ZOOCOENOLOGICAL STATE OF MICROHABITATS AND ITS SEASONAL DYNAMICS IN AN AQUATIC MACROINVERTEBRATE ASSEMBLY
(HYDROBIOLOGICAL CASE STUDES ON LAKE BALATON, №. 1)

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Abstract. In the years 2002, 2003 and 2004 we collected samples of macroinvertebrates on a total of 36 occasions in Badacsony bay, in areas of open water (in the years 2003 and 2004 reed-grassy) as well as populated by reed (*Phragmites australis*) and cattail (*Typha angustifolia*). Samples were taken using a stiff hand net. The sampling site includes three microhabitats differentiated only by the aquatic plants inhabiting these areas. Our data was gathered from processing 208 individual samples. The quantity of macroinvertebrates is represented by biovolume value based on volume estimates. We can identify taxa in abundant numbers found in all water types and ooze; as well as groups associated with individual micro-habitats with various aquatic plants. We can observe a notable difference between the years in the volume of invertebrate macrofauna caused by the drop of water level, and the multiplication of submerged macro-phytes. There are smaller differences between the samples taken in reeds and cattail stands. In the second half of 2003 – which was a year of drought – the *Najas marina* appeared in open waters and allowed to support larger quantities of macroinvertebrates. In 2004 with higher water levels, the *Potamogeton perfoli-atus* occurring in the same area has had an even more significant effect. This type of reed-grass may support the most macroinvertebrates during the summer. From the aspect of diversity relations we may suspect different characteristics. The reeds sampling site proved to be the richest, while the cattail microhabitat is close behind, open water (with submerged macrophytes) is the least diverse microhabitat.
Keywords: *biovolume, reed, cattail, macrophyte, macrofauna, bootstrap, Tukey-test*

Introduction and aims

Lake Balaton, the largest lake in Central Europe has long been in the center of hydrobiological research. Thanks to more than a hundred years of scientific study, a massive body of knowledge has been gathered making it one of the most thoroughly researched shallow lake. Fresh water macroscopic invertebrates had been reseached for a long time in Hungary. At the end of the nineteenth century knowledge was very limited, only 207 invertebrate species of the lake were known. A hundred years later this number has gone up to 1300, but intensive research of fauna will likely push this number over 2000 [49]. The lakeshore is made up of diverse habitats. 58% of the shore is considered to be in natural state, 12% artificially scattered by rocks and the remaining 30% is paved. The natural parts of the north shore are characterized by belts of reeds. The deterioration of these areas covered by reeds is ever increasing. The stock forming dominant species is common reed [*Phragmites australis* (Cav.) Trin.] but the expansion of narrowleaf cattail (*Typha angustifolia* L.) to the determinant of reeds can be observed

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in some areas of lake Balaton [31]. This is one of the reasons why it is worth researching these two plant communities from the aspect of macroinvertebrate fauna.

Lake Balaton is characterized by different reed grass-stands reaching down to 2 meters in depth of which *Potamogeton perfoliatus* is the most common community forming species, next in line is *Myriophyllum spicatum* followed by *Ceratophyllum demersum* and *Najas marina* [25].

The most thorough research of macroinvertebrates living in water vegetations has been carried in reed-grass areas. A sound knowledge base is available in connection with the macrozoobenthon of rocky shores just like the invertebrate fauna of reeds. On the other hand there is very little available data about the characteristics of the different vegetational habitats – especially for narrowleaf cattail – in vicinity of lakeshore from the aspect of the macroinvertebrate fauna.

Previous works primarily concentrated on spatial patterns and are mainly of faunistic nature. From the temporal patterns only descriptive research has been carried out, moreover not enough attention was paid to the research of seasonal changes occurring on a shorter time scale. This is why it is appropriate to engage analysing zoocoenological spatial and temporal patterns, and to broaden our knowledge in this direction.

Today in the ecological literature the different schools of methodology are distinctly separated from each other.

- Pattern descriptions based on field work constitute one of the main directions e.g. [17, 29, 36, 46, 50, 51, 52, 53, 54, 56, 59].
- Modelling research either works with oversimplified situations or deals with purely theoretical questions e.g. [28, 34, 20, 35].
- Experimental research on the other hand often neglects the complexity of ecosystems e.g. [57].

For the elimination of the above mentioned problems recently new approaches emerged which try to merge the previous methods [21]. With our research at lake Balaton we wish to lay a foundation for future research conducted with a similar approach.

For the location of our research we chose a part of Badacsony Bay containing narrowleaf cattail stands, common reed stands as well as open water areas (in the process of being populated with reed-grass). Badacsony Bay is located on the north shore of Lake Balaton. More close up, the sampling site includes three different microhabitats differing from the aspect of the above mentioned vegetation. During 2002, 2003, and 2004 we collected samples on a total of 36 occasions from spring to last in the autumn. Our data was gathered from processing 208 individual samples. The first two years, especially 2002 proved exceptionally draughty with very low water levels.

In accordance with the above written facts, our aims in the current research were the following:

- to explore the zoocoenological patterns of macroinvertebrate assemblies;
- to explore the seasonal changes in zoocoenological conditions in the three characteristic microhabitats of Lake Balaton. As a first step we would only like have an idea of seasonal changes in quantitative conditions.

We would like the knowledge gathered about the seasonal dynamic patterns of different microhabitats to serve as a foundation for further

- ecological modelling research;
- designing of manipulative experimental setting;
- possible research of climate changes.

Figure 1. *Location of Badacsony Bay within Lake Balaton.*

Review of literature

Long-term changes of aquatic plant areas in Lake Balaton and other shallow lakes

In the recent decades degradation of reeds in Lake Balaton can be observed. There are many studies published about the causes of the desolation of reeds [31] but the causes and reasons behind this phenomenon are not known in every case.

The replacement of common reed stands with narrowleaf cattail is a process present in almost all lakes across Europe including Lake Balaton, this process can be attributed the increasing eutrophization of waters and growth in halobity [31, 32].

Reed-grass plays a very important role in the life of lake Balaton. It is known that reed-grass is the antagonist of production of masses of algae, because in the spring the growth of reed grass stands takes away large quantities of nutrition from the ooze and from the water thus the algae population – whose development maximum is reached later on – cannot develop powerfully [63]. Production of algae in large quantities with its shading properties stunts the development of reed-grass. Balaton in its mesotrophic state rooted reed-grasses have a light compensation depth of about 2 meters. This explains why reed-grass was able to penetrate the lake to 2 meters in depth in the 1960’s and why it was driven out to shallower areas in the period of vigorous algae production. [24]. Since 1995 oligotrophization can be observed in Lake Balaton, which can be attributed to decline in external phosphorus loads. In the Keszthely Basin the decline in the biomass of phytoplankton became detectable in 1995, thus following the decline of phosphorus loads with a 7–8 years delay, the change in the combination of plankton took a further 3 years delay [67]. The decrease of algae penetration – which can be observed since 1995 favours the advance of reed-grass. The decreased water levels observed since 2000 should also catalyse this process, however even by 1999 reed grass penetration has not reached the levels of the sixties, and in 2000 even less reed-grass was recorded [24, 25].

Many foreign studies deal with the decline of reed stands. The fragmentation of common reed stands was researched on Poygan lake (Wisconsin, USA) in connection with the changes in water levels and winter conditions [8] The higher stem densities corresponded to larger patch size, greater historical stability, and less fragmentation. In

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addition, larger patches tended to be deeper, and covered a greater range of water depths. Higher stem densities were associated with shallower water, though intermediate depths have experienced the greatest decline.

Although combinations of extreme water levels and winter temperatures did not significantly predict annual changes in area of all common reed stands, these factors explained most of the variance in stands with the greatest loss.

Considerable amount of work to be found about the spreading of reeds and other marsh vegetation in connection with different environmental conditions [10, 30, 33, 65].

Study of macroinvertebrates in various stands of aquatic plant types

There are many references in the literature that the quality and quantity of submerged and emergent macrophyte may play an important role in the spatial and quantitative patterns and the combination of species of the macroinvertebrate fauna [40], thus the relevance of our research is indisputable.

Works written about the flora and fauna tied to the reeds are summarized concisely in the book titled *Fauna of Reeds* [66].

Müller & *al*. researched parts of Lake Tisza with narrowleaf cattail and other aquatic plants [40]. According to their results areas with narrowleaf cattail stands contained the most species and this area also proved to be the richest from the aspect of spiders, insects and mayflies.

There are known results from the aspect of dragonfly and aquatic bug fauna of submerged and emergent macrophyte stands (amongst others *Typha* spp.) of many flatland lakes [43].

Nicolet & *al.* researched wetland plants, macroinvertebrate assemblages and the water's physico-chemical characteristics of 71 temporary ponds in England and Wales [42]. Their work primarily directs attention to the importance of temporary ponds from the point of view of nature conservation.

Dvorak researched the macroinvertebrates and their functional feeding groups in the narrowleaf cattail, common reed and *Nuphar lutea* colonies of a shallow eutrophic lake in the Netherlands [14].

Parson & Matthews' work [45] emphasizes the relation between the macroinvertebrates and the macrophytes, pointing out that this is an insufficiently researched subject in water systems. The authors examined the invertebrate macrofauna of emergent macrophytes (amongst others *Typha latifolia*) and submerged macrophytes (*Potamogeton* and *Ceratophyllum* species) in a small, shallow, eutrophic pond in the USA. They found significant differences in the density of the macroscopic invertebrates of the different aquatic plant types. The biggest differences were observed between the fauna of the emergent and the submerged plants, the causes of this can be traced back to the morphological difference between the plant types.

Olson & *al*. researched the connection of aquatic plants and macroinvertebrates in the USA [44]. The main plants of the area included common reed, *Scirpus acutus*, *Potamogeton spp.* and the narrowleaf cattail which they found to be the colony with most species and also to contain the biggest macroinvertebrate biomass.

Some macroinvertebrate colonies living in different microhabitats were researched in Lake Balaton as well [5]. In this case the different microhabitats were different reed-grass communities. Biró & Hufnagel's works contain important information about Balaton's aquatic and semi-aquatic bug fauna [4, 6], which is very important from our point of view because it includes information about Badacsony Bay as well.

Study of macroinvertebrates in Lake Balaton

The detailed scientific study of Lake Balaton and its surroundings have started over a hundred years ago thanks to the activities of the Hungarian Geographical Society's Balaton Committee. The Committee has started its work on the initiative of Lajos Lóczy with the notion that the lake is endangered by becoming overpopulated with reed-grass. The research materials, the gathered and processed knowledge-base and the conclusions drew from them were published in the monograph titled *The Results of the Scientific Study of Balaton* (BTTE). Sixty writers took part in the completion of the very big, more than 6000 pages long BTTE. The work has also been published in German in its full length.

