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EFFECTS OF WATER LEVEL FLUCTUATIONS ON LITTORAL MACROINVERTEBRATES (LAKE BALATON, HUNGARY)

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A BALATON VÍZSZINTVÁLTOZÁSAINAK HATÁSA A PARTI ÖV MAKROGERINCTELEN ÁLLATAIRA

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ABSTRACT: The water level of Lake Balaton was extremely low in 2003 (80 cm less than the mean depth of several decades- 3.25 m), after a dry period of several years. Due to the intensive precipitation in 2004, a regeneration period started. Altogether 96 macroinvertebrate taxa were identified on the stones of the littoral zone in these two years. Dominant species were Ponto-Caspian immigrants: the invasive bivalve *Dreissena polymorpha* and the amphipods *Chelicorophium curvispinum* and *Dikerogammarus* spp. *(D. haemobaphes* and *D. villosus).* Maximal density of macroinvertebrates (ind m^{-2} stone surface) was 110,700 in 2003 and 132,354 in 2004. *C. curvispinum* was more abundant in 2004 compared with the drought period 2003, when zebra mussel was more abundant. The relative abundance of the amphipod genus *Dikerogammarus* changed the similarly than that of the zebra mussel. Chironomidae also occurred in large numbers. Vertical stratification of animal numbers and specific taxa occurred in May 2003 and throughout the year of 2004, at higher water level. Many more individuals were recorded on the bottom than near the lake water surface. Water level fluctuation mostly influenced the dominance relationships of the alien Ponto-Caspian invasive invertebrates.

Key words: macroinvertebrates, littoral zone, invasive species, water level fluctuation, Lake Balaton

KIVONAT: A Balaton vízszintje több éves száraz periódus után rendkívül alacsony volt 2003-ban (80 cm-el alacsonyabb, mint a sok évi átlag: 3.25 m). A 2004-ben bekövetkezett intenzív csapadék hatására regenerálódási periódus kezdődött. Összesen 96 makrogerinctelen taxont azonosítottunk a köves parti zónában a fenti periódusban. Pontokáspi inváziós fajok alkották a gerinctelen állatok zömét: vándorkagyló *(Dreissena polymorpha),* tegzes bolharák *(Chelicorophium curvispinum) és Dikerogammarus* fajok *(D. haemobaphes* és *D. villosus)*. Az összes makrogerinctelen állat maximális denzitása (ind m^{-2} kőfelszín) 110 700 volt 2003-ban, 132 354 2004-ben. Sokkal több *C. curvispinum* fordult elő 2004-ben, mint az előző évben, a vándorkagyló ellenben 2003-ban volt gyakoribb, mint 2004-ben. A *Dikerogammarus* fajok relative abundanciája a vándorkagylóéval hasonlóan változott. Chironomidae szintén gyakori volt a mintákban. A makrogerinctelen állatok denzitása tekintetében vertikális rétegzettség jellemző 2003 májusában és 2004-ben, magasabb vízállás mellet. Sokkal több állat fordult elő a mélyben, mint a vízfelszín közelében. A vízszint ingadozás főként a pontokáspi inváziós fajok dominancia viszonyait befolyásolta.

Kulcsszavak: makrogerinctelenek, parti öv, inváziós fajok, vízszint változás, Balaton

Introduction

Water level fluctuations of a shallow lake directly influence the littoral zone and invertebrates living in the encrustation of different substrata. About half of the shoreline of Lake Balaton is protected against wave action by large stones (MISLEY 1988). The surface of these stones is important substrate for invertebrates. The water level of Lake Balaton (a large, shallow lake) has dramatically changed in 2000-2003. In 2003, after a dry period of several years, the water level was extremely low (the water level was 80 cm less than the mean depth of several decades – 3.25 m), which was followed by a regeneration period due to the intensive precipitation in 2004.

Despite the numerous references on the invertebrate fauna of Lake Balaton (e. g. BÍRÓ and MUSKÓ 1995, MUSKÓ et al. 2003, MUSKÓ et al. 2007), scarce literature has been published on qualitative and quantitative structure of the macroinvertebrate community living in the encrustation of littoral stones in relation to water level fluctuation (LAKATOS et al. 1997, KOZÁK et al. 1998, MUSKÓ et al 2007). The invertebrates are important food for fishes (BÍRÓ and MUSKÓ 1995, SPECZIÁR et al. 1997) whose behaviour is also influenced by the water level fluctuation (FISCHER and ÖHL 2005).

The aim of the present study is to report on (i) the qualitative and quantitative structure of the recent macroinvertebrate community living on the stone encrustations in the littoral zone of Lake Balaton and (ii) highlight the effects of the recent water level fluctuation on the macroinvertebrate density and diversity.

