*J. Limnol.*, 66(2): 160-169, 2007

# Freshwater molluscs in mountain lakes of the Eastern Alps (Austria): relationship between environmental variables and lake colonization

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*ABSTRACT*

*This study examines the colonization of twelve mountain lakes of the Central Alps in Austria by freshwater gastropods and bivalves. Of the twelve lakes studied, seven are in the montane vegetation level (600 – 1400 m), and five are subalpine (1400 – 2200 m). At each lake, species diversity and abundance was measured by taking 10 samples along the shore, for each parameter. In addition to recording of molluscs, I measured 12 environmental factors, namely, altitude, water temperature, shading, water pH, conductivity, oxygen saturation, biological oxygen demand after 5 days ($BOD_5$), nitrate concentration, total hardness, mean grain size of the bottom substrate, and percentage of submerged vegetation and algal cover, at each sample site. I then used multivariate statistical analysis, specifically Canonical Correspondence Analysis, to detect any relationships between these physico-chemical factors and the distribution of molluscs.*

*The study detected a total of 13 mollusc, 8 gastropod and 5 bivalve species in the lakes, with lakes at the montane vegetation level generally exhibiting higher species diversities than lakes at the subalpine vegetation level.* Pisidium casertanum, Galba truncatula**,** P. subtruncatum, *and* Radix balthica *exhibited the highest species abundance, while* Acroloxus lacustris *and* Musculium lacustre, *both typical of lower altitudes, were very rare. Multivariate analysis revealed an important influence of shading, altitude, nitrate, $BOD_5$, oxygen saturation, substrate grain-size and submerged vegetation on the distribution patterns of most mollusc species. In contrast, the distribution patterns of* P. subtruncatum *and* P. obtusale *were highly independent of the measured environmental factors.*

*Key words: Mountain lake, spatial distribution, molluscs, abundance, Canonical Correspondence Analysis*

## 1. INTRODUCTION

In recent decades, scientists have become increasingly interested in Alpine mountain lakes, leading to research covering a wide range of chemical, physical, and biological aspects (e.g. Köck *et al*. 1995; Sommaruga *et al*. 1999; Sommaruga 2001; Lami & Boggero 2006). Sperling (1975) and Frank (1992, 1996) carried out the first significant investigations of terrestrial and aquatic molluscs in the inner-Alpine region, and provided a preliminary impression of the distribution of the malacofauna in various biotopes of the Austrian Alps. At the same time, Turner *et al*. (1998) conducted a more comprehensive study in the Swiss Alps, and produced partly detailed distribution maps of all gastropod and bivalve species recorded in Switzerland and Liechtenstein. This atlas of the Swiss malacofauna, and its spatial distribution in the Western Alps, still represents a quantum leap in Central European malacological research; no such publication is available, or anticipated, for the Eastern Alps.

Scientific studies of the distribution of freshwater molluscs in the inner-Alpine waters of Austria are still very scarce (e.g. Kuiper 1974; Sperling 1975; Patzner 1995; Sturm 2003, 2004), for two main reasons. First, colonization of mountain lakes and brooks is often limited to the very few species that can tolerate extreme environmental conditions. Second, abundances of such highly tolerant species in their aquatic biotopes are usually very low, which significantly complicates both their detection and quantification. Further, investigations which have attempted to elucidate a possible relationship between distribution patterns of aquatic molluscs and environmental conditions have only been within a close compass (e.g. Sturm 2004, 2005), and have used the mathematical concepts of linear regression as well as Generalized Linear and Generalized Additive Models (GLM and GAM; Hosmer & Lemeshow 2000). The practice of only recording mollusc abundances semi-quantitatively, in defined frequency classes (e.g. class 1 for rare or individual occurrence to class 4 for occurrence in masses; Patzner 1994) has shipwrecked more comprehensive ecological studies. These frequency data were not appropriate for multivariate correspondence analysis, which examines species tolerances over a set of environmental factors (Ter Braak 1986).

This study has two objectives. First, the present work aims to quantitatively study malacological colonization of 12 mountain lakes positioned in the Centrals Alps of Austria (Counties of Salzburg and Styria), and measure environmental factors at each sampling site. Second, the study seeks to use a multivariate ordination technique (Canonical Correspondence Analysis) to decode possible relationships between mollusc distribution patterns and environmental factors. Canonical

Correspondence Analysis permits complex calculations to be displayed in rather simple two-dimensional graphs. This work should advance our knowledge of the colonization of the Eastern Alps by freshwater molluscs.

## 2. MATERIALS AND METHODS

### 2.1. Study site and date of sampling

All 12 of the investigated lakes are located in the Central Alps of Austria (County of Salzburg and Styria), and three of these lakes are within the core zone of the Hohe Tauern National Park (Fig. 1). The altitudes of the mountain lakes range from 1,056 m (Kreuzensee) to 2,170 m (Kratzenbergsee), thus varying between the upper montane and subalpine vegetation zone. All of the lakes are of glacial origin with variable substrate grain-size and content of submerged vegetation (Tab. 1), except for Hintersee, which was formed by a landslip and Lower Bockhartsee and Lower Rotgüldensee, which are both reservoirs dammed for local electricity production. Surrounding vegetation mainly depends upon the geographic position of the lakes, and therefore ranges from diverse grasses, bushes and deciduous trees at lower altitudes to spruce, larch and cembra pines at the subalpine level. At each of the studied lakes, I selected 10 sample points, evenly distributed along the lake shore, for mollusc sampling and measurement of environmental factors, resulting in a total of 120 samples.

Field work occurred from September 2000 to August 2001 during periods of warm weather and decreased rainfall. Sampling and measurement activity along the shore of the lakes took place from late morning ($10^{00}$) to the early evening ($16^{00}$). I strove to have constant weather conditions during the investigation of a single lake.