Zoological research on the other hand, had to be conducted under less fortunate circumstances. For this reason Géza Entz senior the leader of zoological research, emphasized that a well equipped shore side laboratory is needed. Despite this, much later, only in 1926 established the Hungarian National Museum a research base in Révfülöp, which one year later merged into the Hungarian Biological Research Institute (today: Hungarian Academy of Sciences Balaton Limnological Research Institute) at Tihany. The institute's designated mission was to research and get to know the life of Lake Balaton.

After the stagnation of post war years, the fauna research of lake Balaton almost completely stopped during the fifties and the first half of the sixties (due to science policy). The exceptions during these times were the National Museum's department of zoology and the Department of Systematic Zoology of Eötvös Loránd University. A sudden change was caused by the great fish dilapidation of 1965. Balaton was devastated by a number of biological disasters (cyanobacterial blooms, and fish dilapidation) after which studies of plankton and benthos began on the whole open water area of Balaton. Later a program was launched for the zootaxonomic study of the littoral zone. The scientific knowledge accumulated over the years made Lake Balaton one of the most thoroughly researched shallow lakes in the world. A large body of knowledge was gathered about Balaton's open water planktonic and benthonic invertebrates as well as invertebrates of the shore covered by aquatic plants (littoral region). The story of research of invertebrates of lake Balaton was summarised by Ponyi [49] and later by Berczik & Nosek [2]. The story and state of benthos research was reviewed by Dévai on the basis of the 250 existing works [12]. The recent research of invertebrate fauna of littoral zone is reported by G.-Tóth & *al.* [22, 23].

Even in the forties research was conducted by Entz about the macroinvertebrate fauna of different submerged macrophyte stands (*Myriophyllum spicatum* and *Potamogeton perfoliatus*) [15]. He carried out his research around Tihany in submerged macrophyte stands with different water depths. Béla Entz's work primarily concentrated on the description of composition of species, he placed no emphasis on the seasonal changes. Earlier works are characterised by the fact that they neglected seasonal dynamics, just like Ponyi's Crustacea study of Balaton [48]. The author studied beside the above mentioned two main reed-grass types the species *Ceratophyllum submersum* and designated many sampling points all over the Balaton. His work was oriented at the description of the crustacean fauna.

Quantitative research of the macroinvertebrate fauna of *Potamogeton perfoliatus* in Lake Balaton was first conducted by Bíró & Gulyás [7]. The authors took samples from five permanent sampling sites in the north shore of Lake Balaton in the summer months of three years. As they only took samples during two or three summer months, they were not concerned by seasonal changes. The merit of their work lies in quantitative data based on their particular sampling method.

In recent years Muskó & *al.* took quantitative samples of macroinvertebrates for three years in the submerged macrophyte stands of the north shore of Lake Balaton [39] using the sampling method and device described by Bíró & Gulyás. During this research seasonal dynamics were also studied. During a year they took samples on a total of three (May–June, July and October) occasions and in another year they took samples on four occasions (May, July, September and October). Because of the methodology they used, their results are comparable with data gathered in much earlier years. They put special emphasis on the Ponto-Caspian invasive species.

In the scientific literature there are references to the seasonal changes of certain groups that make up the invertebrate macrofauna of Lake Balaton. Seasonal dynamics of certain groups of Balaton invertebrates on offshore bars have also been investigated by Dózsa-Farkas & *al.* [13]. Data about the seasonal fluctuation of certain invertebrates living in settlings and being a part of the fish nutrition were provided by Szító [62].

Materials and methods

Sampling site

The sampling site was designated in a part of Badacsony bay, where different emergent macrophyte stands intersect with open water. The examined plant communities are typical to the littoral zone in this part of Lake Balaton.

Various submerged macrophytes are tipical in front of the emergent macrophyte stands, but did not form continuous vegetation in the year 2002. However large quantities of reed-grass were found in territory of open water in the years 2003 and 2004. We designated three sampling points close to one another. These points were differentiated only by aquatic plant types, which formed the basis for the definition of the three microhabitats. The sampling points are situated 5–7 meters from each other. The sampling site can be reached by boat.

Microhabitats situated close to each other within the determined habitat were chosen in such a way, that differences between samples express exclusively the effect of microhabitats. The goal of our research is not describe the habitat types but to compare the type of microhabitats.

We describe the aquatic plant communities of examined area by Borhidi [9].

- **Reeds**: This type comprises such a community inside the „reed communities" (*Phragmition australis* Koch 1926) where the common reed [*Phragmites australis* (Cav.) Trin.] is dominant. It's called „reeds" (*Phragmitetum communis* Soó 1927 em. Schmal 1926). This community is typical where the littoral zone is in a natural state in Lake Balaton. The common reed is dominant among emergent macrophytes [25]. The lowest water level is noticed in reeds between the three microhabitats. (e.g. if the official water level of Lake Balaton is 60 cm (very shallow), the water level in this place is 70 cm) The stem density is considerable but some smaller inlets are found where the accumulation of vegetable debris may be significant. Samples were taken from marginal zones of reed stands, as well as from dense and from sparse parts. Reeds are never reaped that's why withered reeds provide some shadow in spring.
- **Cattail stands**: It's the "narrowleaf cattail stands" area (*Typhetum angustifoliae* Soó 1927, Pignatti 1953) inside the „reed communities". This species is typical in sublittoral zones of mesotrophic-eutrophic lakes, usually were ooze contains organic matter in large quantities. Cattail stands are sparse in their initial state

but later become dense and high (2.5 m) [9]. In many cases in this part of Lake Balaton these plant communities make up the outer belt surrounding the reeds. Stem density is higher and narrowleaf cattail (*Typha angustifolia* L.) stands are high in this location.
This is where the biggest depth was observed out of the three sampling points probably because this vegetation showed significant advances towards the open water. (e.g. if the official water level of Lake Balaton is 60 cm, the water level in this place is 78 cm). Samples were taken from outer parts of cattail stands as well, from dense parts of cattail and from waters of smaller inlets.

- **Open water**: This expression refers to the place that isn't colonised by emergent macrophytes. In most cases reed-grass stands are found in this area but considerable continuous stands of submerged macrophyte were not observed in the year 2002. Actually all of 2002 may be considered poor in reed-grass because considerable submerged macrophytes wasn't found in even the broader surroundings of the sampling site, which is in contrast with what was observed in earlier years. Continuous spiny naiad (*Najas marina* L.) stands were appeared in the middle of summer in 2003. These reed-grass stands reached the surface by the second half of summer. Spiny naiad frequently constitutes continuous underwater fields in Lake Balaton that are hard to detect. [16]. According to Borhidi, spiny naiad stands (*Najadetum marinae* Fukarek, 1961) are typical in shore side areas with sandy and oozy bottomed shallow lakes that are in the process of salination. This halophyte reed grass is common in shallow waters not inclined to quick warming – areas usually shaded by reeds. According to Felföldy, this cosmopolitan species preferring warm places, with subtropical-mediterranean origin is more common in bays of mesotrophical lakes, where it is found in different reed grass communities, but almost always in a special, to some extent separated position. [18]. Here water depth has a transitional value compared to the shallower reeds and the deeper cattail areas. The claspingleaf pondweed (*Potamogeton perfoliatus* L.) – this submerged macrophyta is the typical reed grass in deeper water in Lake Balaton – appeared by early summer of the year 2004 and densed significantly by the second half of summer. Samples were taken from area of open water surrounded by two emergent macrophyte communities in obtuseangle. When the continuous reed-grass vegetation appeared we took samples from their areas too.
  Actually the *Potamogeton perfoliatus* stands appeared in 2003 but these are found only in deeper waters far away from the sampling site. This reed-grass species constituted of larger continuous fields in the whole area in 2004. We often found some remains of reed-grass in a sampler, in most cases these were the mentioned species and the *Ceratophyllum demersum*. This plant was typical in internal inlets of emergent macrophyte stands farther away from examined locations.

Field work

We strove to take samples frequently from the water body and ooze of the three microhabitats under the period of vegetation during three years. Taking semiquantitative samples by stiff hand net proved to be the most suitable method based on our previous research. The stiff hand net's form is symmetrical hemisphere. The maximum internal diameter is 14.8 cm, mesh size is 0.8 mm.

Taking quantitative samples would be effective but it would lead to difficult problems in area of emergent macrophytes. Nagy & *al* suggest a new sampler and

Figure 2. *Orthophoto of Badacsony Bay taken in the summer of 2002. The sampling site is marked. Areas of cattail form darker territories bordered by the reeds in the littoral zone. (Source: REGINFORM Kft).*

associated sampling procedure for quantitative analysis of the biota in macrophyte-covered water bodies by Aqualex [41]. The Aqualex is a cylinder, it was made of an aluminum plate, its base area is 0.5 m^2 and its height is 1 m. The bottom flange of sampler is sharp, this way it can cut the plants when it is thrown into the water body in vertical position. This method would have been unfortunate to use for two reasons. First this type of sampler is hard to obtain, it has to be manufactured in most cases, and on the other hand it is still unsuitable for collecting samples in an emerged macrophyte type vegetation. During the testing of Aqualex the conclusion was drawn that in case of researching high growth emerged macrophytes, it cannot be viewed as acceptable means of collecting samples [11]. Researchers conducting these tests in the case of this type of vegetation tried the so called "cutting method"(the part of the vegetation above the water level is cut.) This method did not prove to be representative enough, because there were significant differences in the number of taxa and species between samples taken at different times in the treated and untreated areas. The drastic change of the site (cutting of the parts above the water line which provide shade), but mostly the unevenness of the bottom (unevenness makes it impossible to suddenly close the sample taken), make this method unsuitable even on a theoretical basis.

Ten samples were taken from water body by stiff hand net. One drawing includes the whole water column (surface, medium and bottom region). We tried to achieve this objective with S-form drawing. Two samples were taken from upper layer of ooze in every case by the same sampler.

Macrofauna (with some vegetational rubbish were found in sampler) were preserved immediately in 6% formaldehyde. Samples of water body and ooze were handled separately.

Environmental factors concerning the sampling were registered in a notebook on every occasion. In some cases we measured the water depth. Data of official water level were picked up from the homepage of "Országos Vízjelző Szolgálat" (www.hydroinfo.hu). The average difference between official water level and measured water level was calculated.

(This difference is in the case of microhabitat of cattail is: +18 cm, reed: +10 cm, open water: +14 cm.)

