

Zooplankton community composition of high mountain lakes in the Tatra Mts., the Alps in North Tyrol, and Scotland: relationship to pH, depth, organic carbon, and chlorophyll-a concentration

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Abstract: The European EMERGE (European Mountain lake Ecosystems: Regionalisation, diaGnostic & socio-economic Evaluation) project was a survey of high mountain lakes (above tree-line) across Europe using unified methods of sampling and analysis. The sampling was carried out in summer or autumn 2000, and comprised biological samples, and samples for chemical analysis. Data from three lake districts are used in this paper: the Tatra Mts. in Slovakia and Poland (45 lakes), the Alps in Tyrol in Austria (22 lakes), and Scotland (30 lakes). As it is shown by multiple regression analysis, DTOC (dissolved or total organic carbon) is the key variable for most groups of zooplankton. With increasing DTOC and mostly with chlorophyll-a decreasing, pH increasing and depth decreasing, macrofiltrators with coarse filter meshes are replaced by microfiltrators with fine filter meshes. Higher DTOC may increase bacterioplankton production and advantage species able to consume bacteria (microfiltrators). Other zooplankton species also differ in their preference for DTOC, chlorophyll-a, pH and depth, but DTOC being positively correlated with chlorophyll-a and pH positively correlated with depth. It may be caused by their different preference for food quality in terms of C:P ratio.

Key words: zooplankton, alpine, mountain, dissolved organic carbon, food quality

Introduction

It is known that zooplankton species differ in the ratio of algae and bacteria in their food (Geller & Müller 1981; Hessen 1985; Hessen *et al.* 1989). Their ability to collect bacteria is dependent on the density of their filter meshes (Brendelberger 1991).

Bacteria may be an important source of phosphorus for zooplankton, because they have a higher phosphorus content than algae. For example, Vadstein *et al.* (1993) found 10 times lower C:P ratio in bacteria than in algae in Lake Nesjøvatn in Norway. Hessen and Andersen (1990) found bacteria to account for 75% of particulate phosphorus in a humic lake, which made them the most important source of phosphorus for zooplankton. Moreover, assimilation efficiency of phosphorus from bacteria-sized particles was almost 82% (Hessen & Andersen 1990).

At a low ambient phosphorus concentration and elevated carbon content, C:P ratio of phytoplankton is so high that it limits the growth rate of zooplankton consuming it (DeMott *et al.* 1998; Elser *et al.* 2001; Hessen *et al.* 2002; Urabe *et al.* 2002). At high C:P, the gross (growth to ingestion ratio) and net (growth to assimilation ratio) growth efficiencies of *Daphnia* for phosphorus decrease, so that the phosphorus cannot be used for growth, and the growth rate decreases (DeMott *et al.* 1998). Copepods and carnivorous Cladocera have a lower P content in comparison with herbivorous Cladocera (Andersen & Hessen 1991; Hessen & Lyche 1991). These species could be less affected by low P content in food (Urabe *et al.* 2002).

Increasing intensity of light increases carbon to phosphorus (C:P) ratio of phytoplankton due to increased carbon fixation which elevates the carbon content (Hessen *et al.* 2002; Urabe *et al.* 2002; Hessen 2008). Since light intensity decreases with increasing depth of lakes, lake depth may influence food quality for zooplankton in terms of C:P ratio.

The ratio of algal to bacterial production is dependent on the concentration of the substrate for bacterial growth, which is dissolved organic carbon (DOC). In lakes with low primary production, the primary production to bacterioplankton production ratio gradually decreases with increasing allochthonous DOC concentration, because DOC has a positive influence on bacterial production and a negative influence on primary production due to absorption of light (Jansson *et al.* 2000). Based on summer epilimnetic data from oligotrophic clearwater lakes and dystrophic humic lakes, the ratio equals 1 at DOC concentrations around 10 mg dm⁻³ (Jansson *et al.* 2000). In more productive lakes and the ocean, allochthonous DOC is less important, and bacterial production is positively correlated with algal primary production (Cole *et al.* 1988). In mountain lakes, Reche *et al.* (1996) and Panzenböck (2007) found that the amount of carbon released extracellularly by phytoplankton was large enough to satisfy the bacterioplankton demand. The contribution of photosynthetic extracellular release (PER) to primary production was on average 32 % in the alpine lake Gossenköllesee (Panzenböck 2007). The contribution of net PER to total net primary production increased with increasing irradiance. 15 times higher rates of PER were observed during the ice-free season. 37 % of the carbon released during incubation was incorporated into bacterial biomass.

In acidic lakes, extracellular release of DOC by phytoplankton may also be limited by dissolved inorganic carbon concentration (DIC). Low DIC supply may limit the growth and photosynthesis of phytoplankton. At pH less than 6, the DIC resulting from air equilibration is about 10 µM, a value known to be rate limiting for various species in culture (Goldman & Graham 1981; Williams & Turpin 1987), and for natural phytoplankton (Nygaard 1989; Hein 1997). This level of DIC may be even below the photosynthetic compensation point of some algae species, and preclude their growth (Williams & Turpin 1987). However, lake waters are sometimes naturally CO₂ supersaturated, and then inorganic carbon limitation does not occur (Hein 1997).

It follows from the discussion above that bacteria are an important high quality food source for zooplankton. However, the importance of bacteria as food is determined by the size of bacterial production, which is stimulated by DOC. The in-lake photosynthetic production of DOC by algae is important, but decreases with decreasing irradiance caused by depth and also probably decreases at low pH. High levels of DOC may thus be awaited in lakes with high import of allochthonous DOC, or in lakes with high production DOC, which is probable at high chlorophyll-a concentration, high irradiance in shallow lakes and possibly at high pH. In the lakes with high bacterial production stimulated by high DOC, the ability to collect bacteria should advantage microfiltrators in zooplankton. The aim of this work is to confirm that the distribution of micro- and macrofiltrators in high mountain lakes (above the tree-line) is determined by DTOC (dissolved or total organic carbon), chlorophyll-a, pH and depth in three mountain areas in Europe.

Methods

High mountain lakes situated above the tree-line were surveyed. Samples were collected in the lakes of three lake districts covered by the EMERGE project: the Tatra Mts. in Slovakia and Poland (45 lakes), the Alps in Tyrol in Austria (22 lakes) and Scotland (30 lakes) (Fig. 1; Table 1). The Scottish sites were located in the Cairngorm and Grampian Mountains and the northwest Highlands (Kernan *et al.* 2009a). Sampling survey was performed in the ice-free season in late summer or autumn 2000: in the Tatra Mts. in 16.9.–1.10., in the Alps in 16.8.–19.9. and in Scotland in 19.9.–25.10. Sampling and chemical analysis were performed by many colleagues across Europe. The methods of chemical analyses were described by Camarero *et al.* (2009). Water samples