### 2.2. Recording of aquatic molluscs and environmental factors

In order to sample and count aquatic molluscs, I placed a 0.5 x 0.5 m frequency frame at the sample points, respectively, and recorded all molluscs within the frame. At each point, I repeated this procedure four times to cover a total sampling area of 1 m$^2$. I followed the sampling strategy of Patzner (1994) and Glöer & Meier-Brook (2003), which included the investigation plants and stones for possible colonization by molluscs

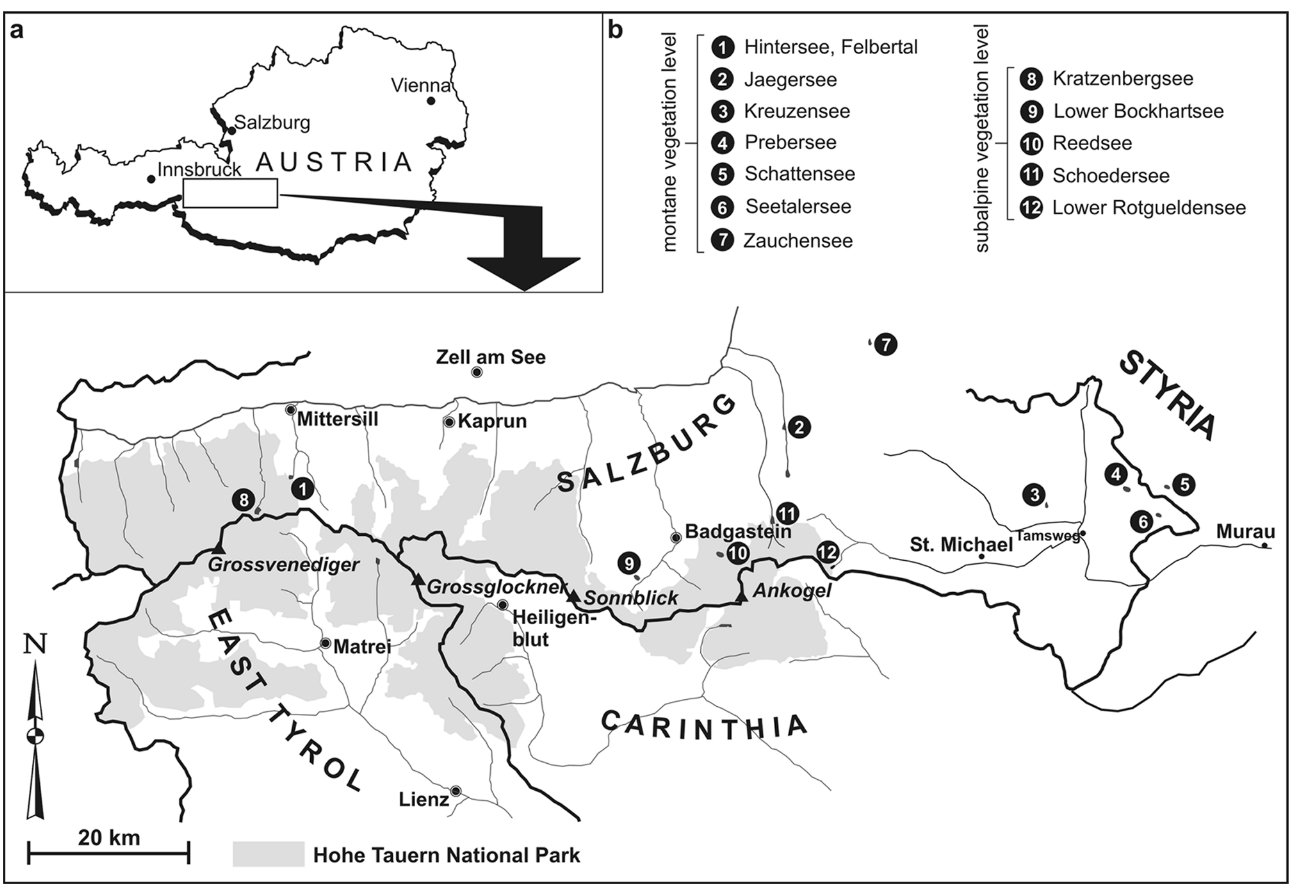


**Fig. 1.** Map illustrating the geographic position of the investigated mountain lakes within the Eastern Alps. Seven lakes belong to the montane vegetation zone (600 – 1400 m) and five lakes to the subalpine vegetation zone (1400 – 2200 m).

**Tab. 1.** Geographic and morphological characteristics of the investigated lakes.

**Brief characterization of the studied lakes**

| Lake | | Geogr. pos./ Altitude | Size, Depth | Vegetation | Ground substrate | Code |
|---|---|---|---|---|---|---|
| Hintersee, Felbertal |  | End of the Felber valley, South of Mittersill, County of Salzburg<br>1315 m | S: 0.08 km$^2$<br>D: max. 6 m | Spruces, larchs, herb vegetation, dense subm. veg. | Organic substrate mixed with sand, blocks of silicate rocks | **HS** |
| Jaegersee |  | End of the Kleinarl valley, South of Kleinarl, County of Salzburg<br>1105 m | S: 0.1 Ø km$^2$<br>D: ca. 5 m | Mixed forest with maples, spruces, etc., herb vegetation along the western lakeside | Organic substrate mixed with sand, blocks of silicate rocks | **JS** |
| Kreuzen-see |  | South of the Lessach valley, 10 km W of Tamsweg, County of Salzburg<br>1056 m | S: 0.01 km$^2$<br>D: ca. 4 m | Rich grass and herb vegetation on the shore, dense subm. veg. | Organic substrate mixed with fine sand | **KS** |
| Prebersee |  | 8 km NE of Tamsweg, County of Salzburg<br>1124 m | S: 0.18 km$^2$<br>D: ca. 5 m | Spruces, pines, and birch, moor and grass veg., sparse subm. veg. | Organic substrate mixed with sand and stones of different size | **PS** |
| Schatten-see |  | Krakauhintermuehlen 15 km NE of Tamsweg, County of Styria<br>1120 m | S: 0.03 km$^2$<br>D: ca. 6 m | Spruces and pines, dense grass veg., dense subm. veg. | Organic substrate, grass, sand, stones | **SS** |
| Seetaler-see |  | End of the Seetal, 10 km E of Tamsweg, County of Salzburg<br>1080 m | S: 0.10 km$^2$<br>D: ca. 10 m | Dense moor and grass veg., trees along the northern lakeside | Organic substrate, grass, mud, moor vegetation | **STS** |
| Zauchen -see |  | End of the Zauchen valley, South of Altenmarkt, County of Salzburg<br>1339 m | S: 0.06 km$^2$<br>D: max. 8 m | Spruces and herb vegetation, partly dense subm. veg. | Organic substrate, sand, stones of different size | **ZS** |
| Kratzen-bergsee |  | End of the Hollersbach valley, County of Salzburg<br>2170 m | S: 0.26 km$^2$<br>D: max. 30 m | Grass vegation rich of species (e. g. sedges) | Silicate stones and blocks | **KBS** |
| Lower Bock-hartsee |  | Above Sportgastein, Gastein valley, County of Salzburg<br>1830 m | S: 0.16 km$^2$<br>D: max. 12 m | Sparse vegetation including herbs and bushes, no subm. veg. | Silicate blocks of cm to dm size | **LBS** |
| Reedsee |  | Koetschach valley, East of the Graukogel, County of Salzburg<br>2070 m | S: 0.06 km$^2$<br>D: max. 6 m | Spruces, larchs, and pines | Medium- to coarse-grained inorganic substrate mixed with organic mass | **RS** |
| Schoeder-see |  | End of the Grossarl valley, South of Grossarl, County of Salzburg<br>1450 m | S: 0.10 km$^2$<br>D: max. 2 m | Moor and grass vegetation | Organic substrate, grass, mud | **SCS** |
| Lower Rot-güldensee |  | North of the Grosser Hafner, above Murwinkel, County of Salzburg<br>1760 m | S: 0.15 km$^2$<br>D: max. 10 m | Sporadic lining by larchs and pines, no subm. veg. | Silicate blocks of cm to dm size | **LRS** |

