Can nutrient pathways and biotic interactions control eutrophication in riverine ecosystems? Evidence from a model driven mesocosm experiment

Christoph G. Jäger[*], Jeske Hagemann, Dietrich Borchardt

Department of Aquatic Ecosystems Analysis and Management, Helmholtz Centre for Environmental Research — UFZ, Magdeburg, Germany

ABSTRACT

Ecological theory predicts that the relative importance of benthic to planktonic primary production usually changes along the rivers' continuum from a predomination of benthic algae in lower stream orders to a predomination of planktonic algae at higher orders. Underlying mechanisms driving the interaction between algae in these habitats, its controlling factors and consequences for riverine ecosystems are, however, only partly understood. We present a mechanistic analysis of the governing ecological processes using a simplified, numerical model and examine how abiotic factors and biotic interactions influence benthic and planktonic algae by changing resource competition. We compare the outcome of the model with the results of a factorial mesocosm experiment mimicking the parameter spaces of the model. The results show a remarkable similarity with regard to the temporal development of benthic and pelagic algal biomass and shifting dominance patterns. In particular we analyse the effects of the pathways of nutrient supply (upwelling from the hyporheic zone, direct supply to the surface water, or via both pathways) and grazing in a gradient of river depths. Our results show that detachment of benthic algae, sinking of planktonic algae and the pathway of nutrient supply are key processes determining the respective algal biomass distributions particularly in shallow and intermediate deep systems. Increasing nutrient supply increases algal biomasses, but does not change the general pattern of the interactions. Decreasing light supply decreases the dominance of planktonic algae, but increases dissolved nutrients. At intermediate to high grazing rates algal biomass can be controlled by grazers, but however, at high grazing rates, dissolved nutrients accumulate in the surface water. Our results indicate that nutrient pathways, resource competition and internal control by grazing need to be considered explicitly for the understanding and explanation of eutrophication phenomena in riverine ecosystems. As a consequence, ecologically effective eutrophication management of running water systems has to go beyond the control of nutrient emissions or the achievement of limiting threshold values in the receiving waters, but requires the consideration of the nutrient pathways (surface water versus groundwater) and the shifting biological controls from lower to higher order stream ecosystems.

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1. Introduction

In aquatic ecosystems two structural different compartments exist, the benthic habitat, where algae are attached to the bottom, and the surface water, in which algae are suspended as phytoplankton. Across the boundary between these compartments algae compete for two different types of essential resources, light and nutrients (Jäger and Diehl, 2014), but also subsidise each other by migration between the habitats (Istvànovic and Honti, 2011; Stevenson and Peterson, 1991; Tekwani et al., 2013). While these biotic interactions modify the respective importance of primary producers in the specific compartments, abiotic conditions determining the light and nutrient availability provide the general setting and boundaries for the extent of possible interactions. For example, low light supply (mediated by low light intensity, high turbidity, dark water colour, or deep water depth) and elevated nutrient supply generally favour the predominance of planktonic algae (Jäger and Diehl, 2014). Moreover, sinking losses of planktonic algae are inversely related to water depth (Reynolds et al., 1990;

* Corresponding author.
E-mail addresses: christoph.jaeger@ufz.de (C.G. Jäger), jeske.hagemann@ufz.de (J. Hagemann), dietrich.borchardt@ufz.de (D. Borchardt).

Visser et al., 1996). Consequently, there is usually a transition from shallow upstream reaches predominated by benthic algae to deep downstream reaches predominated by phytoplankton along the longitudinal gradient from headwaters to estuaries (Vannote et al., 1980).

The competition between benthic and planktonic algae is particularly interesting, when nutrients are supplied by upwelling from the bottom of the system. Then, benthic and planktonic algae face two opposing resource gradients and the general principle of their competition is that planktonic algae shade the benthic habitat, but benthic algae in turn intercept the nutrient flux to the surface water (Hansson, 1988; Jäger and Diehl, 2014). It has been shown, for example, that benthic algae remove 80% of the nitrogen from the upwelling water (Henry and Fisher, 2003) and, as a consequence, the biomass of benthic algae is higher in zones where nutrient rich water from the interstitial is upwelling than in zones of downwelling or no water exchange with the interstitial (Valett et al., 1994; Wyatt et al., 2008). Moreover, intense grazing on phytoplankton reduced the shading of benthic algae and increased the populations in the benthic food web located at about 1 m water depth in the Hudson River (Strayer et al., 2008).

However, when nutrients are supplied directly to the surface water, they bypass the nutrient interception of the benthic algae and should increase production and biomass of planktonic algae (cf. Jäger and Diehl, 2014), which, in turn, can be a major source for hypoxia at nutrient replete conditions (Mallin et al., 2006). Consequently, the pathway and magnitude of nutrient supply may control the degree of eutrophication, which can for example lead to increasing algal biomasses in one or both habitats, taste and odour problems of the water caused by exudates, extreme fluctuations of dissolved oxygen concentrations and pH, and an increased probability for fish kills and other biota caused by the decay of massive algal blooms and subsequent hypoxia (Smith et al., 1999). The biomass production of algae, however, can be reduced and controlled by grazing in both compartments. Grazers have been shown to have a high impact on the biomass of benthic algae (Hill et al., 1995; Hillebrand, 2009; Kjeldsen, 1996) and to affect or even completely control the biomass of phytoplankton (Brown et al., 2005; Caraco et al., 2006; Kathol et al., 2011).

Generalising analyses of the underlying mechanisms in riverine ecology can be very difficult, because of the inherent temporal and spatial heterogeneity of running-water systems. However, analyses of the (temporal and spatial) attractor of a system and its dependency from identifiable processes can provide the fundamental basis for a more mechanistic understanding, which subsequently might be applied to more realistic scenarios (e.g. Speirs and Gurney, 2001). Jäger and Borchardt (submitted) showed recently, that such spatial attractors can be analysed by a simplified (ODE) version of a mathematical model, which simulates the biomasses benthic and planktonic algae and nutrient concentration in riverine ecosystems. Moreover, they showed that systems can be well described by their spatial attractors, when environmental conditions are only slowly and gradually changing (Jäger and Borchardt, submitted).