were collected as surface samples from central part of each lake (Straškrábová *et al.* 2009), and kept in cool and dark conditions until analysis. Chemical analyses were carried out by all involved laboratories according to the methods agreed within the MOLAR Project (Camarero *et al.* 2009), which were described by Wathne & Hansen (1997), and The MOLAR Water Chemistry Group (1999). Total organic carbon (TOC) was determined using catalytic combustion and IR spectrophotometry detection with TOC5000 Analyser, Shimadzu, Kyoto, Japan (Camarero *et al.* 2009). Only one depth with expected maximum chlorophyll-a concentration was sampled for bacterial biomass, chlorophyll-a concentration, and phytoplankton (Straškrábová & Stuchlík 2000). During autumnal mixing, the samples were taken with the top end of a sampler 0.5 m below the surface (so in Scotland according to Kernan *et al.* 2009a), whereas in deeper thermally stratified lakes at the depth of 1.5 times Secchi depth reading, which is where the chlorophyll maximum occurs during summer stratification (Catalan *et al.* 2002). Chlorophyll-a samples underwent filtration and concentration on Whatman GF/F glass fibre filters, and chlorophyll-a was then extracted in acetone and measured spectrophotometrically or fluorometrically (Kernan *et al.* 2009c; Straškrábová *et al.* 2009). In Scotland, the concentration of chlorophyll-a was determined spectrophotometrically after hot extraction in a mixture of acetone and methanol 5:1 (Kernan *et al.* 2009a). Large pelagic zooplankton was sampled quantitatively (quantitative samples) using Apstein type pelagic net (with 200 µm mesh and 0.2 m diameter except 0.1 m diameter in the Alps) hauled several times from the bottom to the surface at the deepest part of the lake (Kernan *et al.* 2009b; Kernan *et al.* 2009c). In Scotland, the net was only hauled from 1.5x Secchi disc depth (Kernan *et al.* 2009a). All pelagic zooplankton was sampled qualitatively (qualitative samples) using pelagic net (with 40 µm mesh and 0.2 m diameter) hauled vertically and laterally. Zooplankton samples were preserved with formaldehyde at the final concentration of 4%. Planktonic organisms in quantitative samples were counted in an Utermöhl type chamber using an inverted microscope. Sub-sampling was used to count at least 400 individuals of large crustaceans in a known part of each sample. Concentrated qualitative samples were observed spread on microscope slides and the found taxa were recorded. A part of each sample covered by 2-5 cover slips was observed.

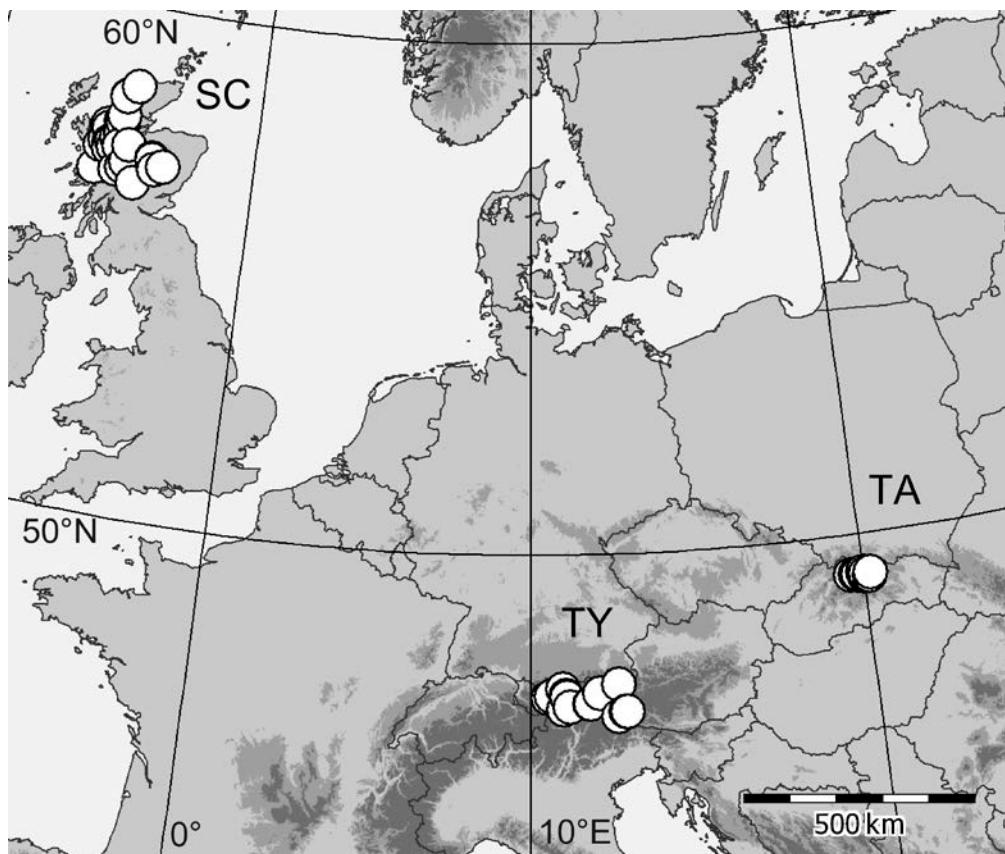


Fig 1: Map of the surveyed lakes belonging to three areas (lake districts): Scotland (SC, 30 lakes), the Alps in Tyrol in Austria (TY, 22 lakes), the Tatra Mts. in Slovakia and Poland (TA, 45 lakes).

Table 1: List of the surveyed lakes in the Tatra Mts. (EMERGE code beginning TA) and the Alps (code TY), in Scotland (code SC) and their characteristics. DTOC – dissolved or total organic carbon concentration (DOC in the Tatra Mts. and the Alps, TOC in Scotland), Chl-a – chlorophyll-a, AA – *Arctodiaptomus alpinus*, AAF – *Alona affinis*, AE – *Acroperus elongatus*, AEX – *Alonella excisa*, AH – *Acroperus harpae*, AL – *Arctodiaptomus laticeps*, AN – *Alonella nana*, AR – *Alona rectangularis*, ARU – *Alona rustica*, AV – *Acanthocyclops vernalis*, BC – *Bryocamptus cuspidatus*, BLR – *Bosmina longirostris*, BLS – *Bosmina longispina*, BP – *Branchinecta paludosa*, CA – *Cyclops abyssorum*, CC – *Chaoborus crystallinus*, CO – *Chaoborus obscuripes*, CQ – *Ceriodaphnia quadrangula*, CS – *Chydorus sphaericus*, DB – *Diaphanosoma brachyurum*, DD – *Drepanothrix dentata*, DG – *Daphnia galeata*, DL – *Daphnia longispina*, DN – *Diacyclops nanus*, DP – *Daphnia pulicaria*, DR – *Daphnia rosea*, EG – *Eudiaptomus gracilis*, EL – *Eurycerus lamellatus*, ES – *Eucyclops serrulatus*, GT – *Graptoleberis testudinaria*, HG – *Holopedium gibberum*, ML – *Mixodiaptomus laciniatus*, MV – *Megacyclops viridis*, PP – *Polyphemus pediculus*, PPI – *Paralona nigra*, RF – *Rhynchotalona falcata*. ^qSpecies was only found in qualitative sample. ^wAbundance in quantitative samples lower than 0.05 dm⁻³.

