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# Waterbird-mediated Productivity of Two Soda Pans in the Carpathian Basin in Central Europe

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**Abstract.—**The effect of aquatic birds on nutrient cycling and energy flow was investigated in two soda pans, one turbid and the other colored, with different physical and chemical characteristics. Primary plankton production and respiration were measured together with an estimation of waterbird carbon, nitrogen and phosphorus loading during 2014. Both pans were hypertrophic and showed net heterotrophy. The nutrient loading of the birds in the turbid pan was approximately five times higher (C: 758 kg/ha/year, N: 122 kg/ha/year, P: 20 kg/ha/year) than in the colored pan, with significant guanotrophication. Despite the high chlorophyll *a* concentrations (turbid: 752 µg/l and colored: 369 µg/l, on average), the annual surface-related planktonic production was relatively low (turbid: 64 mg C/m$^2$/year and colored: 23 mg C/m$^2$/year), by contrast, respiration was similar in the two pans (turbid: 75 C/m$^2$/year and colored: 78 mg C/m$^2$/year). Nutrient loading showed a significant positive correlation with total and soluble reactive phosphorus, chlorophyll *a* and gross planktonic production, supporting the conclusion that the waterbirds significantly affected primary production. By contrast, there was no significant correlation between the nutrient loading and planktonic respiration. The low production and respiration ratio (Pro/Res) in the colored pan was presumably caused by a high dissolved organic carbon concentration (polyhumic). A possible explanation for the difference of Pro/Res between the turbid and colored pans is variation in the decomposition of the bird excrement and surrounding macrophytes. *Received 20 January 2016, accepted 22 August 2016.*

**Key words.—**colored pan, guanotrophication, heterotrophy, Ramsar sites, respiration, turbid pan.

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The role of waterbirds in biochemical cycles and productivity in aquatic ecosystems has been studied in a number of cases. Guanotrophication by waterbirds can have a positive impact on productivity and energy flow. However, waterbirds can cause local habitat degradation. Several supporting and regulatory ecosystem services are provided by waterbirds (Green and Elmberg 2013). The influence of birds in aquatic ecosystems is often indirect, and their importance remains largely unknown because of the lack of essential information about the interactions between waterbirds and other ecosystem components. Thus, effective management of aquatic ecosystems requires a better understanding of how waterbirds can affect ecosystems.

Zavarzin (1993) observed that endorheic soda lakes have closed nutrient cycling, where the input of carbon and nitrogen into the ecosystem comes predominantly from $CO_2$ and $N_2$ fixation by photosynthetic cyanobacteria. On other hand, the soda lakes are not entirely closed systems because of sometimes vast populations of waterbirds (Brian *et al.* 1998; Sorokin *et al.* 2014).The soda pans of the Carpathian Basin are important breeding and stopover sites for African-Eurasian migratory waterbirds traversing the Black Sea and the Mediterranean flyway (Boros *et al.* 2013). The aquatic communities of these habitats are strongly linked to waterbirds in three ways: 1) soda pans with high zooplankton biomass attract planktivorous filter-feeding waterbirds (Boros *et al.* 2006a; Horváth *et al.* 2013); 2) wading shorebirds feed on less abundant nektonic and benthic invertebrates (Boros *et al.* 2006b, 2008b); and 3) large-bodied herbivorous bird species (e.g., geese) provide a significantly high external nutrient load of carbon (C), nitrogen (N), and phosphorus (P), which causes hypertrophic conditions (Boros *et al.* 2008a) and may lead to net heterotrophy (Vörös *et al.* 2008).

The primary objective of this study was to identify the impact of waterbirds on the processes of production and decomposition in two characteristic Hungarian soda pans. Our hypothesis was that waterbirds have a significant impact on both planktonic production and respiration because of the nutrient loading associated with their presence. By selecting two different hypertrophic soda pans, one dominated by open water (80%) and one by macrophyte vegetation (90%), the spatial distribution of marshland macrophytes was also taken into account as a background environmental factor.

## METHODS

### Study Area

The pans were located in the Duna-Tisza Interfluvial region of Hungary. The Zab-szék pan (46° 50' 5.09" N, 19° 10' 17.82" E) was selected as a prototypical turbid type (grayish-white water rich in suspended colloidal minerals), while the Sósér pan (46° 47' 18.62" N, 19° 8' 39.71" E) was selected to represent the colored type (brownish-black water rich in dissolved humic matters). The two pans are located 3 km apart. The pans are situated in the groundwater discharge areas of a closed hydrographic (endorheic) basin, in which groundwater inflow exceeds the surface-related watershed inflow and precipitation (Boros *et al.* 2013). We assume that nutrient input by precipitation, surface and groundwater inflow were the same in both pans.

Submerged macrophytes were absent from the open waters of the pans, but both pans were surrounded by marshland vegetation dominated by saltmarsh bulrush (*Bolboschoenus maritimus*) and common reed (*Phragmites australis*) in varying spatial proportions. The extent of open water and marshland vegetation was estimated from field observations and remote-sensing databases extracted from Google Earth. The mapping procedure and spatial calculations were carried out using ArcMap (Environmental Systems Research Institute 2013). The selected pans differed in the spatial distribution of open water and macrophyte-covered areas: in 2014, the turbid Zab-szék pan (143 ha) consisted of 80% open water and 20% marshland vegetation, whereas the colored Sósér pan (51 ha) consisted of 90% marshland vegetation and only 10% open water at average water-depth levels. As both pans are shallow with intermittent standing water, they are incapable of supporting resident fish populations.

