Acta Zoologica Academiae Scientiarum Hungaricae 54 (Suppl. 1), pp. 189–206, 2008

THE ROLE OF AQUATIC BIRDS IN THE REGULATION OF TROPHIC RELATIONSHIPS OF CONTINENTAL SODA PANS IN HUNGARY

BOROS, E.[1], FORRÓ, L.[2], GERE, G.[3], KISS, O.[4], VÖRÖS, L.[5], and †ANDRIKOVICS, S.[4]

[1]*Naturglob Ltd., H-1196 Budapest, Kossuth L. u. 76, Hungary, E-mail: drborose@gmail.com*
[2]*Hungarian National History Museum, Department of Zoology H-1088 Budapest, Baross u. 13, Hungary*
[3]*Department of Systematic Zoology and Ecology, Eötvös Lóránd University H-1117 Budapest, Pázmány Péter sétány 1/c, Hungary*
[4]*Department of Zoology, Eszterházy Károly College Leányka u. 6 H-3300 Eger, Hungary*
[5]*Balaton Limnological Research Institute of the Hungarian Academy of Sciences Department of Hydrobotany, H-8237 Tihany, P.O. Box 35, Hungary*

The aim of this study was to estimate the population sizes, food resources, food selection and trophic regulation of aquatic birds in these soda pans. We classified the estimated density of birds into 3 simple nutrient cycling guilds: net-importer, exporter-importer and the net-exporter. The most important aquatic bird guild was the net-importer guild (51–70%), and the second was the exporter-importer guild (41–27%), while the relative densities of the net-exporter guild was the lowest (8–3%) in the investigated 2 pans. The captive foraging experiment demonstrated that the filter-feeder wildfowl (*Anas* species) could successfully remove the microcrustacean plankton and invertebrate nekton from the water. The biomass of planktonic crustaceans was significantly more by an order of magnitude than the biomass of the other invertebrates (benthos, nekton). The relatively simple trophic relationships demonstrate the bottom up function of some keystone herbivore aquatic bird species, while the top down control is determined by several wildfowl and wader species. The external nutrient load of the aquatic birds causes hypertrophic level of inorganic nutrient resources for the algae, while the planktonic primary production varied only between oligotrophy and mesotrophy because of the extreme physical conditions of these waters. The observed net heterotrophy and several trophic relationships seem to be regulated by aquatic birds.

Key words: soda pans, aquatic bird guilds, bottom up and top down control, trophic relationships, heterotrophy

INTRODUCTION

The natural shallow intermittent soda (sodic) alkaline pans represent a unique type of inland saline waters all over the world and are also important stopover sites for several migratory aquatic birds (waterbirds). We can find continental soda pans in Africa, Asia, North and South America, Australia and Europe. These ecosystems occur in the border of arid zones where steppe vegetation occurs (HAMMER 1986).

The Carpathian Basin is an important western border area of the sodic ecosystem range of Eurasia where characteristic continental soda pans occurs. Unfortunately, there has been a dramatic loss of soda pans during the last few decades (BOROS & BIRÓ 1999, BOROS *et al.* 2006*c*). Moreover, global climate change may also become an increasingly threatening factor for these intermittent wetlands. According to ecological importance and threatening factors, the international importance of most characteristic soda pans was taken into account by the Ramsar Convention based upon the specific criteria of migratory aquatic bird populations as well as biogeographically unique habitats. BOROS (2003) demonstrated by trend analysis that the numbers of some waterfowl and shorebirds species populations increased on soda pans of Kiskunság National Park during last 3 decades. Several soda pans are also designated as Natura 2000 sites in Hungary according to Directives 79/409/EEC and 92/43/EEC.

The aquatic bird populations of soda pans were studied by several ornithologists, but only a few studies dealt with the ecological importance of the bird population within this ecosystem. STERBETZ (1968*a*, *b*, 1972*a*, *b*, 1988, 1991) studied the waterbird food selection by stomach content of shot individuals and described several plant and animal items on waterbird diet. STERBETZ (1988) found Anostracan *Branchinecta orientalis* SARS, 1901 in large amounts and high frequencies in the stomachs of 15 shorebird species (Scolopacidae) on a characteristic sodic pan (Kardoskut, “Fehér-szék” pan in the southern part of the Great Hungarian Plain), but smaller crustaceans were not an important volume in their diet.

We also found spatial relations between the density of *Branchinecta orientalis* and pelagic foraging waders, but this phenomenon did not prove as evidence between microcrustacean zooplankton and filter-feeder waterfowl species (BOROS *et al*. 2006*a*) except for Avocet (*Recurvirostra avosetta* LINNAEUS, 1758), which feed on microcrustacean zooplankton extensively (FORRÓ & BOROS 1997) on Hungarian soda pans. Nevertheless GURD (2006) proved that filter-feeding dabbling ducks (*Anas* spp.) can actively select particles of food by size.

We have already demonstrated that (BOROS 2001, 2002, BOROS *et al*. 2006*b*) the waders (e.g. Scolopacide) apparently feed on the most abundant macroscopic nektonic or benthic invertebrates (e.g. Corixinae, Hydrophilidae), but we found differences in diets related to the foraging techniques used by each species. We also found *Bolboschoenus maritimus* (L.) PALLA in a high proportion of cores and a few microcrustaceans in the diet of Dunlin [*Calidris alpina* (LINNAEUS, 1758)].

The invertebrate fauna of the investigated soda pans was also extensively studied by zoologists and these previous data give a comprehensive base to evaluate the main food resource of birds. FORRÓ (2003) summarised the microcrustacean, ANDRIKOVICS and MURÁNYI (2003) the macrozoobenthos, and KISS *et al.* (2001) the macroscopic invertebrate fauna of the soda pans of Kiskunság.

OLÁH (2003) and OLÁH *et al.* (2006) worked out a comprehensive waterbird nutrient cycling guild concept for the Hungarian wetlands which explains both the feeding and the nutrient cycling function of the birds. This concept contains 3 main waterbird guild groups: the material transporters group (e.g. grazer geese) which take organic materials from the outside; the decomposition accelerating group which accelerates the organic breakdown inside the water (e.g. ducks); and the bioturbing group which accelerates the recycling directly through mechanical effects on the bottom during feeding (e.g. waders). The three main nutrient cycling waterbird guild groups are divided into 9 subgroups based on feeding characteristics of the waterbirds species.

