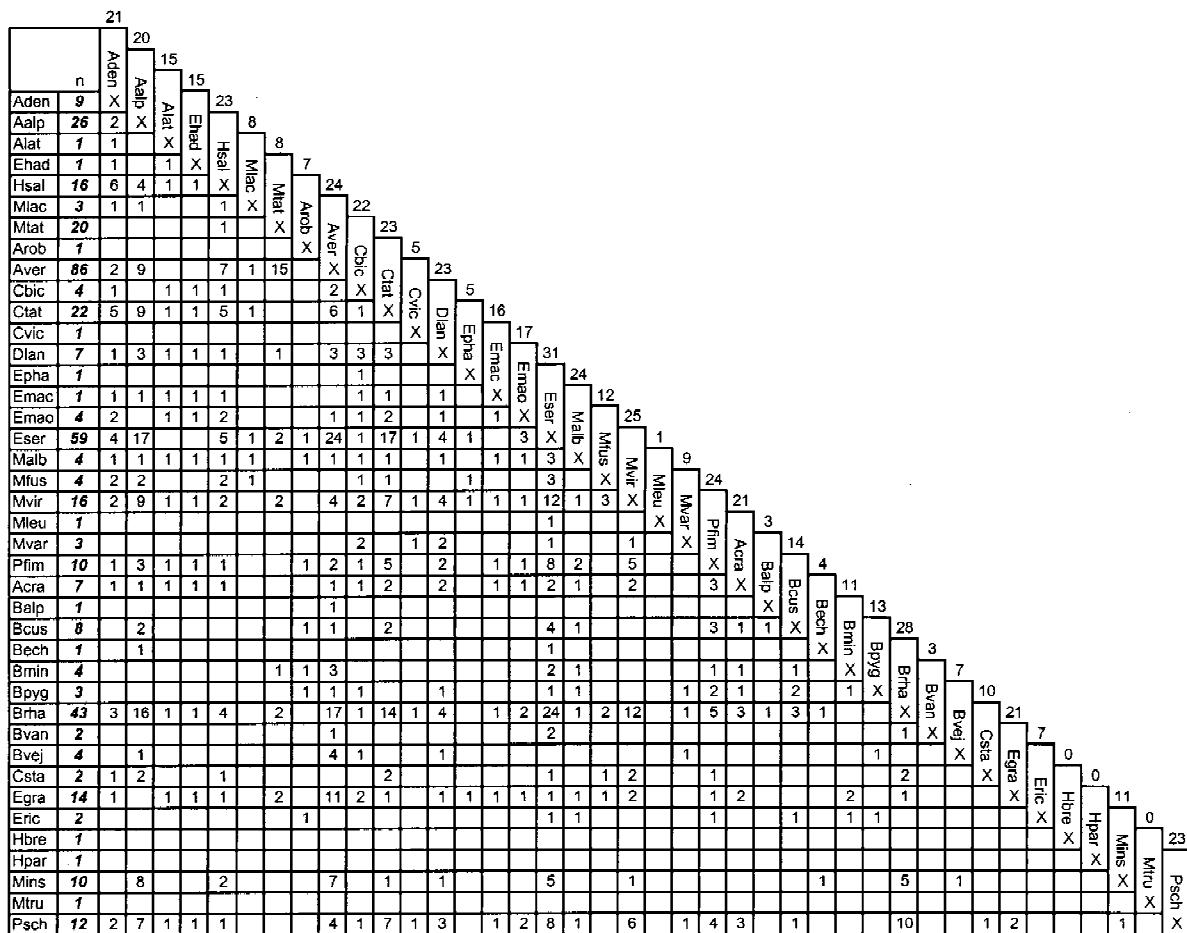


Figure 2. Coexistence chart for copepod species in 150 assemblages. n : number of water bodies in which a species occurred. Numerals given above columns are the total number of species that coexisted with a given species. Stygobiont taxa and species preferring lotic environments are omitted. Species are identified by the labels listed in Table 1.

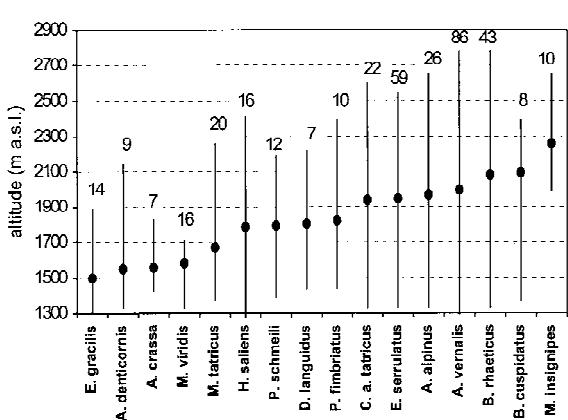


Figure 3. Mean altitude and altitudinal ranges of the more commonly encountered copepods. Numerals represent number of populations encountered in the study area.

gions, but only the last may be regarded as a stenotopic mountain form. It is widespread throughout the Lime-stone Alps and the Austrian Central Alps, but shows a more limited distribution in the Italian Alps, being absent in our samples from dolomitic areas.

