PRIMARY RESEARCH PAPER

Transport of seston in the karstic hydrosystem of the Plitvice Lakes (Croatia)

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Abstract Research into spatial and temporal variation in seston transport was carried out during the year 2000 on three reaches on the longitudinal profile of the karstic cascading system of the Plitvice Lakes in Croatia. The three investigated reaches were (i) a channel over a barrier with low gradient; (ii) flow through a deep lake; and (iii) a channel with cascades and a steep gradient. The aim of the study was to establish the influence of physiographical and hydrological differences of these reaches on the quality and quantity of seston transport and food resources in the seston. To calculate the seston transport, we measured: total suspended matter (TSM), particulate inorganic matter (PIM), particulate organic matter (POM), chlorophyll-a (chl-a), heterotrophic bacteria and discharge. The PIM contribution from TSM ranged between 60 and 90%, while the percentage of POM in TSM was the highest in summer and ranged from 33 to 46%.

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M. Špoljar (⊠) · B. Primc-Habdija · I. Habdija Department of Biology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, Zagreb 10 000, Croatia e-mail: mspoljar@biol.pmf.hr POM and discharge were significantly negatively correlated (r = -0.43, P < 0.05). For the transport of TSM, PIM, POM and chlorophyll-a statistically significant differences between the three reaches were established. In a principal component analysis, 86% of the variance was explained by the first two factors. The first factor corresponded well with net transport of TSM, PIM, POM and chl-a and distinguished investigated reaches in two groups: the 1st group with increasing (reaches with low gradient and with high gradient), and the 2nd group with decreasing net seston transport (reach with flow through a deep lake). The second factor corresponded strongly with discharge and distinguished investigated reaches according to their temporal variability.

Keywords Karstic lakes · Seston · Total suspended matter (TSM) · Particulate inorganic matter (PIM) · Particulate organic matter (POM)

Introduction

Seston is made up of inorganic particles and dead or alive organic particles. Many studies have focused on organic matter in seston, since it is the main food source for benthic organisms, for instance, insect larvae (Eriksson, 2002) and mussels (Cahoon & Owen, 1996; Descy et al., 2003). Furthermore, organic matter size structure in running waters influences the longitudinal arrangement of functional feeding groups of macrozoobenthic organisms (Vannote et al., 1980). Also, many recent studies have examined the relation between seston and hydrological or hydraulic factors, such as discharge, flow velocity, retention and dilution (Sandlund, 1982; Webster et al., 1987; Wallace et al., 1991; Wanner et al., 2002).

In this paper we study the seston transport in the Plitvice Lakes for a few reasons. Firstly, because they are a karstic hydrosystem consisting of sixteen cascading barrage lakes (Ford & Pedley, 1996) and in Croatia, 46% of the country is karstic (Kuhta, 2002). Secondly, investigations of seston have mainly been directed at river mouths or basins in large rivers, such as the Loire River in France (Lair, 1980), the Po River in Italy (Ferrari et al., 1989), the Rhine River in the Netherlands (De Ruyter van Steveninck et al., 1992; Tubbing et al., 1994). In these cases, lentic conditions form only a small part of the river, while lotic stretches are dominant. In the Plitvice Lakes the situation is reversed, and lakes dominate, while the lotic parts are short stretches. Thirdly, organic matter accumulation may have a negative impact on this system, providing the basis for rooted vegetation on the tufa barriers, and preventing travertinisation processes.

According to Roglić (1974), the Plitvice Lakes are riverine lakes that represent the upstream part of the Korana River, and water flows from one lake to the other over the barriers. In regard to physiography and hydrology of the Plitvice hydrosystem, there are three main types of lotic connection between the lakes: channels, cascades and waterfalls. Through the longitudinal profile of the Plitvice Lakes two types of water transition exist and occur repetitively. Firstly, epilimnetic water from extensive lakes flow into short lotic reaches, and secondly, water from the lotic reaches flow into retention zones (lakes).

We hypothesize that the quality and the quantity of seston transport is influenced by the physiographical and hydrological features of the lotic/lentic reaches. The main objectives of this study were to establish: (1) the influence of different physiographical and hydrological lotic reaches on the seston transport from the lentic part; (2) the influence of retention in lakes on seston transport from the lotic part; (3) seasonal and spatial variation of quality and quantity of suspensed matter in seston transport; and (4) seasonal and spatial variation of food resources (POM, phytoseston, heterotrophic bacteria) in the seston transport.