Besides the feeding ecology of the birds, we demonstrated the important effect of aquatic birds on the nutrient load and water quality (BOROS *et al.* 2008), and we also proved that the nutrient input of birds causes net heterotrophy (VÖRÖS *et al.* 2008) on soda pans where internationally important aquatic bird population assemble. We established three simple main nutrient transport guilds concentrated on the nutrient export-import functioning of aquatic bird species: net-importer, exporter-importer, and net-exporter guilds, which are explained in this volume (BOROS *et al.* 2008).

HAMMER (1986) published some models of trophic interactions in saline lake ecosystem on different salinity levels and meromictic environment, but these are not completely implacable to the holomictic intermittent soda pans.

The aim of this study is to estimate the population sizes, nutrient cycling guilds, food resources, and food selection of aquatic birds on soda pans. Based on the previous and current data, we set as an aim the synthesis of our comprehensive knowledge concerning the nutrient loading and feeding parameters of aquatic birds and their regulation effects in the trophic relationships of continental soda pans.

MATERIALS AND METHODS

Study sites

Invertebrate assessments and aquatic bird monitoring were conducted on the open soda water bodies of "Kelemen-szék" (46°47'N, 19°11'E, 120 ha) and "Zab-szék" (46°50'N, 19°10'E, 100 ha) pans of Kiskunság National Park in Hungary. The geographical location of the investigated pans can also be seen in this volume (BOROS *et al.* 2008). The investigated characteristic soda pans are one of the most important stopover sites for the aquatic birds within the middle Hungarian section of the River Danube basin. BOROS (1999) published a comprehensive ecological description of the Hungarian white coloured soda pans, including the study sites, and a short description and detailed physical and chemical data can also be read in this book (BOROS *et al.* 2008, VÖRÖS *et al.* 2008). The most important physical and chemical features of these soda pans are next (numerical data represent year 2002):

– very shallow (max depth: 0.4 m) and intermittent wetlands,
– homomictic (Z_{mix} = Z) white coloured water with high turbidity (average Secchi depth: 0.01–0.02 m) by colloidal fragments,
– dominance of Na^+, HCO_3^- and Cl^- ions (Fig. 1.) with fluctuating hypo-mesosaline ranges of salinity (Average salinity: 8 g L^{-1}, max. 23 g L^{-1}) depending on water level,
– alkaline pH values (pH between 9–10).

Methods

The investigation of the aquatic bird population and the guild conception. The birds were identified and counted through the use of binoculars (8 × 42) and field scopes (30 × 75) on weekly or biweekly occasions on the open water bodies of the two pans in 2002. The monthly average numbers of the birds were considered by average of weekly or biweekly counting data. The density data were calculated by monthly average number of different species and the monthly average surface of the open water table. The surface of the open water tables showed important seasonal variations, and the "Zab-szék" pan completely dried out in July of 2002. Regarding the water table fluctuation, we estimated the edge of open water on working maps by field experiments in each month, and identified the areas by means of ESRI ArcMap 9.1 GIS software.

In order to describe the role aquatic birds play in the regulation of trophic relationships, we implemented a nutrient cycling guild concept which is explained in detail in this volume (BOROS *et al.* 2008). This concept orders the birds into 3 main nutrient cycling guilds: net-importer, exporter-importer, and net-exporter.

Experimental investigation of food selection of filter-feeder waterfowl. Based on former studies, there was no evidence that filter foraging aquatic birds extensively feed on microcrustacean zooplankton after we made a test feeding experiment on captive birds. Mallards (*Anas platyrhynchos* LINNAEUS, 1758), Pintail (*Anas acuta* LINNAEUS, 1758), Garganey (*Anas querquedula* LINNAEUS, 1758), Teal (*Anas crecca* LINNAEUS, 1758), and Wigeon (*Anas penelope* LINNAEUS, 1758) were fed in captivity with characteristic invertebrate food sources that was collected from the investigated soda pans. We collected native microcrustaceans (Cladocera and *Daphnia* ssp.), nekton [Corixinae – *Sigara lateralis* (LEACH, 1817) imagos and eggs], and macrozoobenthos (Odonata larvae) mixed food from the investigated pans by the same method that is used for taking invertebrates samples. The

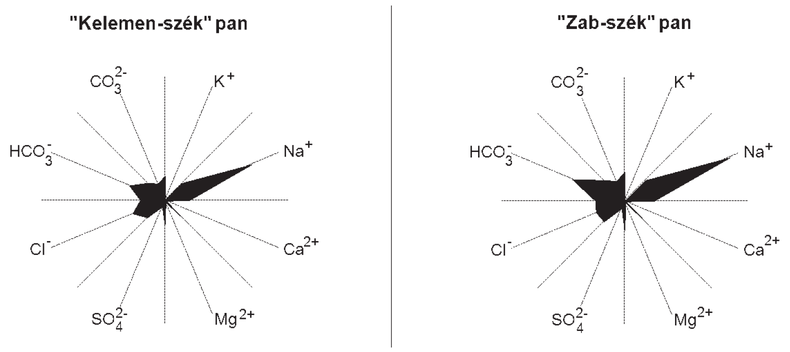

Fig. 1. The ionic composition of the waters of investigated soda pans

biomass (wet weight) of different invertebrate groups was separately measured in the samples before and after the feeding experiment, and the data were expressed in g l^{-1} units based on the water volume of samples.

The investigated birds were not fed for one day before the experiment. The feeding experiment took place during an 8 hour interval during daylight the next day. The different duck species were separated in individual dry boxes. The natural food in original soda water was placed in shallow fixed trays for the ducks in the morning, and the remaining water samples were recycled and investigated again under microscopes.

