Original Articles

Development of submerged macrophyte and epiphyton in a flow-through system: Assessment and modelling predictions in interconnected reservoirs

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A B S T R A C T

Every approach to lake restoration requires the reestablishment of submerged macrophytes. However, macrophyte overgrowth in shallow lakes may lead to deterioration and a consequent necessity for restoration treatments. We assumed that a major threat to the increased trophic level in the Jankovac flow-through system arises from the sediment, where the accumulation of decudicial leaf litter and decayed macrophyte fragments could generate anoxic conditions. The integrated Water Quality Model (WQM) and the Submerged Aquatic Vegetation Model (SAVM) were combined in the Jankovac Model (JanM) and applied during the vegetated season in 2008 and 2014, with the aim to offer a possible approach to the maintenance of good water quality. The impacts of flow velocity and epiphyton growth on submerged macrophyte coverage and biomass were simulated. Biocenotic analyses suggested that epiphyton growth was more extensive in 2014 in comparison to 2008. The results of JanM indicated that increased flow velocities enhanced macrophyte growth and dissolved oxygen concentrations concurrently with the decline of epiphyton biomass. Furthermore, results suggested that epiphyton growth rate of 0.4 d−1 maintained macrophyte coverage and biomass at a satisfactory level of 70% reservoir coverage. Considering the proposed scenarios hydraulic treatment could be applied to regulate submerged macrophytes in shallow reservoirs, as an efficient and less invasive approach than sediment removal, especially in sensitive karst areas.

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1. Introduction

Ratio among primary producers, macrophytes (i.e. charophytes, bryophytes and angiosperms): phytoplankton: periphytic algae, is crucial in maintaining a favourable transparent state in lakes (Schell, 1998). Macrophyte stands have exceptional ability to alter environmental conditions, nutrient cycling, bioenosis assemblages and biotic interactions. Their impact on ecosystem functioning is related to the complexity of macrophyte stems and their physiology (Kuczyńska-Kippen and Nagengast, 2006; Chaparro et al., 2014). Complex submerged macrophytes achieve their best results in the suppression of algal bloom through the competition for nutrient uptake (Jepssen et al., 1997; Lau and Lane, 2002) or by the production of allelopathic substances to mitigate algal growth (van Donk and van de Bund, 2002). Floating-leaved macrophytes increase shading, reduce algal photosynthetic oxygen production and reject zooplankters (Compé et al., 2011), whilst emergant macrophytes prevent coastal erosion (Horppila and Nurminen, 2005). Besides numerous zooplankters (Kuczyńska-Kippen and Nagengast, 2006; Špoljar et al., 2012b), macrophyte stands host many epiphytic organisms, i.e., algae, protozoans and meiofauna (Kralj et al., 2006; Špoljar et al., 2012c: Dražina et al., 2013). Epiphytic biomass and diversity depend on multiple abiotic (light supplies, nutrients, flow velocity, water residence time) and biotic (macrophyte architecture, abundance of grazers) factors.

Interactions among macrophytes, illumination, epiphyton, grazers and fish may reflect the trophic state of the hydrosystem (Beresford and Jones, 2010; Špoljar et al., 2011). Epiphyton biomass
is generally higher in eutrophic lakes, but also, due to better illumination, its ratio can be higher in oligotrophic lakes (Laugaste and Reunanen, 2005). The same authors studied epiphyton on 22 macrophyte species during the summer in the hypertrophic stratified Verevi Lake (Estonia), and concluded that substrate complexity may affect epiphyton biomass. For instance, chlorophyll a amounted to 117–200 μg g−1 DM−1 on floating-leaved plants, 330–360 μg g−1 DM−1 on emergent plants, and the highest values, 820–920 μg g−1 DM−1 on submerged plants. From biotic components, epiphyton-feeding snails as known grazers, have a significant impact on the biomass and species composition in the epiphyton, by reducing and removing old and recovering new epiphyton strata (Brömmark, 1989; Żebek and Szymańska, 2014).

A shift between a transparent vs. turbid state is largely due to macrophyte presence vs. absence. For instance, Scharmützelsee Lake (SE of Berlin, Germany) was characterized by turbid water until 2003. Thereafter, increased water transparency together with a rapid submerged macrophyte colonization, up to 5 m depth corresponded to the light supply of 3 E m−2 d−1 (Hilt et al., 2010). The authors recorded that an upgrowth of submerged macrophyte stands to approximately 24% coverage in 2005–2006, dominated by rootless N. obtusa and Ceratophyllum demersum, contributed to the stabilization of the water transparency. Dense macrophyte stands may also cause low bottom oxygen concentration, release P from the sediment and suppress mineralisation (Stephen et al., 1997; Søndergaard et al., 2003). These conditions indicate a higher trophic level and may transform the lake from a transparent to a turbid state, in accordance with the known chemical process clearly described by Søndergaard et al. (2003): In oxidised conditions, phosphorus is sorbed to iron (III) compounds, while in anoxia iron (III) is reduced to iron (II) and subsequently both iron and sorbed phosphate returned into solution. In two reservoirs of the Paraná basin (South America) Chiba de Castro et al. (2013) observed the negative effects of dense macrophyte stands (80–100% coverage) where a decline in the redox potential was caused by oxygen depletion. In the study of Caraco and Cole (2002) it was established that in the River Hudson (the stretch from New York to Albany, USA) the alien aquatic macrophyte (Trapa natans) may extremely decrease dissolved oxygen concentration to values below 2.5 mg l−1, while within macrophyte stands dominated by a native species (Vallisneria americana) dissolved oxygen did not decrease below 5 mg l−1 during the summer growing season. In the restoration of overgrown lakes important ecological goals are to create diverse macrophyte stands with an open water and mosaic of different, preferably submerged, macrophytes (Moss et al., 1997). A mosaic community of macrophytes will increase habitat heterogeneity between macrophyte stands and the open water and enhance biocenotic diversity and life styles (food preferences, migrations, nesting, molting), facilitate succession of organisms and remove water pollutants and nutrients (Björk, 1994; Wang et al., 2009). Macrophyte diversity provides stands less sensitive to physical disturbances, i.e. waves, bioturbations and herbivores, suppress algal production and reduce losses of total phosphorus (Engelhardt and Ritchie, 2001; Hilt et al., 2006).