Materials and methods

Stones protecting the shore from erosion were sampled in four occasions (May, July, September and October) in two years, 2003 and 2004 from four localities on the shoreline from the westernmost region to the eastern one (Keszthely, Szigliget, Tihany and Balatonalmádi, Fig. 1 and Table 1). Three replicates were taken near the water surface and from the bottom at each station (for further details see MUSKÓ et al., 2007). The encrustation of the stones was brushed, sieved (300 µm mesh size) and preserved in 70 % ethanol. For the calculation of the stone surfaces each surface was drawn to a wrapping paper and the flat surface was cut out and weighed. Wrapping paper was weighed (10 replicates), and using this weight of 100 cm^2 paper, calculated the surface of the stones. Assuming that the stones lay on their own largest surface, the density of animals was calculated as ind m^{-2} lake surface (in the stony littoral zone) taking into account the largest surface of the stones. Water depth and temperature was measured at each site and date. All the animals were identified to the possible lowest taxonomic level and counted, except for Porifera. Data were presented as relative abundance (% of each species) and density (ind m^{-2} stone surface). For more details on the methods see MUSKÓ et al. (2007).

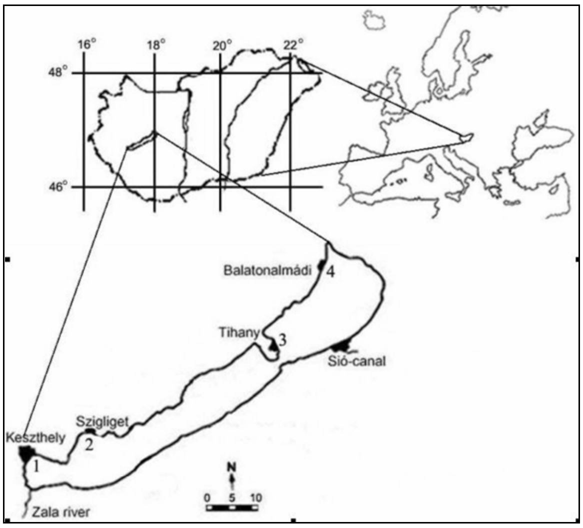

Fig. 1. The location of Lake Balaton and the sampling stations.

Table 2 contains the list of taxa found. Shannon's diversity index was calculated as follows: $H = -\sum_{i=1}^{S} p_i \ln p_i$ where H = Shannon's diversity index, S = total number of species in the community (richness), pi = proportion of N (total number of individuals) made up of the *i*th species. Data were compared using analysis of variance (GLM ANOVA) and Post-hoc Tukey's test with SPSS 11.5. The density data were transformed using a logarithmical (log (x+1)) transformation. The normality of the data was checked with a normal Q-Q plot of the model residuals (SOKAL and ROHLF, 1995). All relationships were considered significant at $p < 0.05$ and all interactions were included in the first models and nonsignificant, higher-order interactions were removed from the final models.

Table 1. Water depth and temperature in 2003 and 2004 (average of three measurements ± Standard Deviation) ns= near the surface, b= at the bottom. B. Almádi = Balatonalmádi. * We measured at the pier, where the water was deeper.

Date (month, day) and station	Depth (cm)		Water temperature (°C)	
2003-2004	2003	2004	2003	2004
May (05.19; 05.18.)				
Keszthely, ns	10	10	21.6±0.0	15.9±0.0
Keszthely, b	40.3±1.2	73	21.5±0.1	15.7±0.1
Szigliget, ns	10	10	22.4±0.1	16.0±0.0
Szigliget, b	50.7±1.2	60	22.4±0.0	16.0±0.0
Tihany, ns	10	10	19.2±0.1	17.0±0.0
Tihany, b	133.0±2.0	150	19.0±0.1	16.0±0.0
B. Almádi, ns	10	10	22.4±0.0	18.0±0.0
B. Almádi, b	36.7±3.1	52	22.5±0.1	18.0±0.0
July (07.07; 07.06)				
Keszthely, ns	10	10	22.1±0.1	ø
Keszthely, b	36.67±3.2	85	22.0±0.0	25±0.0
Szigliget, ns	10	10	23.2±0.2	ø
Szigliget, b	38.0±1.7	70	23.1±0.0	25±0.0
Tihany, ns	10	10	22.1±0.1	ø
Tihany, b	125	168	22.0±0.0	25±0.0
B. Almádi, ns	ø	10		ø
B. Almádi, b	30.7±2.1	30	26.2±1.8	25±0.0
Sept. (09.02; 09.06.)				
Keszthely, ns		10		20.60±0.00
Keszthely, b	23	80	20.3±0.0	20.50±0.00
Szigliget, ns		10		21.73±0.23
Szigliget, b	19	50	19.5±0.1	21.53±0.06
Tihany, ns	10	10	21.0±0.0	22.40±0.00
Tihany, b	100	162	21.1±0.0	21.87±0.06
B. Almádi, ns		10		18.83±0.06
B. Almádi, b	5	35	20.1±0.1	18.80±0.00
Oct. (10.07; 10.11.)				
Keszthely, ns		10		14.8±0,0
Keszthely, b	30	60	14.0±0.0	14.7±0.1
Szigliget, ns		10		14.2±0.0
Szigliget, b	15	45	14.2±0.0	14.2±0.0
Tihany, ns		10		15.0±0.0
Tihany, b	111	152	15.2±0.0	15.0±0.0
B. Almádi, ns		10		13.6±0.1
B. Almádi, b*	25	32	13.3±0.1	13.5±0.0