Several harpacticoid species were restricted to the alpine (*B. alpestris*, *B. vandouwei*, *B. echinatus*, *Hypocamptus* sp. aff. *brehmi*, *H. paradoxus*, *M. vejvodskyi truncatus*) or alpine/subalpine (*M. insignipes*) region. Of these, only *M. insignipes* had a sufficiently high incidence ($n=10$) to relate its occurrence to a strict preference for high-altitude sites. The same seems to hold for some other rare oligothermic species, that have not yet been recorded from lower sites (*B. alpestris*, *B. vandouwei*, *Hypocamptus* spp., *M. alpina*) (Table 1). The coldwater-forms *Bryocamptus cuspidatus* and *B. rhaeticus* were frequently encountered in surface

Table 2. List of Copepoda recorded from the Eastern Alps (> 1300 m a.s.l.). *: species recorded in this study. Unconfirmed records are in brackets (records of *Moraria brevipes* in the Alps are probably *M. alpina*)

Calanoida			
* <i>Acanthodiaptomus denticornis</i> (Wierzejski, 1887)	(<i>Eucyclops speratus</i>) (Lilljeborg, 1901)	<i>Bryocamptus (R.) zschokkei</i> (Schmeil, 1893)	
* <i>Arctodiaptomus (A.) laticeps</i> (Sars, 1863)	(* <i>Macrocylops albidus</i>) (Jurine, 1820)	<i>Bryocamptus (R.) tatraensis</i> Minkiewicz, 1915	
* <i>Arctodiaptomus (R.) alpinus</i> (Imhof, 1885)	(* <i>Macrocylops fuscus</i>) (Jurine, 1820)	* <i>Canthocamptus staphylinus</i> (Jurine, 1820)	
<i>Eudiaptomus gracilis</i> (Sars, 1863)	(<i>Megacyclops gigas</i>) (Claus, 1857)	<i>Canthocamptus st. microstaphylinus</i> (Wolf, 1905)	
(<i>Eudiaptomus graciloides</i> (Lilljeborg, 1888))	(* <i>Megacyclops viridis</i>) (Jurine, 1820)	* <i>Elaphoidella gracilis</i> (Sars, 1862)	
* <i>Eudiaptomus hadzici</i> (Brehm, 1939)	(* <i>Mesocyclops leuckarti</i>) (Claus, 1857)	<i>Elaphoidella phreatica</i> (Chappuis, 1925)	
<i>Eudiaptomus vulgaris</i> (Schmeil, 1898)	(* <i>Microcyclops varicans</i>) (Sars, 1863)	<i>Elaphoidella proserpina</i> Chappuis, 1934	
* <i>Heteropece saliens</i> (Lilljeborg, 1863)	(<i>Paracyclops affinis</i>) (Sars, 1863)	* <i>Epactophanes richardi</i> Mrázek, 1893	
* <i>Mixodiaptomus laciniatus</i> (Lilljeborg, 1889)	(* <i>Paracyclops fimbriatus</i>) (Fischer, 1853)	<i>Hypocamptus brehmi</i> (Douwe, 1922)	
* <i>Mixodiaptomus tetricus</i> (Wierzejski, 1883)	(<i>Thermocyclops dybowskii</i>) (Landé, 1890)	* <i>Hypocamptus sp. aff. brehmi</i> (Douwe, 1922)	
Cyclopoida	(<i>Thermocyclops oithonoides</i>) (Sars, 1863))	* <i>Hypocamptus paradoxus</i> (Kreis, 1926)	
(<i>Acanthocyclops kieferi</i> (Chappuis, 1925))	Harpacticoida	<i>Maraenobiotus brucei carpathicus</i> Chappuis, 1928	
* <i>Acanthocyclops robustus</i> (Sars, 1863)	* <i>Attheyella (A.) crassa</i> (Sars, 1862)	* <i>Maraenobiotus insignipes</i> (Lilljeborg, 1902)	
* <i>Acanthocyclops vernalis</i> (Fischer, 1853)	<i>Attheyella (A.) wierzejskii</i> (Mrázek, 1893)	<i>Maraenobiotus insignipes alpinus</i> (Keilhack, 1909)	
* <i>Cryptocyclops bicolor</i> (Sars, 1863)	<i>Bryocamptus (A.) abnokensis</i> (Kiefer, 1929)	<i>Maraenobiotus vejvodskyi</i> Mrázek, 1893	
<i>Cyclops abyssorum</i> s.l. Sars, 1863	* <i>Bryocamptus (A.) alpestris</i> (Vogt, 1845)	* <i>Maraenobiotus vejvodskyi truncatus</i> Gurney, 1932	
* <i>Cyclops abyssorum tetricus</i> (Kozminski, 1927)	* <i>Bryocamptus (A.) cuspidatus</i> (Schmeil, 1893)	<i>Maraenobiotus vejvodskyi zschokkei</i> (Kreis, 1920)	
(<i>Cyclops strenuus</i> Fischer, 1851)	<i>Bryocamptus (A.) laccophilus</i> (Kessler, 1914)	* <i>Moraria alpina</i> Stoch, 1998	
* <i>Cyclops vicinus</i> Uljanin, 1875	* <i>Bryocamptus (A.) rhaeticus</i> (Schmeil, 1893)	(<i>Moraria brevipes</i>) (Sars, 1862))	
(<i>Diacyclops bisetosus</i> (Rehberg, 1880))	* <i>Bryocamptus (A.) vandouwei</i> (Kessler, 1914)	<i>Moraria (?) monticola</i> (Menzel, 1912)	
<i>Diacyclops aff. clandestinus</i> (Kiefer, 1926)	* <i>Bryocamptus (B.) minutus</i> (Claus, 1863)	<i>Moraria mrázeckii</i> Scott, 1896	
* <i>Diacyclops languidoides</i> s.l. (Lilljeborg, 1901)	* <i>Bryocamptus (B.) vejvodskyi</i> (Mrázek, 1893)	<i>Moraria poppei</i> (Mrázek, 1893)	
* <i>Diacyclops languidus</i> (Sars, 1863)	* <i>Bryocamptus (L.) dacicus</i> (Chappuis, 1923)	<i>Moraria radovnae</i> (Brancelj, 1988)	
* <i>Ectocyclops phaleratus</i> (Koch, 1838)	* <i>Bryocamptus (L.) echinatus</i> (Mrázek, 1893)	* <i>Paracamptus schmeili</i> (Mrázek, 1893)	
* <i>Eucyclops macruroides</i> (Lilljeborg, 1901)	<i>Bryocamptus (L.) hoferi</i> (Douwe, 1907)	<i>Parastenocaris austriaca</i> Kiefer, 1976	
* <i>Eucyclops macrurus</i> (Sars, 1863)	* <i>Bryocamptus (R.) pygmaeus</i> (Sars, 1862)	* <i>Pseudomoraria triglavensis</i> Brancelj, 1994	
* <i>Eucyclops serrulatus</i> (Fischer, 1851)	<i>Bryocamptus (R.) typhlops</i> (Mrázek, 1893)		

standing waters at high altitudes; in the Alps, *B. cuspidatus* is known also from springs (Gerecke et al., 1997) and *B. rhaeticus* from subterranean environments at lower altitudes as well (Stoch, 1993). In the study area, *B. cuspidatus* was restricted to softwater habitats on primary rock, showing a strong preference for submerged mosses, while *B. rhaeticus* tolerated a wide range of habitat conditions, both in limestone and crystalline regions.