Predictions of ecosystem functioning are often requested and can prove to be of great value in protected areas with peculiar karst phenomenon, as in the Papuk Nature Park (Croatia). After sediment-drainage of the Jankovac reservoirs (Papuk Nature Park) in 2003 we analysed invertebrates in plankton, epiphyton and benthos as well as macrophyte coverage, and environmental parameters in 2008 and 2014. According to obtained data (Špoljar et al., 2012a,b,d, 2015) macrophytes tend to overwhelm both reservoirs and thus the eutrophication process could be triggered. We assumed that the increased trophic level in the Jankovac reservoirs originated from the sediment, where the accumulation of deciduous leaf litter and decayed macrophyte fragments probably generate anoxic conditions. In such cases aeration methods for water column (Verner, 1994) and sediment (Hilt et al., 2006) are frequently applied in lakerestorations. Flow velocity also plays an important role in flow-through systems affecting macrophyte stands (Wilby et al., 1998), epiphyton (Špoljar et al., 2012a), planktonic (Špoljar et al., 2012b) and benthic (Sertić-Perić et al., 2011) organisms. For instance, low to medium flow velocities sustain the diversity and density of macrophyte stands (Madsen et al., 2001; Franklin et al., 2008). The same authors recorded that higher flow velocities negatively impact macrophyte stands, while Asaeda and Son (2000) and Horner et al. (2011) noted an increased epiphyton flushing rate. Recently, many modelling efforts have offered solutions for eutrophication reduction (Jin and Ji, 2015; Zhang et al., 2015, 2016). In the present study we considered flow velocity and dissolved oxygen concentrations as the main drivers in the balance between macrophyte coverage and epiphyton biomass and conducted them through a modelling design. The main objectives of this study were: (1) using a model simulation to analyse the influence of the flow velocity and epiphyton on macrophyte coverage and biomass; (2) to analyse environmental properties for sustainable growth of macrophytes and (3) to present an assemblage of zooeiphyton, protozoans and meiofauna, under impact of environmental conditions in the Jankovac flow-through system. The overall aim of this study is to present a hydraulic control strategy in the regulation of submerged macrophytes within shallow reservoirs.

2. Material and methods

2.1. Study area

Jankovac Stream (45°31'07"N, 17°41'11"E, Fig. 1, Table 1) is a small approximately 700 m long hydrosystem, in a submountain area at 475 m asl, situated on sedimentary karst rocks in the Papuk Nature Park, NE Croatia, and is described in detail in our previous studies (Špoljar et al., 2012a,b,d). Most of the stream was anthropogenically modified in two reservoirs (lentic parts), while lotic parts occur as rheorene spring (JS) and the Skakavac Waterfall over the tufa barrier (WJ). The two reservoirs (R1 and R2) exist as an interconnected flow-through system separated by a bank, and water flows through a connection between reservoirs. Across the longitudinal profile, the stream is mostly surrounded by deciduous forest, dominated by beech (Fagus sylvatica L.), followed by common ash (Fraxinus excelsior L.), maple (Acer pseudoplatanus L., A. obtusatum (Waldst. et Kt. ex Willd.), and wych elm (Ulmus glabra Huds.). The reservoir banks are slightly inclined. The bottom is covered with organic mud, which consists of a thick layer (0.5 m) in the littoral zone of mostly fine particulated organic matter, originating from macrophyte decay and deciduous leaf litter.

Both reservoirs were subjected to the sediment-drainage method in September of 2003 in an attempt to increase the water level. Water is transparent through the whole column and thus favours the growth of submerged macrophytes, Hippuris vulgaris as dominant and accompanying Potamogeton natans. Emergent macrophytes, Carex sp., Scirpus sp., Iris pseudacorus and Typha latifolia, constitute a discontinuous narrow belt around both reservoirs.

2.2. Assessment of zooeiphyton, environmental parameters and their interactions

Samples were collected in triplicate in July and the first half of September of 2008 and 2014 (Fig. 1). Within both reservoirs two habitats were identified: nonvegetated habitats, with pelagial (R1N, R2N), inflow (R1I) and outflow (R1O, R2O) parts of reservoirs; and vegetated habitats with H. vulgaris (R1H, R2H). Epiphyton
was sampled from submerged and branched *Hippuris*. This species reaches its maximum growth activity in July. For epiphyton analysis, shoots of both macrophytes (each sample contained a shoot of a single plant) were sampled with a plexiglas core sampler (30 cm high, φ 8 cm, 26 µm mesh) according to Kornijów and Kairesalo (1994). Macrophyte shoots ranging between 10–15 cm in length were cut and epiphyton was scraped off using a small brush and washed into plastic bottles after which they were transported to the laboratory and the living material was identified ≤48 h of collection.