Table 2. List of identified taxa (indet. = the identification was not possible because the animals were too young or we were not able to identify. + = the taxon present)

	Taxon	2003	2004
Hydrozoa	Hydridae indet.	+	+
	Cordylophora caspia (Pallas, 1771)	+	+
Platyhelminthes	Microturbellaria indet.	+	+
	Tricladidae indet.		+
	Dendrocoelum lacteum (Müller, 1774)		+
	Polycelis nigra (Müller, 1774)		+
	Dugesia polychroa (Schmidt, 1861)		+
	Dugesia lugubris (Schmidt, 1861)	+	+
	Planaria torva (Müller, 1774)	+	+
Nematoda	Nematoda indet.	+	+
Nematomorpha	Nematomorpha indet.	+	
Annelida	Oligochaeta indet.	+	+
	Stylaria lacustris (Linnaeus, 1767)	+	+
	Tubificidae indet.	+	+
	Hirudinea indet.	+	
	Piscicola geometra Linnaeus, 1758	+	+
	Glossiphoniidae indet.	+	+
	Glossiphonia complanata (Linnaeus, 1758)		+
	Helobdella stagnalis (Linnaeus, 1758)	+	+
	Haementeria sp. indet.	+	
	Batracobdella paludosa (Carena, 1824)	+	+
	Hirudidae indet.	+	
	Erpobdellidae indet.	+	+
	Erpobdella octoculata (Linnaeus, 1758)	+	+
Bryozoa	*Fredericella* sp. indet. statoblast		+
	Fredericella sultana (Blumenbach, 1779)	+	+
	Plumatella sp. indet.	+	+
	Hyalinella punctata (Hancock, 1850)		+
Mollusca	Gastropoda indet.	+	+
	Valvata sp. indet. juv.	+	
	Valvata piscinalis (Müller, 1774)	+	+
	Valvata pulchella Studer, 1820	+	
	Valvata naticina (Menke, 1845)	+	+
	Potamopyrgus antipodarum (J. E. Gray, 1843)	+	+
	Lithoglyphus naticoides (Pfeiffer)	+	+
	Bithynia sp. indet. juv.	+	
	Bithynia tentaculata (Linnaeus, 1758)	+	+
	Acroloxus lacustris (Linnaeus, 1758)	+	+
	Lymnaea palustris (Müller, 1774)	+	
	Lymnaea truncatula Müller, 1774	+	+
	Lymnaea peregra (Müller)	+	
	Lymnaea peregra v.ovata (Draparnaud, 1805)	+	+
	Physa fontinalis (Linnaeus, 1758)	+	+
	Planorbarius corneus (Linnaeus, 1758)	+	+
	Gyraulus riparius (Westerlund, 1865)	+	+
	Gyraulus laevis (Alder, 1838)	+	+
	Ferrissia wautieri (Mirolli, 1950)	+	
	Dreissena polymorpha (Pallas, 1771)	+	+
	Pisidium pseudosphaerium Schlesch, 1947	+	
Chelicerata	Hydracarina indet.	+	+
Crustacea	Cladocera indet.	+	+
	Sida crystallina (Müller, 1776)		+
	Diaphanosoma mongolianum Ueno, 1938	+	+
	Daphnia indet. ephippium	+	+
	Daphnia cucullata Sars, 1862	+	+
	Daphnia hyalina Leydig, 1860	+	+
	Eubosmina coregoni (Baird, 1857)		+
	Monospilus dispar Sars, 1861	+	

Table 2. cont.

	Taxon	2003	2004
	Alona sp. indet.	+	+
	Chydoridae indet.	+	+
	Chydorus sphaericus (Müller, 1785)		+
	Leptodora kindtii (Focke, 1844)	+	+
	Ostracoda indet.	+	+
	Limnocythere inopinata (Baird, 1843)	+	+
	Harpacticoidea indet.	+	+
	Eudiaptomus gracilis (Sars, 1862)	+	+
	Cyclopoidea indet.	+	+
	Limnomysis benedeni Czerniavsky, 1882	+	+
	Chelicorophium curvispinum (Sars, 1895)	+	+
	Dikerogammarus spp.	+	+
	Jaera istri Veuille, 1979	+	+
Insecta	Insecta indet.		+
	Sminthurides sp. indet. larva	+	+
	Isotomus sp. indet. larva	+	+
	Isotomurus palustris Müller, 1776 larva		+
	Caenis sp. indet. larva	+	+
	Baetidae larva	+	
	Coenagrionidae indet. larva		+
	Hemiptera indet. imago		+
	Mesoveliidae indet. larva	+	
	Micronecta sp. indet. larva	+	+
	Trichoptera indet. larva	+	+
	Agraylea sexmaculata Curtis, 1834 larva	+	+
	Ecnomus tenellus (Rambur, 1842) larva	+	+
	Orthotrichia sp. indet. larva	+	+
	Diptera indet. larva	+	+
	Pericoma sp. indet. larva	+	
	Psychoda sp. larva	+	
	Ceratopogonidae indet. larva	+	
	Palpomyia sp. indet. larva	+	
	Chironomidae indet. larva	+	+
	Coleoptera indet. larva	+	
	Noterus sp. indet. imago	+	
	Hymenoptera indet. imago	+	+
	Prestwichia aquatica Lubbock, 1864 imago		+
Pisces	Pisces indet. eggs and larva	+	+
	Total	81	76