Study site

Our investigation of seston transport was carried out in the Plitvice Lakes National Park. The total area of this region is 19,172 ha, of which 13,500 ha is forested, 192 ha is open water; the rest is mostly meadows. The Plitvice Lakes belong to the karstic region of the NW Dinarid Mts, and have both surface and subterranean drainage systems. The main surface waters that supply the Plitvice Lakes are: the Crna rijeka River with its tributary the Kavga Stream, and the Bijela rijeka River with tributaries the Vukmirovića rijeka River and the Ljeskovački potok Stream. The Rivers Crna and Bijela rijeka connect in the Matica River, which flows into the Prošće Lake (Fig. 1).

The Plitvice Lakes are divided into the Upper (Prošće, Ciginovac, Okrugljak, Batinovac, Veliko and Malo Lake, Vir, Galovac, Milino Lake, Gradinsko Lake, Veliki burget, Kozjak) and Lower Lakes (Milanovac, Gavanovac, Kaluđerovac, Novakovića Brod). The drop between the first and last lake is 134 m and the straight-line distance is 5640 m (Riđanović, 1994). The Upper Lakes are situated in a dolomite $[CaMg(CO_3)_2]$ valley, while the Lower Lakes are situated in well-bedded rudiste limestone $[CaCO_3]$, in the canyon of the Korana River.

The lakes are oligotrophic and dimictic, with spring and the autumn overturn. A thermocline occurs in the summer at a depth of 10–20 m (in the deep lakes, lake Prošće, Kozjak, Galovac), which implies a vertical oxygen distribution during stagnation (Habdija et al., 1993).

Physical and chemical parameters measured in the Plitvice lakes were as follows: temperature ranges from a minimum of 3 (in January) to a maximum of 21.8°C (in August); dissolved oxygen ranges from a minimum of 7.5 (in July and 636.51



Fig. 1 Map of the Plitvice Lakes with stations investigated marked, and reaches investigated: BL1-BL2, BVJ-BLG, BM1-BM2

August) to a maximum of 14.5 mg O₂ l⁻¹ (in January); COD (Chemical Oxygen Demand) ranges from a minimum of 0.9 (in January) to a maximum of 3.2 mg O₂ l⁻¹ (in September); SRP (Soluble Reactive Phosphorus) ranges from a minimum of 0.011 (January) to a maximum of 0.041 mg l⁻¹ (in July); alkalinity is at a minimum of 186.7 in July and a maximum of 256.7 mg CaCO₃ l⁻¹ (in November); and the pH is generally alkaline (in the range 7.6–8.6).

BVJ-BLG

BL1-BL2

Figure 1 shows the Plitvice Lakes watershed areas with the investigated reaches, the subject of this study, identified. We collected samples from six sampling points, representative of three physiographically and hydrologically different types of reach in the hydrosystem of the Upper Plitvice Lakes. Morphometrical characteristics of these reaches, and their locations are shown in Table 1. The first is a channel over a barrier with a low gradient, BL1-BL2 (Barrier Labudovac 1, BL1; Barrier Labudovac 2, BL2); the second involves water flow through a deep lake BVJ-BLG (Barrier Veliko jezero, BVJ; Barrier Lake Galovac, BLG); and the third is a channel with cascades and a steep gradient of barrier BM1-BM2 (Barrier Milanovac 1, BM1; Barrier Milanovac 2, BM2).

