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The effects of *Najas marina* on the zooplankton species composition and water chemistry in a small, shallow lake (Fehér-tó, Fertő-Hanság National Park, Hungary)

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Abstract. Horizontal distribution and diurnal migration of zooplankton as well as a few water chemistry parameters were investigated in the clear-water and the turbid state of the extremely shallow Lake Fehér (Hungary) between 1998-2001. Significant horizontal and diel differences were recorded in the density and composition of zooplankton assemblages as well as a few water chemical parameters between the turbid and clear-water state of lake. In the turbid state copepods dominanted zooplankton assemblages developed with low density and species richness and the cladoceran zooplankton consisted of mainly pelagic species with low abundance values. During the presence of *Najas marina* the zooplankton community was dominated by cladocerans and the ratio of the macrophyta-associated species was high. In case of few cladoceran species significant diel density differences developed between the macrophyte bed and the above macrophyte-free water column however macrophyta-associated species did not show diel vertical migration. Based on the result of diurnal monitoring the importance of DHM (diel horizontal migration) was irrelevant in the uniform and dense *Najas* beds and zooplankton appear to migrate vertically rather than horizontally.

Submerged macrophytes have a major impact on the biological structure and water quality of shallow lakes (SCHEFFER & JEPPESEN, 1998). Macrophytes enhance water clarity through enhanced grazing on phytoplankton, shading, reduction of nutrient and light availability, excretion of allelopathic substances, increase of sedimentation and reduction of resuspension. The role of macrophytes as stabilizing and structuring components in lakes of differing trophy have been emphasized in the stable state theory by SCHEFFER et al. (1993) based on that over a range of nutrient concentrations, shallow lakes can have two alternative equilibria: a clear-water state dominated by aquatic vegetation, and a turbid state characterized by high algal biomass. The biomass and seasonality of zooplankton is connected to lake trophy, in turn reflecting the vegetation density. In eutrophic lakes with high macrophyte density, the zooplankton peak follows plant biomass, coinciding in late summer. On the contrary shallow lakes with scanty vegetation the zooplankton biomass takes place in the beginning of summer or autumn (JEPPESEN et al., 1998). Dense macrophyte beds can act as a refuge for large zooplankton species, which in turn control the phytoplankton (TIMMS & MOSS, 1984), but the refuge effect being diminised at increasing predator density (JEPPESEN et al., 1998). In shallow lakes opposite to deep-lakes, the predator-avoidance strategy of diel vertical migration (DVM) is less advantageous, in these systems the importance of diel horizontal migration (DHM) increases. During the DHM the pelagic zooplankton move into macrophyte beds during daytime, using it as spatial refuge against fish predators, but migrate into open water at night to feed on phytoplankton.

The Fertő-Hanság area is one of the most important wetlands in Central Europe. Limnological research has a long tradition in the Seewinkel and Lake Fertő but only limited information is available on the neighbouring shallow lakes in the Hanság region. In 1998, a four-year project was started to study the faunistics, temporal and spatial distribution of several Crustacean taxa and composition of the

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zooplankton assemblages of the Lake Fehér (KISS, 2002). Besides zooplankton the main water chemical parameters were also recorded because only little information has the diel and horizontal changes of the main water chemical parameters (temperature, pH, conductivity, dissolved oxygen concentration) in extremelly shallow lakes. In this paper the turbid and the clear-water state of the lake is compared and the diel variation in horizontal and vertical distribution of the several species is discovered in the vegetation period.

GENERAL DESCRIPTION OF THE STUDY AREA

Lake Fehér (Fehér-tó) (47° 41' N, 17° 21'E) is situated in the area of the Fertő-Hanság National Park, in the northwestern part of Hungary. It is strictly protected and not influenced by human activities. The lake is small and very shallow (area: 2.69 km^2, open water: 0.25 km^2, mean depth: 50 cm, maximum depth: 110 cm). The hydrology of the lake depends on the interplay of precipitation and evaporation and there is an accidental water supply from the River Rába through a little channel. The littoral zone of the lake is characterised by beds of emergent macrophytes (*Phragmites australis* and *Typha angustifolia*). Since 1994, the lake was devoid of open water macrophytes, whereas in 1999 and 2000 the open water was covered by dense vegetation of *Najas marina* (95 % Plant Volume Infested).

Until 1983 Lake Fehér was a fish pond. Since 1983, when the area became protected, the fish stock has been considerably increased. The fish assemblage is dominated by cyprinids. The most abundant species are *Carassius auratus*, *Rutilus rutilus* and *Perca fluviatilis* (G. GUTI, personal communications).