Photographs of sampling site were taken for the sake of more exact documentation. We took a photo on every occasion in 2003 (from the same angle). These photos were taken from a boat, standing in the place of open water facing the direction of emergent macrophytes. The Badacsony Hill can be seen in background. (e.g. *Fig. 3*).

Figure 3. *Photograph of the sampling site taken on July 13th 2003.*

The period of field work lasted from spring to late autumn. Samples were taken in 2002 between 29 April and 16 November on 16 occasions. Unfortunately due to the extreme weather conditions (remarkably intensive waves) we had to finish the sampling in some cases, therefore some samples were left out. (These data are marked by a "?" in *Fig. 8*)

We took samples on 13 occasions from 31st of March to 9th of November 2003. The *Najas marina* stands were observed on 13th July for the first time. This plant constituted smaller underwater fields in a few places at this time. The spiny naiad reached the surface by the second half of July and this vegetation became dense during August. It sank to the bottom by October and formed an accumulated layer reaching to the borders of the emergent macrophyte stands.

Samples were taken altogether on seven occasions between 17th of April and 29th of November. At first we could observe the *Potamogeton perfoliatus* stands in June in the area of open water sampling site. In the months of June and July it formed a dense stand and in October there was a significant amount of reed grass accumulated in front of the emergent macrophyte stands.

The water level of Lake Balaton was extremely falling in consequence of the drought that begun in 2000. This process reached its negative peak in 2003 when low water levels not seen since the 1920's were recorded (this information is also available at www.hydroinfo.hu) The water level of Lake Balaton was significantly higher in 2004.

Of the sampling occasions the official water level was the highest on 30 June 2004 (82 cm) and the lowest on 19 October 2003 (24 cm). Both values, especially the minimum value in 2003, may be considered to be under the average water level corresponding to season, consequently the field-work was done under very droughty period.

Processing of samples

Maroinvertebrates were selected on the basis of taxon and body size categories (morphon). Animals were classified as the most precise taxon category [3, 19, 37, 47, 58, 60, 61], in several cases identification to species was finished. Remains of animals (e.g. shell, exuvium) were also collected and categorised. Body size categories are important primarily from the aspect of calculating biovolume. We used five fundamental size categories (I–V) and some special size categories. The Ia. category was used for the case of Cladocera and Aphidinea, just over 1 mm size and in the case of Tubificidae, smaller (I–II–III) and larger (IV–V) categories were used. If some individuals proved to be particularly large, their length was registered (only some Tubificidae, on average 7 cm). For the Chi^2 test and the stochastic simulation (bootstrapping) we used the number of specimens, but in all other parts of our work we used the biovolume value of collected animals because both biomass and biovolume values represent quantity of macroinvertebrates rather than the number of individuals. Establishing dry mass is very troublesome it is worth to use biovolume instead. Calculation is based on comparing the form of animals to simple geometrical forms. The volume of geometrical forms may be calculated in a simple way. The invertebrates were compared to sphere ($V \doteq \pi d^2$) or to cylinder ($V = \pi r^2 m$) (V = volume, d = diameter, r = radius, m = length, in millimeters.) The two subversion of cylinder geometrical form are the 'cylinder / 2' and 'thread' counted by cylinder's formula with smaller and smaller radius. Taxa with the corresponding geometrical forms are in *Fig. 2* and the values of length, diameter and radius can be seen in *Fig. 1*. Contracted tables were made for examination of spatial patterns, in which rows contain the microhabitats (samples of ooze and water body are separately) and the columns contain the morphons. Under the multivariate analysis we conducted the hierarchical clustering and ordination (non-metric multidimensional scaling) of morphons based on sampling sites (microhabitat–surface combination) and of sampling sites based on morphons. Based on these results, tables were rearranged. As the similarity measure we used the Morisita index, because this index is not sensitive to the variatons of morphon numbers. We made a new table in which the rows represented the higher taxon categories, the columns the sampling sites (microhabitat-surface combination), and the cells contained

Table 1. *The meaning of size categories and the values of lenght (m), diameter (d) and radius (r) corresponding to the size intervals used during biovolume calculations (in mm).*

size category	meaning	*m*	*d* (sphere)	*r* (cylinder)	*r* (cylinder2)	*r* (thread)
I	>1 mm	1	1	0.15	0.075	0.05
II	1–5 mm	5	5	0.75	0.375	0.25
III	5–10 mm	10	10	1.5	0.75	0.50
IV	10–15 mm	15	15	2.25	1.125	0.75
V	15 mm<	20	20	3	1.5	1.00
Ia	2 mm	2	2	—	—	—
I, II, III	>10 mm	8	—	—	—	0.40
IV, V	10 mm<	20	—	—	—	1.00
V (special case)	e.g. 70 mm	70	—	—	—	3.50

the numbers of the individuals. From every column random samples were taken with an Excel macro developed by ourselves. With the aim of this stochastic simulation (bootstrapping) we can generate arbitrary number of pseudo-replicates. In this case 10 new objects, each containing 1000 macroinvertebrate specimens, have been randomly generated. The comparisons of each year and microhabitats based on certain significant taxa were conducted with Turkey's pairwise comparisons.

For the examination of diversity the use of morphons proved to be the most suitable method – since the full list of species is not available – as any type of abundant object system's diversity, falling into any disjunct category may be in question [27].

We used the biovolume values for calculations instead of the number of species. Based on this we examined the morphon's biovolume diversity. The table used for the calculations included the value of biovolume in mm^3 in each microhabitat in each year. To compare diversity relations, Rényi's diversity ordering has been applied.

The seasonal dynamics of volume of macroinvertebrates collected during the three years are rendered in graphs.

The PAST program [55] has been used for multivariate data analysis.

Use of concepts

Macroinvertebrate assemblies

The macroinvertebrate category categorises the invertebrate animals found in the particular habitat by their sizes. The bottom size category is defined by the mesh (0.8 mm) on the hand net serving as the sampling device. This term is used in a very wide sense, because according to the principles of zoocoenological sampling [1], every animal in the sample were accounted with. Thus the samples include animals under the mash size that got into the sample with debris (e.g. some Cladocera and Copepoda) and larval or juvenile stage of fishes. Separating the larval and juvenile stage of fishes and other groups from "real" macroinvertebrates would lead to great loss of information. Mostly because of the larval and juvenile fishes it would be worth to use a different term instead of macroinvertebrates but we feel it is more adequate to use and to interpret the term along with the known limitations. In the light of the above said: the term "macroinveretbrate assemblies" is to be interpreted along with the groups that otherwise would not fit into this category, either because of their size range (certain planktonic invertebrates) or taxonomical state (larval and juvenile fish).

Microhabitat

The smaller part of the researched water habitat which has externally well identifiable structural properties (such as water depth, bottom type, vegetation, water current characteristics) based on which it may be viewed as a homogenus habitat part from the aspect of the given research [26]. Our samples were taken from three microhabitats, which differ mostly in terms of vegetation, thus their naming was done accordingly: reeds, narrowleaf cattail stands and open water

Morphon

A category that takes into account the given animal's taxonomical position, ontological state and body size at the same time. The use of this category is justified for more reasons. The body size is important for the calculation of biovolume, on the other hand different sized individuals of certain species (in addition larvae and adults) may be typical to different microhabitats and/or different time intervals.

Results

Faunistic overview

Table 2 shows all the identified species and other taxa. The geometrical forms – needed for biovolume calculation – are shown in the second column. The next three columns contain average biovolume values (mm^3) of animals which were collected during the three years. Samples of three microhabitats differ significantly based on the results of Chi^2 test.

Based on *Table 2*, following statements can be made about macroinvertebrate fauna:

- Considerable quantities of Ponto-Caspian species were found in samples. *Limnomysis benedeni* has a particurarly large biovolume. This species was introduced in 1950's as a source of nutrition for fish [68]. Together with this species the *Dikerogammarus* species (Amphipoda) appeared and multiplied [48], these were collected too. Other typical representative of Amphipoda suborder is the *Corophium curvispinum*, it appeared together with zebra mussel (*Dreissena polymorpha*) in the lake in 1930's [38].
- Particurarly large quantities of Tubificidae and Chironomidae were found. These benthic animals primarly live in ooze.
- *Leptodora kindtii* considered to be typical in Lake Balaton are also found together with the other Cladocera.
- The most taxa are detectable in the reeds microhabitat.
- Bivalvia, Gastropoda, Hirudinea and larvae of Ephemeroptera and Zygoptera were found in significant quantities in reeds compared to other microhabitats.
- The most of Arachnoidea are spiders fallen to the water or semi-aquatic spiders, the smaller part is comprised of Hydrachnidae. Probably the reeds provide the most suitable habitat for these groups.
- Biovolume of Chironomidae larvae and Tubificidae are the most significant in cattail stands microhabitat.
- The most larval and juvenile stage of fishes are also found in cattail stands.
- *Dikerogammarus* spp. and *Argulus* spp. belong mostly to cattail stands among crustaceans.
- The least taxa are found in open water and usually in the smallest biovolume values too.
- The most planktonic crustaceans (Cladocera and Copepoda) belong to open water.

Spatial zoocoenological patterns

Under the multivariate analysis we conducted the hierarchical clustering and ordination of morphons based on sampling sites (microhabitat-surface combination) and of sampling sites based on morphons. Samples of ooze and water body were separated based on results of classification of sampling sites. Samples of reeds and cattail stands were situated close to each other in 2002, on the other hand in other years samples of cattail stands and open water were close to each other. Ordination results of morphons (based on sampling sites) are depicted in *Figs. 4–6*, and for the list of morphons with the appropriate serial numbers see *Table 3*.