EMERGE code	Name	Geographical coordinates	Lake area ha	Depth m	Altitude m	pH	DTOC mg C dm ⁻³	Chl-a µg dm ⁻³	Crustacean taxa found in zooplankton	Fish
SC0002	Loch Coir' a' Ghrunnda	57°12'7"N, 6°13'16"W	2,87	9,2	750	6,1	0,7	0,3	BLS,AE ^w ,RF ^w	yes
SC0010	Lochan Bac an Lochain	56°43'24"N, 5°39'25"W	1,76	4,3	590	6,3	2,4	0,76	DB,CQ ^q ,BLS,AAF ^q ,AEX ^w ,AN ^q ,EG,CA	yes
SC0029		57°10'25"N, 5°35'34"W	2,52	1	720	6,1	5,2	0,78	DD,BLS,AE ^q ,AH ^w ,AAF ^q ,AEX ^w ,AN ^w	?
SC0067	Loch Coire na Caime	57°33'57"N, 5°28'33"W	3,21	5,1	530	6	1	0,65	DD ^q ,DR,BLS,AH ^w ,AN,GT ^q ,CA	yes
SC0068	Loch Bhuic Moir	57°16'43"N, 5°26'53"W	3,55	7,8	540	6,5	5,6	0,62	DB ^w ,HG,BLS,AH ^w ,AAF ^q ,EG,CA	?
SC0076	Loch Coire Mhic Fhearchair	57°35'28"N, 5°26'42"W	10,05	24	600	6,2	1,5	0,27	HG ^w ,BLS,AE ^w ,AH ^w ,CA	yes
SC0084		57°31'0"N, 5°23'32"W	9,65	32	670	5,5	0,9	0,23	HG ^w ,BLS,AE ^q ,AH ^q ,AAF ^q ,EG ^w ,CA	yes
SC0101	Loch a' Chleirich	57°15'3"N, 5°18'19"W	1,44	1,7	750	6,9	3	0,88	BLS,AH,AEX ^q ,AN,EG,CA,DN,ES	no
SC0108		57°8'34"N, 5°17'14"W	1,9	8,1	720	5,9	2	0,19	BLS,AH ^w ,PPI ^q ,EG,CA	?
SC0124	Loch an Fhraoich-choire	57°16'29"N, 5°13'34"W	4,42	6,2	660	6,6	2,4	0,6	DR,BLS ^w ,AH ^w ,AN ^q ,EG,ES ^w ,CC ^w	?
SC0140	Gorm Lochan	57°10'19"N, 5°6'13"W	1,64	9,8	870	6,8	1,4	1,96	DR ^q ,BLS ^q ,AH ^q ,EG ^q	yes
SC0153	Loch Beag	57°22'19"N, 5°5'4"W	2,45	13	660	6,7	2,7	0,32	DR,BLS,AE ^w ,AH,AAF ^q ,AN ^q ,EG	yes
SC0165	Loch a' Mhadaidh	57°42'45"N, 5°1'28"W	31,1	46	570	5,9	1,9	0,3	BLS,AE ^q ,AH ^q ,PPI ^q ,EG,CA	yes
SC0172		56°44'48"N, 4°54'15"W	9,32	9,1	740	6,6	2,6	1,18	DP,BLS,AE ^q ,AH ^q ,AAF ^q ,AEX ^q ,PPI ^q ,EG,CC	yes
SC0180	Loch Toll Lochan	57°29'44"N, 4°57'18"W	7,54	14	520	6,2	6,7	0,4	DR,BLS,AE ^w ,AH ^q ,AN ^q ,EG,CA	yes
SC0189	Loch an Fhuar-thuill Mhoir	57°27'9"N, 4°56'12"W	5,36	15	770	6,2	0,7	0,36	DR,BLS,AE ^q ,AN ^q ,AL,CA	?
SC0190	Loch Gorm	57°40'53"N, 4°57'16"W	21,61	47	540	6,2	2	0,44	DR,BLS,AH ^w ,AL,CA	yes
SC0191	Loch Carn a' Chaochain	57°13'13"N, 4°54'56"W	2,29	5	660	6,2	6,7	2,04	DB ^w ,BLS,AEX ^w ,AN ^w ,ML	?
SC0197	Loch a' Choire Dhairg	58°11'57"N, 4°58'35"W	4,22	11,5	530	6,8	1,7	0,63	HG,DR,BLS,AE ^q ,AH ^w ,AAF ^q ,PPI ^q ,CA	yes
SC0204	Lochan a' Chnapaich	57°48'35"N, 4°56'8"W	5,6	8,8	690	6,5	2,4	0,36	DR,BLS,AH ^w ,EG,ML	?
SC0211	Loch Bealach na h-Uidhe	58°11'6"N, 4°57'13"W	2,9	3,5	530	6,2	3,5	0,83	DR,BLS,AH,ML,CA	yes
SC0271	Lochan Coire an Lochain	56°49'53"N, 4°41'3"W	5,06	4,7	740	6,9	3,2	0,37	HG,BLS,AE ^w ,AH ^w ,AN ^q ,MV ^w	yes
SC0330	Lochan Coire Choille-rais	56°56'43"N, 4°34'37"W	7,4	27	810	6,7	1,3	0,41	HG ^q ,DR,BLS,AH ^w ,AAF ^q ,CA	?
SC0335		57°16'9"N, 4°34'58"W	1,92	6	540	6,8	9,2	0,44	DB ^q ,DL ^q ,BLS,AH ^q ,AAF ^q ,AEX ^w ,AL,CA,ES ^w	?
SC0349		58°25'1"N, 4°35'43"W	3,82	7,3	530	6	2,6	0,63	DR,BLS ^q ,AH ^q ,AN ^q ,ML ^w ,CA ^q ,CC ^w	?
SC0366	Lochan nan Cat	56°33'22"N, 4°12'23"W	12,37	14	720	7,1	2,9		HG,DG,BLS,AE ^w ,AH ^w ,AN ^q ,MV	yes
SC0379		57°6'20"N, 3°40'60"W	0,91	5,6	920	5,8	0,8	0,14	DR ^w ,BLS,AH ^w ,ARU ^w ,CS ^w ,EG,ML,CA,ES ^w	no
SC0382	Lochan Uaine	57°3'47"N, 3°38'55"W	3,78	21	910	5,9	1,1	0,31	HG,BLS,AE ^w ,AH ^w ,CS ^q ,MV ^w	no