BM1-BM2

Name of the stretch	Description of the stretch	Bottom	Altitude (m a.s.l.) starting-ending point	Length (m)	Gradient (%)
BL1-BL2	Channel with low incline	sand, few cataracts moss overgrowth	636.6–633.8	280	1
BVJ-BLG	Water flowing throughout the deep lake	sand	607.5–586	600	3.6
BM1-BM2	Channel with cascades and sharp incline	sand, barrier moss overgrowth	563.5–541	145	7.6

Table 1 The morphometrical features of the investigated reaches

Reach BL1-BL2: Channel over a barrier with a low gradient (Barrier Labudovac 1, BL1-Barrier Labudovac 2, BL2)

The upstream point BL1 was situated on the inflow of the water from the Prošće Lake (maximum depth 37.4 m, surface of 68.2 ha) into the Labudovac channel (mean width 7 m, mean depth 1 m). The sandy bottom is covered with submerged vegetation, and the littoral zone of the channel with emerged vegetation. Trees in the riparian zone shade the left bank, while sciophilic mosses, from the genera *Bryum* and *Cratoneu-rum*, cover the cataracts in the Labudovac channel. The downstream point BL2, was situated before water flows over the Labudovac barrier.

Reach BVJ-BLG: Water flow through a deep lake (Barrier Veliko jezero, BVJ-Barrier Lake Galovac, BLG)

The upstream point, BVJ, was shaded with riparian trees and surrounded with moss-grown barriers and small waterfalls (up to 2.5 m). It was situated at the downstream end of the barrier of the Lake Veliko jezero. Then, water flows through the large (12.5 ha) and deep lake Galovac (maximum depth 25 m). Downstream point, BLG, was situated on the outflow of the water from the Galovac Lake.

Reach BM1-BM2: Channel with cascades and a steep gradient of barrier (Barrier Milanovac 1, BM1-Barrier Milanovac 2, BM2).

The upstream point, BM1, was situated at the outflow of water from the Kozjak Lake (maximum depth 46.4 m, surface of 82 ha) into the right border channel (mean width 2.5 m, mean depth 0.5 m) on the Milanovac barrier. At the beginning of the stretch, bed inclination was low, and the bottom was covered with gravel and sand. A population of *Salix caprea* dominated on the channel bank. About one hundred meters from

the starting point, the barrier dropped relatively steeply. In this area tree tops (*Fagus silvatica*, *Fraxinus ornus*) shaded the channel what supported the development of sciophilic mosses on the barrier. The downstream point, BM2, was situated after the water flow over the Milanovac barrier (Fig. 1, Table 1).

Materials and methods

The investigation was conducted from March until December 2000. Seston samples were collected monthly at the three reaches, from the upstream and the downstream points of each reach. Samples for chemical analysis and food resources were also taken with the same sampling strategy. Samples for heterotrophic bacteria were collected from April until the end of the year, except in July.

Water samples of 200 l were filtered through a plankton net (mesh 26 μ m). The samples were dried at 104°C for 4 h, and ashed at 600°C for 6 h. The amount of dry weight (DW) after 104°C/4 h was considered as the amount of total suspended matter (TSM). Ash weight (AW) was considered as the amount of particulate inorganic matter (PIM) while ash free dry weight (AFDW) as particulate organic matter (POM). For the suspended particulate organic matter we took into consideration ultra-fine particulate organic matter (UPOM) size particles, 0.5–50 μ m, because plankton net mesh size was 26 μ m.

We took 3 l of water samples for chlorophyll-*a* (chl-*a*) estimation. Ethanol extraction according to Nusch (1980) was used for the estimation of chl-*a*. Heterotrophic bacteria were analysed by the spread plate method, after serial dilution of samples. Colony forming units (CFU) were

counted after incubation at 22°C for 72 h (APHA, 1985).

The transport of TSM, PIM, POM, chl-*a* and heterotrophic bacteria was calculated by multiplying the concentrations of DW, AW, AFDW, chlorophyll-*a* and CFU number by the discharge. The net seston transport in the reach was defined as the difference between the upstream and downstream ends of the reach.

Data for daily water discharge was obtained from the State Meteorological and Hydrological Service. The most complete data for 2000 were obtained from the gauging station at Plitvički Ljeskovac, in the water catchment of the Matica River.

Statistical analysis used the STATISTICA software (copyright©StatSoft). Pearson product moment correlation and two-way analysis of variance with a post hoc Tukey HSD test were calculated. The principal component analysis (PCA) was used to ordinate space-time localization (investigated reach, month) as a function of TSM, PIM, POM, and chl-*a* net transport. Data for heterotrophic bacteria were not included because no statistically significant spatial or temporal differences were recorded. Sestonic variables were centered and standardized prior to PCA analysis. Projections of the individual cases were plotted onto the factorplane (factor $1 \times factor 2$).