The most widespread species, *A. vernalis*, *E. serrulatus* and *B. rhaeticus* were also the first species to appear in newly emerged lakes and ponds at the edge of retreating glaciers in the Central Alps.

Species richness

Within the major habitat groups (cf. Table 1), the lowest mean species numbers were found in temporary ponds ($n=1.45$), followed by bog ponds ($n=2.11$) and permanent ponds ($n=2.29$). An average of 4.0 species was found in lakes, of which lakes in limestone areas harboured significantly more copepods ($n=6.24$) than did soft-water lakes on metamorphic bedrock ($n=2.96$,

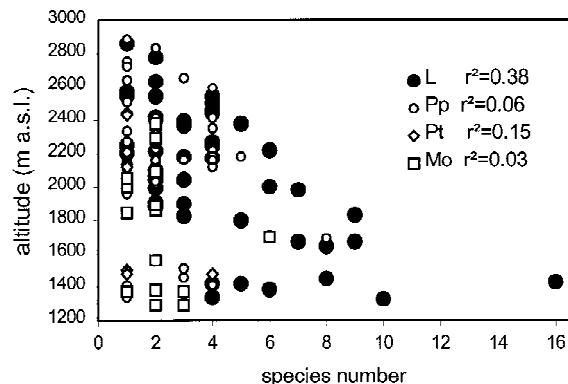


Figure 4. Species richness in major habitat types along the altitudinal gradient. Habitat labels are the same as in Table 1.

$P<0.02$). Similarly, a higher species number was encountered in ponds of the Limestone Alps ($n=2.90$) compared with the Central Alps ($n=2.0$; n.s., $P=0.23$). Lakes on the southern slope of the Alps tended to support more species than lakes situated on the northern slope, both in the Central Alps (Austria: $n=2.75$; Italy: $n=3.25$; n.s., $P=0.43$) and in the Limestone Alps (Aus-

tria: $n=5.00$; Slovenia: $n=6.62$; n.s., $P=0.31$). With increasing altitude, a distinct trend towards species impoverishment is apparent (Fig. 4). Out of 44 species encountered along the whole altitudinal gradient, 38 occurred at altitudes above 1500 m, 22 above 2000 m, and only 10 species were recorded in the upper alpine belt above 2500 m.

However, low regression coefficients reflect a rather weak correspondence between altitude and species richness in a distinct habitat type (Fig. 4), because of the strong heterogeneity of environmental conditions, both between (different geology) and within sampling (different habitat types) areas.

Habitat requirements – Ordination results

Our results indicate that among the abiotic variables, water body size, trophic conditions, temperature, altitude, pH and conductivity were the most important variables associated with the distribution of species (Fig. 5). Some inconsistencies arise from the short period of data collection (only during summer). Temperatures, therefore, generally reflect values close to the annual maximum, and are thus more closely related to the size of a water body than to the altitude, as small ponds may warm up considerably even in high alpine regions in summer. The percentage of explained variance on the two major axes was 43.6% (60.1% on axes 1–3) with the whole species set. By including only more frequent species (≥ 7 encounters), 57.4% (76.1%) of the variance could be explained. Probably much of the unexplained variance is linked with stochastic fluctuations, microhabitat structures, and with top-down or bottom-up regulated biotic variables.

In general, the ordination results reflect the habitat requirements of the species. A strong positive correlation with altitude and negative correlation with temperature was shown by several oligothermic harpacticoids characteristic of high-altitude sites (see above), and also, although less pronounced, by *A. alpinus* and *C. a. tetricus*. These species were mainly found in lakes and were, therefore, also positively associated with the areal factor. Conversely, pond species (*M. tetricus*) or species commonly encountered in bog ponds (*Elaphoidella gracilis*, *B. vejvodskyi*) were grouped at the opposite end of ordination axis 1, indicative of warm and/or dystrophic conditions. Except for species that occurred only once or twice, only *Macrocylops albidus* was restricted to lakes. Species that were restricted to carbonate waters in the Limestone Alps or the Dolomites were positively correlated with con-

ductivity along axis 2 (*A. denticornis*, *Cryptocyclops bicolor*, *Eucyclops macruroides*, *Macrocylops fuscus*, *Megacyclops viridis*, *Microcyclops varicans*, as well as a number of species that were encountered only once or twice in the Limestone Alps) (Fig. 5).

In order to reveal the influence of fish predation, and to reduce the area-temperature-inconsistency, a second CCA was carried out by including all lakes and species encountered in >10% of the lakes (Fig. 6 A). By plotting the sites together with the species scores, the strong effect of geology is visualised, with species preferring a higher trophic level and being more strongly associated with conductivity ordinated along axis 1, together with lakes from the Limestone Alps (Fig. 6 B). There was also a strong negative correlation of temperature with altitude, and all planktonic species showed strong negative correlations with the presence of fish. The percentage of variance explained on the two major axes was 69.4% (86.4% on axes 1–3).

Information on habitat structure such as substrate type or presence/absence of submersed vegetation were not available for all sites, and therefore not included in the ordination. However, it was obvious that waterbodies harbouring mosses were more frequently occupied by a diverse harpacticoid fauna (e.g. *B. alpestris*, *B. cuspidatus*, *B. minutus*, *B. pygmaeus*, *B. rhaeticus*, *M. insignipes*, *Paracamptus schmeili*).