and sampling the bottom substrate with a hand sieve (mesh size: 0.5 mm). Sampling of fine inorganic sediment mixed with plant fragments and detritic components generally took place to a depth of about 10 cm, in order to include endobenthic molluscs such as pill clams. Sampling was exclusively conducted along the lake shore, to a maximum water depth of 1 m. For aquatic gastropods and bivalves, I only recorded adult and subadult living animals, larval forms and empty shells were excluded. Whenever possible, counting occurred at the sample points, and collected animals were then released to their natural habitats. For muddy ground substrate, sieving occurred in the laboratory and retained material was carefully examined under the stereomicroscope. For each sample point, representatives of the occurring species were stored in 70 % ethanol.

At each sample site, I measured 12 environmental factors, namely, water temperature, pH, conductivity, oxygen saturation, biological oxygen demand after 5 days [$BOD_5$], nitrate content, total hardness, altitude, mean grain-size of the bottom substrate, submerged vegetation, and algal cover, and shading. Water measurements occurred in the water layer directly above the sediment, between late morning and early evening. Except for $BOD_5$, which was analyzed in the laboratory after taking a water sample and storing it in a dark box at 10 °C, I measured all physical and chemical properties using portable instruments or single use analysis probes (Stelzner GmbH). I determined the mean grain size of the bottom substrate by sampling ca. 1 kg of the sediment and sieving the substrate in the laboratory, using mesh sizes of 20 mm, 5 mm, 2 mm, 0.5 mm, 0.1 mm, and 0.063 mm. I then plotted relative sediment mass against grain size in a double-logarithmic graph in order to determine mean grain size. I estimated the density of submerged vegetation and the extent of algal cover of stones and plants by counting, with 0 % indicating no vegetation or algae and 100 % representing extremely dense occurrence of submerged plants or algae.

Environmental factors were analyzed statistically by computing mean values and standard deviations for each mountain lake (Tab. 2), in order to assess the heterogeneity of physical and chemical water properties along the lake shores. I also performed statistical analysis on the samples as a whole, in order to assess the total range covered by the environmental factors.

### 2.3. Multivariate statistical analyses

In order to determine the relationships, if any, between the occurrence of aquatic molluscs and abiotic/biotic factors, I assembled two types of matrices (mollusc taxa abundance by sites and environmental variables by sites), to which I applied a multivariate gradient analysis. I followed the mathematical method of

**Tab. 2.** Results of environmental variable measurement at the studied lakes. Standard deviations in parentheses (n = 10 for each lake). For abbreviations see Table 1 and Figure 4.