Results

Hydrology. The variation of discharge in 2000 is shown in Fig. 2. The minimum occurred in summer $(6.20 \text{ m}^3 \text{ s}^{-1})$, and the maximum in

10.0

Fig. 2 Discharge regime on the hidrological station Plitvički Ljeskovac (Matica River) during the year and average seasonal discharge values (Q_A). Rhombs mark sampling date December (8.79 m³ s⁻¹). The seasonal discharge was highest in winter (at 7.80 m³ s⁻¹), decreased slightly in spring (to 7.04 m³ s⁻¹), and was lowest in summer (6.32 m³ s⁻¹). In the autumn a slight increase to 6.87 m³ s⁻¹ was noted. The seasonal discharge differences were statistically significant (two-way ANOVA, df = 3; F = 12.7; P = 0.0001).

On the longitudinal profile (all six points, from BL1 to BM2) the Pearson product-moment correlation coefficient suggested a weak but significantly negative correlation between the transport of TSM and discharge (r = -0.22, P = 0.05), while that between the transport of POM and discharge suggested a more strongly negative correlation (r = -0.43, P < 0.05).

Spatio-temporal fluctuation of measured parameters in seston transport

In the three investigated reaches, from March until August, temporal fluctuations of TSM, PIM, POM and chl-*a* were low, while after that period fluctuations were higher (Fig. 3). Also, the magnitude of the measured parameters in seston rose from August to December. Values for chl-*a* transport reached their peak in September, except at the downstream point of the reach BVJ-BLG. The number of heterotrophic bacteria oscillated during the investigated period.

Transport of TSM, PIM and POM through the reach with retention in a lake, BVJ-BLG, decreased by approximately 50%, while over the reach with a steep slope, BM1-BM2, the equivalent amounts doubled. The situation was differ-





Fig. 3 Seasonal fluctuations of total suspended matter (TSM); particulate inorganic matter (PIM) and particulate organic matter (POM), chlorophyll-*a* and heterotrophic bacteria transport on the three investigated reaches

ent with chl-*a*. Chlorophyll-*a* in transport through the lotic reach BM1-BM2 decreased by 19%, while its transport through the reach BVJ-BLG lost only 1% of the input amount. On the lotic reach BL1-BL2 a slight decrease of TSM, POM, chl-*a* and increase of PIM and hetrotrophic bacteria were observed.

According to the values for measured parameters in the seston, the Pearson product-moment correlation suggested that TSM and PIM were strongly and positively related in all three reaches (from r = 0.93 to r = 0.99). The PIM contribution

 Table 2
 Two-factor ANOVA of measured parameters in seston

	df	F	Р
TSM			
Reaches	2	10.0	0.001
Seasons	3	0.7	0.590
Reaches*Seasons	6	3.5	0.017
Reaches	2	93	0.002
Seasons	3	0.6	0.002
Reaches*Seasons	6	37	0.007
POM	0	5.7	0.014
Reaches	2	6.4	0.008
Seasons	3	1.0	0.426
Reaches*Seasons	6	1.9	0.142
Chl-a			
Reaches	2	3.7	0.044
Seasons	3	0.8	0.510
Reaches*Seasons	6	2.4	0.068
Heterotrophic bac	teria		
Reaches	2	2.0	0.171
Seasons	3	0.1	0.937
Reaches*Seasons	6	0.8	0.564
Multiple comparis	ons		
	IISU	IIA	
IW			
IS		TSM*, PIM*	
ISU		CHL-a*	
IA		TSM*, PIM*, CHL-a*	
IIW			
IIS		TSM*, PIM*	
IISU			
IIA			
IIIW			
IIIS		TSM*, PIM*	
IIISU	POM*	TSM*, PIM*,POM*	
IIIA	TSM*	TSM*, PIM*, POM*	

Results of multiple comparisons (Tukey test) are shown Symbols: I-BL1-BL2; II-BVJ-BLG; III-BM1-BM2; BVJ-BLG; BM1-BM2. Seasons: W, Winter; S, Spring; SU, Summer; A, Autumn

 $^*P < 0.05$

to TSM was estimated as between ca. 60 and 90%. Also, TSM and POM were significantly positively correlated (r = 0.63-0.94), where the percentage of POM in TSM was highest in the summer and ranged from 33 to 46%. Between the transport of POM and the amount of chl-*a* in seston, statistically significant and positive relations (r = 0.76) were established only on the lotic reach BL1-BL2.