Presence of fish

The proportion of sampled lakes stocked with fish was highest in the Southern Central Alps and Dolomites in Italy (86%, $n=14$), followed by the Northern Limestone Alps (38%, $n=13$), the Northern Central Alps (29%, $n=17$), and the Southern Limestone Alps (23%, $n=13$). The presence of planktivorous fishes normally excluded the occurrence of calanoid copepods. In only 3 out of 29 ‘fish-lakes’ the presence of either a single diaptomid species (*A. denticornis*, *A. alpinus*) or *H. saliens* was observed. Also, *C. a. tetricus*, the sole euplanktonic cyclopoid in high-altitude lakes, had a low incidence in fish-stocked lakes ($n=3$). The different intensity of fish stocking in the investigated areas was also reflected in the distribution of *A. alpinus*, which was almost entirely restricted to ponds ($n=7$) in the Italian Alps, where it was found only once in a lake. In contrast, only one ‘pond-population’ but 8 lake-records were noted from Austria, and the species occurred exclusively in lakes in Slovenia ($n=10$).

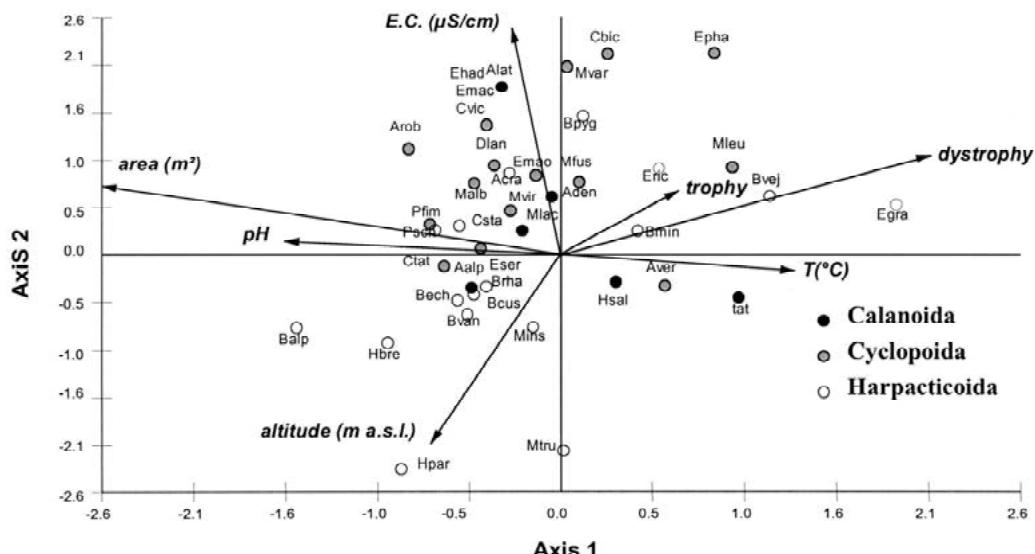


Figure 5. Ordination diagram based on canonical correspondence analysis (CCA) of copepod species scores with respect to environmental variables (arrows). Species are identified by the labels listed in Table 1.

Biogeography

Species of the family Diaptomidae encountered in the Alps may have a clear preference for high-altitude sites (*A. alpinus*), may show a distinct north-south disjunction in Europe (*M. laciniatus*, *A. laticeps*), may exhibit a relatively wide geographical range throughout the Holarctic (*A. denticornis*), or are predominantly (*M. tetricus*) or exclusively (*E. hadzici*) restricted to the Balkans (Figs 7–9). *Eudiaptomus hadzici* reaches its northernmost distribution in the Julian Alps, as does *A. laticeps* in its southern distribution. Our records of *M. laciniatus* in the Northern Limestone Alps are the first for this species in high-altitude regions within the Alps. The only temorid species, *H. saliens*, is widely distributed throughout the western Palaearctic, with one centre of occurrence in the Alps. With the sole exception of *C. a. tetricus*, no cyclopoid species may be regarded as being typical for alpine waters. Most species have a wide distribution at least throughout the Holarctic or are cosmopolites (Table 1). In contrast, several harpacticoids are typical mountain species (*B. alpestris*, *B. vandouwei*, *H. sp. aff. brehmi*, *H. paradoxus*, *M. alpina*, *P. triglavensis*), even if they were extremely rare in the present study, with not more than one or two populations encountered. Another harpacticoid (*M. insignipes*) has a boreo-alpine distribution.

None of the species is definable as a narrow endemic. Only four taxa may be considered endemic

to the Alps, but the degree of uncertainty is high: *H. paradoxus* (possible records from Eastern Europe should be checked), *H. sp. aff. brehmi* (probably a new species), *Pseudomoraria triglavensis* and *M. alpina* (Stoch, 1998; some records from Germany are under study: Moura, pers. com.). The specific status of some other possible endemic species (*Bryocamptus unisetiger*, *Maraenobiotus insignipes alpinus* and *Moraria (?) monticola*), not present in our samples, is highly doubtful. Moreover, the taxonomic position of a further endemic taxon, *Maraenobiotus vejvodskyi zschorkei*, is under revision by one of us (F.S.). Previous records of *Moraria brevipes* in the Alps are probably related to *M. alpina*. More taxonomic work is needed to clarify the geographical distribution of these harpacticoids.