In this study we analyse how biotic and abiotic factors influence the interactions between benthic and planktonic algae and investigate their relevance for mechanistically explaining eutrophication in riverine ecosystems with the aim to provide an advanced science base for measures of eutrophication control. To this end, we use a mechanistic mathematical model, which is similar to the model recently published by Jäger and Borchardt (submitted). We use a spatial (PDE) variant of the model to give an example of the full, longitudinal river gradient and a simplified (ODE) variant to analyse the effects of specific environmental parameter and ecosystem processes. In particular we analyse: (i) the influence of the pathways of nutrient supply. To get a fundamental understanding of the

systems we analyse boundary cases of natural systems in which we assume that nutrients are continuously supplied from the bottom, directly to the surface water, or via both pathways. To test if the assumptions of the model are also valid for natural communities, we compare the model results with the results of a mesocosm experiment using a factorial design of the control variables. (ii) The influence of emigration of benthic algae and sinking of planktonic algae, (iii) the magnitude of incoming light and nutrient supply, and (iv) the influence of selective grazing of benthic or planktonic algae. All model analyses were conducted in a gradient of river depths to evaluate the different impact on the systems when they are predominated by benthic algae at shallow depths, by phytoplankton at deep depths, or can be predominated by algae in both habitats.

2. Material and methods

2.1. Model structure

We assume a uniform riverine ecosystem along the longitudinal dimension x, which comprises two vertically well-mixed habitats: a surface water body, ranging from the surface (with $z = 0$) to the bottom (with $z = z_{max}$), and a benthic layer below, with thickness of $z_{bl} = 1$ mm (note that the thickness of the benthic layer has no effect on the model outcomes). While the surface water moves with flow velocity v and is longitudinally mixed with turbulent diffusion coefficient D, the benthic compartment does not move or mix along x-direction. Within the ecosystem there is one algal taxon, which can grow in both habitats, as a benthic form within a thin biofilm (B, calculated per area), or a planktonic form (A, calculated per volume). Their dynamics is described as:

$$\frac{\partial A}{\partial t} = \frac{A}{z_{max}} \int_0^{z_{max}} P_A(I(z), R_{sw})dz - l_A \cdot A - \frac{s_A}{z_{max}}A - \frac{a_{is} + a_{sw}}{z_{max}}A$$

$$+ \frac{r_e}{z_{max}}B - v\frac{\partial A}{\partial x} + D\frac{\partial^2 A}{\partial x^2} \qquad (1)$$

$$\frac{\partial B}{\partial t} = B \cdot P_B(I_{zmax}, R_{bl}, B_K) - l_B \cdot B - r_e \cdot B + \beta \cdot s_A \cdot A \qquad (2)$$

All state variables and parameters are defined with units in Table 1. Algal population produce new biomass at gross production rate P_A in the surface water and at P_B in the benthic layer, and suffer grazing and maintenance losses at rates of l_A and l_B in the specific habitats, respectively. Planktonic algae sink out of the surface water at velocity s_A and are diluted by incoming water from the interstitial layer at rate a_{is} and from surface runoff at rate a_{sw}. The amount β of sinking algae can settle in the benthic layer and algae from the benthic layer detach and emigrate to the surface water at rate r_e. Algal production is co-limited by light (I) and one mineral nutrient, which we assume to be phosphorus (R_{sw} in the surface water and R_{bl} in the benthic layer). Areal benthic primary production is additionally limited by space with a carrying capacity of B_K:

$$P_B(I_{zmax}, R_{bl}, B_K) = p\frac{I_{zmax}}{I_{zmax} + h}\frac{R_{bl}}{R_{bl} + m}\left(1 - \frac{B}{B_K}\right) \qquad (3)$$

Because we assume the surface water to be vertically well-mixed, depth integrated algal production of phytoplankton can then be solved following (Huisman and Weissing, 1995) as:

$$\int_0^{z_{max}} P_A(I(z), R_{sw})dz = \frac{p}{k \cdot A + k_{bg}}\log\left(\frac{h + I_0}{h + I_{zmax}}\right)\frac{R_{sw}}{R_{sw} + m} \qquad (4)$$

Table 1
Definition, units and values of parameters and variables used for the general model analyses (Model) and for the adjusted model compared with the results of the experiment (Exp.). The model parameter are default parameter values. Deviations are specified at the specific figures.

Parameter	Value		Definition & Unit
	Model	Exp.	
a_{bl}	0.1		Nutrient exchange rate between benthic layer and surface water [m day^{-1}]
a_{is}	0	0	Nutrient exchange rate between interstitial water and benthic boundary layer [m day^{-1}]
	0.05	0.005	
	0.1		
a_{sw}	0.1	0.005	Nutrient influx from surface runoff [m day^{-1}]
	0.05	0	
	0		
B_K	15,000		Carrying capacity of benthic algae [mg C m^{-2}]
c	0.02	0.0035	Phosphorus to carbon quota of algae [mg P mg C^{-1}]
D	10	–	Turbulent diffusion coefficient [m^2 s^{-1}]
h	25		Half saturation constant for light-limited production [μmol photons m^{-2} s^{-1}]
I_0	300	100	Light intensity at the surface [μmol photons m^{-2} s^{-1}]
k	0.0003		Light attenuation coefficient of algae [m^2 mg C^{-1}]
k_{bg}	2.5		Background light attenuation coefficient [m^{-1}]
l_A	0.1	0.025	Loss rate of phytoplankton [day^{-1}]
l_B	0.1	0.025	Loss rate of benthic algae [day^{-1}]
m	5		Half saturation constant for nutrient-limited production [mg P m^{-3}]
p	1		Maximum production rate [day^{-1}]
r_e	0.01	0.005	Emigration rate of benthic algae [day^{-1}]
R_{in}	200	30	Concentration of dissolved nutrients in the influx [mg P m^{-3}]
		100	
s_A	0.4	0.002	Sinking velocity of phytoplankton algae [m day^{-1}]
v	0.1	–	Stream flow [m s^{-1}]
z_{bl}	0.001		Depth of the benthic layer [m]
z_{max}	0.1–10	0.4	Depth of the surface water [m]
β	0.01	1	Amount of algae immigrating to the benthic layer
ε	0.1		Recycling coefficient of algae
A			Biomass of algae in the surface water [mg C m^{-3}]
B			Biomass of algae in the benthic layer [mg C m^{-2}]
R_{bl}			Concentration of dissolved nutrients in the benthic layer [mg P m^{-3}]
R_{sw}			Concentration of dissolved nutrients in the surface water [mg P m^{-3}]
x			Longitudinal dimension of the river [km]