Differences in quality and quantity of seston transport between the investigated reaches

An analysis of discharge and net changes in transport of TSM, PIM, POM, chlorophyll-*a* and heterotrophic bacteria over the three reaches gave us results shown in Table 3. The results of twoway ANOVA suggested statistically significant differences between the investigated lotic stretches in terms of net changes of TSM, PIM, POM and chlorophyll-*a*. Also, results showed that net changes of TSM and PIM transport had the major influence on the difference between the lotic stretches. For heterotrophic bacteria spatio-temporal changes were not statistically significant.

Multiple comparisons (to determine significant differences between stretches and/or between seasons) were provided by the Tukey test (Table 2). The results of this test suggested that the autumn period on the reach BVJ-BLG showed the most difference relative to other reaches and seasons. These differences implied losses of TSM, PIM and POM in the reach BVJ-BLG in contrast to an increase in seston over the lotic reach, BM1-BM2. Also, significant differences were evident in the net change of chl-*a* concentration between autumn amounts on the reach BVJ-BLG and summer and autumn

Table 3 Results from PCA. Eingenvector loading and percent of variability in the data set attributed to each principal component (F1, F2)

	F1	<i>F</i> 2
Percent of variable explained Eingevector loading	63.88	21.75
TSM	-0.975	-0.136
PIM	-0.951	-0.179
POM	-0.891	0.051
Chl-a	-0.736	0.291
Q	0.040	-0.974

amounts on the reach BL1-BL2 because of the highest values of chl-a concentration on the lotic reach BL1-BL2 (Fig. 3).

In the PCA analysis, 86% of the variance was explained by the first two factors (Fig. 4, Table 3). The ordination of temporal changes on the investigated reaches from the first factor corresponded with the mass of measured sestonic parameters (TSM, PIM, POM, chl-a) and explained 64% of variance. Factor 1 distinguished investigated reaches into two groups: the first with increasing (reaches with low gradient and with high gradient); and the second with decreasing net seston transport (reach with flow through a deep lake). The second factor explained 22% of the variance and corresponded strongly with discharge, what implied arrangement of the investigated reaches according to temporal changes. Furthermore, reaches where increase or decrease of POM and chl-a strongly determine net seston transport, during the period of low water (mostly summer months), are grouped in the 1st and 2nd quadrants. Reaches where increase or decrease of TSM and PIM strongly influenced net seston transport, during the period of high water (mostly spring and autumn months), are grouped in the 3rd and 4th quadrants.



Fig. 4 Relative ordination of investigated reaches for each month as a function of investigated parameters. Symbol: I-BL1-BL2; II-BVJ-BLG; III-BM1-BM2. Months mark with numbers (started with 3 for March until 12 for December)

Discussion

Hydrological influence on seston transport

In many investigations, discharge is a very important factor in seston transport (Sandlund, 1982; Wallace et al., 1991, Wanner et al., 2002). In our study, data for the year 2000 existed only for the hydrological station Plitvički Ljeskovac. This is situated on the bank of Matica River, which is the main supply of the Plitvice hydrosystem and inflows into the first, Prošće Lake. We considered this station as the reference which shows the quantity of inflow to the Plitvice Lakes. In this investigation, the discharge fluctuated slightly, and the curve of daily discharge reflects a nivopluvial water regime, as noted by Riđanović (1994). We explain the low discharge as a result of numerous retentions (lakes) in the Plitvice hydrosystem. In spite of low fluctuation, there were statistically significant differences of discharge between the seasons.

The relationship between discharge and seston is very complex and influenced by many factors: meteorological conditions, seasons of the year, torrents, topography of the watershed, composition of the riparian vegetation (forest, grass) etc. Some investigators observe that an increase of organic particles in the seston is significantly and positively correlated with discharge (Young & Huryn, 1999), while others note an inverse relation between discharge and the concentration of organic matter (Pace et al., 1992). We observed a significant inverse relationship between the POM and discharge (BL1-BL2). Because of the large lake surface area in the investigated longitudinal profile, related to short lotic stretches, we presume that increase of POM occurs during the summer, with a positive correlation between longer retention time and higher production in the lake (Welker & Walz, 1998).

