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RESEARCH ARTICLE

Organic matter governs N and P balance in Danube Delta lakes

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Abstract The transformation of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorous (SRP), and the release of dissolved organic and particulate N and P, were analyzed in two lake complexes (Uzlina–Isac and Puiu–Rosu–Rosulet) of the Danube Delta wetland during flood conditions in May and at low water level in September 2006. The Uzlina–Isac complex was hydrologically tightly-connected with the Danube River and was flushed with river-borne nutrients and organic matter. These lakes acted as effective transformers for nutrients and produced large amounts of fresh biomass, that promoted the excretion of dissolved organic N and P during active growth. Biomass breakdown created particulate matter (<0.45 μm), which was widely liberated during low flow in the fall. The Puiu–Rosu–Rosulet complex was characterized by a more distant position to the Danube and proximity to the Black Sea, and received dominantly transformed organic compounds from the flow-through water and vast vegetation cover. Due to reduced nutrient input, the internal production of organic biomass also was reduced in these more remote lakes. Total N and P export from the lake nearest to the shelf was governed by dominantly dissolved organic and particulate compounds (mean 58 and 82%, respectively). Overall, this survey found that these highly productive wetlands efficiently transform nutrients into a large pool of dissolved organic and particulate N and P. Hence, wetland lakes may behave widely as net sources of organic N and P to downstream waters and coastal marine systems.

Keywords Wetland · Nutrient transformations · Organic N and P production

Introduction

The Danube Delta wetland is the second largest river delta in Europe (5,800 km^2) after the Volga Delta (Fig. 1). It forms a highly heterogeneous and productive transition zone between the main branches of the River Danube and the coastal Black Sea (Oosterberg et al. 2000). The fluvial part of the Delta on the Romanian territory is strongly influenced by water from Sfantu Gheorghe, the southern branch of the River Danube. The fluvio-marine part is partially influenced by the Sulina channel, the middle Danube branch, and by saltwater intrusion from the Black Sea. However, the hydraulic gradient mostly prevents inflow of brackish water into lakes, and the flow is maintained by a sequence of artificial channels (Panin 1996).

The delta represents a vast compact zone of reed beds found in the world (Hanganu 2002), and primary productivity effectively removes dissolved compounds, such as nutrients, from the flow-through water (Friedrich et al. 2003). In relation to other deltas in the world, the Danube Delta is still relatively unaffected by anthropogenic inputs (Oosterberg et al. 2000). Nonetheless, man-induced transition towards eu- and hypertrophy has affected biodiversity and productivity of most aquatic and wetland

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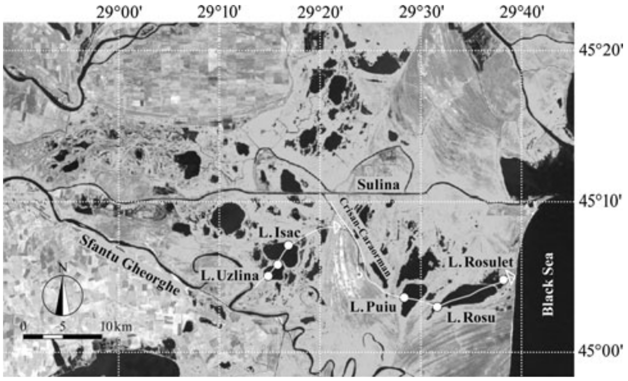

Fig. 1 Selected Danube Delta lakes with the main sampling stations indicated by *open circles*: Uzlina-in, Uzlina-out, Isac-out, Puiu-in, Rosu-in, and Rosulet-out. *-in* and *-out* represent inflow and outflow, respectively. Sulina and Sfantu Gheorghe represent the main branches of the River Danube in the delta influencing the studied lakes. The *white arrow* visualizes the approximate direction of the flow path through the two lake complexes. On average, 183 $m^3 s^{-1}$ are discharged in the Sfantu Gheorghe branch (Bondar 2000), and water travel times to Lake Uzlina are ~0.2 days (Oosterberg et al. 2000). Average channel water inflows into the Puiu–Rosu–Rosulet complex were 150 and 30 $m^3 s^{-1}$ in May and September, respectively, with corresponding outflows amounting to 165 and 50 $m^3 s^{-1}$ (Bondar 2000). The travel times to the Black Sea coast were estimated to range from 0.1 to 0.2 days (also see "Discussion")

systems in the delta and the associated coastal Black Sea (Cristofor et al. 2003). From the early 1960s to late 1980s, riverine loads of inorganic N and P increased five- and threefold, respectively (Almazov 1961; Kroiss et al. 2006; Teodoru et al. 2007). However, since the 1990s nutrient loads started to gradually recede, mainly due to economic breakdown and reduction in agriculture and manure release (Zessner and van Gils 2002; Ludwig et al. 2009).

The Danube Delta lakes investigated in this study (Fig. 1) are eutrophic in respect to inorganic N and P concentrations (Oosterberg et al. 2000). These lakes act as efficient sinks for nutrients during the growing season (Durisch-Kaiser et al. 2008). It was further observed that inorganic N input and nutrient retention rates decrease with increasing hydrological distance from the main rivers of the delta. Friedrich et al. (2003) estimated from in-lake benthic effluxes and external inflows that more than 76% of the inorganic N and P input were internally removed from the water column during the growing season. However, they did not quantify the formation of dissolved organic and particulate N and P, and recommended to include them in future studies because they should not be neglected in highly productive wetland systems.

Assimilation of nutrients into phytoplankton and plant biomass, and decomposition of organic compounds, channels N and P into either particulate or dissolved organic matter (POM, DOM), and controls nutrient availability (Findlay and Sinsabaugh 2003). Several studies have shown that organic matter may constitute an important fraction exported by wetlands as well as rivers to the sea (Harrison et al. 2005; Seitzinger and Sanders 1997). This material may either be rather old and partially aged (e.g. Raymond and Bauer 2001) or rather freshly produced and highly bioavailable due to intense phytoplankton growth within wetland lakes (Findlay et al. 1990; Boon 2006) and due to exudation from living macrophyte biomass (Stepanauskas et al. 2000). Royer and Minshall (1997) also found that breakdown rates of macrophyte species were highly variable seasonally, and particle load liberated from this process was partly stored in sediments and released at later stages of decomposition. In accord with these findings, the Danube Delta lakes may transform inorganic nutrients loads in large proportions into organic N and P, which may partially become internally stored, remineralized or exported to the northwestern shelf of the Black Sea.