Discussion

In mountain waters, a distinct decrease in species richness and individual densities with increasing altitude is obvious. Representing small biogeographic ‘targets’, remote high-altitude settings are less likely to receive colonists from a disseminating source (Starkweather, 1990). Upper altitudinal limits imposed on the distribution of species result from the harshness of the physical environment, reduced resource diversity along with a decreasing habitat complexity, and the young age of some water bodies. There are fairly

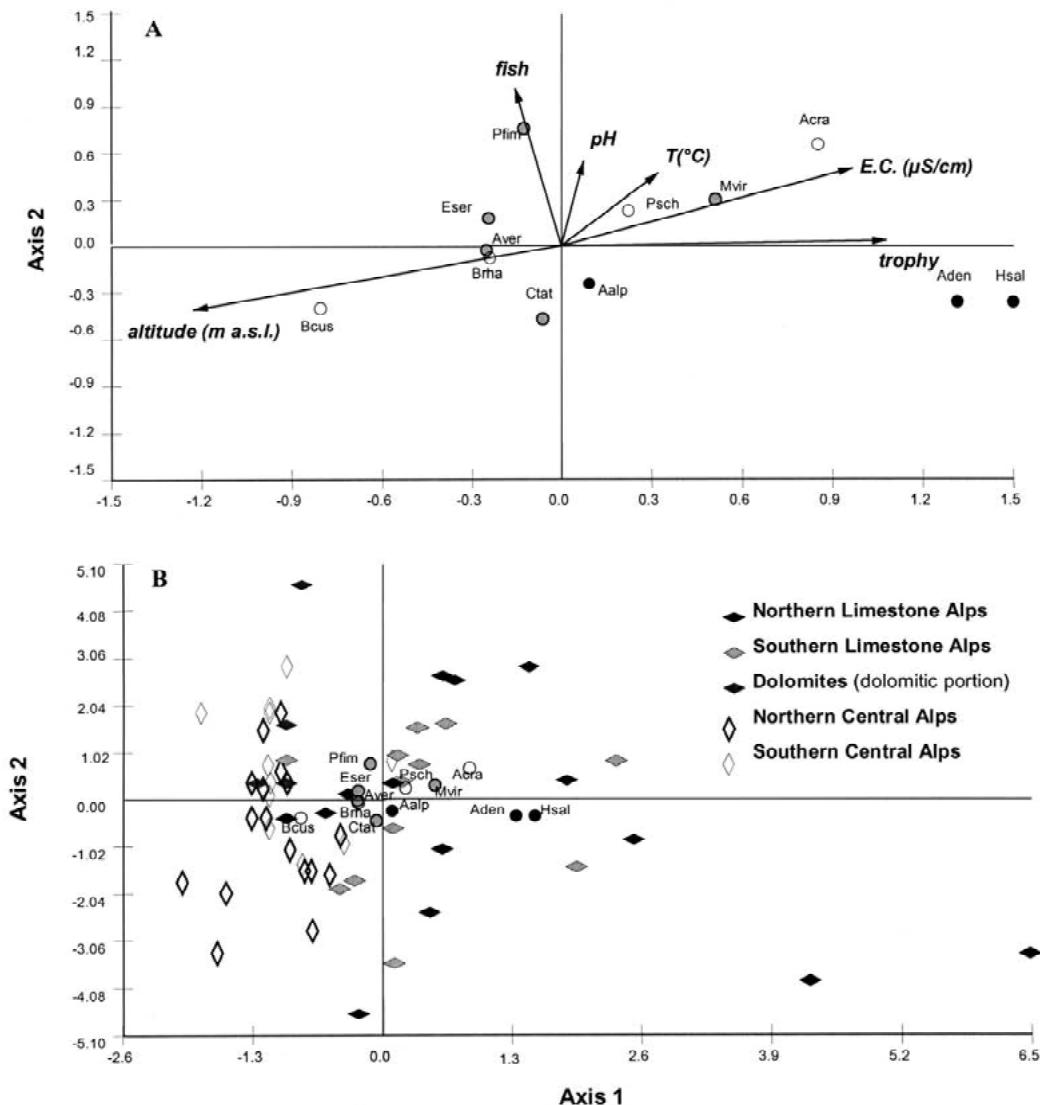


Figure 6. CCA-ordination of copepod species scores with respect to environmental variables (A) and together with lake scores (B). Only lake records and more frequently encountered species are included. Different geological regions are indicated by different symbols. Species are identified by the labels listed in Table 1.

stringent ecological requirements for many species that prevent colonization. However, in our samples most copepods were observed to exploit a rather wide altitudinal range. This less clear-cut restriction to distinct altitudinal belts, as is generally observed for terrestrial communities (Sfenthourakis, 1992, and references therein), is probably because of the moderating effect of water on physical conditions such as temperature and radiation. Nilssen (1976) concluded that the effect of altitude on the composition of pelagic crustacean assemblages plays a minor role compared

to such parameters as acidity, humic content, lake morphometry and fish predation.

Remarkably, in the alpine copepod fauna calanoids and harpacticoids evolved a number of typical high-altitude taxa, but in cyclopoid taxocoenoses mainly widespread species predominate, some even thought to be cosmopolites (according to Dussart & Defaye, 1985). However, taxonomic uncertainties obscure the picture, because some of these copepods belong to species complexes in urgent need of revision (e.g. most species of the genera *Eucyclops*, *Acanthocyc-*

