Longitudinal patterns and response lengths of algae in riverine ecosystems: A model analysis emphasising benthic-pelagic interactions

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A B S T R A C T

In riverine ecosystems primary production is principally possible in two habitats: in the benthic layer by sessile algae and in the surface water by planktonic algae being transported downstream. The relevance of these two habitats generally changes along the rivers' continuum. However, analyses of the interaction of algae in these two habitats and their controlling factors in riverine ecosystems are, so far, very rare. We use a simplified advection-diffusion model system combined with ecological process kinetics to analyse the interaction of benthic and planktonic algae and nutrients along idealised streams and rivers at regional to large scales. Because many of the underlying processes affecting algal dynamics are influenced by depth, we focus particularly on the impact of river depth on this interaction. At constant environmental conditions all state variables approach stable spatial equilibria along the river, independent of the boundary conditions at the upstream end. Because our model is very robust against changes of turbulent diffusion and stream velocity, these spatial equilibria can be analysed by a simplified ordinary differential equation (ode) version of our model. This model variant reveals that at shallower river depths, phytoplankton can exist only when it is subsidised by detaching benthic algae, and in turn, at deeper river depths, benthic algae can exist only in low biomasses which are subsidised by sinking planktonic algae. We generalise the spatial dynamics of the model system using different conditions at the upstream end of the model, which mimic various natural or anthropogenic factors (pristine source, dam, inflow of a waste water treatment plant, and dilution from e.g. a tributary) and analyse how these scenarios influence different aspects of the longitudinal spatial dynamics of the full spatial model: the relation of spatial equilibrium to spatial maximum, the distance to the spatial maximum, and the response length. Generally, our results imply that shallow systems recover within significantly shorter distances from spatially distinct disturbances when compared to deep systems, independent of the type of disturbance.

1. Introduction

In riverine ecosystems primary producers usually show a transition between habitats along the longitudinal gradient from headwaters to estuaries: shallow upstream reaches are predominated by benthic algae, while deep downstream reaches are predominated by phytoplankton ("River Continuum Concept", Vannote et al. 1980). In contrast to this conceptual large scale pattern, most experiments and models in riverine ecology have been focused on rather small scales, such as specific reaches or sites. Consequently, studies of streams and smaller rivers mainly focus on benthic communities, while studies of larger rivers focus mainly on planktonic communities (e.g. Dodds et al. 2002, Ochs et al. 2013, Graba et al. 2014, Istvánovics et al. 2014). Studies and models analysing primary producers in both habitats and their interactions, however, are rather rare (but see e.g. Flipo et al. 2004, Abdul-Aziz et al. 2010).

Nevertheless, many processes that influence the interaction between benthic and planktonic algae act on local scales. Benthic and planktonic algae, for example, compete for light and nutrients across the boundary of their habitats (Jäger and Diehl 2014). The general principle of their competition is that phytoplankton shades the benthic habitat, but benthic algae, in turn, reduce the nutrient flux to the surface water from nutrient rich interstitial water (Hansson 1988, Henry and Fisher 2003, Jäger and Diehl 2014). With increasing water depth this competitive interaction leads to an increasing dominance of phytoplankton. At deep river depths benthic algae are usually more light limited than planktonic algae, as they

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are located at the bottom of the system, while the proportional sinking losses of planktonic algae are reduced (Reynolds et al. 1990, Visser et al. 1996, Jäger and Diehl 2014). Besides these competitive interactions, the benthic and planktonic habitat can also be coupled by migration of algal cells. A high amount of planktonic algae can originate from the benthic habitat and sinking planktonic algae can settle in the benthic layer (Stevenson and Peterson 1991, Istvánovics and Honti 2011, Tekwani et al. 2013).

However, particularly challenging in riverine ecosystems is the spatial scale of the interaction between benthic algae and phytoplankton: while benthic algae react locally to the specific conditions at specific sites, planktonic algae are transported downstream while they respond. Consequently, their response to specific conditions shows a spatial delay (cf. Anderson et al. 2005). The spatial scale of their response is influenced by stream velocity, turbulent diffusion, algal production, and loss processes like sinking and grazing (Speirs and Gurney 2001, Lucas et al. 2009). Consequently, the analysis of the interaction of benthic algae and phytoplankton in riverine ecosystems needs to be extended beyond local scales. Existing concepts that address processes over larger scales include the "River Continuum Concept" or the "Serial Discontinuity Concept" (Vannote et al. 1980, Ward and Stanford 1983). While the "River Continuum Concept" assumes more or less steady natural gradients along the river course with changing dominance from benthic to planktonic algae, the "Serial Discontinuity Concept" extends this concept for spatially distinct anthropogenic disturbances, e. g. flow regulation by dams. However, not only dams and reservoirs can alter the river continuum, but in addition also other human impacts can influence river systems dramatically, like for example nutrient rich discharges from waste water treatment plants. A measure to analyse and quantify the spatial scale of such impacts is the response length, which was initially developed to analyse the response of a population of drifting benthic organisms (invertebrates) to a local spatial disturbance in an otherwise spatially homogeneous and temporally constant environment (Anderson et al. 2005).