MATERIALS AND METHODS

Sampling was carried out from June to September at monthly intervals in 1998 and 2001 and biweekly in 1999 and 2000. The temperature, pH, conductivity and dissolved oxygen were measured in the field by using MULTILINE-P4 portable meter as well as the laboratory analyses were carried out with DX-120 ion chromatograph. The quantity of the zooplankton sample usually was 50 litre, but from the *Najas* beds only 5 litre sample was collected because of the high crustacean density. As zooplankton distribution is characterized by a high degree of horizontal patchiness we attempted to reduce this problem by collecting and pooling five subsamples on each occasion and each sampling. Samples were filtered through a 70 μm mesh net then preserved in 5 % formaldehyde solution. The diel changes of the zooplankton assemblages and the in situ measured water chemical parameters were followed in August of 1998, 1999, 2000 and 2001 in every two hours between 2 a.m. and 11 p.m. from three vertical zones of the lake: 1. water surface, 2. middle of the water column, 3. sediment surface. To test the horizontal distribution of the crustacean species, the monthly, biweekly and diurnal zooplankton samples were collected from three sampling points along the 100 m long transect: 1. mid-lake (approximately 100 m from the shore, 2. between 1. and 3., approximately 20 m from the emergent macrophyta zone, 3. outer side of the *Typha angustifolia* stand. When *Najas marina* occured using the same methods zooplankton were also sampled in a *Najas*-free patches close to the *Typha* zone (4. sampling site).

Microcrustaceans were enumerated by using inverted microscopy and identified to species level. Very dense samples were subsampled.

RESULT AND DISCUSSION

Environmental parameters

Turbid state (1998, 2001)

In the turbid state the open water was devoid of macrophytes. In 1998 and 2001 hypertrophic conditions were recorded, dense blooms of blue-green algae developed in the lake. The most frequent species were *Anabaena spiroides* and

Microcystis reinboldii (K. T. KISS, personal comments).

In the vegetation period the turbidity (140 FTU) and the suspended solid content (84 mg l^{-1}) was high especially in August. In summer because of the high pH values there was no bicarbonate (HCO_3^-) in the water and the CO_3^{2-}-concentration (mean: 23.2 mg l^{-1}) increased. The temperature ranged from 15.2-31.3^{0}C. The mean temperature was 1-3^{0}C lower on the outer side of the *Typha* zone than the open water. There was no significant vertical temperature difference in the water column, the average deviation was only 0.4-0.5^{0}C. The pH ranged from 9.10–10.73, the maximum was in August of 2001. The pH values decreased inshore and except August there was no vertical pH difference in the water column. The conductivity ranged from 333-521 μS/cm^{-1} and there were no significant vertical and horizontal conductivity differences in the lake. The dissolved oxygen concentration ranged from 8.75-20.7 mg l^{-1} and decreased inshore an average 2.9 mg l^{-1} in 1998 and 7.6 mg l^{-1} in 2001. The mean vertical oxigen difference in the water column was 0.52 mg l^{-1} in 1998 and 3.51 mg l^{-1} in 2001. The vertical differences increased inshore both years.

In August of 1998 and 2001 the lake was extremelly shallow (34 and 31 cm) and considerable cyanophyta blooms were developed. During the diurnal monitoring the horizontal differences between the water surface *temperature* in the mid-lake (mean: 26.76^{0}C in 1998 and 27.49^{0}C in 2001) and the outer side of the *Typha* zone (mean: 26.32^{0}C in 1998 and 26.52 in 2001) were insignificant. The temperature decreased inshore both years. Significant diurnal temperature fluctuations were detected both in the mid-lake (9.0^{0}C in 1998 and 8.6^{0}C in 2001) and the *Typha* zone (8.6^{0}C in 1998 and 6.3^{0}C in 2001). The maximum was at 3 p.m. (30.9^{0}C in 1998 and 31.2^{0}C in 2001) and the minimum was at 2 a.m. (21.9^{0}C in 1998 and 22.6^{0}C in 2001). The vertical temperature differences in the water column were inconsiderable (mean: 0.39^{0}C in 1998 and 0.9^{0}C in 2001) at all sampling sites of the transect. The horizontal differences between the water surface *pH* in the mid-lake (mean: 8.93 in 1998 and 10.14 in 2001) and the outer side of the *Typha* zone (mean: 9.11 in 1998 and 9.8 in 2001) were insignificant (mean difference: 0.18 in 1998 and 0.39 in 2001). The mean diurnal pH difference was 1.02 in 1998 and 1.15 in 2001. The maximum was at 3 p.m. (9.64 in 1998 and 10.73 in 2001) and the minimum was at 5 a.m. (8.48 in 1998 and 9.47 in 2001). The mean vertical pH differences in the water column were inconsiderable (0.128 in 1998 and 0.184 in 2001) at all sampling points of the transect. The *conductivity* increased inshore in 1998 and 2001 too, and the mean horizontal differences between the mid-lake (mean: 359 μs cm^{-1} in 1998 and 463.6 μs cm^{-1} in 2001) and the outer side of the *Typha* zone (mean: 368 μs cm^{-1} in 1998 and 472 μs cm^{-1} in 2001) were 8.67 μs cm^{-1} in 1998 and 7.6 μs cm^{-1} in 2001. Significant interannual differences were recorded in the mean diurnal conductivity fluctuation - in 1998 the diurnal difference was 11.7 μs cm^{-1}, but 107 μs cm^{-1} in 2001. The conductivity maximum was in daytime and the minimum was at night. The mean vertical conductivity differences in the water column were low (1.66 μs cm^{-1} in 1998 and 4.45 μs cm^{-1} in 2001).