Table 2. *The identified species and other taxa with the corresponding geometrical forms (to which invertebrates were compared to during biovolume calculations) and the average biovolume values of taxa (mm^3) gathered during the three years in all three microhabitats.*

taxa	form	cattail	reed	open water
HYDROZOA				
Hydra circumcincta Shulze	cylinder	0	0.9	0.5
OLIGOCHAETA				
(other) Tubificidae**	thread	690.9	493.0	400.6
Branchiura sowerbyi Beddard*	thread	423.3	227.7	321.7
Pristina sp.	thread	3.4	3.9	3.6
HIRUDINEA				
Piscicola geometra L.	cylinder/2	3.9	11.3	0.4
Glossiphonia heteroclita L.	cylinder	1.0	2.7	0.1
Erpobdella octoculata L.	cylinder	8.1	12.7	0
Helobdella stagnalis L.	cylinder	0.5	2.2	0.1
BIVALVIA				
Dreissena polymorpha Pall.	sphere	30.3	96.2	28.1
Pisidium sp.	sphere	0	1.1	0
GASTROPODA				
Acroloxus lacustris L.	cylinder	0.1	0.6	0.1
(other) Gastropoda	sphere	85.3	157.6	57.4
ARACHNOIDEA				
Hydrachnidae	sphere	1.5	6.1	1.9
Araneidea	sphere	7.9	18.8	1.2
CRUSTACEA				
Limnomysis benedeni Czern.	cylinder	502.8	460.7	577.5
Dikerogammarus sp.	cylinder	48.0	15.2	2.1
Corophium curvispinum G.O. Sars	cylinder	5.3	6.7	1.1
Argulus sp.	cylinder	3.2	1.5	0.4
Leptodora kindtii Focke	cylinder	42.8	16.4	32.6
(other) Cladocera	sphere	21.9	13.1	100.8
Asellus aquaticus L.	cylinder	1.0	4.2	0
Copepoda	cylinder	0.04	0.02	0.04
COLLEMBOLA	cylinder	0	0.1	0
EPHEMEROPTERA				
Caenidae	cylinder	0.3	10.0	0.3
Baetidae	cylinder	26.4	66.8	39.2
ODONATA				
Ischnura sp.	cylinder	22.3	172.1	12.7
Anisoptera	cylinder	0	0	3.6
HOMOPTERA (Aphidinea)	sphere	0	5,9	0

**The particurarly big sized Tubificidae were separated. These were identified down to species level (Branchiura sowerbyi).*

***Other Tubificidae: Species identification was finished in some cases, where the big part of them were Pothamotrix sp.*

****We identified the larval and juvenile stage of fishes (Cyprinidae) [47] but species identification happened in only some of the cases. Three species are likely to be found in most cases: Rutilus rutilus L., Scardinius erythrophthalmus L. or Alburnus alburnus L. (one individual may be Rhodeus sericeus amarus Bloch).*

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Table 2 **(continued).**

taxa	form	cattail	reed	open water
HETEROPTERA				
Aquarius paludum paludum Fabr.	cylinder	16.7	1.0	0
(other) Gerridae	cylinder	0.4	0.5	0
Micronecta meridionalis Costa.	cylinder	13.5	3.5	15.0
Sigara sp.	cylinder	0	1.0	3.4
Sigara striata L.	cylinder	1.0	3.0	0
(other) Corixidae	cylinder	0.1	0	0.4
Microvelia sp.	cylinder	0.3	0	0.1
Microvelia reticulata Scholtz.	cylinder	0	2.6	0
Mesovelia furcata Mulsant & Rey	cylinder	0.6	0.2	0
Ranatra linearis L.	cylinder	0	8.0	0
TRICHOPTERA				
Hydroptilidae	cylinder	0.3	0	0
Polycentropodidae	cylinder	0.5	1.6	0.1
Limnephilidae	cylinder	0	0	0.1
(other) Trichoptera	cylinder	0.003	0.002	0.3
DIPTERA				
Chironomidae	cylinder/2	185.4	138.2	170.2
Ceratopogonidae	cylinder/2	10.3	12.5	6.1
Tipulidae	cylinder	1.0	0	0
Tabanidae	cylinder	0.3	0.2	0
Syrphidae	cylinder	0.3	0	0
„Diptera puparium”	cylinder	8.1	2.9	16.0
„Diptera imago”	cylinder	5.8	4.2	1.6
PISCES (Cyprinidae)***	cylinder	134.4	20.4	3.2

The groups that are typical of ooze and of the water body may be sharply isolated based on results of classification and ordination of morphons.

Making statements about observed macroinvertebrate groups is troublesome in most of the cases. Exact statements can be made about only abundant morphons.

The following groups are typical considering all three years at the same time:

- **Typical in ooze**. Tubificidae, Chironomidae and Ceratopogonidae have significant biovolume values in ooze of every examined microhabitats. It seems the snails are also more likely to come out of ooze, tied less to microhabitats.
- **Primarily living in ooze of reeds**. Mostly *Helobdella stagnalis* and *Glossiphonia heteroclita* leech species.
- **Primarily living in water body of cattail stands.** Bigger individuals of *Dikerogammarus* species, *Argulus* sp., in general the *Aquarius paludum* (with the exception of 2004 when it hardly came into the samples.), *Mesovelia furcata* (primarily its adults) and certain larval and juvenile Cyprinidae
- **Primarily living in water body of reeds**. In general the *Dreissena polimorpha*, *Erpobdella octoculata* and Aphidinea taxa – if any – mostly come out of waters of reeds. The *Ischnura* sp. and *Sigara striata* adult in 2002 and 2003 were found in the reeds, while in 2004 it could be found in cattail stands just as much as in reeds. Caenidae proves to be more of a reeds type. *Hydra circumcincta* is found in the reeds but there are more found in the open water in 2004

Table 3. *The list of morphons with the appropriate serial number (S) derived from the taxonomic name, the category of body size, and in some cases from the state of ontogenesis (larva, pupa, adult).*

S	morphon		S	morphon	
1	*Hydra circumcincta*	II	45	Collembola	II
2	Tubificidae	I, II, III	46	Caenidae larvae	II
3	Tubificidae	IV, V	47	Caenidae larvae	III
4	*Branchiura sowerbyi*	V	48	Baetidae larvae	II
5	*Pristina* sp.	I	49	Baetidae larvae	III
6	*Pristina* sp.	II	50	Ischnura sp. larvae	II
7	*Piscicola geometra*	II	51	Ischnura sp. larvae	III
8	*Piscicola geometra*	III	52	Ischnura sp. larvae	IV
9	*Piscicola geometra*	IV	53	Ischnura sp. larvae	V
10	*Glossiphonia heteroclita*	II:	54	Anisoptera larvae	IV
11	*Erpobdella octoculata*	II	55	Gerridae larvae	II
12	*Erpobdella octoculata*	III	56	*Aquarius paludum* larvae	III
13	*Erpobdella octoculata*	IV	57	*Aquarius paludum*	IV
14	*Erpobdella octoculata*	V	58	*Microvelia* sp. larvae	II
15	*Helobdella stagnalis*	II	59	*Microvelia reticulata*	II
16	*Dreissena polymorpha*	II	60	*Mesovelia furcata* larvae	II
17	*Dreissena polymorpha*	III	61	*Mesovelia furcata*	II
18	*Dreissena polymorpha*	V	62	Corixidae larvae	II
19	*Pisidium* sp.	II	63	*Micronecta meridionalis* larvae	II
20	other Gastropoda	Ia	64	*Micronecta meridionalis*	II
21	other Gastropoda	II	65	*Sigara* sp. larvae	II
22	other Gastropoda	III	66	*Sigara* sp. larvae	III
23	*Acroloxus lacustris*	II	67	*Sigara striata*	III
24	Hydrachnidae	Ia	68	*Ranatra linearis* larvae	V
25	Hydrachnidae	II	69	Aphidinea	I
26	Araneidea	II	70	Aphidinea	Ia
27	Araneidea	III	71	Coleoptera	II
28	*Limnomysis benedeni*	I	72	Coleoptera larvae	II
29	*Limnomysis benedeni*	II	73	other Trichoptera larvae	I
30	*Limnomysis benedeni*	III	74	Hydroptilidae larvae	II
31	*Dikerogammarus* sp.	I	75	Polycentropodidae larvae	II
32	*Dikerogammarus* sp.	II	76	Limnephilidae larvae	II
33	*Dikerogammarus* sp.	III	77	Chironomidae larvae	I
34	*Dikerogammarus* sp.	IV	78	Chironomidae larvae	II
35	*Dikerogammarus* sp.	V	79	Chironomidae larvae	III
36	*Corophium curvispinum*	II	80	Chironomidae larvae	IV
37	*Argulus* sp.	II	81	Chironomidae larvae	V
38	*Argulus* sp.	III	82	Ceratopogonidae larvae	II
39	*Leptodora kindti*	II	83	Ceratopogonidae larvae	III
40	other Cladocera	I	84	Ceratopogonidae larvae	IV
41	other Cladocera	Ia	85	Ceratopogonidae larvae	V
42	*Asellus aquaticus*	II	86	Tipulidae larvae	III
43	*Asellus aquaticus*	III	87	Tabanidae larvae	III
44	Copepoda	I	88	Syrphidae larvae	IV
89	Diptera pupa	II	94	Cyprinidae young larvae	III
90	Diptera pupa	IV	95	Cyprinidae intermediate larvae	III
91	Diptera adult	II	96	Cyprinidae older larvae	IV
92	Diptera adult	III	97	Cyprinidae young juveniles	IV
93	Diptera adult	IV	98	Cyprinidae young juveniles	V

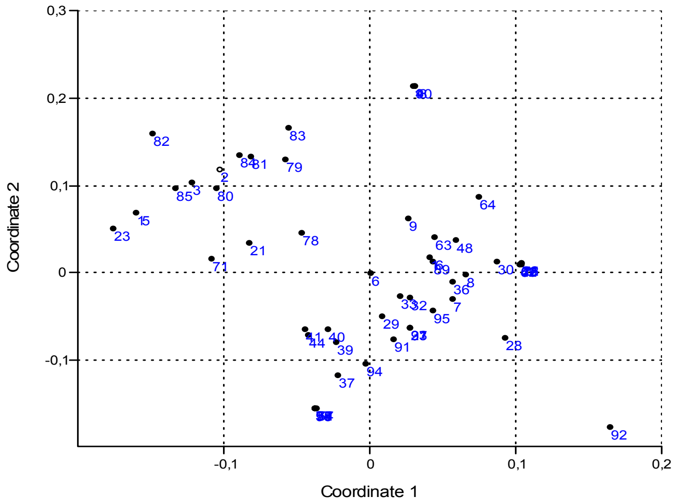

Figure 4. *Ordination results of morphons based on sampling sites – 2002 (non-metric multidimensional scaling). For the meaning of the numbers see Table 3. Results of cluster analysis support the results of ordination.*

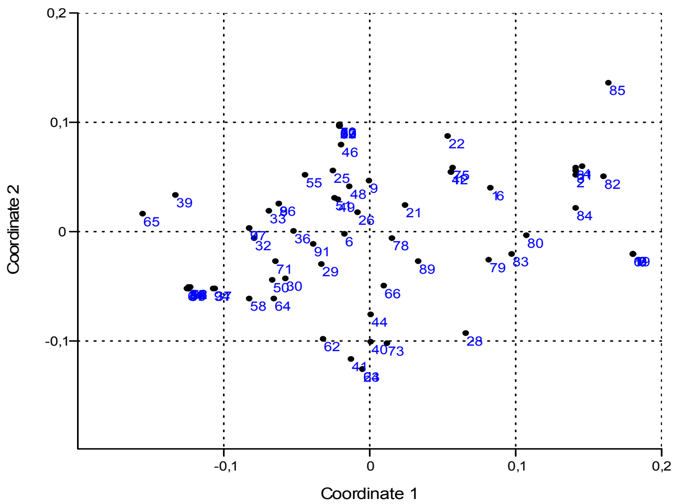

Figure 5. *Ordination results of morphons based on sampling sites – 2003 (non-metric multidimensional scaling) For the meaning of the numbers see Table 3. Results of cluster analysis support the results of ordination.*

- **Typical in water body of reeds and cattail stands alike**. *Corophium curvispinum* definitely belongs to this category. Part of *Piscicola geometra* and smaller sized *Dikerogammarus* taxa also belong here. In 2004 *Ischnura* sp., most of *Acroloxus lacustris*, and smaller Caenidae and *Sigara striata* belonged here.
- **Primarily living in water body of open water**. There was no such group in 2002. Cladocera (including *Leptodora kindtii*) is definitely typical here. And in 2003 larvae of Corixidae.
- **Typical in water body (generally) and – in small quantities – in ooze**. Cladocera which, at other times is typical in open waters belonged to this category in 2002.

