



**Effects of Global Warming on
Phytoplankton and its Biocontrol in Large Rivers:
Insights from a Model Analysis**

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Insights from a Model Analysis**

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ABSTRACT

Benthic filter feeders (BFF) can reduce phytoplankton concentration (abundance) thereby controlling eutrophication in several ecosystems, including rivers. However, experiments suggest warming can alter the relationship between BFF grazing rate and the growth rate of (heterotrophic) planktonic prey. To investigate how eutrophication control by grazers is altered with temperature under the influence of other important abiotic (water depth, and speed, light, and turbidity) and biotic factors (initial phytoplankton concentration [hereafter: P_{in} value], BFF density and spatial BFF distribution), we developed a spatially-explicit computer simulation model. This model simulates the dynamics of a phytoplankton population traveling through a simplified river channel while being grazed by BFF. Our model includes the thermal responses of BFF grazing and phytoplankton growth. The results show that BFF grazing can qualitatively alter and, in some circumstances, even reverse the response of phytoplankton to warming. Moreover, the response of grazer-controlled phytoplankton to warming, water depth and P_{in} value is non-linear and phytoplankton can increase steeply with slight changes within some ranges of these variables. In addition, these variables can interact causing their combined effects on eutrophication to differ from what is expected considering their isolated effects. Generally, the effect of most variables, including temperature, P_{in} value and BFF density and spatial distribution, is larger at shallow waters. Moreover, our study shows that phytoplankton control can be substantially improved by heterogeneous BFF distributions where the BFF are located at the extremes of the river either upstream or downstream instead of homogeneously distributed along the whole river. However, warming can cause a switch between these two optimal distributions or even can cause differences among the spatial distributions to disappear. In general, the homogeneous BFF distribution can be used as conservative estimate of eutrophication control. In conclusion, this work shows that trophic control can qualitatively alter the response of eutrophication to warming, supporting previous studies suggesting that the prediction of global warming effects requires considering not only the thermal responses of organisms but also their trophic interactions. In addition to these biotic variables, this thesis reveals that considering the interactions between abiotic and biotic variables and including their spatial distribution are important for eutrophication control. Especially, the detection of thresholds in the response of grazer-controlled phytoplankton to temperature, water depth, P_{in} value, and spatial BFF distribution indicates that one should be careful with predictions because of potential abrupt changes. Although further studies are needed to make specific recommendations for water quality management, our work provides preliminary suggestions on the conditions where grazers or P_{in} reductions can be more efficient to control eutrophication.

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CHAPTER 1 - INTRODUCTION

1.1 BACKGROUND

Phytoplankton, i.e. pelagic algae, is the dominant primary producer in aquatic ecosystems (e.g. Vannote *et al.*, 1980, Minshall *et al.*, 1985). However, excessive phytoplankton production (i.e. eutrophication¹) can cause severe water quality problems affecting the biota and physical environment as well as the economy and society. These problems include: instability in oxygen concentration and pH value; blooming of undesirable species such as toxic blue-green algae; increasing water turbidity and therefore affecting the light regime of benthic algae and macrophytes; threatening endangered and sensitive species; water treatment problems; and reducing the recreational use of sites (e.g. Quinn, 1991 as cited in US-EPA, 1996; Smith, 1998; Dodds & Welch, 2000; Smith, 2003). Moreover, eutrophication is an important challenge in many freshwater and coastal marine ecosystems worldwide (Smith, 1998, Abell *et al.*, 2012).

Freshwater ecosystems where phytoplankton contributes to eutrophication include lakes, reservoirs and large rivers (e.g. Smith, 2003). In large rivers eutrophication may appear in middle and lowland stretches because their long water residence times allow, under the right circumstances, the development of abundant phytoplankton (e.g. the Danube, Istvánovics & Honti, 2012; the Rhine, Friedrich & Pohlmann, 2009; the Elbe, Scharfe *et al.*, 2009). This is important because rivers provide many important ecosystem services including being a source of water for human and animal consumption, for irrigation and industrial uses, for domestic and industrial waste disposal as well as for navigation and recreational purposes. Moreover, as rivers are connected to, and sometimes form the connection between, other water bodies, riverine eutrophication is likely to affect not only the river and its adjacent areas but also the receiving waters. Therefore, the impact of eutrophication can be considerable. For example, in England and Wales, the damage costs and policy response costs (i.e. those spent to address the damage) of freshwater eutrophication were together estimated at \$182-237 million yr⁻¹ (Pretty *et al.*, 2003).

¹ Eutrophication has been defined in at least four different ways (Edmondson 1995). The meaning most closely associated with the etymology of the word refers to the increase of the rate of nutrient supply to a water body. However, the consequences of such increase in nutrient supply have also been referred to as eutrophication itself (Edmondson 1995). Here we use the second definition, focusing on phytoplankton concentration, one of the main causes of water quality problems and a quality variable which is widely cited and easily perceived by people (Smith, 1998).

Given the impact of eutrophication and its extension, its control is an important management goal. Although eutrophication is usually managed by reducing nutrients, this is often impossible or unaffordable in reasonable time (Shapiro *et al.*, 1975). Fortunately, eutrophication can also be controlled by grazers (also called “top-down” control; hereafter: grazer control). Note, however, that grazer control is intended to complement, *not* substitute, eutrophication control by nutrients.

Grazer control has been studied mainly on fish (e.g. Carpenter *et al.*, 1995, Benndorf, 1995, Winkelmann *et al.*, 2014). Nonetheless, eutrophication seems to decrease in several freshwater ecosystems due to benthic filter feeders (BFF) (e.g. Cohen *et al.*, 1984, Effler *et al.*, 1996, Caraco *et al.*, 1997; 2006, Hardenbicker *et al.*, 2015b). BFF are animals living in the substrate of aquatic habitats (i.e. benthos), which feed by filtering particles from the water, e.g. clams and mussels. Some invasive BFF species (e.g. the Asiatic clam, *Corbicula fluminea*) have invaded ecosystems worldwide (e.g. Araujo *et al.*, 1993; such ecosystems include large rivers such as the Rhine, e.g. Hardenbicker *et al.*, 2015b) and have very high clearance rates, i.e. can filter particles such as phytoplankton from the water column very fast².

Eutrophication control by nutrients or grazers, however, seems to be influenced by different factors (see next paragraphs). It is likely that among such factors the initial, i.e. at the source, phytoplankton concentration (hereafter: P_{in}) of the river stretch is relevant. Therefore, to support management decisions regarding the most efficient manner to control eutrophication in different sites, a systematic study of the effect of relevant factors is needed. Such study can thereby support the achievement of relevant legislation, such as the WFD (European Commission, 2000).

Regarding the factors influencing grazer control, the high clearance rates and wide-ranging distribution of some (invasive) BFF species, has motivated several studies, many of which focus on rivers, where several of such species inhabit. For example, laboratory and mesocosms experiments have analyzed the factors determining the effects of BFF grazing on eutrophication, mainly BFF clearance rate (such mesocosms facilities are found, for example, in large rivers such as the Rhine and the Elbe; e.g. Weitere *et al.*, 2009). These factors include temperature (Lauritsen, 1986) and phytoplankton traits including concentration (Lauritsen, 1986, Vohmann *et al.*, 2010), composition (Lauritsen & Mozley, 1983) and individual (i.e. particle, organism) size (Way *et al.*, 1990).

² Although the nuisances caused by such species are important, here we advocate their use only in sites already invaded by them (see Appendix 5).

These experimental studies have improved our understanding of factors determining BFF grazing and, based on their results, preliminary estimations of potential BFF effects in rivers have been attempted (e.g. Lauritsen, 1986). However, estimating the impact of BFF on riverine phytoplankton requires considering several other abiotic factors affecting both phytoplankton growth and the impact of BFF grazing on phytoplankton.

Several of these factors have actually been considered in simulations with relatively complex models, which have allowed to reproduce phytoplankton concentration in certain rivers taking into account the impact of BFF (e.g. Schöl *et al.*, 2002, Descy *et al.*, 2012, Pigneur *et al.*, 2014). However, the complexity of these models, e.g. complex river morphology and inclusion of several phytoplankton groups (e.g. Descy *et al.*, 2012, Pigneur *et al.*, 2014), hinders the mechanistic understanding that systematic model simulations (also called a “virtual lab approach”) can foster about the effects of particular variables on eutrophication control by BFF.

A virtual lab approach³ can help us to understand factors such as phytoplankton concentration (eutrophication), by testing the effect that different values of certain parameters have on such factor, while keeping constant the values of the remaining parameters. A virtual lab approach can benefit from several things: field observations and measurements, experimental data, theories providing hypotheses on functional relationships to be tested, and models (linking experimental data and theories, and providing formulations). In addition to providing such information, previous experiments and simulations (with BFF or other organisms) can suggest research directions for virtual lab approach studies. For example, Viergutz *et al.*, 2007 observed that the balance between the rates of phytoplankton growth and BFF grazing depends on temperature. Therefore, climate change, with its associated warming, will likely alter such balance. That global warming effects on ecosystems will likely depend on the interplay of species traits and physiological responses to warming is also supported by other studies, e.g. Deutsch *et al.*, 2008, Tewksbury *et al.*, 2008, Huey *et al.*, 2009, Bonebrake & Mastrandrea, 2010, see also review by Urban *et al.*, 2016.

³ In models designed for a virtual lab approach, many variables are often oversimplified to facilitate understanding the effect of the variables of interest. For example, our model oversimplifies the effects of nutrients and the river morphology to focus in the thermal responses of phytoplankton growth and BFF grazing. Such models are also called “stylized models” and the model here developed and applied is one of them.

However, there is only one previous study using a virtual lab approach addressing eutrophication control by BFF in rivers (which revealed the impact of water depth and residence time, on such control; Lucas & Thompson, 2012). Hence, there is gap in our knowledge of riverine eutrophication control by BFF, including the potential effects of climate change on such eutrophication control. Simultaneously, the potential of a virtual lab approach to improve our knowledge on this topic is promising but still unrealized.

1.2 KNOWLEDGE GAP AND AIMS

In particular, our knowledge gap includes several unanswered questions. First, it is unclear *how warming affects eutrophication control by BFF grazing and how these effects depend on BFF density and the thermal responses of phytoplankton growth and BFF grazing. Moreover, the role of river morphology such as water depth, and its associated flow velocity, in relation to temperature effects is unknown.* Second, although the initial phytoplankton concentration (at the source; P_{in}) can vary considerably within and between rivers (see Appendix 3, Section A3.2), it is unclear *how eutrophication control by reducing P_{in} (hereafter: source control) interacts with grazer control under warming in relation to water depth, BFF density and the thermal responses of phytoplankton growth and BFF grazing.* Third, although spatial BFF distribution in rivers naturally varies (e.g. Leff *et al.*, 1990, Jantz & Schöll, 1998, Caraco *et al.*, 1997, Hardenbicker *et al.*, 2015b), it is unknown *how such distribution affects eutrophication control and how such effects depend on temperature, P_{in} value, water depth and BFF density.*

The aim of this work is to answer these questions for large rivers using a virtual lab approach. To do this, we develop and apply a spatially explicit computer simulation model (see Chapter 2 for model description) which considers the interplay between abiotic (river depth and length, flow velocity, temperature) and biotic factors (P_{in} , phytoplankton growth, BFF grazing and, in particular, the *thermal responses for phytoplankton growth and BFF grazing*; Appendix 1). The model simulates the population dynamics of phytoplankton traveling along a large river stretch, starting with an incoming phytoplankton concentration (P_{in}) to estimate phytoplankton concentration at the outlet of such stretch (hereafter: P_{out}).

While several of our model formulations (equations) come from previous models, we use information from observations and experimental studies as a guide for suggesting factors important for eutrophication control (e.g. temperature) and to parameterize our model (Table 2-1 and Appendices 1-3). We tried to keep our parameters within realistic values using data from certain rivers, regions and taxa (see Table 2-1 in Chapter 2 for the values and Appendices 1-3 for the justification of such values). However, we also

kept the model stylized, i.e. focused on the potentially most important factors, to make it systematically tractable and generalizable to large rivers. Therefore, simulated river morphology is stylized and very simple in our model, while the river dimensions are in the range of the Rhine and the Elbe. Moreover, the BFF grazing mechanism is similar in different species in nature. Hence, even when we parameterized our model with data from *C. fluminea*, an invasive BFF, our model and its main conclusions may also apply or be applied to other rivers and BFF species (including native BFF).

We used this model to study the effects of unstudied or poorly studied factors on, and perform techniques that were poorly applied to, eutrophication control. First, we perform one of the very first applications of a virtual lab approach to analyze riverine eutrophication control by BFF. Second, we analyze systematically for the first time the effects of Pin value and BFF distribution on eutrophication control in a riverlike system.

1.3 CHAPTER OUTLINE

This thesis consists of five chapters additional to the present one. The next chapter (Chapter 2) describes the simulation model presenting its rationale, spatial dimensions, equations and variables. The following three chapters (Chapter 3 to 5) describe the application of the model to study the effects of different variables on eutrophication control (see chapter comparison in Table 1-2).

Chapter 3 has an ecosystem functioning perspective. It studies how warming and water depth determine phytoplankton growth and BFF grazing and thereby eutrophication at the outlet (Pout) of a large river. Chapters 4 and 5, in contrast, have a management perspective. Chapter 4 studies to what extent can eutrophication control be achieved at the outlet (Pout) through source control (managing Pin) and enhanced by grazer control under different temperatures, water depths, BFF densities, and thermal responses of phytoplankton growth and BFF grazing. Chapters 3 and 4 assume that BFF distribute homogeneously throughout the river. Chapter 5 studies how the BFFs' spatial distribution affects the performance of grazer control of eutrophication (comparing a spatially homogeneous distribution with several heterogeneous ones), at the outlet (Pout) and also along the river. Chapter 5 also analyzes the influence of all the parameters studied in the preceding chapters, namely, temperature, water depth and the thermal responses of phytoplankton growth and BFF grazing. Chapter 6 presents the general discussion and conclusions of the thesis. This thesis concludes with the references and five appendices.

Chapter	2	3	4	5
Type	Model description	Model application		
Focus	-	Ecosystem functioning under warming	Eutrophication control management under warming	Eutrophication control management under warming
BFF spatial distribution	-	Homogeneous	Homogeneous	Homogeneous and heterogeneous
Abiotic and biotic factors studied	-	Temperature, depth, thermal responses*, BFF density	Same as in Chapter 3 + Pin	Same as in Chapter 4 + BFF spatial distribution

Table 1-2. Chapter contents. *Thermal responses of phytoplankton growth and BFF grazing.

CHAPTER 2 - METHODS

This chapter describes the simulation model developed to study the effects of benthic filter feeders (BFF) grazing on phytoplankton (eutrophication) during its travel from the source to the outlet of a large river stretch under warming. BFF can reduce phytoplankton concentration on water bodies (e.g. Cohen *et al.*, 1984, Effler *et al.*, 1996, Caraco *et al.*, 1997; 2006). However, such reductions are likely determined by warming, which can alter the relationship between the rates of plankton growth and BFF grazing (Viergutz *et al.*, 2007). Moreover, these reductions are affected by water depth, which determines the water volume and time that BFF have to graze (e.g. Lucas & Thompson, 2012).

2.1 OVERVIEW

We developed a spatially explicit time-discrete population model able to simulate phytoplankton dynamics and the effects of BFF grazing on them in large river stretches (500 km length; LR) under a wide range of abiotic and biotic conditions. Abiotic factors include temperature (T ; varied from 0 to 32°C), light, water depth (D ; varied from 1 to 8m) and water speed. Biotic conditions include optimum temperatures for phytoplankton growth and benthic grazing under various BFF densities (G ; 0, 50, 100, 300 and 500 ind./m²). Benthic grazing was modelled based on measurements of the Asiatic clam (*Corbicula fluminea*; Appendix 2) but due to the simulation of different thermal responses for grazing (Appendix 1), results are likely to account, at least to some extent, for intra- and interspecific variability (see also Appendix 5).