The aim of this study is to analyse the interaction between benthic and planktonic algae in riverine ecosystems with a particular focus on the spatial scale of this interaction. Because many of the underlying processes are influenced by river depth, we focus particularly on the impact of river depth on the interaction of benthic and planktonic algae. To this end, we use a simplified advection-diffusion-model, which for example has been used to analyse factors influencing population persistence and spatial patterns of drifting organisms in running water systems (Speirs and Gurney 2001, Pachepsky et al. 2005, Lutscher et al. 2007) and combine it with mechanistic processes of a resource competition model of benthic and planktonic algae Jäger and Diehl 2014). Particularly, we analyse the (1) sensitivity of our model against changes of stream velocity and turbulent diffusion and show that all state variables approach stable densities along the river (spatial equilibria), when environmental conditions are homogenous. (2) We analyse if the spatial pattern of the model system can be approximated by the temporal dynamics of a simplified, ordinary differential equation (ode) version of our model. (3) Focusing on spatial equilibria, we examine the competitive and subsidising processes of the interaction between benthic algae and phytoplankton for systems of different river depths. (4) We analyse if the spatial gradient of a river course can be approximated by spatial equilibria of rivers of respective depths. (5) Finally, we simulate different scenarios for natural or anthropogenic factors (pristine source, dilution from a tributary, dam, and inflow of a waste water treatment plant) and analyse how these scenarios influence different aspects of the longitudinal spatial pattern: the relation of spatial equilibrium to spatial maximum, the distance to the spatial maximum, and the response length (in an adjusted definition).

2. Methods

2.1. Model system

The spatial model assumes a river channel of the longitudinal dimension x. Within the river channel exist two vertically well-mixed habitats: a surface water body ranging from the surface ($z = 0$) to the top of the benthic layer at $z = z_{max}$, and the benthic layer with thickness of $z_{bl} = 1$ mm. The model assumes one algal taxon that can grow in both habitats, as phytoplankton in the surface water and as a thin biofilm in the benthic layer (like e.g. species of the genera *Navicula, Dinobryon, Scenedesmus*, etc.), and which needs light and nutrients to produce new biomass. We assume that the surface water, including phytoplankton and dissolved nutrients, moves with a constant flow velocity v and is longitudinally mixed with a constant turbulent diffusion coefficient D; the benthic compartment does not move or mix along x-direction. The temporal and spatial dynamics of carbon biomasses of phytoplankton (A, calculated as concentration per volume) and biofilm (B, calculated per area), the concentrations of one limiting inorganic nutrient (phosphorus) in the surface water (R_{sw}) and the benthic layer (R_{bl}), and light intensity at the bottom of the surface water ($I_{z_{max}}$) are described by Eqs 1–5:

$$\frac{\partial A}{\partial t} = \frac{A}{z_{max}} \int_0^{z_{max}} P_A(I(z), R_{sw})dz - l_A \cdot A - \frac{s_A}{z_{max}}A - \frac{a_{is} + a_{sw}}{z_{max}}A$$
$$+ \frac{r_e}{z_{max}}B - v\frac{\partial A}{\partial x} + D\frac{\partial^2 A}{\partial x^2} \tag{1}$$

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

$$\frac{\partial B}{\partial t} = B \cdot P_B(I_{zmax}, R_{bl}, B_K) - l_B \cdot B - r_e \cdot B + \beta \cdot s_A \cdot A \tag{3}$$

$$\frac{\partial R_{bl}}{\partial t} = \frac{a_{is}}{z_{bl}}(R_{in} - R_{bl}) - \frac{a_{bl}}{z_{bl}}(R_{bl} - R_{sw}) - \frac{c \cdot B}{z_{bl}}P_B(I_{zmax}, R_{bl}, B_K)$$
$$+ \varepsilon \cdot c \cdot l_B \cdot B \tag{4}$$

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

All state variables and parameters are defined with units in Table 1. Algae produce new biomass at gross production rate P_A in the surface water and at P_B in the benthic layer. Algal populations suffer losses, mainly from grazing, at rates of l_A and l_B in the specific habitats, respectively. Planktonic algae are diluted by incoming algal-free water from the interstitial layer (via the benthic layer) at rate a_{is} and from surface runoff at rate a_{sw}. Due to gravity, planktonic algae additionally sink out of the surface water at velocity s_A. 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 cells take up dissolved nutrients 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. Nutrients are transferred between a stable pool in the interstitial water with constant concentration R_{in} and the benthic layer at rate a_{is} and between the benthic layer