The vertical light gradient follows Lambert-Beer's law with light intensities I_0 at the surface and $I_{z_{max}}$ at the bottom of the surface water body. Light is vertically attenuated by the biomass of phytoplankton with specific attenuation coefficient k and by non-algal components with coefficient k_{bg}:

$$I_{z_{max}} = I_0 e^{-(k \cdot A + k_{bg}) z_{max}} \qquad (5)$$

The nutrient dynamics in the surface water (R_{sw}) and benthic layer (R_{bl}) are described as:

$$\frac{\partial R_{sw}}{\partial t} = \frac{a_{bl}}{z_{max}}(R_{bl} - R_{sw}) + \frac{a_{sw}}{z_{max}}(R_{in} - R_{sw})$$
$$- \frac{c \cdot A}{z_{max}} \int_0^{z_{max}} P_A(I(z), R_{sw}) dz + \varepsilon \cdot c \cdot l_A \cdot A - v \frac{\partial R_{sw}}{\partial x} + D \frac{\partial^2 R_{sw}}{\partial x^2}$$
$$\qquad (6)$$

$$\frac{\partial R_{bl}}{\partial t} = \frac{a_{is}}{z_{bl}}(R_{in} - R_{bl}) - \frac{a_{bl}}{z_{bl}}(R_{bl} - R_{sw}) - \frac{c \cdot B}{z_{bl}} P_B(I_{zmax}, R_{bl}, B_K)$$
$$+ \varepsilon \cdot c \cdot l_B \cdot B$$
$$\qquad (7)$$

The concentration of dissolved nutrients in the benthic layer (R_{bl}) is affected by an influx of nutrients from an infinite pool in the interstitial water with concentration R_{in} at rate a_{is} and by an exchange of nutrients with the surface water at rate a_{bl}. The concentration of nutrients in the surface water (R_{sw}) is affected by the exchange with the benthic layer and by a direct supply of nutrients to the surface water with concentration R_{in} at rate a_{sw}. Dissolved nutrients are taken up by algal cells from the respective habitat in proportion to their production assuming a constant algal nutrient to carbon ratio c, and, in turn, the amount ε of nutrients stored inside grazed algal cells becomes instantly recycled by e.g. sloppy feeding. In our analyses we investigate the effects of different pathways of nutrient supply by assuming that nutrients are spatial and temporal uniformly supplied either only from the bottom via interstitial water ($a_{is} = 0.1$ m day^{-1}, $a_{sw} = 0$ m day^{-1}), only to the top directly into the surface water ($a_{is} = 0$ m day^{-1}, $a_{sw} = 0.1$ m day^{-1}) or equally from the bottom and to the top ($a_{is} = 0.05$ m day^{-1}, $a_{sw} = 0.05$ m day^{-1}).

The main focus of this study is set on the spatial equilibrium values and how they are influenced by biotic and abiotic factors. Therefore, we used a simplified variant of the model for most analyses, in which the PDEs (1) and (6) were transferred to ODEs. The full spatial model was only used to give a complete overview of the model behaviour in Fig. 2. For these analyses, the boundary conditions were set to fixed concentrations of planktonic algae and nutrients in the surface water ($A = 10$, $R_{sw} = 5$) at x = 0 mimicking a pristine groundwater source and convective fluxes at the mouth. We run the model until temporal equilibrium using COMSOL, version 3.5a with a space grid size of 100 m along x- direction.

2.2. Experimental design and analyses

To test the evidence of theoretical predictions, we analysed the effects of the nutrient pathway and magnitude of nutrient supply in mesocosm experiments with natural algal communities in a factorial design. We used circular flumes with an outer diameter of 0.5 m and an inner diameter of 0.2 m, which consisted of a "hyporheic chamber" with the height of 1.5 cm, a benthic layer with

a perforated metal plate covered with a net of 1 μm pore size, and a surface water chamber with the height of 0.5 m. The surface water was mixed by metal combs and the groundwater chamber by magnet balls with 9.6 rotations per minute, resulting in a water speed of 0.1 m s^{-1} at the inner end and 0.25 m s^{-1} at the outer end of the flume. We used water from the river Holtemme, upstream of the city of Wernigerode (51°49′04.3″N, 10°43′43.9″E), Germany, as inoculum. At this location the river Holtemme has an average discharge of 0.34 m^3 s^{-1} and is almost free of anthropogenic impacts (Wollschlaeger et al., 2016), with low background phosphorus and nitrogen concentrations (concentrations of soluble reactive phosphorus < 3 mg P m^{-3} and nitrate = 305 mg N m^{-3} at the start of the experiment), as the upstream area is located in the Harz National Park. Before the experiment, the flumes were filled to a height of 0.1 m with 100 μm pre-filtered water for two weeks, to allow the benthic algae to colonise the benthic layer. The light intensity during the colonisation phase and the experiment was fixed at 100 μmol photons m^{-2} s^{-1} at the surface of the water level with a light-dark cycle of 12:12 h. At the start of the experiment the flumes were carefully drained and re-filled up to an outlet at the height of 0.4 m with fresh, 100 μm pre-filtered water. As medium for the experiment we used ultra-filtered river water (0.45 μm) and added phosphorus to a final concentration of 30 mg P m^{-3} for the low nutrient treatment and of 100 mg P m^{-3} for the high nutrient treatment. To ensure that phosphorus is the only limiting nutrient, we also added nitrogen to a final concentration of 3000 mg N m^{-3} (i.e. a molar relation of N:P of 221:1 and 66:1 in the low and high nutrient treatment, respectively). The medium was supplied either to the hyporheic chamber or directly to the surface water with a rate of 0.005 m day^{-1}. The experiment was conducted in a full factorial design with three replicates resulting in 12 mesocosms. The experiment was conducted in a climate room at 15° C ($\pm$1°) for five weeks from 14. May until 18. June 2014.

The mesocosms were sampled weekly for chlorophyll a using an AlgaeTorch for phytoplankton and a BenthoTorch for benthic biomass (both bbe moldaenke GmbH, Schwentinetal, Germany), particular organic carbon (POC) of plankton and benthos, using high-temperature combustion (Elementar Vario cube; Elementar Analsensysteme GmbH, Hanau, Germany) after filtration on precombusted glass fibre filters (GF/F, Whatman), and total phosphorus (TP) of the surface water, using the ammonium molybdate spectrometric method (DIN EN ISO 6878, 2004).

3. Results

3.1. Comparison of experiment and model

For the comparison of the experimental results and the model predictions we used the default parameter values mentioned above, but had to adjust depth, nutrient concentrations and influx rates, and light intensity according to the experimental set-up. Furthermore, we adjusted the phosphorus to carbon ratio of algae to the results of the experiment. Because the losses in the experiment were only driven by maintenance and micrograzing we reduced the loss rate of algae by a factor of four. We used an emigration rate of benthic algae which gave a good fit with the experimental results (half of its default value). Planktonic algae were not able to sink out of the water column; however, we assumed that a fraction of their population can settle in the benthic habitat by setting β to 1. Subsequently, we adjusted their sinking velocity to obtain equal migration losses in both habitats ($s_A/z_{max} = 0.005$).