The *dissolved oxygen concentration* decreased inshore and the mean horizontal differences between the mid-lake and the outer side of the *Typha* zone was 1.91 mg l^{-1} in 1998 and 5.59 mg l^{-1} in 2001. The mean oxygen concentration as well as the maximum values (14.73 mg l^{-1} in 1998 and 26.2 mg l^{-1} in 2001) was notably higher in 2001 because of the photosyntetic activity of the notably higher blue-green algae biomass. The mean diurnal concentration fluctuation was 8.81 mg l^{-1} in 1998 and 11.91 mg l^{-1} in 2001. The concentration maximum was between 5-7 p.m and the minimum was at 5 a.m. The mean vertical differences in the water column were low, 2.19 mg l^{-1} in 1998 and 2.29 mg l^{-1} in 2001.

Clear-water state (1999, 2000)

In the clear-water state of the lake the open water was covered by the homogeneous stand of *Najas marina*. In 1999 the *Najas* appeared at the end of June. In July the *Najas* entirely covered the open water (95 % Plant Volume Infested) and above the macrophyte beds there was a 20-25 cm deep *Najas*-free water column (mean water depht: 69 cm). It was particular that in the *Najas* beds the phytoplankton was very diverse (60-80 species) and the phytoplankton biovolume was high. The dominant species were *Microcyctis aeruginosa* and *Meriosmopedia tenuissima* (5000-30000 ind ml^{-1}) (K. T. KEVE, personal comment). From July to August in the macrophyte beds the density of *Notonecta glauca* and the juvenile fish were high. In 2000 *Najas marina* appeared at the end of June and opposite to 1999 in front of the *Typha* zone, there was a 2-3 m wide zone which was devoid of *Najas*. The mean water depth (53 cm) was lower than the previous year therefore the *Najas*-free water column was only 10-15 cm deep. In August, rich periphyton assemblages developed on the *Najas* which in August in the open water entirely colonized the macrophyte beds and that by shading reduces the *Najas* photosynthesis (SAND-JENSEN 1977). In the macrophyte beds the phytoplankton biovolume was low. The density of the YOY fish was high like in 1999, but *Notonecta glauca* was not present.

In the clear-water state the water turbidity (mean: 12.66 FTU) and the suspended solid content were low (mean: 0.012 mg l^{-1} in 1999 and 10.8 mg l^{-1} in 2000). From June to September the water surface *temperature* ranged from 18.1–26.1^{0}C. The horizontal differences were insignificant (mean: 1.72^{0}C) however the vertical temperature differences, opposite to turbid state, notably increased (mean: 2.81^{0}C, maximum: 6.4^{0}C). The *pH* ranged from 7.63–10.08. The mean horizontal pH difference was low (0.70) and the values fluctuated horizontally. The vertical pH differences in the water column increased with the expansion of the *Najas* and the maximum was in August 2000 (1.2). The *conductivity* ranged from 233-619 µs cm^{-1}, increased inshore and the conductivity differences increased horizontally with the expansion of the *Najas*. The *dissolved oxygen concentration* ranged from 1.14-21.34 mg l^{-1} and as compared with the turbid state the mean vertical oxigen difference in the water column significantly increased (mean: 3.57 mg l^{-1}, max: 10.82 mg l^{-1}). In the end of September, when *Najas* was disintegrated, the pH and the dissolved oxygen content decreased (mean: 5.66 mg l^{-1}, min: 1.14 mg l^{-1}), as well as the turbidity and conductivity increased because of the intensive *Najas* degradation.

During of the diurnal monitoring the water depth was 67 cm in 1999 and 40 cm in 2000. The horizontal *temperature* differences between the mid-lake and the outer side of the emergent macrophyta zone were insignificant (mean: 0.83^{0}C). The diurnal temperature changes decreased with water depth (mean water surface: 8.1^{0}C, mean sediment surface: 2.9^{0}C) and the vertical temperature differences in the water column were considerably increased compared with the turbid state (mean turbid state: 0.4^{0}C, mean clear-water state: 2.85^{0}C, max: 7.0^{0}C). In case of *pH* there were no significant horizontal differences in the lake (mean: 0.47 in 1999 and 0.86 in 2000). The pH decreased with the water depth in accordance with several observations - that plant beds frequently have high pH in the surface layers, but lower values in the darker, deeper layers (FRODGE et al 1990). The mean diurnal pH difference also decreased with water depth (mean water surface: 1.9, mean sediment surface: 0.92). The minimum values (7.35-9.61) were at night (between 11 p.m and 2 a.m.) and the maximum values (8.86-10.47) were between 3 and 9 p.m. The *conductivity* increased inshore and significant horizontal differences were detected between the mid-lake (mean: 250 µs cm^{-1} in 1999 and 293 µs cm^{-1} in 2000) and the outer side of the *Typha* zone (mean: 272 µs cm^{-1} in 1999 and 463 µs cm^{-1} in 2000). The mean vertical conductivity differences in the water column increased comparing to the turbid state (mean turbid state: 3.05 µs cm^{-1}, mean clear-water state: 12.69 µs

cm^{-1}) and the maximum vertical differences (40-22 μs cm^{-1}) were in daytime. Significant diurnal and vertical *dissolved oxygen concentration* differences were recorded both years of the clear-water state (Fig. 1). The diurnal differences decreased with water depth (mean water surface: 12.38 mg l^{-1}, mean sediment surface: 5.63 mg l^{-1}) and the mean vertical difference was 9.04 mg l^{-1} in 1999 and 5.57 mg l^{-1} in 2000. The horizontal differences were higher in the water surface (mean: 4.38 mg l^{-1}) than in the *Najas* bed (mean: 1.57 mg l^{-1}).