Net seston transport

The greatest differences between the three investigated reaches were recorded in the transport of TSM and PIM, which was not surprising, while inorganic particles constituted the main part of TSM and significantly influenced its fluctuation. There was no temporal regularity in the investigated seston parameters, resulting in no statistically significant differences between the seasons.

On the lotic reaches BL1-BL2 and BM1-BM2 processes of drift, erosion and sedimentation were simultaneously evident. At the head of these reaches was a large lake. We considered that net change of transport depended firstly on the processes which reflect the physiographical characteristics of the reach (gradient, bottom sediment), and secondly, on the plankton fluctuation in the lake above a lotic reach that had a great influence on the quality and quantity of organic seston transport. We presume that on the reach with low gradient, BL1-BL2, a strong influence of the lake prevailed to influence the process of sedimentation. For instance, Spoljar (2003) reported that over the whole lotic reach BL1-BL2, euplanktonic organisms prevailed in seston. Values of POM and chl-a transport on the lotic reach BL1-BL2 were higher compared to the reach BM1-BM2, especially at the upstream limit (BL1). A high level of organic matter was present over the whole length of the reach BL1-BL2, due to the low gradient of the reach. We conclude that changes in quality and quantity of seston transport through this reach were a consequence of the strong influence of plankton fluctuation in the lake above. On the lotic reach with a steep gradient, BM1-BM2, increase of TSM, PIM, POM could be attributed to the strong influence of high gradient, bottom cover (mosses) and high water current, respectively. Consequently, processes of drift and erosion prevailed there.

We presume that there is a high input of inorganic matter and benthic elements at the head of the reach, BVJ-BLG, which is encircled with small waterfalls. After this, the water passes through the retention of the wide, deep Galovac Lake, which results in a significant loss of seston mass because of sedimentation in the lake, for all measured parameters in seston except chl-*a*. We explain this by suggesting that high primary production in this lake compensates for the loss of phytobenthos inflows in the seston at the upstream limit, BVJ. We considered seston particulate organic matter as the main food source for benthic organisms, such as the functional feeding groups of collector-filterers and collector-gatherers and have available data for POM (UPOM fraction), heterotrophic bacteria and phytoseston (measured as chl-a). According to Habdija et al. (1994, 2004) at higher water velocity the greatest concentration of UPOM is retained in the bryophytic mats, where collector fauna, mostly caddis larvae, oligochaetes and small dipteran larvae, dominate. The coarse and fine particulate organic matter increases in those habitats with a low current velocity. Furthermore, bryophyte biotopes dominate in the channels and barriers of the Plitvice Lakes so we conclude that collectors (1052 ind m^{-2}) are the main consumers of particulate organic matter. Also in the littoral regions of the lakes collectors formed the highest percentage (55%) of the total biomass with 1469 ind 0.1 m⁻².

During the investigation period, POM content consisted mostly of organic detritus particles, except in September, where zooseston played an important role in seston constitution (Špoljar, 2003). A positive correlation between POM and chl-*a*, noted only on the lotic reach BL1-BL2, suggests a higher primary production in the upper Lake Prošće in comparison to lower Lake Kozjak. The explanation for higher production could be in the higher ortho-phosphate concentration which inflows into the Prošće Lake from the Matica River (Špoljar et al., 2001).

We suppose that temporal fluctuations of chl-a in seston transport occurs as a result of nutrient concentrations in the epilimnion of the lakes. The late summer turnover in lakes results in an increase of chl-a concentration, with an annual peak in September (Špoljar, 2003). We explain this as a reflection of low discharge, which results in a longer retention time that positively influences the growth of phytoplankton in riverine lakes.

