Limnologica 42 (2012) 65–71

Contents lists available at SciVerse ScienceDirect

Limnologica

journal homepage: www.elsevier.de/limno

Distribution of benthic microcrustaceans along a water depth gradient in an Austrian Alpine lake – Sedimentary evidence for niche separation

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ARTICLE INFO

Article history:
Received 23 May 2011
Received in revised form 18 August 2011
Accepted 27 August 2011

Keywords:
Cladocera
Community thresholds
Habitat specificity
Mountain lakes
Paleolimnology

ABSTRACT

Distribution of benthic microcrustacean (Crustacea: Cladocera) was investigated with paleolimnological approach by using their fossil surface sediment assemblages within a thermally extreme lake in the Niedere Tauern, Austrian Alps. The results from 20 surface sediment samples suggested that the spatial distribution of chydorids is clearly heterogeneous along the water depth gradient (1.8–6.1 m); *Alona quadrangularis* dominated in shallow (warm, minerogenic) habitats, *Chydorus sphaericus*-type succeeded at intermediate depths, and *Alona affinis* dominated in deep (cold, organic) sites. Apparently, these benthic cladocerans exhibit clear habitat and resource segregation. The distributional patterns revealed local community thresholds at approximately 2.5 and 4.5 m water depths and these thresholds were likely to be forced by variances in habitat quality (minerogenic–organic), food resources (periphyton/detritus), thermal properties (warm–cold), and UV-exposure (high–low). The results emphasize the usability of the paleolimnological approach in distributional investigations and its applicability in providing information on species–environmental relationships for environmental change evaluations and paleoecological interpretations.

Introduction

Environmental variation at different geographical scales has a major influence on local species assemblages, as species dispersal abilities, biotic interactions, and adaptation potential to local environmental conditions affect species distributional patterns (Lavergne et al. 2010; White et al. 2010). Environmentally generated heterogeneous species distribution is evident as ecological thresholds, which can be characterized as points at which there is an abrupt change in a property or phenomenon in an ecosystem, e.g. maintenance of particular species (Groffman et al. 2006). In freshwater lakes, which are severely affected by anthropogenic environmental changes, such as climate warming and pollution (Brönmark and Hansson 2002; Heino et al. 2009), the identification and evaluation of such thresholds have become explicitly more important during the period of major anthropogenic environmental perturbations because they can be valuable in global change assessments, environmental quality classifications, and in biodiversity conservation efforts (Catalan et al. 2009).

Paleolimnological approach (Smol 2008) for examining fossil biotic assemblages in lakes' surface sediments provide a cost-efficient and quick way to estimate modern species distribution patterns and diversity of aquatic organisms preserving as fossils. Despite the fact that only a small fraction of aquatic organisms preserve as fossil remains in lake sediments, research on surface sediment assemblages of such organisms has become an important and valid method in contemporary ecological studies (Bjerring et al. 2009; Catalan et al. 2009; Brancelj et al. 2009). In addition to using paleolimnological approach in determining wide geographical distribution patterns (Bjerring et al. 2009; Brancelj et al. 2009; Catalan et al. 2009), it has recently been utilized in identifying patterns at local-scale too, unraveling habitat-specificity of various organisms (Laird et al. 2010; Luoto 2010; Nevalainen 2011). Local species assemblages and site-specific thresholds, however, are not governed solely by local processes, as biogeographical processes have a major contribution (Bilton et al. 2001).

Distributional borders of many organisms, such as mountain lakes located at remote high altitude zones, can be regarded as sensitive indicators of environmental change (Marchetto and Rogora 2004). It is important to evaluate the present species distribution and biodiversity at such sites, because they are likely to respond fast and abruptly to the modern climate warming (Holt and Keitt 2005; Parker et al. 2008). In the current study, with an objective to determine local patterns of Cladocera distribution and to examine local community thresholds within a homogeneous Alpine lake basin, fossil Cladocera from a set of surface sediment samples along a water depth gradient were analyzed. It was hypothesized, based

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doi:10.1016/j.limno.2011.08.003