The model covers all processes necessary to describe the interplay and feedbacks between the above mentioned abiotic and biotic factors in a large river stretch (but see last paragraph of this section on the feedback between phytoplankton and BFF). In particular, it accounts for the relationship between river morphology (such as slope, roughness, and water depth) and water speed (and, therefore, water residence time at the outlet i.e. the time it takes the water to go through the river). As the model is spatially explicit, both spatially homogeneous and heterogeneous conditions can be considered. Parameters values and ranges are taken from general empirical data and from specific data of the Rivers Rhine and Elbe, see

Table 2-1). The main interactions between the model components are depicted in Figure 2-1. Details of these components are given below together with a summary of parameters.

The model simulates the dynamics of a phytoplankton population traveling through a large river stretch from a source to the outlet. We describe the abundance of the phytoplankton population in terms of concentration (mass/volume) and, although the water volume containing such population is not described explicitly (the population is simulated as a non-dimensional "cloud"), we consider it implicitly in our simulations. We assume a turbulent water regime with well mixed water. Thus, we assume that phytoplankton concentration is homogeneously distributed in the vertical dimension (see Figure 2-2) and BFF grazing occurs with the same rate throughout the whole phytoplankton population (note that river depth affects this rate, see next sections for details).

Main input quantities were the initial (i.e. at the source) phytoplankton concentration (P_{in}), the river channel properties including the temperature conditions, and the grazer density. Main output quantity was the phytoplankton concentration at the outlet of the river stretch, i.e. after water residence time at the outlet has passed, (P_{out}) under varied abiotic (in particular temperature and water depth) and biotic (BFF density and species temperature optima) conditions. See a list of parameters in Table 2-1 and a list of variables in Table 2-2.

It is worth noting that, in our system, i.e. (large) rivers, there is a constant flow of water continuously washing out planktonic organisms and suspended material in a few days, which makes the system very dynamic. In other words, the time during which the travelling phytoplankton and the locally fixed BFF grazers can interact at all is much shorter than in many other ecosystems. Moreover, in contrast to other systems, the life span of the consumers and producers studied here differs considerably: while the producer's (i.e. phytoplankton) life is very short and its biomass is transported to the river outlet within just a few days, the consumers (i.e. BFF) have a considerably longer life (ca. 2-3 years). For these reasons, our model neglects the feedback from phytoplankton to BFF, focusing exclusively on phytoplankton dynamics.

Our work therefore focuses on **short term** dynamics. Moreover, our study addresses **single river channels** with **homogeneous morphology** and **well-mixed** waters (see below). Although long term dynamics and water stratification as well as (ramified) river networks and heterogeneous channel morphology may alter our results, our work can serve as a baseline for future and more complex models.

2.2 TEMPORAL AND SPATIAL STRUCTURE AND SCALES

2.2.1 Time scale

The model is time discrete and runs at hourly time steps. This temporal resolution was chosen as an agreement between model simplicity and accuracy in the description of both phytoplankton growth and BFF grazing. The duration of a simulation depended on channel characteristics such as water depth (see following section).

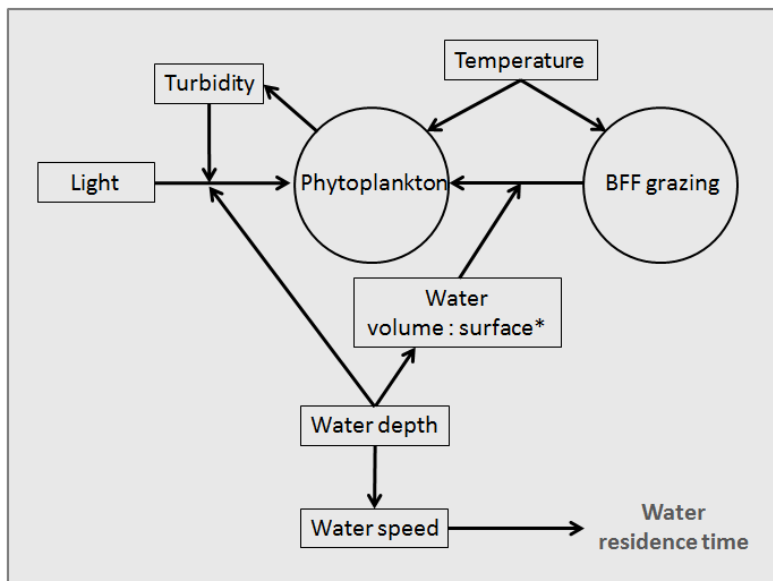


Figure 2-1. Schematic representation of the model structure depicting the interaction between phytoplankton concentration (eutrophication) and the environment, including biotic (i.e. BFF grazing) and abiotic (temperature, light, turbidity and water depth and speed) factors. Water depth and turbidity modify the availability of light for phytoplankton, which in turns alters the turbidity of the water column (self-shading effect). Moreover, water depth determines the water volume : surface (*), i.e. the ratio of the volume of the water column to the surface of the river below such water column. Water volume : surface in turn affects how BFF grazing impacts phytoplankton. Water speed is a function of water depth, and it determines the water residence time at the outlet, which is the time span within which all system interactions take place.

2.2.2 Spatial structure and water movement (water speed, water residence time and mixing)

The water speed (v ; m/s) in the horizontal dimension (with respect to the river bed) was modelled according to Manning equation:

$$Eq. 1 \quad v = \frac{R^{2/3} * S^{1/2}}{n}$$

where S and n are the channel slope and the roughness coefficient, respectively (both parameters are unitless; see values in Table 2-1 and justification in Appendix 3). R is the hydraulic radius (m; Eq. 2), i.e. the relation of the cross-sectional area (CA) of the water in the river channel and its wetted perimeter (WP). The cross-sectional area and the wetted perimeter refer to the area and the perimeter that the water occupies in the cross section of the river channel, respectively. Since we assume here that the river channel has a cubic shape, the cross-sectional area of the river is rectangular, and therefore also CA (Eq. 2).

$$Eq. 2 \quad R = \frac{CA}{WP} = \frac{D * W}{(2 * D) + W}$$

Water residence time at the outlet ($t_{res,out}$; hours), i.e. the time it takes the water to go through the river, is inversely proportional to the water speed (v ; m/s):

$$Eq. 3 \quad t_{res,out} = \frac{LR}{v * 3,600}$$

where LR (m) is the length of the river stretch, v (m/s) is the speed of the water in the downstream direction of the river, and 3,600 is a factor to convert units from seconds to hours. The simulation was stopped whenever the simulation time (t ; hours) was equal or larger than t_{res} . Using Eqs. 1 to 3 and the parameter values employed here, increasing water depth (D) leads to a fast but relatively constant increase in water speed (v) but to a dramatically decrease in water residence time at the outlet ($t_{res,out}$) in shallow waters followed by a much slower decrease at deeper waters (Fig. A3-1).

We assumed that the phytoplankton population and water move with the same speed in relation to the river bed (i.e. “plug flow”; the same assumption used by Lucas & Thompson, 2012). Thus, the distance a phytoplankton population moves during each time step (hereafter named “river segment”) is:

$$Eq. 4 \quad LS = v * \Delta t$$

where LS is the length of the river segment (m) crossed and Δt the length of the time step (in seconds). Since we used hourly time steps Δt is equal to 3,600s in all our simulations. Due to the discrete temporal structure, spatial water movement representation is also discrete (Fig. 2-2). Therefore, the distance travelled by the phytoplankton population at the end of simulation time was often actually slightly larger than river length (LR ; 500km).

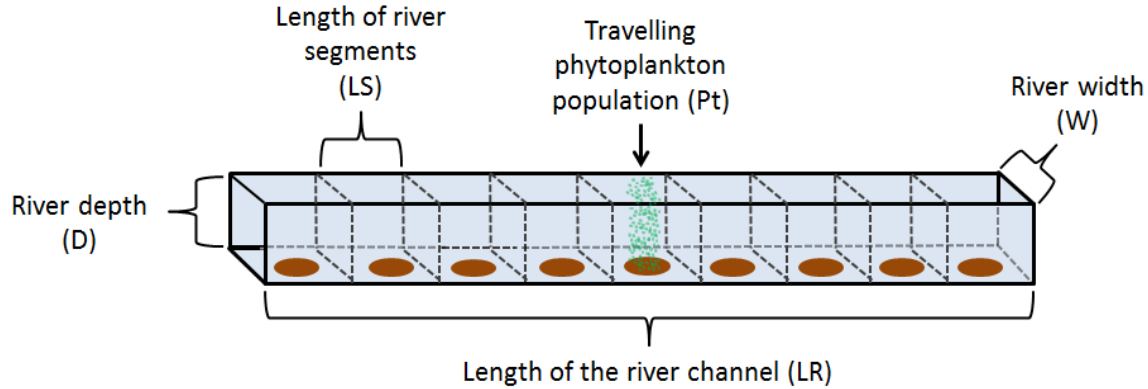


Figure 2-2. Schematic representation of the spatial structure of the modelled river system (lateral view). The river channel (blue rectangle) contains a travelling phytoplankton population (green dots) which moves in each time step from one segment (of length LS) to another one along the river. Note that the depicted proportion between LS and LR is much larger than in the model.

2.3 PHYTOPLANKTON DYNAMICS

Phytoplankton dynamics were simulated using an exponential (Ricker like) equation (de Ruyter van Steveninck *et al.*, 1992; Kremer & Nixon, 1978):

$$Eq. 5 \quad P_{t+\Delta t} = e^{(p(T,L,D,SC,N,P_t) - l(T,L,D,P_t) - g(T,D,G_t,P_t))\Delta t} * P_t$$

where P_t is the phytoplankton concentration (mgC/l) at time t , p the phytoplankton gross growth rate (d^{-1} ; Eq. 6), l the phytoplankton losses not due to benthic grazing (d^{-1}), g the phytoplankton losses due to benthic grazing (d^{-1}), T the water temperature ($^{\circ}C$), N the nutrient concentration (mg/l), D the depth of the river (m), SC is the seston content without phytoplankton in the river water (mg/l), and G_t the grazer density at time t (ind./m²; see “Simulation details” for the relationship between G_t and grazer density in the river, G). We assumed in all simulations hourly time steps ($\Delta t = 1h$). Note that the rates in Table 2-1 are given in daily time steps and have to be transformed accordingly. The initial phytoplankton concentration (P_{in}) was equal to 1 mgC/l (i.e. $P_{t=0} = 1$ mgC/l) in Chapter 3 but varied from 0.02 to 10.02 mgC/l in Chapters 4 and 5. For presentation of the results we report P_t when $t \geq t_{res,out}$ and call it P_{out} .

Although similar exponential equations to Eq. 5 have been used formerly (e.g. de Ruyter van Steveninck *et al.*, 1992, Kremer & Nixon, 1978) and considered the dependence on temperature and phytoplankton

density for both phytoplankton growth and grazing (Kremer & Nixon, 1978), our study is novel in several respects. We make a systematic exploration of the effect of temperature (0-32°C) on eutrophication. Moreover, we investigate different thermal responses of both phytoplankton growth rate and benthic grazing rate. Finally and most importantly, we consider the river in a spatially explicit way and combine these studies with a systematic analysis of the impact of water depth (D) and its relation to water residence time at the outlet ($t_{res,out}$; see previous section) in rivers. The effect of both D and t_{res} on eutrophication biocontrol by benthic grazers have been analyzed separately before (Lucas & Thompson, 2012). However, it is an open question, how these factors interact with temperature effects and thermal responses. The combination of these abiotic and biotic factors and their spatial heterogeneity proved as essential for the phytoplankton dynamics and the extent of eutrophication as demonstrated in our results.

The three basic processes considered in Eq. 5 (phytoplankton growth $p(T, L, D, SC, N, P_t)$ losses without grazing $l(T, L, D, P_t)$ and losses due to grazing $g(T, D, G_t, P_t)$ and their dependencies on the abiotic and biotic factors are now explained in detail.

2.3.1 Phytoplankton gross growth

We define phytoplankton gross growth rate (p ; d^{-1}) as:

$$Eq. 6 \quad p(T, L, D, SC, N, P_t) = p_{max} * j(T) * u(L, D, SC, P_t) * h(N)$$

where p_{max} is the maximum phytoplankton growth rate (d^{-1}), $j(T)$ the thermal response, $u(L, D, SC, P_t)$ the light dependency (including shading and self-shading) and $h(N)$ the nutrient dependency (these dependencies impact p_{max} and are unitless).

Maximum phytoplankton growth rate (p_{max}) varies among algae groups (Lüring *et al.*, 2013) and characteristics of the species such as the surface-volume ratio (Reynolds, 1989). Thus, choosing a single value to represent the growth of an entire phytoplankton community is challenging. Natural phytoplankton communities are likely to have a higher productivity than that expected from the average productivity of the species forming that community, due to the increase in productivity and resource use efficiency with functional richness (Ptacnik *et al.*, 2008, Striebel *et al.*, 2009). Therefore, we have chosen a rather high maximum (specific) rate of algae growth (p_{max}): 1.8 day^{-1} . This value is close to the 90th percentile of the growth of green algae at the optimum temperature reported in a recent literature survey (for cyanobacteria

the same percentile has a value of about 1.3 day⁻¹ in that survey; Lürling *et al.*, 2013). Moreover, this value is used by Schöl *et al.*, 2002 for diatoms in simulations of the River Rhine phytoplankton under benthic grazing.

2.3.1.1 Thermal response for phytoplankton growth

We modelled the thermal response for phytoplankton ($j(T)$) according to the equation described in O'Neill *et al.*, 1972 determined by the parameters T_{opt}^p , T_{max}^p and Q_{10}^p (Table 2-1, Eq. A1-1 in Appendix 1). This type of equations describing the shape of the thermal response of a biological rate or fitness are usually called “thermal performance curves” and have been used to assess or predict the impact of temperature on species performance (e.g. Huey & Hertz, 1984, Huey & Kingsolver, 1989, Deutsch *et al.*, 2008, Clusella-Trullas *et al.*, 2011, Vasseur *et al.*, 2014; see also Kingsolver, 2009 for an explanation of the basic features of such curves).

Although we were interested mainly in the effects of high temperatures such as those found in spring and summer (which are about 8.5-28.5°C for the Rhine River at Cologne; data from 1999 in Weitere *et al.* 2005), we tested an extended temperature range of 0-32°C (see Appendix 3 for the justification on this large temperature range). Stream temperature is likely to vary throughout the day due to the influence of solar radiation, but it is subject to several other factors which depend on the landscape and the riparian vegetation (Johnson, 2003). For simplicity, we assumed temperature was constant throughout the simulation time.

2.3.1.2 Light dependency for phytoplankton growth

The light dependency $u(L, D, SC, P_t)$ is defined according to Di Toro *et al.*, 1971:

$$Eq. 7 \quad u(L, D, SC, P_t) = \frac{e * PF * (e^{-a1} - e^{-a0})}{atte(SC, P_t) * D}$$

$$a1 = \frac{I_{sur}}{I_{opt}} * e^{-atte(SC, P_t) * D_{pro}(L, P_t)}$$

$$a0 = \frac{I_{sur}}{I_{opt}}$$

where e is the Euler number, PF the photoperiod fraction (unitless; Eq. 8), I_{sur} the mean photosynthetically active radiation just below the water surface during the photoperiod ($\mu E/(m^2*s)$; Eq. 11 below), I_{opt} the optimum light intensity for phytoplankton growth ($\mu E/(m^2*s)$), $atte(SC, P_t)$ the light attenuation coefficient (m^{-1} ; Eq. 9) and $D_{pro}(L, P_t)$ the depth of the euphotic layer (m; Eq. 10), i.e. the

depth of the water layer where light is enough for phytoplankton photosynthesis. Note that for simplicity we comprised the light dependency in $u(L, D, SC, P_t)$ to L instead of stating all components of the light (and phytoplankton light-dependency) $DL, DR, I_{lim}, I_{opt},$ and I_{sur} separately. The same is true for $D_{pro}(L, P_t)$ (Eq. 10).