The main objective of this study was therefore to determine the role of dissolved organic matter and particles in the N and P budget of Danube Delta lakes situated within a network of flow-through systems. The proportions of inorganic, dissolved organic and particulate N and P were determined in lakes directly receiving Danube water and, by contrast, also in lakes located far downstream and receiving autochthonous and diagenetically aged organic materials and internally regenerated nutrients. We characterized N and P availability for in-lake biomass formation and studied benthic remineralization in the various lakes. Based on this data-set, we addressed the question of which fractions of N and P were exported in dissolved organic and particulate forms to the coastal Black Sea.

Materials and methods

Study sites

Water samples where taken from five flow-through lakes (Table 1) located in the Romanian part of the Danube Delta (Fig. 1). The Lakes Uzlina and Isac form the Uzlina–Isac complex, and the three other lakes form the Puiu–Rosu–Rosulet-complex. The sampling sites were called Uzlina-in, Uzlina-out, Isac-out, Puiu-in, Rosu-in, and Rosulet-out. The abbreviation—in attached to the different names of lakes represents inflow and the abbreviation—out represents outflow. All lakes sampled are shallow (max. depth during flooding <6 m, Table 1) and exhibit a rich vegetation, constituted of macrophytes, periphyton, and floating algae. The surroundings of lakes is dominated by reed belts, which are regularly flooded during high runoff (Table 1). The two lake complexes mainly differ in their supply of Danube water, which is loaded with nutrients and affects productivity within the lakes. Regarding the whole

Table 1 Hydrological data and Chl_a concentrations of sampling sites in Lakes Uzlina, Isac, Puiu, Rosu, and Rosulet during post-flood conditions in May and low flow in September 2006

Parameters	Lake Uzlina		Lake Uzlina		Lake Isac		Lake Puiu		Lake Rosu		Lake Rosulet	
Open water surface area (km^2)	4.83				10.2		8.25		13.65		3.71	
Reed surface area (km^2)	9.73				15.4		21.08		26.03		14.02	
Sampling locations*	Uzlina-in		Uzlina-out		Isac-out		Puiu-in		Rosu-in		Rosulet-out	
Sampling time (month)	May	Sept.	May	Sept.	May	Sept.	May	Sept.	May	Sept.	May	Sept.
Depth at sampling site (m)	3	2	3	2	4.2	3	2.8	3.4	6.4	5.8	4.3	2
Average depth (m)	3.7	2.3	3.7	2.3	4.0	2.7	3.9	3.4	4.9	3.8	4.2	3.1
Lake volume ($n \times 10^6$ m^3)	17.9	11.1	17.9	11.1	40.8	27.5	32.2	28.1	66.9	51.9	15.6	11.5
Average through-flow (m^3 s^{-1})	19	13	19	13	39	21	22	15	34	21	18	12
Hydraulic residence time (d)	11	10	11	10	12	15	17	22	23	29	10	11
Chl_a (μg L^{-1})	14	20	16	34	19	36	11	60	10	60	14	47
Oxygen (mg L^{-1})	8.8	9.3	11.2	8	10.5	7.5	4.0	5.6	7.8	8.1	9.9	3.3

Surface areas and hydraulic residence times were taken from Oosterberg et al. (2000) and Bondar (2000)

* At all sampling sites: *in* inflow, *out* outflow

Danube Delta, the channels taking off from the main Danube branches supply approximately 75% of the river water discharged into the delta (Bondar 2000). The Uzlina–Isac complex belongs to the fluvial delta, and is strongly influenced through the Uzlina channel by water from the Sfantu Gheorghe branch of the Danube. On average, 183 m^3 s^{-1} are discharged in the Sfantu Gheorghe (Bondar 2000), and water travel times to Lake Uzlina are ~0.2 days (Oosterberg et al. 2000). Both lakes also show high loads of suspended particles, and high cover of floating and submerged vegetation (Coops et al. 2008). The other three Lakes, Puiu, Rosu, and Rosulet, are situated further distant to the Sulina branch and belong to the fluvio-marine delta. They receive river water through the Crisan-Caraorman channel and through-flow from the Uzlina–Isac complex through the Litcov channel. During times of low flow the Sulina branch contributes only ~50% to the total inflow, whereas during flooding, inflow of river water through the Crisan-Caraorman channel to these lakes rises. Average water inflows into the Puiu–Rosu–Rosulet complex are 150 m^3 s^{-1} and 30 m^3 s^{-1} in May and September, respectively (Bondar 2000) (Fig. 1). This complex encompasses large and isolated lakes, where the water quality is also highly influenced by black water input from large floating reedbeds (Coops et al. 2008). Lake Rosu is separated only by partially submerged sand bars, reed, and floating reed islands (*Phragmites* sp. plaurs) from Lake Rosulet, and represents the largest freshwater lake in the Danube Delta. Based on aquatic vegetation and turbidity, Lakes Uzlina, Rosu, and Rosulet qualify as turbid systems, whereas Lakes Isac and Puiu behave as intermediate between clear and turbid and lack floating vegetation and large loads of suspended solids (Coops et al. 1999).

The water table of the River Danube and the associated delta rises to highest levels between April and June, and then decreases to low levels between July and October (Panin 1996; Oosterberg et al. 2000). In late fall and winter, when the water table in the Danube Delta is very low, water inundating reed areas flows back into the lakes and severe easterly winds might additionally push water from the Black Sea into the Puiu–Rosu–Rosulet complex. The hydraulic residence time during the sampling campaigns varied between 10 and 29 days (Table 1). In May 2006, we encountered flooding conditions with extremely high water flow of the River Danube, which resembled discharges recorded from other extreme floods (Mikhailov et al. 2008). The annual water discharge of the River Danube increased up to ~15,000 m^3 s^{-1} (as determined for extreme floods) compared to the average of 6,460 m^3 s^{-1} (ICPDR 2004). In September, hydrological conditions resembled values as those reported by the ICDPR report.