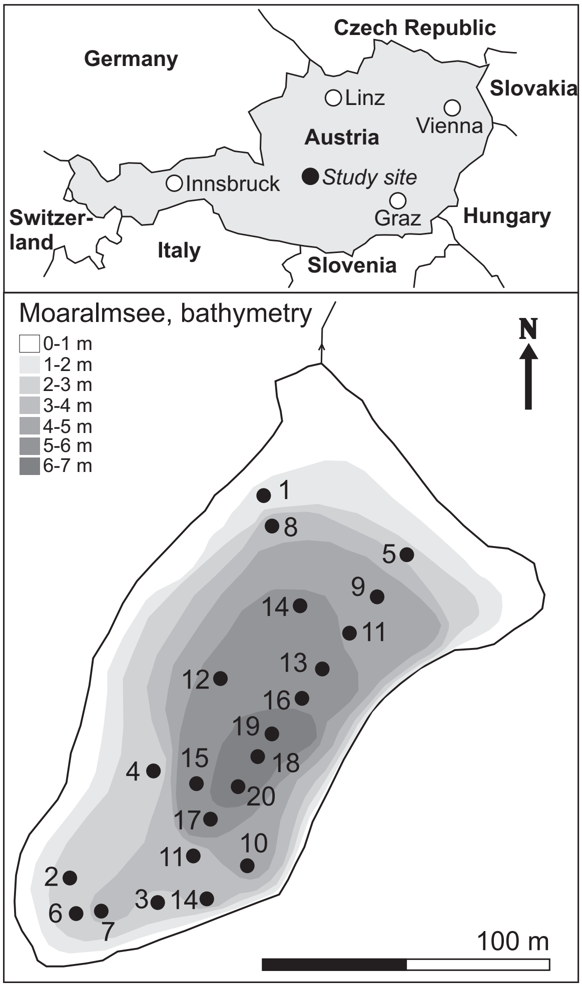

Fig. 1. Location of Lake Moaralmsee in the Niedere Tauern region of the Austrian Alps and distribution of the examined surface sediment samples along the depth gradient within the basin.

on previous results from a limnologically heterogeneous basin (Nevalainen 2011), that no distinct distributional features could be recognized and that no clear site-specific thresholds could be determined due to uniform habitats and environmental extremity (Thompson et al. 2005) in this Alpine lake basin.

Study site

Lake Moaralmsee (47°21.5′N, 13°47.5′E) is located at an altitude of 1825 m a.s.l. in the Niedere Tauern region of the Eastern Alps in Austria (Fig. 1). The lake was chosen for the present study because as a remote high altitude mountain lake it can be regarded to be close to pristine state, although it is most likely affected by long-range atmospheric transport and deposition of pollutants (Marchetto and Rogora 2004), and have homogeneous benthic habitats without any effects of dense aquatic vegetation or river inflows. In addition, the lake is shallow (max. depth 6.1 m, Fig. 1), which reduces thermal stratification of the water column (Fig. 2). Therefore, the effects of water depth and interconnected environmental parameters on benthic fauna can be considered to be maximized in this lake. The lake basin has a maximum length of 232 m, maximum width of 127 m, and maximum depth of 6.1 m (Fig. 1).