Investigation of the microcrustacean plankton, macroscopic invertebrate nekton, and benthos. The quantitative sampling of invertebrates was carried out with a cylinder shaped standard sized plastic exclusion tool (diameter: 0.58 m; height: 0.60m) in 2002 (9th March, 2th April, 23th April, 17th May, 13th June, 5th July, 26th July, 22th August). Three sampling points were marked on both pans. Three random samples were repeatedly taken within a circle with a 100 m radius around each marked point (n = 9 within a pan per every sampling event). The distance (in meter unit) between random and marked points was generated by means of a random table on the field, and was approached by wading in the shallow water. The whole microcrustacean plankton and macroscopic invertebrate nekton specimens were removed with a zooplankton net (100 μm) from the cylinder tool soon after it was put into the water. The sampled volume of water was calculated based on water depth inside and diameter of sampling device. The macrozoobethos was sampled by core samples (diameter: 0.58 m; height: 0.1m) and each sample was taken from inside the standard cylinder. The whole core samples were flushed through bronze mesh (0.12 mm). The whole filtered specimen was preserved in formaldehyde until laboratory investigation.

Invertebrate specimens from preserved samples were identified and counted after preparation in a laboratory under a stereomicroscope. All macroscopic invertebrate species were counted individually and microcrustacean densities were estimated. To estimate the number of microcrustaceans, the samples were filtered and diluted to 100 ml, after which 5 ml subsamples were taken and individuals were counted. Subsamples were taken from every sample and counted until there was less than 10% difference between three subsamples. If a sample contained only a few hundred individuals, the whole sample was counted, while in the case of samples containing more than 5000 items, 2 ml subsamples were used.

The abundance data were calculated based on sampled volumes of water and parameters of the core sampling tool and expressed in g m^{-2} unit. The biomass (dry weight) of invertebrate nekton and macrozoobenthos were weighed with an analytical scale (precision 0.01 mg) after a standardised dehydration procedure for different sizes of specimens for each species. The biomass (dry weight) was estimated by body length and weight calibrations for each species and sample. The length of individuals ($n_{min.}$ = 10) of the dominant species in each sample was measured with an ocular micrometer. The biomass (dry weight) of microcrustacean plankton species was estimated through the use of published regression relationships between body length and biomass (BOTTRELL *et al.* 1976, DUMONT *et al.* 1975). The non-normal and homogeneous invertebrate population biomass data were compared with a nonparametric Kruskal-Wallis test.

The basis of the determination of trophic relationships. We discussed the ecological role of aquatic birds in the regulation of the trophic relationship of intermittent soda pans, and summarised and synthesized the former relevant published data, these current data, and the related studies in this volume (BOROS *et al.* 2008, VÖRÖS *et al.* 2008). The applied environmental factors and involved processing on different trophic levels are listed below:

- physical and chemical characteristics of white coloured soda water,
- planktonic primary production (GPP) and respiration
- bacterial activity in the water and in sediment

– density of the aquatic bird communities,
– nutrient load (C, N, P) of aquatic birds,
– nutrient transporting and cycling guilds of aquatic birds,
– food selection of aquatic birds,
– potential food resources of aquatic birds.

RESULTS

Densities of aquatic bird guilds of soda pans

The density of aquatic birds obviously fluctuated during the year according to migrating, breeding, and wintering seasons. The yearly mean densities of observed species and standard errors of means are summarised in Table 1. Although we found that the relative yearly mean densities of aquatic bird guilds were different between the "Kelemen-szék" and "Zab-szék" pans, the most important guild was the net-importer guild (51–70%) with the second being the exporter-importer guild (41–27%), while the relative density of the net-exporter guild was the lowest (8–3%) in both pans in 2002 (Fig. 2).

We observed 18 species that belong to the net-importer guild group, which is primarily comprised of large herbivore grazing species (e.g. *Anser* species) which collect their food outside the soda pans. The most abundant species (yearly mean density > 1 ind. ha^{-1}) in this guild were the White-fronted Goose (*Anser albifrons*), Greylag Goose (*Anser anser*), Mallard (*Anas platyrhychos*), Crane (*Grus grus*), Curlew (*Numenius arquata)*, and the Yellow-legged Gull (*Larus cachinnans*).

We observed 16 species that belong to the exporter-importer guild, which forage both outside and inside soda waters (e.g. most *Anas* species and certain

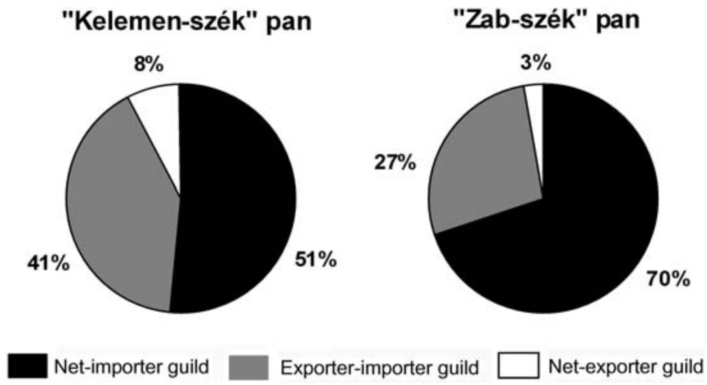

Fig. 2. The composition of aquatic bird guilds by densities on the investigated soda pans in 2002

Table 1. The densities (ind.ha^{-1}) data of aquatic bird guilds on the investigated soda pans in 2002

Sites	"Kelemen-szék" pan						"Zab-szék" pan					
Guilds	Net-importer		Exporter-importer		Net-exporter		Net-importer		Exporter-importer		Net-exporter	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Actitis hypoleucos (LINNAEUS, 1758)					0.053	0.078					0.007	
Anas acuta LINNAEUS, 1758			0.052	0.052					0.172	0.235		
Anas clypeata LINNAEUS, 1758			1.178	1.403					1.685	2.104		
Anas crecca LINNAEUS, 1758			4.721	5.481					4.838	6.077		
Anas penelope LINNAEUS, 1758			0.978	1.068					0.920	1.313		
Anas platyrhynchos LINNAEUS, 1758	3.086	3.057					17.129	37.223				
Anas querquedula LINNAEUS, 1758			0.037	0.029					0.309	0.278		
Anas strepera LINNAEUS, 1758			0.010	0.005					0.047	0.034		
Anser albifrons (SCOPOLI, 1769)	12.372	19.215					19.751	19.419				
Anser anser (LINNAEUS, 1758)	5.075	6.345					10.804	22.845				
Anser erythropus (LINNAEUS, 1758)							0.006					
Anser fabalis (LATHAM, 1787)	0.670	1.425					0.955	1.589				
Ardea cinerea LINNAEUS, 1758	0.014	0.010					0.018	0.006				
Ardea purpurea LINNAEUS, 1766	0.026	0.031										
Aythya ferina (LINNAEUS, 1758)					0.030	0.016					0.064	
Aythya fuligula (LINNAEUS, 1758)					0.008	0.004						
Branta leucopsis (BECHSTEIN, 1803)	0.010						0.010	0.005				
Branta ruficollis (PALLAS, 1769)	0.023	0.013					0.017	0.011				
Calidris alba (PALLAS, 1764)											0.047	0.028
Calidris alpina (LINNAEUS, 1758)					2.152	2.037					1.317	2.359
Calidris ferruginea (PONTOPPIDAN, 1763)					0.820							