| Factor | JS | ZS | HS | KBS | UBS | URS | RS | SCS | PS | STS | KS | SS | MIN | MAX | MEAN | SD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **ALT (m)** | 1105 | 1339 | 1315 | 2170 | 1830 | 1760 | 2070 | 1450 | 1124 | 1080 | 1056 | 1120 | 1056 | 2170 | 1439 | 376 |
| **T (°C)** | 8.9 | 8.5 | 10.2 | 8.1 | 14.3 | 11.7 | 8.4 | 9.9 | 19.3 | 18.8 | 19.6 | 17.6 | 7.9 | 19.8 | 13.3 | 4.5 |
| | (0.5) | (0.2) | (0.5) | (0.2) | (0.2) | (0.2) | (0.3) | (0.1) | (0.3) | (0.3) | (0.1) | (0.3) | | | | |
| **$O_2$%** | 93.0 | 96.0 | 93.5 | 96.3 | 95.3 | 94.0 | 92.7 | 93.0 | 84.0 | 90.0 | 90.5 | 87.8 | 78.0 | 98.0 | 91.6 | 4.4 |
| | (1.4) | (1.0) | (2.6) | (1.7) | (1.2) | (1.0) | (1.2) | (1.6) | (4.3) | (1.8) | (4.8) | (1.7) | | | | |
| **PH** | 7.6 | 6.8 | 6.5 | 6.6 | 6.9 | 6.8 | 7.4 | 6.2 | 6.1 | 5.9 | 6.4 | 5.8 | 5.5 | 7.8 | 6.5 | 0.6 |
| | (0.2) | (0.2) | (0.2) | (0.2) | (0.2) | (0.2) | (0.3) | (0.1) | (0.4) | (0.4) | (0.3) | (0.3) | | | | |
| **TH (mg $l^{-1}$)** | 2.6 | 2.0 | 2.8 | 3.5 | 3.0 | 2.8 | 2.5 | 1.6 | 1.2 | 1.4 | 1.2 | 1.4 | 1.0 | 3.8 | 2.1 | 0.8 |
| | (0.2) | (0.3) | (0.1) | (0.2) | (0.7) | (0.1) | (0.3) | (0.7) | (0.1) | (0.1) | (0.1) | (0.1) | | | | |
| **EC ($\mu$S $cm^{-1}$)** | 112.5 | 88.3 | 85.0 | 66.8 | 112.0 | 105.7 | 68.7 | 76.0 | 105.0 | 99.3 | 77.5 | 128.8 | 56.0 | 158.0 | 98.1 | 25.3 |
| | (12.4) | (6.1) | (9.3) | (11.5) | (6.1) | (3.5) | (9.5) | (10.6) | (21.1) | (9.0) | (10.4) | (3.6) | | | | |
| **N (mg $l^{-1}$)** | 2.9 | 1.9 | 1.6 | 1.7 | 1.3 | 0.7 | 0.9 | 1.3 | 3.5 | 3.6 | 3.5 | 3.5 | 0.2 | 4.6 | 2.2 | 1.3 |
| | (1.5) | (0.9) | (1.3) | (0.5) | (0.2) | (0.3) | (0.7) | (0.1) | (0.3) | (0.2) | (0.3) | (0.2) | | | | |
| **$BOD_5$ (mg $l^{-1}$)** | 2.1 | 1.3 | 1.9 | 0.8 | 1.9 | 1.5 | 1.3 | 2,2 | 3.8 | 3.2 | 3.2 | 3.2 | 0.3 | 4.1 | 2.2 | 1.0 |
| | (0.4) | (1.0) | (0.3) | (0.6) | (0.7) | (0.5) | (0.5) | (0.9) | (0.3) | (0.6) | (0.2) | (0.3) | | | | |
| **S (%)** | 45.0 | 48.3 | 20.0 | 17.5 | 0.0 | 3.3 | 63.3 | 47.5 | 30.0 | 35.0 | 15.0 | 60.0 | 0,0 | 80.0 | 30.4 | 22.1 |
| | (23.8) | (7.6) | (14.1) | (5.0) | (0.0) | (5.8) | (15.3) | (9.6) | (8.2) | (12.9) | (5.8) | (8.2) | | | | |
| **SV (%)** | 44.5 | 61.7 | 37.1 | 13.1 | 0.0 | 3.3 | 15.8 | 69,4 | 43.8 | 77.5 | 80.0 | 66.3 | 0.0 | 90.0 | 45.0 | 27.5 |
| | (26.1) | (2.9) | (8.6) | (2.4) | (0.0) | (3.8) | (3.8) | (10.9) | (6.6) | (6.5) | (10.2) | (7.8) | | | | |
| **ALG (%)** | 31.3 | 33.3 | 18.8 | 0.0 | 0.0 | 0.0 | 8.3 | 56.3 | 25.0 | 68.8 | 59.8 | 72.5 | 0.0 | 75.0 | 35.0 | 27.5 |
| | (12.1) | (14.4) | (23.9) | (0.0) | (0.0) | (0.0) | (14.4) | (12.3) | (0.0) | (12.5) | (10.7) | (15.3) | | | | |
| **SUB (mm)** | 2.5 | 1.2 | 5.6 | 10.5 | 22.0 | 14.0 | 5.8 | 2.4 | 4.1 | 3.5 | 4.5 | 6.5 | 1.2 | 22.0 | 6.1 | 5.4 |
| | (0.4) | (0.2) | (1.5) | (7.8) | (10.7) | (3.1) | (2.9) | (0.8) | (1.4) | (1.1) | (1.7) | (3.2) | | | | |

Canonical Correspondence Analysis (CCA; Ter Braak 1986, 1988; Palmer 1993; Ter Braak & Verdonschot 1995), which uses a combination of ordination and regression techniques to evaluate the response of animal community compositions to environmental gradients. By applying this method, I assumed that animals occuring in a specific range of habitats, are most abundant around an optimum, and community composition changes along a gradient. Following convention, I plotted the results of CCA into graphs, with species represented as points and environmental factors represented by arrows starting from the origin. Goodness of fit for the CCA model used in this study was obtained using the Monte Carlo permutation test outlined by Verdonshot and Ter Braak (1994). All modelling was done with the computer program Multi-Variate Statistical Package (MVSP, version 3.1). Values for species abundance were log-transformed, resulting in a better approximation to the normal distribution. While a down-weighting procedure for rare mollusc species was applied, forward selection was not possible within MVSP.

## 3. RESULTS

### *3.1. Environmental variables*

Water temperature was remarkably heterogeneous, ranging from 7.9 °C to 19.8 °C, with a mean temperature of 13.3 °C (Tab. 2). Oxygen saturation varied between 78 % and 98 %, indicating that the sample sites had a slight under-saturation of $O_2$ due to, perhaps, metabolic processes or decomposition. Water pH ranged from 5.5 to 7.8. Total hardness was quite low among the lakes, with a maximum value of 3.8 mg $l^{-1}$ and a mean value of 2.1 mg $l^{-1}$. Like total hardness, conductivity was generally low in all of the study lakes (mean value: 98.1 $\mu$S $cm^{-1}$), which is characteristic for lakes situated in the silicate rocks of the Central Alps.

Nitrate and $BOD_5$ of the water showed a somewhat similar behaviour, with a wide range of values and a