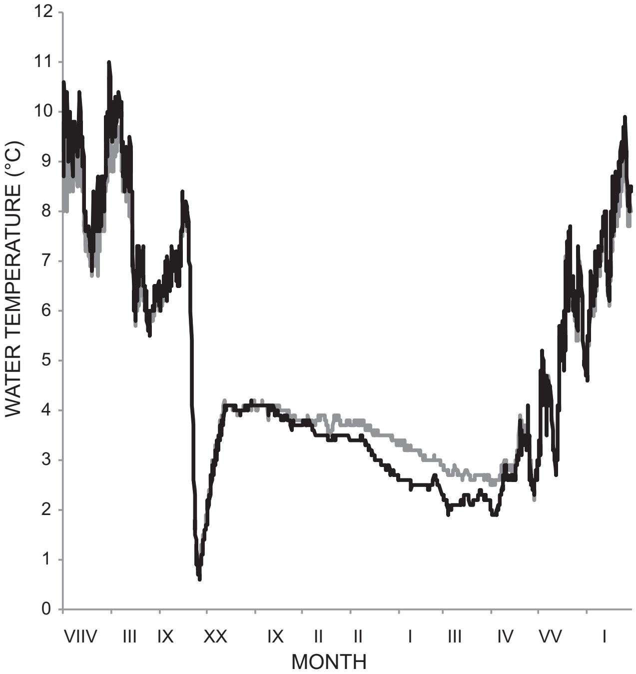

Fig. 2. Annual record (23 July, 2009 to 21 July, 2010) of water temperature at depths of ~1 m (black line) and 3 m (gray line) in Lake Moaralmsee, measured at 4-hour intervals.

Vertical limnological variability within the water column (Table 1), performed using a multiparameter sonde 6600V2 (YSI Inc., Yellow Springs, OH, USA), indicated that Lake Moaralmsee is oligotrophic (average chlorophyll concentration in the water column: 0.27 RFU) and has a pH of ~8 (Table 1). The secchi depth (August 2010) was 6.1 m, down to the deepest location in the lake. The lake can be regarded as an ultra-sensitive high altitude mountain lake because it is unusually cold compared to other lakes at similar altitude; its summer water temperatures are generally 6–7 °C cooler. This fact is caused by its catchment morphology, which causes extensive cold water inflow from snowmelt and groundwater during the summer (Thompson et al. 2005). The annual water temperature measurements (July 2009 to July 2010) from water depths of ~1 and 3 m were measured with 4-hour intervals using 8-bit MINILOG-TR thermistors (Vemco Ltd., Halifax, Nova Scotia, Canada) and the measurements indicated that water temperature hardly exceeds +10 °C even during the summer months (Fig. 2). Although water temperature range during 2009–2010 at depths of ~1 and 3 m in the lake showed no distinct

Table 1
Vertical limnological variation in the water column (0–6 m) of Lake Moaralmsee in July 2010.

Measurement depth	(m)	0	1	2	3	4	5	6
Temperature	(°C)	11.7	11.7	10.0	8.2	7.7	7.2	7.2
Conductivity	(μS cm^{-1})	27	27	28	27	27	27	27
pH	(units)	8.1	8.2	8.4	8.3	8.2	8.0	8.0
Chlorophyll a	(RFU)	0.1	0.2	0.3	0.3	0.3	0.3	0.4
Phycocyanin	(RFU)	0.2	0.1	0.1	0.1	0.1	0.1	0.1
Dissolved oxygen	(mg l^{-1})	11.0	10.9	10.9	11.5	11.4	11.3	11.3
Oxygen saturation	(%)	101.7	100.1	96.9	96.5	95.6	94.2	93.6