In the spatial fluctuation of chl-*a* concentration, we observed its decrease on the lotic reaches BL1-BL2 and BM1-BM2. Phytoplankton from the lake epilimnion was lost from the seston as a result of sedimentation, which could be the reason for chl-*a* decreasing at the downstream limits of the lotic reaches BL1-BL2 and BM1-BM2. This may be compared with the similar conclusions of Vadeboncoeur (1994) in an analysis of chl-a concentration at the water outlet from Lake Placid to the Owl Creek backwater, where concentrations of chl-a markedly decreased with distance from the lake, because of phytoplankton sedimentation in lotic habitats. However, we have also observed the opposite case during the investigation period, where at the downstream limit of a reach, the concentration of chl-a increased. We explain this in terms of bed drift and the input of benthic algae into the seston. Vadeboncoeur (1994) also explained an increase of chl-a concentration with distance from a lake outlet by an input of benthic algae from the bottom.

The net transport of heterotrophic bacteria increased from spring to summer on the lotic reaches. We concluded that a higher density of heterotrophic bacteria at the downstream limits of the lotic reaches BL1-BL2 and BM1-BM2 is the result of bed drift and intake of bacteria from benthos into the seston. Also, the low depth of the channels (mean depths of 0.5-1 m) contributes to bacteria input into the seston. We presume that the decrease in June and September is a result of grazing microfilterers from lake zoo-plankton and benthic filterers, with a high percentage of caddis larvae from the genus *Hydropsyche* (Kučinić, 2002). Both reached maximum population densities at these times.

Seston transport in the Plitvice Lakes system, compared with running water, is very low because the hydrosystem includes more lentic then lotic habitats. Thus a low rate of TSM transport (36–87 t year⁻¹) in the Plitvice Lakes occurs with low discharge (6–9 m³ s⁻¹). A second reason for low seston mass in the Plitvice Lakes could be a low trophic status of the hydrosystem. By comparison, the Rivers Ariége and Garonne (France) have discharges ranging from 50 to 500 m³ s⁻¹, and annual values for transport of suspended matter of between 34,000 and 86,400 t year⁻¹ (Chauvet & Fabre, 1990).

Conclusions

The results of our study show that physiographical and hydrological features significantly influence the transport of TSM, PIM, POM and chlorophyll-a. The highest downstream changes in the lotic reaches studied were recorded in the transport of TSM and PIM. Since PIM contributes a high percentage to the seston mass, it correlates positively with TSM and strongly influences the fluctuation of TSM transport. The biggest difference in the net seston transport for measured parameters was observed between the reach with retention, and a lotic reach with a steep gradient. Measuring seston sedimentation rate, drift and bed erosion, could be an important objective of further investigations, especially to understand the controls of the travertinization process, and to explain the balance of allochthonous and autochthonous food resources for the benthic community.

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References

- APHA, AWWA & WPCF, 1985. Standard Methods for Examination of Water and Wastewater, 16th ed. Washington.
- Cahoon, L. B. & D. A. Owen, 1996. Can suspension feeding by bivalves regulate phytoplankton biomass in Lake Waccamaw, North Carolina? Hydrobiologia 325: 193–200.
- Chauvet, E. & A. Fabre, 1990. Dynamics of seston constituents in the Ariege and Garonne rivers (France) Hydrobiologia 192: 183–190.
- De, Ruyter van Steveninck E. D., W. Admiraal, G. M. Breebaart, J. Tubbing & B. van Zanten, 1992. Plankton in the River Rhine. Structural and functional changes observed during down-stream transport Journal of Plankton Research 14: 1351–1368.
- Descy, J. P., E. Everbecq, V. Gosselain, L. Viroux & S. Smitz, 2003. Modelling the impact of benthic filterfeeders on the composition and biomass of river plankton Freshwater Biology 48: 404–417.
- Eriksson, A. I., 2002. Can predation by net-spining caddids larvae (Trichoptera: *Hydropsyche siltalai*) cause longitudinal changes in zooplankton species composition in lake outlet streams? Archiv für Hydrobiologie 153: 231–244.
- Ferrari, I., A. Farabegoli & R. Mazzoni, 1989. Abundance and diversity of planktonic rotifers in the Po River Hydrobiologia 186/187: 201–208.