Sampling and analyses

Water column and sediment porewater samples were collected from each lake either close to the in- or outflow in May and September 2006 (Fig. 1). In May and September 2006, water samples at each site were retrieved using a Niskin bottle from three depths (~0.5 m and ~1.5–3 m depth, and ~0.5 m above sediment). Water samples for measurements of dissolved oxygen were collected bubble-free in gas-tight crimp-seal bottles. Dissolved oxygen concentrations were measured with the Winkler method (Grasshoff 1983). Water samples for $chlorophyll_a$ (Chl_a) analysis were collected in muffled 100 mL glass bottles. Thereafter, aliquots (50 mL) were filtered through pre-combusted GF/F Filter (Whatman). Filters were extracted in 70% ethanol and spectrophotometrically analysed after the ISO method 10260 (ISO 1992). For analyses of N and P fractions, samples (200 mL) were collected in acid-rinsed HDPE bottles, and stored at 4°C in the dark during transport to the laboratory aboard ship. Thereafter, all samples were stored frozen at −20°C until further analysis. Aliquots (~100 mL) of water column samples were used unfiltered for analyses of total N and P. Remaining aliquots (~100 mL) were filtered (0.45 μm pore size, cellulose nitrate, Nucleopore) and used for analyses of total dissolved N, nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), total dissolved P, and soluble reactive P (SRP). All filters used were pre-cleaned in Milli-Q UV water to avoid contamination of the filtrate with N and dissolved organic C (DOC). After cleaning, only 1 ± 0.3 μM N (nitrate) and 10 ± 7 μM DOC were leached from cellulose nitrate filters. Hence, we collected filter blanks during filtration, and used blank values to correct data measured from samples. The filters introduced an error of 1–10% to nitrate and of 2–3% to DOC concentrations in all samples collected. Subsamples of unfiltered and filtered water samples were digested with a peroxodisulfate solution for 1 h at 120°C to completely oxidize organic N and P to NO_3^- and SRP. In non-digested and digested samples, NO_3^-, NO_2^-, NH_4^+, and SRP concentrations were determined spectrophotometrically using a Technicon autosampler and standard methods (DEV 2004). The analytical error of the method was ~5%. For analyses of particulate and dissolved organic carbon, samples (40 mL) were collected in acid-washed and combusted glass bottles, sealed with Teflon-lined caps and stored frozen until analysis. Concentrations of total organic C (TOC) and DOC were measured from unfiltered and filtered (0.45 μm pore size, cellulose nitrate, Nucleopore) water samples, respectively, on a Shimadzu TOC 5050A analyzer using high-temperature catalytic oxidation (Benner and Strom 1993). Concentrations of individual fractions are reported as mean ± 1 standard deviation ($n = 3$). We use the notation particulate N and P (PN and PP) in the whole text because particles may have contained adsorbed inorganic N and P. POC was calculated as TOC−DOC, PN as total N−total dissolved N, PP as total P−total dissolved P. DIN represents $[NO_2^-] + [NO_3^-] + [NH_4^+]$. DON was calculated as total dissolved N−DIN, and DOP as total dissolved P−SRP.

In May and September 2006, porewater samples were collected at all sampling sites at 1 cm intervals from the top sediment to ~0.5 m depth using dialysis porewater samplers or ‘peepers’ (Hesslein 1976; Urban et al. 1997). A total of ten samples was extracted at each depth to gain enough sample volume, and a total of 450 samples were collected at each site. Peepers consisted of a plexiglas plate (50 × 15 × 1.5 cm) containing about 480 milled cells. Before sampling, all cells were filled with ultrapure and almost oxygen-free water (Nanopure), and sealed with a dialysis membrane (0.2 μm pore size, Truffyn, Gelman). Peepers were positioned by a diver in the top sediment of the sampling sites and recovered 4 days later. Equilibration happened through diffusion of solutes across the dialysis membrane into the cells. The porewater then was extracted with medical syringes from the cells. For NH_4^+ and SO_4^{2-} analysis, 5 mL porewater were stored in a clean Polypropylene-tube (Greiner) at 4°C in the dark. Ammonium concentrations were immediately analyzed aboard ship, and SO_4^{2-} concentrations were measured by ion chromatography (IC Metrohm 690) at Eawag. For analysis of methane (CH_4) concentrations, 3 mL porewater were transferred to a 25 ml crimp-seal vial, poisoned with Cu-(I)-Cl, sealed gas-tight, and stored for further analyses. Quantification of CH_4 was accomplished by injecting 500 μl of headspace from the serum vials into a Carlo Erba HRGC 5160 gas chromatograph equipped with a J&W GSQ column (30 m × 0.53 mm). Injection temperature was 70°C, FID temperature was 250°C, and the oven temperature was held at 100°C.

Benthic fluxes (mmol m^{-2} h^{-1}) of NH_4^+, CH_4, and SO_4^{2-} across the water–sediment interface were calculated along linear changes in concentrations (concentration gradient, the magnitude of the interface), with sediment depth using Fick’s first law of diffusion. Regression analysis across the concentration gradient using 3 or more data points were additionally run to control calculated flux values. Molecular diffusion coefficients (m^2 s^{-1}) of 1.19×10^{-9} for ammonium, 1.57×10^{-9} for methane, and 9.4×10^{-10} for sulphate were used (after Furrer and Wehrli 1996). Note that due to the coarse depth resolution of peepers, NH_4^+, CH_4, and SO_4^{2-} fluxes calculated over the water–sediment interface represent only crude approximations. Furthermore, fluxes are derived from two different methods used to measure concentrations of NH_4^+, CH_4, and SO_4^{2-} in porewater.

We applied a simple box model approach to our data in order to calculate N, P, and C transformation and production rates in both lake complexes during the sampling campaigns in May and September 2006. Based on the average concentrations along the flowpaths of the two lake complexes and on hydrological conditions documented in Table 1, specific transformation and production rates (mmol m^{-2} d^{-1}) were calculated as follows:

$$R^i = \left[C^i(\text{out}) - C^i(\text{in})\right] \times Q/A$$

where R^i stands for the transformation rate of species i, C denotes the concentrations at the inflow and the outflow of a lake complex, respectively, Q represents the average flow-through (L d^{-1}), and A stands for the total lake surface area in a complex. As a result, positive terms denote production and negative terms indicate transformation of a dissolved or particulate N, P, or C species.

According to the empirical model by Smith (1979), water column TP concentrations were used to predict system primary production ($R^2 = 0.94$) during the two sampling periods (Table 1). We used the relationship

$$v = 10.4 \times \mathrm{TP} - 79$$

in which v represents the daily mean photosynthesis (mg C cm^{-3} d^{-1}) and TP represents the mean total P concentration (mg m^{-3}), in order to estimate system primary productivity. Because the model covers oligo- to eutrophic conditions, different lake sizes and different depths, we assume that it is applicable to the rather shallow and wetland-dominated Danube delta lakes.