Epiphyton, protozoans and meiofauna (benthic or periphytic heterogenous groups of metazoaons: rotifers, nematodes, gastrotrichs, cladocerans, copepods, ostracods; defined as organisms that can pass through a 1000 µm sieve and retained on a 44 µm sieve; Giere, 2009) were identified and counted in three subsamples under an Optron-Axiovert 35 inverted microscope (125×–400× magnification). For species determination, the following literature was consulted: Voigt and Koste (1978), Ogden and Hedley (1980), Amoros (1984), Einsle (1993), Foissner and Berger (1996), and Rundle et al. (2002). Bdelloidea and Nematoda were counted but not identified. Microfaunal biomass in epiphyton, presented in dry weight, was calculated by assuming a biovolume based on their geometric shapes, and converted to dry mass for protozoans (Gilbert et al., 1998), rotifers, cladocerans and copepods (Dumont et al., 1975; Malley et al., 1989). All shoots were dried and weighed and epiphytic biomass was estimated as µg g⁻¹ DM (epiphyton dry mass per gram dry mass of macrophyte).

At each sampling point, in parallel with biocoenoses samples, field measurements and samples for laboratory analyses were taken. Temperature, dissolved oxygen concentration, pH (Hatch HQ30d), conductivity (HACH sensION 5) and flow velocity (P600 flow meter, DOSTMANN electronic GmbH) were determined in the field. All nutrients, orthophosphates, total phosphorus (TP), nitrates and Kjeldahl total nitrogen (TN) were determined according to APHA (1995). Nitrites and ammonium were measured using

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**Table 1**

Main hydromorphological and environmental features of the Jankovac Stream, Papuk Nature Park.

<table>
<thead>
<tr>
<th>Localities</th>
<th>JS</th>
<th>R1</th>
<th>R2</th>
<th>JW</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Area (m²)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lengthmax (m)</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Widthmax (m)</td>
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<td></td>
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</tr>
<tr>
<td>zmax (m)</td>
<td></td>
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<tr>
<td>Height (m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Total volume (m³)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Main reservoir stations</th>
<th>R1N</th>
<th>R1H</th>
<th>R2N</th>
<th>R2H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat specification</td>
<td>Lotic</td>
<td>Lentic</td>
<td>Lentic</td>
<td>Lentic</td>
</tr>
<tr>
<td>Flow velocity (m s⁻¹)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>WRD (day)</td>
<td></td>
<td></td>
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<tr>
<td>Bottom granulometry</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Bed and dominant macrophyte coverage</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Abbreviations: JS – Jankovac Spring, R1 – Reservoir 1, R2 – Reservoir 2, JW – Jankovac Waterfall, R1N – nonvegetated pelagial in R1, R1H – *Hippuris* stands in R1; R2N – nonvegetated pelagial in R2, R2H – *Hippuris* stands in R2. *According to Špoljar et al. (2012b).*
ion chromatography (Dionex ICS-3000). Dissolved organic matter (DOM, mg O$_{2\text{Ma}}$ g$^{-1}$) was measured through the estimation of chemical oxygen demand, COD$_{\text{Ma}}$ (Spoljar et al., 2011). Algae, measured as chlorophyll $a$ (Chl $a$) according to Nusch (1980), in plankton (PChl-$a$) and epiphyton (EChl-$a$), and concentration of particulate organic matter (POM) were considered as food resources. POM values were measured as ash-free dry mass (AFDM) according to the procedure described in Spoljar et al. (2012b). Macrophyte dry mass (DM) was measured after epiphyton removal and weighed after drying in a thermostat at 104 °C for 24 h.

Before the statistical analysis, all the data were logarthimically transformed [$\log(x+1)$] and their normality was checked using Shapiro-Wilk's test. Results of this test showed that data did not follow normal distribution, and then a non-parametric Mann-Whitney $U$ test (comparison between two independent samples for zoöepiphyton biomass between two years) was used. Relationships between environmental and biotic parameters were correlated using Spearman rank.

2.3. The JanM

Jankovac Water Quality and the Macrophyte Model (JanM) composed the water quality model coupled with the sub-model M-SAVM (Modified-Submerged Aquatic Vegetation Model). The JanM was developed under the framework of the Environmental Fluid Dynamics Code (EFDC, Hamrick, 1992), model to simulate hydrodynamics and water quality in the Jankovac Reservoirs. Based on the Submerged aquatic vegetation Model, SAVM (Cerco et al., 2002; Jin et al., 2007), the submodel M-SAVM (Zhang et al., 2015) was developed by modification of the light attenuation equation. The JanM structure accompanying the embedded subroutine for nutrients (orthophosphates and nitrates) and dissolved oxygen (DO) cycles has been described previously (Zhang et al., 2016), and the governing hydrodynamics and mass-balance equations together with the numerical solution algorithm (Zhang et al., 2013; Jin and Ji, 2015) are attached in the Supplementary Material. The kinetic mass balance equations for shoot, root, and epiphyton have also been described previously (Ji, 2008; Jin and Ji, 2013; Zhang et al., 2015). The main biomass-balance equations of the JanM and the numerical solution algorithm can be found in the Supplementary Material.