Table 1 (continued)

Sites	"Kelemen-szék" pan						"Zab-szék" pan					
Guilds	Net-importer		Exporter-importer		Net-exporter		Net-importer		Exporter-importer		Net-exporter	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Calidris minuta (LEISLER, 1812)					0.054	0.037					0.400	0.377
Charadrius alexandrinus LINNAEUS, 1758					0.110	0.204					0.033	0.027
Charadrius dubius SCOPOLI, 1786					0.026	0.014					0.034	0.009
Charadrius hiaticula LINNAEUS, 1758					0.043	0.031					0.031	0.019
Chlidonias hybridus (PALLAS, 1811)									0.113			
Chlidonias niger (LINNAEUS, 1758)			0.004									
Cygnus olor (GMELIN, 1789)					0.008	0.002					0.024	0.023
Egretta alba (LINNAEUS, 1758)	0.094	0.129					0.018	0.009				
Egretta garzetta (LINNAEUS, 1766)	0.005											
Gallinago gallinago (LINNAEUS, 1758)					0.012							
Gelochelidon nilotica (GMELIN, 1789)			0.012	0.000								
Grus grus (LINNAEUS, 1758)	2.687	3.174					2.707	2.768				
Himantopus himantopus (LINNAEUS, 1758)					0.037	0.041					0.040	
Larus cachinnans PALLAS, 1811	2.392	4.720					9.156	20.418				
Larus canus LINNAEUS, 1758	0.043	0.058					0.070	0.077				
Larus melanocephalus TEMMINCK, 1820			0.034	0.027					0.012	0.006		
Larus ridibundus LINNAEUS, 1766			6.965	8.763					5.620	10.225		
Limosa lapponica (LINNAEUS, 1758)					0.004							
Limosa limosa (LINNAEUS, 1758)					1.188	1.528					0.041	0.059
Mergus albellus LINNAEUS, 1758					0.029	0.018						
Numenius arquata (LINNAEUS, 1758)	2.323	3.718					1.152	2.550				

Table 1 (continued)

Sites	"Kelemen-szék" pan						"Zab-szék" pan					
Guilds	Net-importer		Exporter-importer		Net-exporter		Net-importer		Exporter-importer		Net-exporter	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Numenius phaeopus (LINNAEUS, 1758)	0.070	0.031					0.120	0.151				
Nycticorax nycticorax (LINNAEUS, 1758)	0.005											
Phalacrocorax carbo (LINNAEUS, 1758)	0.052	0.024					0.051					
Philomachus pugnax (LINNAEUS, 1758)			4.688	5.730					3.604	5.544		
Platalea leucorodia LINNAEUS, 1758					0.032							
Pluvialis apricaria (LINNAEUS, 1758)			4.697	6.649					1.553	1.955		
Pluvialis squatarola (LINNAEUS, 1758)					0.250	0.236					0.484	0.729
Podiceps cristatus (LINNAEUS, 1758)					0.003	0.000						
Podiceps nigricollis C. L. BREHM, 1831											0.023	0.024
Recurvirostra avosetta LINNAEUS, 1758					1.148	1.605					0.521	0.561
Sterna caspia PALLAS, 1770			0.004									
Sterna hirundo LINNAEUS, 1758			0.043	0.009								
Tadorna tadorna (LINNAEUS, 1758)											0.033	
Tringa erythropus (PALLAS, 1764)					0.223	0.232					0.218	0.443
Tringa glareola LINNAEUS, 1758					0.352	0.638						
Tringa nebularia (GUNNERUS, 1767)					0.025	0.030					0.040	0.024
Tringa ochropus LINNAEUS, 1758											0.009	0.007
Tringa stagnatilis (BECHSTEIN, 1803)					0.016						0.053	0.028
Tringa totanus (LINNAEUS, 1758)					0.057	0.051					0.051	0.036
Vanellus vanellus (LINNAEUS, 1758)			3.549	5.937					8.700	16.208		
Total sum	3.393	7.758	1.676	3.846	2.181	3.844	7.237	19.380	2.562	7.472	1.351	3.365

Charadriiformes species). The most abundant species (yearly mean density > 1 ind. ha^{-1}) in this guild were the Teal (*Anas crecca*), Shoveler (*Anas clypeata*), Golden Plover (*Pluvialis apricaria*), Lapwing (*Vanellus vanellus*), Ruff (*Philomachus pugnax)*, and the Black-headed Gull (*Larus ridibundus)*.

The most numerous observed species (28) belong to the net-exporter guild which feed on different food resources exclusively inside soda waters (e.g. most Charadriformes species), but only the density of Dunlin (*Calidris alpin*a) and Bar-tailed Godwit (*Limosa limos*a) exceed the 1 ind. ha^{-1}.

The nutrient loads of different guilds are proportionate to the densities, which are also demonstrated in this volume (BOROS *et al.* 2008) in the example of 6 soda pans.

Food selection of filter-feeder waterfowl

The data of test feeding experiment are summarised in Table 2, which lists the wet weight of 4 food items from soda water before and start of experiment for 5 waterfowl species. The data show that Corixinae biomass (wet weight) dominated in the food samples before the feeding experiment (6.710–8.144 g l^{-1}) while these were almost totally exploited during the feeding experiment (0.037–0.271 g l^{-1}) by all duck species. The mallard reduced the Corixinae biomass by 98.5 %, the Pintail by 97.6%, Garganey by 99.4%, Teal by 98.7%, and the Wigeon by 96.6%. Although the biomass of Odonata (0.015–0.157 g l^{-1}) and microcrustacean (0.024–0.184 g l^{-1}) were less than the biomass of Corixinae before the feeding experiment, both of their biomasses were zero after the feeding, meaning that all duck species can also actively select and intake small sized microcrustaceans.