Although we did no parameter calibration procedure, the model simulations show a remarkable similarity to the experimental results (Fig. 1). The only major difference can be seen for the benthic

carbon biomass when nutrients are supplied directly to the surface water (green lines). For these treatments the results of the experiment were higher than expected from the model. Comparing the model results with the biomass of chlorophyll a in the benthic layer, the qualitative pattern fits very well again. A reason for that deviation of the pattern between carbon biomass and biomass of chlorophyll a or model results might be that the bacteria biomass or extracellular carbon in the benthic layer was elevated when nutrients were supplied from the top.

3.2. Pathways of nutrient supply in the full spatial model

In shallow systems (0.3 m) algal biomass and production are predominated by benthic algae (i.e. low biomass and proportional production of planktonic algae, high biomass of benthic algae, Fig. 2a, b, f). Nutrient influx from the bottom supports the highest total production and biomass of benthic algae, which intercept the nutrient flux to the surface water most efficiently (Fig. 2b–e). Consequently, the concentration of dissolved and total nutrients in the surface water are highly reduced when nutrients are supplied from the bottom compared to when they are supplied directly to the surface water (87× and 19× lower at spatial equilibrium, respectively, Fig. 2c and d). There are only weak longitudinal gradients and spatial equilibrium values are reached within short distance (<100 km) after the source (Fig. 2).

At intermediate river depth (1.0 m) algae can grow efficiently in both habitats. Although the pathway of nutrient supply has almost no effect on total production at spatial equilibrium, it has enormous impact on specific algal biomasses and specific production (Fig. 2g, h, k, l); the system can be predominated by either benthic or planktonic algae. When nutrients are supplied from the bottom, benthic algae predominate and intercept the nutrient supply for planktonic algae, when nutrients are supplied to the surface water planktonic algae build up high biomass and shade the benthic habitat (Fig. 2g–l). The concentration of dissolved and total nutrients in the surface water at spatial equilibrium are 18× and 9× lower when nutrients are supplied from the bottom compared to when they are supplied directly to the surface water, respectively (Fig. 2i and j). When nutrients are supplied from the bottom, spatial gradients are weak and equilibrium is reached within short distance (<100 km). When nutrients are supplied directly to the surface water, planktonic algae take about 300 km to reach spatial equilibrium, resulting in higher biomass of benthic algae and higher concentration of nutrients in the upstream reaches (Fig. 2g–l).

In deep rivers (2.0 m) the system is predominated by planktonic algae (Fig. 2m, n, r). Because the system is mainly limited by light, there is only weak influence of the pathway of nutrient supply, but the total influx of nutrients to the surface water is slightly reduced when nutrients are supplied from the bottom because they have to diffuse through an additional habitat (Fig. 2m–r). The low light availability reduces specific production rate per biomass (not total production) when compared to shallower systems and algal biomass takes more time (distance) to reach spatial equilibrium (Fig. 2m). Consequently, there is only a low concentration of algal biomass in the first 250 km but a high concentration of dissolved nutrients, followed by a peak of biomass at about 500 km, until algal biomass reaches spatial equilibrium after 750 km (Fig. 2m–r).