The growth limiting function for light intensity, $f_2(l)$, was described as Eq. (1) in the M-SAVM. The $\mu_e$ was determined by the water transparency (Secchi depth) and epiphyton in the M-SAVM (Zhang et al., 2015). The effect of epiphyton was included in the light attenuation equation, which is the main difference between M-SAVM and SAVM.

\[
f_2(l) = \frac{2.718}{\mu_e - H_b}\left[\exp(-\alpha - \exp(-\beta))\right]
\]

\[
\mu_e = \mu_0 + K_e \frac{B_e}{CChl_e}
\]

where $\mu_e$ is the light attenuation coefficient (m$^{-1}$); $H_b$ is the average shoot height above the bed (m); the coefficients $\alpha$ and $\beta$ are described in detail in Ji (2008); $\mu_0$ is the background light attenuation coefficient (m$^{-1}$), which reflects the water transparency; $B_e$ are the epiphyton biomass (g C m$^{-2}$); $K_e$ is the coefficient for EChl $a$ (m$^{-1}$ mg C m$^{-2}$); and $CChl_e$ is the carbon/EChl $a$ ratio for epiphyton (g C: mg EChl $a$).

2.4. Model application

2.4.1. Framework of the simulations

The horizontal plane of reservoirs was divided into 278 grid cells (DX 1.57 – 13.8m, DY 3.57 – 16.7m) with two layers in JanM. The hydrodynamic time step was 1 s, water quality and macrophyte model were 0.4 s. The semi-monthly averaged data for hydraulic and meteorological boundary conditions were used and water quality and loads, also on a semi-monthly basis. Both initial shoot and root carbon biomass values were assumed to be 5 g C m$^{-2}$ in the bottom layer.

2.4.2. Calibration and validation

JanM was calibrated and verified to a hydrodynamic with the water depth ($z$) and flow velocity ($FV$), using two datasets, 07/01–09/30, 2008 and 07/01–09/30, 2014. The model simulations of constituents were good with RMSE of depth (0.17 m). Hydrodynamic model calibration was carried out by changing the roughness (calibrated from 0.025 to 0.035), RMSE of velocity is 0.36 cm s$^{-1}$ The calibration and validation results of $z$ and $FV$ at R1H and R2H are presented in the Supplementary Material (Fig. S1).

JanM was calibrated and verified with the five water quality parameters, DO, DOM, TP, TN, chlorophyll-$a$ (EChl-$a$ and PChl-$a$), using two datasets, 07/01–07/31, 2014 and 09/01–09/30, 2014. The calibrated values of the major coefficients in JanM are presented in the Supplementary Material (Table S1 in Supplementary material). The results of the main limnological parameters at R1H and R2H are presented in the Supplementary Material (Figs. S2 and S3 in Supplementary material). The model simulations of main water properties showed a good fit with RMSE, R-RMSE, and the absolute error values <30% (Table S2 in Supplementary material).

JanM was calibrated and verified respectively with macrophyte biomass in two datasets, 07/01–10/10, 2008 and 07/01–10/10, 2014. The values of the major coefficients for calibration in M-SAVM are given in Table 2. The model simulations are acceptable, based on RMSE, R-RMSE, and the absolute error values (Table 3).

2.4.3. Sensitivity analysis

A sensitivity analysis was conducted to elucidate how the uncertainty of the model outputs can be apportioned to the parameters (Arhonditsis and Brett, 2005). The sensitivity analyses for light attenuation coefficient and maximum growth rate of plant shoots were carried out in M-SAVM as part of a previous study (Zhang et al., 2015). The epiphyton maximum growth rate ($PMe$) for this study was chosen because the impact of epiphyton in mitigation of macrophytes growth is focused.

3. Results

3.1. The coverage and biomass of macrophytes influenced by flow velocity

Simulated macrophyte coverage is consistent with the trends of measured data in reservoirs R1 and R2 (Fig. 2, Table 3). Three scenarios were simulated by the JanM with the purpose of establishing the effect of $FV$ on macrophyte growth, measured as coverage and biomass, dissolved oxygen, light attenuation and epiphyton biomass.

The original scenario (OS) was the calibration from 2008. Three, five, and ten times higher $FV$ were assumed in the scenarios. The modelled macrophyte coverage in the OS reached maximums of 73% in R1 and 90% in R2 (Fig. 3a). Results suggested that macrophyte coverage and biomass both increased with higher $FV$ in the simulated scenarios. By applying the $FV$10 scenario, results indicated an extension of macrophyte coverage up to 78% and 92%, in R1 and R2, respectively. Similarly, macrophyte biomass also amounted to higher values in the $FV$10 scenario, with a maximum of 167.5 g DM m$^{-2}$ at R1H and 132.4 g DM m$^{-2}$ at R2H (Fig. 3b).

Significant oscillations for DO were observed in the $FV$10 scenario at R1H ($p < 0.01$). The concentrations of DO by $FV$10 varied
Fig. 2. Modelled coverage and biomass of macrophytes for calibration (a, b) and validation (c, d) period.