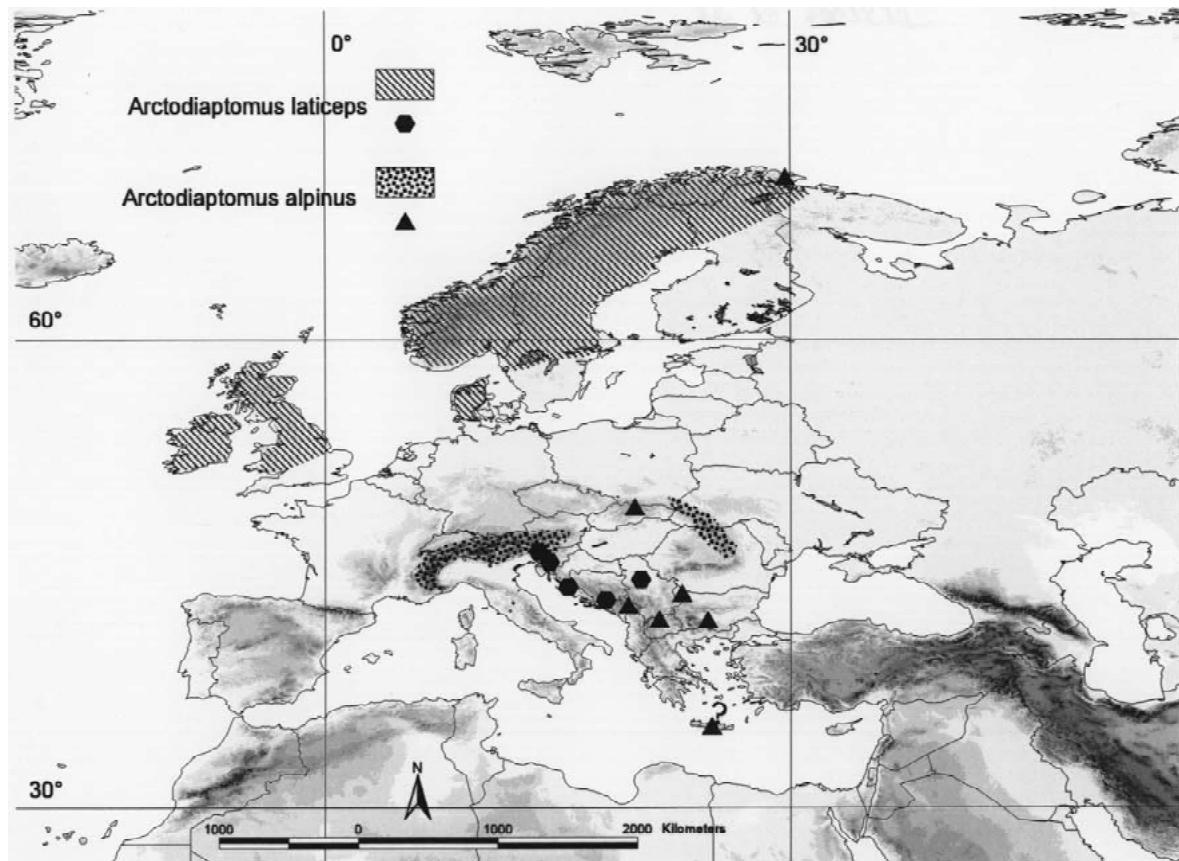


Figure 7. Geographic distribution of *Arctodiaptomus alpinus* and *A. laticeps*. Hatched areas indicate a widespread distribution, symbols are restricted single records.

lops and *Diacyclops*). *Paracyclops fimbriatus*, another ‘species-complex’ hitherto recorded from all over the world, but now believed to be restricted to Eurasia, has recently been revised by Karaytug & Boxshall (1998), and a reappraisal of alpine records is needed. An increase of taxonomic resolution certainly will bring about a more realistic picture of the ecological requirements of these taxa. Likewise, as refinements of alpha-taxonomic methods and comparisons of copepod populations from different continents indicate, several species nowadays considered to be cosmopolites or to have a holarctic distribution, may finally prove to have a more restricted range (Reid, 1998, and references therein; Stoch, this volume).

Another striking aspect of copepod incidence in the Alps is the extreme rarity of some harpacticoid species considered to be typical elements of the alpine fauna. In several of the species encountered, only one (*Bryocamptus alpestris*, *Hypocamptus paradoxus*, *H. sp. aff. brehmi*, *Maraenobiotus vejvodskyi truncatus*,

Moraria alpina, *Pseudomoraria triglavensis*) or two populations (*B. vandouwei*) were recorded, although well over 150 sites were sampled. Some populations may simply have been overlooked because of low individual densities, or the proper microhabitat was not sampled (e.g. sparse stocks of submersed mosses, interstitial environments). However, recent collections by one of us (F.S.) indicated that *M. alpina* and *B. alpestris* probably prefer lotic environments such as springs, and the same may apply to *P. triglavensis* as well. Also, seasonality of population development may affect sampling results, as most sites were sampled only once.

Very likely, general abiotic conditions are most important, and with altitude increasingly important in determining the composition of assemblages. However, the most commonly encountered copepods are capable of adapting to a wide range of environmental conditions, and the distributional patterns of, for instance, planktonic assemblages cannot be explained