Results

Input of N, P, and C and concentration changes along the flow path

In this section, we report on relevant input terms of N, P, and organic C, and explain the distribution of their concentrations in the two different lake complexes. Water entering at Uzlina-in dominantly supplied DIN to the Uzlina–Isac complex (82% of TN in May and 97% of TN in September), whereas at Puiu-in the inflowing water provided increased concentrations of DON and PN in May (79% of TN) and September (90% of TN) (Fig. 2a, b). Although Danube water was supplied through the Crisan-Caraorman canal, backwash from extensive reedbeds loaded the Puiu–Rosu–Rosult lake complex with plenty of organic substrates as previously observed by Coops et al. (2008). The inorganic nutrient concentrations showed a clear decrease along the flow path in both lake complexes, except for the Puiu–Rosu–Rosult complex in the fall (Fig. 2). The dramatic drop in DIN concentrations was partially compensated by a buildup in the concentrations of DON and PN, which resulted in almost constant TN concentrations in the Puiu–Rosu–Rosulet system in both seasons. However, in September, Lake Rosulet exhibited a DIN release accompanied by a decrease in DON concentrations.

Similar to N, inflowing water provided dominantly dissolved inorganic P (63% of TP in May and 74% of TP in September) to the Uzlina–Isac complex (Fig. 2c, d). The input of SRP into Lake Uzlina was about two to three times higher at low runoff in September compared to flooding in May. In both seasons, the Uzlina–Isac complex effectively transformed the SRP input into DOP and PP, hence keeping TP inputs and exports closely balanced. In contrast, the Puiu–Rosu–Rosulet complex received highest loads of SRP only with the spring flood (69% of TP in Lake Rosu), while in the fall 99% of TP input into Lake Puiu was in dissolved organic and particulate form. Internal processes eliminated about 24% of the autumn TP load from the Puiu–Rosu–Rosulet-complex.

Water entering both complexes mainly carried DOC and this relationship stayed rather unchanged in both seasons (Fig. 2e, f). The external loading was highest in May for both lake complexes. Only the Uzlina–Isac complex showed distinct seasonality in DOC and POC, with concentrations about twice as high during the spring flood compared to low flow in the fall. The Puiu–Rosu–Rosulet complex was characterized by a constant spatial and temporal distribution of concentrations along the flow path.

Nutrient transformation and organic matter production rates

In the Uzlina–Isac complex, DIN transformation was almost equal in both seasons, and the production of dissolved organic and particulate N was highest in spring (Table 3). High primary productivity, especially in fall, was estimated for Lakes Uzlina and Isac. Similarly, along flow-through in the Lakes Puiu, Rosu, and Rosulet, DON was dominantly produced in May, and transformed in September (Table 3). This trend aligned with the dynamics observed for the DIN pool, in which transformation prevailed in spring and release in the fall. In the Puiu–Rosu–Rosulet-complex, PN was transformed in both seasons. Considering the TN pool, we calculated that N was transformed in Lakes Uzlina and Isac, and in the Puiu–Rosu–Rosulet complex was transformed in May and produced in September.

Transformation rates of SRP were elevated in the Uzlina–Isac complex in fall due to higher P loading. Interestingly, in both seasons SRP removal rates were balanced by almost equally high production rates of DOP and PP, with proportionally high PP formation in the fall (Table 3). We also found that TP transformation occurred in both complexes, and prevailed in the Puiu–Rosu–Rosulet complex in the fall. Production rates of TOC prevailed in the Uzlina–Isac complex in the fall, and were perfectly aligned with estimated rates of primary productivity (Table 4). We noticed a removal of TOC in the Puiu–Rosu–Rosulet complex in the spring, mainly resulting from transformation of organic particles.

Nutritional limitations for biomass formation

We found that the availability of P relative to N was limited due to a TN:TP > 50 in Lake Uzlina, whereas the ratio decreased towards 34 along the flowpath to Lake Puiu, and was again exhibiting limited P availability in the Lakes Rosu and Rosulet in spring (Table 4). A limited availability of P did not occur in fall when the delta lakes received high riverine SRP input (Fig. 2), but limited N availability developed in Lake Puiu and Rosu in the fall (Table 4). We observed that, in most cases and especially in spring, DOM was