Table 2. Food selection biomass data (wet weight [g]) of filter-feeder waterfowl in the captive foraging experiment

Species		Experiment (wet weight g)	Corixinae	Odonata larvae	*Daphnia* spp.
Mallard	*Anas platyrhynchos*	before	7.081	0.112	0.125
Mallard	*Anas platyrhynchos*	after	0.103	0	0
Pintail	*Anas acuta*	before	7.393	0.105	0.105
Pintail	*Anas acuta*	after	0.179	0	0
Garganey	*Anas querquedula*	before	6.716	0.072	0.156
Garganey	*Anas querquedula*	after	0.037	0	0
Teal	*Anas crecca*	before	7.788	0.157	0.184
Teal	*Anas crecca*	after	0.102	0	0
Wigeon	*Anas penelope*	before	8.154	0.015	0.024
Wigeon	*Anas penelope*	after	0.279	0	0

Composition and biomass of food resources of aquatic birds in the soda pans

According to the previous studies, there were three dominant species in the microcrustacean plankton: the soda water indicator *Arctodiaptomus spinosus* (DADAY, 1891) and *Moina branchiate* (JURINE, 1820) as well as the widely tolerant *Daphnia magna* STRAUS, 1820. Although the seasonal and territorial variation was considerable in the total biomass (dry weight), 60–70% of the yearly average biomass of microcrustaceans (1.57–2.25 g m^{-2}) was caused by the high density of the most characteristic *Arctodiaptomus spinosus* in the soda pans.

The anostracans and Coroxinae dominated in the invertebrate nekton and showed a typical seasonal pattern. The *Branchinecta orientalis* and *B. ferox* (H. MILNE-EDWARS, 1840) [anostracans] occurred exclusively from March until the beginning of May, while *Sigara lateralis* and *Paracorixia concinna concinna* (FIEBER, 1848) [Corixinae] can be found almost throughout the whole season with the population peak occurring in May and June. There were also considerable differences between the pans in yearly average biomass (dry weight) of nekton ("Kelemen-szék" pan: 0.02 g m^{-2}; "Zab-szék" pan: 0.13 g m^{-2}). Anostracans dominated in the nekton of Zab-szék pan, while Corixinae dominated the "Kelemen-szék" pan.

Eight species representing the holometabolous aquatic insect Chironomidae were found in the macrozoobenthos, which was the dominant (65%) group of yearly biomass (dry weight) of macrozoobenthos in "Zab-szék" pan, while their biomass was almost negligible in the "Kelemen-szék" pan. The Chironomiinae subfamily species were: *Camptochironomus tentans* FABRICIUS, 1805; *Chironomus annularius* authors, cf. ASHE et CRANSTON 1990*; Chironomus dorsalis* authors, cf. ASHE et CRANSTON 1990; *Dicrotendipes tritomus* (KIEFFER in THIENEMANN et KIEFFER, 1916); *Glyptotendipes barbipes* (STAEGER, 1839); *Polypedilum nubeculosum* (MEIGEN, 1838); *Tanytarsus* sp. VAN DER WULP, 1874; *and Cryptotendipes* sp. LENZ, 1941. The *Camptochironomus tentans* and *Chironomus annularius* are typical halophil species. *Dicrotendipes tritomus* and *Glyptotendipes barbipes* live mainly in brackish waters. *Chironomus dorsalis* is characteristic to the intermittent waters. Ceratopogonidae sp. dominated (67%) the yearly biomass of macrozoobenthos in "Kelemen-szék" pan, but their proportion was 30% of yearly biomass of macrozoobenthos even in "Zab-szék" pan.

A few characteristic species of Ephydridae, Stratiomydae were found in the pans. Locally, the *Berosus spinosus* (STEVEN, 1808) [Hydrophylidae] was also found. In bottom without aquatic macrophytes, the representatives of hemimetabolus aquatic insects were not found. Among the snails, only the *Anisus spirorbis* (LINNAEUS, 1758) was collected a few in living form but the empty houses of 12 other mollusc species were also registered.

Generally there were significant differences [Kruskal–Wallis-teszt: H (5, n = 405) = 266.967; p = 0.0001] among the biomasses (dry weight) of investigated groups within the site factor ($p < 0.05$). Because of microcrustacean zooplankton, biomass was more by an order of magnitude (average 1.876 g m^{-2}) than all of other invertebrates, and there was no significant difference between nekton (average 0.062 g m^{-2}) and macrozoobenthos (average 0.112 g m^{-2}) yearly biomass. The tested medians and minimum maximum ranges of biomass data are demonstrated in Fig. 3, as well as the summarised density and biomass data (with min., max., and SD values) of the invertebrate species (or taxon) are shown in Table 3.

DISCUSSION

According to our results, the contribution of aquatic birds to the total external nutrient load of the soda pans was approximately 50% in the case of organic carbon (OC), 35% of the nitrogen (N) and 70% of the phosphorus (P). Within the total ex-

Table 3. The biomass data (dry weight, gm^{-2}) of food resorces of aquatic birds on the investigated soda pans in 2002

	"Kelemen-szék" pan	n	Mean	Min.	Max.	SD
Microcrustacean plankton	*Arctodiaptomus spinosus* (DADAY, 1891)	66	1.344	0.110	9.739	1.689
	Daphnia magna STRAUS, 1820	66	0.696	0.000	6.189	1.332
	Moina brachiata (JURINE, 1820)	66	0.208	0.000	2.817	0.553
Nekton	*Branchinecta* spp.	66	0.005	0.000	0.094	0.017
	Corixinae spp.	66	0.015	0.000	0.124	0.026
Macrozoobenthos	*Berosus spinosus* (STEVEN, 1808)	57	0.012	0.000	0.213	0.038
	Ceratopoginidae sp.	57	0.026	0.000	0.249	0.059
	Chironomidae sp.	57	0.000	0.000	0.028	0.004
	"Zab-szék" pan					
Microcrustacean plankton	*Arctodiaptomus spinosus* (DADAY, 1891)	54	1.201	0.003	7.721	1.743
	Daphnia magna STRAUS, 1820	54	0.002	0.000	0.034	0.007
	Moina brachiata (JURINE, 1820)	54	0.362	0.000	5.260	1.034
Nekton	*Branchinecta* spp.	54	0.108	0.000	0.520	0.155
	Corixinae spp.	54	0.022	0.000	0.327	0.051
Macrozoobenthos	*Berosus spinosus* (STEVEN, 1808)	45	0.015	0.000	0.133	0.030
	Ceratopoginidae sp.	45	0.086	0.000	0.416	0.119
	Chironomidae sp.	45	0.185	0.000	0.930	0.200