3.3. Detachment, sinking, and quantity of nutrient and light supply

Without immigration of detaching benthic algae a population of sinking planktonic algae cannot persist at shallow water depth and, consequently, detaching benthic algae should be the main source of planktonic algae in shallow systems (Fig. 3a, e). In turn the low
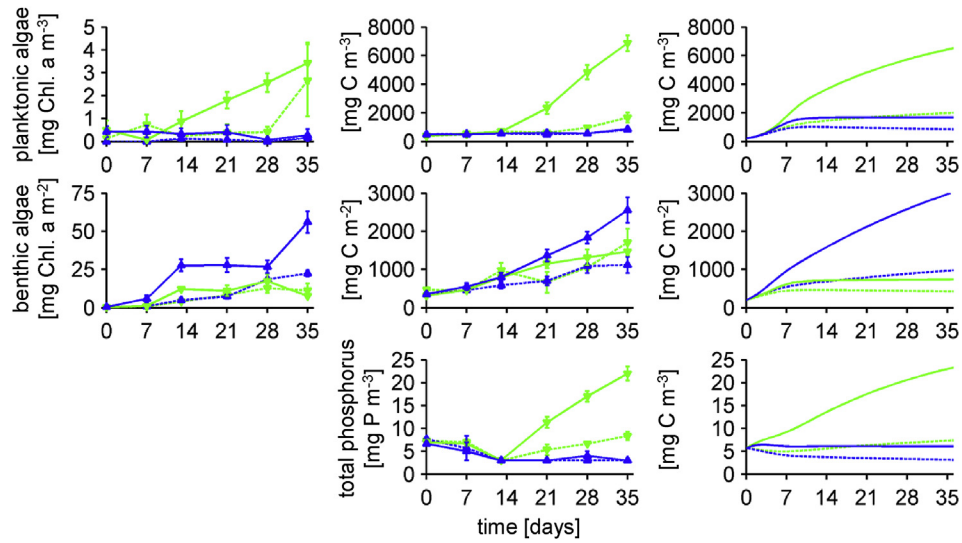
Fig. 1. Comparison of the temporal dynamics of the experiment (left and middle column) and the model (right column). Effects of the way of nutrient influx (line colours: blue = bottom, green = top) and nutrient concentration (full lines: 100 mg P m^{-3}, dashed lines: 30 mg P m^{-3}) on: concentration of planktonic algae, biomass of benthic algae, and total nutrients (TP) in the surface water. The results from the experiments for algal biomass are shown in chlorophyll a and POC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
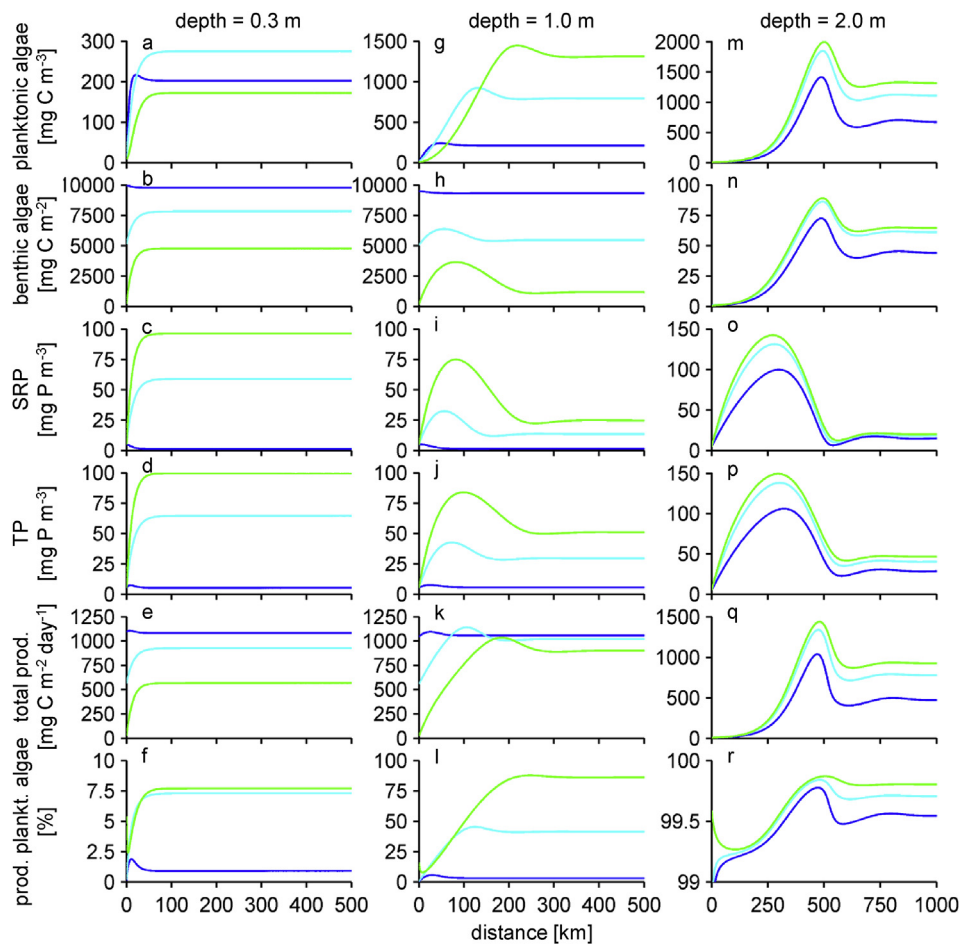
Fig. 2. Model results of the full spatial model: effects of the way of nutrient influx (line colours: blue = bottom, green = top, cyan = bottom & top) and river channel depth (see caption on top) along a longitudinal river gradient on: concentration of planktonic algae, biomass of benthic algae, concentration of dissolved nutrients (SRP) and total nutrients (TP) in the surface water, total algal production and proportional production of planktonic algae. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
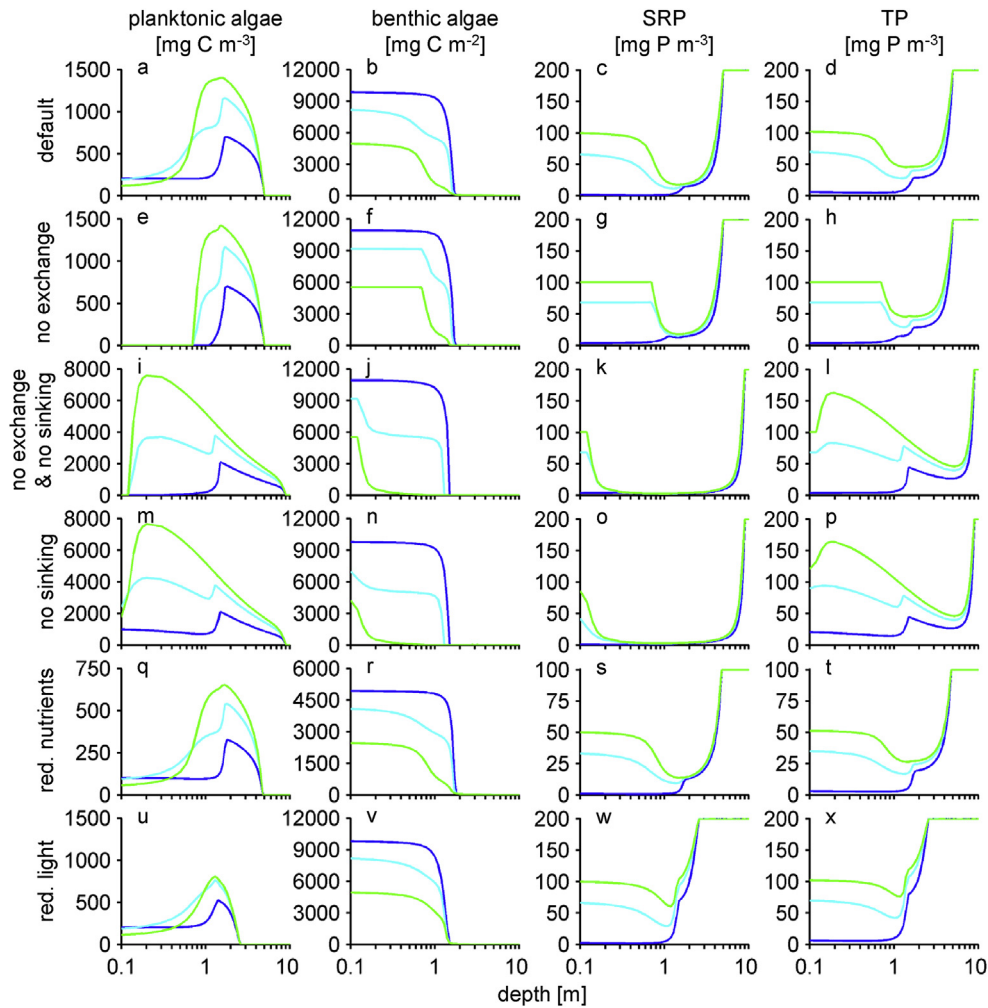
Fig. 3. Results of the spatial equilibrium values of the simplified model: effects of the way of nutrient influx (line colours: blue = bottom, green = top, cyan = bottom & top) in a gradient of river channel depths on concentration of planktonic algae, biomass of benthic algae, concentration of dissolved nutrients (SRP) and total nutrients (TP) in the surface water, for systems with, default values (first row), no exchange of algae between habitats (r_e & $\beta = 0$) (second row), no exchange between habitats and no sinking of planktonic algae (r_e & $s_A = 0$) (third row), no sinking of planktonic algae ($s_A = 0$) (fourth row), reduced nutrient concentration (100 mg P m^{-3}) (fifth row), and reduced incoming light intensity (150 μmol photons m^{-2} s^{-1}) (sixth row). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

biomass of benthic algae in deep systems is build up mainly by sinking planktonic algae (Fig. 3b, f). When nutrients are supplied only from the bottom the depths-area where algae can coexist in both habitats without exchange is very small (from 1.2 to 1.7 m river depth), the coexistence area is wider when nutrients are supplied to the surface water (0.8—1.5 m) and widest when nutrients are supplied to both habitats (0.8—1.6 m) (Fig. 3e and f). However, the competitive predominance of benthic algae in shallow systems decreases and the area of coexistence increases when planktonic algae do not suffer from sinking losses as long as (parts) of the nutrients are supplied directly to the surface water (Fig. 3i, j, m, n). Moreover, the reduction of sinking losses increases efficiently the biomass of phytoplankton and, consequently, the concentration of total nutrients in the surface water, particularly at low to intermediate river depths (Fig. 3i—p). Without sinking losses also the maximum depth at which planktonic algae can persist within the system increases from 5.0 to 9.0 m (Fig. 3i, m).