The photoperiod fraction (PF) is the fraction of the day with sunlight and was calculated from day length (DL; h) according to:

$$Eq. 8 \quad PF = \frac{DL}{24}$$

The attenuation coefficient for light passing through the water column ($atte(SC, P_t)$; m^{-1}) was calculated according to Schöl *et al.*, 2002 and assuming a carbon to chlorophyll *a* (chl-*a*) ratio (C_{chl_r} ; unitless) of 25 (Admiraal *et al.*, 1992):

$$Eq. 9 \quad atte(SC, P_t) = atte_{chl} * \frac{P_t * 1000}{C_{chl_r}} + atte_S * SC + atte_W$$

where $atte_{chl}$ ($l/(mgC*m)$), $atte_S$ ($l/(mg*m)$), $atte_W$ (m^{-1}) are the attenuation coefficients of light in the water column due to phytoplankton, seston and water, respectively (see values in Table 2-1). Note that the attenuation coefficient ($atte(SC, P_t)$) incorporates the self-shading effect of phytoplankton, which limits the growth of phytoplankton via the light dependency ($u(L, D, SC, P_t)$; Eq. 7).

The depth of the euphotic zone ($D_{pro}(L, P_t)$; m) was simulated according to Schöl *et al.*, 2002:

$$Eq. 10 \quad D_{pro}(L, P_t) = \frac{\ln(I_{sur}) - \ln(I_{lim})}{atte(SC, P_t)}$$

where I_{sur} is the mean photosynthetically active radiation intensity just below the water surface during the photoperiod ($\mu E/(m^2*s)$; Eq. 11) and I_{lim} the minimum light intensity that phytoplankton needs to grow ($\mu E/(m^2*s)$; Table 2-1). Note that the values chosen here as optimum light intensity (I_{opt}) and limiting light intensity for phytoplankton growth (I_{lim} ; see value in Table 2-1) correspond to diatoms (Richardson *et al.*, 1983). Although adaptation of phytoplankton to certain light intensity is likely to occur and some approaches have been suggested to model it (Kremer & Nixon, 1978) here we have neglected such adaptation for simplification. In addition, $D_{pro}(L, P_t)$ was restricted to sensible values (see ‘‘Simulation details’’ section).

The mean photosynthetically active radiation intensity just below the water surface during the photoperiod (I_{sur} ; $\mu E/(m^2*s)$) was estimated according to the following equation:

$$Eq. 11 \quad I_{sur} = HR * PAR_r * (1 - WRC) * 4.5$$

where HR is the hourly solar radiation intensity (HR; W/m²; Eq. 12) received on the water surface, PAR_r the fraction of photosynthetically active radiation (PAR) in the incoming light (unitless), WRC the water surface reflection coefficient, i.e. the fraction of PAR which is reflected by the water surface (unitless) and 4.5 is the factor to convert units from W/m² to $\mu E/(m^2*s)$ (Williams, 2006). In addition, I_{sur} was restricted to positive non-zero values (see Section “Simulation details”).

In turn the hourly solar radiation intensity (HR; W/m²) was estimated as follows (modified from Park & Clough, 2014):

$$Eq. 12 \quad HR = \frac{\pi}{2 * 24} * \frac{DR}{PF} * \sin \left(\pi * \frac{DP - \frac{1 - PF}{2}}{PF} \right)$$

where DR is the daily solar radiation (Wh/(m²*d)), PF the photoperiod fraction (unitless; Eq. 8) and DP the fraction of the day that has passed (unitless); i.e. the time of the day, and 24 the factor needed to convert from Wh/(m²*d) to W/m². Eq. 12 assumes that the entire site is unshaded. The hourly solar radiation was computed every hour from 00:30 to 23:30.

DP was estimated as follows:

$$Eq. 13 \quad DP = \frac{th}{24}$$

where th is day time (*hours*, for example, when the day time is 11:30 $th= 11.5$) (We assumed that all simulations started at 00:30 hrs, i.e. $th_{t=0}= 0.5$).

2.3.1.3 Nutrient dependency for phytoplankton growth

Nutrients are assumed not to limit phytoplankton growth. Therefore, the nutrient limitation factor ($h(N)$) has a value of one in all simulations. However, to account for nutrient depletion at high phytoplankton densities (and, therefore, avoid unrealistically high phytoplankton concentrations), in the following section we incorporated a density-dependent mortality which aggregates the effects of several factors which limit phytoplankton growth at high phytoplankton concentration (Eq. 14).

2.3.2 Phytoplankton losses due to processes other than benthic grazing

The loss of phytoplankton in Equation 5 is a simplified representation of several processes that reduce phytoplankton concentrations:

$$Eq. 14 \quad l(T, L, D, P_t) = m_{max} * mb^{(T^*-20)} * \frac{P_t}{k_m + P_t} + rb + rp * p(T, L, D, SC, N, P_t)$$

The first term describes a density-dependent mortality rate comprising zooplankton grazing, parasitism, and nutrient depletion according to Nyholm, 1978. These processes affect phytoplankton at high densities and are therefore modelled as a density-dependent saturating equation. m_{max} is the maximum density-dependent mortality rate (d^{-1}), mb (unitless) is the base coefficient for the thermal response of phytoplankton mortality and k_m (mgC/l) is the half-saturation coefficient of the density-dependence. T^* ($^{\circ}C$) is equal to the temperature (T) if $T \leq 25^{\circ}C$, otherwise $T^*=25^{\circ}C$. Note that m_{max} is the maximum mortality rate at $20^{\circ}C$ but higher maximum mortality rates are possible up to $0.42 d^{-1}$ for $T \geq 25^{\circ}C$. (See parameter values on Table 2-1.) Because higher temperatures than those in Nyholm (1978) are analyzed here, we set the temperature limit of T^* at $25^{\circ}C$ instead of employing the usual Van't Hoff equation (as Nyholm (1978) did). This limit avoids overestimating mortality at high temperatures. Although phytoplankton mortality due to e.g. zooplankton grazing or parasitism is likely to be high in hot waters, it is unlikely that it increases above the assumed $0.42 d^{-1}$. Note that m_{max} is relatively low ($0.8 d^{-1}$) and k_m is relatively high (50 mgC/l), so it is unlikely that the exact shape of this curve alters our main conclusions.

The second term, rb , is the basal (dark) respiration rate (d^{-1}) and, in the third term, rp is the photorespiration factor (unitless) (see variable values in Table 2-1) and $p(T, L, D, SC, N, P_t)$ the gross growth rate of phytoplankton (d^{-1}). Photorespiration accounts for the energy lost when cells produce biomass. Therefore, the photorespiration factor is a constant proportion of the gross growth rate.

2.3.3. Phytoplankton losses due to benthic grazing

The Asian clam (*Corbicula fluminea*) was used in this study as a model species. The Asian clam is one of the most conspicuous BFF invaders thorough the world (e.g. Araujo *et al.*, 1993, Sousa *et al.*, 2008) and the second most studied freshwater BFF invader (Sousa *et al.*, 2014). Moreover, this species physiology

and ecology have been subject to considerable study (e.g. Aldridge & McMahon, 1978, McMahon, 2002, Weitere *et al.*, 2009).

The grazing rate of the BFF population ($g(T,D,P_t,G_t); d^{-1}$) incorporates the dependence of grazing on temperature, T, depth, D, grazer density, G_t , and phytoplankton concentration, P_t (e.g. Descy *et al.*, 2003):

$$Eq. 15 \quad g(T,D,P_t,G_t) = \min(f_{max}, f(P_t,T)) * \frac{G_t}{D * 1000}$$

where *min* is an operator that selects the minimum value from two quantities, f_{max} , the maximum daily filtration rate per individual BFF (l/(ind.*d)), and $f(P_t,T)$ the daily filtration rate per individual BFF (l/(ind.*d)) dependent on phytoplankton concentration, P_t , and temperature, T. G_t is the BFF density at time step, t (G_t ; ind./m²; see “Simulation details” for the relationship between G_t and grazer density in the river, G). The factor 1000 converts units from m³ to liters. See parameter values in Table 2-1 and the section “Temporal and spatial structure” for a description of the spatial structure of the river.

Filtration rate under high phytoplankton concentrations ($f(P_t,T)$) was estimated as:

$$Eq. 16 \quad f(T,P_t) = \frac{i_{max} * i(T)}{P_t + k_g}$$

where i_{max} is the maximum daily ingestion rate per individual BFF (mgC/(ind.*d)), k_g is a coefficient for BFF ingestion (mgC/l) and $i(T)$ (unitless) is the thermal response for benthic grazing. Such thermal response $i(T)$ is a unimodal curve defined by the parameters T_{opt}^g , T_{max}^g and Q_{10}^g (Eq. A1-1). In some simulations we varied T_{opt}^g and with it T_{max}^g (T_{max}^g was always equal to $T_{opt}^g + 10^\circ C$), but Q_{10}^g always remained unchanged (see parameter values in Table 2-1 and parameter estimation in Appendix 2). $i(T)$ in eq. (16) is an essential functional relationship of our model, because its deviation from the thermal response of phytoplankton growth rate ($j(T)$; Eq. A1-1 in Appendix 1) determines the difference in optimal temperature conditions for phytoplankton growth and grazing, which in turn determines the extent of eutrophication as will be shown in our results. Both i_{max} and k_g were estimated by fitting field data from Vohmann *et al.*, 2010 by linear regression (see values in Table 2-1 and estimation in Appendix 2).

Eq. 16 produces a decline in the filtration rate with increasing phytoplankton concentrations. Such a decline has been observed at higher phytoplankton concentrations in several BFF species (e.g. *Dreissena polymorpha*, Sprung & Rose, 1988; *C. fluminea*, Lauritsen, 1986; *Cerastoderma edule* and *Venerupis*

pullastra; Foster-Smith, 1975) (Fig. A2-3). Note that at lower phytoplankton concentrations, the filtration rate is set to f_{\max} (see *min* operator in eq. (15) and below for quantifying f_{\max}).

Although BFF filtration rate varies with the body size of individuals (e.g. Bayne & Newell, 1983), for simplification we assumed an equal shell length of 10.5mm for all individuals in the simulations. This value is in the range of that of the BFF used in Vohmann *et al.*, 2010 (their shell length was 10-11mm) and is in the lower range of sizes exhibited in *C. fluminea* (which can reach nearly four times this size; e.g. Aldridge & McMahon, 1978; note that the size of this species is highly variable among different populations, Araujo *et al.*, 1993). Moreover, in several mussel species the filtration rates reported in different studies are highly variable and *Corbicula fluminea* is no exception (e.g. Viergutz & Weitere, 2013).

We set the maximum filtration rate of BFF (f_{\max}) to 5 l/(ind.*d), which, although may appear high when compared with some experiments feeding phytoplankton to BFF (Viergutz *et al.*, 2012 reports f_{\max} values of ca. 3 l/(ind.*day); but Lauritsen, 1986 reports values larger than 18 l/(ind.*day)), is conservative compared with measurements of BFF feeding on natural phytoplankton assemblages (Vohmann *et al.*, 2010 reported filtration rates of about 2-18 l/(ind.*day), Table A2-1 in Appendix 2. Moreover, Mattice (1979) found f_{\max} values to be about 19 l/(ind.*day)). In addition, this is near the value used in other modelling studies of 86 l/(gC*d) or ca. 4.8 l/(ind.*d), (considering the transformation factor they estimated: ca. 0.056g/ind.) for *Corbicula spp.*, which was obtained based on published values (Descy *et al.*, 2012, Pigneur *et al.*, 2014). Furthermore, a recent study on the filtration rate of four invasive BFF (*Dreissena polymorpha*, *D. rostriformis* and two *Corbicula* lineages: R and S), indicated that maximum filtration rates surpass this value (being ca. 200 l/(gC*d) for both *Corbicula* lineages and even higher for the dreissenids: ca. 200-700 l/(gC*d); Marescaux *et al.*, 2016).

Note that f_{\max} has the same effect as BFF density (ind./m²). Therefore, any over- or underestimation of this value would follow the trends testing different BFF densities. Moreover, note that Eq. 15 assumes that BFF graze on all phytoplankton taxa with the same efficiency, i.e. all taxa have the same edibility. Although this is unlikely in nature (Bastviken *et al.*, 1998), it is a useful simplification and helps us to analyze the effects of other variables. Moreover, we assumed active filtration all the time, although bivalve seem to have resting periods in which they close their valves and presumably do not filter (e.g. Englund & Heino, 1996, Ortmann & Grieshaber, 2003, McIvor, 2004).

Although the grazing rate of different phytoplankton taxa can differ strongly (Bastviken *et al.*, 1998), the phytoplankton community is represented here as a single population and we simulated a single grazing rate for the whole community. However, because BFF can reduce most phytoplankton taxa (Bastviken *et al.*, 1998) and because we use a conservative grazing rate (Appendix 2) the main pattern of our results is unlikely to differ substantially from simulations of different phytoplankton taxa with their particular BFF grazing rate.

2.4 EXTINCTION THRESHOLDS, PARAMETER RANGE RESTRICTIONS AND RELATIONSHIP BETWEEN BFF DENSITY AT TIME t AND IN THE ENTIRE RIVER (G_t VS G)

In our model, whenever the phytoplankton concentration (P_t) is lower than a defined threshold value (P_{ext} ; 10^{-5} mgC/l) the simulation stops (this limit is set in order to avoid nonsensical results, such as negative phytoplankton concentrations).

Moreover, the euphotic zone ($D_{pro}(L, P_t)$) values were restricted to avoid nonsensical results (euphotic zone can neither be negative nor can it be larger than the depth of the river (D)). If $D_{pro}(L, P_t) > D$ then $D_{pro}(L, P_t) = D$. Moreover, if $D_{pro}(L, P_t) < 0$ then $D_{pro}(L, P_t) = 0$.

In addition, the mean photosynthetically active radiation intensity just below the water surface (I_{sur}) was restricted to avoid negative values (impossible in nature) and zero values (the logarithm of zero is not defined): if $I_{sur} \leq 0$ then $I_{sur} = 1e-9$. Moreover, no light means that there is no euphotic zone, i.e., if $I_{sur} = 1e-9$ we set $D_{pro}(L, P_t) = 0$.

Finally, in Chapters 3 and 4 the BFF density at time t (G_t ; i.e. the density of BFF actually grazing on phytoplankton) is equal to the BFF density in the entire river (G). In other words G_t is temporally and spatially constant in these chapters. This is because we assumed a homogeneous BFF distribution in the river. In Chapter 5, however, we assumed heterogeneity in BFF distribution and thus G_t differs from G in most cases.