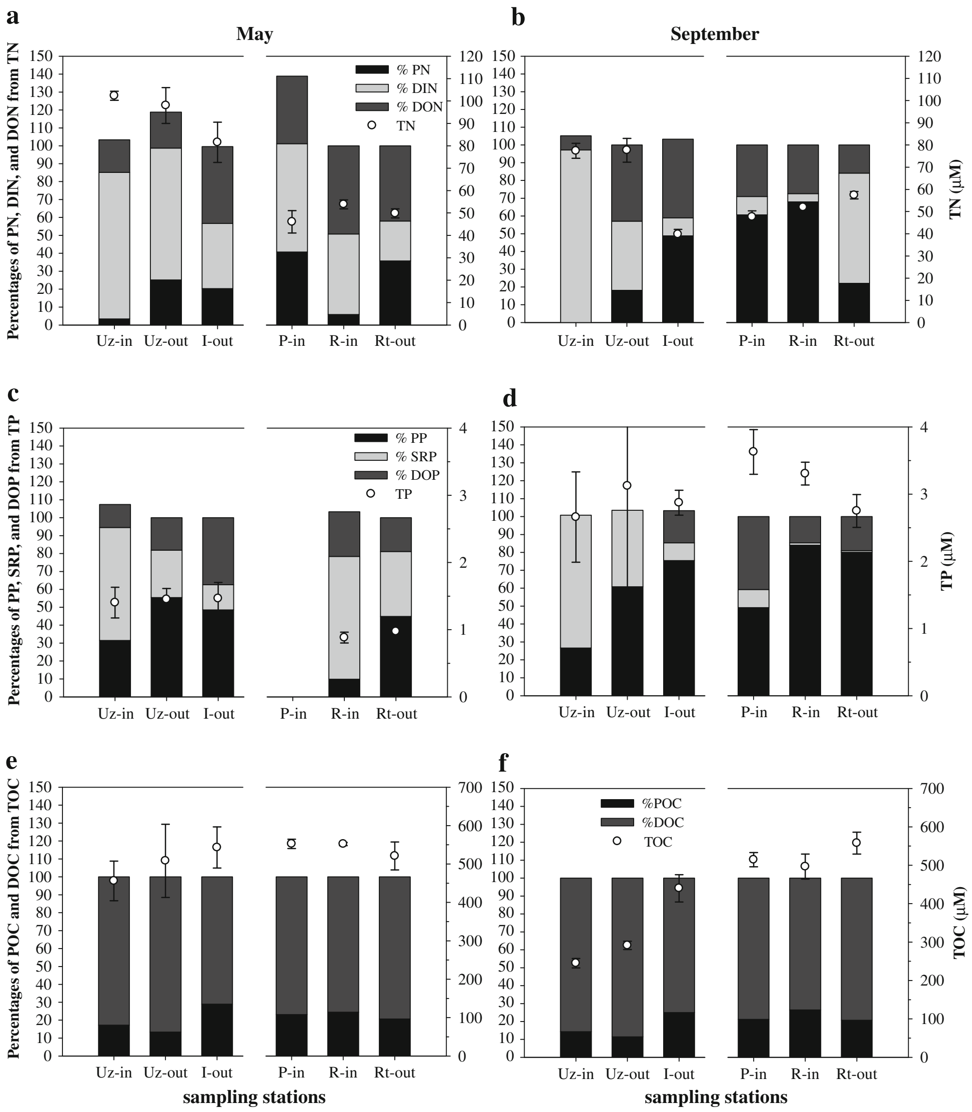

Fig. 2 The percentages of *PN*, *DIN*, and *DON* from *TN*, percentages of *PP*, *SRP*, and *DP* from *TP*, and percentages of *POC* and *DOC* from *TOC* are shown along the flow path in the two lake complexes (Fig. 1) in May and September 2006. Mean concentrations (±standard deviation, $n = 3$) of *TN*, *TP*, and *TOC* are shown on the second *Y*-axis (*open circles*). Note, that percentages are in certain cases deviating from 100% because percentages were calculated from means over the whole water column ($n = 3$), and filtration and sample processing of the different subsamples may have introduced contamination to the samples. Note that all samples were filter blank corrected (see "Materials and methods"). Three depths (~0.5 m and ~1.5–3 m depth, and ~0.5 m above sediment) were sampled at each site ($n = 3$). By creating stack plots of the different percentages, we were unable to plot the standard devations. *Uz-in* Uzlina-inflow, *Uz-out* Uzlina-outflow, *I-out* Isac-outflow, *P-in* Puiu-in, *R-in* Rosu-inflow, *Rt-out* for Rosulet-out

P-deficient, whereas particles were deficient in N. Different source materials for DOM and particles may explain this result. The observed switch in N:P ratios between the two lake complexes can be related to differences in phytoplankton, algae, and macrophyte biomass and species composition as described by Oosterberg et al. (2000). Seasonal differences may also be explained by changes in species composition. It was, for example, reported that cyanobacteria start to increase their biomass Lake Rosulet after June (Coops et al. 2008), indicating reduced relative N availability in the fall.

Discussion

Nutrient dynamics along a chain of delta lakes

Lake Uzlina exhibited highest DIN and SRP concentrations among all sampling stations due to an intense hydrological connectivity with the Danube branch Sfantu Gheorghe. Nutrient concentrations resembled those in Danube river water (119 µM DIN and 1.3 µM SRP) published for the year 2006 in the ICPDR Report (ICPDR 2009). These data further corroborate other studies (e.g. Oosterberg et al. 2000), which reported that river water enters Lake Uzlina within about 0.2 days travel time from the Sfantu Gheorghe branch, and therefore represents the main source of lake water and dissolved nutrients in the Uzlina–Isac complex. Benthic release of NH_4^+ (~3.8 mmol m^{-2} d^{-1} in both seasons) represented an additional substantial internal source of N to this lake complex (Table 2) and contributed ~10% of TN input in May and ~18% in September. Relative to the abundant inorganic nutrient pool, both dissolved organic and particulate N and P played subordinate roles in the inflow by covering 21% of TN and 44% of TP in May and 8% of TN and 27% of TP in September.

Table 2 Benthic fluxes of ammonium, methane, and sulphate were calculated from porewater profiles across the sediment–water interface in the different lakes in May and September 2006

	NH_4^+ (mmol m^{-2} d^{-1})		CH_4 (mmol m^{-2} d^{-1})		SO_4^{2-} (mmol m^{-2} d^{-1})	
Sampling time	May	September	May	September	May	September
Uzlina-in*	6.4	4.9	7.2	2.1	−7.8	−0.5
Uzlina-out*	2	n.d.	1.6	n.d.	−2.2	n.d.
Isac-out	3.2	2.7	3.6	3.3	−2	−0.4
Mean	3.8 ± 2.3	3.8	4 ± 2.8	2.7	−4 ± 3.3	−0.4
Puiu-in	8.8	8.26	9	2.4	−4.5	−1.9
Roşu-in	4. 8	7.11	7	4.9	−6.4	−0.1
Roşulet-out	2.7	0.89	1.9	2.8	−6	−2.7
Mean	5.4 ± 3.1	5.4 ± 4	6 ± 3.7	3.4 ± 1.3	−5.6 ± 1	−1.6 ± 1.3

Mean of the whole lake complex is given plus the standard deviation ($n = 3$)

At each sampling site, 45 depth layers were sampled

nd not determined

* At all sampling sites: *in* inflow *out* outflow

In the Uzlina–Isac complex, dissolved inorganic nutrients were strongly withdrawn from the water column (Fig. 2) emphasizing the finding by Arrigoni et al. (2008) that wetlands efficiently trap inorganic N and P species. System DIN transformation rates in May and September were widely comparable to nitrate + ammonium uptake rates measured by Friedrich et al. (Friedrich et al. 2003) (Table 3). Lake Isac, covering almost twice the area of Lake Uzlina and embedded in extensive reedbeds, was most efficient for DIN and SRP transformation during low flow in the fall (Fig. 2). Higher system net SRP uptake rates in fall than in spring were also found by previous investigators (Cristofor et al. 1993; Friedrich et al. 2003), and were explained by two to three times larger SRP concentrations compared to May (Table 3; Fig. 2). The high September rates also aligned, by almost a factor of 2, with the elevated Chl_a concentrations compared to May and increased system primary productivity (Tables 1, 3). The temperature was ~20°C in both months, and hence may have inserted a similar impact on the different rates in the studied seasons.