EMERGE code	Name	Geographical coordinates	Lake area ha	Depth m	Altitude m	pH	DTOC mg C dm ⁻³	Chl-a µg dm ⁻³	Crustacean taxa found in zooplankton	Fish
SC0386	Loch nan Eun	56°53'6"N, 3°32'18"W	14,46	10	790	6,7	5,1	1,6	DR,BLS,EL ^q ,PPI ^q ,EG,ML,CA,ES ^q	yes
SC0399	Lochnagar	56°57'33"N, 3°13'53"W	9,9	24	790	5,4	1,6	0,47	HG,BLS,AH ^w ,EG	yes
TA0001	Horné Roháčske pleso	49°12'21"N, 19°37'37"E	1,45	8,1	1718	6,4	0,44	0,72	DR,AH,AAF ^q ,AV ^q	no
TA0003	Nižné Jamnícke pleso	49°12'11"N, 19°46'18"E	1,12	9,2	1728	7,2	0,43	0,67	DR,AH ^w ,AAF ^q ,CA,ES ^q	no
TA0004	Vyšné Račkove pleso	49°12'0"N, 19°48'23"E	0,73	12,7	1697	7,2	0,13	0,65	DR,AAF ^q ,CS,CA	yes
TA0006	Veľké Bystré pleso	49°10'59"N, 19°50'37"E	0,89	12,7	1876	7,3	1	0,55	CA	yes
TA0007	Zielony Staw Gąsienicowy	49°13'44"N, 20°0'4"E	3,84	15,1	1672	6,8	0,67	5,75	AH ^w ,AAF ^w ,CA	yes
TA0008	Zelené krivánske pleso	49°9'34"N, 20°0'31"E	4,32	23,1	2017	6,7	0,274	1,4	DP,CS,CA	no
TA0009	Dlugi Staw Gąsienicowy	49°13'38"N, 20°0'39"E	1,58	10,6	1784	6,2	0,223	0,11	CS,AV ^w	no
TA0010	Zadni Staw Gąsienicowy	49°13'32"N, 20°0'43"E	0,53	8	1852	6,4	0,234	0,03	CS,AV ^w	no
TA0011	Nižné Terianske pleso	49°10'11"N, 20°0'51"E	4,91	43,2	1941	6,7	0,255	2,4	CS ^w ,CA,ES ^q	no
TA0012	Zadni Staw Polski	49°12'48"N, 20°0'51"E	6,46	31,6	1890	6,3	0,446	0,57	AAF ^w ,CS ^w ,CA,ES ^q	no
TA0013	Czarny Staw Gąsienicowy	49°13'52"N, 20°1'12"E	17,79	51	1620	6,4	0,51	3,09	AH ^q ,AAF ^w ,CA	yes
TA0014	Vyšné Terianske pleso	49°10'5"N, 20°1'18"E	0,55	4,2	2109	5	0,554	1,83	CS,AV	no
TA0015	Zmarzly Staw Gąsienicowy	49°13'28"N, 20°1'26"E	0,28	3,7	1787	6	0,14	0,05	CS ^w ,AV ^q	no
TA0017	Vyšné Wahlenbergovo pleso	49°9'51"N, 20°1'38"E	4,96	21,1	2145	6,3	0,15	1,23	CS ^w ,CA,ES ^w	no
TA0018	Czarny Staw Polski	49°12'17"N, 20°1'40"E	12,65	50,4	1722	6,6	0,95	3,84	CS ^w ,CA	yes
TA0019	Nižné Temnosmrečinské pleso	49°11'34"N, 20°1'50"E	10,48	40,5	1674	7,2	0,354	0,83	DG,DP,CS ^w ,CA	no
TA0020	Okrúhle pleso	49°10'15"N, 20°2'11"E	0,75	10,2	2096	6,1	0,27	0,39	AA	no
TA0021	Capie pleso	49°10'6"N, 20°2'16"E	2,43	16,8	2072	6,3	0,22	0,96	CS ^w ,AA ^w ,CA ^w ,ES	no
TA0022	Vyšné Temnosmrečinské pleso	49°11'21"N, 20°2'22"E	4,95	20	1716	7,2	0,204	1,43	DP,CS ^w ,CA	no
TA0023	Wielki Staw Polski	49°12'48"N, 20°2'25"E	34,14	79,3	1655	6,7	0,41	0,61	DP,CA	yes
TA0026	Malé Hincovo pleso	49°10'26"N, 20°3'31"E	2,22	6,1	1923	7,3	0,58	0,86	DP ^w ,AH ^w ,CS ^w ,AA,CA,ES ^w	no
TA0027	Veľké Hincovo pleso	49°10'47"N, 20°3'38"E	18,19	53,2	1946	6,9	0,42	1,14	AH ^w ,AAF ^w ,CS ^w ,AA,CA	yes
TA0029	Czarny Staw pod Rysami	49°11'20"N, 20°4'40"E	20,54	76,4	1580	7	0,264	0,96	DP,CA	no
TA0030	Veľké Žabie pleso	49°10'19"N, 20°4'43"E	2,26	6,9	1919	6,5	0,15	0,75	CS,ES ^w	no
TA0031	Dračie pleso	49°9'59"N, 20°5'15"E	1,71	16	1998	6,9	0,05	0,41	AA	no
TA0032	Vyšné Žabie bielovodské pleso	49°11'39"N, 20°5'39"E	8,08	24,3	1699	6,6	0,43	0,53	DP,AAF ^w ,CS ^w ,CA	no
TA0036	Litvorové pleso	49°10'38"N, 20°7'52"E	1,67	18,6	1863	6,9	0,14	1,18	DP,AH ^q ,CA	no
TA0037	Batizovské pleso	49°9'8"N, 20°7'53"E	2,78	11,2	1879	6,3	0,1	0,57	CS ^w	no
TA0039	Zelené javorové pleso	49°12'22"N, 20°8'34"E	0,75	8,3	1811	6,6	0,36	1,28	DP,CS,AA,CA	no
TA0042	Pusté pleso	49°10'56"N, 20°9'18"E	1,2	6,82	2055	6,9	0,28	0,84	CS ^w ,AA,CA ^q	no
TA0043	Vyšné zbojnícke pleso	49°10'44"N, 20°9'34"E	0,66	7	1972	6,9	0,27	0,39	CS ^w ,AA	no
TA0044	Prostredné zbojnícke pleso	49°10'42"N, 20°9'42"E	0,62	5,4	1969	6,8	0,31	0,32	AA,AV ^q ,CA ^w	no

EMERGE code	Name	Geographical coordinates	Lake area ha	Depth m	Altitude m	pH	DTOC mg C dm ⁻³	Chl-a µg dm ⁻³	Crustacean taxa found in zooplankton	Fish
TA0045	Ľadové pleso	49°11'3"N, 20°9'46"E	1,72	18	2057	6,6	0,33	0,69	CS,AA,CA	no
TA0047	Starolesnianske pleso	49°10'48"N, 20°10'4"E	0,73	4,1	1986	5,3	1,37	5,26	CQ ^w ,CS,AV	no
TA0049	Žabie javorové pleso	49°11'28"N, 20°10'12"E	0,83	16	1886	7	0,1	0,33	DP,CA	no
TA0051	Prostredné sivé pleso	49°11'3"N, 20°10'36"E	0,88	5,2	2011	5,8	0,33	0,04	CS ^w ,BC	no
TA0054	Veľké spišské pleso	49°11'36"N, 20°11'47"E	2,43	9,6	2014	6,2	0,056	0,14		no
TA0056	Prostredné spišské pleso	49°11'29"N, 20°11'56"E	1,82	5,1	2013	6	0,141	1,42	CS	no
TA0101	Wyżni Siwy Stawek	49°12'18"N, 19°50'14"E	0,05	1,8	1716	7,2	3,33	0,27	CS ^w	no
TA0102	Dwoisty Staw Wschodni	49°13'60"N, 20°0'25"E	1,41	9,2	1657	5,8	0,23	0,95	HG,AH,EL ^q ,CS ^w ,ES ^q	no
TA0105	Vyšné Furkotské pleso	49°8'37"N, 20°1'53"E	0,46	3,4	1698	6,5	0,32	1,04	BP,DR,AR ^q ,CS,AA	no
TA0106	Wyżni Mnichowy Stawek IX	49°11'42"N, 20°3'17"E	0,06	2,3	1870	4,8	0,74	1,75	AAF,CS	no
TA0108	Morskie Oko	49°11'52"N, 20°4'20"E	34,54	50,8	1395	6,9	0,47	1,38	HG,DG,BLR,PP,CA ^q ,ES ^w	yes
TA0109	Slavkovské pleso	49°9'9"N, 20°11'5"E	0,1	2,91	1676	5	5,15	11,17	AAF,AEX ^q ,CS ^w ,AV,CO	no
TA0110	Čierne pleso kežmarské	49°12'28"N, 20°13'35"E	0,31	3,6	1579	7	0,35	0,97	AAF,AEX ^q ,CS ^w ,AA	no
TY0047	Unterer Seewiese	47°11'38"N, 10°28'55"E	1,78	2,2	2229	8,8	1,644	0,49	AAF,CS ^q ,AA,CA ^q ,ES ^q	no
TY0048	Oberer Seewiese	47°11'16"N, 10°29'9"E	1,43	13,5	2469	8,1	0,286	0,45	CS ^q ,AA,CA ^w	no
TY0049	Mittlerer Seewiese	47°11'27"N, 10°29'26"E	0,52	4,7	2425	8,3	0,355	0,24		no
TY0077	Steinsee	47°13'31"N, 10°35'47"E	1,87	8,3	2222	8,6	0,708	0,73	DR,AH ^w ,CS,AA,CA ^w	yes
TY0166	Drachensee	47°21'15"N, 10°56'5"E	5,01	24	1874	8,3	1,054	2,12	AV ^w	yes
TY0170	Schwarzsee ob Sölden	46°57'42"N, 10°56'46"E	3,72	18	2796	5,7	0,542	1,61	CS,AV	yes
TY0188	Gossenköllesee	47°13'31"N, 11°0'50"E	1,59	9,9	2413	7	0,398	2,89	AEX ^w ,CS,CA	yes
TY0189	Rotfelssee	47°13'35"N, 11°0'29"E	1,01	5	2485	7,3	0,354	0,53	CS ^w ,AV ^q	yes
TY0194	Oberer Plenderlessee	47°11'56"N, 11°2'17"E	2,23	7,5	2344	7,1	0,248	0,88	CA	yes
TY0195	Mittlerer Plenderlessee	47°12'17"N, 11°2'30"E	1,46	5,76	2317	6,5	0,766	1,26	AEX ^w ,CA	yes
TY0229	Mutterbergersee	47°0'43"N, 11°7'43"E	3,07	8,1	2479	5,7	0,44	0,42	CS ^w ,CA	yes
TY0303	Friesenbergsee	47°3'53"N, 11°41'60"E	1,88	4,5	2450	7,6	0,32	0,21	ES ^q	?
TY0305	Oberer Wesendlekarsee	47°4'21"N, 11°43'1"E	1,72	16,5	2660	7,3	0,415	1,99	AEX ^q	?
TY0306	Unterer Wesendlekarsee	47°4'3"N, 11°43'11"E	2,46	21,5	2368	7,2	0,624	1,33		yes
TY0338	Vorderer Langersee in der Wilden Krimml	47°15'40"N, 11°59'17"E	3,65	15,4	2232	7,1	1,639	7,49	BLR,CS ^q ,CA	yes
TY0339	Oberer Scheibensee	47°15'46"N, 11°58'54"E	1,53	4	2290	7,5	0,861	1,49	BLR,AH ^q ,CS ^q ,AV ^q	yes
TY0427	Aschersee	46°48'10"N, 12°30'11"E	1,38	7	2532	7	1,027	0,49	DR,AEX ^q ,CA	yes
TY0428	Anraser See	46°48'25"N, 12°31'4"E	2,07	6,5	2538	7,2	0,779	0,95	DR,AAF ^q ,AA,CA	yes
TY0444	Wildsee ob Fieberbrunn	47°25'36"N, 12°32'21"E	3,23	14,5	1840	7,4	0,867	0,78	DR,CA,ES ^q	yes
TY0459	Alkusersee	46°54'1"N, 12°43'59"E	7,19	44,6	2432	7,1	0,416	2,68	BLR,AV ^q	yes
TY0463	Südlicher Neualplsee	46°53'17"N, 12°45'57"E	1,95	13,2	2438	7	0,862	18,65	AAF ^w ,AEX ^w ,AV ^q	yes
TY0464	Nördlicher Neualplsee	46°53'24"N, 12°46'3"E	2,08	7,2	2440	7,1	1,031	1,36	BLR,CA	yes