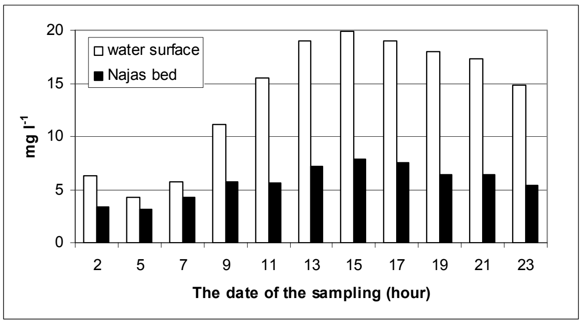

Figure 1. The diurnal variation of the mean diel dissolved oxygen concentration (mg l^{-1}) differences between the water surface and the *Najas* bed (n = 66, average values of the diurnal experiments in August 1999 and 2000)

Crustacean assemblages

Turbid state (1998, 2001)

Like most shallow lakes in the turbid state due to the low refuge availability, the highest zooplankton biomass occured in the beginning of the growing season. In summer in Lake Fehér the zooplankton density, especially the large-bodied cladocerans were extremely low as well as cyclopoid copepods dominated in the Crustacean assemblages. The mean density of copepods (3.76 ind l^{-1} in 1998 and 2.06 ind l^{-1} in 2001) was higher than the mean density of cladocerans (0.85 ind l^{-1} in 1998 and 1.24 ind l^{-1} in 2001) both years. The mean Crustacean density was 4.6 ind l^{-1} in 1998 and 3.32 ind l^{-1} in 2001. In 1998 the cladoceran zooplankton consisted of mainly pelagic species with low abundance values and out of the recorded 7 Cladocera species *Moina brachiata* (39.67% of the total Crustacean density) was completely dominant from June to September. The copepods community consisted of 6 species, *Diacyclops bicuspidatus* and *Mesocyclops leuckarti* appeared with extremely low abundance values and *Megacyclops viridis* (mean: 0,53 ind 50 l^{-1}) existed only close to the *Typha* zone. The dominant species were *Acanthocyclops vernalis* (42.65% of the total density), *Cyclops vicinus* (33.21%) and *Eucyclops serrulatus* (5.24%). In 2001 16 species were identified and the dominant species were *Moina brachiata* (13.18%), *Eucyclops serrulatus* (27.78%), *Cyclops vicinus* (18.74%) and *Acanthocyclops vernalis* (8.37%). Horizontal differences were detected in the distribution of several species, the mean density of *Diaphanosoma brachyurum*, *Moina brachiata* and *Acanthocyclops vernalis* decreased inshore as well as *Simocephalus vetulus*, *Chydorus sphaericus, Alona intermedia* and *Megacyclops viridis* increased inshore.

During the diurnal monitoring there was a significant difference in the species richness in 1998 (9) and 2001 (18) indicating that the clear-water state in 2000 could promote the colonization of several species in the open water (Table 1). The species richness (mid-lake: 3 (1998), 11 (2001), *Typha* edge: 8 (1998), 18 (2001) inceased inshore both years, but in respect to the mean density there were interannual differences. In 1998 the mean density (mid-lake: 0.93 ind l^{-1}, *Typha* edge: 1.12 ind l^{-1}) increased inshore. The zooplankton consisted of only 3 pelagic species (*Moina brachiata*, *Cyclops vicinus* and *Acanthocyclops vernalis*) in the mid-lake with low and fluctuating density values and the total zooplankton abundance was below 2 ind l^{-1} all day. The mean density was higher at night (1.33 ind l^{-1}) than in daytime (0.9 ind l^{-1}) and the differences between the night and daytime density increased inshore because of the higher night appearance of the littoral zone species (*Megacyclops viridis*, *Mesocyclops leuckarti*, *Eucyclops serrulatus*) (Fig. 2). The mean density of the pelagic *Moina brachiata* and *Acanthocyclops vernalis* decreased inshore while the density of *Chydorus sphaericus* increased inshore and the edge of the *Typha* stand a few individual of *Pleuroxus aduncus*, *Eucyclops serrulatus* and *Megacyclops viridis* were presented.