### Field Measurements and Water Sampling

Water sampling was carried out monthly between January and December 2014 in the open waters of the pans. Water depth was measured at each sampling location, and underwater light conditions were measured with a Secchi disc (Secchi) except when the pan bottom was visible (Wetzel and Likens 1991). Water temperature, pH and conductivity were measured using a WTW MultiLine P4 field instrument. The diel variation in water temperature was determined using HOBO Pendant Temperature/Light Data Loggers (64K-UA-002-64). Salinity (Sal) was calculated from conductivity using the following formula: salinity (g/l) = 0.8 × conductivity (mS/cm) (Boros *et al.* 2014).

### Laboratory Measurements

The concentration of colored dissolved organic matter (CDOM) was expressed as Pt (platina) units (mg Pt/l) using the method of Cuthbert and del Giorgio (1992). Acid-washed glassware was used for the analyses. Samples for total organic carbon (TOC) and dissolved organic carbon (DOC) analyses were acidified (to pH 2 with HCl) and bubbled to remove dissolved inorganic carbon. Next, the samples were filtered through a precombusted GF-5 glass fiber filter (pore size = 0.4 μm), and both TOC and DOC concentrations were measured using an Elementar High TOC (V.-Balogh *et al.* 2009, 2010). Particulate organic carbon (POC) was defined as the difference between TOC and DOC concentrations (POC = TOC – DOC).

For the determination of total nitrogen (TN), samples were digested by sodium hydroxide and potassium-persulfate in an autoclave at a temperature of 121 °C, and TN was measured with a Shimadzu UV-160A spectrophotometer (Eaton *et al.* 1995). The quantity of soluble reactive phosphorus (SRP) was determined from filtrates based on the method of Murphy and Riley (1962), while total phosphorus (TP) content was measured spectrophotometrically after potassium-persulfate digestion from unfiltered water samples (Menzel and Corwin 1965).

Total suspended solids (TSS) were determined gravimetrically (Eaton *et al.* 1995) after filtration through cellulose acetate filters (pore size = 0.4 μm). For the chlorophyll *a* (Chl) measurement, 5-100 ml of each sample (depending on turbidity) was filtered through a GF-5 glass fiber filter, after which chlorophyll *a* concentration was determined spectrophotometrically with hot methanol extraction (Wetzel and Likens 1991). Algal-free suspended solids (TSS-Alg) concentration was calculated by assuming a 1:100 ratio between chlorophyll *a* concentration and the dry weight of phytoplankton (Reynolds 1984). Subtracting the latter from the total suspended solids (TSS) concentration yielded the algal-free suspended solids (TSS-Alg) concentration.

### Planktonic Primary Production and Respiration

Planktonic primary production (Pro) and community respiration (Res) were measured monthly using the 'light-dark bottle' method (Vollenweider 1969). The measurements began after ice melt from 1 February 2014 to 31 December 2014, except in July, when the pans were almost completely dry. Seasonal variation was monitored with two measurements per month during the vegetation period from March to October 2014, except in July and August, again because of low water levels. To estimate production and respiration rates, samples were collected in 300 ml Karlsruhe bottles in the field. For each pan, three light bottles and three darkened bottles were placed into the water along the shoreline. The bottles were fully submerged in an upside-down position, with the bottom of the bottles at the surface and the height of the Karlsruhe bottles extending beyond the euphotic depth of the ponds. Incubations lasted from 10 to 14 hr. Dissolved oxygen before and after the incubations was measured with a WTW Oxi 539 dissolved oxygen meter and a TriOxmatic 300 electrode. Daily production was calculated from the hourly values by assuming that Production(daily) = Production(hourly) × daylight hours. Daily respiration (for 24 hr) was calculated on the basis of the measured hourly respiration rates taking into account the diel variability of respiration as a consequence of temperature dependence (del Giorgio and le B. Williams 2005). Oxygen concentration data were transformed into carbon concentration (mg C/l) by applying a constant parameter of 0.313.

### Estimation of the Nutrient Loading of Waterbirds

The nutrient loading of birds was estimated by determining the abundance of waterbird populations and the nutrient content of their excrement. Waterbirds on the open water of the pans were counted with binoculars (8×42 and 10×42) and spotting scopes (30×75 and zoom 20-60×78) during daylight at 7-day intervals throughout 2014. Daily bird abundance (individuals/ha) was calculated from the average of the weekly counts for each month. The contribution of waterbird populations to the daily nutrient load was estimated using daily net rates of C, N, and P excretion (Table 1). Daily carbon, nitrogen and phosphorus excretion data (g/day/individual) were modified by a species-residency time correction factor (RTF: residence time in hours on the pans during 24 hr) on the water surface based on observed diurnal and nocturnal activity. Daily net C, N, and P excrement data and waterbird species RTFs are listed in Table 2. The monthly total loading of waterbirds = Σ species (A × E × RTF × D), where A is the daily mean of abundance of waterbird species for each month, E is the daily net rate of C, N, and P in the excrement of each bird species, RTF is the daily residency time factor of each species on the open water and D is the number of days of each month. The annual summarized net C, N, and P loads were determined by summing the monthly average loads. Surface-related data were calculated as the sum of monthly loading volumes divided by the actual size of the open water of each month.