Organisms were identified using keys by Bartoš (1959), Šrámek-Hušek *et al.* (1962), Ruttner-Kolisko (1972), Kiefer (1978), Koste (1978), Rozkošný (1980), Negrea (1983), Einsle (1993), Segers (1995), De Smet (1997), and Flössner (2000). The identity of a misidentified *Daphnia* species from the Nižné Temnosmrečinské Lake was corrected to *D. galeata* according to the genetical study by Petrusek *et al.* (2007). The harpacticoid copepod *Bryocamptus cuspidatus* (Schmeil, 1893) was identified by Anton Brancelj.

The presence of fish in the Scottish lakes was determined from historical or anecdotal sources (Kernan *et al.* 2009a). Because these data may not be reliable (Kernan *et al.* 2009c) and only three lakes were fishless, no comparison of Scottish lakes with and without fish was possible. The three fishless lakes had not unique composition of zooplankton. In the Alps and the Tatra Mts., species composition of the fish populations was known at the sampling date (Hořická *et al.* 2006; Tolotti *et al.* 2006). Vulnerability to fish predation is dependent on fish density (Knapp *et al.* 2005), but the density of fish population was not known.

Only a qualitative zooplankton sample was available for SC0140 Gorm Lochan, and only a quantitative zooplankton sample for TY0049 Mittlerer Seewisee.

Data on TOC were available only for the Scottish lakes and data on DOC only for the continental lakes. The median DOC/TOC ratio in oligotrophic lakes is 0.9 (Wetzel 2001). In alpine and mountain forest lakes in Europe, DOC/TOC ranges from 0.69 to 0.92 with Pearson correlation coefficients r^2 being from 0.53 to 0.98 (Camarero *et al.* 1999; Winder *et al.* 2001; Rosén 2005; Nedbalová *et al.* 2006). In this paper, DOC and TOC were thus regarded as a single variable and named DTOC (dissolved or total organic carbon).

Multiple regression analysis and principal component analysis (PCA) of data were performed using PAST software version 1.94b (the description of PAST give Hammer *et al.* 2001). Linear regression was used to find a linear relationship between dependent variable y and explanatory variables x_n ($y = a + b_1x_1 + b_2x_2 + \dots$). The values of the dependent variable y were assigned to zooplankton species or groups of species according to their expected preference for different size categories of food. For example, value 1 was assigned to *Diaphanosoma brachyurum* with fine filter meshes, value 0 to *Daphnia rosea* with intermediate filter meshes and value -1 to *Holopedium gibberum* with coarse filter meshes. If two species were present in one lake, both values were averaged. Principal component analysis is a procedure for finding hypothetical variables (components) which account for as much of the variance in multidimensional data as possible (Hammer *et al.* 2001). These new variables are linear combinations of the original variables. PCA results were displayed in a correlation biplot (information on correlation biplots give Legendre & Legendre 1998).

Results

A list of all surveyed lakes with their geographical coordinates, area, depth, altitude, crustacean taxa found in zooplankton, pH, dissolved or total organic carbon concentration (DTOC), chlorophyll-a (chl-a) concentration, and fish presence is shown in Table 1. Mean characteristics of lakes grouped in the three lake districts are compared in Table 2.

Tab 2: Comparison of characteristics of lakes in three areas (lake districts): Scotland (code SC), the Alps (code TY), the Tatra Mts. (code TA). TN – total nitrogen, TP – total phosphorus, DTOC – dissolved or total organic carbon, chl-a – chlorophyll-a concentration, bacteria – total bacteria and filamentous biomass, bare ground – bare ground (without vegetation) in catchment, ice cover – ice cover duration

Code		Latitude	Longitude	Altitude	pH	Cl	TP	DTOC	Chl-a	Bacteria	Bare ground	Ice cover
				m		mg dm ⁻³	µg dm ⁻³	mg C dm ⁻³	µg dm ⁻³	µg C dm ⁻³	%	days
SC	mean	57,33	-4,88	679	6,31	5,1	2,8	2,83	0,64	21,33	32,9	127
SC	minimum	56,56	-6,22	520	5,42	1,67	2,5	0,7	0,14	1,97	0,5	113
SC	median	57,26	-4,95	680	6,19	4,65	2,5	2,4	0,44	20,61	22,8	127
SC	maximum	58,42	-3,23	920	7,14	9,72	6	9,2	2,04	45,67	81,9	140
TA	mean	49,19	20,05	1843	6,5	0,17	2,6	0,54	1,37	17,04	62,4	198
TA	minimum	49,14	19,63	1395	4,83	0,11	0,7	0,05	0,03	0,47	0	168
TA	median	49,19	20,04	1870	6,62	0,17	2,1	0,32	0,84	12,05	65	199
TA	maximum	49,23	20,23	2145	7,28	0,23	14,7	5,15	11,17	169,82	85	223
TY	mean	47,11	11,55	2376	7,31	0,12	3,7	0,71	2,23	19,23	47	212
TY	minimum	46,8	10,48	1840	5,66	0,07	1,6	0,25	0,21	3,48	3	179
TY	median	47,19	11,41	2429	7,21	0,1	2,6	0,67	1,11	19,07	47,8	216
TY	maximum	47,43	12,77	2796	8,82	0,25	8,5	1,64	18,65	30,49	95	231

Tab 3: The results of linear regression analyses fitting lines ($y = a + b_1x_1 + b_2x_2 \dots$) to data. The values assigned to zooplankton groups were used as dependent variable (y) and pH, depth (m), chlorophyll-a ($\mu\text{g dm}^{-3}$) and DTOC (mg C dm^{-3}) were explaining variables (x). P values of b_i coefficients are the results of t-tests. R^2 is the coefficient of determination. Area codes: SC – Scotland, TY – the Alps, TA – the Tatra Mts. In the Tatra Mts. and the Alps, only zooplankton occurrences in quantitative samples with abundances higher than 0.05 dm^{-3} were included. If only lakes without fish are included in an analysis, it is stated in the Group column.