Table 1. The composition of Crustacean assemblages as well as the mean diel density of the species during the diurnal monitoring (n= 33 in each monitoring years)

	1998	1999	2000	2001
Alona intermedia	-	201.86	160.4	31.72
Alonella excisa	-	0.52	25.2	-
Bosmina longirostris	-	0.66	27.65	5.72
Ceriodaphnia quadrangula	-	14.95	420.9	1.78
Ceriodaphnia reticulata	-	1.09	525.6	3.14
Chydorus sphaericus	11.97	2458.4	138.8	-
Diaphanosoma brachyurum	0.315	151.9	286.4	18.72
Disparalona rostrata	-	-	9,8	5,75
Graptoleberis testudinaria	-	4.7	836.7	-
Leydigia acanthocercoides	-	-	-	2.25
Moina brachiata	11.48	0.79	-	155.9
Pleuroxus aduncus	0.27	226.3	358.3	-
Polyphemus pediculus	-	-	6.41	-
Pseudochydorus globosus		2.46	-	-
Scapholeberis mucronata	-	2.7	163	10.18
Simocephalus serrulatus	-	-	0.9	-
Simocephalus vetulus	-	1185.5	5434.4	5.84
Cyclocypris ovum	-	0.4	4.66	-
Physocypria kraepelini	-	2.02	3.74	1.87
Pseudocandona compressa	-	0.9	3.19	1.51
Acanthocyclops vernalis	20.45	650.9	860.1	34.57
Canthocamptus staphylinus	-	-	-	0.66
Cyclops vicinus	2.55	0.8	5.15	-
Ectocyclops phaleratus	-	0.13	5.06	-
Eucyclops serrulatus	3.09	21.16	455	104.3
Macrocyclops albidus	-	3.63	184.3	0.85
Megacyclops viridis	1	16.66	90.5	2.75
Mesocyclops leuckarti	2.91	624.4	1622.2	54.91
SUM /50L	54.035	5572.83	11628.36	441.57
ind l^{-1}	1.08	111.45	232.56	8.83

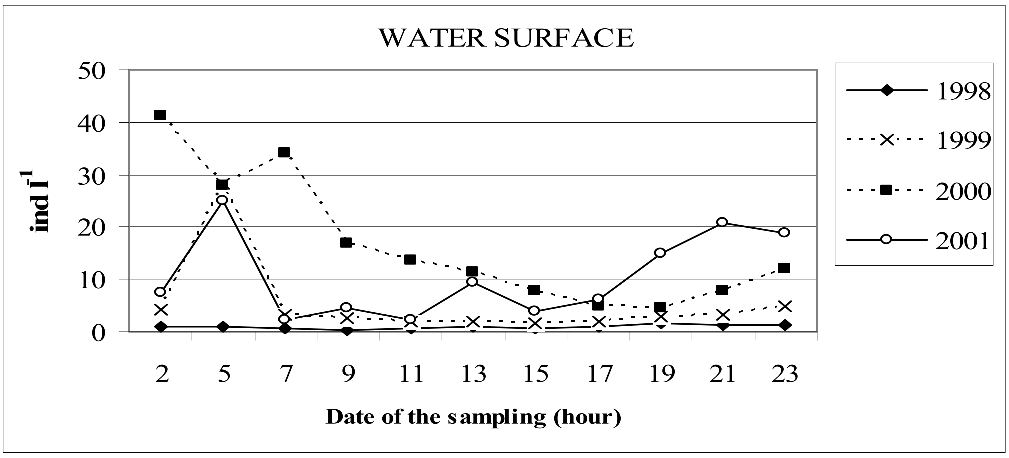

Figure 2. Diel density differences of the Crustacean assemblages in the mid-lake during the diurnal monitoring

Opposite to 1998 in 2001 the mean density decreased inshore (mid-lake: 10.55 ind l^{-1}, macrophyta zone: 0.53 ind l^{-1}) because of the inshore density decrease of the pelagic *Moina brachiata* (mid-lake: 6.32 ind l^{-1}, *Typha* zone: 0.52 ind l^{-1}). Like in 1998 the mean density was higher at night (13.3 ind l^{-1}) than daytime 7.18 ind l^{-1}) because the mean density of *Moina brachiata*, *Alona intermedia* and *Mesocyclops leuckarti* were notably higher at night. At the edge of *Typha* zone the representative species of the reed-belt appeared (*Simocephalus vetulus*, *Ceriodaphnia reticulata*, *Pseudocandona compressa*, *Macrocyclops albidus* and *Megacyclops viridis*).

Besides the low refuge availability the direct and indirect effects of high pH are also important in controlling the density of filter-feeding zooplankton (JEPPESEN et al., 1990). The enhanced pH in the turbid state caused by high photosynthetic activity of the blooming phytoplankton probably affected cladoceran density because cladocerans are generally more sensitive to elevated pH than cyclopoid copepods. The summer presence of *Cyclops vicinus* and *Acanthocyclops vernalis* also supported the finding that some cyclopoid copepods are tolerant to high pH (HANSEN et al., 1991). In 1998 and 2001 because of the unfavourable environmental conditions (cyanophyta bloom, high temperature and pH values) the open water were unsuitable for fish, but cladoceran density was low also because of the decreased phytoplankton edibility and the high concentration of suspended sediment which are known to decrease fecundity and survivorship of cladocerans via reduced ingestion rates of phytoplankton cells (ARRUDA et al., 1983).