ternal load, the large bodied herbivore net-importer guild dominated, producing 77% of the OC, 71% of the N and 61% of the P load. The role of the exporter-importer guild contribution was moderate, giving 21% of the OC, 24% of the N and 31% of the P load, while the external nutrient load of the net-importer guild was negligible. This high contribution of the birds in the external nutrient load reflects the fundamental bottom up function of the net-importer aquatic bird guild within this ecosystem. In these waters, the nutrient load of the birds causes hypertrophic levels (concentration) of inorganic nutrient resources for the algae, while the planktonic primary production varied only between oligotrophy and mesotrophy. This paradoxical phenomenon can be explained by the extreme physical conditions of these waters, where the high inorganic turbidity causes severe light limitation of phytoplankton. The low primary production coupled with high respiration of planktonic organisms (bacteria and zooplankton). The observed net heterotrophy seems to be one of the main ecological characteristics of these waters is the result of the significant external organic carbon load of aquatic birds.

The observed net heterotrophy indicates that the high external organic and inorganic nutrient load of the aquatic birds has a great impact on the whole trophic structure. This can also be seen at higher trophic levels as well and affects the production of macrozoobenthos (Chironomidae, Ceratopogonidae, Hydrophilidae), crustacean plankton (Copepoda, Cladocera) and invertebrate nekton (Anostraca, Corixinae) communities. The trophic structure of the characteristic turbid alkaline

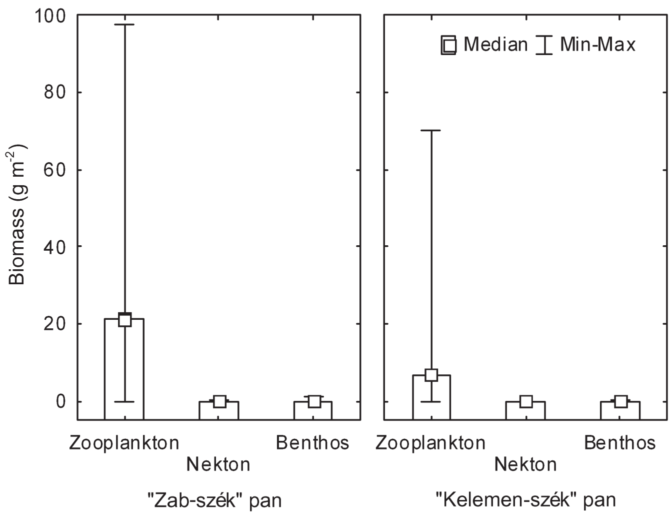

Fig. 3. The biomass (dry weight) of the food resources of aquatic birds on the investigated soda pans in 2002

soda waters is relatively simple. The main ecological factors and trophic relationships are summarised in Fig. 4.

The bacterioplankton and microzooplankton is primarily supplied by avian excrements. The mineralization of the organic matter supplies the phytoplankton with excessive amounts of inorganic nutrients. The planktonic crustaceans and some nektonic species also utilise the suspended organic avian excrements besides the heterotroph microplankton and phytoplankton organisms. The avian bottom up function coincides with the lack of fish support the relatively high biomass of planktonic crustaceans which exceeds the biomass of nekton and benthos. Certain species of nekton (e.g. anostracans) feed on bacterioplankton, algae and crustaceans (DIMENTMAN 1979), while other nektonic groups (e.g. Corixinae) feed on dead invertebrates and living crustaceans (MURILLO & RECASENS 1986). All dead planktonic and nektonic organisms sink to the bottom and supply zoobenthos. The

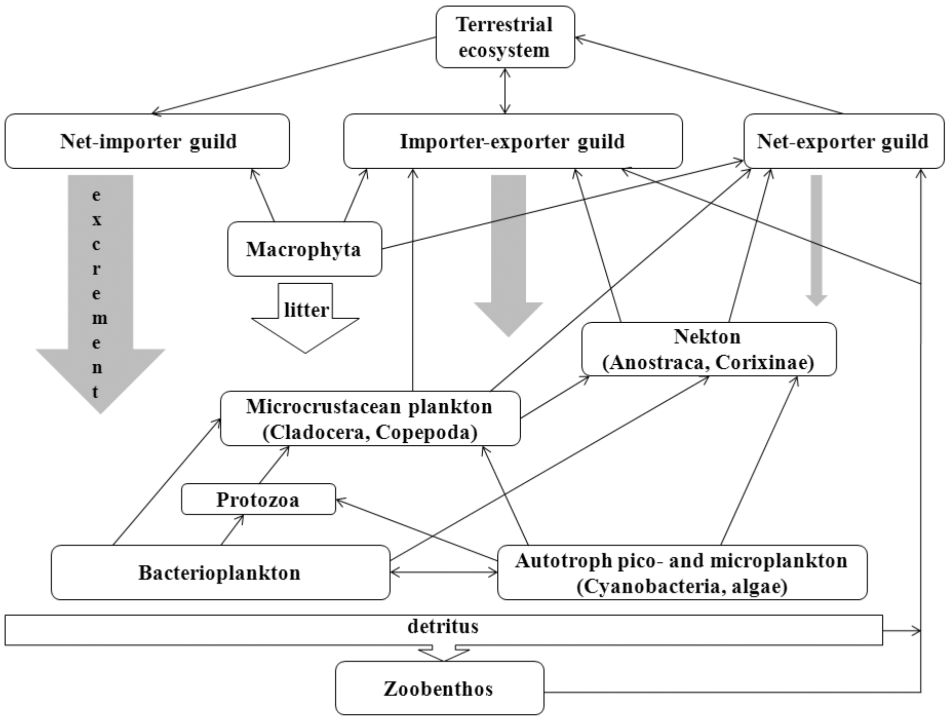

Fig. 4. The most important trophic relationships of the characteristic turbid alkaline soda waters. The grey arrows represent the volume of inorganic and organic excrements of aquatic birds, serving as inorganic nutrients for autrotrophic plankton and organic nutrients for heterotrophic organisms. The white arrows represent the litter of macrophytes and other detritus of the water column. The simple arrows represent the most important trophic relationships.

main group of macrozoobenthos (e.g. Chironomidae) feed on detritus, but some larvae are predatory (e.g. Hydrophylidae and Odonata).