### Statistical Analyses

We tested for relationships between waterbird-related nutrient loading and the investigated water variables with pairwise Spearman rank correlations. To reveal any possible relationship between measured and estimated parameters, we also carried out a Principal Component Analysis (PCA). Basic statistical analyses, graph preparation, PCA ordination with standardized scores and Spearman rank correlations were performed using Origin software (OriginLab 2015).

## RESULTS

### Waterbird Population and Nutrient Loading

Both waterbird species richness and abundance were higher on the Zab-szék pan than on the Sósér pan, likely because of the difference in the size of the open water area. Altogether, 45 waterbird species were observed on the two pans, but only 14 of them were observed on the Sósér pan whereas only 44 of them were found on the Zab-szék pan (Table 2). Bird abundance and nutrient loading displayed notable seasonal variation, which was associated with peaks in the passage of migratory birds. The abundance of waterbirds observed on the Zab-szék pan was highest in early spring (February-March), with a second peak (July) of post-breeding birds occurring prior to the drying out of the pans (Fig. 1A). On the Sósér pan, only moderate population peaks occurred in spring and summer (Fig. 1B). The highest observed waterbird abundance was 171 individuals/ha on Zab-szék pan in February, while there were only 26 individuals/ha on the Sósér pan at the beginning of July as the pan was drying out. The cumulative yearly sum of the monthly average number of waterbirds was two orders of magnitude higher and the yearly sum of the monthly average abundance was one order of magnitude higher on the Zab-szék pan (55,453 individuals; 385.10 individuals/ha) compared to Sósér pan (495 individuals; 41.24 individuals/ha). The species composition of the waterbird community differed between the pans. Based on the number of individuals/ha, the primary species contributing to the allochthonous nutrient loads on the Zab-szék pan were the Greater White-fronted Goose, Greylag Goose, Eurasian Teal, Mallard, Eurasian Curlew, Caspian Gull, Yellow-legged Gull, and Black-headed Gull, while on the Sósér pan, the Northern Lapwing and the Black-headed Gull were the only abundant species (scientific names in Tables 1 and 2).

In 2014, the yearly total nutrient loading of waterbirds was estimated to be 7,582 mg C/m$^2$/year, 1,221 mg N/m$^2$/year and 197

**Table 1. Daily net Carbon (C), Nitrogen (N), and Phosphorus (P) excrement data (g/day/individual) and residency time factors (RTF: residency time hours on the pans during 24 hours) of the observed waterbird species. International English and scientific names are from the British Ornithologists' Union (2013).**

| Waterbird Species | | RTF | C | N | P | Source |
|---|---|---|---|---|---|---|
| Tundra/Taiga Bean Goose | *Anser fabalis* | 0.6 | 9.76 | 0.49 | 0.11 | Oláh (2003) |
| Greylag Goose | *Anser anser* | 0.6 | 9.76 | 0.49 | 0.11 | Oláh (2003) |
| Greater White-fronted Goose | *Anser albifrons* | 0.6 | 8.60 | 0.69 | 0.08 | Kear (1963) |
| Dabbling ducks | *Anas* spp. | 0.8 | 9.12 | 0.58 | 0.18 | Manny *et al.* (1994); Oláh (2003) |
| Diving ducks | *Aythya and Mergus* spp. | 1.0 | 9.69 | 0.61 | 0.19 | Manny *et al.* (1994); Oláh (2003) |
| Great Egret | *Ardea alba* | 1.0 | 14.50 | 1.38 | 3.78 | Marion *et al.* (1994) |
| Grey Heron | *Ardea cinerea* | 1.0 | 14.50 | 1.38 | 3.78 | Marion *et al.* (1994) |
| Grebes | *Podiceps* spp. | 1.0 | 9.69 | 0.61 | 0.19 | Manny *et al.* (1994); Oláh (2003) |
| Common Crane | *Grus grus* | 0.6 | 8.40 | 3.48 | 0.58 | Oláh (2003) |
| Pied Avocet | *Recurvirostra avosetta* | 1.0 | 5.00 | 2.16 | 0.36 | Oláh (2003) |
| Black-winged Stilt | *Himantopus himantopus* | 1.0 | 5.00 | 2.16 | 0.36 | Oláh (2003) |
| Curlews | *Numenius* spp. | 0.6 | 3.00 | 1.30 | 0.22 | Oláh (2003) |
| Northern Lapwing | *Vanellus vanellus* | 0.6 | 2.52 | 0.65 | 0.12 | Oláh (2003) |
| Plovers | *Charadrius* spp. | 1.0 | 3.00 | 0.93 | 0.11 | Oláh (2003) |
| Ruff | *Philomachus pugnax* | 0.6 | 2.52 | 0.65 | 0.12 | Oláh (2003) |
| Sandpipers 1 | *Calidris* spp. | 1.0 | 3.00 | 0.93 | 0.11 | Oláh (2003) |
| Sandpipers 2 | *Tringa* spp. | 1.0 | 4.20 | 1.08 | 0.20 | Oláh (2003) |
| Common Snipe | *Gallinago gallinago* | 1.0 | 4.20 | 1.08 | 0.20 | Oláh (2003) |
| Black-headed Gull | *Chroicocephalus ridibundus* | 0.6 | 3.48 | 0.36 | 0.23 | Gould and Fletcher (1978) |
| Mediterranean Gull | *Larus melanocephalus* | 0.6 | 3.48 | 0.36 | 0.23 | Boros *et al.* (2008a) |
| Caspian Gull | *Larus cachinnans* | 0.6 | 7.68 | 0.66 | 0.62 | Gould and Fletcher (1978) |
| Mew Gull | *Larus canus* | 0.6 | 4.32 | 0.48 | 0.30 | Gould and Fletcher (1978) |
| Terns | *Chlidonias* spp. *and Sterna* spp. | 1.0 | 4.50 | 0.60 | 0.38 | Boros *et al.* (2008a) |
| Yellow-legged Gull | *Larus michahellis* | 0.6 | 7.68 | 0.66 | 0.62 | Gould and Fletcher (1978) |