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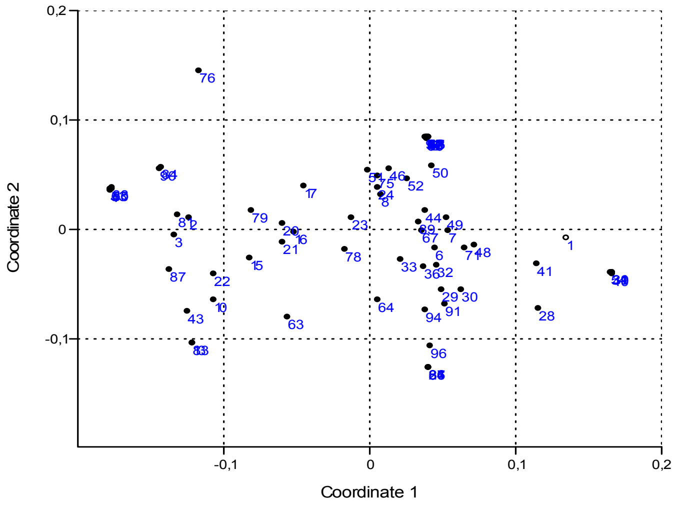


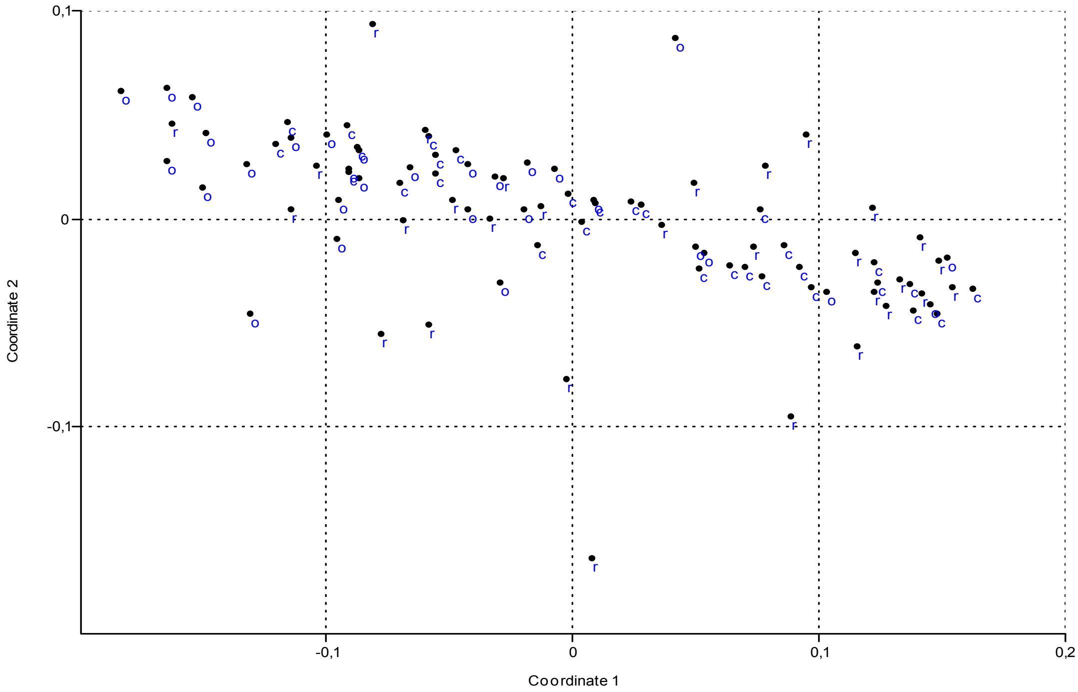
Figure 6. *Ordination results of morphons based on sampling sites – 2003 (Non-metric Multidimensional Scaling) For the meaning of the numbers see Table 3. Results of cluster analysis support the results of ordination.*

Also belonging to this group are the planktonic crustacean: Copepoda. In general *Pristina sp*, *Baetidae*, an certain individuals of *Piscicola geometra* and most of the *Limnomysis benedeni* belonged here.

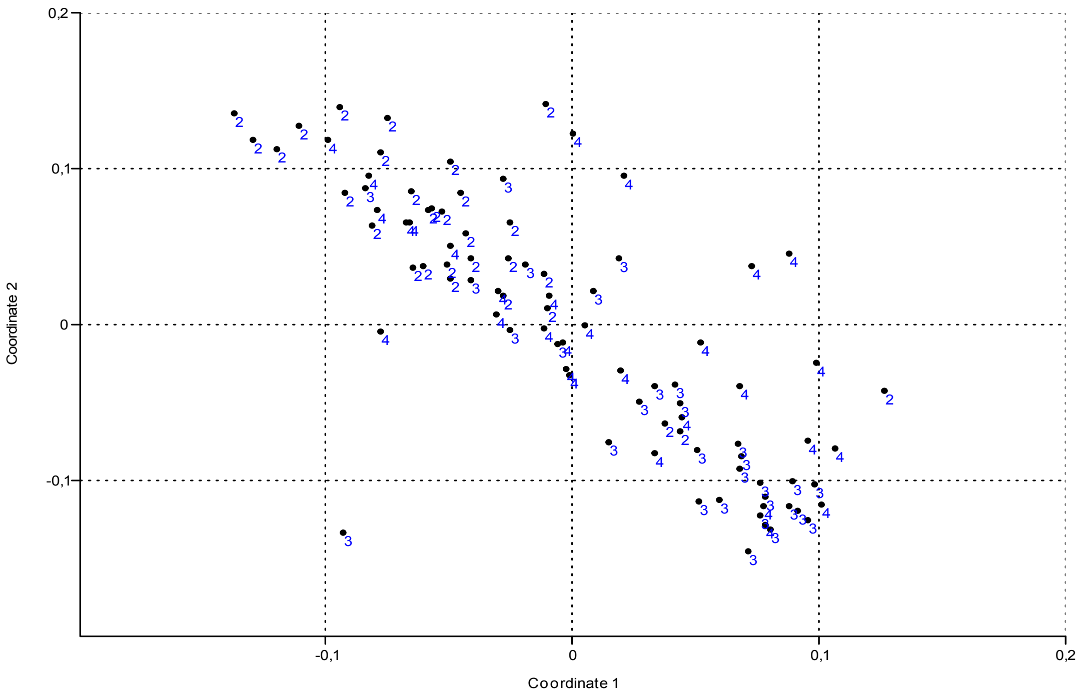
- In the years 2002 and 2003 *Argulus sp* and the young larvae of Cyprinidae together formed a separate group. In 2002 they were linked exclusively to reeds and in 2003 they were linked to the open water and the waters of cattail stands. They belonged into the same group in 2004 too amongst other species characterised by the waters of cattail stands.

Table 4. *Value of higher level taxa (number of individuals) in th examined three years and the three microhabitats (open w. = open water). With the aim of stochastic simulation (boot-strapping) we generated pseudo-replicates based on this data matrix.*

Taxa	**2002**			**2003**			**2004**		
	cattail	**reed**	**open w.**	**cattail**	**reed**	**open w.**	**cattail**	**reed**	**open w.**
Hydrozoa	—	—	—	—	6	—	—	1	4
Oligochaeta	649	658	261	1244	821	845	662	477	574
Hirudinea	6	2—	2	5	17	—	19	49	4
Bivalvia	13	29	1	4	14	3	4	18	5
Gastropoda	8	2	1	17	51	25	13	58	21
Arachnoidea	1	4	—	3	7	6	3	5	—
Crustacea	1525	1318	88—	27—	115	1149	577	216	851
Collembola	—	—	—	—	—	—	—	1	—
Ephemeroptera	1	3	—	2—	112	42	36	96	75
Odonata	—	2	—	11	46	11	7	33	4
Heteroptera	3	9	6	36	28	33	87	24	91
Aphidinea	—	—	—	—	26	—	—	8	—
Coleoptera	1	6	—	4	1	2	1	2	1
Trichoptera	2	1	—	6	9	2	2	5	2
Chironomidae	228	286	175	164	138	164	76	75	86
(Other) Diptera	12	19	9	19	29	14	15	9	8
Pisces/Cyprinidae	8	5	—	23	2	3	31	4	—



a



b

***Figure** 7. Similarity pattern of the objects (unfiltered data matrix; see Table 4) by stochastic simulation (bootstrapping).* **a.** *Objects mean the microhabitats (c = cattail, r = reed, o = open water).* **b.** *Objects mean the years (2 = 2002, 3 = 2003, 4 = 2004)*

Table 5. *The results of Turkey's pairwise comparisons of microhabitat-year combinations' stochastic simulated data (c = cattail, r = reed, o = open water) in case of Hirudinea (unfiltered data matrix; see Table 4).*

	c 2002	r 2002	o 2002	c 2003	r 2003	o 2003	c 2004	r 2004	o 2004
c 2002		0.663	**1.000**	**1.000**	0.253	**1.000**	0.225	*0.000*	**1.000**
r 2002	2.587		0.521	0.792	**0.999**	0.283	**0.998**	*0.000*	0.739
o 2002	0.297	2.884		**1.000**	0.165	**1.000**	0.144	*0.000*	**1.000**
c 2003	0.297	2.290	0.594		0.367	**0.996**	0.332	*0.000*	**1.000**
r 2003	3.520	0.933	3.817	3.223		0.065	**1.000**	*0.000*	0.315
o 2003	0.848	3.435	0.551	1.145	4.368		0.055	*0.000*	**0.998**
c 2004	3.605	1.018	3.902	3.308	0.085	4.453		*0.000*	0.283
r 2004	11.490	8.907	11.790	11.200	7.974	12.340	7.889		*0.000*
o 2004	0.170	2.417	0.467	0.127	3.351	1.018	3.435	11.320	