Analysis Nr.	Area code	Group	Dependent variable value (y)	N	Explanatory variables (x)	Slope (b)	P value (slope)	R^2	P value (overall)	
1 SC		<i>Diaphanosoma brachyurum</i>		123	DTOC	0,15	0,005	0,32	0,005	
		<i>Daphnia rosea</i>	0							
		<i>Holopedium gibberum</i>	-1							
2 SC		<i>Conochilus hippocrepis</i>		118	DTOC	-0,21	0,044	0,23	0,044	
		<i>Conochilus unicornis</i>	-1							
3 SC		Pelagic Rotifera: <i>Ascomorpha ovalis</i> , <i>Asplanchna priodonta</i> , <i>Collotheca mutabilis</i> , <i>Conochilus hippocrepis</i> , <i>Conochilus unicornis</i> , <i>Gastropus stylifer</i> , <i>Kellicottia longispina</i> , <i>Keratella cochlearis</i> , <i>Keratella quadrata</i> , <i>Ploesoma hudsoni</i> , <i>Polyarthra remata</i> , <i>Polyarthra vulgaris</i> and <i>Synchaeta</i> sp.		Number of species in one lake						
					29	DTOC	0,58	0,025	0,17	0,025
						pH	2,44	0,058		
4 SC		Pelagic Rotifera: <i>Ascomorpha ovalis</i> , <i>Asplanchna priodonta</i> , <i>Collotheca mutabilis</i> , <i>Conochilus hippocrepis</i> , <i>Conochilus unicornis</i> , <i>Gastropus stylifer</i> , <i>Kellicottia longispina</i> , <i>Keratella cochlearis</i> , <i>Keratella quadrata</i> , <i>Ploesoma hudsoni</i> , <i>Polyarthra remata</i> , <i>Polyarthra vulgaris</i> and <i>Synchaeta</i> sp.		Number of species in one lake						
					29	DTOC	0,65	0,013	0,38	0,006
						$\log_{10}(\text{depth})$	3,36	0,018		
5 SC		<i>Keratella cochlearis</i> , <i>Polyarthra remata</i>		126	DTOC	0,08	0,038	0,17	0,038	
		<i>Keratella hiemalis</i> , <i>Polyarthra dolichoptera</i>	-1							
6 TATY		<i>Keratella cochlearis</i> , <i>Polyarthra remata</i>		138	DTOC	0,19	0,009	0,18	0,009	
		<i>Keratella hiemalis</i> , <i>Polyarthra dolichoptera</i>	-1							
7 TATY		<i>Daphnia rosea</i>		119	pH	0,58	0,012	0,56	0,002	
		<i>Daphnia pulicaria</i>	0		$\log_{10}(\text{depth})$	-1,02	0,003			
		<i>Holopedium gibberum</i>	-1							
8 TATY		<i>Daphnia rosea</i>		119	DTOC	1,25	0,037	0,23	0,037	
		<i>Daphnia pulicaria</i>	0							
		<i>Holopedium gibberum</i>	-1							
9 TATY		<i>Daphnia rosea</i>		119	chlorophyll-a	-0,85	0,077	0,17	0,077	
		<i>Daphnia pulicaria</i>	0							
		<i>Holopedium gibberum</i>	-1							
10 TATY		<i>Daphnia rosea</i> , no fish		113	pH	0,92	0,011	0,61	0,009	
		<i>Daphnia pulicaria</i> , no fish	0		$\log_{10}(\text{depth})$	-1,14	0,008			
		<i>Holopedium gibberum</i> , no fish	-1							
11 TATY		<i>Daphnia rosea</i> , no fish		113	DTOC	2,72	0,027	0,37	0,027	
		<i>Daphnia pulicaria</i> , no fish	0							
		<i>Holopedium gibberum</i> , no fish	-1							
12 TATY		<i>Arctodiaptomus alpinus</i>		144	chlorophyll-a	-0,13	0,038	0,1	0,038	
		<i>Cyclops abyssorum</i> , <i>Acanthocyclops vernalis</i>	-1							
13 TATY		<i>Arctodiaptomus alpinus</i>		144	pH	0,43	0,006	0,31	0,001	
		<i>Cyclops abyssorum</i> , <i>Acanthocyclops vernalis</i>	-1		$\log_{10}(\text{depth})$	-0,92	0,003			
14 TATY		<i>Arctodiaptomus alpinus</i> , no fish		126	pH	0,53	0,007	0,45	0,001	
		<i>Cyclops abyssorum</i> , <i>Acanthocyclops vernalis</i> , no fish	-1		$\log_{10}(\text{depth})$	-1,3	0,002			
15 TATY		<i>Arctodiaptomus alpinus</i> , no fish		126	DTOC	0,82	0,056	0,24	0,041	
		<i>Cyclops abyssorum</i> , <i>Acanthocyclops vernalis</i> , no fish	-1		chlorophyll-a	-0,47	0,016			
16 TATY		<i>Cyclops abyssorum</i> , no fish		117	pH	0,78	<0,001	0,87	<0,001	
		<i>Acanthocyclops vernalis</i> , no fish	-1		$\log_{10}(\text{depth})$	0,55	0,041			
17 TATY		<i>Cyclops abyssorum</i> , no fish		117	DTOC	-0,45	0,003	0,46	0,003	
		<i>Acanthocyclops vernalis</i> , no fish	-1							
18 TATY		<i>Cyclops abyssorum</i> , no fish		117	chlorophyll-a	-0,22	<0,001	0,57	<0,001	
		<i>Acanthocyclops vernalis</i> , no fish	-1							
19 SC		<i>Arctodiaptomus laticeps</i> , <i>Eudiaptomus gracilis</i> , <i>Mixodiaptomus laciniatus</i>		113	$\log_{10}(\text{DTOC})$	2,81	0,029	0,36	0,029	
		<i>Cyclops abyssorum</i> , <i>Megacyclops viridis</i>	-1							
		(lakes with both groups are not included)								
20 SC		<i>Arctodiaptomus laticeps</i>		121	chlorophyll-a	-0,47	0,037	0,46	0,012	
		<i>Eudiaptomus gracilis</i>	0		pH	0,82	0,012			
		<i>Mixodiaptomus laciniatus</i>	-1		$\log_{10}(\text{depth})$	0,89	0,015			
21 TATY		<i>Daphnia galeata</i> , <i>D. rosea</i> , <i>D. pulicaria</i>		123	DTOC	-1,21	0,005	0,32	0,005	
		<i>Bosmina longirostris</i>	-1							
22 TATY		<i>Daphnia galeata</i> , <i>D. rosea</i> , <i>D. pulicaria</i>		123	chlorophyll-a	-0,35	0,001	0,4	0,001	
		<i>Bosmina longirostris</i>	-1							
23 TATY		fish present		158	$\log_{10}(\text{chlorophyll-a})$	0,72	0,042	0,07	0,042	
		fish absent	-1							
24 TATY		fish present		158	$\log_{10}(\text{DTOC})$	1,16	0,002	0,16	0,002	
		fish absent	-1							

The relationship of zooplankton species groups to the biotic variables DTOC and chlorophyll-a and the abiotic variables pH and depth inferred from regression or multiple regression analyses is shown in Table 3. Regression analysis is used to find out whether the variable y describing in most cases the food size preference of zooplankton species is dependent on various environmental characteristics (x_i). Nearly all slope coefficients (b_i) from regressions are statistically significant (P value <0.05). If a slope coefficient is positive, then the dependent variable y increases with the increase of this explaining variable. If a slope coefficient is negative, then the dependent variable y increases with the decrease of this explaining variable. In other words, species represented by high values of y prefer high values of environmental characteristics with positive slope coefficients and low values of environmental characteristics with negative slope coefficients.