Decreasing nutrient concentration in the influx decreases the biomasses of both algae and the concentration of nutrients in the systems, but does not change the overall qualitative pattern at spatial equilibrium (compare Fig. 3 a—d with q-t, note: nutrient concentration and scales of panels q—t are half of a-d).

Decreasing light intensity increases the light limitation of algal production particularly at intermediate and deep river systems. Consequently, the impact on shallow systems is rather small (Fig. 3u—x). At intermediate depths increasing light limitation reduces the biomass of planktonic algae, when nutrients are at least partly supplied directly to the surface water (Fig. 3a, u). Interestingly, then the effect of reduced shading by planktonic algae is higher than the effect of reduced incoming light intensity and the biomass of benthic algae increases (Fig. 3b, v). The depth beyond which no algal production is possible decreases with decreasing light intensity to 2.5 m. Over a wide range of depths (from about 0.5 to 5 m) decreasing light availability increases the concentration of nutrients within the surface water (Fig. 3 c, d, w, x).

3.4. Effects of algal grazing

Generally, increasing grazing on algae in one habitat, results in decreasing biomass of the respective algae. This effect, however, is rather weak, when the systems are usually predominated by algae in the other habitat, i.e. the magnitude of planktonic grazing has only weak effects at shallow water depth, particularly when nutrients are supplied from the bottom, and the magnitude of benthic

grazing has only weak effects at deep water depths, particularly when nutrients are supplied to the top (Figs. 4 and 5). In shallow to intermediate deep systems benthic production and, as a consequence, nutrient retention in the benthic habitat is low at low grazing rates, because benthic algae are close to their carrying capacity, and at high grazing rates, because the biomass of benthic algae is strongly reduced (Fig. 4d–f and m-o). The characteristic of this pattern decreases with increasing depth and with increasing nutrient supply directly to the surface water (Fig. 4d–f and e-q). At shallow water depth this results in inverse-unimodal concentration of dissolved and total nutrients along benthic grazing rates (Fig. 4g–l). At intermediate water depths, when nutrients are (partly) supplied from the bottom, planktonic algae can benefit from the increased nutrient fluxes to the surface water at low and high grazing rates (Fig. 4 a, b). Therefore it is possible that one specific system can be dominated by algae in both habitats at low grazing rates, benthic algae can predominate at intermediate grazing rates, or planktonic algae can predominate at high grazing rates (Fig. 4 a, b, d, e). The total losses of benthic biomass to the grazers follow mainly benthic production (Fig. 4m–r).

In intermediate to deep systems phytoplankton biomass, production, and, consequently, nutrient uptake stay rather constant over a wide gradient from low to intermediate or high grazing rates (Fig. 5a–c, g-o). With a further increase of the grazing rate, algal biomass, production, and nutrient uptake decrease rapidly (Fig. 5a–c, g-o). The grazing rates, at which this decline appears, decrease with increasing depth (Fig. 5). The highest biomass of planktonic algae is used by the grazers around the grazing rates where the decline appears (Fig. 4p–r). At higher grazing rates benthic algae can use parts of the available nutrients at depth below about 1.9 m or nutrients accumulate within the surface water in deep systems (Fig. 5 d–l).