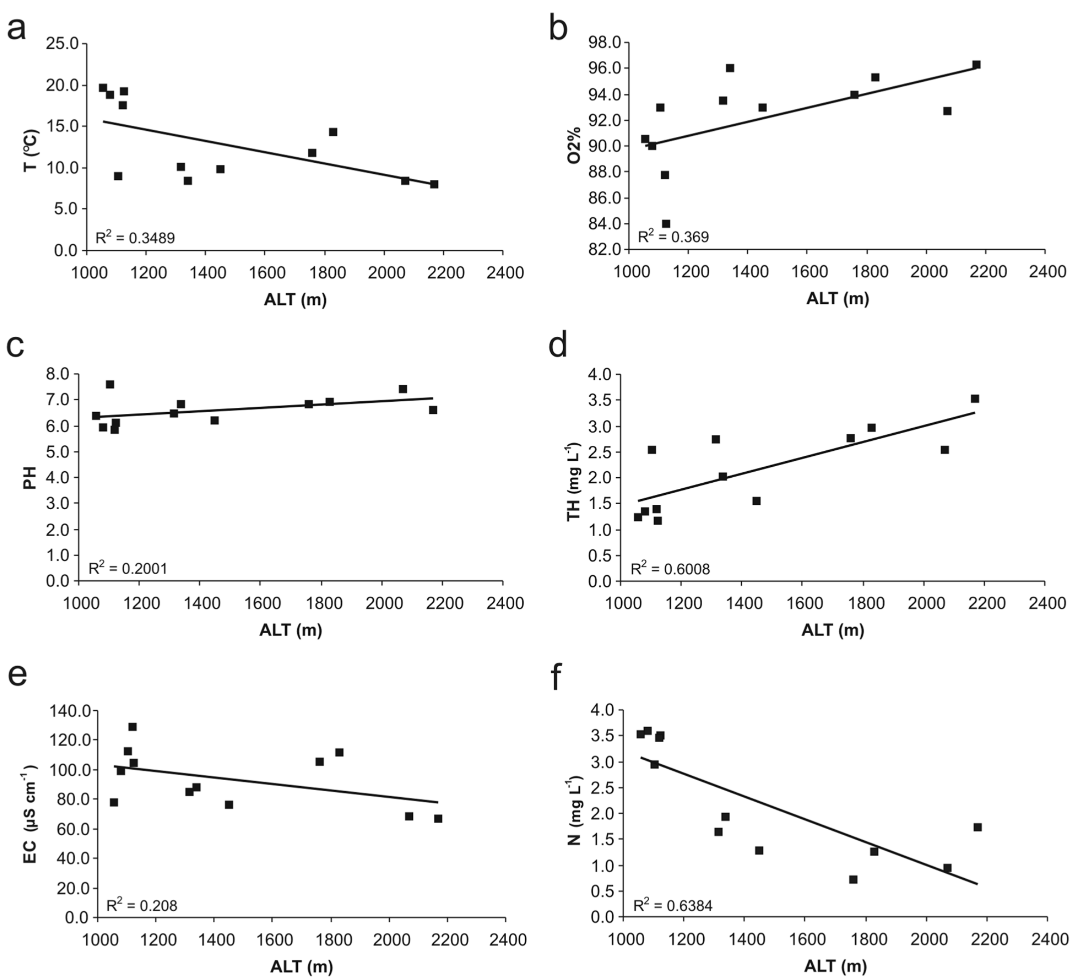


**Fig. 2.** Relationships between environmental variables and altitude: Temperature (a), oxygen saturation (b), pH (c), total hardness (d), conductivity (e), and nitrate (f).

mean of approximately 2 mg $l^{-1}$ (Tab. 2). With respect to shading of the lake shore, there was high fluctuation among the studied lakes, with values ranging from 0 % to 80 %, and a mean value of 30.4 % (Tab. 2). Submerged vegetation and algal cover of the sediment showed similar mean values (45 % and 35 %) and standard deviations (27.5 %) in all studied lakes. Mean grain size of the bottom substrate varied between 1.2 mm, indicating sandy substrate, and 22 mm, suggesting a stony bottom.

In addition to varying widely between lakes, in certain lakes, the measured abiotic and biotic parameters also varied widely between sample sites. In general, lakes that were highly influenced by terrestrial and/or aquatic vegetation showed a higher variation in measurements between sample points (e.g. Jägersee), than lakes characterized by very sparse vegetation (e.g. Kratzenbergsee; Tab. 2). Linear regression analysis also showed that variables measured at the sample points changed significantly with altitude (Figs 2 and 3). While water temperature, $BOD_5$, nitrate content, submerged vegetation and algal cover decreased with increasing altitude, oxygen saturation, total hardness, and mean grain size of the bottom substrate, shading, water pH, and conductivity did not exhibit a significant dependence upon altitude.

### *3.2. Mollusc diversity and abundances*

The highest number of freshwater mollusc species, namely 7 gastropod and 5 bivalve taxa, was recorded at Jägersee, followed by Schödersee with a total of 8 species and Seetalersee with 7 species (Tab. 3). The lowest species diversity occurred at Kratzenbergsee, where I recorded only the pill clam *Pisidium casertanum* (Poli 1791) and the pulmonate mud snail *Galba truncatula* (O. F. Müller 1774). Over all of the lakes, I recorded a total of 13 mollusc species (8 gastropods and 5 bivalves)