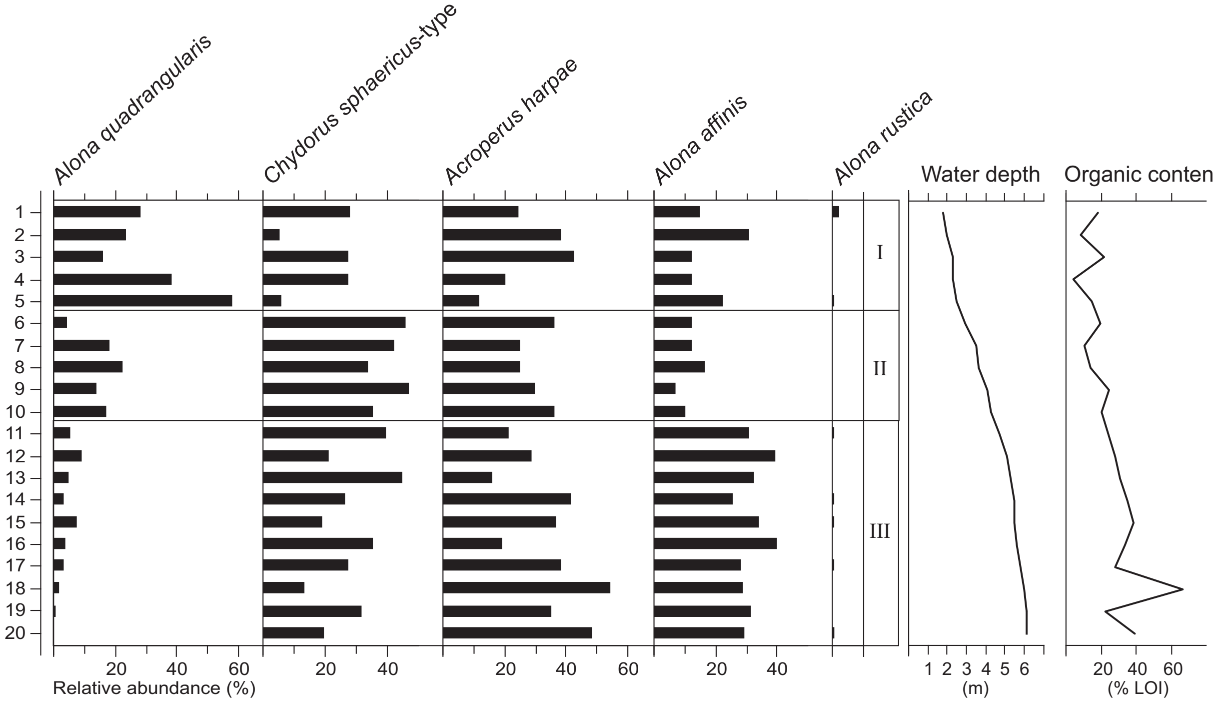

Fig. 3. Relative abundance of Chydoridae in the surface sediments from Lake Moaralmsee along the water depth and organic content gradients. The horizontal lines indicate local community thresholds and the roman numerals (I–III) illustrate sample groups according to the water depth (<2.5 m, 2.5–4.5 m, >4.5 m), which were separated by cluster and similarity analyses.

thermal stratification during summer months, the multisonde measurements from July indicated a difference of ~4 °C between epi- and hypolimnetic waters (Table 1).

Methods

A total of 31 surface sediment samples (topmost 0–1 cm) from Lake Moaralmsee were collected from a small boat with a Kajak gravity corer (August 2010), and the sampling sites were distributed along a water depth gradient (up to 6 m). The water depth was measured at each sampling site from a boat during the sediment sampling. The retrieved sediment samples were stored in plastic bags at +4 °C in a cold room and prepared later for fossil Cladocera analysis following the methods described in Szeroczyńska and Sarmaja-Korjonen (2007). In the laboratory, the samples were heated in 10% KOH for approximately 15–20 min and washed and sieved through a 51-μm mesh under running tap water. The residues were then centrifuged for approximately 10 min to concentrate the fossil cladoceran remains and dyed with a few drops of glycerol–safranine.

The prepared samples were mounted on microscopic slides and analyzed for their cladoceran species composition under a Leitz Diaplan light microscope with magnifications between 100- and 400-times. Minimum of 100 cladoceran individuals (Kurek et al. 2010), enumerated as the number of most abundant body part (carapaces, headshields, postabdomens, ephippia), were identified following the identification key by Szeroczyńska and Sarmaja-Korjonen (2007). Only 20 of the 31 samples contained enough fossil cladoceran remains (Fig. 1), while the remnants were extremely scarce in the 11 remaining samples.

The organic content of the sediment, measured as loss-on-ignition (LOI, Dean 1974), was determined from 10 to 12 g wet sediment samples, which were first dried at 105 °C for 12 h and then ignited in an oven at 550 °C for 2 h. The LOI analysis could not be performed with the sample #11 (Fig. 1) because there was not enough sediment material available.

To characterize cladoceran communities and community thresholds, constrained cluster analysis (unweighted pair-group average, UPGMA), using Euclidean similarity measure, was applied to the cladoceran data (relative abundances). These thresholds were further validated with one-way analysis of similarity (ANOSIM), which used the Euclidean distance. Cluster and similarity analyses were performed using the software PAST 2.08 (Hammer et al. 2001). Furthermore, generalized additive modeling (GAM) was applied to the cladoceran relative abundances and water depth data to identify significant ($p \leq 0.05$) relationships between taxon distribution and water depth in the data set. Poisson distribution and total maximum value of the data were used in the individual GAM settings. The GAM models were produced with CanoDraw, a component of the program CANOCO 4.5 (ter Braak and Šmilauer 2002).