Table 6. *The results of Turkey's pairwise comparisons of microhabitat-year combinations' stochastic simulated data (c = cattail, r = reed, o = open water) in case of Gastropoda (unfiltered data matrix; see Table 4).*

	c 2002	r 2002	o 2002	c 2003	r 2003	o 2003	c 2004	r 2004	o 2004
c 2002		**1.000**	**1.000**	**0.999**	*0.001*	**0.949**	**1.000**	*0.000*	**0.994**
r 2002	0.619		**1.000**	**0.973**	*0.000*	0.767	**0.996**	*0.000*	**0.929**
o 2002	0.707	0.088		**0.962**	*0.000*	0.730	**0.994**	*0.000*	**0.909**
c 2003	0.937	1.555	1.644		0.011	**1.000**	**1.000**	*0.003*	**1.000**
r 2003	6.186	6.804	6.893	5.249		0.055	*0.004*	**1.000**	0.020
o 2003	1.732	2.351	2.439	0.795	4.454		**0.995**	0.019	**1.000**
c 2004	0.530	1.149	1.237	0.407	5.655	1.202		*0.001*	**1.000**
r 2004	6.716	7.334	7.423	5.779	0.530	4.984	6.186		*0.006*
o 2004	1.219	1.838	1.926	0.283	4.966	0.513	0.689	5.496	

Table 7. *The results of Turkey's pairwise comparisons of microhabitat-year combinations' stochastic simulated data (c = cattail, r = reed, o = open water) in case of Ephemeroptera (unfiltered data matrix; see Table 4).*

	c 2002	r 2002	o 2002	c 2003	r 2003	o 2003	c 2004	r 2004	o 2004
c 2002		**1.000**	**1.000**	**0.980**	*0.000*	0.772	0.424	*0.000*	*0.006*
r 2002	0.089		**1.000**	**0.987**	*0.000*	0.807	0.464	*0.000*	*0.008*
o 2002	0.022	0.111		**0.978**	*0.000*	0.763	0.414	*0.000*	*0.006*
c 2003	1.475	1.386	1.497		*0.001*	**1.000**	**0.965**	*0.000*	0.118
r 2003	7.762	7.673	7.784	6.287		*0.007*	0.037	0.010	0.802
o 2003	2.340	2.251	2.362	0.865	5.422		**1.000**	*0.000*	0.394
c 2004	3.094	3.005	3.116	1.619	4.668	0.754		*0.000*	0.744
r 2004	13.040	12.950	13.060	11.570	5.278	10.700	9.947		*0.000*
o 2004	5.500	5.411	5.522	4.025	2.262	3.160	2.406	7.540	

We generated pseudo-replicates based on stochastic simulation (bootstrapping). The unfiltered data matrix is shown in *Table 4*. We can make the following statements based on results of ordination of these groups (*Fig. 7*):

Strongly separated differences aren't observed between microhabitats because the points that symbolized microhabitats are situated closely to one another *Fig. 8a*. The years are separated better. (*Fig. 8b* 2002 more in the upper part of the figure, in the lower parts 2003, and finally 2004 mostly in the centre and lower parts.)

Table 8. *The results of Turkey's pairwise comparisons of microhabitat-year combinations' stochastic simulated data (c = cattail, r = reed, o = open water) in case of Odonata (unfiltered data matrix; see Table 4).*

	c 2002	r 2002	o 2002	c 2003	r 2003	o 2003	c 2004	r 2004	o 2004
c 2002		**1.000**	**1.000**	**0.951**	*0.000*	**0.961**	**0.997**	*0.000*	**0.987**
r 2002	0.241		**1.000**	**0.980**	*0.000*	**0.985**	**1.000**	*0.000*	**0.997**
o 2002	0.000	0.241		**0.951**	*0.000*	**0.961**	**0.997**	*0.000*	**0.987**
c 2003	1.718	1.478	1.718		*0.001*	**1.000**	**1.000**	*0.000*	**1.000**
r 2003	8.008	7.767	8.008	6.289		*0.001*	*0.000*	*0.003*	*0.000*
o 2003	1.650	1.409	1.650	0.069	6.358		**1.000**	*0.000*	**1.000**
c 2004	1.100	0.859	1.100	0.619	6.908	0.550		*0.000*	**1.000**
r 2004	13.850	13.610	13.850	12.130	5.843	12.200	12.750		*0.000*
o 2004	1.375	1.134	1.375	0.344	6.633	0.275	0.275	12.480	

Table 9. *The results of Turkey's pairwise comparisons of microhabitat-year combinations' stochastic simulated data (c = cattail, r = reed, o = open water) in case of Heteroptera (unfiltered data matrix; see Table 4).*

	c 2002	r 2002	o 2002	c 2003	r 2003	o 2003	c 2004	r 2004	o 2004
c 2002		**1.000**	**1.000**	0.609	0.045	0.429	*0.000*	*0.004*	*0.000*
r 2002	0.400		**1.000**	0.787	0.093	0.618	*0.001*	0.010	*0.000*
o 2002	0.533	0.133		0.836	0.117	0.680	*0.001*	0.013	*0.000*
c 2003	2.702	2.302	2.169		**0.923**	**1.000**	0.087	0.473	*0.001*
r 2003	4.566	4.167	4.034	1.865		**0.980**	0.772	**0.997**	0.081
o 2003	3.082	2.683	2.550	0.381	1.484		0.163	0.654	*0.004*
c 2004	6.907	6.507	6.374	4.205	2.340	3.824		**0.994**	**0.914**
r 2004	5.689	5.289	5.156	2.987	1.123	2.607	1.218		0.412
o 2004	8.809	8.410	8.277	6.107	4.243	5.727	1.903	3.120	

Table 10. *The results of Turkey's pairwise comparisons of microhabitat-year combinations' stochastic simulated data (c = cattail, r = reed, o = open water) in case of larval and juvenile fish (Cyprinidae) (unfiltered data matrix; see Table 4).*

	c 2002	r 2002	o 2002	c 2003	r 2003	o 2003	c 2004	r 2004	o 2004
c 2002		**0.955**	0.541	0.445	**0.944**	**0.931**	*0.000*	**1.000**	0.541
r 2002	1.693		**0.996**	0.032	**1.000**	**1.000**	*0.000*	0.880	**0.996**
o 2002	2.843	1.151		*0.002*	**0.998**	**0.999**	*0.000*	0.385	**1.000**
c 2003	3.047	4.739	5.890		0.028	0.024	*0.000*	0.606	*0.002*
r 2003	1.760	0.068	1.083	4.807		**1.000**	*0.000*	0.860	**0.998**
o 2003	1.828	0.135	1.016	4.875	0.068		*0.000*	0.837	**0.999**
c 2004	11.100	12.800	13.950	8.057	12.860	12.930		*0.000*	*0.000*
r 2004	0.339	2.031	3.182	2.708	2.099	2.166	10.760		0.385
o 2004	2.843	1.151	0.000	5.890	1.083	1.016	13.950	3.182	

Some characteristics observed in the similarity relation of certain years and certain microhabitats based on significant taxon categories (Turkey's pairwise comparisons; *Tables 5–10*).

- Generally there are only minimal differences between the microhabitats within the same year. This is especially true for the year 2002 and 2003 mostly in the case of Heteroptera. The same can be said about Gastropoda, Ephemeroptera

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and Odonata in the year 2002. In this case data corresponding to cattail in 2003 are completely identical to those of 2002.

Table 11. *The morphon/biovolume diversity indexes belonging to the three microhabitats (c = cattail, r = reed, o = open water) during 2002, 2003 and 2004.*

	2002 c	2002 r	2002 o	2003 c	2003 r	2003 o	2004 c	2004 r	2004 o
morphons	43	46	29	53	56	41	52	58	38
biovolume	30874	49733	32370	77059	58198	42792	54167	35176	45850
dominance	0.14	0.19	0.28	0.22	0.14	0.16	0.20	0.11	0.40
Shannon index	2.42	2.23	1.92	2.09	2.51	2.34	2.22	2.80	1.61
Simpson index	0.86	0.81	0.72	0.78	0.86	0.84	0.80	0.89	0.60
Menhinick	0.24	0.21	0.16	0.19	0.23	0.20	0.22	0.31	0.18
Margalef	4.06	4.16	2.70	4.62	5.01	3.75	4.68	5.45	3.45
equitability	0.64	0.58	0.57	0.53	0.62	0.63	0.56	0.69	0.44
Fisher alpha	4.92	5.00	3.14	5.56	6.11	4.47	5.67	6.78	4.07
Berger–Parker	0.25	0.35	0.50	0.35	0.28	0.34	0.37	0.21	0.61

- In 2004 data of reeds often differ completely from all other data in the same period. In the case of Hirudinea and Odonata the difference is complete and in the case of Gastropoda and Heteroptera there are only a few exceptions.
- Data of reeds in 2003 also differ in a lot of cases (Gastropoda and Ephemeroptera) from all others but mostly from those of 2002.
- In 2004 data of cattail and open water show great similarity with all the data of 2002 (Gastropoda, Odonata).
- However, in the case of Heteroptera samples taken 2004 differ in almost every case from the ones taken in 2002.
- In the case of Ephemeroptera in 2002 the data corresponding to open water differ from all others, and in the case of Cyprinidae data of cattail in 2004 differ.