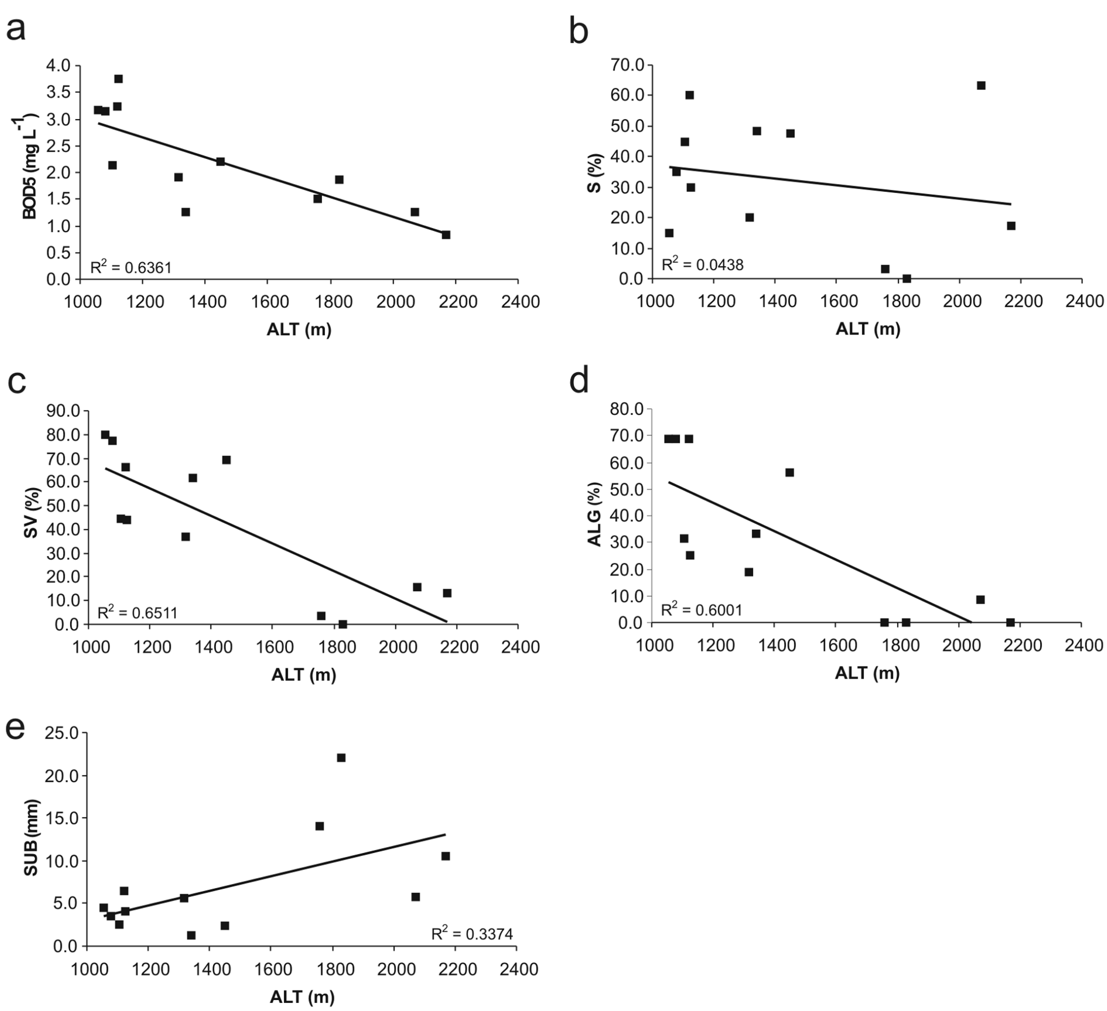


**Fig. 3.** Relationships between environmental variables and altitude: Biological oxygen demand (a), shading (b), submerged vegetation (c), cover algal (d), and substrate grain size (e).

in the Alpine water bodies, with the highest abundances occurring for *P. casertanum*, *G. truncatula*, *Radix balthica* (Linnaeus 1758), and *Pisidium subtruncatum* Malm 1855. Lowest individual numbers were found for *Pisidium nitidum* Jenyns 1832, *Musculium lacustre* (O. F. Müller 1774), *Acroloxus lacustris* (Linnaeus 1758), and *Planorbis planorbis* (Linnaeus 1758), each occurring with an average population density of less than 1 ind. $m^{-2}$. Generally, there were significant differences in species number and specific abundances among and within study lakes (Tab. 3). The most remarkable differences were between water bodies of the montane vegetation zone and the subalpine vegetation zone. Lakes from the higher Alpine level had lower average number of species, and showed a sharp decrease in the population density of molluscs, for example *P. casertanum* occurred at a density of 19.3 $\pm$ 5.1 ind. $m^{-2}$ in the Seetalersee, but fell to 3.5 + 4.1 ind. $m^{-2}$ in the Kratzenbergsee.

As the moderately high standard deviations in Table 3 indicate, species abundances also exhibited significant variation among the sample sites of each lake. This finding underscores the heterogeneous distribution of most mollusc species along the lake shore, which, in most cases, was linked to variable distribution of terrestrial and submerged vegetation.

### *3.3. Canonical Correspondence Analysis*

I performed multivariate analysis on both the malacological and physico-chemical data set in order (1) to elucidate possible relationships between the spatial distribution of mollusc species and environmental conditions and (2) to test a classification of the sample sites according to the 12 environmental variables measured (Fig. 4). The first two axes accounted for 24 % of the variance, with axis 1 (13.5 % of the variance) representing water pH, shading, and oxygen saturation against conductivity. Axis 2 (10.5 % of the variance) consisted mainly of algal cover, submerged vegetation, and nitrate content against total hardness. Except for water temperature, which had to be excluded from further consideration, possible multi-colinearity among environmental variables was insignificant, because respective variance inflation factors ranged from 1.22 (shading) to 3.75 (altitude).

In the projection of mollusc species together with the environmental variables, most of the species are clustered in the third quadrant of the graph (Fig. 4 a). This suggests that *P. planorbis*, *Anisus spirorbis* (Linnaeus 1758), and *M. lacustre* showed an enhanced affinity for increased amounts of submerged vegetation, while *A. lacustris* preferred higher values of oxygen saturation.

**Tab. 3.** Results of mollusc recording and counting at the studied lakes (ind. $m^{-2}$). Standard deviations in parentheses (n = 10 for each lake). For abbreviations see Table 1 and Figure 4.

| Species | JS | ZS | HS | KBS | UBS | URS | RS | SCS | PS | STS | KS | SS | MIN | MAX | MEAN | SD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Rl** | 3.3 | 5.0 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 6.8 | 3.8 | 1.8 | 5.0 | 6.3 | 0.0 | 9.0 | 2.8 | 3.1 |
| | (1.5) | (3.6) | (1.9) | (0.0) | (0.0) | (0.0) | (0.0) | (2.1) | (3.9) | (2.1) | (2.2) | (3.5) | | | | |
| **Rb** | 0.0 | 3.7 | 5.5 | 0.0 | 0.0 | 0.0 | 6.3 | 4.5 | 1.5 | 5.0 | 10.0 | 9.8 | 0.0 | 17.0 | 4.5 | 5.0 |
| | (0.0) | (3.2) | (4.0) | (0.0) | (0.0) | (0.0) | (2.1) | (2.4) | (3.0) | (6.6) | (7.4) | (2.6) | | | | |
| **Gt** | 6.0 | 10.7 | 0.0 | 5.0 | 0.0 | 0.0 | 8.7 | 0.0 | 13.3 | 7.5 | 13.0 | 10.3 | 0.0 | 23.0 | 6.5 | 5.7 |
| | (2.2) | (1.5) | (0.0) | (6.6) | (0.0) | (0.0) | (2.1) | (0.0) | (7.4) | (3.4) | (2.2) | (2.9) | | | | |
| **As** | 8.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 8.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 11.0 | 1.4 | 3.1 |
| | (2.2) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (1.5) | (0.0) | (0.0) | (0.0) | (0.0) | | | | |
| **Al** | 6.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.8 | 0.0 | 1.8 | 1.5 | 0.0 | 0.0 | 10.0 | 1.1 | 2.5 |
| | (3.7) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (4.3) | (0.0) | (2.4) | (2.4) | (0.0) | | | | |
| **Bc** | 4.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 6.5 | 0.0 | 9.0 | 0.0 | 0.0 | 0.0 | 12.0 | 1.6 | 3.2 |
| | (2.4) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (1.3) | (0.0) | (2.9) | (0.0) | (0.0) | | | | |
| **Pp** | 8.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 11.0 | 0.7 | 2.5 |
| | (2.2) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | | | | |
| **Acl** | 4.5 | 3.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 9.0 | 0.6 | 1.6 |
| | (3.1) | (1.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | | | | |
| **Ml** | 3.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 8.0 | 0.7 | 2.0 |
| | (3.9) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (1.7) | (0.0) | (0.0) | (0.0) | (0.0) | | | | |
| **Pc** | 8.0 | 12.7 | 3.8 | 3.5 | 0.0 | 0.0 | 7.3 | 18.5 | 11.0 | 19.3 | 11.3 | 8.0 | 0.0 | 24.0 | 9.5 | 7.5 |
| | (3.7) | (6.4) | (4.8) | (4.1) | (0.0) | (0.0) | (8.1) | (2.6) | (3.5) | (5.1) | (4.6) | (5.4) | | | | |
| **Ps** | 8.0 | 8.7 | 5.8 | 0.0 | 0.0 | 0.0 | 6.0 | 9.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 15.0 | 2.8 | 4.2 |
| | (2.9) | (5.5) | (1.7) | (0.0) | (0.0) | (0.0) | (2.6) | (4.1) | (0.0) | (0.0) | (0.0) | (0.0) | | | | |
| **Po** | 3.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 8.0 | 6.3 | 0.0 | 0.0 | 12.0 | 2.0 | 3.4 |
| | (1.3) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (4.2) | (3.4) | (0.0) | | | | |
| **Pn** | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 8.0 | 0.4 | 1.6 |
| | (2.6) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | (0.0) | | | | |