Results

The water depth at the 20 sampling sites ranged between 1.8 and 6.1 m and LOI of the 19 samples (#11 omitted) varied between 4.4 and 66.7% in Lake Moaralmsee (Figs. 1 and 3), having a strong positive correlation ($R = 0.74$, $p < 0.001$). A total of five species of Chydoridae from three different genera were recovered from the 20 surface sediment samples (Fig. 3); *Acroperus harpae* (Baird, 1935) was most abundant (average proportion 32%), followed by *Chydorus sphaericus*-type (29.3%), *Alona affinis* (Leydig, 1860) (24%), *Alona quadrangularis* (Müller, 1785) (14.4%), and *Alona rustica* Scott, 1895 (0.4%). In addition, two *Daphnia pulex*-type ephippia were encountered (in samples #1 and #17), but these were not included into the further analyses (see discussion).

The cluster analysis separated three major sample groups according to cladoceran communities that corresponded to water level thresholds; samples 1–5 (<2.5 m), samples 6–10 (2.5–4.5 m),

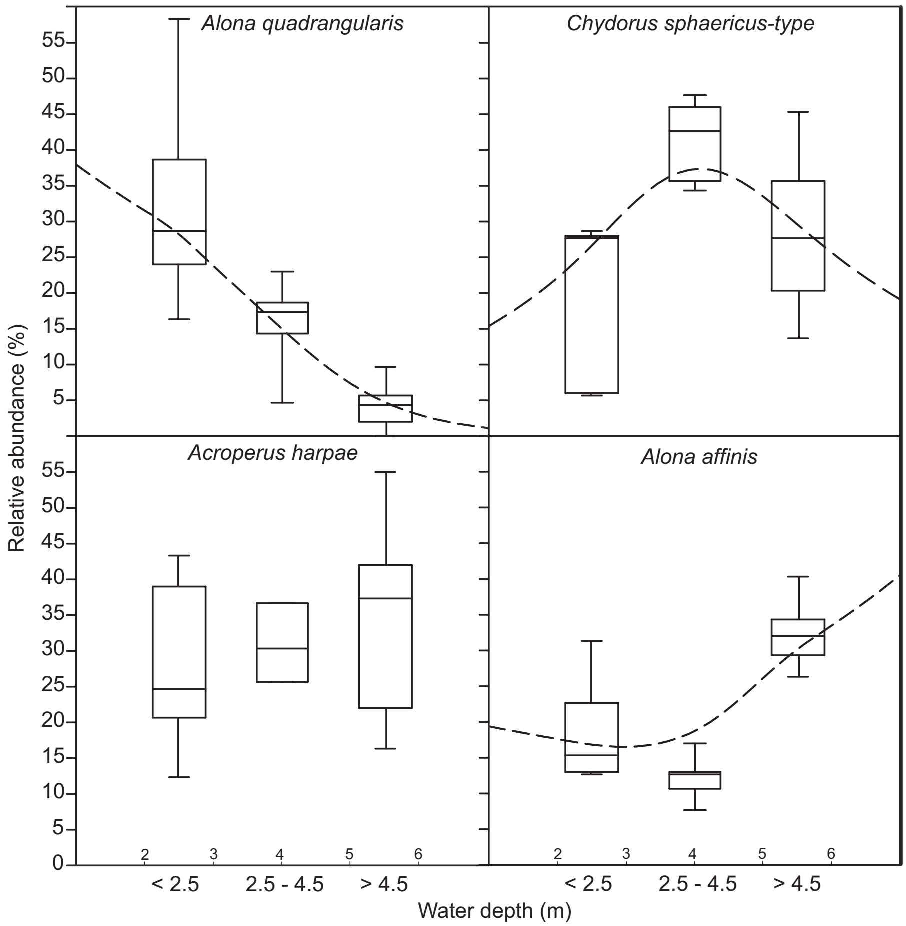

Fig. 4. Box plots summarizing the proportional abundance of the four most common chydorid taxa along the three sample groups (illustrated in Fig. 3) and significant ($p \leq 0.05$) species response curves (dashed lines) to water depth fitted with generalized additive models (GAM) from the Lake Moaralmsee data. The box plots indicate the median (horizontal line), the 25–75 percent quartiles (box), and the minimal and maximal values (short horizontal lines).