Fig. 3. Modelled macrophyte coverage and biomass, DO, light attenuation $f(I)$, and epiphyton biomass in three different flow velocity scenarios (FV3, FV5, FV10).
Table 2
Major M-SAVM coefficients and constants of the calibrated model *.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Reported in literature</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( f_r )</td>
<td>fraction of production directly transferred to the root</td>
<td>0.15</td>
<td>0.15 Ji (2008)</td>
<td></td>
</tr>
<tr>
<td>( L_{0r}, L_{1r}, L_{2r} )</td>
<td>non-respiration loss rate for plant shoots, roots, and epiphytes</td>
<td>0.01</td>
<td>0.01 Ji (2008)</td>
<td>d⁻¹</td>
</tr>
<tr>
<td>( PM_s )</td>
<td>maximum growth rate under optimal conditions for plant shoots</td>
<td>0.15</td>
<td>0.1 Cerco and Moore (2001)</td>
<td>d⁻¹</td>
</tr>
<tr>
<td>( \gamma PM_s )</td>
<td>maximum growth rate under optimal conditions for epiphytes</td>
<td>0.2</td>
<td>0.065 Zhang et al. (2015)</td>
<td>d⁻¹</td>
</tr>
<tr>
<td>( \gamma KN_{half}KN_{half} )</td>
<td>half-saturation constant for nitrogen uptake from water and bed</td>
<td>1.0</td>
<td>0.13 Thursby and Harlin (1982)</td>
<td>gNm⁻¹</td>
</tr>
<tr>
<td>( \gamma KP_{half}KP_{half} )</td>
<td>half-saturation constant for phosphorus uptake from water and bed</td>
<td>0.03</td>
<td>0.02 Madden and Kemp (1996)</td>
<td>gPm⁻³</td>
</tr>
<tr>
<td>( I_{LS} )</td>
<td>maximum value for optimum light intensity for plant growth</td>
<td>90</td>
<td>20–100 Ji (2008)</td>
<td>Wm⁻²d⁻¹</td>
</tr>
<tr>
<td>( \gamma K_{Pr}, K_{Re} )</td>
<td>effect of temperature below optimal temperature on shoot production</td>
<td>0.001</td>
<td>0.001 Ji (2008)</td>
<td>C⁻²</td>
</tr>
<tr>
<td>( \gamma K_{Pr}, K_{Re} )</td>
<td>effect of temperature above optimal temperature on shoot production</td>
<td>0.001</td>
<td>0.001 Ji (2008)</td>
<td>C⁻²</td>
</tr>
<tr>
<td>( \gamma K_{O} )</td>
<td>maximum respiration for plant shoots at reference temperature</td>
<td>0.04</td>
<td>0.019 Madsen et al. (1991)</td>
<td>d⁻¹</td>
</tr>
<tr>
<td>( \gamma K_{M}, K_{M} )</td>
<td>maximum respiration for plant roots at reference temperature</td>
<td>0.015</td>
<td>0.022 Cerco and Moore (2001)</td>
<td>d⁻¹</td>
</tr>
<tr>
<td>( \gamma K_{M}, K_{M} )</td>
<td>maximum respiration for epiphytes at reference temperature</td>
<td>0.025</td>
<td>0.0005 Zhang et al. (2015)</td>
<td>d⁻¹</td>
</tr>
<tr>
<td>( \gamma K_{Re}, K_{Re} )</td>
<td>effect of temperature on plant shoots and roots respiration</td>
<td>0.001</td>
<td>0.001 Ji (2008)</td>
<td>C⁻¹</td>
</tr>
<tr>
<td>( \gamma \mu_{a} )</td>
<td>root-to-shoot transfer rate for light dependence</td>
<td>0.35</td>
<td>0.35 Zhang et al. (2015)</td>
<td>d⁻¹</td>
</tr>
<tr>
<td>( \gamma \mu_{a} )</td>
<td>half-saturation light at shoot surface</td>
<td>120</td>
<td>120 Zhang et al. (2015)</td>
<td>Wm⁻²d⁻¹</td>
</tr>
<tr>
<td>( \mu_{a} )</td>
<td>half-saturation light at shoot surface</td>
<td>0.6</td>
<td>0.5 van Nes et al. (2002); Janse et al. (2010)</td>
<td>m⁻¹</td>
</tr>
<tr>
<td>( K_{r} )</td>
<td>coefficient for epiphyte chlorophyll</td>
<td>0.04</td>
<td>0.04 Zhang et al. (2015)</td>
<td>m⁻¹mg⁻¹m²</td>
</tr>
<tr>
<td>( H_{b} )</td>
<td>the average shoot height above the bed</td>
<td>0.3</td>
<td>0.3</td>
<td>m</td>
</tr>
<tr>
<td>( \theta_{np} )</td>
<td>phosphorus to carbon ratio for plant shoots, roots, and epiphytes</td>
<td>0.167</td>
<td>0.167 Cerco and Cole (1994)</td>
<td>gN:gC</td>
</tr>
<tr>
<td>( \alpha_{Chl} )</td>
<td>carbon to chlorophyll ratio for epiphytes</td>
<td>0.12</td>
<td>0.15 Mao et al. (2009); 0.12 Zhang et al. (2015)</td>
<td>gC:mgEChl α</td>
</tr>
</tbody>
</table>

* The parameters with the symbol "*" are in the equations for \( f_{1}(N), f_{2}(T), f_{3}(D), P_{r}, R_{r}, R_{r}, \) and \( f_{3r} \), which are detailed elsewhere (Ji, 2008).