Water leaving the Uzlina–Isac complex flowed through a series of channels and extended reed beds until it was diverted mainly through the Litcov channel into the Puiu–Rosu–Rosulet complex (Bondar 2000) (Fig. 1). The flow was maintained by confluence with the Crisan-Caraorman channel, directing river water of the Sulina branch into Lake Puiu. Channel water as well as backwash from extensive reed beds provided nutrients and remineralized organic biomass to these lakes. Macrophytes and reed stands are known as sources of remineralized nutrients (Carpenter and Lodge 1986), and this release can be substantial in the littoral zone, particularly during high water levels (Cristofor et al. 1993). Therefore, input of nutrients from reedbeds was particularly active during May, when the Delta was flooded (Table 1). High mineralization rates may also be inferred from low O_2 concentrations (Table 1) and highest benthic ammonium and methane release at Puiu-in in May (Table 2). Large delta lakes like Lake Puiu exhibit very high sediment organic matter content (Coops et al. 2008), which may trigger extensive mineralization. Hence, the average input of benthic NH_4^+ to the Puiu–Rosulet–Rosu complex was substantial relative to the external DIN input (5.4 mmol m^{-2} d^{-1} in both seasons), and made up ~34% of TN input in May and ~42% in September compared to the Uzlina–Isac complex (Table 2). Hence, external inorganic nutrient input declined with decreasing hydrological connectivity with the main river, as previously described (Cristofor et al. 1993; Heiler et al. 1995).

Due to reduced nutrient input to the fluvio-marine delta, system DIN transformation rates were also reduced in May (Table 3). Spring rates were comparable to nitrate + ammonium uptake rates by Friedrich et al. (2003), while in fall DIN was even released and rates were much higher than in this earlier study. Despite the DIN release, N-deficient growth reflected in a POC:PON > 14.6 and TN:TP < 20 (Table 4) was encountered. Nitrate conversion to N_2 and NH_4^+ may particularly occur in the heavily vegetated Lake Rosulet in late summer because senescence of macrophytes easily develops deoxygenated conditions (Carpenter and Lodge 1986), and may therefore stimulate denitrification. We recorded an intense odor of hydrogen-sulfide, high benthic sulphate removal, and lowest water column oxygen concentrations during the fall campaign in this lake (Tables 1, 3). An increasing abundance of cyanobacteria in Lake Rosulet in late summer (Coops et al. 2008) suggested N-fixation as an additional DIN source to

Table 3 N, P, and C loading (mmol m^{-2} d^{-1}) of the lake complexes and internal transformation and production rates (mmol m^{-2} d^{-1}) during flooding in May and low flow in September 2006

Loading and reaction (mmol m^{-2} d^{-1})	May				September			
	Uzlina–Isac		Puiu–Rosu–Rosulet		Uzlina–Isac		Puiu–Rosu–Rosulet	
	Inflow	Reaction	Inflow	Reaction	Inflow	Reaction	Inflow	Reaction
TN	11.8	−2.7	5.3	−1.2	5.7	−2.8	2.6	+1.3
DIN	9.3	−6.0	2.3	−1.4	5.3	−4.9	0.3	+1.7
DON	2.1	+1.8	1.4	+0.3	0.4	+0.8	0.7	−0.3
PN	0.4	+1.5	1.6	−0.1	0.0	+1.3	1.6	−0.1
TP	0.17	−0.01	0.10	0.00	0.3	−0.04	0.2	−0.05
SRP	0.10	−0.08	0.08	−0.05	0.2	−0.18	0.02	−0.02
DOP	0.02	+0.04	0.02	+0.01	0.0	+0.04	0.08	−0.05
PP	0.05	+0.03	0.0	+0.04	0.1	+0.10	0.10	+0.02
TOC	51	+10	46	−2.6	16	+13	28	+2.3
DOC	44	+2	35	+0.01	14	+8	22	+2.0
POC	7	+8	11	−2.6	2	+5	6	+0.3
Primary productivity (mmol m^{-2} d^{-1})	8 ± 0.3		4 ± 1		29 ± 4		26 ± 4	

Production is indicated by positive values and transformation by a negative sign. Observations for each sampling site ($n = 3$) were averaged in order to calculate inflow and net concentrations in the individual lake complexes. Primary productivity (mmol m^{-2} d^{-1}) was calculated with an empirical model (Smith 1979) and averaged ($n = 9$) for each lake complex

the system, helping to overcome this N limitation. Likewise to DIN, system SRP transformation was also remarkably reduced in both seasons. The higher uptake in May was explained by increased ambient SRP concentrations supplied to the Puiu–Rosu–Rosulet complex during the spring flood (Fig. 2).

Formation and dynamics of dissolved organic matter and particles in Danube Delta lakes

Organic matter and particle production

In the delta lakes, inorganic nutrients are efficiently converted into biomass or lost due to denitrification in anoxic lake sediments (Friedrich et al. 2003; Wetzel 2006). Living biomass in wetlands is an important source of DOM, and senescing detritus mainly contributes to the formation of particles and regenerated nutrients (Wetzel 1979; Childers 2000; Stepanauskas et al. 2000). In such systems, organic N and P can constitute the dominant fractions of TN and TP in flowing water. An investigation on riverine nutrient transport to the Baltic Sea demonstrated that 52% of TN and 64% of TP occurred in the organic form (Stepanauskas et al. 2002). Another study by Seitzinger and Sanders (1997) showed that in the Delaware and Hudson River (USA), organic N can account for 20–90% of the total riverine N load.

In this study, we calculated the load of dissolved organic and particulate N and P to both lake complexes. As described in detail above, we further determined transformation and production rates for these compound classes and compared them to TP-based estimates of the internal primary productivity in the individual complexes (Table 3). In the Uzlina–Isac complex, the inflow of dissolved organic and particle N and P at Uzlina-in was small relative to the inflow of DIN and SRP. However, the inflow of riverine organic matter reached a maximum during the spring flood, possibly because transport of dissolved organic carbon and particulate matter tends to increase during flooding (e.g. Aspetsberger et al. 2002; Eimers et al. 2008).