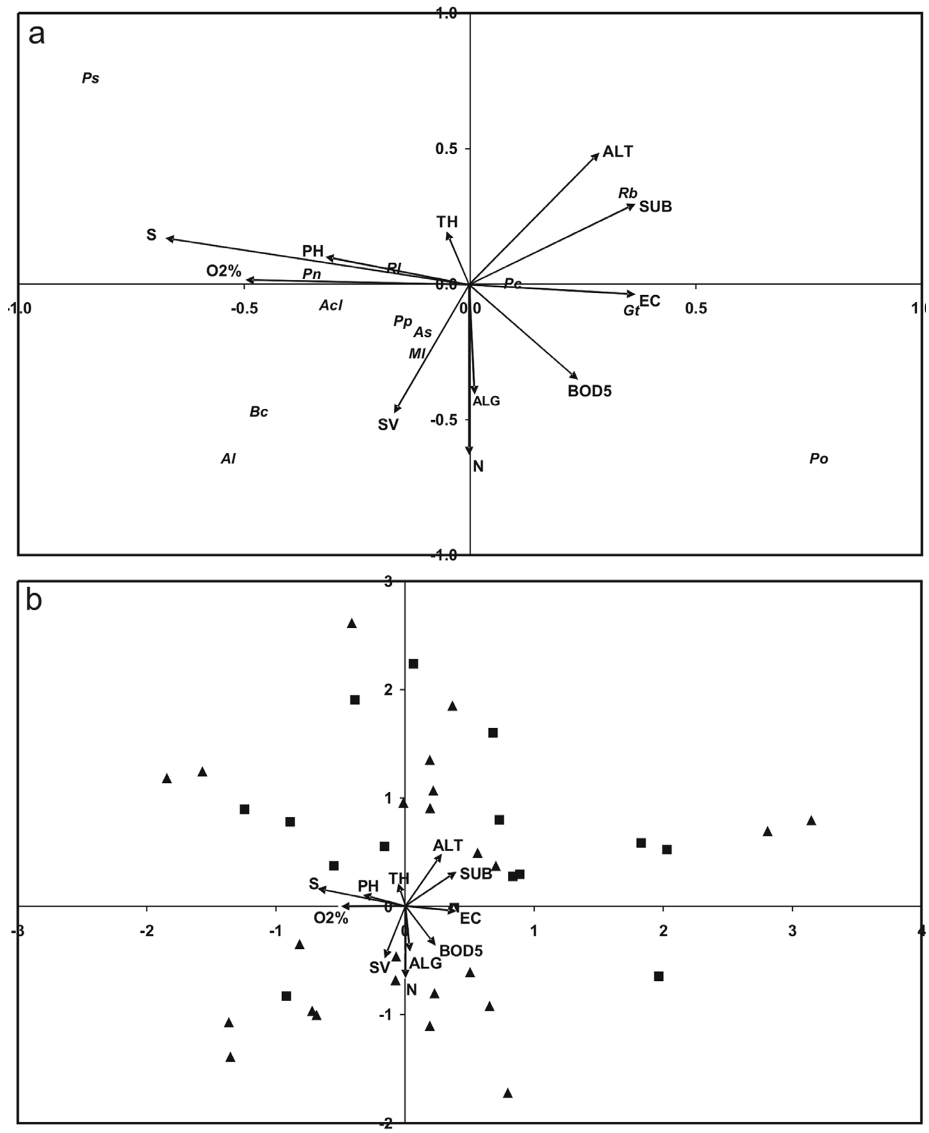


**Fig. 4.** Results of multivariate statistics. a) Relationships between environmental variables (vectors) and species (Abbreviations: *Acl…Acroloxus lacustris*, *Al…Anisus leucostoma, As…Anisus spirorbis, Bc…Bathyomphalus contortus, Gt…Galba truncatula, Ml…Musculium lacustre, Pc…Pisidium casertanum, Pn…P. nitidum, Po…P. obtusale, Pp…Planorbis planorbis, Ps…Pisidium subtruncatum, Rb…Radix balthica, Rl…R. labiata*; ALG… algal cover, ALT…altitude, BOD5…biological oxygen demand, EC…conductivity, N…nitrate content, $O_2$%…oxygen saturation, PH…water pH, S…shading, SUB…substrate grain size, SV…submerged vegetation, TH…total hardness). b) Relationships between environmental variables (vectors) and sampling sites: (see text).

While *Bathyomphalus contortus* (Linnaeus 1758) and *Anisus leucostoma* (Millet 1813) did not exhibit a strong dependence on the variables defining the quadrant, their position in the graph indicates that they preferentially occurred at sites with higher values of the measured biotic and abiotic parameters. In the second quadrant of the graph, 3 species were positioned, indicating that *P. nitidum* and, to a minor extent, *Radix labiata* (Rossmaessler 1835) have an affinity for higher values of oxygen saturation, shading, and water pH. The position of *P. subtruncatum* suggested a tolerance of the variables defining this quadrant. *R. balthica* and *P. casertanum* are situated in the first quadrant of the graph, indicating that the gastropod had an affinity for higher altitudes and larger grain-sizes of substrate, while the bivalve preferred medium substrate grain-size and conductivity. *G. truncatula* and *Pisidium obtusale* (Lamarck 1818) appear in the fourth quadrant of the graph, with the mud snail exhibiting a strong affinity for high conductivity while the pill clam is characterized by a remarkable independence of the environmental variables.