and samples 11–20 (>4.5 m) (Fig. 3). The significant separation between these sample groups was also supported by the ANOSIM results ($R = 0.59$, $p < 0.001$) suggesting dissimilarities between the groups. *A. harpae* occurred steadily in all samples, *A. quadrangularis* dominated in the shallowest sample group, *C. sphaericus*-type was most abundant in the samples from intermediate depths, and *A. affinis* occurred most frequently in the deepest samples (Fig. 3). The community-based sample groups were used further for box plotting, which summarized the different abundances of the four most common taxa at each depth cluster (Fig. 4).

According to GAMs *A. quadrangularis* ($F = 21.20$, $p < 0.001$), *C. sphaericus*-type ($F = 4.09$, $p = 0.036$), and *A. affinis* ($F = 8.85$, $p = 0.002$) had significant ($p \leq 0.05$) relationship to water depth and taxon response curves to water depth were generated for these taxa (Fig. 4). The taxon response curves indicated that *A. quadrangularis* had low water depth optimum, *C. sphaericus*-type intermediate optimum, and *A. affinis* high water depth optimum. The response curves also show that all these taxa had wide tolerance for water depth.

Discussion

Diversity and distribution

High altitude and latitude lakes are usually poor in their species assemblages due to extremely harsh physical characteristics, because low annual and summer temperature, short ice-free period, and low habitat diversity restrict the number of successful colonizers. Accordingly, also chemical environment, e.g. low nutrient status and conductivity (Table 1), in high latitude and altitude lakes may inhibit species richness. In the current study, only five cladoceran taxa (Fig. 3), all belonging to the benthic family Chydoridae, were recovered from the surface sediment samples across the basin of Lake Moaralmsee. In addition, two *Daphnia* ephippia were recovered from the samples, but according to contemporary zooplankton samples from summer 2010 (R. Kurmayer, pers. comm.), *Daphnia* was not present in the lake. Thus, is likely that the ephippia found were due to passive dispersal and have not resulted in colonization. This extremely low cladoceran species richness, restricted only to benthic cladocerans, is comparable to the results of Brancelj et al. (2009), who studied nearly 300 cold lakes (high altitude and latitude) across Europe and found on average four cladoceran taxa at European high altitude lakes. Lake Moaralmsee is situated at a high altitude, it has a small surface area, and it is oligotrophic; these factors inhibit the capacity to support more diverse communities (Fryer 1985; Brancelj et al. 2009).

Furthermore, Lake Moaralmsee is unusual in its thermal characters (Thompson et al. 2005, Fig. 2, Table 1), being extremely cold (summer temperature generally <10 °C) due to its catchment characteristics (see study site description). Since temperature is extremely important in the succession of aquatic vegetation and niche development, which are important for cladocerans (Rautio 1998) and for promoting phytoplankton success, the low temperatures have most likely prevented diverse succession of niches reducing cladoceran species richness. According to field observations, a well-developed aquatic macrophyte zone is completely absent from the lake and since macrophytes and habitat complexity are generally considered to boost chydorid species diversity (Whiteside and Harmsworth 1967; Rautio 1998; Nevalainen 2010), it seems obvious that the chydorid species richness is extremely low. Accordingly, cold alpine lakes are primarily inhabited by a few cold-tolerant cladoceran taxa (Kamenik et al. 2007; Brancelj et al. 2009). In addition to low temperatures, high altitude location and high transparency of the lake causes higher UV-radiation exposure, which has detrimental effects on species diversity in general (Sommaruga 2001; Rose et al. 2009).