Clear-water state (1999, 2000)

During the presence of *Najas marina* the composition of the zooplankton assemblages remarkably changed, the density and the species richness both increased. Especially the density of plant-associated cladoceran species were high because the homogeneous macropyte beds with low edge:area ratio would favour the non-migrating macrophyta-associated cladoceran species (PATERSON, 1993). Opposite to the turbid state the mean density of Cladocera assemblages (48.5 ind l^{-1} in 1999 and 146.4 ind l^{-1} in 2000) was significantly higher than Copepoda assemblages (25.68 ind l^{-1} in 1999 and 37.4 ind l^{-1} in 2000). Considerable density differences were formed between the *Najas*-free water surface (mean: 3.5 ind l^{-1} in 1999 and 17.7 ind l^{-1} in 2000) and the *Najas* beds (mean: 181.7 ind l^{-1} in 1999 and 408.61 ind l^{-1} in 2000) and these differences increased with the expansion of the *Najas*. From June to September there was no interannual difference in the species richness (26 species in 1999, 27 species in 2000) but the density of several species differed.

In 1999 high abundance cladoceran community with macrophyte-associated species (*Simocephalus vetulus*, *Alona intermedia*, *Pleuroxus aduncus*) formed in the *Najas marina* beds, as well as a few individuals of *Moina brachiata*, *Ceriodaphnia quadrangula*, *Bosmina longirostris*, *Alona guttata* and the necrophagous *Pseudochydorus globosus* were also identified. The dominant species were *Simocephalus vetulus* (28.9%), *Chydorus sphaericus* (28.2%), *Acanthocyclops vernalis* (17.72%) and *Mesocyclops leuckarti* (16.22%). The mean density decreased inshore (mid-lake: 102.8 ind l^{-1}, *Typha* edge: 53.23 ind l^{-1}) especially because of the density decrease of *Diaphanosoma brachyurum* and *Acanthocyclops vernalis.* The lower inshore densities could explain the lower refuge availability of the less dense *Najas* beds where small fish usually aggregated during the day, preferably outside the dense emergent vegetation.

In 2000 the dominant species were *Simocephalus vetulus* (51.36%), *Graptoleberis testudinaria* (14.87%) and *Mesocyclops leuckarti* (16.45%) and opposite to previous year the abundance of *Chydorus sphaericus* (1.88%) and *Acanthocyclops vernalis* (0.95%) significantly decreased. In 2000, among the new species in the *Najas* bed, *Ceriodaphnia reticulata, Alonella excisa, Scapholeberis mucronata, Graptoleberis testudinaria* and *Polyphemus pediculus* appeared that previously had been detected from the reed-belt. From the *Najas* beds a small population of *Simocephalus serrulatus* was detected for the first time in the lake in August of 2000.

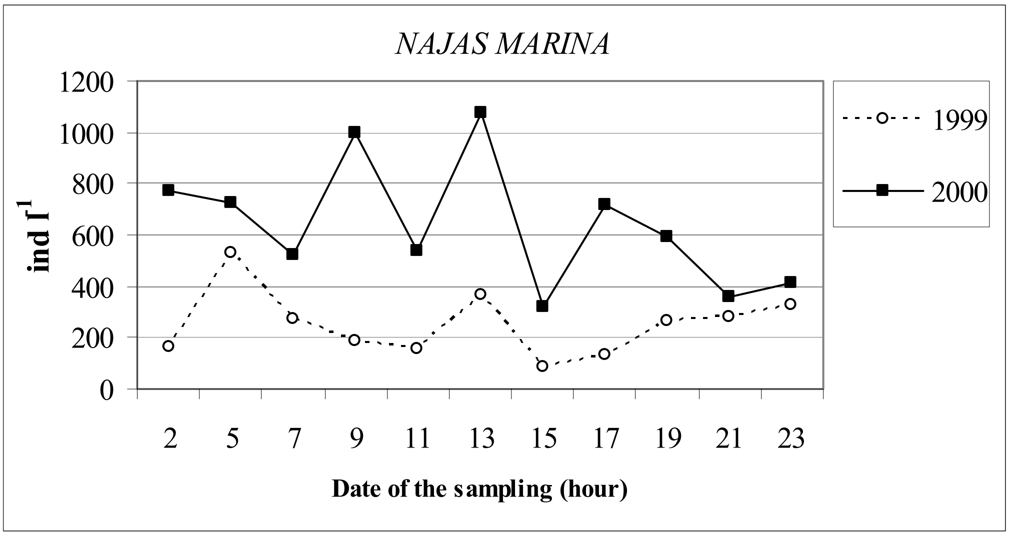

Figure 3. Diel density differences of the Crustacean assemblages in the *Najas* beds of the mid-lake during the diurnal monitoring in August 1999 and 2000

The abundance of the Crustacean assemblages was significant higher in 2000 (mean: 184 ind l^{-1}, max: 1291 ind l^{-1}) than in 1999 (mean: 74.24 ind l^{-1}, max: 365 ind l^{-1}) as well as the mean density notably decreased inshore (mid-lake: 2477.6 ind l^{-1}, *Typha* zone: 617.5 ind l^{-1}) in 2000 especially the massive occurrence of *Simocephalus vetulus* in the mid-lake. These interannual differences and the lower density values in 1999 could explain by the increased predation pressure of the invertebrate predator, *Notonecta glauca* and small fish in the *Najas* beds. The massive presence of *Notonecta glauca* usually produced a top-down effect in small lakes which was similar to that reported in case of planktivorous fish (ARNÉR et al., 1998). In 2000 the absence of invertebrate predators and the rich periphyton assemblages on *Najas marina* contributed on the increrased Crustacean density. In 2000 the abundance of small fish also decreased in the macrophyte beds (personal observation) because the expansion as well as the structural complexity of the *Najas* bed increased and zooplanktivorous fish tend to avoid dense macrophyte beds (ENGEL, 1987). It was particular that the ostracods did not found in high density in the *Najas* beds (mean: 3.51 ind 50 l^{-1} in 1999 and 6.95 ind 50 l^{-1} in 2000) and a significant part of the individuals were juvenile. The density and species number of ostracods increased inshore both years.