DTOC is the key variable in Scotland. As to cladocerans, *Diaphanosoma brachyurum* prefers high DTOC, *Daphnia rosea* intermediate, and *Holopedium gibberum* low values (Table 3, analysis 1). In the Tatra Mts. and the Alps, *Daphnia rosea* prefers high DTOC (Table 3, analysis 8) and low chlorophyll-a (Table 3, analysis 9), *Daphnia pulicaria* intermediate, and *Holopedium gibberum* low DTOC and high chlorophyll-a. In Scotland, the calanoid copepods *Arctodiaptomus laticeps*, *Eudiaptomus gracilis*, and *Mixodiaptomus laciniatus* prefer higher DTOC than the cyclopoid copepods *Cyclops abyssorum* and *Megacyclops viridis* (Table 3, analysis 19). This relationship is significant if only lakes with either cyclopoid copepods or calanoid copepods are included, while lakes with both groups not. In the fishless lakes of the Tatra Mts. and the Alps, the calanoid copepod *Arctodiaptomus alpinus* prefers higher DTOC and lower chlorophyll-a (Table 3, analysis 15) than the cyclopoid copepods *Cyclops abyssorum* and *Acanthocyclops vernalis*. Both in the Scottish lakes (Table 3, analysis 5) and the lakes of the Tatra Mts. and the Alps (Table 3, analysis 6), the rotifers *Keratella cochlearis* and *Polyarthra remata* prefer higher DTOC than *Keratella hiemalis* and *Polyarthra dolichoptera*. In Scotland, the rotifer *Conochilus unicornis* prefers higher DTOC than *C. hippocrepis* (Table 3, analysis 2). In Scotland, the number of the pelagic rotifer taxa *Ascomorpha ovalis*, *Asplanchna priodonta*, *Collotheca mutabilis*, *Conochilus hippocrepis*, *Conochilus unicornis*, *Gastropus stylifer*, *Kellicottia longispina*, *Keratella cochlearis*, *Keratella quadrata*, *Ploesoma hudsoni*, *Polyarthra remata*, *Polyarthra vulgaris* and *Synchaeta* sp. present in one lake increases with increasing DTOC (Table 3, analysis 3).

In the Tatra Mts. and the Alps, zooplankton species groups preferring different DTOC values prefer usually different pH and depth values, with pH and depth negatively correlated. *Daphnia rosea* prefers high pH and small depth, *Daphnia pulicaria* intermediate, and *Holopedium gibberum* low pH and big depth (Table 3, analyses 7 and 10). In the lakes of the Tatra Mts. and the Alps, the calanoid copepod *Arctodiaptomus alpinus* prefers higher pH and smaller depth than the cyclopoid copepods *Cyclops abyssorum* and *Acanthocyclops vernalis* (Table 3, analyses 13 and 14). In PCA analysis of all lakes, the direction of increasing depth and chlorophyll-a, and decreasing pH and DTOC approximately agrees with the axis 2 (Fig. 2).

Some other species are also dependent on pH and depth, but pH and depth are positively correlated. As regards calanoid copepods in Scotland, *Arctodiaptomus laticeps* prefers high pH and depth and low chlorophyll-a, *Eudiaptomus gracilis* intermediate, and *Mixodiaptomus laciniatus* low pH and depth and high chlorophyll-a (Table 3, analysis 20). As regards cyclopoid copepods in the Tatra Mts. and the Alps, *Cyclops abyssorum* prefers higher pH and depth and lower chlorophyll-a and DTOC than *Acanthocyclops vernalis* in fishless lakes (Table 3, analyses 16, 17 and 18). In PCA analysis of all lakes, the direction of pH and depth both decreasing and DTOC and chlorophyll-a both increasing approximately agrees with the axis 1 (Fig. 2).

In the Tatra Mts. and the Alps, fish are found in lakes with high DTOC and chlorophyll-a (Table 3, analyses 23 and 24). Species often tolerating fish presence are *Bosmina longirostris*, *Daphnia rosea*, and *Cyclops abyssorum*, whereas *Arctodiaptomus alpinus* and *Daphnia pulicaria* are usually found in fishless lakes (Table 4). In the Tatra Mts. and the Alps, the cladoceran *Bosmina longirostris* prefers higher chlorophyll-a and DTOC than the cladocerans *Daphnia galeata*, *D. rosea* and *D. pulicaria* (Table 3, analyses 21 and 22). Species tolerating fish are species occurring at high DTOC and chlorophyll-a: *C. abyssorum* occurs mostly at high chlorophyll-a (Table 3, analysis 12), *B. longirostris* at high both DTOC and chlorophyll-a (Table 3, analyses 21 and 22), and *D. rosea* at high DTOC (Table 3, analyses 8 and 11).

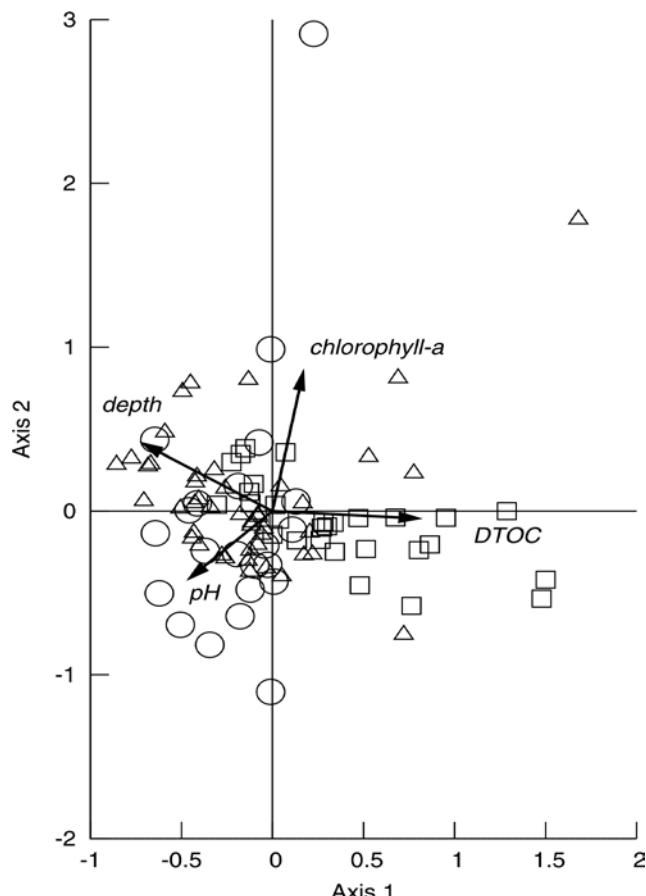


Fig. 2: Correlation biplot based on PCA of characteristics of 96 lakes in the Tatra Mts. (Δ), the Alps (\circ) and Scotland (\square). Depth was logarithmically transformed ($\log_{10}(\text{depth})$). Axes 1, 2, and 3 explained 34%, 26%, and 23% of variance, respectively. The species scores (points) were multiplied by 0.5 for display purposes.