The current results (Figs. 3 and 4) suggested, controversially to what was hypothesized, that there was high heterogeneity in surface sediment cladoceran communities across the water depth gradient in Lake Moaralmsee. Although considerable spatiotemporal variation is expected in Cladocera on a lake-specific scale (Tremel et al. 2000; Örnólfsdóttir and Einarsson 2004), paleolimnological approach in Cladocera research has relied on the fact that one surface sediment sample from the center of a lake basin are representative of local species assemblages. However, recent studies on intrabasin variability of biotic species assemblages (Laird et al. 2010; Luoto 2010) have shown the changeability of species compositions across water depth gradients. The diverse intralake distribution of cladocerans in surface sediment samples, forced by changes in sampling site depth, has also been evidenced previously (Kattel et al. 2007; Nevalainen 2011) and in overall, together with the Moaralmsee results (Figs. 3 and 4), they suggest that cladoceran remains are deposited post-mortem or after moulting in proximity of their original habitats. This perspective may thus allow distinguishing species' habitat-specificities and, accordingly, provide valuable autecological implications for ecological and paleoecological interpretations.

There was an evident separation in the percentage abundance and distribution of *A. quadrangularis*, *A. affinis*, and *C. sphaericus*-type (Figs. 3 and 4), suggesting a clear niche separation of these benthic taxa. In Lake Moaralmsee, *A. quadrangularis* showed strong preference to shallow habitats and had maximum occurrence (58.3%) at the depth of 2.5 m (sample #5), whereas *A. affinis* was related to deep sites (max. 40.2% at 5.6 m depth in sample #16). *C. sphaericus*-type appeared to succeed mostly at intermediate depths (2.5–4.5 m) and had a maximum of 47.6% at a depth of 4.1 m. These distribution patterns were further reflected into the shapes of the generated response curves (Fig. 4), showing clearly the modeled preference of *A. quadrangularis* to shallow, *C. sphaericus*-type to intermediate, and *A. affinis* to deep habitats in Lake Moaralmsee. Following the change in the water depth in Lake Moaralmsee, the quality of substrata changed from minerogenic (shallow habitats) to organic (deep habitats) and, therefore, it is likely that chydorids do not respond to water depth *per se*, but diverse environmental gradients associated to bottom-up and top-down controls along the water column. Of these controls, bottom substrata (minerogenic/organic), food type (benthic algae/detritus), and fish predation may vary significantly at different water depths and along horizontal littoral-offshore transect (Amsinck et al. 2006; Sweetman and Smol 2006; Nevalainen 2011). The two *Alona* species are known to be strongly associated to bottom substrata, both minerogenic and organic, and to show preference for a true benthic bottom-dwelling lifestyle (Fryer 1968; Flössner 2000).

The two abundant *Alona* species showed contradictory depth optima in Lake Moaralmsee (Fig. 4) than in a previous study from a boreal lake in Finland (Nevalainen 2011). In the boreal lake, *A. quadrangularis* showed a distinct preference for deep habitats (~5 m) with organic sediment and *A. affinis* succeeded in shallow (~2 m) vegetative habitats. These opposite depth and substrate preference in two different geographical regions suggest that chydorids are highly tolerant to environmental gradients in water depth and substrate, and exhibit patterns of local adaptation in niche segregation. This seems rational, because local limnological conditions, e.g. in temperature and primary production, are highly variable and dependent on the larger-scaled geographical location. Although chydorids are generally thought to form a compact ecological entity, associated to lakes' littoral zone, it is evident from the literature (Fryer 1968; Kotov 2006; Flössner 2000; Van Damme and Dumont 2010) and from the present results (Figs. 3 and 4) that individual species are highly segregated according to their habitats.

Community thresholds

The cluster analysis, further supported by the ANOSIM, recognized two major thresholds in the community assemblages according to the water depth at the sampling sites in Lake Moaralmsee (Fig. 3); at ~2.5 m and ~4.5 m depths. These thresholds separated communities dominated by *A. quadrangularis*, *C. sphaericus*-type, or *A. affinis*, which apparently have different environmental optima according to water depth in Lake Moaralmsee (Fig. 4). In addition to sediments' organic content, which correlated strongly with water depth in Lake Moaralmsee (Fig. 3) and is indicative of substrate type and possibly different types of benthic food resources (epiphyton/detritus), there exist several environmental and limnological factors associated with water depth gradient that may affect the local distribution of species. The limnological measurements of the water column (Table 1) in Lake Moaralmsee showed that primarily temperature, and to lesser extent primary production (chlorophyll a), vary along the water depth and may contribute to the observed thresholds (Fig. 3).