4. Discussion

Recently, Jäger and Borchardt (submitted) showed that, the spatial variant of the model is independent of both, stream velocity, when distance is expressed as travel time of surface water, and longitudinal turbulent diffusion, except at high and rather uncommon values for natural systems. Consequently, at uniform environmental conditions, planktonic and benthic algae and nutrients approach stable spatial equilibria, which are identical in the
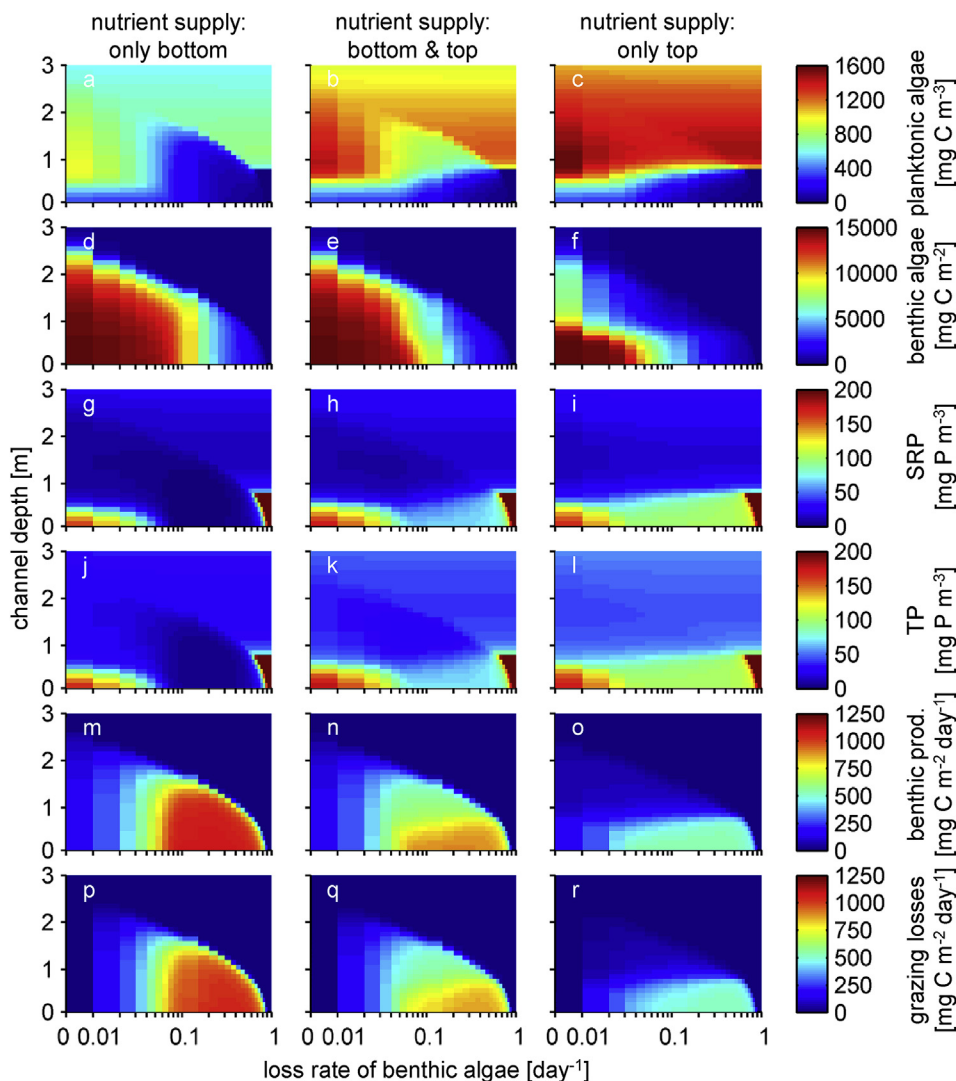
Fig. 4. Results of the spatial equilibrium values of the simplified model: effects of loss rate of benthic algae (x-axes), river channel depth (y-axes), and way of nutrient influx (see caption on top) on: concentration of planktonic algae, biomass of benthic algae, concentration of dissolved nutrients (SRP) and total nutrients (TP) in the surface water, production of benthic algae, and total grazing losses of benthic algae.
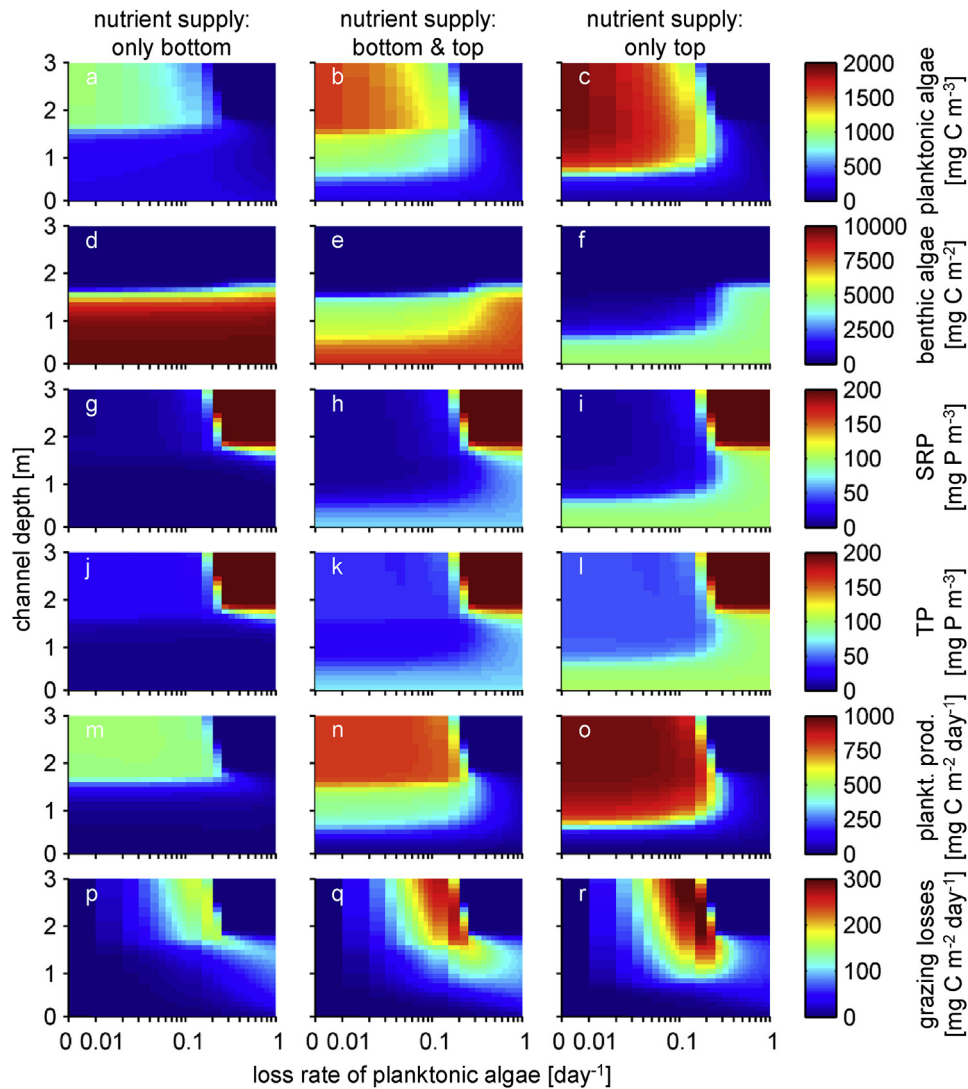
Fig. 5. Results of the spatial equilibrium values of the simplified model: effects of loss rate of planktonic algae (x-axes), river channel depth (y-axes), and way of nutrient influx (see caption on top) on: concentration of planktonic algae, biomass of benthic algae, concentration of dissolved nutrients (SRP) and total nutrients (TP) in the surface water, production of planktonic algae, and total grazing losses of planktonic algae.

spatial (PDE) variant and the simplified (ODE) variant of their model system. They showed in their analyses of the spatial pattern, that the spatial dynamics to these spatial equilibria depend on starting values and environmental conditions and can be very diverse. These spatial dynamics, however, can be well approximated by the temporal dynamics of the simplified model, if the starting conditions for the benthic algae are similar to the equilibrium conditions at the source in the spatial model (Jäger and Borchardt, submitted). In our experimental system we tried to meet these preconditions by allowing the benthic algae to colonise the benthic layer before the start of the experiment. The temporal development of the mesocosms, consequently, should roughly simulate the spatial development within a river channel. Although, we did no systematic parameter adaptation for the comparison between the model and the results of the mesocosm experiment, the qualitative and even quantitative fit is remarkable. Therefore, we conclude that our model includes most important mechanisms, which also might be relevant for natural communities. Model and experiment, however, were not designed to mimic reality, but to analyse specific key-processes, which determine the degree of eutrophication as a function of fundamental river characteristics,

pollution pathway of nutrients, the role of resource competition, and internal controls by grazing. The knowledge and the findings of our process analyses indicate that management options for eutrophication in rivers may go beyond the current focus of controlling the nutrients with limit concentrations (Dodds, 2007).

A major problem of eutrophication are excessive algal blooms particularly of phytoplankton (but also benthic algae), which can lead to oxygen deficient conditions and can consequently cause fish kills (Mallin et al., 2006; Smith et al., 1999). The reduction of algal biomass at a focal site, however, is only of limited benefit when it simultaneously increases the nutrient concentration, due to reduced uptake by algae or recycling within the system. Then, the problem of eutrophication is just displaced to downstream reaches or to coastal and marine systems. For a sustainable control of eutrophication nutrients have to be withdrawn and locked or exported from the systems. This is, for example, possible when grazers reduce algal biomass (and associated nutrients) and leave the system (e.g. by emerging insects), when the biomass and nutrients locked in grazers are effectively transferred in the food-web up to higher trophic levels like fish, which are eventually eaten by birds or mammals, or if nutrients are precipitated from the system

by bio-geochemical reactions (e.g. sedimentation of particle bound phosphorous, calcite precipitation).