Results

The water level drastically decreased by September 2003, continually increased until July 2004 and decreased a little thereafter (Table 1). Due to the dry season of 2003, at Balatonalmádi from July until October and at Szigliget in October only stones from the bottom could be collected.

Altogether 96 animal taxa were indentified (Table 2), among these the Ponto-Caspian invaders: *Chelicorophium curvispinum* and *Dikerogammarus* species (*D. haemobaphes and D. villosus)* (Amphipoda) as well as zebra mussels *(Dreissena polymorpha)* dominated (Tables 3 and 4). Chironomidae also occurred in large relative abundance. The relative abundance of *C. curvispinum* ranged between 0 and 58.8 % in 2003 and between 0.51 and 72.7 % in 2004 that of of *D. polymorpha* ranged between 0.6 and 86.7 % in 2003 and between 0.6 and 75.0 % in 2004. Large seasonal, spatial and vertical variations of macroinvertebrates were observed in 2003: There was a vertical stratification of animals in May, when the water level was the highest in 2003 (Table 3). Significantly higher relative abundance of *D.*

polymorpha and *C. curvispinum* occurred on the stones at the bottom than near the surface in May and July (ANOVA, $p < 0.0001$, Table 5b and c). *D. polymorpha* dominated in September (ANOVA, $p < 0.0001$, Table 5d). There was no consequent stratification in September and October even if we could sample from both strata. The relative abundance of the *Dikerogammarus* species was high in May and July almost everywhere (Table 3). Among non invasive taxa Chironomids prevailed in the encrustation of the stones in 2003.

Other Ponto-Caspian immigrants were also sampled: the hydrozoa *Cordylophora caspia*, the mysid *Limnomysis benedeni* and the isopod *Jaera istri*. To be mentioned *Cordylophora caspia*, a new species for Lake Balaton (BENCE and MUSKÓ 2004, MUSKÓ et al. 2008), found at Keszthely and Tihany.

The fauna of the stones was dominated by the amphipod *C. curvispinum* at the higher water level in 2004, especially at the bottom (Table 4). Zebra mussels were also important in the regeneration period, in 2004, but the dominance differed from 2003 values (Tables 3 and 4, ANOVA, $p < 0.0001$, Table 5e). Fewer individuals of *Dikerogammarus* spp. were found. Chironomids were more abundant in 2004 than in 2003. Vertical stratification of relative abundance occurred during the year.

Zebra mussels were dominant mainly on the stones at the bottom (Table 5). The amphipod *Dikerogammarus* spp. found near the surface and *C. curvispinum* were not associated with zebra mussels. This separation was more striking in 2004, when water level was higher. *C. curvispinum* characterized the samples at Tihany and Szigliget, while zebra mussels at Keszthely and Balatonalmádi, both at the bottom and near the surface in 2004. *Dikerogammarus* spp. were significantly less important in 2004 than in 2003 (ANOVA, $p< 0.001$, Table 5f), when they remained basically near the water surface. The importance of Chironomidae changed in 2004 as compared to 2003. *C. curvispinum* and *Dikerogammarus* spp. showed large differences in relative abundance between the two years. *D. polymorpha* dominated the invertebrate community in 2003, while *C. curvispinum* dominated in 2004.

Cordylophora caspia, a species new for Lake Balaton (BENCE and MUSKÓ 2004, MUSKÓ et al. 2008) was found during this project. Porifera were also found but not counted.

The range of the Shannon diversity index near the surface was higher in 2003 than in 2004 (Fig. 2), but the difference was not significant. The biodiversity was significantly higher near the surface than at the bottom at Szigliget and Tihany in 2004 (Fig. 2, ANOVA, $p < 0.003$, Table 5 g).

The species richness (the number of taxa) was somewhat higher at the bottom than near the surface in both years (Fig. 3), but the differences were not significant. The species richness was larger near the surface at Keszthely, while at Balatonalmádi the situation was the opposite in 2004, no significant differences occurred at the stations and data. The number of taxa decreased in 2004 as compared to 2003 (Table 2), but the differences were not significant.

Population density was found higher on the bottom than near surface in May 2003 (ANOVA, $p < 0.0001$, Table 5 a). This was observed all the year 2003 at Tihany, where the deepest depth was recorded (Fig. 4a and b). The density of invertebrates ranged between 1256 and 110,700 ind m^{-2} stone surface and between 3550 and 335,671 ind m^{-2} lake surface (Fig. 4a and b) in 2003. In 2004 the density of invertebrates was low in May, then increased, ranging between 1266 and 132,354 ind m^{-2} stone surface and between 4782 and 448,124 ind m^{-2} lake surface (Fig. 4c and d), significant differences only occurred between July and September (ANOVA, $p < 0.0001$, Table 5h).