Of the limnological properties measured (Table 1), water temperature is known to be an important factor in determining cladoceran community composition at a large geographical scale (Korhola 1999; Kamenik et al. 2007; Bjerring et al. 2009). This is due to the fact that temperature directly interacts in reducing or enhancing metabolism and reproductive rates (Gillooly and Dodson 2000; de Eyto and Irvine 2001) and that it has multiple indirect effects on cladoceran habitats altering aquatic vegetation patterns, sediment properties, and food resources. Furthermore, temperature primarily controls the seasonal succession of cladoceran reproductive modes (Frey 1982); under favorable temperature cladoceran populations can multiply rapidly or reproduce only a few generations under low temperatures (Green 1966; Poulsen 1940). Although there is very little direct knowledge about the taxon specific temperature optima and tolerances of chydorids, all chydorid taxa (Fig. 3) occurring in Lake Moaralmsee are widely characterized as cold-tolerant (Harmsworth 1968; Bigler et al. 2006; Brancelj et al. 2009) but most likely exhibit variance in their optimal temperature conditions. The chydorid community thresholds occurred approximately at 2.5 and 4.5 m depth in Lake Moaralmsee (Fig. 3). The annual temperature measurements (Fig. 2) showed that there is a difference of roughly 1–2 °C between 1 and 3 m depth and the measurement performed in July (Table 1), the warmest month, suggested a difference of ~3 °C. The water temperature differences are higher when going deeper in the water column and Table 1 suggested a difference ~4 °C between shallow and deep waters. Accordingly, local temperature ranges along the water depth gradient may be significant for the community patterns observed here (Fig. 3).

As stated above, a major physical component in influencing biological functions in alpine lakes is solar UV-radiation (Sommaruga 2001; Rose et al. 2009) and this is due to thinner atmosphere and higher water transparency than in low-land lakes. UV-exposure in transparent alpine lakes is strongly related to water depth (Rose et al. 2009), generally decreasing with increasing water depth. Accordingly, it is regarded that shallow littoral habitats (<2.5 m) are more exposed to UV-radiation than deeper benthic habitats (>4.5 m) and therefore the observed thresholds may have been driven by UV-attenuation and taxon specific UV-tolerances. In cladoceran zooplankton, UV-exposure has been shown to have detrimental effects (Rautio and Korhola 2002; Rautio and Tartarotti 2010), but UV-tolerance has not thus far been investigated with benthic cladocerans. However, Vinebrooke and Leavitt (1999) suggested that littoral benthic communities of motile invertebrates responded to UV-exposure by seeking physical refuge among sediments. Despite the ability to seek refuge among the benthic substrata, it seems likely that also chydorid taxa show different tolerances to UV-radiation and are able to adapt to high exposure via pigmentation in alpine lakes (Manca et al. 1998).

Conclusion

As apparent from the current results benthic cladocerans exhibit clear habitat and resource segregation and therefore should not be considered to form a littoral ecological entity. Unraveled here, *A. quadrangularis* preferred shallow (warmer) and minerogenic habitats and *A. affinis* favored deep (colder) habitats. Although paleolimnological approach in examining distributional ranges of aquatic organisms is well established at wide geographical gradients, this study emphasizes the usability of the approach also at the local-scale. Not only can intralake investigations provide valuable autecological information of individual taxa, which can be further used in paleoecological interpretations and as indicators of environmental change, they may contribute in describing local ecological thresholds.

Acknowledgements

Tomi P. Luoto, Johann Knoll, Rainer Kurmayer, and Guntram Christiansen are thanked for their assistance with the fieldwork. Additionally, J. Knoll is acknowledged for preparing the Cladocera samples and performing the LOI analysis and T.P. Luoto is thanked for valuable remarks on the manuscript. This work is a contribution to the DETECTIVE (DEcadal deTECTion of biodIVErsity in alpine lakes) project. Constructive comments of two anonymous reviewers improved the quality of the manuscript and are thanked for.

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