Regarding a possible relationship between sampling sites and environmental variables, sampling points in the montane vegetation zone (solid triangles) exhibited a very irregular distribution with most points falling to the right of axis 2 (Fig. 4 b). Sampling points in the subalpine vegetation zone (solid squares) chiefly plotted in quadrants 1 and 2 of the graph. Most points did not show a significant correlation with the environmental variables, but, more generally, subalpine lakes were characterized by higher values for substrate grain size and total hardness, whereas montane water bodies exhibited higher values for submerged vegetation, nitrate content, algae, and $BOD_5$. Based on these findings, montane lakes may experience a higher influence of terrestrial and aquatic vegetation and have a substrate that consists of fine particles, mixed with plant components. Subalpine lakes, on the other hand, are only sparsely affected by terrestrial and aquatic vegetation, and have a bottom substrate that mainly consists of stones and larger blocks that are only partly crushed by transport processes.

## 4. DISCUSSION

As demonstrated by Turner *et al.* (1998) for the Swiss Alps, both species number and abundance of freshwater molluscs decline remarkably with increasing altitude. According to the authors, malacological diversity at 2000 m (the subalpine vegetation level) declines to a total of 15 species, while at 3000 m no mollusc species have yet been found. In the same altitude range, species abundances decrease from up to 100 ind. $m^{-2}$ to zero ind. $m^{-2}$. The results of the study presented here greatly correspond with the findings of Turner *et al.* (1998) for the Western Alps. As such, according to this field study, subalpine water bodies have a significantly reduced malacofauna as compared to lakes in the montane level. This investigation underscores that the dependence of mollusc distribution upon altitude results from changing environmental conditions.

It is well known that water bodies at high altitudes are dominated by generalist species (some pill clams and lymnaeids), while, on the other hand, montane lakes are also colonized by specialists when levels of submerged vegetation and nutrients are high (Glöer & Meier-Brook 2003). During this investigation, within the group of aquatic snails, *G. truncatula* and *R. labiata* were collected most frequently (Tab. 3). At least one of these two species occurred in all of the lakes colonized by aquatic molluscs. According to Turner *et al.* (1998), Glöer (2002), and Glöer & Meier-Brook (2003), *G. truncatula* are a widely distributed species, and particularly colonize the shores of larger lakes and are more or less independent of $CaCO_3$ concentration. Turner *et al.* (1998) describe this gastropod species as a *ubiquist*, which has already reached the upper-Alpine (2800 m) waters in Switzerland. A very similar distribution is reported for *R. labiata*, which, at the moment, is found at a maximum altitude of 2700 m. The third detected species of Lymnaeidae is *R. balthica*, which prefers small ponds that are rich in macrophytes (Sturm 1999; Glöer & Meier-Brook 2003; Jaeckel 2004), but also occurs in fast flowing brooks and rivers (Patzner 1996). According to Turner *et al.* (1998), *R. balthica* has already reached altitudes of 2500 m in Switzerland.

All species of Planorbidae recorded in this study preferred lakes in the montane vegetation zone. According to previous publications (e.g. Sturm 1998; Glöer & Meier-Brook 2003), *A. leucostoma*, *A. spirorbis*, *B. contortus*, and *P. planorbis* mainly colonize small ponds with thick vegetation or bays within rivers and brooks, and can reach high population densities. For *A. leucostoma*, Turner *et al.* (1998) describe a distribution up to 2250 m in the Swiss Alps, while the other species have been found at maximum altitudes of about 1500 m. According to this contribution, the occurrence of *A. lacustris* is limited to a maximum altitude of 1300 m and is characterized by low frequencies. This gastropod is mainly found on stalks and leaves of plants, but can also colonize the surface of stones covered with layers of algae.

Regarding the bivalves, I only recorded species of the family Sphaeriidae. A rather homogeneous distribution throughout the colonized lakes was observed for *P. casertanum* and, with some exceptions, also for *P. subtruncatum*. Both pill clams are widely distributed in Middle Europe, being extremely tolerant of any changes in environmental conditions (i.e. temperature, pH, $CaCO_3$ content), and, in many cases, are characterized by high abundances (e.g. Kuiper 1974; Meier-Brook 1975; Falkner 1990; Glöer & Meier-Brook 2003). Turner *et al.* (1998) describe an occurrence of *P. casertanum*, in Switzerland, up to 2750 m (Rifflsee at Zermatt), whereas *P. subtruncatum* was limited to a maximum altitude of 2000 m. With respect to *P. obtusale* and *P. nitidum*, ecological requirements outlined in the literature are different to those of *P. casertanum* (Meier-Brook 1975; Glöer & Meier-Brook 2003). The occurrence of *M. lacustre* is limited to two lakes with high vegetation density (Jägersee, Schödersee). In Switzerland, the maximum altitude reached by this species is 1350 m (Turner *et al.* 1998). Regarding its ecology, *M. lacustre* mainly prefers shallow ponds and slowly flowing rivers, thereby often acting as a pioneer species that colonizes a habitat before its competitors (e.g. Sturm 1999).

As documented in the results section, the two lakes dammed for electricity production (Lower Bockhartsee, Lower Rotgüldensee) do not bear any malacofauna. Besides several other parameters, the most reasonable cause for this phenomenon are the periodic fluctuations of the water level that are typical for such lakes. Due to significant water level fluctuations, the shore vegetation is very sparse and cannot provide enough micro-habitats for molluscs. Additionally, the ground of both lakes is mainly composed of medium- to coarse-grained mineral substrate and therefore does not provide optimum conditions for gastropods and bivalves. As documented in previous studies (e.g. Kuiper 1974), storage lakes are rarely colonized by molluscs.

Based on the results of the present study, colonization of Alpine waters by aquatic molluscs depends highly upon the ecological demands of single gastropod and bivalve species, with generalistic species penetrating to higher biotopes than specialists. However, further investigations seem necessary to document this colonization process and to verify the present findings.

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*Received: July 2007*
*Accepted: November 2007*