However, the significance of the benthos community was much lower than that of the planktonic organisms. The yearly benthic bacterial activity was lower than the planktonic bacterial activity (Borsodi *et al.* 2003, Szabó *et al.* 2004); similarly, our unpublished experimental results suggest that the contribution of the benthos to the total community respiration was only 15%. In this ecological system, the planktonic organisms play a key role in organic matter decomposition and nutrient cycling. The frequent drying of these lakes makes possible the periodic oxidation of sediment, and the wind action can transport some part of buried materials, which is an important regulation of natural succession in this intermittent environment.

The members of different guilds of aquatic birds extensively feed on macroscopic invertebrates on the soda pans. The filter feeder ducks (mainly exporter-importer guild) can also feed on crustacean plankton, invertebrates nekton (Boros *et al*. 2006*a*), as well as on macrophytes inside and outside of the water. We proved that the filter feeder ducks can successfully intake the microcrustaceans, consequently they are important food resources for them because of the high density and biomass of zooplankton in the soda pans.

The most wader species belong to the net-exporter guild (bioturbing guild in other demonstrated concept) rather feed on macrozoobenthos and invertebrate nekton (Boros *et al*. 2006*b*), which is a typical top-down control regulation. Székely and Bamberger (1992) proved that the waders can remove 87% of their invertebrate prey in a short period. This result was demonstrated in a Hungarian fishpond, where high density (10,000 ind. m^{-2}<) of food resources (predominantly chironomid larvae) was available. In general, the abundance of benthic animals was much less (200–1000 ind. m^{-2}) than 10,000 ind. m^{-2} in the soda pans, consequently the top down control of waders on their benthic food resource must be more intensive in this environment.

The above-mentioned trophic relationships demonstrate a well balanced unique ecosystem, where the aquatic birds play a key role in bottom up and top down regulation at the same time. The bottom up function is determined by some keystone species, for instance White-fronted Goose (*Anser albifrons* (Scopoli, 1769)], Graylag Goose (*Anser anser* (Linnaeus, 1758)] and Black-headed Gull (*Larus ridibundus* Linnaeus, 1766), while the top down control regulation is determined by several wildfowl and wader species. By comparing this trophic structure with other continental saline lakes (Hammer 1986) or with other shallow lakes (Scheffer 1998), we can demonstrate that Hungarian intermittent alkaline soda pans are unusual wetland ecosystems.

*

Acknowledgements – Our studies were supported by the Hungarian Scientific Research Fund (OTKA, T/038033), and the determination of non-biting midge larvae was made by KÁLMÁN BÍRÓ, for him we express our gratitude. We thank GYÖRGY DÉVAI for his advices, the Kiskunság National Park Directorate and CSABA BIRÓ for their technical and GIS supports. We also thank the Kecskemét Zoo and ANDRÁS BARKÓCZI for the collaboration and for helping us in the captive foraging experiment.

REFERENCES

ANDRIKOVICS, S. & MURÁNYI, D. (2003) Zoobentosz együttesekről a Szabadszállás–Fülöpszállás környéki fehér szikes vizekben. (Zoobenthic assemblages in white sodic waters near Szabadszállás–Fülöpszállás (Hungary).) *Természetvédelmi Közlemények* **10**: 251–271. [in Hungarian]

BOROS, E. (1999) A magyarországi szikes tavak és vizek ökológiai értékelése. (Ecological state of sodic water bodies in Hungary.) *Acta Biologica Debrecina* **9**: 13–80. [in Hungarian]

BOROS, E. (2001) Vonuló partimadarak (Charadriiformes) speciális táplálékkínálata szikes vizekben. [Special food resource of migrating waders on soda pans.] *Hidrológiai Közlöny* **81**: 332–333. [in Hungarian]

BOROS, E. (2002) Partimadarak (Charadrii) potenciális táplálékkínálata és az élőhelykezelés összefüggései kiskunsági szikes gyepterületeken. (Investigations on the relation between potential food resource of shorebirds (Charadrii) and habitat management practices on sodic grassland in the Kiskunság.) *Aquila* **107–108**: 15–35. [in Hungarian]

BOROS, E. (2003) Vízimadár populációváltozások és környezeti okai a Kiskunsági Nemzeti Park szikes tavain és mocsarain (KNP II. sz. területének térségében). (Waterbird population changes and their environmental reasons on sodic lakes of the Kiskunság National Park.) *Természetvédelmi Közlemények* **10**: 289–312. [in Hungarian with an English summary]

BOROS, E. & BIRÓ, CS. (1999) A Duna–Tisza-közi szikes tavak ökológiai állapotváltozásai a XVIII–XX. századok időszakában. (Ecological change of sodic water bodies in the plain between Danube and Tisza from 18th to 20th centuries.) *Acta Biologica Debrecina* **9**: 81–105. [in Hungarian]

BOROS, E., BÁNFI, SZ. & FORRÓ, L. (2006) Anostracans and microcrustaceans as potential food sources of waterbirds on sodic pans of the Hungarian plain. *Hydrobiologia* **567**: 341–349.

BOROS, E., ANDRIKOVICS, S., KISS, B. & FORRÓ, L. (2006) Feeding ecology of migrating Waders (Charadrii) at sodic-alkaline pans in the Carpathian Basin. *Bird Study* **53**: 86–91.