**Table 2. Monthly average individuals and abundance of the observed bird species on the pans in 2014. International English and scientific names are from the British Ornithologists' Union (2013).**

| Waterbird Species | | Zab-szék Pan (# individuals) | Sósér Pan (# individuals) | Zab-szék Pan (# individuals/ha) | Sósér Pan (# individuals/ha) |
|---|---|---|---|---|---|
| Greater White-fronted Goose | *Anser albifrons* | 36,930 | | 256.46 | |
| Greylag Goose | *Anser anser* | 1,643 | 100 | 11.41 | 8.33 |
| Tundra/Taiga Bean Goose | *Anser fabalis* | 2 | | 0.01 | |
| Red-breasted Goose | *Branta ruficollis* | 5 | | 0.03 | |
| Northern Pintail | *Anas acuta* | 91 | | 0.63 | |
| Northern Shoveler | *Anas clypeata* | 793 | | 5.51 | |
| Eurasian Teal | *Anas crecca* | 5,818 | | 40.40 | |
| Eurasian Wigeon | *Anas penelope* | 224 | | 1.56 | |
| Mallard | *Anas platyrhynchos* | 2,723 | | 18.91 | |
| Garganey | *Anas querquedula* | 43 | | 0.30 | |
| Gadwall | *Anas strepera* | 20 | | 0.14 | |
| Common Pochard | *Aythya ferina* | 5 | | 0.03 | |
| Common Shelduck | *Tadorna tadorna* | 151 | | 1.05 | |
| Great Egret | *Ardea alba* | 37 | | 0.26 | |
| Grey Heron | *Ardea cinerea* | 1 | | 0.01 | |
| Common Crane | *Grus grus* | 60 | | 0.42 | |
| Common Sandpiper | *Actitis hypoleucos* | 2 | | 0.01 | |
| Dunlin | *Calidris alpina* | 629 | 1 | 4.37 | 0.08 |
| Curlew Sandpiper | *Calidris ferruginea* | 4 | | 0.03 | |
| Little Stint | *Calidris minuta* | 15 | 1 | 0.10 | 0.08 |
| Temminck's Stint | *Calidris temminckii* | 3 | 3 | 0.02 | 0.25 |
| Kentish Plover | *Charadrius alexandrinus* | 8 | | 0.06 | |
| Little Ringed Plover | *Charadrius dubius* | 20 | | 0.14 | |
| Common Ringed Plover | *Charadrius hiaticula* | 8 | 24 | 0.06 | 2.00 |
| Common Snipe | *Gallinago gallinago* | | 3 | 0.00 | 0.25 |
| Black-winged Stilt | *Himantopus himantopus* | 21 | 15 | 0.15 | 1.25 |
| Broad-billed Sandpiper | *Limicola falcinellus* | 1 | | 0.01 | |
| Eurasian Curlew | *Numenius arquata* | 163 | | 1.13 | |
| Whimbrel | *Numenius phaeopus* | 1 | | 0.01 | |
| Ruff | *Philomachus pugnax* | 2,475 | 126 | 17.19 | 10.50 |
| Pied Avocet | *Recurvirostra avosetta* | 709 | 3 | 4.92 | 0.25 |
| Common Tern | *Sterna hirundo* | 1 | | 0.01 | |
| Spotted Redshank | *Tringa erythropus* | 334 | 31 | 2.32 | 2.58 |
| Wood Sandpiper | *Tringa glareola* | 75 | 58 | 0.52 | 4.83 |
| Common Greenshank | *Tringa nebularia* | 11 | | 0.08 | |
| Marsh Sandpiper | *Tringa stagnatilis* | 5 | 3 | 0.03 | 0.25 |

**Table 2. (continued) Monthly average individuals and abundance of the observed bird species on the pans in 2014. International English and scientific names are from the British Ornithologists' Union (2013).**

| Waterbird Species | | Zab-szék Pan (# individuals) | Sósér Pan (# individuals) | Zab-szék Pan (# individuals/ha) | Sósér Pan (# individuals/ha) |
|---|---|---|---|---|---|
| Common Redshank | *Tringa totanus* | 77 | | 0.53 | |
| Northern Lapwing | *Vanellus vanellus* | 1,355 | 20 | 9.41 | 1.67 |
| Whiskered Tern | *Chlidonias hybrida* | 3 | | 0.02 | |
| Black Tern | *Chlidonias niger* | 5 | | 0.03 | |
| Black-headed Gull | *Chroicocephalus ridibundus* | 749 | 107 | 5.20 | 8.92 |
| Mew Gull | *Larus canus* | 4 | | 0.03 | |
| Mediterranean Gull | *Larus melanocephalus* | 3 | | 0.02 | |
| Yellow-legged Gull & Caspian Gull | *Larus michahellis & Larus cacchinnans* | 226 | | 1.57 | |
| TOTAL | | 55,453 | 495 | 385.10 | 41.24 |

mg P/m$^2$/year for the Zab-szék pan, and 1,376 mg C/m$^2$/year, 226 mg N/m$^2$/year and 54 mg P/m$^2$/year for the Sósér pan. The yearly total nutrient loads and the seasonal dynamics of waterbird abundance show that the monthly mean carbon, nitrogen and phosphorus loading by waterbirds was six, five, and four times higher in the Zab-szék pan, respectively, than in the Sósér pan (Table 3; Fig. 1B, 1C).