Symbol	Parameter	Units	Value	Reference
<i>Phytoplankton</i>				
C_{chl_r}	Carbon to chlorophyll <i>a</i> ratio	Unitless	25	Admiraal <i>et al.</i> , 1992. This value has also been employed in estimations of the carbon flow in the Rhine (Weitere <i>et al.</i> , 2005).
I_{lim}	Light intensity at which the phytoplankton growth becomes limited	$\mu E/(m^2*s)$	6	Value for diatoms (Richardson <i>et al.</i> , 1983). A very similar value (7) is used by Schöl <i>et al.</i> , 2002 for simulations in the Rhine.
I_{opt}	Optimum light intensity for phytoplankton growth	$\mu E/(m^2*s)$	84	Value for diatoms (Richardson <i>et al.</i> , 1983). A very similar value (86) is used by Schöl <i>et al.</i> , 2002 for simulations in the Rhine.
k_m	Half-saturation coefficient for the density-dependent mortality rate	mgC/l	50	Calibrated to keep Pout in a realistic range when $P_{in} = 10\text{mgC/l}$, i.e. ca. 12.5mgC/l at shallow waters (depth= 1m) but above 5mgC/l at deeper ones (depth= 4m) ⁵
Mb	Base coefficient for the thermal response of phytoplankton mortality rate	d^{-1}	1.07	Nyholm, 1978
m_{max}	Maximum density-dependent mortality rate	d^{-1}	0.8	Calibrated to keep Pout in a realistic range (see note on k_m) ⁵
$P_{in} (P_{t=0})$	Initial phytoplankton concentration	mgC/l	1.0*, 0.02-10.02**	* Chapter 3. ** Chapters 4 and 5. See Appendix 3 for a justification of these values.
p_{max}	Maximum gross growth	d^{-1}	1.8	In the higher range of values from Lüring <i>et al.</i> , 2013; Schöl <i>et al.</i> , 2002 (for diatoms)
Q_{10}^p	Rate of change of the thermal response function given a 10°C increase	Unitless	1.88	Bissinger <i>et al.</i> , 2008; this value is also very close to that used by Schöl <i>et al.</i> , 2002 for both diatoms and green algae (1.85; based in Straškraba & Gnauck, 1983 as cited in Schöl <i>et al.</i> , 2002)
Rb	Basic (dark) respiration	d^{-1}	0.085	Schöl <i>et al.</i> , 2002
Rp	Photorespiration factor	Unitless	0 or 0.04*	0.04 was used during day time while zero was used during the night. The values are taken from Schöl <i>et al.</i> , 2002 but our implementation of the values is slightly different. (According to Schöl <i>et al.</i> , 2002 0.04 was used inside the euphotic layer and zero was used outside the euphotic layer and during the night.)
T_{max}^p	Maximum temperature for phytoplankton growth	°C	36	See Appendix 1
T_{opt}^p	Optimum temperature for phytoplankton growth	°C	24, 27 and 30	See Appendix 1
<i>Benthic filter feeders (BFF)</i>				
G	Density of BFF population in the river	ind./m ²	0, 100, 300 and 500	These concentrations are in the range of the values reported for <i>D. polymorpha</i> and <i>C. fluminea</i> in several sites (see Appendix 3). Note, however, that the BFF distribution is patchy so that the BFF density in the entire river length is difficult to estimate
i_{max}	Maximum ingestion rate	mgC/(ind.*day)	4.35	Fitted to Vohmann <i>et al.</i> (2010) data (assumes the body size (shell length) of BFF is 10.5mm). See Appendix 2
f_{max}	Maximum BFF filtration rate	l/(ind.*d)	5	See Section 2.3.3
k_g	Coefficient for BFF ingestion	mgC/l	0.39	Fitted to Vohmann <i>et al.</i> (2010) data; see Appendix 2

Symbol	Parameter	Units	Value	Reference
Q_{10}^g	Rate of change of ingestion rate given a 10°C temperature increase	Unitless	2.0	See Appendix 1
T_{max}^g	Maximum temperature for BFF ingestion	°C	$T_{opt}^g + 10$	See Appendix 1
T_{opt}^g	Optimum temperature for BFF ingestion	°C	19, 22 and 25	See Appendix 1
<i>Physical parameters</i>				
<i>atte_chl</i>	Attenuation coefficient of light in the water column due to phytoplankton (measured in chlorophyll <i>a</i> concentration)	l/ (µgchl- <i>a</i> *m)	0.013	Schöl <i>et al.</i> , 2002
<i>atte_S</i>	Attenuation coefficient of light in the water column due to seston	l/(mg*m)	0.052	Schöl <i>et al.</i> , 2002
<i>atte_W</i>	Attenuation coefficient of light in the water column due to water	m ⁻¹	1.06	Schöl <i>et al.</i> , 2002
<i>D</i>	Depth of the river (i.e. water depth)	M	1 - 8	In the range of values found in some rivers including the Rhine (Admiraal <i>et al.</i> , 1993, Uehlinger <i>et al.</i> , 2009) and Middle Elbe (Scharfe <i>et al.</i> , 2009).
<i>DL</i>	Day length (amount of hours per day with solar radiation)	H	15.03	Palz & Greif, 1996 ^{1,2,5}
<i>DR</i>	Average daily radiation	Wh/(m ² *d)	4643.33	Palz & Greif, 1996 ^{1,3,5}
<i>LR</i>	Length of the river stretch	M	500,000	In the range of long rivers, e.g. the Elbe (1,094km; Scharfe <i>et al.</i> , 2009), the Rhine (ca. 1,250km; Uehlinger <i>et al.</i> , 2009), the Danube (2,780km; WWF, 2002), the Volga (3,531km; WWF, 2002)
<i>N</i>	Roughness coefficient of the river channel	Unitless	0.04	See Appendix 3
<i>PAR_r</i>	Fraction of the light which is photosynthetically active radiation	Unitless	0.5	Approximate value for different atmosphere types at solar altitudes greater than 40°C (Kirk, 1994)
<i>S</i>	Slope of the river channel	m/m	0.0004	See Appendix 3
<i>SC</i>	Seston content without phytoplankton	mg/l	25	In the range of values from the River Rhine (24mg/l) ⁴ and Elbe (26mg/l) ⁴ .
<i>T</i>	Temperature	°C	0 - 32	See A3.4 Section in Appendix 3
<i>W</i>	Width of the river	M	100	In the lower range of values of the upstream segments of Rhine River (Bleninger <i>et al.</i> , 2006; Uehlinger <i>et al.</i> , 2009)
<i>WRC</i>	Water reflection coefficient	Unitless	0.05	In the range of values for midday solar angle at latitude 50°N (Kirk, 1994)
<i>Technical details of the simulations</i>				
<i>P_{ext}</i>	Minimum phytoplankton concentration below which the simulation stops	mgC/l	10 ⁻⁵	-
<i>th_{t=0}</i>	Initial value of day time (<i>th</i>) for each day	Hours	0.5	-

Table 2-1. Parameters employed in the model. Notes: 1) Data from Cologne/Wahn station (latitude 50°52'N), for the years 1966-1975; values are means of three months (April, May and June), to represent spring conditions; 2)

Monthly mean of astronomical sunshine duration ; 3) Estimated monthly mean of daily global irradiation; 4) For the Rhine mean seston content is for 1992–2009 (data International Commission for the Protection of the Rhine/BfG) and for the Elbe it is for 1994–2009 (data River Basin Community Elbe), both sources cited in Hardenbicker et al., 2014; 5). See A3.5 Section on Appendix 3 for information on the impact of day length and average daily radiation and mortality parameters (k_m and m_{max}) on phytoplankton growth.

Symbol	Variable	Units	Equation
<i>Phytoplankton</i>			
$j(T)$	Thermal response for phytoplankton growth	unitless	A 1-1
$h(N)$	Nutrient dependence for phytoplankton growth	unitless	-
$l(T, L, D, P_t)$	Phytoplankton losses due to processes other than benthic grazing	d^{-1}	14
$p(T, L, D, SC, N, P_t)$	Phytoplankton gross growth rate	d^{-1}	6
P_t	Phytoplankton concentration at time t	mgC/l	5
$u(L, D, SC, P_t)$	Light dependence for phytoplankton growth	unitless	7
<i>Benthic filter feeders (BFF)</i>			
$f(P_t, T)$	Filtration rate of BFF individuals (at high phytoplankton concentrations)	l/(ind.*d)	16
$g(T, P_t, G_t)$	Grazing rate of the BFF population	mgC/(l*d)	15
G_t	Density of BFF population at time t	ind / m ²	See “Simulation details”
$i(T)$	Thermal response for BFF grazing rate	unitless	A 1-1
<i>Physical variables</i>			
$atte(SC, P_t)$	Attenuation coefficient of light in the water column	m ⁻¹	9
DP	Fraction of the day that has passed	unitless	13
D_{pro}	Depth of the productive (i.e. euphotic) water layer	m	10
HR	Hourly radiation	W/m ²	12
I_{sur}	Mean photosynthetically active radiation intensity just below the water surface	$\mu E/(m^2*s)$	11
LS	Length of a river segment	m	4
PF	Photoperiod fraction (fraction of the day with sun light)	unitless	8
R	Hydraulic radius of the river stretch	m	2
t	Simulation time step	hours	-
$t_{res,out}$	Water residence time at the outlet of the river stretch	hours	3
Th	Day time for each day	hours	See text below Eq. 13
T^*	Exponent coefficient for the thermal response of phytoplankton mortality	°C	See text below Eq. 14
v	Water speed (in downstream direction)	m/s	1

Table 2-2. Variables employed in the model.

CHAPTER 3 - EFFECTS OF WARMING ON GRAZER-CONTROLLED PHYTOPLANKTON IN RIVERS WITH IMPLICATIONS FOR EUTROPHICATION

This chapter studies the effect of temperature, water depth and the thermal response of phytoplankton growth and BFF grazing on the phytoplankton concentration (eutrophication) at the outlet of a river stretch (Pout). We assumed a constant initial (upstream) phytoplankton concentration in such river stretch (Pin= 1.0 mgC/l) in all simulations. Moreover, we assumed a homogeneous distribution of BFF throughout such river stretch in all simulations. However, the effects of Pin and of the spatial BFF distribution on eutrophication (Pout) are explored in Chapters 4 (Pin) and 5 (Pin and BFF distribution).

3.1. INTRODUCTION

Climate change effects on ecosystems and reliable methods for predicting them are currently intensely debated. There is consensus that traditional correlative climate-envelope approaches assuming that species just follow their shifted environmental niche are of limited applicability (e.g. Davis *et al.*, 1998, Singer *et al.*, 2016). The reason is that they do not consider ecological mechanisms determining species dynamic responses to climate change besides the abiotic niche. A recent review lists six essential ecological mechanisms and reminds that they should be considered to improve the predictions of climate change in ecosystems (Urban *et al.*, 2016).

Two of these mechanisms, physiology and species interactions, seem interlinked in some food webs. For example, thermal responses to increasing temperature [physiology] may differ between resource and consumers and this can change community structure and dynamics [species interactions] (Yvon-Durocher *et al.*, 2011, Dell *et al.*, 2014). These differential thermal responses seem supported by evidence suggesting that the indirect effects of temperature, mediated by trophic interactions, may be equal or more important than the direct effects on single trophic levels (O'Connor, 2009, Alsterberg *et al.*, 2013). Moreover, these differential effects of temperature can be widespread in nature as suggested by the differences in the thermal responses of consumers and resources (Dell *et al.*, 2014).

A consumer-resource interaction which is relevant in several aquatic systems and seems to respond differently to warming is that of phytoplankton and benthic filter feeders (BFF; Viegutz *et al.*, 2007).

Phytoplankton is the main primary producer in large rivers, providing the main source of energy in deep channels (e.g. Vannote *et al.*, 1980). However, when its abundance becomes high it can damage the ecosystem and its services (Smith, 2003, Smith *et al.*, 2006, see introduction to Chapter 4 for examples).

Phytoplankton growth can respond to several factors. Although, it can be limited by nutrients, this limitation is likely moderate in rivers with high nutrient concentrations such as those from several industrial and agricultural areas (e.g. Smith *et al.*, 1993; 1997). Importantly, phytoplankton growth increases with temperature, up to an optimum (e.g. Butterwick *et al.*, 2005, Lürling *et al.*, 2013). Nonetheless, temperature also determines a common loss process of phytoplankton in rivers, namely grazing by benthic filter feeders (BFF; e.g. Mattice, 1979, Reeders & Bij de Vaate, 1990, Viergutz *et al.*, 2007). In fact, experiments suggest that warming can alter both BFF grazing rate and the growth rate of (heterotrophic) planktonic prey (Viergutz *et al.*, 2007) and it is an open question what are their combined effects on river eutrophication under warming.

In addition, the thermal responses of BFF grazing rate and phytoplankton growth rate may differ among species and sites (or at least among studies; Appendix 1 shows some variations in BFF filtration rate with temperature; see Weitere *et al.*, 2008 for an intraspecific comparison of BFF. Moreover, see Thomas *et al.*, 2016 for the variability of phytoplankton growth with temperature according to latitude, ecosystem and functional group).

Despite their relevance, warming effects on grazer-controlled phytoplankton have never been analyzed using systematic model simulations. Moreover, to the best of our knowledge, the effects of variations in thermal responses have never been analyzed systematically for this consumer-resource interaction. In fact, there are scarce studies of such variations for consumer-resource interactions in general (for preliminary work see Dell *et al.*, 2014 for a general framework focusing on the rising part of the thermal response and Öhlund *et al.*, 2015 for an analysis of such variations in a specific consumer-resource pair focusing on consumer response, i.e. attack rate). Instead, certain specific thermal responses are often assumed when modelling the effects of BFF grazing on phytoplankton in a particular site (e.g. Schöl *et al.*, 2002, Pigneur *et al.*, 2014). In addition, although the effect of BFF grazing on phytoplankton is determined by both water depth (e.g. Caraco *et al.*, 1997, Lucas & Thompson, 2012) and residence time (Lucas & Thompson, 2012), the effects of the interplay of these factors with warming is unknown. River temperature and depth are not independent (Smith, 1972) and climate change is likely to affect these two variables simultaneously in several systems (IPCC, 2013).

Our aim here is to test how phytoplankton abundance in river channels responds to warming in the short term, i.e. during the time in which the phytoplankton is travelling to the outlet of the river (a few days) and BFF populations are relatively unchanged. We investigated how this response depends on grazing by BFF of different densities and how it is altered by water depth and residence time. To focus on this and as a baseline, we assume homogeneous river morphology and well-mixed waters. We used the spatiotemporal simulation model of phytoplankton dynamics in rivers developed in Chapter 2. This model considers the differences in thermal responses of both phytoplankton growth and benthic grazing over a large temperature range. We studied how these differential thermal responses of the two trophic levels interact in this consumer-resource interaction and how the hydrological characteristics of the river, particularly water depth, alter the responses of phytoplankton to warming.

3.2. SPECIFIC METHODS

We used the simulation model described in Chapter 2 to study the effect of BFF grazing on phytoplankton (eutrophication) in rivers under warming. We focused on the resulting phytoplankton concentration at the outlet (P_{out}) as a measure for eutrophication and studied its dependence on BFF density in the river (G), varying from 0 to 500 ind./m², under a wide range of temperatures (T ; varied from 0 to 32°C) and water depths (D ; varied from 1 to 8m). We explored the effect of different thermal responses by varying the optimum temperature of phytoplankton growth (T_{opt}^p ; from 24 to 27°C) and of BFF grazing rate (T_{opt}^g ; from 19 to 25°C). The initial phytoplankton concentration at the source ($P_{in} = P_{t=0}$) was set to 1.0 mgC/l in this chapter (see Appendix 3 for a justification of this value). In Chapters 4 and 5 we explore the effects of varying P_{in} value.

3.3. RESULTS

3.3.1. Influence of temperature, depth and grazing on downstream phytoplankton concentration (P_{out})

Under grazer absence, the downstream phytoplankton concentration (P_{out}) was maximum at its optimum growth temperature ($T_{opt}^p = 27^\circ\text{C}$) and gradually decreased as temperature departed from this optimum (Fig. 3-1). This resulted in a non-monotonic unimodal response of P_{out} to temperature. This unimodal response was flattened and its P_{out} values lowered with increasing water depth (Fig. 3-1; Fig. 3-2, left

plots). Therefore, very shallow waters with temperatures around T_{opt}^P promoted the highest Pout in the range of conditions tested (Fig. 3-2).