In contrast to loading, production rates of dissolved and particulate N and P were high in the Uzlina–Isac complex in both seasons, and compensated DIN and SRP removal (Table 3). For example, we attributed the spring surplus of DOP along flow-through to secretion of freshly synthesized DOM from living macrophytes, which is high (up to 100%) during active photosynthesis (Wetzel 2006; Stepanauskas et al. 2000). Due to increased internal DOP input, DOC:DOP ratios progressively decreased along the flowpath in the Uzlina–Isac complex (Table 4). Estimated rates of internal primary productivity were comparable to those from eutrophic lakes (Lampert and Sommer 2007), and were highest in the fall. This may be explained by twofold higher Chl_a concentrations relative to spring (Tables 1, 3) and by the vegetation encountered in the Uzlina–Isac complex. In May, macrophytes and filamentous algae dominated Lake Uzlina, whereas mostly macrophytes dominated in Lake Isac. In September, an intense development of phytoplankton biomass was

Table 4 Average molar ratios of C, N, and P contained in POM, DOM, and the dissolved inorganic and total dissolved nutrient pool

	POM			DOM		Total
May 2006						
Sampling locations	POC:PN:PP	POC:PN	POC:Chl$_a$	DOC:DON:DOP	DOC:DON	TN:TP
Uzlina-in	155:2:1	22	5	2109:112:1	22	74
Uzlina-out	123:9:1	4	6	1627:83:1	23	68
Isac-out	198:13:1	22	7	799:66:1	12	34
Puiu-in	n.d.	6	13	1563:91:1	45	43
Rosu-in	780:28:1	23	12	2039:125:1	17	61
Rosulet-out	261:44:1	8	8	1580:88:1	21	51
September 2006						
Sampling locations	POC:PN:PP	POC:PN	POC:Chl$_a$	DOC:DON:DOP	DOC:DON	TN:TP
Uzlina-in	34:n.d.:1	a	12	b	35	31
Uzlina-out	29:12:1	2	9	b	11	29
Isac-out	51:9:1	6	16	677:37:1	19	14
Puiu-in	63:16:1	4	9	275:9:1	30	13
Rosu-in	48:13:1	4	9	791:30:1	26	16
Rosulet-out	52:6:1	15	12	850:18:1	73	21

According to Guildford and Hecky (2000), TN:TP < 20 indicates N-deficient growth, whereas TN:TP > 50 indicates P-deficient growth. Average POC:Chl$_a$ (μmol μg^{-1}) ratios are shown for POM source association. Values relate to the means of samples collected from surface, intermediate, and bottom waters ($n = 3$), and for TN and TP the variability among these three samples can be inferred from data presented in Fig. 2

n.d. not determined, *a* PN below detection limit, *b* DOP below detection limit

observed in both lakes next to an increase in algal and macrophyte biomass. The estimated primary productivity added approximately 1.2 mmol m^{-2} d^{-1} of organic N and ~0.08 mmol m^{-2} d^{-1} of organic P to the Uzlina–Isac complex in May, and 4.4 mmol m^{-2} d^{-1} and ~0.3 mmol m^{-2} d^{-1}, respectively, in September. These estimates were in the order of production rates calculated from outflow and inflow concentrations. Hence, we were confident that they express trends in biomass production in these delta lakes.

In sharp contrast to the Uzlina–Isac complex, Lakes Puiu, Rosu, and Rosulet, received TN and TP in dominantly dissolved organic and particulate form. For example, in fall the organic fraction in the inflow (Puiu-in) could even make up 90% of TN and TP. Similarly to the lakes in the fluvial delta, the spring flooding increased the likelihood for increased organic matter input, except for P (Table 3). During flooding, black water was flushed from large floating reedbeds into the relatively deep water column of the large and isolated Lakes Puiu and Rosu (Jones 1992), thereby facilitating the supply of reed and macrophyte exudates to the flowing water. The dominance of C and N in imported DOM was also reflected in DOM elemental composition (Table 4).

Comparable to the Uzlina–Isac complex, internal production of dissolved organic and particulate N and P was high in the spring season, whereas in fall only PP formation could partially compensate the internal transformation of DOP and SRP (Table 3). Hence, the overall N and P balance in the Puiu–Rosu–Rosulet complex showed that along the flow path, TN and TP were transformed in spring, while in fall only TN was produced and mainly in the form of DIN. The estimated primary productivity was found to be high in September (Table 3), and perfectly matched with production rates or release of PP based on concentration changes along the flowpath. We also attributed the high primary productivity to 6 times larger Chl$_a$ concentrations measured in the two larger and deeper Lakes Puiu and Rosu in fall (~60 μg L^{-1}) than in spring. They were also comparable to long-term estimates by Oosterberg et al. (2000), and may be explained by the finding that both lakes exhibited higher phytoplankton densities in both seasons than the Uzlina–Isac complex. In Lakes Puiu and Rosu, turbidity increased from spring to fall, due to intense phytoplankton growth, except in Lake Rosulet, where the prevalence of humic substances (black water), leaching from by intense vegetation cover (Covaliov et al. 2003), may have inhibited microalgal growth (Jones 1992).

Particle dynamics

Internal biomass leaching and breakdown caused an increase in DON and DOP concentrations in May. However, next to biomass breakdown of senescent vegetation, several other processes as described below may have caused an increase of PN and PP concentrations in September (Fig. 2). Royer and Minshall (1997) found that macrophytes show significantly higher breakdown rates in spring than in fall. Interestingly, the particle load liberated from this process was prone to storage in sediments and released at later stages of decomposition. Other studies also observed that particulate material (N and P) was to a great extent retained in sediments during high flood and vegetation periods and then released in the fall season (Sand-Jensen 1998; Schulz and Gucker 2005). Tockner et al. (1999) found that the Danube floodplain close to Vienna behaved as a trap for POM, whereas it exported DOM and very coarse particles. These findings were widely applicable to N, P, and C dynamics in the Uzlina–Isac complex. Severe flooding in May promoted storage of breakdown products in sediments, while low flow in September allowed its liberation. High net PP release in fall further aligned with the finding that release of P from aquatic plant detritus mainly occurs via decomposition. Especially shoots store P next to N and their decay provides an important source of these elements to flowing waters (Carpenter and Lodge 1986). Coops et al. (2008) reported remobilization of P from decaying macrophytes and from reedbeds in Danube delta lakes, a process that was certainly enhanced at the end of the vegetation period.

Concerning PP, its selective liberation throughout both seasons may be also based on abundant phytoplankton biomass, forming an important proportion of suspended particle mass in the large lakes. Microalgae have a much higher P requirement (C:P $\approx$ 106, Redfield 1958) than macrophytes (C:P $\approx$ 550, see above), and therewith may also selectively enrich the particle pool in P.

Effects on C:N:P stoichiometry along the flow-path

Comparison of molar C:N and N:P ratios in particulate and dissolved matter (Table 4) allowed specifying N and P availability for water column biomass production (Sommer 1990; Guildford and Hecky 2000; Wetzel 2001) along transport in the two lake complexes. This approach is conservative because we lack data on internal P loading, which may be substantial in these shallow systems (Friedrich et al. 2003). Furthermore, massive benthic CH_4 release and removal of SO_4^{2-} indicated high anoxic organic matter decomposition rates in lake sediments (Table 2), and therefore implied concomitant high internal P loading.