- Ford, T. D. & H. M. Pedley, 1996. A review of tufa and travertine deposits of the world Earth-Science Reviews 41: 117–175.
- Habdija, I., B. Primc-Habdija & I. Belinić, 1994. Functional community organization of macroinvertebrates in lotic habitats of the Plitvice Lakes Acta hydrochimica et hydrobiologica 22: 85–92.
- Habdija, I., Primc-Habdija B., Erben R. & Radanović I., 1993. Trophic role of rotifers in the plankton of Lake Kozjak (Plitvice Lakes) Hydrobiologia 257: 101–106.
- Habdija, I., B. Primc-Habdija, R. Matoničkin, M. Kučinić, I. Radanović, M. Miliša & Z. Mihaljević, 2004. Current velocity and food supply as factors affecting the composition of macroinvertebrates in bryophyte habitats in karst running water Biologia, Bratislava 59: 577–593.
- Kučinić, M., 2002. Diversity and distribution of caddis flies (Trichoptera, Insecta) in the biotopes of the Plitvice Lakes. PhD. University of Zagreb, Faculty of Science. 138 pp.
- Kuhta, M., 2002. Croatia, II. Karst and caves In Gottstein-Matočec S., (ed), Encyclopaedia Biospeologica. III Société de Biospéologie Moulis 2237– 2287.
- Lair, N., 1980. The rotifer fauna of the River Loire (France) at the level of the nuclear power plants Hydrobiologia 73: 153–160.
- Nusch, E. A., 1980. Comparison of different methods for chlorophyll and phaeopigment determination Archiv für Hydrobiologie. Ergebnisse der Limnologie 14: 14– 36.
- Pace, M. L., S. E. G. Findlay & D. Lints, 1992. Zooplankton in advective environments. The Hudson River community and a comparative analysis Canadian Journal of Fisheries and Aquatic Sciences 49: 1060– 1069.
- Ridanović, J., 1994. The geographical position and hydrogeographical characteristics of the Plitvice Lakes. In Plitvice Lakes – Croatian national good world heritage. The management of Plitvice Lakes National Park, Zagreb, pp. 29–42.
- Roglić, J., 1974. Morphological characteristics of the Plitvice Lakes national Park. In Man and Nature, Plitvice Lakes, pp. 5–25.
- Sandlund, O. T., 1982. The drift of zooplankton and microzoobenthos in the river Strandaelva, western Norway Hydrobiologia 94: 33–48.

- Spoljar, M., 2003. Transport of seston in the cascading system of the Plitvice Lakes. PhD. University of Zagreb, Faculty of Science. 113 pp.
- Špoljar, M., B. Primc-Habdija & A. Plenković-Moraj, 2001. Overflow effect on the dynamics of the rotifer community in cascade lake system Verhandlungen Internationale Vereinigung fr Limnologie 27: 3409– 3412.
- Tubbing, G. M. J., W. Admiraal, D. Backhaus, G. Friedrich, E. D. De Ruyter van Steveninck, D. Mueller & I. Keller, 1994. Results of the international plankton investigation on the River Rhine Water Science and Technology 29: 9–19.
- Vadeboncoeur, Y., 1994. Longitudinal dynamics of seston concentration and composition in a lake outlet stream Journal of the North American Benthology Society 13: 181–189.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.
- Wallace, J. B., T. F. Cuffney, B. S. Goldowitz, K. Chung & G. J. Lugthart, 1991. Long-term studies of the influence of invertebrate manipulations and drought on particulate organic matter export from headwater streams Verhandlungen Internationale Vereinigung für Limnologie 24: 1676–1680.
- Wanner, S. C., K. Ockenfeld, M. Brunke, H. Fischer & M. Pusch, 2002. The distribution and turnover of benthic organic matter in a lowland river: Influence of hydrology, seston load and impoundment River Research and Applications 18: 107–122.
- Webster, J. R., E. F. Benfield, S. W. Golladay, B. H. Hill, L. E. Hornick, R. F. Kazmierczak & W. B. Perry, 1987. Experimental studies of physical factors affecting seston transport in streams Limnology and Oceanography 32: 848–863.
- Welker, M. & N. Walz, 1998. Can mussels control the plankton in rivers? – a planktological approach applying a Lagrangian sampling strategy Limnology and Ocenography 43: 753–762.
- Young, R. G. & A. D. Huryn, 1999. Effects of land use on stream metabolism and organic matter turnover Ecological Applications 9: 1359–1376.