It is generally accepted, that the ultimate reason for eutrophication is an increase of nutrients in the aquatic environments (Smith et al., 1999). Although the biomass of algae in both habitats increases, increasing nutrients do not really influence the general pattern and processes of interaction between benthic and planktonic algae, at least in the parameter space of our study. In contrast, the pathway of nutrient supply can have a strong impact on the systems of shallow to intermediate depths. In shallow systems the pathway of nutrient supply has only weak impact on phytoplankton, but intermediate impact on benthic algae and high impact on nutrients. At intermediate depth it has high impact on the biomasses of both algae and intermediate impact on nutrients (Figs. 2 and 3).

One important process that limits the biomass of phytoplankton in shallow and intermediate deep systems is the loss by sinking. High sinking losses and nutrient supply mainly from the bottom can be supported by a high hydraulic connectivity between the surface and interstitial water (Brunke and Gonser, 1997; Minshall et al., 2000). In contrast, clogging of the river bottom probably leads to reduced sinking losses of planktonic algae, which increases their biomass extremely, particularly when nutrients are supplied directly to the surface water (Fig. 3a, m). These results imply that the avoidance of surface run-off and clogging should be two central aims of management in shallow and intermediate deep systems. Moreover, river depth itself might be a possible management option. The systems can change very abruptly between the two states of predomination by benthic or planktonic algae within a short range of depth, particularly at low detachment rates of benthic algae (Fig. 3e–h) and, moreover, depending on algal trait values even alternative stable states might be possible (Hilt et al., 2011; Jäger and Diehl, 2014). There, a minor change of river depth can have high impact on algal biomasses in the respective habitats.

Reducing the light intensity is an often discussed option for managing eutrophication particularly in upstream areas where a shading of the stream can be easily implemented by e.g. planting trees (Bowes et al., 2012; Hutchins et al., 2010). Our results show that at intermediate to deep systems the biomass of phytoplankton can be reduced by decreasing light availability (Fig. 3a, u). A reduction of biomass, however, results always in increasing nutrient availability and, consequently, might transfer the problem of eutrophication only toward downstream reaches or costal systems (Fig. 3u–x).

In contrast, a sustainable control of eutrophication is possible by grazers, when they feed on algae of the predominating habitat. High impact on the biomass of benthic algae has been reported, for example, from snails (Hill et al., 1995; Kjeldsen, 1996). Moreover, Hillebrand (2009) showed in a meta-analysis of experimental studies that grazers removed on average 59% of the benthic biomass, independent of lake, costal, or riverine ecosystem. High grazing rates on phytoplankton have been shown from case-less caddisfly larvae, ciliates, rotifers, and mussels (Brown et al., 2005; Caraco et al., 2006; Kathol et al., 2011). An example of an effective top down control of phytoplankton is shown from the invasive zebra mussels in the Hudson River (Caraco et al., 2006; Strayer et al., 2008). However, high grazing rates on phytoplankton might increase respiration of the grazers in the benthic habitat and decrease oxygen concentration (Caraco et al., 2006). A possible control of phytoplankton by grazers might also be sensitive to temperature (Ruiz et al. in prep.). Moreover, according to our results effective eutrophication control is only possible at intermediate grazing rates. At low rates the grazing pressure is too low, at high rates algal biomass and, consequently, algal production is too low and dissolved nutrients accumulate in the water (Figs. 4 and 5). It is

unclear, however, which management options in particular maintain such intermediate grazing rates. In lakes the reduction of planktivorous fish by increasing the abundance of piscivorous fish has been reported as a possibility to increase grazing on phytoplankton and to control eutrophication (Benndorf et al., 2002; Hansson et al., 1998). It has been shown, that the presence of a forth trophic level increases the grazers and decreases algae also in riverine ecosystems (Wootton and Power, 1993). In conclusion it is evident, that enhanced grazer control of eutrophication in riverine ecosystems has a huge management potential, but needs further detailed and quantified analyses.

In particular, studies analysing both, benthic and planktonic algae, in riverine ecosystems are very rare. Therefore, the aim of this study is to gain a general understanding of dominant processes determining the interaction of benthic and planktonic algae in riverine ecosystems and to give some general suggestions for a possible control of mass developments of algal biomass (eutrophication) with emphasis on the role of nutrient pathways entering the receptor system, resource competition, and ecosystem internal control by grazing. We show that the interaction of benthic and planktonic algae is particularly important at intermediate deep systems. In such systems small changes of river characteristics can have high impacts (threshold behaviour) and river management of the critical factors might be a promising tool to reduce adverse eutrophication effects. However, to develop specific river management options for specific sites and problems probably more realistic models are needed, which may consider stream networks of various orders and transient conditions as fundamental characteristic of lotic ecosystems. Such models should therefore include realistic hydrology (e.g. transient discharge and stream velocity) because hydrologic parameters influence many processes and environmental conditions as, for example, detachment of benthic algae and light availability by increasing turbidity and water depth (Davies-Colley and Smith, 2001; Uehlinger et al., 1996). Moreover, stream flow, light, nutrients and grazing are also known to change algal and grazer species (Hilton et al., 2006; Law, 2011).

We are convinced, however, that the simplifications of our model help to determine and understand key processes of autotrophic production and losses in riverine ecosystems including their interactions. We hope that this study will serve as a stepping stone towards a more ecosystem based understanding and management of eutrophication in riverine systems. This knowledge is badly needed as pointed out by Jarvie et al. (2013) who stated that here is "an 'inconvenient truth' that phosphorus (P)-based nutrient mitigation, long regarded as the key tool in eutrophication management, in many cases has not yet yielded the desired reductions in water quality and nuisance algal growth in rivers and their associated downstream ecosystems".

5. Conclusions

- Detachment of benthic algae, sinking of planktonic algae and the pathway of nutrient supply are key processes determining the respective algal biomass distributions particularly in shallow and intermediate deep systems.
- Increasing nutrient supply increases algal biomasses, but does not change the general pattern of the interactions.
- Decreasing light supply decreases the dominance of planktonic algae, but increases dissolved nutrients.
- At intermediate to high grazing rates algal biomass can be controlled by grazers, but however, at high grazing rates, dissolved nutrients accumulate in the surface water.
- Our results indicate that nutrient pathways, resource competition and internal control by grazing need to be considered

explicitly for the understanding and explanation of eutrophication phenomena in riverine ecosystems.

- As a consequence, ecologically effective eutrophication management of running water systems has to go beyond the control of nutrient emissions or the achievement of limiting threshold values in the receiving waters, but requires the consideration of the nutrient pathways (surface water versus groundwater) and the shifting biological controls from lower to higher order stream ecosystems.

Acknowledgments

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