During the diurnal monitoring 23 species were recorded in 1999 and 24 in 2000. (Table 1) The density of Crustacean assemblages, especially of the macrophyte-associated species (*Simocephalus vetulus*, *Graptoleberis testudinaria*, *Alona intermedia, Pleuroxus aduncus* and *Chydorus sphaericus)* was significantly higher in the *Najas* bed than the *Najas*-free open water and there were notably interannual differences in the density of these species (Fig. 2, 3). The mean density of *Simocephalus vetulus*, *Ceriodaphnia quadrangula*, *C. reticulata*, *Scapholeberis mucronata, Graptoleberis testudinaria, Pleuroxus* *aduncus*, *Eucyclops serrulatus*, *Macrocyclops albidus* and *Mesocyclops leuckarti* was significant higher in 2000 in the mid-lake and *Typha* edge alike however the density of *Chydorus sphaericus* remarkably decreased. The typical littoral predator, *Polyphemus pediculus* was recorded only 2000 and its density was increased inshore. The dominant copepod species were *Acanthocyclops vernalis* in 1999, and *Acanthocyclops vernalis*, *Eucyclops serrulatus* and *Mesocyclops leuckarti* in 2000. The predators, *Macrocyclops albidus* and *Megacyclops viridis* were presented only inside the *Najas* beds. The mean density of copepods considerably higher in the *Najas* beds (mean: 59.53 ind l^{-1} in 1999 and 135 ind l^{-1} in 2000), than in the open areas (mean: 1.38 ind l^{-1} in 1999 and 8.95 ind l^{-1} in 2000) but except *Acanthocyclops vernalis* no diel changes in density were observed. The density of copepods was notably higher than the turbid state and opposite to the observation of several authors (JEPPESEN et al., 1990) that the appearance of submerged macrophytes was the cause of the decline in cyclopoid abundance

The mean total density of the Crustacean assemblages in the water column were considerable higher in the mid-lake (mean: 11.68 ind l^{-1} in 1999, 15.3 ind l^{-1} in 2000) than in front of the *Typha* zone (mean: 6.2 ind l^{-1} in 1999 and 8.76 ind l^{-1} in 2000). These horizontal differences could explain that cyprinid fish usually aggregate close to the emergent macrophyte zone hence the predation pressure on zooplankton is higher (HALL, 1979).

In case of few species diel migration pattern were detected. The mean density of *Alona intermedia*, *Bosmina longirostris Ceriodaphnia* spp., *Chydorus sphaericus Diaphanosoma brachyurum* and *Scapholeberis mucronata* increased at night close to the water surface and parallel to this decreased in the *Najas* beds so these species show diel verical migration between the *Najas* beds and the above *Najas*-free water column (Fig. 4). Like other results (LAURIDSEN & BUENK, 1996) macrophyte-associated species did not show diel vertical migration between the macrophyta bed and the *Najas*-free water surface layer, however, density values fluctuated all day in the *Najas* beds at all sampling sites of the transect. (Fig. 5) In 2000 the density of plant-associated species was considerable decreased inshore (mean mid-lake: 435 ind l^{-1}, mean *Typha* zone: 204.4 ind l^{-1}) especially because of the decreased density of *Najas* close to the *Typha* zone.

In the *Najas*-free sampling site the zooplankton density was low and the mean day-night density of *Ceriodaphnia* spp. (day: 0.95 ind 50 l^{-1}, night: 34.83 ind 50 l^{-1}), *Scapholeberis mucronata* (day: 7.63 ind 50 l^{-1}, night: 48.67 ind 50 l^{-1}) and *Acanthocyclops vernalis* (day: 190.5 ind 50 l^{-1}, night: 1302 ind 50 l^{-1}) differed, but in case of the other species the day-night abundance did not change significantly indicating that the importance of DHM is little in Lake Fehér because the PVI is nearly 100 %. Like other observations (CERBIN et al., 2003) this result indicate that in lakes with extensive and uniform macrophyte vegetation, zooplankton appear to migrate vertically rather than horizontally.

CONCLUSION

Significant horizontal and diel differences were recorded in the density and composition of zooplankton assemblages as well as a few water chemical parameters between the turbid and clear-water state of Lake Fehér. In the turbid state in case of the examined water chemical parameters there were no vertical differences in the water column however in case of temperature, dissolved oxigen concentration and conductivity horizontal differences were detected between the mid-lake and the emergent macrophyte vegetation. In the clear-water state the horizontal water chemical differences in the lake except conductivity were insignificant because of the relative homogeneous environmental conditions in the *Najas* beds. Opposite to the turbid state the vertical water chemical differences significantly increased in the water column because of the photosyntetic activity and shading of *Najas marina*.