Table 3
Statistical error quantification analysis results of calibration and validation for biomass *.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>July R1</th>
<th>July R2</th>
<th>September R1</th>
<th>September R2</th>
</tr>
</thead>
<tbody>
<tr>
<td>i. Calibration period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Measured coverage (%)</td>
<td>75</td>
<td>60</td>
<td>75</td>
<td>60</td>
</tr>
<tr>
<td>Modeled coverage (%)</td>
<td>68</td>
<td>84</td>
<td>68</td>
<td>52</td>
</tr>
<tr>
<td>Absolute error</td>
<td>11.5</td>
<td>13.6</td>
<td>20.1</td>
<td></td>
</tr>
<tr>
<td>RMSE</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-RMSE (%)</td>
<td>20.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ii. Validation period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coverage of Macrophytes (%)</td>
<td>87</td>
<td>97</td>
<td>97</td>
<td>94</td>
</tr>
<tr>
<td>Modeled coverage (%)</td>
<td>86</td>
<td>97</td>
<td>97</td>
<td>94</td>
</tr>
<tr>
<td>Absolute error</td>
<td>0.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RMSE</td>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-RMSE (%)</td>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* R-RMSE = RMSE/Mean.

between 7.0 and 20.2 mg O₂ l⁻¹ in both reservoirs (Fig. 3c). In particular, some trends of a slight decline during the establishment of macrophytes were observed after which a rapid increase in the growth period was exhibited.

According to the original scenario of JanM, the light intensity limitation coefficient among macrophytes reached an average of 0.537 ± 0.158 at R1H and 0.357 ± 0.173 at R2H in OS (Fig. 3d). The FV10 scenario resulted in the highest averages among the three scenarios, with 0.627 ± 0.132 (R1H) and 0.373 ± 0.180 (R2H). The
light intensity limitation coefficient was slightly lower (~0.007) at R2H in comparison to R1H by FV10 during macrophyte decay, but was not indicative of a significant decline of biomass.

Epiphyton biomass decreased with increased FV in the scenarios. The modelled epiphyton biomass in the OS achieved maximum values of 28.9 g DM m\(^{-2}\) in R1H and 19.9 g DM m\(^{-2}\) in R2H (Fig. 3e). The FV10 scenario indicated a meaningful decline of epiphyton biomass in comparison with the OS, 63.1% and 40.2%, in R1H and R2H, respectively.

3.2. The impact of epiphyton in mitigation of macrophytes growth

A sensitivity analysis was performed to test the influence of a wide spectrum of parameter values for the epiphyton maximum growth rate (PMe). In Jankovac Reservoir, macrophyte coverage should be reduced and remain at a max of 70% of the lake area. Therefore, we designed a test to simulate the increase of epiphyton growth rates in the M-SAVM, i.e. 0.25, 0.3, and 0.4 d\(^{-1}\).

The modelled macrophyte coverage and biomass both decreased with increased epiphyton growth (PMe) in sensitivity analysis scenarios. The results show that macrophyte coverage is restricted at 61.0% in R1 and 51% in R2 comprising the highest epiphyton growth rate scenario, PMe0.4 (Fig. 4a). Similarly, the macrophyte biomass declined in PMe0.4, with maximum values of 79.5 g DM m\(^{-2}\) at R1H and 59.8 g DM m\(^{-2}\) at R2H (Fig. 4b). Results of PMe0.3 and PMe0.4 scenarios suggested that the maximum macrophyte coverage could be undermined and coverage could be below ~70% of the lake area.

3.3. Zooepiphyton assemblage and interactions with environmental parameters

The diversity of meiofauna remained similar, 30 and 25 taxa, in 2008 and 2014 respectively, with rotifers as the most diverse group. Biomass of total zooepiphyton notably increased from 2008 to 2014. Ciliates and rotifers made a prominent contribution in 2008 and nematodes and copepods in 2014 (Fig. 5). Instead of distinctive variations in zooepiphyton biomass, temporal as well as spatial (between reservoirs) oscillations were not statistically different (Mann-Whitney, \(p < 0.05\)).

Zooepiphyton was significantly and negatively affected by flow velocity. Macrophyte coverage, substrate size (considered through macrophyte DM) and biomass of epiphytic algae enhanced the biomass of zooepiphyton dominant groups (Table 4). Copepods also showed similar trends of interactions with environmental parameters, but a significantly positive relationship was revealed with dissolved oxygen concentrations among macrophytes (\(r = 0.425\)). EChl-a was significantly (\(p < 0.001\)) positively impacted by substrate size (0.760) and coverage (0.815).