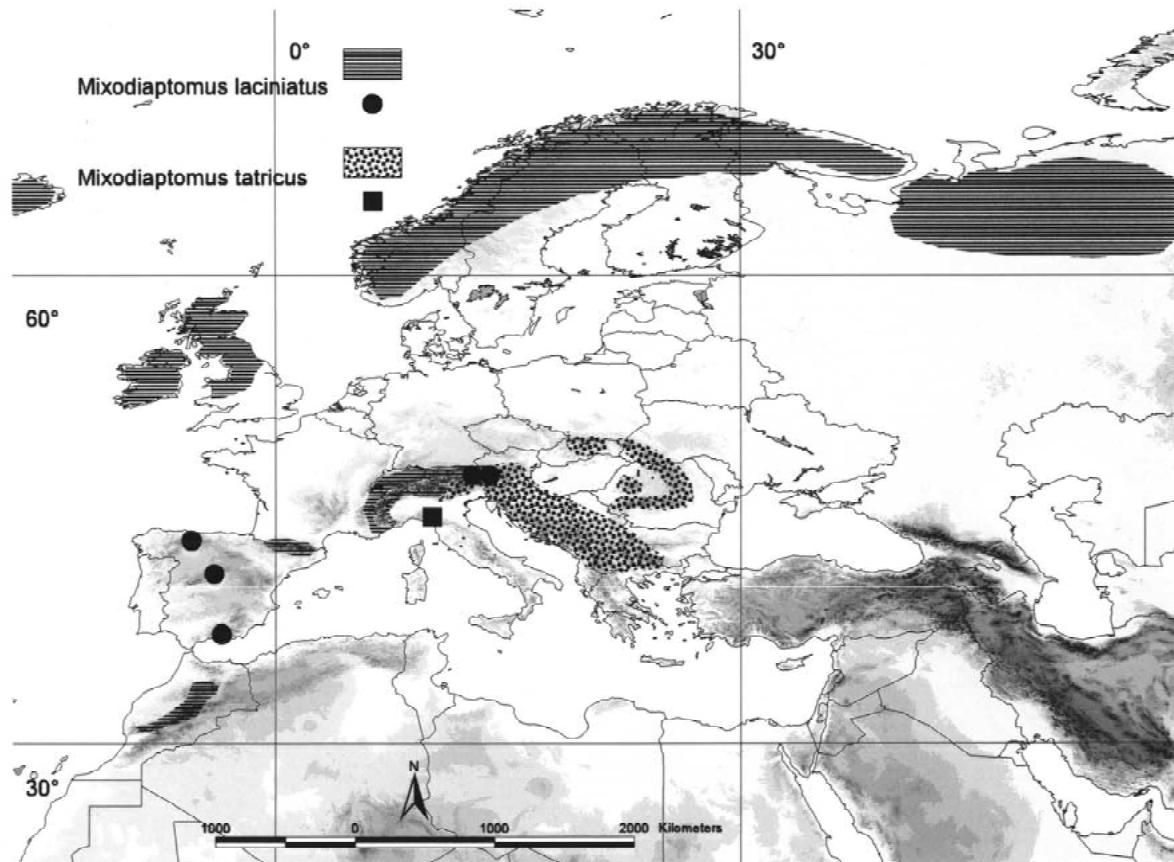


Figure 8. Geographic distribution of *Mixodiaptomus laciniatus* and *M. tetricus*. Hatched areas indicate a widespread distribution, symbols are restricted single records.

within the frame of abiotic conditions alone. Thus, competition and/or predation may be of major importance in simply structured aquatic environments such as mountain lakes and ponds (Anderson, 1974).

Fish predation is believed to be another key factor limiting the diversity of planktonic crustaceans in alpine lakes (Starkweather, 1990; Schabetsberger et al., 1995), together with suboptimal conditions for growth and reproduction. High-altitude copepods are highly vulnerable to introduced fish if they are conspicuous because of noncryptic coloration (Hairston, 1979) or show a slow, food-limited development of their population. However, there is evidence that large, pigmented copepods are in some cases able to survive fish introduction. Donald et al. (1994) found *Hesperodiaptomus* species to coexist with introduced fish in large subalpine and alpine lakes in Canada, but not in small lakes less than 2–16 ha in area and a maximum depth of 4–16 m. They argued that offshore pelagic habitats of large lakes provide a refuge

from salmonid predation. In deep high-altitude lakes in the Tatra Mountains Gliwicz (1986) found that *Cyclops abyssorum tetricus* may react to the presence of planktivorous fish by increased diel vertical migration. Gliwicz & Rowan (1984), however, concluded that *C. abyssorum tetricus* may not only survive in lakes stocked with planktivorous fish, but may even profit from salmonid predation on egg-carrying females. As eggs proved to be resistant to fish digestive enzymes, they argued that both direct (reduced cannibalism on nauplii) and indirect effects (reduced interspecific competition by extinction of coexisting crustaceans) should increase the survivorship of the younger generation. However, our results do not confirm this idea, as the distribution pattern of all planktonic species, including *C. abyssorum tetricus*, was negatively associated with that of fish. The stocking of a small mountain lake in Slovenia caused the extinction of *A. alpinus* and a sharp decline of *C. abyssorum tetricus* after only a few years (Brancelj, 1999). On the other