Table 3. Relative abundance of invertebrates in 2003 (taxa that occur at least once in larger than 5%). ns = near near surface. b =on the bottom.

Taxa	May		July		Sept.		Oct.	
	ns	b	ns	b	ns	b	ns	b
Keszthely								
Nematoda	21.8	0.3	0.1	0.0	0.3	0.0	0.3	0.0
Oligochaeta	17.8	5.2	3.0	0.9	3.3	2.9	0.5	0.7
D. polymorpha	0.8	24.0	12.6	33.7	62.4	55.8	11.3	5.7
Hydracarina	0.2	1.0	1.8	0.3	2.1	1.0	1.4	0.1
C. curvispinum	2.8	20.3	14.4	5.2	0.2	9.6	7.6	0.9
Dikerogammarus spp.	21.5	23.1	58.3	29.8	1.9	8.2	7.0	3.1
J. istri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	14.2	20.7	6.8	23.5	5.6	6.5	13.9	17.7
Pisces (eggs)	14.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Others	6.2	5.3	3.0	6.7	24.3	16.1	58.1	71.8
Szigliget								
Nematoda	0.4	0.0	0.1	0.0	0.0	0.1		0.0
Oligochaeta	14.6	2.8	0.4	1.6	0.0	1.8		0.7
D. polymorpha	6.8	20.4	4.9	46.1	86.7	7.7		71.3
Hydracarina	2.4	0.8	1.3	1.7	0.0	0.1		0.4
C. curvispinum	9.7	33.2	2.4	7.0	0.3	1.5		0.4
Dikerogammarus spp.	25.4	27.3	79.4	16.4	6.9	14.6		10.3
J. istri	4.7	1.1	0.2	0.5	0.0	0.0		0.0
Chironomidae	22.3	13.8	3.9	8.1	5.6	25.3		15.2
Pisces (eggs)	7.3	0.0	0.0	0.0	0.0	0.0		0.0
Others	6.4	0.5	7.4	18.6	0.4	48.9		1.8
Tihany								
Nematoda	9.0	0.1	0.0	0.0	1.9	0.4	10.8	0.1
Oligochaeta	8.4	6.4	5.7	1.0	15.2	1.9	13.2	0.8
D. polymorpha	1.6	51.3	2.8	70.2	0.8	51.3	0.6	25.0
Hydracarina	17.4	1.9	8.3	1.0	4.2	0.4	2.0	0.4
C. curvispinum	5.4	17.2	6.9	16.4	30.0	31.3	49.7	58.8
Dikerogammarus spp.	9.1	4.3	32.0	3.1	28.4	1.8	17.0	3.3
J. istri	10.4	11.1	4.3	3.8	1.5	1.4	1.1	2.9
Chironomidae	9.9	1.9	27.9	3.5	12.5	9.5	4.1	7.3
Pisces (eggs)	15.9	0.0	7.2	0.1	0.0	0.0	0.0	0.0
Others	13.0	5.8	4.9	1.1	5.5	2.2	1.5	1.4
Balatonalmádi								
Nematoda	0.7	0.8		0.0		1.0		0.4
Oligochaeta	34.3	15.7		1.7		31.5		12.5
D. polymorpha	3.2	5.8		66.0		32.5		44.2
Hydracarina	0.5	2.6		0.3		0.2		0.1
C. curvispinum	3.1	14.2		11.5		0.9		0.0
Dikerogammarus spp.	27.1	8.7		11.6		0.0		0.1
J. istri	0.5	0.7		0.1		0.0		0.0
Chironomidae	24.1	35.9		7.9		11.6		2.6
Pisces (eggs)	0.5	0.3		0.0		0.0		0.0
Others	6.1	15.4		0.9		22.4		40.1

The deepest point, Tihany, seemed to be the most favourable site for invertebrates in the stone encrustation in 2003 (the density ranged between 4,915 and 98,980 ind m^{-2} stone surface) (Fig. 4a), while Szigliget in 2004 (the density ranged between 11,713 and 132,354 ind m^{-2} stone surface) (Fig. 4c). Tihany was favourable for invertebrates also in 2004 (the density ranged between 11,181 and 126,850 ind m^{-2} stone surface) (Fig. 4c). Significantly more animals occurred at Tihany, than at other stations in both years (ANOVA, $p<0.0001$, Table 5i and j).

Table 4. Relative abundance of invertebrates in 2004 (taxa that occur at least once in larger than 5%). ns = near near surface. b =on the bottom.