4. Discussion

4.1. Medium–term alterations in studied reservoirs

The results of this modelling reveal possibilities for the regulation of submerged macrophyte growth in small and shallow reservoirs of the temperate zone. Any treatments in an ecosystem request prior preparation and selection, peculiarly in a hydro system situated in a karst area, known worldwide for its habitats, species diversity and sensitivity to anthropogenic disturbance (Williams, 2008; Buzan and Pallavicini, 2014). In spite of being a protected area, Jankovac reservoirs were subjected to sediment-drainage restoration in 2003, which resulted in a decline of macrophyte diversity. According to Razlog-Grlica and Grlica (2004), 30 macrophyte species were recorded before treatment but by the following year there were 10 fewer species, suggesting that sediment removal eliminated propagules (Hilt et al., 2006). During 2008 and 2014, we conducted comprehensive ecological research of environmental parameters and aquatic bioeocenosis, thus we were able to observe and record the possible signs of an increased trophic level (Špoljar et al., 2012a,b,d, 2014). Firstly, a notable increase in phytoplankton biomass (2.18 ± 0.57 µg l\(^{-1}\) Chl a in 2008 and 4.91 ± 2.01 µg l\(^{-1}\) Chl a in 2014) indicating a transition from an oligotrophic to a mesotrophic level. Secondly, uniform macrophyte stands dominated by Hippuris and Potamogeton, which successively increased their infestation and by 2014 occupied almost the whole reservoir bed. According to Perrow et al. (1994) and Hilt et al. (2006) monocultures of macrophyte stands indicate a higher trophic level, while a diverse macrophyte assemblage is highly preferred and better sustains the balance between bioeocenosis and nutrient. Thirdly, macroinvertebrate assemblages were present in 2008, indicating clean and not significantly altered water quality, while in 2014 pollution and a deterioration in water quality had become apparent (Špoljar et al., 2014, 2015). We presumed that in aquatic bioeocenosis macroinvertebrates were initially negatively impacted by decreased oxygen, probably due to the dissolved organic matter decomposition in the sediment (Bianchini et al., 2008). Namely, hypoxic conditions in the bottom water layer as well as in sediment, could be explained by the presence of the surrounding deciduous forest which contributes to a higher accumulation of leaf litter and decayed macrophyte fragments. Both lead to anoxic conditions, confirmed by a slight increase of phosphates and sulphates above the permisssible concentrations in the sediment (Špoljar et al., 2014). Similarly, Kuczy´nska-Kippen and Joniak (2010) in a study of mid-field and mid-forest ponds in NW Poland, also pointed out the significant impact of the catchment area on limnological parameters and aquatic bioeocenoses.

4.2. Interactions among flow velocity, macrophytes and epiphyton

The main intention of this study was to invent and suggest a treatment against macrophyte overgrowth and anoxic conditions that is less invasive than sediment removal, and to prevent the occurrence of eutrophication processes in a particular karst situated flow–through system. Simultaneously, we combined an interpretation of ecological interactions from the results of epiphyton bioeocenotic analysis and modelling simulations. The application of such modelling can offer solutions as well as predictions for lake restoration. Numerous approaches have been developed to reduce eutrophication in water bodies, i.e. EFDC (Hamrick, 1992), WASP (Wool et al., 2002) together with models designed to predict and manage macrophyte growth, i.e., SAVM (Cerco and Moore, 2001; Jin and Ji, 2013) and the modified SAVM by Zhang et al. (2015, 2016).

In the JanM simulation we included flow velocity with the aim to obtain data anticipated in the regulation of macrophyte cover and biomass. Commonly, the diversity and density of macrophytes are promoted at low to medium and suppressed by increased flow velocities (Madsen et al., 2001; Franklin et al., 2008). Recently, hydrological treatments in lake restoration based on macrophyte regulation, have been presented as a result of water level fluctuations (Moss et al., 1997; Bekioglu et al., 2006; Zhang et al., 2015), hypolimnetic withdrawal of nutrient rich water (McComas, 2003), or dilution of high nutrient concentration, by adding nutrient-poor water, reducing algal growth by flushing faster than they can reproduce (Cooke et al., 1993). The modelled results of interactions among macrophytes, flow velocity, epiphyton and environmental parameters may be explained as follows: firstly, higher flow velocity probably flushes epiphyton, thus enables light supply and increases macrophyte coverage and biomass; secondly, oxy-
gen concentrations are increased by the photosynthetic activity of macrophytes and mixing is enhanced as a result of higher flow velocity and the inflow of highly oxygenated water; thirdly, aeration enhances the mineralisation of organic matter and contributes to phosphorous precipitation, its uptake by macrophytes and prevention of algal bloom. Asaeda and Son (2000) experimentally established flow velocity as a key factor in epiphyton erosion, and Wilby et al. (1998), further investigating this interaction, concluded that higher flow velocities limit epiphyton and enhance macrophyte growth. Moreover, the resilience of Hippuris to higher flow velocity could be explained by their flexible but strong stem, and it is likely that this species is more restricted by a low trophic level and higher pH than by flow velocity. The extent of submerged macrophyte coverage is also important in nutrient reduction efforts and evaluating the success of water quality management (Jin and Ji, 2013; Zhang et al., 2016). In the Yuqiao Reservoir, NE China, Zhang et al. (2015) suggested that the decline in nutrient concentrations was due to uptake of Potamogeton crispus growth during periods of exponential growth. Simulations

Fig. 5. Spatio-temporal oscillations of dominant groups and total zooepiphyton on the studied sampling points.

Table 4
Spearman rank correlations \( r; p < 0.05 \) among main groups and total zooepiphyton against environmental parameters.