Besides the non-linearity of the relationship between Pout and temperature, it is worth noting the non-linearity of the relationship between Pout and water depth: for any given change in depth and grazer density, Pout changed more rapidly at shallow waters than at deeper ones.

However, grazing can strongly alter, or even reverse, the unimodal relationship between Pout and temperature, particularly at high BFF densities (Figs. 3-1 and 3-2; see also Appendix 4 for BFF densities of 100 and 500 ind./m²). The closer the temperature was to the optimum for benthic grazing (T_{opt}^g ; in Fig. 3-1 equal to 22°C), the stronger the grazer-mediated decrease in Pout (with respect to the condition without BFF) (Figs. 3-1 and 3-2). As temperatures departed from the optimum for benthic grazing, Pout was less affected by BFF grazing (Figs. 3-1 and 3-2). This resulted in a non-monotonic (but also not unimodal) relationship between Pout and temperature under certain conditions, e.g. at high BFF densities (300-500 ind./m²) at 2-4m depth.

Moreover, grazing can also reverse the relationship between Pout and water depth: when grazers were present at moderate or high densities (i.e. 300-500 ind./m²) the shallowest waters yielded, at several temperatures, the minimum Pout (Figs. 3-1 and 3-2). Hence, the variability in Pout at different grazer densities was larger at shallow waters.

Nevertheless grazer-controlled Pout can increase rapidly within small temperature changes when optimum grazing temperature (T_{opt}^g) was exceeded (Figs. 3-1 and 3-2). These rapid increases therefore reveal a temperature threshold beyond which grazer control is not effective anymore. This threshold was more pronounced in shallow waters and it usually augmented at high BFF densities. Under these conditions, Pout can rise from almost zero to ca. 3 mgC/l within a few degrees °C (Figs. 3-1 and 3-2; see also Appendix 4 for grazer densities of 100 and 500 ind./m²). This was true even when higher BFF densities produced a large range of temperatures and depths where Pout was low (compare different BFF densities in Figs. 3-1 and 3-2 and from Appendix 4). However, the steepness of the threshold effect depended not only on BFF density but also on the difference between the thermal responses of grazing and phytoplankton growth (T_{opt}^g and T_{opt}^P , respectively; see next section).

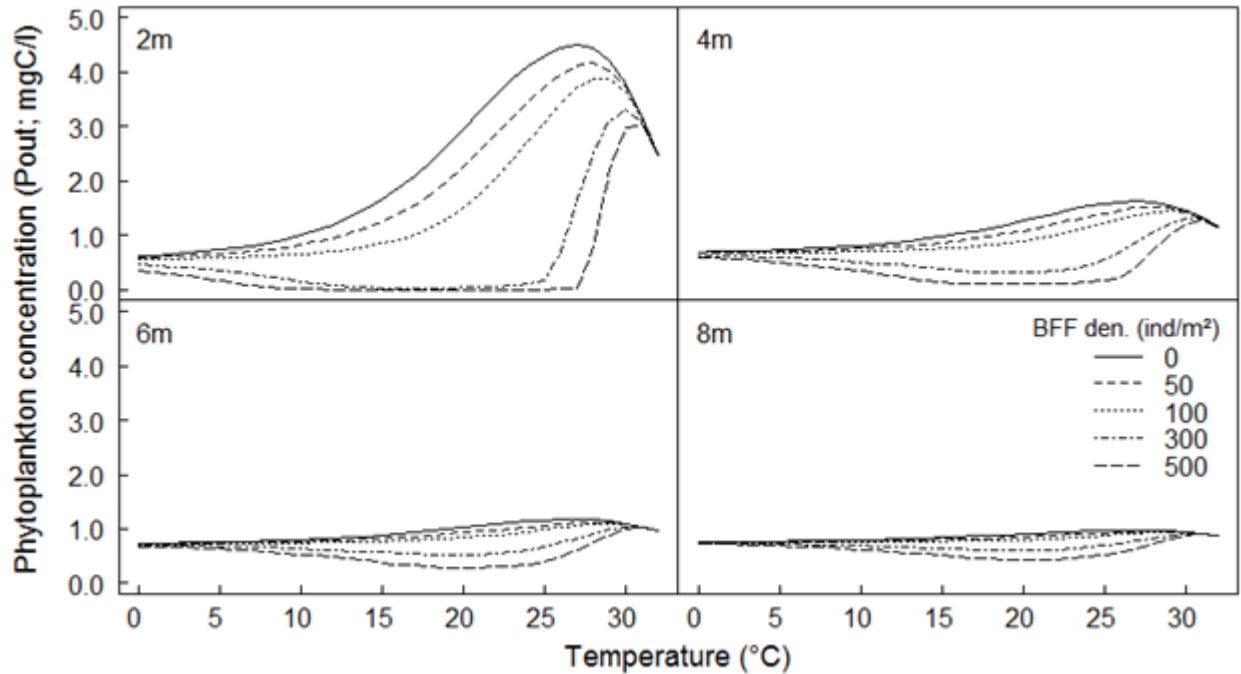


Figure 3-1. Phytoplankton concentration versus water temperature for different BFF densities and water depths (T_{opt}^P : 27°C, T_{opt}^g : 22°C).

In general, deep waters with extreme temperatures were the least affected by grazing, but were also the ones, especially cold waters, which yielded the lowest Pout in the absence of grazers. In most cases, the highest Pout values developed in shallow hot waters even when grazer density was high (Figs. 3-1 and 3-2).

3.3.2 Influence of thermal response of both grazing and phytoplankton growth

The preceding results were derived using certain values for the thermal responses of both BFF grazing rate ($T_{opt}^g = 22^\circ\text{C}$) and phytoplankton growth rate ($T_{opt}^P = 27^\circ\text{C}$). However, thermal responses can vary between taxa and studies (see introduction and Appendix 2) and are expected to change with succession, in the case of phytoplankton communities, and/or adaptation, in the case of both BFF and phytoplankton. Therefore, to test the effect of the thermal responses in our results we simulated phytoplankton dynamics with values 3°C above and below the ones used in the preceding results for both T_{opt}^P and T_{opt}^g , i.e. $T_{opt}^P = 24$ and 30°C and $T_{opt}^g = 19$ and 25°C . Throughout this text we refer to the impact of the thermal response of grazing rate

using its optimum value T_{opt}^g although maximum temperature for grazing T_{max}^g changes together with T_{opt}^g ; T_{max}^g being always equal to $T_{opt}^g + 10^\circ\text{C}$. In the case of the thermal response of phytoplankton growth rate, however, T_{opt}^p is independent of T_{max}^p ; T_{max}^p being always equal to 36°C (see Appendix 1 for details).

Our results show that the effect of temperature on grazer-controlled downstream phytoplankton concentration (Pout) depends on the thermal response of grazing (T_{opt}^g) and phytoplankton growth (T_{opt}^p) (Fig. 3-2).

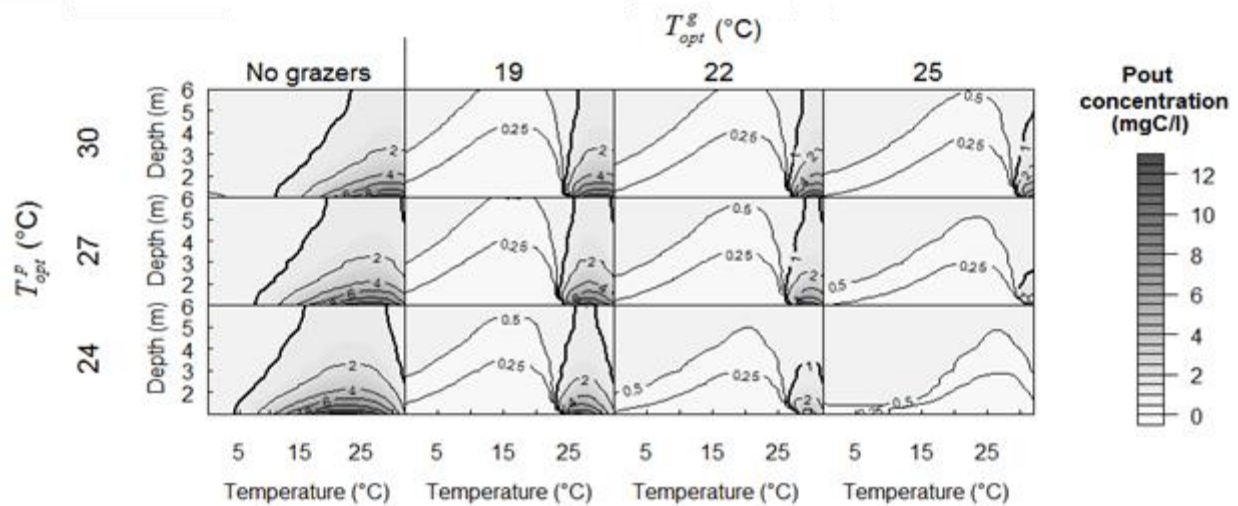


Figure 3-2. Contour plots of downstream phytoplankton concentration (Pout) versus water temperature and depth for different optimum temperatures for phytoplankton growth rate (T_{opt}^p) and BFF grazing rate (T_{opt}^g). The ‘No grazers’ panel (column in the left edge of the figure) shows results without BFF grazing, while the rest of the panels shows results with BFF grazing at a density of 300 ind./m².

Without grazers the number of high Pout values (e.g. $> 8\text{mgC/l}$) and the maximum Pout values increased with decreasing T_{opt}^p . With grazers, as the difference between T_{opt}^p and T_{opt}^g decreased, both (high) Pout values and the number of combinations of depth and temperature where Pout was low (i.e. $< 0.5\text{mgC/l}$) declined. This decline flattened the temperature threshold by producing less extreme Pout values throughout the range of temperatures and depths tested. Increasing BFF density usually amplified these patterns (compare Fig. 3-2; with figures in Appendix 4).

3.4. DISCUSSION

This study investigated how the phytoplankton concentration at the outlet of a large river, Pout, responds to warming and how this response is altered by benthic grazing at different BFF densities. In addition, we tested how the water depth, and its associated water volume (discharge) and residence time ($t_{res,out}$) interact with the temperature effects and altered the response of Pout to warming. Moreover, we analyzed how variations in thermal responses of phytoplankton and grazers affected phytoplankton abundance.

Our main findings are:

(1) The relationship between grazer-controlled phytoplankton concentration (Pout) and water temperature is generally non-linear and non-monotonic, i.e. warming may either increase or decrease Pout depending on its intensity, starting temperature and grazer density, (2) grazing can even reverse the effects of warming on Pout up to a certain temperature; (3) there is a certain threshold temperature above which grazer control fails i.e., grazer-controlled phytoplankton can rapidly increase within small temperature increments, (4) water depth reduces the effects of temperature and grazing on eutrophication (Pout), and (5) the matching of thermal responses of phytoplankton and grazers determines both the temperature range where such control is efficient and the steepness of the effects of temperatures thresholds.

An advantage of our study is that we consider a large range of temperatures (0-32°C), depths (1-8m) and grazer densities (0-500 ind./m²) and to explore their combined effects on Pout in a mechanistic way. This allows us to identify the nonlinear and non-monotonic relationship between Pout and temperature, to monitor its change from a unimodal relationship at zero and low grazer densities to a threshold like relationship under moderate to high grazer densities and just a weak relationship at large depths, thus reconciling seemingly contradictory findings on the effects of warming (see below).

3.4.1. Grazing can reverse the response of phytoplankton to temperature

The non-linear and non-monotonic (unimodal) relationship between downstream phytoplankton (Pout) and temperature that arises under grazer absence (Fig. 3-1) can be explained by the impact of the thermal response curve of phytoplankton growth (Eq. 6 in Chapter 2), which has a unimodal shape (see Appendix 1 for the description of such thermal dependency and for justification of its shape). Note that the term for phytoplankton losses non-due to BFF grazing also increases nonlinearly below 25°C but reaches saturation above this temperature (see Eq. 14 in Chapter 2). Hence, phytoplankton growth and loss both

increase nonlinearly with temperature below 25°C but their patterns differ above it. However, because phytoplankton losses are relatively low at the phytoplankton concentrations studied here, their impact is relatively small.

The changes in the temperature effects on Pout due to grazing (relative to the situation without grazers) are caused by the thermal response curve of BFF grazing. The low Pout reductions in cold waters are caused by low grazing rates because these temperatures are far from the thermal optimum for grazing ($T_{opt}^g = 22^\circ\text{C}$) (Fig. 3-1). However, as temperature increases and approaches T_{opt}^g , BFF grazing rate increases and this reduces Pout. At moderate to high grazer densities, this can even reverse the response of Pout to temperature. This means that, in temperature ranges where Pout increases with warming under low grazer densities (or BFF absence), Pout decreases with warming under high grazer densities. Nonetheless, above T_{opt}^g , the grazing rate decreases strongly and this causes a steep increase in Pout within small additional temperature increments, i.e. a temperature threshold, particularly at high grazer densities and shallow waters (Figs. 3-1, 3-2 and A4-1, A4-2; see Section 3.4.4 for the effects of water depth). Note that the thermal dependency of BFF grazing is asymmetric and this causes faster Pout increases as temperatures depart from T_{opt}^g at hotter than at colder waters (see description of the thermal dependencies in Appendix 1).

The qualitative difference in the temperature effects on Pout between rivers without, or with low, BFF densities and those with higher BFF densities, i.e. a unimodal pattern vs a bimodal pattern with temperature thresholds (Figs. 3-1 and 3-2, A4-1 and A4-2) suggests *we should consider the absence or presence of grazers when making predictions about climate change effects* (Figs. 3-1 and 3-2). Moreover, this finding supports other studies which indicate that the indirect effects of warming, through trophic cascading in the food web, may counteract or even overrule direct effects on a single trophic level (Thompson *et al.*, 2004, Suttle *et al.*, 2007; Barton *et al.*, 2009; O'Connor, 2009, Alsterberg *et al.*, 2013). Our results are particularly in line with a recent review by Urban *et al.*, 2016 claiming that ecological mechanisms such as physiology and species interactions govern the response of ecological systems to climate change. The strength of our approach is that it enables conclusions on warming effects on riverine ecosystems (here: eutrophication) by accounting for these interlinked mechanisms in terms of (mis)matching between the thermal responses of phytoplankton growth rate and grazing rate over a large temperature range and its dependence on a further abiotic factor, the water depth.

The release of resource, i.e. phytoplankton, from grazing at a certain temperature was expected from theoretical and empirical considerations of the thermal responses of resource and consumers (e.g. Pörtner & Farrell, 2008; Dell *et al.*, 2011; Kordas *et al.*, 2011; Dell *et al.*, 2014). Certainly, in some studies warming *decreases* grazer control on resources (see below). However, this study is the first, to the best of our knowledge, reporting a unimodal (first increase, then decrease) response of the performance of grazer control to temperature. It is also the first report revealing the existence of a temperature threshold beyond which resource control suddenly fails, leading to steep resource increases at shallow waters (Figs. 3-1 and 3-2). Undeniably, a study by Öhlund *et al.* (2015), has some similarities but also important differences (see below).

The finding of the non-monotonic response to temperature of resource control by grazing contrasts with experimental studies showing that warming has monotonic effects. Such studies showed ambiguous, partly contradicting effects of warming: (i) warming reduces resource *biomass*, in spite of increased resource growth, apparently due to increased grazing (e.g. O'Connor *et al.*, 2009, Kratina *et al.*, 2012, Shurin *et al.*, 2012); (ii) it increases resource biomass even when grazing increases (e.g. Eklöf *et al.*, 2012); (iii) it has weak or no (net) effects on resource biomass (even when its direct and indirect effects, exposed by partitioning, are strong; Alsterberg *et al.*, 2013).