Discussion

In the lakes in the Tatra Mts. and the Alps, microfiltrators with fine filter meshes are replaced by macrofiltrators with coarse filter meshes in the direction of increasing depth and decreasing pH, or increasing chlorophyll-a and decreasing DTOC (Table 3). Filter mesh size is known to predict retention efficiency for bacteria (Brendelberger 1991). The calanoid copepod *Arctodiaptomus alpinus* is replaced by the cyclopoid copepods *Cyclops abyssorum* and *Acanthocyclops vernalis* (Table 3). Both cyclopoid and calanoid copepods are macrofiltrators with coarse filter meshes and low ability to feed on bacteria (Hessen 1985; Hessen *et al.* 1989; Hopp & Maier 2005a). Cyclopoid copepods generally prefer larger, often

animal, food than calanoid copepods do (Fryer 1957; Einsle 1993). For example, *Cyclops* spp. have lower clearance rates (Adrian 1991) and ingest less and larger algae (Tóth *et al.* 1987) in comparison to *Eudiaptomus gracilis*. Similarly, *Daphnia rosea* is replaced by *D. pulicaria*, and *D. pulicaria* by *Holopedium gibberum* (Table 3). *Daphnia rosea* has probably smaller filter mesh size than *D. pulicaria*. The distance of setulae on filter combs is 0.5-0.9 in *D. longispina* (Hessen 1985), whereas it is 0.6-1.8 in *D. pulicaria* (Geller & Müller 1981). American *D. pulicaria* was found to have mostly higher ratio of algae clearance rate to bacterial clearance rate than American *D. rosea* (DeMott & Kerfoot 1982). *H. gibberum* has coarse filter meshes and low ability to feed on bacteria (Geller & Müller 1981; Hessen 1985; Hessen *et al.* 1989). The change from micro- to macrofiltrators with decreasing pH and increasing depth may be the consequence of decreasing DTOC and increasing chlorophyll-a concentration. The primary production to bacterioplankton production ratio decreases with increasing allochthonous DOC concentration (Jansson *et al.* 2000).

Microfiltrators are replaced by macrofiltrators in the direction of decreasing DTOC also in Scotland. As to cladocerans, *Diaphanosoma brachyurum* is replaced by *Daphnia rosea*, which is replaced by *Holopedium gibberum* (Table 3). From *Diaphanosoma* over *Daphnia* to *Holopedium*, the filter mesh size increases and the efficiency of feeding on bacteria decreases (Geller & Müller 1981; Hessen 1985; Hessen *et al.* 1989). Smaller (Bartoš 1959) rotifers *Keratella cochlearis* and *Polyarthra remata* prefer higher DTOC than bigger rotifers *Keratella hiemalis* and *Polyarthra dolichoptera* both in Scotland and the lakes of the Tatra Mts. and the Alps (Table 3). Because they are smaller species, they may also prefer smaller prey, and they may possibly be microfiltrators. Similarly, *Conochilus unicornis* is a smaller species (Bartoš 1959) and prefers higher DTOC than *C. hippocrepis* in Scotland (Table 3). The rotifers *Keratella cochlearis* and *Conochilus unicornis* are known to efficiently ingest bacteria (Bogdan & Gilbert 1987).

Some species are replaced by other species with pH and depth both increasing, while DTOC and chlorophyll-a both decreasing (Table 3). Thus, the ratio of chlorophyll-a and DTOC probably little varies in this direction and these species may differ in other properties than in their food size preference. It may be food quality, because reduced light with increasing depth may cause a change from low (high C:P ratio) to high quality (low C:P ratio) food. Increasing intensity of light increases carbon to phosphorus (C:P) ratio of phytoplankton (Hessen *et al.* 2002; Urabe *et al.* 2002; Hessen 2008). So, calanoids form a series in the direction of pH and depth both increasing in Scotland, in order *Mixodiaptomus laciniatus*, *Eudiaptomus gracilis*, and *Arctodiaptomus laticeps* (Table 3). Food quality may increase in this direction. To avoid low quality food, *M. laciniatus* may have other mode of feeding than *A. laticeps*, selecting only high quality particles. There is also a difference in their life cycles: *A. alpinus* is scarce in the winter and more abundant in the summer, *E. gracilis* has both summer and winter generations, and *M. laciniatus* reproduces in the winter, while it is absent in the summer (Einsle 1993). *A. alpinus* has one population peak during the ice-free period, whereas *M. laciniatus* is present year round in the alpine Seehornsee Lake in Austria (Luger *et al.* 2000). In the Tatra Mts., the distribution of other species of the genera *Mixodiaptomus* and *Arctodiaptomus* is similar to the distribution of these genera in Scotland. In the Tatra Mts., *Mixodiaptomus tetricus* (Wierzejski, 1883) lives in small acidic lakes with fluctuating water level in the altitudinal zone of dwarf mountain pine, which are rich in organic matter (Brtek 1977). *A. alpinus* lives there in the zone of meadows with lower export of organic matter. In the Tatra Mts. and the Alps, the cyclopoid copepod *Acanthocyclops vernalis* is replaced by the cyclopoid copepod *Cyclops abyssorum* in the direction of pH and depth both increasing (Table 3). *A. vernalis* is smaller than *C. abyssorum* (Maier 1994; Hopp & Maier 2005a). In *Cyclops abyssorum* and *C. vicinus*, the duration of the postembryonic development increases with decreasing food concentration, whereas smaller species *Mesocyclops leuckarti*,

Acanthocyclops robustus, and *Thermocyclops crassus* are less affected (Hopp & Maier 2005b). Similarly, they may grow better on low quality food. In Scotland, the number of pelagic rotifer taxa increased in the direction of increasing pH and depth (Table 3). It may be caused by increasing food quality. Further, the number of the taxa increased with DTOC, which may be caused by increasing bacterioplankton production.

Three species were found to resist fish predation in the Tatra Mts. and the Alps: the cyclopoid copepod *Cyclops abyssorum*, and the cladocerans *Bosmina longirostris* and *Daphnia rosea* (Table 4). *C. abyssorum* is known to be not seriously preyed upon by fish except egg-carrying females, whose eggs pass viable through fish guts (Gliwicz & Rowan 1984). *B. longirostris* and *D. rosea* are resistant thanks to their small size (Lynch 1979; Knapp *et al.* 2001; Knapp *et al.* 2005).

Tab 4: Number of occurrences of the zooplankton species in the Tatra Mts. and the Alps in lakes with and without fish. Only occurrences in quantitative samples with abundances higher than 0.05 dm^{-3} are included.

	fish present	fish absent
<i>Bosmina longirostris</i>	5	0
<i>Daphnia galeata</i>	1	1
<i>Daphnia pulicaria</i>	1	8
<i>Daphnia rosea</i>	5	3
<i>Holopedium gibberum</i>	1	1
<i>Acanthocyclops vernalis</i>	1	3
<i>Cyclops abyssorum</i>	16	14
<i>Arctodiaptomus alpinus</i>	3	12

Concluding, I have shown that the zooplankton composition is determined by four variables pH, depth, chlorophyll-a and DTOC. Because DTOC and chlorophyll-a concentrations often correlate with the abiotic variables pH and depth, DTOC and chlorophyll-a may sometimes be omitted and zooplankton composition may be successfully predicted using only pH and depth. However, introduction of fish induces changes of zooplankton composition together with an increase of chlorophyll-a and DTOC concentrations. These changes are not dependent on abiotic variables and the prediction of zooplankton composition using only pH and depth fails.

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