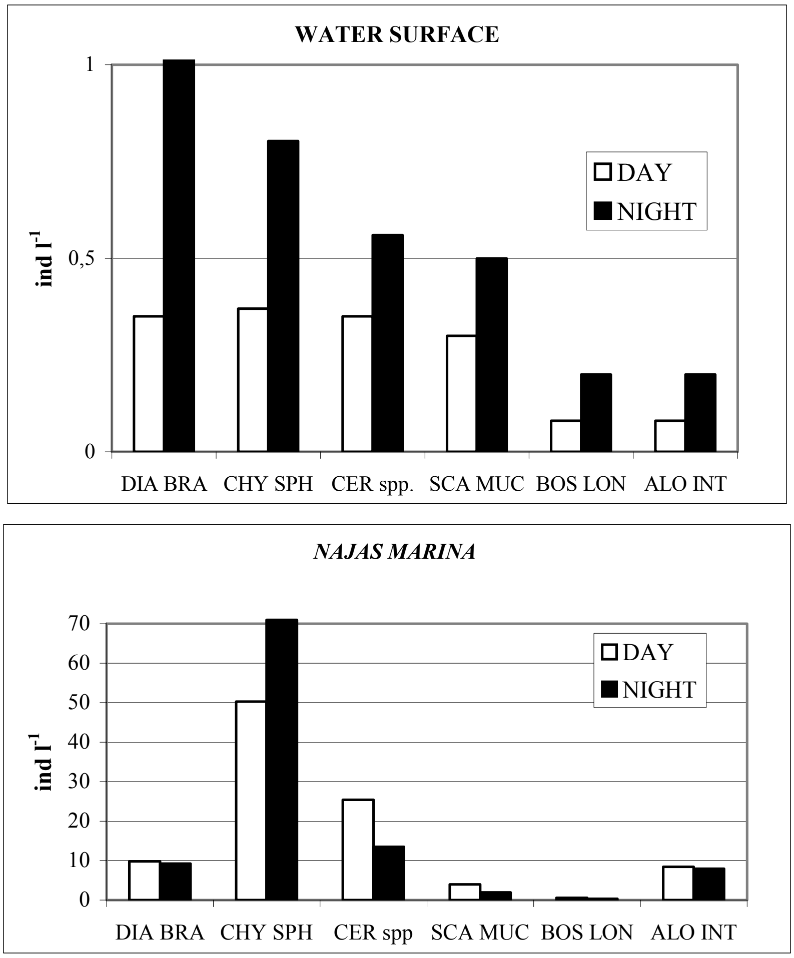

Figure 4. Mean day-night differences of the vertically migrating species (*Diaphanosoma brachyurum*, *Chydorus sphaericus*, *Ceriodaphnia* spp., *Scapholeberis mucronata, Bosmina longirostris* and *Alona intermedia*) in the *Najas*- free water surface and the *Najas* bed (n = 66, average values of the diurnal experiments in August 1999 and 2000)

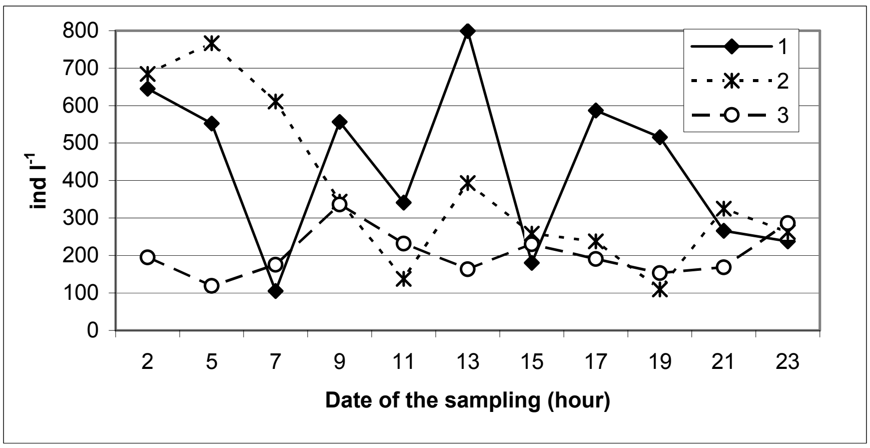

Figure 5. Mean diel and horizontal density differences of the plant-associated species in the mid-lake (1), in the near-shore (2) and close to the emergent macrophyte vegetation (3)

In the turbid state copepods dominanted zooplankton assemblages developed with low density and species richness and the cladoceran zooplankton consisted of mainly pelagic species with low abundance values. In case of *Diaphanosoma brachyurum*, *Moina brachiata*, *Acanthocyclops vernalis, Simocephalus vetulus*, *Chydorus sphaericus, Alona intermedia* and *Megacyclops viridis* horizontal density differences were formed.

During the presence of *Najas marina* the zooplankton community was dominated by cladocerans and the ratio of the macrophyta-associated species was high. In case of few cladoceran species significant diel density differences developed between the *Najas* bed and the above *Najas*-free water column however macrophyta-associated species did not show diel vertical migration. Based on the result of diurnal monitoring the importance of DHM was irrelevant in the uniform and dense *Najas* beds and zooplankton appear to migrate vertically rather than horizontally.

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