## Physical and Chemical Conditions of the Pans

For both pans, the salinity was within the hyposaline range (5.6-5.7 g/l) and the pH was alkaline (> 9). Both pans were very shallow with water depths ranging from 2 to 50 cm, and a monthly period of drying out from the middle of July through August. The transparency, as measured with Secchi, was very low in the turbid Zab-szék pan; the mean transparency for the Zab-szék pan was 1.9 cm, with a minimum of 0.3 cm, due to the high concentration of algal-free suspended solids. However, transparency was also low in the colored Sósér pan, with a much lower concentration of algal-free suspended solids and a mean CDOM concentration an order of magnitude higher than in the Zab-szék pan (Table 3).

There was a strong positive correlation between CDOM and DOC (r = 0.862), and, on the basis of the DOC concentrations, both pans (Sósér in particular) were polyhumic (> 16 mg C/l). The proportion of POC was 32% for the Zab-szék pan and only 9% for the Sósér pan. The mean total nitrogen concentration was higher (2.6x) in the Sósér pan compared to the Zab-szék pan. Conversely, both mean total and soluble reactive phosphorus concentration was higher (3.6x and 4.3x, respectively) in the Zab-szék pan compared to the Sósér pan (Table 3).

## Planktonic Primary Production and Respiration

Mean chlorophyll *a* concentration was two times higher in the Zab-szék pan than

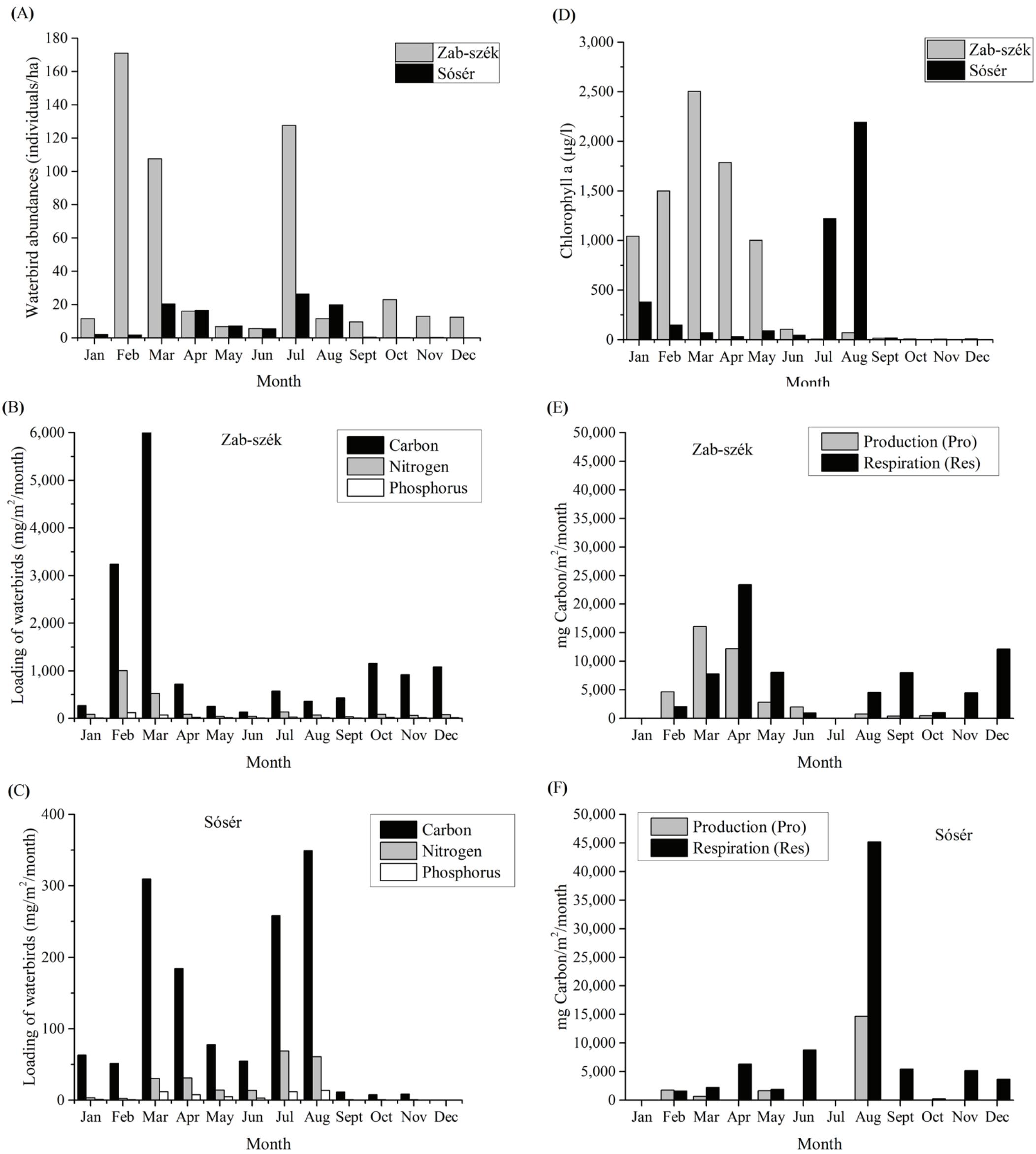


**Figure 1. Seasonal dynamics of waterbird abundance (A), nutrient loading of waterbird excrement (B and C), chlorophyll *a* concentration (D), planktonic production (E), and respiration (F) on the investigated pans (Zab-szék and Sósér pans) in 2014.**

in the Sósér pan. The seasonal dynamics of chlorophyll *a* concentration was also different. In the Zab-szék pan, the annual peak occurred in spring, while in the Sósér pan it was observed in summer (Fig. 1D).