Taxa	May		July		Sept.		Oct.	
	ns	b	ns	b	ns	b	ns	b
Keszthely								
Hydridae	6.9	3.2	5.1	0.2	2.6	4.5	38.2	7.6
Nematoda	0.7	0.1	1.3	0.0	0.0	0.0	0.2	0.2
Oligochaeta	14.6	8.5	30.9	7.0	1.8	2.5	0.5	2.7
D. polymorpha	0.1	32.1	1.4	37.3	46.4	50.5	10.4	62.8
Hydracarina	0.0	0.5	0.2	3.1	3.8	3.0	0.5	0.0
Harpacticoidea	7.5	14.3	1.3	5.6	4.0	5.5	0.1	0.2
C. curvispinum	1.7	2.9	8.3	13.9	3.5	0.6	1.8	0.5
Dikerogammarus spp.	38.1	18.2	19.8	12.5	8.9	2.7	10.6	3.6
J. istri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	13.4	5.9	19.3	14.9	24.0	17.5	28.6	15.0
Pisces (eggs)	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Others	24.0	17.5	17.4	5.7	7.7	17.6	47.4	15.1
Szigliget								
Hydridae	0.5	0.8	1.2	0.1	0.3	0.2	0.0	0.0
Nematoda	25.0	33.1	0.0	0.1	0.1	0.1	0.9	0.0
Oligochaeta	10.5	14.8	0.6	2.0	1.5	2.8	4.9	7.5
D. polymorpha	0.1	0.7	0.8	6.5	7.2	49.0	41.3	26.4
Hydracarina	0.1	0.4	0.8	3.3	0.6	0.9	2.0	0.5
Harpacticoidea	1.6	4.7	0.1	1.2	0.0	0.0	0.0	0.1
C. curvispinum	0.7	23.2	2.9	72.7	54.8	38.1	29.1	54.3
Dikerogammarus spp.	24.9	11.9	43.1	6.2	17.6	4.7	17.4	5.5
J. istri	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Chironomidae	34.8	7.7	40.6	6.9	16.3	0.0	3.0	5.1
Pisces (eggs)	0.9	0.0	5.8	0.0	0.0	0.0	0.0	0.0
Others	1.4	3.7	5.2	1.1	2.1	4.2	1.4	0.5
Tihany								
Hydridae	4.9	7.4	3.9	2.5	0.2	2.2	0.0	0.7
Nematoda	24.9	0.4	0.0	0.8	0.3	0.9	45.1	1.0
Oligochaeta	13.0	2.1	0.7	0.8	0.5	1.0	0.2	0.9
D. polymorpha	0.1	21.1	0.5	11.9	1.2	13.1	0.5	11.4
Hydracarina	0.5	2.2	7.4	5.1	2.4	1.4	2.1	1.2
Harpacticoidea	0.2	0.5	0.7	0.4	0.5	0.0	0.0	0.1
C. curvispinum	9.4	51.9	7.3	55.0	49.0	72.0	21.0	69.8
Dikerogammarus spp.	26.2	2.9	11.5	3.1	14.5	2.8	7.5	1.9
J. istri	3.6	8.2	2.6	13.7	7.5	3.8	4.4	8.5
Chironomidae	12.5	2.2	60.9	0.0	21.7	1.3	17.9	2.7
Pisces (eggs)	2.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0
Others	7.8	8.5	6.2	9.3	2.4	3.8	1.3	2.5
Balatonalmádi								
Hydridae	0.0	0.0	0.8	0.3	0.0	0.2	0.0	0.0
Nematoda	0.4	0.4	0.1	0.6	0.0	0.4	0.0	0.3
Oligochaeta	7.2	10.9	2.2	3.3	1.0	5.8	0.5	5.1
D. polymorpha	2.0	1.9	20.5	23.6	68.5	44.6	75.0	25.5
Hydracarina	0.0	0.1	0.0	0.1	0.4	0.6	0.2	0.0
Harpacticoidea	2.2	8.5	0.2	0.6	0.3	0.3	0.0	0.4
C. curvispinum	6.7	42.5	14.1	28.3	13.5	13.0	9.6	35.7
Dikerogammarus spp.	35.8	8.9	20.4	13.7	6.5	2.4	6.9	8.7
J. istri	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Chironomidae	35.2	17.0	37.7	23.2	5.2	8.0	1.7	17.0
Pisces (eggs)	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	10.0	9.9	4.8	6.5	4.7	25.0	6.2	7.3