Diversity

Table 11 contains the values of the diversity indexes. The diversity profiles are shown in pairs on *Figs. 8a–f.* The most morphons belong to the reeds in each year and the least to the open water. In 2003 and 2004 the total biovolume values show a different picture. The dominance index is highest in the open water except of 2003 when it is highest in the cattail stands. In case of equitability similar incidents can be observed with the opposite signs. Based on the Shannon and Simpson indices and Menhinick index the reeds proved to be the most diverse, except 2002 when the cattail stands were the most diverse. According to the Margalef index the highest value belongs to the reeds in each year. The Berger-Parker index yields a different value for each year. Based on the diversity ordering the following characteristics may be observed:

- In 2002 cattail and reed cannot be put in order because the profiles intersect. Based on the position and shape of the profiles we may make the assumption that in case of dominant morphons the cattail stands are richer but in the case of rare morphons there is no significant difference on the side of reeds. In the same year the open water may be considered less diverse than the cattail and common reed stands in every domain of the scale parameter.
- In 2003 reeds proves to be more diverse than open water and cattail in every domain of the scale parameter. In 2003 cattail and open water cannot be put in order because the profiles intersect. Based on the position and shape of the profiles we may assume

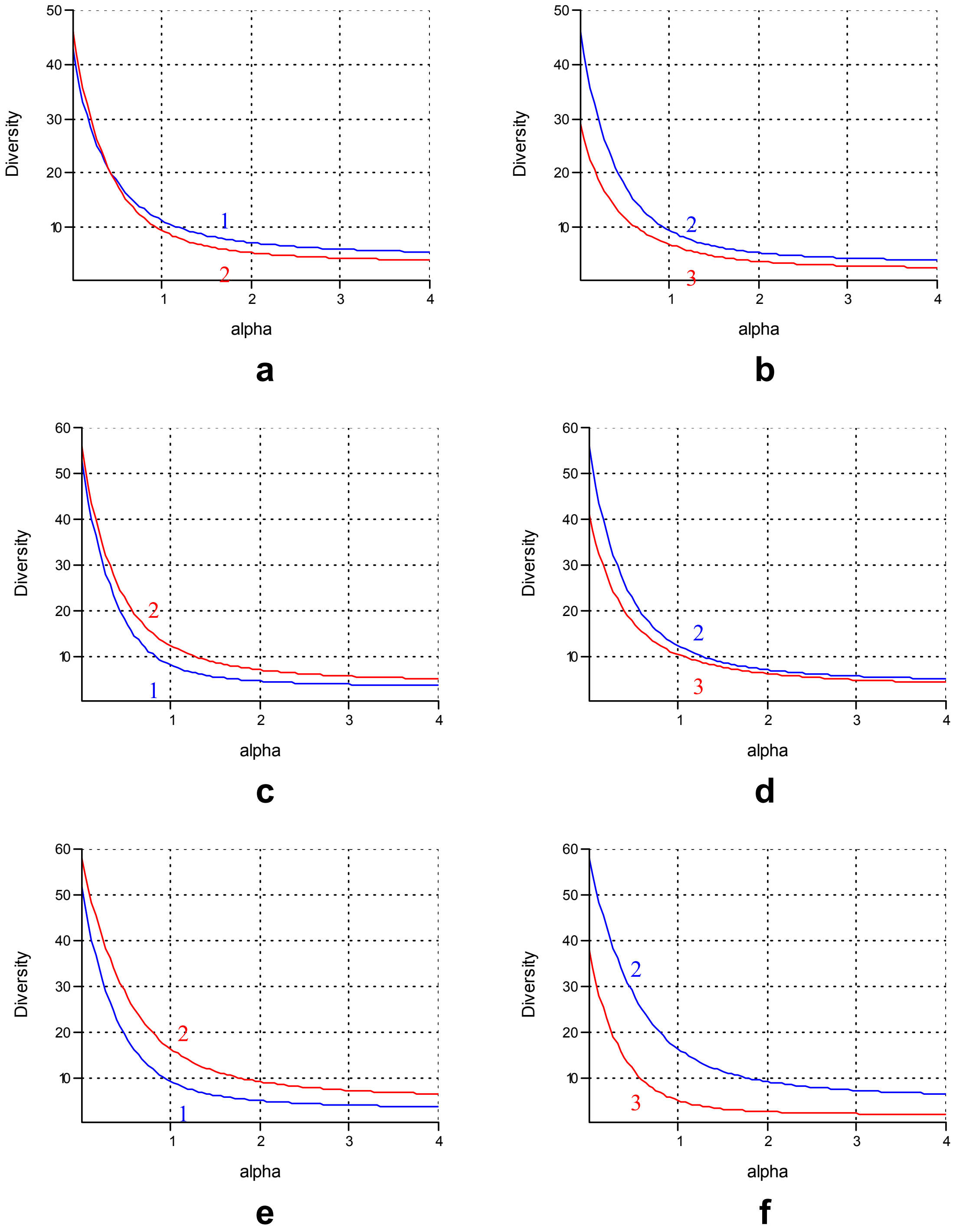

Figure 8. *Diversity ordering of microhabitats in the years 2002 (***a*** and* ***b****), 2003 (***c*** and* ***d****) and 2004 (***e*** and* ***f****). 1 = cattail, 2 = reed, 3 = open water. „Alpha" means the scale parameter (Rényi-diversity).*

that in case of rare morphons the cattail stands are richer but in the case of dominant morphons open water may be a richer environment.

- In 2004 reed stands are the most diverse followed by cattail, and last the open water (in every domain of the scale parameter).

Seasonal dynamics of macroinvertebrates in the three microhabitats

The examination was based on a table in which the sum of the value of the biovolume of the macroinvertebrates collected that day belongs to the sampling date, moreover the serial numbers corresponding to the dates are also included (*Table 12*). In each year the number of the first sampling day is 1.

Based on the *Figs. 9*, *10* and *11*, we can make the following statements:

- In total the most macroinvertebrate matter was observed in 2003 in all three microhabitats, and the year 2002 was the lowest compared to the other two years.
- Looking at the three years at the same time we can state that the low biovolume values in the spring were followed by a slight increase only to fall back at the beginning of summer (around June). From here during the whole summer a steady increase follows and we can record the highest values in the autumn (beginning of October). Late in the autumn decreasing starts.

Table 12. *The data of sampling, their serial numbers (S), and the total biovolume quantities of macroinvertebrates (mm^3) corresponding to the three microhabitats.*

date	S	cattail	reed	open water
29 April 2002	1	1863,2	2197,3	
10 May 2002	12	2198,7	1733,4	770,45
26 May 2002	28	1099,7	1190,2	1745,1
09 June 2002	42	1879,9	1037,3	1120,3
23 June 2002	56	713	1494,2	290,58
01 July 2002	64	678,91	519,06	
16 July 2002	79	2307	1029,6	345,62
28 July 2002	91	3161,7	3387,2	1684,4
08 August 2002	102	1604,4	3220,6	1108,5
15 August 2002	109	2088	1661,9	159,18
220August 2002	116	1075	3075,8	390,83
04 September 2002	129	2543,3	5287,8	15682
22 September 2002	147	2077,2	7611,6	671,47
06 October 2002	161	2904,1	7363,4	3817,3
26 October 2002	181	2043,4	3715,9	3629
16 November 2002	202	2639,2	5205,1	953,22
31 March 2003	1	2373,4	1717,7	729,41
22 April 2003	23	4071,4	6802	3547,9
03 May 2003	33	12799	423,84	1861,1
25 May 2003	55	2073,8	675,28	904,99
09 June 2003	66	1236	730,94	3129,3
26 July 2003	83	2079,3	2250,1	1330,7
13 July 2003	100	1565,6	5298,3	30,034
26 July 2003	113	3561,6	5599,5	2223,9
12 August 2003	131	4274,5	7006,9	2019,5
31 August 2003	150	2323,7	4290,6	3435,4
17 September 2003	167	2419,8	2749,6	6931,2
19 October 2003	199	30219	13179	5184,5
09 November 2003	220	8061,1	7470,7	11461
17 April 2004	1	7191,6	5869,7	3965,5
30 May 2004	44	9844	2233,3	596,18
30 June 2004	75	2477,6	4308,7	1478,6
30 July 2004	105	5670,1	3133,2	7475,6
23 August 2004	129	8431	4603,6	22929
5 October 2004	172	12371	12155	7859,4
29 November 2004	227	8179	2868,3	1542,1

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- In 2002 the following statements may be made about the distribution of the macroinvertebrate biovolume between the microhabitats: From the second half of summer to the end of the year the biggest volume was found in the reeds. In the spring and early summer very steady values were recorded just about the same as in the other microhabitats. Cattail stands have an even value throughout the whole year. Open water shows the lowest values and the highest fluctuations. (the peak of September is very hard to interpret and may be an error).

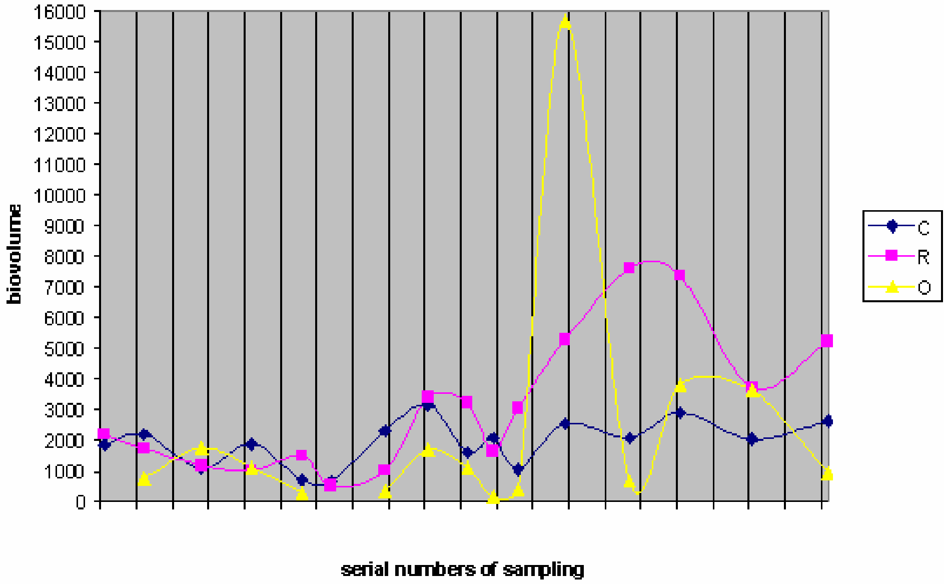

Figure 9. *The seasonal changes in biovolume values (mm^3) of macroinvertebrates in the three microhabitats during 2002. (C = cattail stands, R = reeds, O = open water) Due to extreme weather conditions samples were not taken on the 28th of April on the open water sampling site, on the 10th of May (?) samples were only taken from the ooze and on the 1st of July (?) samples were not taken from the open water and from the water of cattail.*