Since these three response types are present in our model results, our study can help to explain and synthesize the divergent responses to warming in these studies. Our study shows that the determinant of the response type of grazer-controlled phytoplankton to temperature (increasing, decreasing or no relationship) is the relation between grazing pressure and phytoplankton growth, regardless of their absolute values. This finding supports studies showing the importance of *relative* consumer efficiency, i.e. how much consumption rate increases in relation to resource growth, when assessing warming effects (e.g. O'Connor, 2009, Eklöf *et al.*, 2012).

In particular, we found that the relation between grazing pressure and phytoplankton growth depends on: (1) the temperature range considered, i.e., the initial (before warming) and final (after warming) temperature, (2) the water depth, through its effect on water volume (influencing grazing pressure), light availability (influencing phytoplankton growth) and residence time (influencing the time for both grazing and phytoplankton growth) (see Section 3.4.4), (3) the grazer density and (4) the thermal response curves of grazing rate and phytoplankton growth rate (see Appendix 1 for the description of these curves), including their optima (Section 3.4.3), determining the (mis)match of such rates.

Among these factors, we believe that testing a large temperature range and, particularly, using unimodal thermal response curves for both phytoplankton growth and grazing rate are fundamental to encompass the manifold relations between grazing pressure and phytoplankton growth and therefore to reveal and synthesize the three different response types of phytoplankton biomass to warming (increasing or decreasing or no response at increasing temperature) found in other studies.

Moreover, our analysis suggests three possible reasons why other studies show only monotonic relationships between warming and resource biomass (and not non-monotonic patterns) and, in particular, why these studies do not show temperature thresholds in grazer control.

First, the temperature range investigated was too narrow to include the threshold even when it existed. Several experiments tested warming using only one temperature or a relatively limited temperature range above the control temperature (e.g. Barton *et al.*, 2009; O'Connor, 2009; Eklöf *et al.*, 2012; Kratina *et al.*, 2012; Shurin *et al.*, 2012). Accordingly, it has been argued that threshold effects may be unreported in the literature since experiments are usually done in temperature ranges where predators consume prey (Öhlund *et al.*, 2015).

Second, the temperature threshold does not exist or is very attenuated under the studied biotic and abiotic conditions. Regarding abiotic factors, water depth can highly attenuate the effect of the temperature threshold (e.g. when BFF density is 300 ind./m² the threshold at 8m is much less pronounced than at 2m; Fig. 3-1). Regarding biotic factors, some grazer species may be greatly efficient (or inefficient) over most of their temperature range and this may reduce or eliminate the temperature threshold, e.g. low grazing efficiency exemplified by a BFF density of 100 ind./m² did not show thresholds at depths 2-8m (Fig. 3-1). Moreover, compensatory feeding at high temperatures when such temperatures decrease food quality is a probable explanation that high temperatures did not decrease grazing in a study with *D. polymorpha* (Hardenbicker *et al.*, 2015a).

Third, in the case of simulation studies, in addition to the previous reasons, results are influenced by the choice of the thermal response function. Using functions that increase monotonically with temperature will, evidently, not decrease grazing at high temperatures and, thus, resource abundance is unlikely to increase sharply with temperature (e.g. O'Connor *et al.*, 2009).

3.4.2. Thresholds in ecosystems and comparison with the findings of Öhlund et al. (2015)

Our finding of a temperature threshold for eutrophication control by grazers agrees with Öhlund *et al.* (2015), who, using both a simple model and empirical data, showed that consumer (northern pike) *attack rates* on resources (brown trout) fell sharply below certain temperature. Öhlund *et al.* (2015) modelled thermal responses as both exponential and unimodal functions and, although they used different trophic levels than here, some of their conclusions are similar to ours (compare the general shape of our Figure 3-1 at 2m with BFF density of 300ind./m² with Figure S1f in Appendix 1 of Öhlund *et al.* (2015)). However, it is worth noting some differences between our study and Öhlund *et al.*, 2015:

- (1) The temperature thresholds refer to different variables: while Öhlund *et al.*, 2015 refers to thresholds in *consumer attack rates* here we focused on thresholds of *resource biomass*. Undeniably, these variables are related because attacks, if successful, reduce resource biomass.
- (2) The thermal responses studied are from different processes: regarding resources, Öhlund *et al.*, 2015 studied prey escape speed, which helps resources to *avoid* being eaten, while here we focus on resource dynamics, which does *not* help to avoid such consumption (even when its effect on resource biomass can *oppose*, if net growth is positive, that of consumption). Regarding consumers, Öhlund *et al.*, 2015 studied attack speed while here we focus on grazing rate.
- (3) The foraging strategies differ: Öhlund *et al.*, 2015 studied active capture (both predator and prey move in space) and here we study a particular type of grazing (sessile BFF grazing on a phytoplankton population advected by river water).

Regarding (1), here we have expanded the conclusion from Öhlund *et al.* (2015) concerning the effects of warming including not only effects on consumer (attack rates), but also on resulting resource dynamics (phytoplankton concentration, Pout). Hence, our study shows effects on resource biomass (abundance), rather than only in a behavioral trait. This is important, because resource abundance is an important determinant of the flow of energy and matter in the food webs.

Regarding (2) and (3), the thresholds studied by Öhlund *et al.* (2015) require mobile prey and predators with an attack rate that is temperature-dependent. With our study we show that the temperature threshold also exists for other foraging strategies, including grazing, where prey (resources) cannot escape from consumers (but may compensate grazing with growth).

Finally, it is very interesting that although the fall in grazing rate above T_{opt}^g is not extremely steep (Figure A1-2 in Appendix 1), the resource abundance (Pout) does increase steeply with temperature in such a range. Hence, our results seem to expand conclusions from Öhlund *et al.* (2015) that warming may lead to ecological regime shifts when ecological rates show thresholds in the thermal responses to cases where rates are just moderately declining but interact through species interactions. Such regime shifts are of special concern because, due to their abrupt nature, they give little time for species and societies to adapt (Mastrandrea & Schneider, 2001, Scheffer *et al.*, 2001, NRC, 2013).

3.4.3. Matching in thermal response curves determines the outcome of grazer-controlled phytoplankton and the conditions where it occurs

The analysis of varying the thermal responses of BFF grazing and phytoplankton growth showed the influence of these responses on eutrophication control and on the presence and intensity of temperature thresholds for eutrophication control (Fig. 3-2).

Generally, Pout values, and the temperature threshold, were less extreme throughout the range of depths and temperatures tested if the difference between thermal responses was small (i.e. $T_{opt}^p \approx T_{opt}^g$). For example, if T_{opt}^p is 24°C and T_{opt}^g is 25°C (Fig. 3-2) Pout is lower and the temperature threshold less evident than when such difference is larger (e.g. T_{opt}^p of 30°C and T_{opt}^g of 19°C; Fig. 3-2). This is because the coincidence between thermal responses of phytoplankton growth and BFF grazing (i.e. $T_{opt}^p \approx T_{opt}^g$) makes it harder for phytoplankton to grow and for grazers to deplete phytoplankton as high grazing rates coincide with high phytoplankton growth rates. In contrast, large differences in the thermal responses (i.e. $T_{opt}^p \gg T_{opt}^g$) produce a mismatch between high phytoplankton growth rates and high grazing rates. This mismatch causes, on the one hand, high Pout values at hot waters, where grazing rate is low but phytoplankton growth rate is high. On the other hand, it produces low Pout values at warm waters where grazing rate is high but phytoplankton growth rate lower⁴.

⁴ Note that without grazers we observed a pattern which contradicts the expectation that, in nature, phytoplankton growth and thus maximum Pout values increase with the thermal optimum for phytoplankton growth, T_{opt}^p (e.g. Eppley RW (1972) Temperature and phytoplankton growth in the sea. *Fish. Bull.*, **70**, 1063-1085.). We observed, however, more maximum Pout values as T_{opt}^p decreased (Fig. 3-2). This seems caused by two factors. First, because, lower T_{opt}^p values are farther away from the higher limit of temperature range tested (32°C) and from the maximum

This study is, to the best of our knowledge, the first one testing the influence of varying *thermal optima* on consumer-resource interactions. Dell *et al.*, 2014, however, provided a general framework on the impact of thermal response curves focusing on *the rising part* of them, i.e. the part below the thermal optima. In fact, Dell *et al.* (2014) predicted that when thermal optima are different enough, mismatches in the thermal responses of resource and consumers would be important. Our results support this prediction showing that large mismatches in thermal optima (i.e. between T_{opt}^p and T_{opt}^g) reduce grazer control (Figs. 3-2, A4-1 and A4-2).

Our results also support the expectation of Englund *et al.* (2011) that community responses to climate change will reflect the differential thermal optima of species. Importantly, it is worth noting that mismatches in the thermal responses of resource and consumers are likely to be common in nature according to an analysis of a large dataset (Dell *et al.*, 2014). Therefore, grazing limitation and the consequent increase in resource abundance at high temperatures can be a widespread phenomenon in several ecosystems.

These results underline that, at least for some biotic processes, species and temperature ranges, the use of unimodal (“hump-shaped”) thermal response curves (e.g. Gilchrist, 1995, Bulté & Blouin-Demers, 2006, Pörtner & Farrell, 2008, Bonebrake & Mastrandrea, 2010, Englund *et al.*, 2011, Kordas *et al.*, 2011, Dell *et al.*, 2014, Vasseur *et al.*, 2014) instead of monotonic (e.g. linear or exponential) ones (e.g. Gillooly *et al.*, 2001, O'Connor, 2009, O'Connor *et al.*, 2011, Eklöf *et al.*, 2012) is pivotal. A highly efficient consumer within a given temperature range may become (perhaps, within a very short temperature range) inefficient when a temperature threshold is exceeded. Hence, efficiency and inefficiency are always coupled to certain temperature ranges. This is particularly relevant considering that most biological traits have a unimodal response to temperature (Dell *et al.*, 2011). (Note that we are not suggesting that using monotonic functions to model thermal responses is always wrong, but we believe that it has limitations

temperature for phytoplankton growth, T_{max}^p implying more Pout in this temperature range. Second, because phytoplankton losses non-due to benthic grazing decrease with temperature (below 25°C; Eq. 14 in Chapter 2) implying again larger Pout.. However, note that even if phytoplankton growth and loss processes would result in maximum Pout values increasing with T_{opt}^p as expected in nature, it would likely strengthen the main pattern of our results and support our conclusions.

under some conditions and systems, e.g. Englund *et al.*, 2011, Lemoine & Burkepile, 2012. See other arguments for the use of unimodal thermal responses in Appendix 1).

Regarding the shape of the performance curve, it is worth considering that, as long as the thermal response of *grazing* rate is unimodal, using a linear, saturating or even exponential thermal response for phytoplankton growth is unlikely to alter the main pattern of our results: a low phytoplankton abundance, due to strong grazer control at warm temperatures but a subsequent increase in phytoplankton abundance, due to low grazer control, at hot waters.

For a discussion of the realism of the values of thermal optima in relation to river temperature see Chapter 4, Section 4.4.5.

3.4.4 Temperature effects on eutrophication biocontrol decrease with water depth

Under grazer absence the decrease of phytoplankton growth with depth can be explained by the shorter residence time ($t_{res,out}$), i.e. the time that phytoplankton travels through the river stretch and by the light attenuation. The shorter residence time limits the time available for phytoplankton growth (see Eqs. 1-3 for the relationship between water depth and $t_{res,out}$). Deeper waters also have less light available for phytoplankton growth. This is because, if phytoplankton concentration (mgC/l) and therefore light attenuation (per meter) are held constant, increasing water depth increases the length over which the light is attenuated (see Eqs. 9-10 for the effect of self-shading on light availability in the model). This decreases the light available for phytoplankton growth at the lower water layers and therefore the carrying capacity (K) in deeper waters.

The effects of depth on Pout depend on grazing, i.e. the fact that, without grazers, increasing water depth decreases phytoplankton growth while with enough grazers increasing water depth increases phytoplankton growth, can be explained by the shorter $t_{res,out}$ and larger water volumes of deeper waters. Under grazer presence, $t_{res,out}$ defines not only the time available for phytoplankton growth but also the time available for grazing. A longer $t_{res,out}$, hence, decreases phytoplankton concentration (Pout) if phytoplankton losses, including grazing, are larger than its growth (Lucas *et al.*, 2009, Lucas & Thompson, 2012). On the other hand, shallow waters have a lower water volume, to be filtered by BFF, per unit of river area. This decreases the phytoplankton biomass (mgC) that BFF need to graze to reduce phytoplankton concentration (mgC/l) by a certain amount. This finding has important implications for

river management. The deepening of river channels is often thought to reduce eutrophication in some cases (e.g. Sagehashi *et al.*, 2001). However, we showed that under the presence of BFF grazers, such deepening can increase eutrophication by reducing grazer control and that under warming this deterioration effect can become particularly critical (Figs. A3-1, A3-2).

The non-linear response of Pout to water depth, which confirms the findings of Lucas & Thompson (2012), seems to be caused in our model by the non-linearity of three factors. First, by the non-linear relationship between water depth and residence time, $t_{res,out}$ (see Eqs. 1-3 and Fig. A3-1). In particular, decreasing depth at relatively shallow waters increases $t_{res,out}$, and thus the time for both phytoplankton growth and BFF grazing, more than decreasing depth by the same amount at deeper waters does. Second, by the fact that light attenuation through water depth is exponential (see Eqs. 9-10 in Chapter 2). Therefore, light at upper water layers is much more intense than at lower ones. This allows larger increases of phytoplankton gross growth with decreasing water depth at shallower waters (at least within the not-so-extremely-shallow waters tested here). Third, by the non-linear relationship between grazing rate and water depth (see Eq. 15 in Chapter 2; Lucas & Thompson, 2012).

Although we simulated simultaneously the effect of residence time ($t_{res,out}$) together with other effects of water depth (i.e. on water volume and light regime), our results agree, in general, with a previous study using modelling and field data to test the effects of water depth and $t_{res,out}$ separately (Lucas & Thompson, 2012). In particular, our results in cold and warm waters (Figs. 3-1 and 3-2) confirm previous findings on the inversion of the relationship between water depth and phytoplankton due to BFF grazing (and thus, on the largest variability of Pout values at different BFF densities at shallow waters; Lucas & Thompson, 2012). However, our analysis shows that this reversal varies with temperature and may be very small or absent at extreme temperatures.

Therefore, our model results clearly show the interplay between the effects of temperature and water depth on Pout. Importantly, they suggest that the effects of one variable may be compensated or enhanced by changes on the other (Figs. 3-2, A4-1 and A4-2). For example, under grazer absence and at temperatures below T_{opt}^P an increase in Pout due to warming can be compensated by an increase in water depth (Fig. 3-2).

Combined effects of temperature and water depth are relevant because these variables are likely to vary simultaneously in nature for three reasons. First, water temperature and depth depend on each other in

rivers. This is because water volume in rivers impacts both water depth and their heat storage capacity, as well as water speed which, in turn, determines the time water interacts with the temperature of the atmosphere and the stream bed (Smith, 1972). Moreover, water temperature is also determined by the influx of water into the river (which also alters its depth). For example, groundwater, meltwater of glaciers and reservoir deep-water can decrease water temperature (e.g. Mellina *et al.*, 2002, Hari *et al.*, 2006). Second, both water temperature and depth are likely to be affected by climate change impacts on the energy and water cycles (IPCC, 2013). Third, some anthropogenic activities may alter both water depth and temperature (although not necessarily simultaneously). Such activities include land use changes (e.g. Johnson & Jones, 2000, Nelson & Palmer, 2007), power plant effluents (Edinger *et al.*, 1968) and reservoir releases (Lowney, 2000).