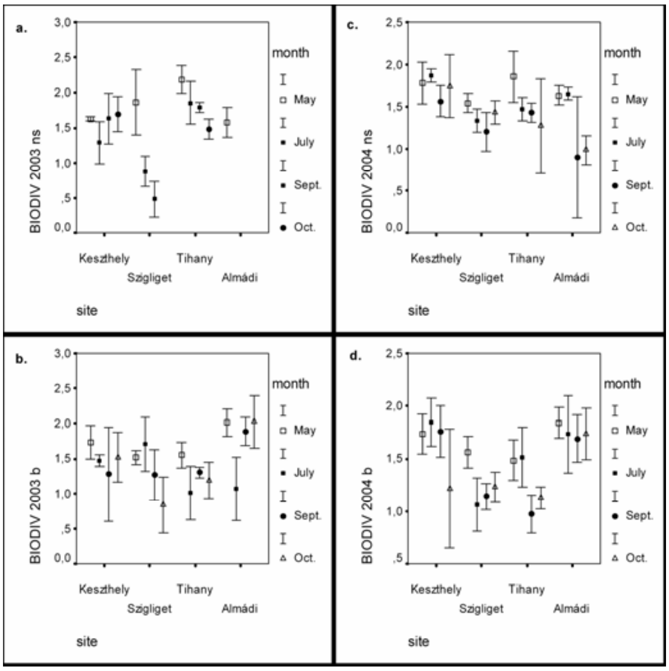

Fig. 2. Biodiversity (Shannon's index) (Mean and Standard Error) depending on the sampling stations near surface (ns) and at the bottom (b) in 2003 and 2004. Almádi = Balatonalmádi.

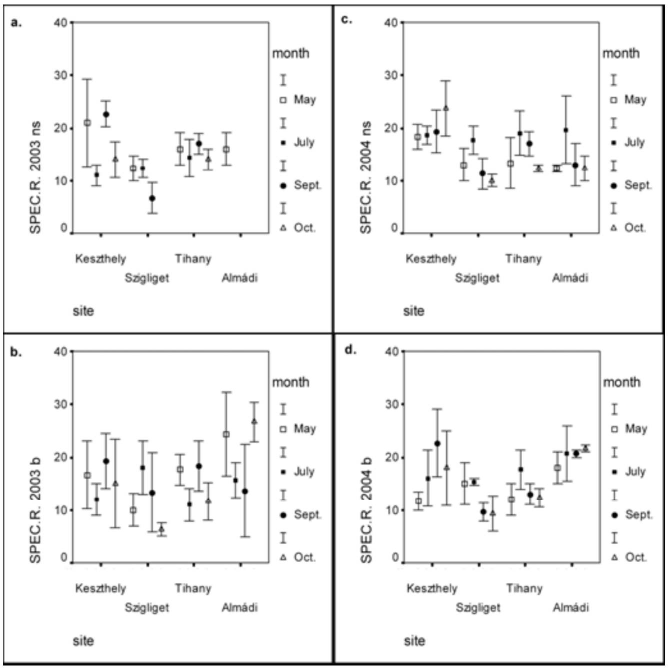

Fig. 3. Species richness (number of animal taxa) (Mean and Standard Error) depending on the sampling stations near surface (ns) and at the bottom (b) in 2003 and 2004. Almádi = Balatonalmádi.

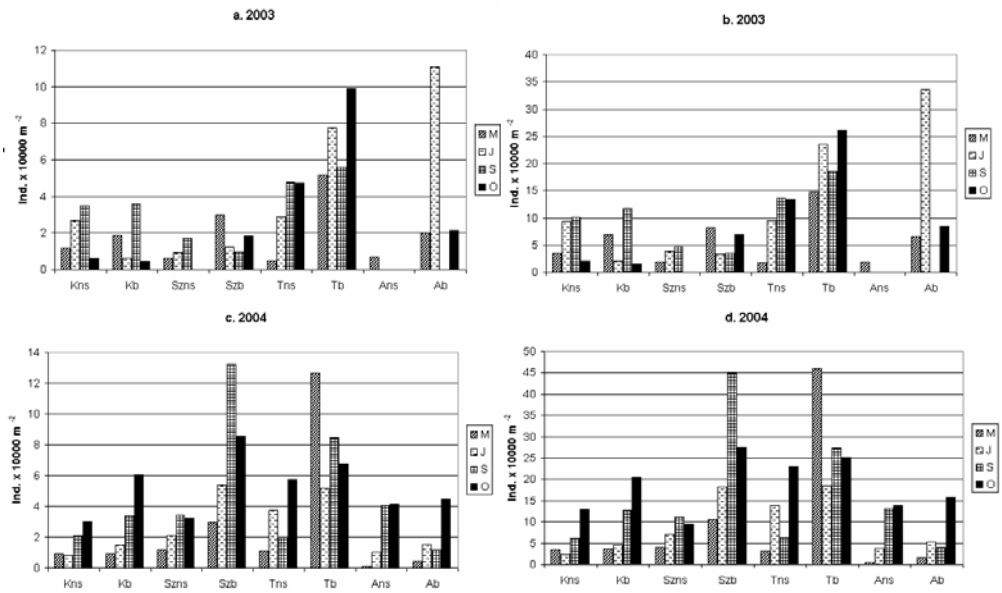

Fig. 4. Density of macroinvertebrates in 2003 and 2004. a and c : ind m^{-2} stone surface, b and d: ind m^{-2} lake surface. K = Keszthely, Sz = Szigliget, T = Tihany, A = Balatonalmádi, ns = near surface, b = at the bottom, M = May, J = July, S = September, O = October.