There was a significant correlation (r = 0.596) between the monthly Pro and Res of the pans, and the rate of respiration was higher than the rate of production for both pans. The yearly Pro/Res ratio was 0.85 in the Zab-szék pan but only 0.29 in the Sósér pan. The estimated mean monthly production rates (Pro: mg C/m$^2$/month) were twice as high in the Zab-szék pan (Fig. 1E)—where the nutrient loading of waterbirds was also higher (C: 6x; N: 5x; P: 4x)—compared to the Sósér pan, while the mean monthly respiration rates (Res: mg C/m$^2$/month) were similar (Table 3).

The seasonal dynamics of production and respiration also differed between the

**Table 3. Basic statistical summary of the soda pans in 2014.**

| Parameter | Abbreviation | Number | Mean | Minimum | Maximum |
|---|---|---|---|---|---|
| **Zab-szék Pan** | | | | | |
| Water depth (cm) | Z | 18 | 13.00 | 2.00 | 40.00 |
| Secchi disc transparency (cm) | Secchi | 18 | 1.90 | 0.30 | 4.00 |
| Algal-free suspended solids (mg/l) | TSS-Alg | 18 | 2,182.80 | 111.20 | 7,637.90 |
| Salinity (g/l) | Sal | 18 | 5.60 | 1.70 | 17.00 |
| pH | pH | 18 | 9.60 | 8.90 | 10.20 |
| Colored dissolved organic matter (mg Pt/l) | CDOM | 17 | 470.40 | 199.30 | 926.10 |
| Dissolved organic carbon (mg/l) | DOC | 18 | 69.12 | 29.43 | 217.19 |
| Total organic carbon (mg/l) | TOC | 18 | 140.67 | 34.15 | 407.29 |
| Total nitrogen (µg/l) | TN | 14 | 8,885.12 | 2,026.39 | 27,441.16 |
| Soluble reactive phosphorus (µg/l) | SRP | 14 | 3,044.00 | 207.30 | 15,239.07 |
| Total phosphorus (µg/l) | TP | 13 | 7,170.08 | 2,012.47 | 17,703.67 |
| Chlorophyll *a* (µg/l) | Chl | 18 | 751.95 | 6.06 | 2,750.84 |
| Planktonic gross primary production (mg C/$m^2$/month) | Pro | 14 | 3,941.31 | 0.00 | 16,092.38 |
| Planktonic respiration (mg C/$m^2$/month) | Res | 14 | 7,236.42 | 920.93 | 23,356.43 |
| Carbon loading of waterbird excrement (mg C/$m^2$/month) | C | 12 | 631.80 | 66.36 | 2,679.31 |
| Nitrogen loading of waterbird excrement (mg N/$m^2$/month) | N | 12 | 101.75 | 17.91 | 445.18 |
| Phosphorus loading of waterbird excrement (mg P/$m^2$/month) | P | 12 | 16.45 | 3.94 | 56.30 |

Table 3. (continued) Basic statistical summary of the soda pans in 2014.

| Parameter | Abbreviation | Number | Mean | Minimum | Maximum |
|---|---|---|---|---|---|
| **Sósér Pan** | | | | | |
| Water depth (cm) | Z | 18 | 18.05 | 5.50 | 50.00 |
| Secchi disc transparency (cm) | Secchi | 18 | 7.20 | 1.50 | 20.00 |
| Algal-free suspended solids (mg/l) | TSS-Alg | 18 | 97.40 | 0.00 | 470.70 |
| Salinity (g/l) | Sal | 18 | 5.70 | 1.30 | 12.90 |
| pH | pH | 18 | 9.30 | 8.40 | 10.10 |
| Colored dissolved organic matter (mg Pt/l) | CDOM | 17 | 5,388.70 | 1,148.40 | 9,644.70 |
| Dissolved organic carbon (mg/l) | DOC | 18 | 437.25 | 95.38 | 988.49 |
| Total organic carbon (mg/l) | TOC | 18 | 479.20 | 98.61 | 1,138.15 |
| Total nitrogen (µg/l) | TN | 14 | 22,725.31 | 3,520.12 | 62,661.46 |
| Soluble reactive phosphorus (µg/l) | SRP | 14 | 710.89 | 33.89 | 2,521.83 |
| Total phosphorus (µg/l) | TP | 14 | 2,015.78 | 292.29 | 3,979.60 |
| Chlorophyll *a* (µg/l) | Chl | 18 | 369.12 | 1.16 | 3,144.48 |
| Planktonic gross primary production (mg C/m$^2$/month) | Pro | 14 | 1,872.05 | 0.00 | 14,645.27 |
| Planktonic respiration (mg C/m$^2$/month) | Res | 14 | 8,039.55 | 207.65 | 45,162.81 |
| Carbon loading of waterbird excrement (mg C/m$^2$/month) | C | 12 | 114.65 | 0.00 | 349.32 |
| Nitrogen loading of waterbird excrement (mg N/m$^2$/month) | N | 12 | 18.80 | 0.00 | 68.61 |
| Phosphorus loading of waterbird excrement (mg P/m$^2$/month) | P | 12 | 4.51 | 0.00 | 13.46 |