Therefore, our analysis of the combined effects of water temperature and depth can help understanding the impacts of climate change and other human activities on eutrophication biocontrol by BFF. Moreover, our results support the conclusion that changes in temperature and precipitation (in this study through their impacts on water temperature and depth) can have interacting effects on organisms and that climate change impacts are likely to be more complex than what can be predicted based on a single variable such as temperature (e.g. Bonebrake & Mastrandrea, 2010; note that interactions between climatic variables may not always occur, e.g. Eklöf *et al.*, 2015).

3.4.5. Temperature effects on other biotic and abiotic variables: outlook for future investigations

In this study we have shown that indirect effects of temperature via the consumer-resource interactions can be more important than its direct effects on resources. Moreover, we revealed the impact that an abiotic factor such as water depth can have on temperature effects on such interactions. However, temperature may impact other abiotic and biotic variables complicating its effects on resource-consumer interactions.

Regarding abiotic variables, although we have focused on well-mixed waters in this study, temperature may affect water stratification in some systems. It has been suggested that temperature effects on transient microstratification can be responsible for changes in phytoplankton community composition in the Hudson River through its effects on BFF grazing (Fernald *et al.*, 2007).

Regarding biotic variables, temperature effects on other organisms that interact with the considered consumer-resource pair can alter the outcome of their interaction of such pair. A relevant example for our system, are the interactions with zooplankton. Zooplankton are phytoplankton grazers but also BFF prey (e.g. Strayer *et al.*, 1999, Pigneur *et al.*, 2014). Although zooplankton grazing is implicitly accounted for in our model in the density-dependent mortality term of phytoplankton (Eq. 14 in Chapter 2), a more explicit consideration of zooplankton dynamics and their interaction with phytoplankton and BFF might modify the results of the BFF-phytoplankton interaction. This would increase, however, complexity and data requirements (note that zooplankton themselves can be herbivores and carnivores and thus have different thermal responses; Seifert *et al.*, 2014, Dell *et al.*, 2014).

Another biotic variable which can be affected by temperature is the food quality for BFF though impacts on the composition of the phytoplankton community (Hardenbicker *et al.*, 2015a). A change in food quality may augment BFF grazing rate, due to compensatory feeding (Hardenbicker *et al.*, 2015a).

Moreover, although our study focuses on the short-term dynamics it is worth noting that experimental warming on *C. fluminea* (Weitere *et al.*, 2009) showed that in the long-term grazer metabolism (and its relationship with ingestion) may cause starvation at higher temperatures (studies on other species seem to support this finding, e.g. Rall *et al.*, 2010, Vucic-Pestic *et al.*, 2011, Lemoine & Burkepille, 2012).

Therefore, consideration of these other temperature impacts in future studies will further improve our understanding and prediction of climate change effect on ecosystems.

3.5. CONCLUSIONS

Our results show that trophic control, by benthic filter feeders (BFF), can qualitatively alter the response of eutrophication to warming. In particular and for the first time, we show that *eutrophication can respond non-monotonically and with thresholds to warming* depending on the grazer density. Thus, our findings support conclusions of other studies indicating that *indirect effects of climate warming* through trophic interactions *can be more important than its direct effects* on single trophic levels. Moreover, this non-monotonic response implies that eutrophication can increase, decrease or be insensitive to warming depending on the starting temperature and grazer density. These findings allow explaining and unifying divergent results of some previous studies. To make these findings possible, it was essential to consider: (1) a large temperature range, (2) the interplay of temperature with other abiotic variables such as depth

and (3) unimodal functions for the thermal responses of both consumer (BFF) grazing rate and resource (phytoplankton) growth rate. Our findings support previous studies indicating that the prediction of global warming effects on ecosystems requires considering ecological mechanisms such as the physiological responses of the organisms and their trophic interactions as well as the interplay between temperature and other environmental stressors. In particular, we provide evidence that a temperature threshold exists beyond which eutrophication control by grazers may fail.

CHAPTER 4 - PHYTOPLANKTON CONTROL IN LARGE RIVERS: WARMING EFFECTS ON THE PERFORMANCE OF SOURCE AND GRAZER CONTROL

So far, the analysis was focused on the effect of warming on the ecosystem functioning of grazer-controlled phytoplankton in large rivers and the implications for the eutrophication status at the outlet. In this chapter, the focus was changed from ecosystem functioning to management aspects, namely the performance of phytoplankton control and its sensitivity to warming for different success criteria.

4.1. INTRODUCTION

Phytoplankton, i.e. pelagic algae, is the dominant primary producer in most aquatic ecosystems markedly influencing energy and matter fluxes and thereby the functioning of the entire ecosystem (e.g. Minshall *et al.*, 1985). In running water ecosystems, the role of autochthonous planktonic production for the flux of matter within food webs increases with water residence time and becomes predominant in rivers (Vannote *et al.*, 1980, Throp and Delong 2002). However, excessive phytoplankton production (i.e. eutrophication) can cause severe water quality problems such as: instability in oxygen concentration and pH value; blooming of problematic species (such as toxic blue-green algae); increasing water turbidity which can affect the light regime of benthic algae and macrophytes; threatening endangered and sensitive species and thus biodiversity; water treatment problems; and reducing the aesthetic value and recreational use of sites (e.g. Quinn, 1991 as cited in US-EPA, 1996; Smith, 1998; Dodds & Welch, 2000; Smith, 2003). Eutrophication is an important problem for lakes, but also rivers and estuaries (e.g. Smith, 2003).

Given these multiple problems, assessing and controlling eutrophication are important management tasks. Therefore, the eutrophication status of a water body is internationally among the criteria for water quality (e.g. United States Congress (92nd), 1972). Eutrophication refers to the increase in primary production. However, most authors evaluate the eutrophication status along the algal standing stock, often estimated by chlorophyll concentration. The European Water Framework Directive (EU-WFD; European Commission, 2000) sets such success criteria. In Germany, Mischke *et al.*, 2011 specified a threshold value below (above) which the seasonal mean phytoplankton concentration of large rivers is 'non-eutrophic' ('eutrophic'). Consequently, management measures are successful, if the water body reaches a non-eutrophic stage.

The dominant focus in eutrophication control is the reduction of nutrients, i.e. the so-called bottom-up control (e.g. Smith *et al.*, 1999). Elevated nutrient loads are the primary reason for eutrophication (e.g. Basu & Pick, 1996, Van Nieuwenhuysse & Jones, 1996). Reduction of nutrients has been successful in controlling eutrophication many cases (e.g. Smith, 1998, Smith *et al.*, 1999). Particularly phosphate has been reduced significantly in recent decades and consequently excessive eutrophication decreased. However, despite considerable effort, today's nutrient concentrations in lakes and rivers is distinctly above the natural background concentration and usually too high to limit algal growth. Further nutrient reduction is often impossible in reasonable time scales or unaffordable (e.g. in the case of diffuse inflow of nutrient-contaminated groundwater) (Shapiro *et al.*, 1975). Moreover, resilience of chemical and/or biological factors may delay the recovery of the water quality, at least in lakes, after nutrient loading decreases (Jeppesen *et al.*, 2012). Hence, nutrient reduction, although necessary, is often insufficient to control eutrophication and must thus be accompanied by other measures.

Fortunately, other factors such as light or grazing also influence eutrophication. However, their potential to supplement nutrient reduction for controlling eutrophication is often ignored. Especially control by grazers, also called “top-down” control, can efficiently control algae biomass. In lakes, filter-feeding zooplankton strongly reduces phytoplankton concentration, resulting in clear water phases after times of highest grazing pressure (Sommer *et al.*, 2012). The process of grazer-induced phytoplankton control can be stimulated by biomanipulation by activating a trophic cascade (e.g. Carpenter *et al.*, 1995, Benndorf, 1995): by introducing predator fish (+), planktivorous fish is reduced (-), which increases filter-feeding zooplankton (+), and this, in turn, reduces phytoplankton (-). Top-down control with fish and trophic cascading has also been tested in rivers, but only for benthic algae (periphyton): benthivorous fish reduce benthic grazers and, thereby, increase periphyton (Winkelmann *et al.*, 2014).

The situation in rivers differs from lakes. Here, zooplankton appears often in very low densities (Weitere *et al.*, 2005) and dominant filter feeders are located in the benthos. Benthic filter feeders (BFF) can significantly decrease phytoplankton in these habitats (e.g. Cohen *et al.*, 1984, Effler *et al.*, 1996, Caraco *et al.*, 1997; 2006, Hardenbicker *et al.*, 2015b). If total grazing rate surpasses phytoplankton growth, phytoplankton concentration can even decrease along the river stretch (Weitere and Arndt 2002). Whether or not a river stretch is a source (i.e., net increase) or a sink (net decrease) for phytoplankton can also be a success criterion for management. However, note that grazer control is passive, i.e. an ecosystem service which is naturally provided, as opposed to an active management measure such as reducing nutrient

inflow. Even though it is likely that grazer densities and thus grazing pressure for phytoplankton can be altered by habitat improvements, today's knowledge to manipulate BFF densities is insufficient.

Another strong predictor for phytoplankton concentration at a given river location is influenced by the phytoplankton concentration at the source (hereafter: P_{in}). Although riverine phytoplankton seems to start with almost plankton-free water at the source, water is then inoculated via different paths from side-waters, tributaries and benthic drift (e.g. Reynolds & Descy, 1996) as well as by stagnant waters, e.g. lakes or reservoirs. Moreover, P_{in} is altered by within-river control mechanisms, e.g. BFF grazing (e.g. Lauritsen, 1986 and Ortmann & Grieshaber, 2003, but see Viergutz *et al.*, 2012). Therefore, even if P_{in} complies with a water quality threshold, phytoplankton can grow or decline while traveling downstream, depending on river conditions.

This leads to question under what conditions can the phytoplankton concentration at the outlet (hereafter: P_{out}) be controlled in such a way that it remains below a certain quality threshold (e.g. that suggested by Mischke *et al.*, 2011) or declines substantially, depending on the success criterion considered. A related question is the effectiveness of source control (actively regulating P_{in}) and grazer control (passively benefiting from naturally existing BFF grazers) for achieving the respective success criteria. To answer these questions, however, it is important to note that phytoplankton growth and BFF grazing depend on several environmental factors. For example, temperature has been observed to alter the balance between these two rates (Viergutz *et al.*, 2007; see also Chapter 3). Hence, such balance will likely change with global warming as the mean temperature of river water is predicted to increase worldwide by 0.8-1.6°C by the end of this century, relative to the temperatures at the end of the last century (van Vliet *et al.*, 2013). Moreover, water depth and the traits of the species in the riverine ecosystem, such as the thermal responses of the rates of phytoplankton growth and BFF grazing, also influence the impact of BFF grazers on the relationship between P_{out} and P_{in} value (Lucas & Thompson, 2012, Chapter 3). This generates the question of how the effectiveness of both source and grazer control change with warming, water depth and the thermal responses of BFF and phytoplankton as well as with the success criterion considered. The outcomes can help clarifying whether and when top-down control with BFF grazers would be an effective supplementary approach to control phytoplankton at the outlet of large rivers.

Answering these questions requires systematically analysing the relationship between P_{out} and P_{in} under different temperatures, river depths, BFF densities, and thermal responses of the rates of phytoplankton growth and BFF grazing. To the best of our knowledge, such systematic analyses are missing so far for

rivers or stream systems. To fill this gap by applying the grazer-controlled phytoplankton model developed in Chapter 2 is the aim of the present chapter. This knowledge is required for tailoring eutrophication control in large rivers under climate change.

4.2. SPECIFIC METHODS

4.2.1 Overview

As in the preceding chapter, we used the simulation model previously developed in this thesis (see Chapter 2) and the river ‘Rhine’ as case study to analyze warming effects on grazer-controlled phytoplankton and their implications for eutrophication. In this chapter, we specifically assessed the performance of two approaches to control phytoplankton at the outlet (P_{out}) - (1) source control, i.e. reducing phytoplankton at the river source (P_{in}), and (2) grazer control, i.e. benefitting from BFF grazing during the travel of the phytoplankton from river source to its outlet. We investigated the impact of P_{in} on P_{out} as a function of river characteristics (temperature and depth) for zero to high BFF densities. In order to avoid an overloading with too many details at this stage, we assumed a spatially homogeneous BFF distribution along the river (in Chapter 5, we will expand our perspective and consider the effect of heterogeneity in the BFF distribution explicitly). The resulting P_{out} values were used to assess the effectiveness of source and grazer control for different river characteristics and for three different criteria of success of phytoplankton control: (i) compliance with a water quality threshold defining a ‘non-eutrophic’ status at the outlet, (ii) net phytoplankton decline during the travel from the source to the outlet, and (iii) substantial P_{out} reduction after management intervention (for detailed explanations see below).

4.2.2. Simulation experiments

We assessed the dependence of the phytoplankton concentration at the outlet, P_{out} , on the phytoplankton concentration at the source, P_{in} (varied between 0.02 and 10.02 mgC/l; see justification of these values on Appendix 3), over a wide range of temperatures (T ; varied from 0 to 32°C) and BFF densities in the river (G ; varied from 0 to 500 ind./m²) for two water depths (D ; 1 and 4m). We also explored the effect of varying ecological traits such as the optimum temperature characterizing the thermal responses of phytoplankton growth (T_{opt}^p ; from 24 to 27°C) and BFF grazing (T_{opt}^g ; from 19 to 25°C).

4.2.3. Definition of three criteria of success for phytoplankton control at the outlet

Three criteria of success will be used for assessing the effectiveness of source and grazer control and its sensitivity to warming.

CRITERION 1: *Compliance with a water quality threshold defining a 'non-eutrophic' status at the outlet*

This criterion reflects the achievement of mitigating eutrophication at the outlet by keeping the respective phytoplankton concentration, Pout, below a certain absolute threshold value. Simulated Pout-values below or above the threshold are classified as 'non-eutrophic' or 'eutrophic', respectively. In this sense, the threshold value used to differentiate between 'non-eutrophic' and 'eutrophic' status, 0.87 mgC/l, was derived from the study of Mischke *et al.* (2011).

Mischke *et al.* (2011) categorized large German rivers in four groups according to their chlorophyll *a* response to total phosphorus because phytoplankton growth depends on catchment properties such as specific run-off and water residence time. For each of these groups Mischke *et al.* (2011) defined the boundaries between the five ecological classes required by the WFD (European Commission, 2000) for the *seasonal mean* of chlorophyll *a* concentration (uncorrected for phaeophytin *a*). The threshold value here used, 0.87 mgC/l, is intermediate between the extremes of the river groups determined by Mischke *et al.* (2011), for the boundary between "good" and "moderate" quality status of the WFD. (This threshold value is transformed assuming a carbon to chlorophyll *a* ratio of 25; Admiraal *et al.*, 1992).

Note that such boundaries are defined for the *seasonal mean* of chlorophyll *a* concentration (uncorrected for phaeophytin *a*; Mischke *et al.*, 2011). The used values given by Mischke *et al.* (2011), are in good agreement with high performance liquid chromatography (HPLC) determinations (Stich & Brinker, 2005, Mischke *et al.*, 2011). Moreover, measurements of chlorophyll *a* concentration can vary considerably, according to the technique used (see e.g. Stich & Brinker, 2005 and references therein). Variation is also present in the ratio between carbon and chlorophyll *a* (C_{chl_r} ; unitless), used here to transform units, depending on environmental properties and taxonomic group (Geider, 1987, Cloern *et al.*, 1995). Therefore, our estimations of the quality threshold are only an approximation.

CRITERION 2: *Net phytoplankton decline during the travel from the source to the outlet*

This criterion assesses the attainment of a ‘net phytoplankton decline’, i.e. a phytoplankton concentration decrease when starting with P_{in} at the source and traveling to the outlet. It is implemented as $P_{out} < P_{in}$.