According to Guildford and Hecky (2000), the TN:TP ratio is most indicative for N- or P-deficient growth in lakes and oceans. We recorded a change in the TN:TP ratio between lakes of both complexes, with an obvious P deficiency relative to N in water supplied from the River Danube to the Uzlina–Isac complex in spring, and decreased P deficiency in Lakes Isac and Puiu (Table 4). Likewise in fall, a decreased availability of N was identified in the Puiu–Rosu–Rosulet complex. Hence, the water leaving this complex to the shelf region exhibited a significantly changed TN:TP ratio as compared to the water entering the delta lakes at Uzlina-in. The spatial and temporal shifts in the TN:TP ratio may be linked to a difference in species composition and vegetation cover between the two lake complexes (Oosterberg et al. 2000). For example, it was reported that cyanobacteria start to increase their biomass in Lake Rosulet after June (Coops et al. 2008), indicating reduced relative N availability in the fall.

Next to the TN:TP ratio, the particulate matter and DOM elemental composition sampled at Uzlina-in in May widely differed from those in September. This effect can be explained either by different particle and DOM input from the river with changing hydrological connectivity (Table 4) or by the different P availability between May and September. During high water, backwash of biomass from abundant reed and macrophyte stands clearly showed an impact on the water column particle and DOM composition. Reed tissues are C-rich, and breakdown enriches DOM, suspended particles, and POC:Chl$_a$ ratios in C. For comparison, the molar C:N:P of marine macrophytes is typically 550:30:1 (Atkinson and Smith 1983) because these plants have an approximately 50-fold lower requirement per unit time for P than microalgae (Sand-Jensen and Borum 1991). The study by Tockner et al. (1999) conducted at the Danube floodplain close to Vienna also suggests that changes in hydrological connectivity resulted in changes in the composition of particulate organic matter transported.

Export of N and P to the Black Sea

In line with the above findings, water leaving Lake Rosulet, the last lake within this flow-through chain, delivered on average 58% of TN and 82% of TP as dissolved organic and particulate species to the coastal shelf of the northwestern Black Sea. Our data confirmed the general notion that wetlands are significant sources of organic matter, which may constitute a major portion of the TN and TP pool exported (Harrison et al. 2005). In order to better gauge the function of the delta wetland lakes in riverine N and P transport to the Black Sea, we assumed that approximately 10% of river discharge flows through the delta (Friedrich et al. 2003). We further assumed that seasonal variability in nutrient removal and biomass formation was widely reflected by spring and fall data, because spring usually covers the largest flood event of the year and fall represents low flow, which also prevails during winter (Oosterberg et al. 2000). Based on our measurements, roughly 4% of TN and 1.4% of TP transported in Danube river water were removed and transformed in the delta per year. Using an average discharge of 6,460 $m^3 s^{-1}$ (ICPDR 2004), transformation in the delta amounted in a reduction of the river's N and P load by ~10,300 t N $year^{-1}$ and ~200 t P $year^{-1}$, representative for abstraction of 3% N and 0.7% P from the total riverine N and P load per year to the Black Sea (Teodoru et al. 2007). Hence, the delta represents a sink for N, whereas a minor sink for P. The immobilization of N and P in the delta lakes was overall lower than expected from former studies (Friedrich et al. 2002, 2003), because we accounted for the presence of organic and particulate N and P.

In accord with the above calculations, ~10,000 t N and ~1,000 t P were potentially exported from Lake Rosulet to the shelf per year, with on average 58% of TN and 82% of TP residing in dissolved organic and particulate form. The water leaves Rosulet-out mainly through an artifical channel, and water travel times to the coast were estimated to range from 0.1 to 0.2 days. Because flow-through at Uzlina-in and Rosulet-out were comparable (Table 1), and water travels over a stretch of ~3.8 km from Sfantu Gheorghe to Lake Uzlina within ~0.2 days (Oosterberg et al. 2000), we assume that water will flow from Rosulet-out to the coast (~2.5 km) within 0.1–0.2 days. During high water, the water also leaves through littoral outlets by breaking through the littoral bars (Bondar 2000). Most of the P leaves this lake in particulate form, and is prone to precipitation in the river plume on the shelf. Because organic and particulate N and P have different bioavailabilities to the primary and secondary producers than their inorganic counterparts (Seitzinger and Sanders 1997; Stepanauskas et al. 1999), we also conclude that their input to the shelf may have severe impacts on coastal N and P cycling. A deficiency in inorganic relative to organic N may enhance the dominance of heterotrophic over autotrophic processes in coastal water, as was observed by Glibert et al. (1991) in the Chesapeake Bay. Monaghan and Ruttenberg (1999) found that DOP formed an important and bioavailable P source for the microbial community during times of high biological productivity in the coastal ocean. However, we may also argue that if the nutrient load of the River Danube can be further reduced, internal nutrient transformations may certainly become more effective in diminishing the flux of N and P to the Black Sea.

Conclusions

The Danube Delta as a system of hundreds of lakes, ponds, reed beds, channels, stream banks and alluvial forests, efficiently transforms nutrients from flowing water into dissolved organic and particulate matter, which therefore dominate N and P cycling in the delta lakes and export to the coastal Black Sea. Especially the larger lakes, such as Isac and Rosu, act as effective transformation "reactors" of nutrients. The Uzlina–Isac complex, characterized by high hydrological connectivity with the River Danube, effectively removes nutrients from flow-through and produces a myriad of dissolved organic compounds and particles. Inorganic nutrient input is diminished with hydrological distance to the main Danube branches and the Puiu–Rosu–Rosulet complex receives widely transformed organics. Nevertheless, this remote complex also shows high productivity due to effective internal nutrient recycling. In summary, along a chain of highly heterogeneous delta lakes we found that DOM release was of general importance in spring, while particle release widely dominated in fall. On a seasonal average, 90% of TN and 69% of TP were flushed in inorganic form to Lake Uzlina, whereas in contrast, 58% of TN and ~82% of TP were potentially exported in dissolved organic and particulate form to the coastal Black Sea. Regarding net N and P export, DOP and PP production rates nearly compensated SRP transformation rates along the flow path, and we therefore conclude that the Danube delta lakes generally act as N transformers and P transporters.

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