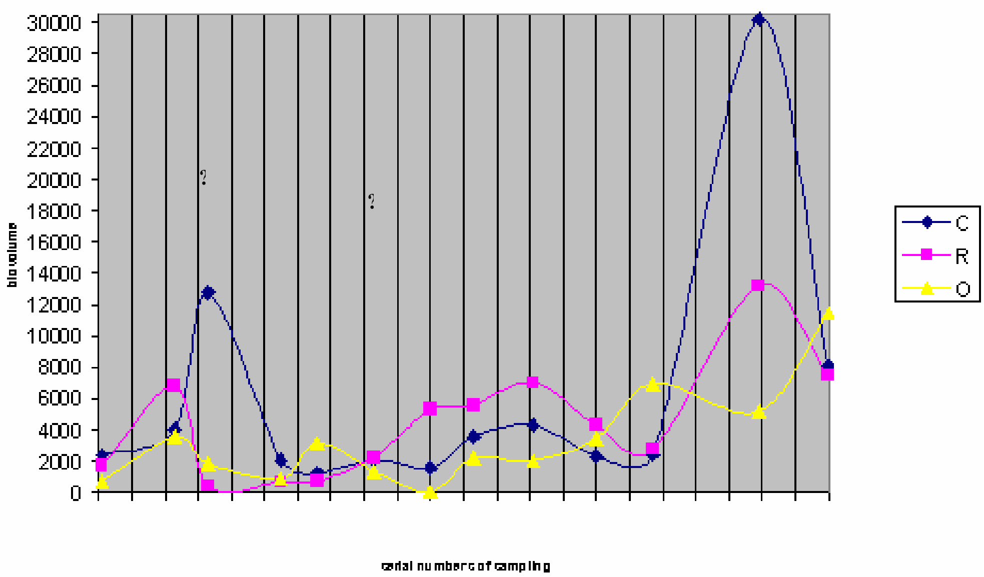

Figure 10. *The seasonal changes in biovolume values (mm^3) of macroinvertebrates in the three microhabitats during 2003 (C = cattail stands, R = reeds, O = open water).*

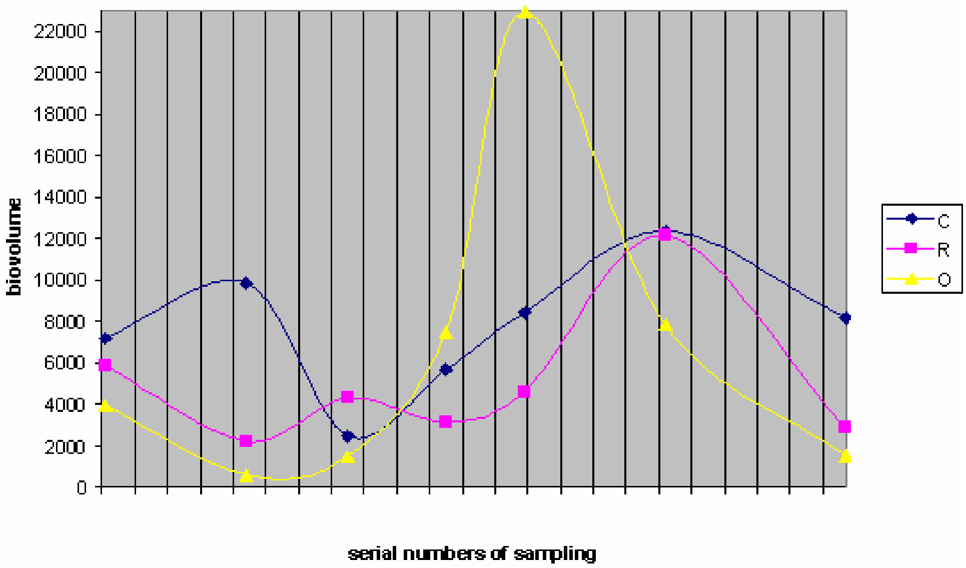

Figure 11. *The seasonal changes in biovolume values (mm^3) of macroinvertebrates in the three microhabitats during 2004 (C = cattail stands, R = reeds, O = open water).*

- In 2002 and 2003 after the peak of August a slight decline can be observed until the end of the month followed by the rise in the autumn. This decline was not observed in 2004 but in this year only one sample was taken during August and there was no sample taken in September.
- In 2003 during the summer the highest biovolume values are linked with the reeds followed by cattail and open water. However during the spring and especially during the autumn the highest increase belongs to the cattail stands. The highest biovolume values were recorded during October of this year. In the case of open water a steady increase of biovolume was recorded from the middle of summer to the end of the year.
- In the spring of 2004 the biggest biovolume may be observed in the case of cattail stands. In the increase that lasts from the summer to autumn reeds is right behind the cattail stands and in the end catches up. In the second half of summer open water shows an ever stronger increase – overtaking the other microhabitats - , it reaches its peak in August and then decreases gradually.

Discussion

Faunistical features

Generally determinable characteristics do not include anything surprising about the current situation of fauna in Lake Balaton. According to the scientific literature, currently in Lake Balaton the *Dikerogammarus* and the *Corophium curvispinum* species are found of the Amphipoda crustaceans. This only differs from what we found in the aspect that the *C. curvispinum* dominates every habitat [38]. On ther contrary in our samples the *Dikero-gammarus* sp. was represented with a larger biovolume value (in terms of the number of individuals the *C. curvispinumis* almost as high as the *Dikerogammarus* species).

Based on the total biovolume amount and the number of taxa it may be suspected that most macroinvertebrates live in the area of the common reed stands. This may be explained in a number of ways:

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- The lowest water depth is recorded in common reed areas, this is where the shore effects have the biggest impact. According to this, it is not the common reed as a species, but other environmental conditions may be decisive.
- The observation may be explained with the characteristics of reed stands. For example the harder stem that may provide a better surface for certain creatures forming biotecton that the vegetation found in the other two microhabitats.

Certain conclusions may be drawn from the cattail sampling site, based on the average volume taxons observed in the sampling area:

- In this area the loose ooze serves as an important substance because more of the species can be found here – living in the ooze in large masses – than in the other two microhabitats (Chironomidae larva and Tubificidae).
- In the cattail stands there are many *Argulus* sp. furthermore there are many larval and juvenile fishes. According to this, the presence of fish is most perceptible in this microhabitat. If this statement is acceptable then cattail stands may be considered the most important microhabitat from the aspect of fish.

It is obvious even from the taxonlist and the average volume of biomass that the fewest macroinvertebrates may be found in the sampling site called open water, this emphasizes the importance of emergent macrophyte stands. This more open area with submerged macrophytes may be most suitable for large volumes of planktonic crustaceans.

Spatial zoocoenological patterns

Up to this point our results did not show strongly separated differences in the three microhabitats. The cause of this is considered to be the marginal effect since the three sampling sites are next to each other, so that samples were taken from the sites' border zones. Therefore it may be worth to set more sampling points within the observed vegetations (inside the stands as well), if we would like to see what differences there are in terms of the macroinvertebrate fauna.

The groups that do not prefer one particular microhabitat are primarily masses of taxa (Tubificidae, Chironomidae, Ceratopogonidae) associated with ooze or in the open water – also found in masses – are the groups of *Limnomysis benedeni*, the *Pristina* sp. and the Baetidae group.

In connection with the water and ooze of reeds, we can find the not fish-parasite leeches. We can also find the most zebra mussel and occurrences of *Hydra circumcincta* too. These groups without a doubt require the surface provided by reeds. The leaf louse (Aphidinea) found presumably only damage the reeds but not other vegetation.

Of the groups belonging to cattail stands we would point out *Argulus* sp. and juvenile fish that emphasize the presence of fish.

There are more than one significant groups that appear in the water body of emergent macrophyte stands or in the ooze beside these areas. This indicates the importance of emergent macrophyte areas, regardless of the actual species that forms the main colony in the area.

The significance of reed-grass is highlighted by the fact that in 2002 a group typical of open water hasn't been separated. With the occurrence of submerged macrophyte the planktonic crustaceans that was distributed evenly in all areas was now concentrated in reed-grass. It seems that the Corixidae larvae prefer the *Najas marina*, because in 2003 they were a characteristics species in this area. It is presumable that for the *Hydra*

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circumcincta the *Potamogeton perfoliatus* is a more ideal microhabitat, in lack of such environment it can only be found in the reeds.

Results based on bootstrapping show significant differences between the different years rather than between the microhabitats. This is backed by characteristics observed in the case of certain taxa. Reeds seems to be the most separated microhabitat based on the defining water macro invertebrate taxa (Hirudinea, Gastropoda, Ephemeroptera, Odonata).

Diversity

The Rényi's diversity ordering method includes more diversity functions by special cases [64] this is why we primarily focus on discussing characteristics based on diversity ordering.

In 2002 the two kinds of emerged macrophytes hardly differed from one another, and the open water areas may definitely be considered poorer. This could mean that emergent macrophyte type habitat is the important factor for the macroinvertebrates and not the actual plant species forming the vegetation.

In 2003 the richest microhabitat in every domain of the scale parameter are the reeds, the open water and cattail areas display only smaller differences. This latter statement may be explained by the open water being populated by reed-grass.

In 2004 – with higher water levels and a more considerable reed-grass population – the unambiguous order in the diversity profiles (reeds – cattail stands – open water) directs attention again to the importance of emergent macrophytes. Altogether, we can declare that diversity is greatest in the reeds microhabitat.

Seasonal dynamics of macroinvertebrates in the three microhabitats

In 2003 higher biovolume values could be observed than in previous years. The highest biovolume values were recorded in October 2003 when the official water level of lake Balaton reached its lowest level at 24 cm. (At this time the water level at the sampling site was 34–42 cm) The observed characteristics indicate the effects of the drop in water levels, because shallower water warms up more powerfully, and the level of available light also changes. This influences significantly the littoral zone's flora and fauna. In our case this meant the increase in macroinvertebrates in the sampling site.

The strong increase in biomass in the open water area in the second half of 2003 coincides with the appearance and densing of *Najas marina* stands which stayed in its place falling to the bottom even in the autumn. The more "reed-grassy" quality of 2003 is due to the appearance of *Najas marina* in the open water area and because in the broader surroundings of the sapmpling site patches of reed-grass was appeared (mainly *Potamogeton perfoliatus*). It is important to know about the *Najas marina* that in Lake Balaton (as elswhere) it forms mainly underwater colonies, during its life cycle not one part of this plant emerges above the water level [16]. Therefore it is presumable that the extremely low water level is the reason for it reaching the surface of the water in 2003. This plant may have been present underwater in 2002 as well, but definitely not in such abundant quantities.

While reeds may be considered the most diverse, this may not be started for the whole of the macroinvertebrates. In general the most macroinvertebrates emerge from reeds compared to the other microhabitats, only in the summer period, and in 2004 even this was not true. In 2004 (more or less) during the whole year cattail attracted larger

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quantities than reeds. When the *Potamogeton perfoliatus* fields became significant this reed-grass area supports the largest quantity of macroinvertebrates.

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