<table>
<thead>
<tr>
<th></th>
<th>Cilophora</th>
<th>Rotifera</th>
<th>Nematoda</th>
<th>Gastrotricha</th>
<th>Copepoda</th>
<th>Total Zooepiphyton</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macrophytes coverage</td>
<td>0.659**</td>
<td>0.696*</td>
<td>0.227</td>
<td>0.353</td>
<td>0.024</td>
<td>0.641</td>
</tr>
<tr>
<td>EChl a (( \mu \text{g g}^{-1} \text{ DM} ))</td>
<td>0.748**</td>
<td>0.898***</td>
<td>0.210</td>
<td>0.549*</td>
<td>0.235</td>
<td>0.797***</td>
</tr>
<tr>
<td>Macrophyte DM (g)</td>
<td>0.679*</td>
<td>0.771***</td>
<td>0.335</td>
<td>0.491*</td>
<td>0.383</td>
<td>0.813***</td>
</tr>
</tbody>
</table>

\* \( p < 0.05 \), 
\* \( p < 0.001 \).
\* \( p < 0.0001 \).

with increased flow velocity reinforce mixing and dissolved oxygen concentrations through the whole water column in shallow reservoirs, as previously confirmed by Chu and Jirka (2003) and Demars and Manson (2013). The turbulence caused by macrophyte stands could positively impact oxygen supplies and mineralisation in the bottom water layer and sediment (Huai et al., 2010). In laboratory conditions it was confirmed that reaeration rates are also enhanced by macrophyte complexity (Moog and Jirka, 1999). Moreover, the relationship between flow velocity and epiphytic biomass implies inverse interactions, i.e., non-filamentous algae were markedly and negatively affected in comparison to filamentous algae at higher flow velocity (Asaeda and Son, 2000), and there is an increase in epiphyton biomass at lower flow velocity (Rovira et al., 2016). Both effects are pronounced through time, and are in compliance with our results, where modelled and field assessment indicated water movement as the main stressor to have a significant impact on biomass decrease of algae, small protozoans and epiphytic meiofauna. Different ecological protozoan and meiofaunal groups responded differently to the oscillation of flow velocity. Due to higher flow velocities, observed in 2008, small-bodied and r-strategist organisms (protozoans, rotifers) developed higher abundances (Špoljar et al., 2012a,b). Additionally, most of the rotifers present were microfilter-feeders that can consume the large amounts of suspended organic matter transported in the water of higher flow velocity (Duggan, 2001; Dražina et al., 2013), which brings them a greater amount of that food type. Nematodes prefer long periods of habitat stability, which prevailed in 2014 (Majdi et al., 2012). They are a heterogeneous trophic group (predators, bacterivores, algivores and omnivores) and thus, in a thick epiphyton layer they can utilize different food sources. Overall, results collected in Jankovac reservoirs indicated that the biomass of ciliates and rotifers, as small-bodied attached organisms highly dependent on microhabitat properties, was strongly and significantly affected by macrophyte coverage and substrate complexity (Špoljar et al., 2012c; Kuczyńska-Kippen and Basińska, 2014).
4.3. Interactions among light, macrophytes and epiphyton

Macrophyte coverage and growth can be controlled by light intensity, water turbidity, epiphytic biofilm as well as snail grazers upon epiphyton on macrophyte stems (Köhler et al., 2010; Žebek and Szymańska, 2014). Submersed macrophyte stands retained suspended particles, increased light attenuation and showed downstream transparency, i.e. light supply (Köhler et al., 2010). Simulations in our study reveal a significant relationship between the biomass of macrophytes and epiphyton (Zhang et al., 2015). Higher epiphyton growth implies a negative effect on macrophytes due to the restriction of light availability and macrophyte photosynthesis (Franklin et al., 2008). Rich epiphyton could result higher nutrient concentrations, as confirmed in standing water bodies (Hill and Harvey, 1990). In the lentic part of running waters, short water residence time promotes nutrient increase and the growth of benthic and epiphytic algae, while long residence time leads to phytoplankton turbidity (Hilton et al., 2006).

5. Conclusions

The results of this modelling demonstrated that hydraulic simulations could be effective in the alteration of transparent and turbid states i.e. in the balance between macrophytes and epiphyton, especially in small and shallow water bodies. The model for Jankovac reservoirs (JanM) is the result of a combination of the integrated Water Quality Model (WQM) and the Submerged Aquatic Vegetation Model (SAVM). These reservoirs are small hydrosystems in an isolated karst and protected area, so common hydrological restoration methods, i.e. water pumps, should be avoided. The adjusted methods should be able to achieve the most sustainable option, fit within the scope of esthetical value of this landscape and protected area. Increased flow velocity could have a positive impact on macrophytes and accompanying epiphyton assemblages. Thus, we are suggesting some less invasive and debilitating restoration methods: cutting macrophytes to form a mosaic community of macrophytes and open water would increase flow velocity. Increased flow velocity, habitat complexity and biodiversity would enable better oxygen supply and mineralization in the sediment through the constant horizontal and vertical mixing of these small and shallow reservoirs. The presented results offer encouragement for the application of hydraulic management in lake restoration, and such application would achieve a favourable quality of sediment, water column and aquatic biocenosis.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.12.038.

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