Table 5. Results of ANOVA for the density, the relative abundance and the Shannon diversity of the all animals in the encrustation. Rank order between positions (P1: on the bottom, P2: near the surface), months (M1: May, M2: July, M3: September, M4: October), years (Y1: 2003, Y2: 2004), and sites (S1: Keszthely, S2: Szigliget, S3: Tihany, S4: Balatonalmádi) was determined using a Tukey-HSD test (if df>1). *Significant after sequential Bonferroni adjustment.

Variables	**Factors**	**Rank order**	**F-value**	**d.f.**	**p-value**
a.) Density of all animals in May of 2003	Position	P1>P2	48.009	1	<0.0001*
b.) relative abundance of *D. polymorpha* May, July of 2003-2004	Position	P1>P2	124.892	1	<0.0001*
c.) relative abundance of *C. curvispinum* May, July of 2003-2004	Position	P1>P2	95.666	1	<0,0001*
d.) relative abundance of *D. polymorpha* 2003-2004	Month	M1<M2<M3>M4	25.607	3	<0.0001*
e.) relative abundance of *D. polymorpha* 2003-2004	Year	Y1>Y2	44.024	1	<0.0001*
f.) relative abundance of *Dikerogammarus spp.* 2003-2004	Year	Y1>Y2	12.319	1	<0.001*
g.) Shannon diversity index at Szigliget and Tihany in 2004	Position	P1<P2	10.48	2	<0.003*
h.) Density of all animals in 2004	Month	M2<M3	8.861	3	<0.0001*
i.) Density of all animals in 2003	Site	S3>S1,S2,S4	10.001	3	<0.0001*
j.) Density of all animals in 2004	Site	S1<S3>S4	19.859	3	<0.0001*

Discussion

Alien invasive species (Ponto-Caspian immigrants) (zebra mussel, *C. curvispinum* and a *Dikerogammaru*s spp) dominated the littoral zone of Lake Balaton, both in 2003, when the water level of the lake was extremely low, and in 2004, when a regeneration started due to intensive precipitation. However, the relative dominance was different in the two years: at low water level zebra mussels dominated, and the amphipod *Dikerogammarus* spp were numerous, while higher water favoured the amphipod *C. curvispinum*. At low water level, many stones remained dry and animals, mainly zebra mussels, died on them. When the water level increased, more stones were covered by water, offering places for zebra mussel larvae to settle. Zebra mussel typically reaches maturity after more than one year; consequently, it needs longer time for regeneration than the amphipods, whose generation time is shorter than a year (MUSKÓ 1992b, 1993). The dominance of the two Ponto-Caspian invasive immigrants, zebra mussels and *C. curvispinum* is a unique phenomenon. Both of these species invaded Lake Balaton in the 1930's, and propagated shortly thereafter (SEBESTYÉN 1934, 1938, ENTZ and SEBESTYÉN 1946). They also were the dominant invertebrates on the submerged macrophytes between 2000 and 2002 (MUSKÓ and BAKÓ 2005, BALOGH and MUSKÓ 2004, MUSKÓ et al. 2004). Moreover, they were the most successful colonizers of different substrates in Lake Balaton (KOZÁK et al. 1998, MUSKÓ and RUSSO 1999, MUSKÓ and GÖRÖG 2000, MUSKÓ et al. 2003). While the density of *D. polymorpha* drastically decreased after invasion by *C. curvispinum* to the Rhine river (VAN DER VELDE et al. 1994), successful coexistence of these two invasive species in Lake Balaton may be explained by their simultaneous invasion and reduced inter-specific competition as observed during the present study.

Dikerogammarus species appeared in Lake Balaton in 1950, when *Limnomysis benedeni* was introduced into the lake as fish food (WOYNÁROVICH 1955), and accidentally, *Dikerogammarus* spp. were also introduced. There were some systematic studies done on these species (see MUSKÓ 1992a, 1994, MUSKÓ et al 2007); *D. villosus*, *D. heamobaphes* and *D. bispinosus* were found on submerged macrophytes in 2000 – 2002 with the dominance of *D. haemobaphes* (MUSKÓ and LEITOLD 2003) but only *D. villosus* and *D. haemobaphes* (with the dominance of *D. villosus* – MUSKÓ et al 2007) were found in 2003-2004 in the encrustation of the stones. However, *D. bispinosus* was also found on the stones in 2005 (MUSKÓ et al. 2006).

The stratification in the relative abundance of *C. curvispinum*, which occurred at higher water level (May 2003 and all the year 2004), disappeared at the extremely low water level (July-October 2003), except for the deepest station Tihany. *Dikerogammarus* spp. did not react very much to water level in this respect.

The highest density of *C. curvispinum* did not reach that found in Lake Balaton 1996 (152,000 ind m^{-2} stone surface, MUSKÓ, 2001). It is possible that the elbowing of *D. villosus,* which is an aggressive competitor (DICK and PLATVOET 2000), competitively interfered with *C. curvispinum.*

The stratification in density of macroinvertebrates on the stones according to deepness supported the results of KOZÁK et al (1998) who have described larger density of macroinvertebrates on the stones at the bottom than near the surface..

Water level fluctuation mostly influenced the dominance relationships of the alien Ponto-Caspian invasive invertebrates.

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