BOROS, E., MOLNÁR, A., OLAJOS, P., TAKÁCS, A., JAKAB, G. & DÉVAI, GY. (2006) Nyílt vízfelszínű szikes élőhelyek elterjedése, térinformatikai adatbázisa és természetvédelmi helyzete a Pannon biogeográfiai régióban. (Geographical distribution, GIS database and nature conservation status of opened sodic (alkaline) water bodies in Pannonic Biogeographical Region.) *Hidrológiai Közlöny* **86**(6): 146–147. [in Hungarian]

BOROS, E. NAGY, T., PIGNICZKI, CS., KOTYMÁN, L., BALOGH, V., K. & VÖRÖS, L. (2008) The effect of aquatic birds on the nutrient load and water quality of soda pans in Hungary. *Acta Zoologica Academiae Scientiarum Hungarica* **54**(Suppl. 1): 205–222.

BORSODI, A., RESKÓNÉ NAGY, M., GEDEON, G., VLADÁR, P., BOROS, E. & MÁRIALIGETI, K. (2003) Szikes tavak baktériumközösségeinek szénforrás értékesítési vizsgálata BIOLOG rendszerrel. (Bacteriological investigations on community-level BIOLOG carbon source utilisation pattern in Hungarian soda lakes.) *Hidrológiai Közlöny* **83**(1–12): 25–28. [in Hungarian]

BOTTRELL, H. H., DUNCAN, A., GLIWICZ, Z. M., GRYGIEREK, E., HERZIG, A., HILLBRICHT-ILKOWSKA, A., KURASAWA, H., LARSSON, P. & WEGLENSKA, T. (1976) A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* **24**: 419–456.

DIMENTMAN, C. (1979) Biology, ecology and distribution of anostracan crustaceans in Israel. *Israeli Journal of Zoology* **28**(1): 57.

DUMONT, H. J., VAN DE VELDE, I. & DUMONT, S. (1975) The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* **19**: 75–97.

FORRÓ, L. (2003) A Fülöpszállás–Szabadszállás környéki szikes vizek rákfaunája. (The microcrustacean fauna of the sodic waters in the of Szabadszállás–Fülöpszállás.) *Természetvédelmi Közlemények* **10**: 241–250. [in Hungarian with an English summary]

FORRÓ, L. & BOROS, E. (1997) Microcrustacean zooplankton as potential food of *Recurvirostra avosetta* in sodic waters of the Hungarian Plain. *Wetlands International Publication* **43**: 239–250.

GURD, D. (2006) Filter-feeding dubling ducks (Anas spp.) can actively select particle by size. *Zoology* **109**: 120–126.

HAMMER, U. T. (1986) *Saline lake ecosystems of the World.* Dr W. Junk Publishers, The Hague, 616 pp.

KISS B., LENGYEL, SZ., MÜLLER, Z., JUHÁSZ, P., OLAJOS, P., SZÁLASSY, N., DÉVAI, GY. & GRIGORSZKY, I. (2001) A Kiskunsági Nemzeti Park szikes víztereiben élő vízi makroszervezetek mennyiségi vizsgálata (Hirudinea, Gastropoda, Odonata and Heteroptera). (Quantitative studies on macroinvertebrates (Hirudinea, Gastropoda, Odonata and Heteroptera) inhabiting sodic ponds of Kiskunsági National Park.) *Hidrológiai Közlöny* **81**(5–6): 385–388. [in Hungarian]

MURILLO, J. & RECASENS, L. (1986) Feeding habits of Sigara lateralis (Heteroptera, Corixinae). *Miscellaneous Zoology Barcelona* **10**: 135–140.

OLÁH, J. JR. (2003) Vízimadár anyagforgalmi guildek. (Waterbird trophic guilds.) *Magyar Vízivad Közlemények* **10**: 381–423. [in Hungarian]

OLÁH, J. JR., LAKATOS, G., KOVÁCS, G., ANDRIKOVICS, S. & OLÁH, J. (2006) Waterbird guilds in Hungarian wetlands. *Canadian Wildlife Service Technical Report* **474**: 92–102.

SCHEFFER, M. (1998) *Ecology of shallow lakes.* Chapman & Hall, London, 343 pp.

STERBETZ, I. (1968*a*) A vadrécék környezetvizsgálata a kardoskúti természetvédelmi területen. (Studie über die Umgebung der im Kardoskúter Naturschutzgebiet lebenden Wildenten) *Aquila* 75: 45–77.

STERBETZ, I. (1968*b*) A magyarországi bőjti- és csörgőrécék (Anas querquedula L. és Anas crecca L.) összehasonlító táplálkozásvizsgálata. [The comparative feed-examination of Garganey and Teal (Anas querquedula L. and Anas crecca L.) in Hungary.] *Állattani Közlemények* **7**: 119–122. [in Hungarian]

STERBETZ, I. (1972*a*) A magyarországi vízivad táplálékbázisa. [The food resource of Hungarian waterfowl.] *Állattani Közlemények* **59**: 119–125. [in Hungarian]

STERBETZ, I. (1972*b*) *Vízivad. [The waterfowl.]* Mezőgazdasági Kiadó, Budapest, 204 pp. [in Hungarian]

STERBETZ, I. (1988) Parti madarak (Limicolae sp.) táplálkozásvizsgálata a Kardoskúti-Fehértón, Dél-kelet Magyarországon. [The investigation of food of waders on the Kardoskúti-Fehértó, South-East part of Hungary.] *Aquila* **95**: 142–161.

STERBETZ, I. (1991) Adatok a Magyarországon védett úszóréce (Anas sp.) fajok táplálkozásához. (On the feeding patterns of Anas species protected in Hungary.) *Aquila* **98**: 37–45. [in Hungarian]

SZABÓ, G., BORSODI, A., VLADÁR, P., CECH, G., TÓTH, E., BOROS, E. & MÁRIALIGETI, K. (2004) A Kiskunsági Nemzeti Park szikes tavainak bakteriológiai vizsgálata. (Studies on the alkaliphilic bacterial communities of two Hungarian soda lakes located in Kiskunság.) *Hidrológiai Közlöny* **84**(5–6): 147–150. [in Hungarian with an English summary]

SZÉKELY, T. & BAMBERGER, ZS. (1992) Predation of waders (Charadrii) on prey population: exclosure experiment. *Journal of Animal Ecology* **61**: 447–456.

VÖRÖS, L., SOMOGYI, B. & BOROS, E. (2008) Birds cause net heterotrophy in shallow lakes. *Acta Zoologica Academiae Scientiarum Hungarica* **54**(Suppl. 1): 23–34.

Revised version received April 21, 2008, accepted May 30, 2008, published December 30, 2008