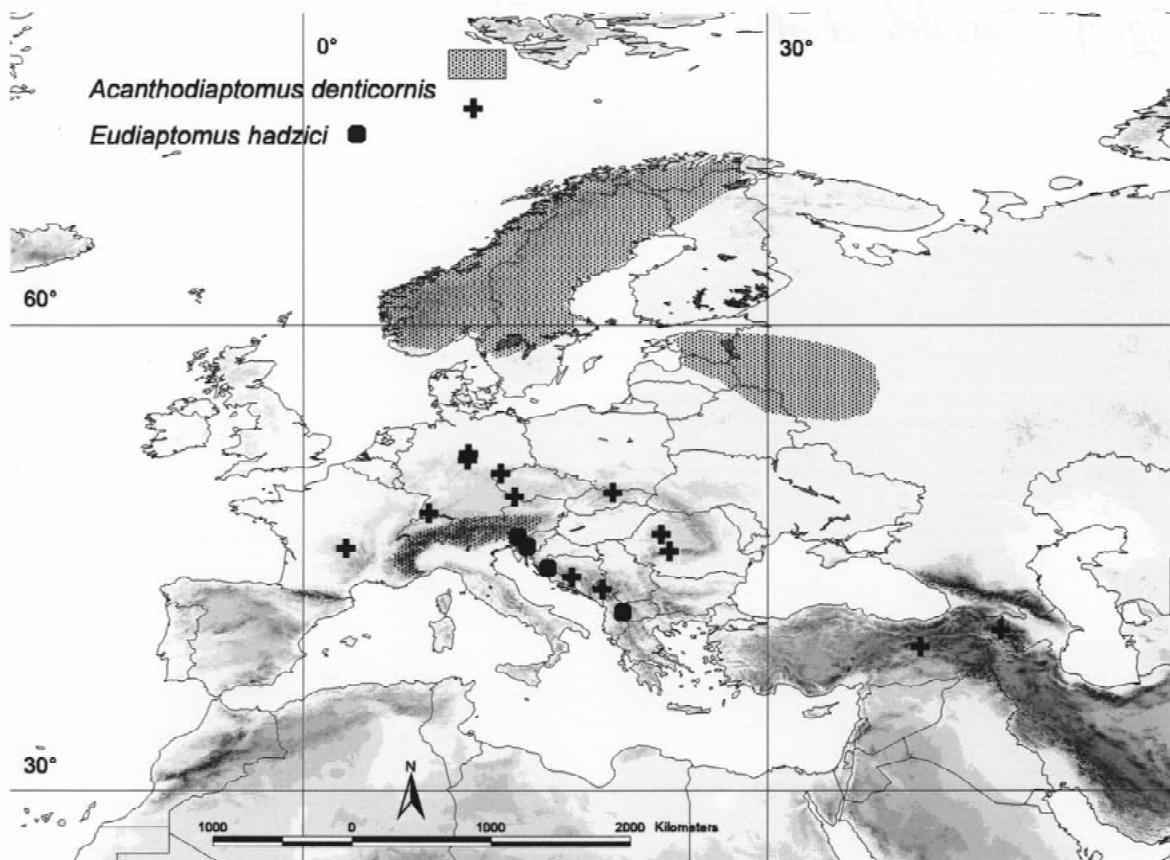


Figure 9. Geographic distribution of *Acanthodiaptomus denticornis* and *Eudiaptomus hadzici*. Hatched areas indicate a widespread distribution, symbols are restricted single records. The entire holarctic range of *A. denticornis* includes localities in North America (Canada) and Asia (Turkistan, Tibet, Altai) as well.

hand, a population of *C. abyssorum taticus* that has coexisted with salmonids in an alpine lake since medieval times is well documented (Praptokardiy, 1979). Most probably, factors such as average size and density of stocked fish, age structure of an established fish population, availability of alternative prey items, together with abiotic environmental characteristics such as lake morphometry and substrate composition, differently modulate the planktivore predation pressure. Hence, it might be possible for a copepod population to adjust to increased mortality in one case, but to become extinct in another.

Cases of coexistence of calanoid species were widespread in the investigated area, but generally restricted to the association of one temorid species (*Heterope saliens*) with one diaptomid species. While the association of one large predatory species (*H. saliens*) with one small omnivorous species (diaptomid) implies little interspecific competition for food, simil-

arities in the niche requirements of diaptomid species are likely to explain their low frequency of coexistence. Syntopic diaptomids were restricted exclusively to karst lakes in the Limestone Alps, probably because of the higher productivity of such lakes, which therefore have a higher carrying capacity for planktonic filter feeders. Furthermore, lakes in limestone areas are frequently subjected to unstable conditions, such as strong between-years variations, for instance in hydrology, temperature and oxygen content (Jersabek & Schabetsberger, 1996), which may further promote coexistence of similar species by changing competitive advantages (cf. Connell, 1980). Unstable conditions were also suggested to explain the coexistence of three diaptomid species in a small alpine lake in Canada (Anderson, 1971).

Considering the distribution of boreo-alpine taxa, one may ask whether the rather stringent environmental conditions in cold and oligotrophic waters

provide optimum conditions for them, or if it is simply a low competitive ability that excludes them from habitats occupied by superior competitors. The latter may add to explain the geographical distribution of alpine diaptomids, as all species had a higher incidence in more productive environments, such as limestone solution lakes, and even true mountain species such as *A. denticornis* and *A. alpinus* may significantly enhance their reproductive output at eutrophic, warm 'lowland-conditions' (Jersabek & Schabetsberger, 1995). Also the puzzling biogeography of predominantly alpine (*A. alpinus*) or boreal (*A. laticeps*) species, that occur in lowland sites on the Balkan Peninsula as well (Kiefer, 1971; Petkovski, 1983) underlines a more generalist nature of these copepods. Furthermore, all species proved to tolerate a wide range of environmental conditions, that may differ significantly between their northern and southern geographical limits, and can produce both subitaneous and resting eggs. *Mixodiaptomus laciniatus*, for example, in Central Europe is restricted almost entirely to large postglacial prealpine lakes (Kiefer, 1978) but on the Iberian Peninsula is only known from high-altitude lakes (Rey & Capblancq, 1975; Cruz-Pizarro, 1983). While in its southern range it is mostly perennial by producing subitaneous eggs, it frequently occurs even in small temporary waters in the Arctic, and shows a strong tendency toward production of resting eggs (Einsle, 1993). In recently deglaciated regions of Sweden, it is among the first species to occupy newly emerged lakes (Nauwerck, 1980). It is amazing that our records of *M. laciniatus* are the first proof of this species to occur within the Alps, although it is widespread in large oligotrophic lowland lakes at the northern, southern and western edges of the Alpine Chain. We can only speculate whether a low dispersal ability of lowland populations that produce predominantly subitaneous eggs impedes crossing the Alps, or colonization events fail as a result of a low competitive ability of the species. Low competitive ability was invoked to explain the frequently observed diaptomid succession *M. laciniatus*–*A. denticornis*–*Eudiaptomus graciloides* in arctic mountain lakes (Nauwerck, 1980). The possibility that a very slow dispersal from areas in which the species survived the Pleistocene explains its scarcity, merits consideration. Similarly, the present-day distribution of *M. tetricus*, a species of predominantly southeastern origin (Kiefer, 1978), in the outermost East and Southeast of the Alps may be a result of dispersal history, rather than of its inability to survive in a broader range of localities. With respect to arctic

pond microcrustacean assemblages, Hebert & Hann (1986) suggested that many thousands of years are required following deglaciation to establish a complete zooplankton community in sites remote from glacial refuges.

Although obviously lacking desiccation-resistant dormant stages, some species (e.g. *E. serrulatus*, *C. abyssorum tetricus*, several harpacticoids?) are widespread in high-altitude regions, and thus seem to be highly effective in colonising remote environments in an early stage. To understand which dispersal mechanism cause(d) the present-day distribution patterns in remote areas such as mountain tops is central to our perception of alpine crustacean assemblages organisation. Investigation of related topics could be a challenging task of future studies.

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