pans. In the Zab-szék pan, maximum production and respiration both occurred in the spring, during February-April (Fig. 1E), when the nutrient loading of waterbirds was also at its peak (Fig. 1B). In contrast, in the Sósér pan, both production and respiration peaked in August (Fig. 1F), due to the presence of a dense population of blue-green algae, with an extremely high maximum chlorophyll *a* concentration in the shallow water occurring after a month-long dry period. This peak was of a brief duration, and production was almost zero from the middle of September to the end of the year.

The estimated annual planktonic production was 2.8 times higher in the Zab-szék pan (63,468 mg C/m$^2$/year) than in the Sósér pan (22,796 mg C/m$^2$/year). In contrast to production, annual planktonic respiration was more or less the same in the two pans (Zab-szék pan: 74,748 mg C/m$^2$/year; Sósér pan: 77,460 mg C/m$^2$/year).

### Principal Component Analysis of the Variables

The first four principal components explain 85.67% of the variance, the remaining components each contribute 4% or less, and several variables are highly correlated. According to the PCA ordination and pairwise correlations, most of the physical and chemical variables related to the first, second or third component, and they varied together in three groups. The first group was composed of T, Sal, pH, SRP and TP, the second comprised Z, Secchi and TN, and the third included Pt, TOC and DOC. TSS-Alg varied separately along the second component. The C, N, and P loading of waterbirds varied closely together with Chl and Pro along the second component, while only Res varied mostly with the fourth component, and it had no significant correlation with any measured variables (Fig. 2).

The C loading of waterbirds was significantly and positively correlated with the TSS-Alg, TP, SRP and Pro variables, and negatively correlated with the Secchi, CDOM and DOC variables. The N loading of waterbirds significantly and positively correlated with the TSS-Alg, pH, CDOM, TP, SRP, Chl and Pro variables, and negatively correlated with the Z, Secchi and DOC variables. The P loading of waterbirds significantly and positively correlated with the TSS-Alg, pH, TP, SRP, Chl and Pro variables, and negatively correlated with the Secchi, CDOM and DOC variables (Table 4).

## DISCUSSION

Both the turbid and colored pans were considered to be hypertrophic based on the concentration of inorganic plant nutrients and chlorophyll *a* (Organization for Economic Cooperation and Development 1982), but the depth-integrated production level was very low compared to the chlorophyll *a* concentration, and the gross primary production and respiration ratio was smaller than 1 for both pans. Although some studies have found that a Pro/Res ratio below 1 is common at different trophic states in temperate zone lakes (del Giorgio and Peters 1994; Hanson *et al.* 2003; Urabe *et al.* 2005; Cornell and Klarer 2008), we found that a Pro/Res < 0.5 may be common in soda pans. Del Giorgio and Peters (1993) demonstrated that the Pro/Res ratio varies with trophic status. Oligotrophic lakes are considered to be net heterotrophic, with chlorophyll *a* concentrations of 17 μg/l set as the dividing point. Eutrophic and hypertrophic lakes are considered to be net autotrophic due to the higher levels of primary productivity and lower allochthonous organic matter. Our results are inconsistent with these findings despite the fact that the average chlorophyll *a* concentration of the pans was an order of magnitude higher (means of turbid: 752 μg/l and colored: 369 μg/l) than the suggested limit (17 μg/l) of heterotrophy; there was no question that the pans were net heterotrophic.

Waterbird-related nutrient loading in inland waters can vary widely (Manny *et al.* 1994; Post *et al.* 1998; Hahn *et al.* 2008). However, in the current study phosphorus and nitrogen loads were found to be three and six times higher, respectively, compared to a

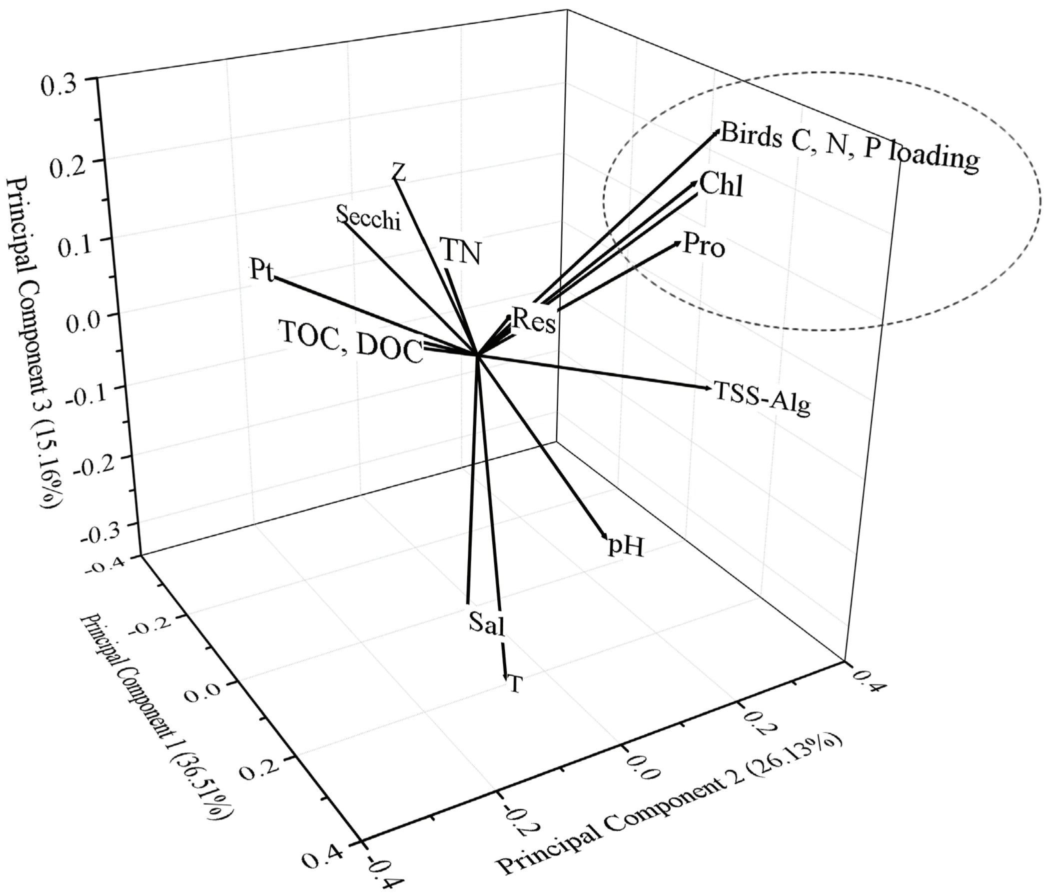


**Figure 2. Presentation of the principal component analysis (PCA) of Carbon (C), Nitrogen (N), and Phosphorus (P) loading of waterbird excrement and the environmental parameters. Dashed lined ellipse symbolizes that nutrient (C, N, P) loading of waterbirds closely varied together with Chl and Pro along the second component (see in Table 3 for abbreviations and units of variables).**

prototypical example of guanotrophication (Manny *et al.* 1994) on Wintergreen Lake, Michigan, USA, where the estimated loading of waterbirds was 297 kg/ha/year for C, 19 kg/ha/year for N and 6 kg/ha/year for P. Thus, our study represents an example of extreme guanotrophication in a continental environment; guanotrophication may be a consequence of the relatively small size of the pans and the high abundance and diversity of waterbirds present.

Some previous studies (Unckless and Makarewicz 2007; Özbay 2015) did not find any significant differences in the plant nutrient pool and concentration of chlorophyll *a* at a 1.5- to 2-m water depth when treated with bird excrement, indicating that feces and associated nutrients settled quickly to the bottom sediments. By contrast, the two soda pans of the current study were very shallow, with a mean depth of 0.13 m and 0.19 m, respectively, which allowed for the continuous mixing of the water column. Therefore, feces and associated nutrients did not settle to the bottom sediments, which explains the significant positive correlation among the nutrient loading of waterbirds, TP and SRP.

The current study also demonstrated that the nutrient loading of waterbirds has an important role in soda pan phosphorus cycling, which was already suggested in a bird-free control investigation (Boros *et al.* 2008a). Our hypothesis was supported, as waterbirds significantly affected planktonic gross pri-

**Table 4. Spearman's rank correlation coefficients between Carbon (C), Nitrogen (N), and Phosphorus (P) loading of waterbird excrement and physical, chemical, and biological variables (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).**

| Carbon Loading of Waterbirds | | Nitrogen Loading of Waterbirds | | Phosphorus Loading of Waterbirds | |
|---|---|---|---|---|---|
| Variable | Correlation coefficient | Variable | Correlation coefficient | Variable | Correlation coefficient |
| Secchi disc transparency | −0.653*** | Water depth | −0.485* | Secchi disc transparency | −0.748*** |
| Algal-free suspended solids | +0.813*** | Secchi disc transparency | −0.705*** | Algal-free suspended solids | +0.857*** |
| Colored dissolved organic matter | −0.491* | Algal-free suspended solids | +0.823*** | pH | +0.495* |
| Dissolved organic carbon | −0.553** | pH | +0.608** | Colored dissolved organic matter | −0.549** |
| Total phosphorus | +0.556* | Colored dissolved organic matter | +0.606** | Dissolved organic carbon | −0.416* |
| Soluble reactive phosphorus | +0.535* | Dissolved organic carbon | −0.420* | Total phosphorus | +0.692*** |
| Planktonic gross primary production | +0.468* | Total phosphorus | +0.654** | Soluble reactive phosphorus | +0.642** |
| | | Soluble reactive phosphorus | +0.590** | Chlorophyll *a* | +0.435* |
| | | Chlorophyll *a* | +0.427* | Planktonic gross primary production | +0.635** |
| | | Planktonic gross primary production | +0.590** | | |

mary production in the studied soda pans, presumably as a consequence of the biological availability of their excrement. Despite the high nutrient (N, P) concentrations and high phytoplankton biomass, depth-integrated primary production was low due to limited light availability caused by extremely high turbidity and high CDOM concentration. In contrast to production, there was no significant correlation between the nutrient loading of waterbirds and planktonic respiration. Thus, this aspect of the hypothesis was not supported. The low Pro/Res in the colored pan was presumably caused by a high dissolved organic carbon concentration (polyhumic). A possible explanation for the difference of Pro/Res between the turbid and colored pans is variation in the decomposition of the bird excrement and surrounding macrophytes.

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