CRITERION 3: *Substantial reduction of P_{out} after management intervention*

This criterion assesses the phytoplankton reduction at the outlet due to a management intervention. It is implemented as $P_{out,a} \ll P_{out,b}$, where ‘a’ and ‘b’ refer to situations after and before a management intervention (e.g. source control i.e., a reduction in P_{in}).

4.3. RESULTS

4.3.1. P_{out} vs. P_{in} relationships and the effects of BFF density and water depth

We start with analyzing the phytoplankton concentration at the outlet, P_{out} , as a function of phytoplankton concentration at the source, P_{in} , under various BFF densities for warm temperature as reference, comparing the results between shallow and deep rivers. This preliminary analysis is conducted to understand grazer-control of eutrophication and its effect on the P_{out} vs. P_{in} curves.

Shallow rivers (1m depth): Figure 4-1a shows the P_{out} vs. P_{in} curves in shallow rivers with a water residence time of 11.7 days (resulting from the assumptions of a river with 1m depth, 500km length and certain width, slope and roughness; see formulas in Eqs. 1-3 and Table 2-1 for parameter values and their justification; Chapter 2). When grazers are absent or scarce (≤ 100 ind./m²), the P_{out} vs. P_{in} curve is nonlinear and P_{out} achieves saturation above a certain critical P_{in} value. To be more specific, P_{out} initially increases steeply with P_{in} , but then only slowly further increases with higher P_{in} values. This reflects the logistic-like phytoplankton growth and the limiting effect of a carrying capacity (K) in the river. When BFF density increases, e.g. to 300 ind./m², however, two important characteristics of the P_{out} vs. P_{in} nonlinearity change: (1) the saturation level of P_{out} decreases, and (2) a critical P_{in} -threshold emerges below which P_{out} is negligible, i.e. phytoplankton is completely removed by the grazers. This response agrees with standard findings from the theory of harvested populations. At very high BFF densities (500 ind./m²), P_{out} is reduced to approx. 0 mgC/l, regardless of P_{in} -value, reflecting its complete control by BFF (Fig. 4-1a).

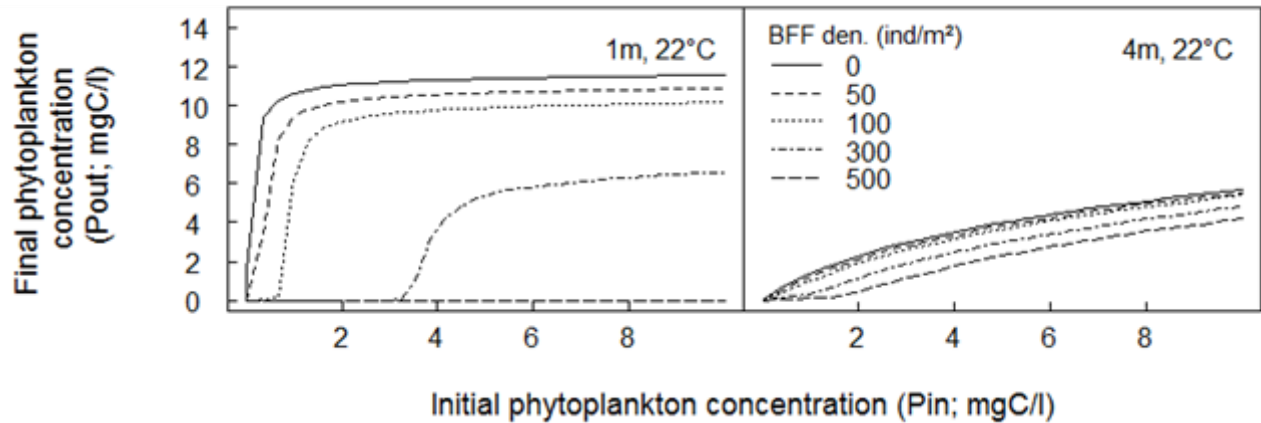


Figure 4-1. Phytoplankton concentration at the outlet, P_{out} , as a function of the phytoplankton concentration at the source, P_{in} , for four BFF densities and two river depths (shallow (1m, a), deep (4m, b)). Water temperature is 22°C.

Deeper rivers (4m depth): Figure 4-1b shows the same analysis for a deeper river of the same length resulting in a residence time of 4.9 days (resulting from the same parameter values as in shallow rivers but with 4m depth). The P_{out} vs. P_{in} relationship is qualitatively different than that for the shallow river: above a certain critical P_{in} -threshold, the P_{out} vs. P_{in} curves are almost linear, regardless of BFF density, and they show no saturation. Moreover, the deeper river yields much lower P_{out} values than the shallow one (Fig. 4-1a). However, the effect of grazers on P_{out} and on the P_{in} thresholds is also low, regardless of their density. The reason for these effects is that the travelling from the source to the outlet is so quick that the phytoplankton cannot grow till the carrying capacity (K) and the time of exposure to the grazers is too short for a substantial phytoplankton reduction. Moreover, the water column to be filtered is higher compared to the case of the shallower river that also diminishes the effectiveness of grazer control.

4.3.2. Temperature effects on the P_{out} vs. P_{in} relationship for different BFF densities and water depths

Our previous analysis used a water temperature of 22°C as an example. However, one of our main interests is studying the temperature effects on source and grazer control. Therefore, we repeated the previous analysis for three additional temperatures (6, 14 and 30°C; Fig. 4-2). Additionally, we analyzed under which conditions phytoplankton experiences net growth on the way to the outlet, i.e. $P_{out} > P_{in}$.

Shallow rivers: Our model results show that the water temperature alters the shape of the Pout vs. Pin curves and the effectiveness of grazer control (Figs. 4-2). Net phytoplankton growth (decline) of Pout compared to Pin is shown when the Pout-Pin-curve is above (below) the grey line (that is where Pout=Pin; Fig. 4-2). At 22°C (the same temperature used in the previous analysis; Figs. 4-1 and 4-2c) and when grazers are absent or scarce, net phytoplankton growth is substantial (Pout markedly above the grey line). However, when BFF density is above a certain minimum, there is a net phytoplankton decline. At hot waters (30°C, Fig. 4-2d), the effectiveness of grazers is markedly reduced, regardless of their density, as indicated by the closeness of Pout vs. Pin curves with and without grazers. Moreover, since phytoplankton growth is high in these waters, the Pout vs. Pin curves reach high values, regardless of BFF density. However, as temperatures decrease (14 and 6°C), the Pout vs. Pin curves reach lower values, regardless of BFF density (Fig. 4-2a-b). Moreover, these curves become more linear, the Pout values do not reach any saturation, and their increase with Pin beyond the Pin-threshold is less steep. In addition, the impact of grazers also decreases with temperature, as is shown by the closeness of Pout vs. Pin curves with grazers and without grazers (Fig. 4-2a).

Deep rivers: The pattern of temperature effects in deep rivers (Figs. 4-2e-h) is similar to shallow ones (Figs. 4-2a-d) but their magnitude is much lower. In fact, the values of Pout and the effect of grazer control are markedly reduced in deeper rivers. Moreover, the Pout values show a net phytoplankton decline, regardless of water temperature and Pin value, except for very low Pin-values and for absent or scarce grazers. Interestingly, Pout vs. Pin curves are much more linear than in shallow waters, showing no, or much lower, Pout saturation and Pin thresholds (particularly in cold waters).

Since grazer control is poor in these waters, in the following, we focus exclusively on shallow waters.

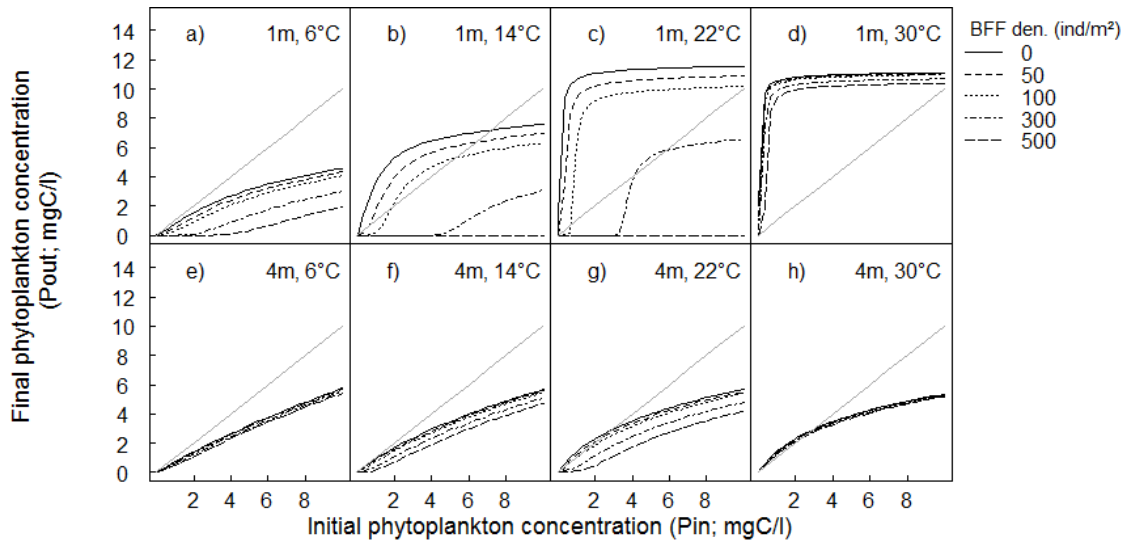


Figure 4-2. Phytoplankton concentration at the outlet, P_{out} , as a function of the phytoplankton concentration at the source, P_{in} , for different BFF densities, four water temperatures (cold to hot) and two water depths (shallow, a - d) and deep (e - h). The gray line shows where the phytoplankton concentrations at source and outlet are equal. P_{out} values above (below) this line indicate a net growth (decline) of phytoplankton during its passage through the river.

4.3.3. Temperature effects on the effectiveness of source and grazer control

Now we come to the main points of interest of this study: (1) the conditions under which the outlet can be kept ‘non-eutrophic’, i.e. P_{out} remains below the quality threshold of 0.87mgC/l (see also the Methods section of this chapter), (2) the effectiveness of source and grazer control in meeting these requirements, and (3) the effect of warming. As we have seen in the preceding analyses, P_{out} responds differently to changes in P_{in} and BFF density, depending on water temperature.

Although the previous analyses (Figs. 4-2) helped to reveal the main pattern in the P_{out} vs. P_{in} curves and their dependence on water temperature, they did not consider whether P_{out} meets the quality threshold (e.g. 0.87mgC/l; see Methods section) and only included four temperature values.

Hence, we now perform a more systematic study by assessing the effect of 33 different temperature values (from 0 to 32°C in 1°C intervals) on both the P_{out} vs. P_{in} relationship (see the contour lines in Fig. 4-3) and the range of P_{in} values which keep the P_{out} values below the quality threshold and assure a ‘non-eutrophic’ status at the outlet (hereafter: tolerable P_{in} values; see “white zones” in Fig. 4-3). Additionally, we compare the outcomes for three different BFF densities. This is relevant for determining the need of

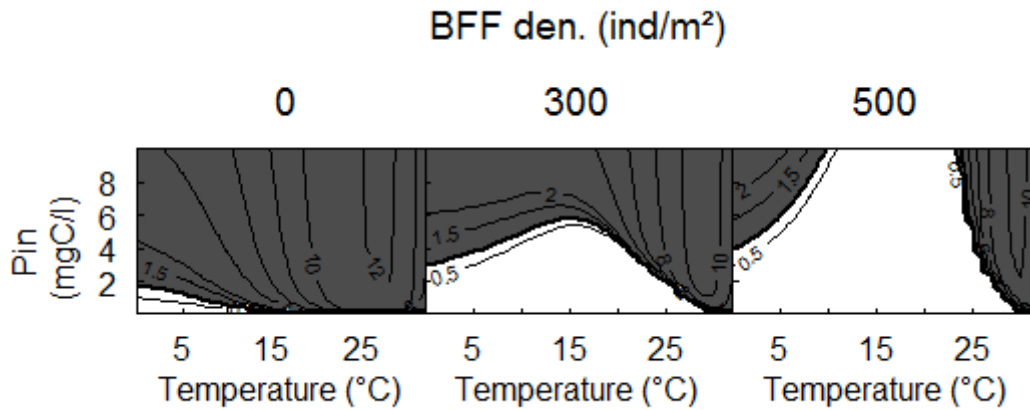


Figure 4-3. Contour plot for the phytoplankton concentration at the outlet, P_{out} , as function of phytoplankton concentration at the source, P_{in} , and water temperature for a shallow river (1m depth) and three BFF densities (0, 300, 500 ind./m²). The white zone shows when P_{out} is below the quality threshold of 0.87 mgC/l and, thus ‘non-eutrophic’ (estimated following Mischke *et al.*, 2011; see Methods section in this chapter).

source control and the influence of grazer control, and for assessing their response to warming. We perform the analyses by referring to specific species traits, namely the default values for the optimum temperatures for the thermal response of phytoplankton growth ($T_{opt}^p = 27^\circ\text{C}$) and BFF grazing ($T_{opt}^g = 22^\circ\text{C}$) (see the characterization of the thermal response in Appendix 1).

The contour plot for the case without grazers (Fig. 4-3, BFF = 0 ind./m²) confirms the previously observed nonlinear increase of P_{out} with P_{in} up to a saturation value (Figs. 4-2). The steepness of the raise of P_{out} with P_{in} increases (indicated by the increasing closeness of the contour lines) when temperature approaches the optimum for BFF growth ($T_{opt}^g = 22^\circ\text{C}$). Consequently, above approx. 15°C , there are no tolerable P_{in} values. Moreover, although P_{out} complies with the quality threshold in cold waters, the maximum tolerable P_{in} values, $P_{in}^{tol,max}$ (i.e. the P_{in} -values yielding a P_{out} -value equal to the quality threshold, see the thick line in Fig. 4-3), are low and even further declining with warming. This indicates that complying with the quality threshold in the absence of grazers requires strong source control (below 15°C) or is even impossible (above 15°C). Note, however, that some of the P_{in} -values above the quality threshold can yield P_{out} -values below this threshold even in the absence of grazers. This occurs when P_{in} is above the carrying capacity (K), due to density-regulation during the travel from the source to the outlet.

Grazer presence (Figs. 4-3, BFF = 300, 500 ind./m²) alters the shape of the contour plots considerably. Now there are large ranges of tolerable Pin-values for a given temperature (see the ‘white zones’). Only above the respective maximum tolerable Pin-value, $P_{in}^{tol,max}$ (bold line at the frontier of the white zone), Pout substantially increases with Pin till it reaches a saturation value. The $P_{in}^{tol,max}$ values show a unimodal dependence on water temperature, i.e. are highest at warm waters. Their decline to low $P_{in}^{tol,max}$ values is faster under further warming (temperature increase to hot waters) than under further cooling (temperature decrease to cold waters). Increasing BFF density can further enlarge the $P_{in}^{tol,max}$ values and, hence, reduce the need for source control, but mainly at moderate temperatures (approx. 10-22°C).

Moreover, Fig. 4-3 reveals a temperature threshold at approx. 24-27°C (depending on Pin), under grazing where the situation changes qualitatively in two ways. First, under temperatures above this threshold, $P_{in}^{tol,max}$ is low, i.e. there are very few tolerable Pin-values, indicating that compliance with the quality threshold is very difficult, even at high BFF densities. Second, while below this temperature threshold, Pout tends to decrease or remain relatively stable with warming, above it, Pout increases steeply with warming (see, for example, contour lines above ca. 24-27°C in Fig. 4-3 under BFF= 500 ind./m²).

4.3.4. Influence of the thermal responses of phytoplankton growth and BFF grazing on eutrophication control

The previous results have revealed that the maximum tolerable Pin-values, $P_{in}^{tol,max}$, show a unimodal response to temperature under grazing. We hypothesize that this characteristic response is caused by the thermal responses of phytoplankton growth and BFF grazing, which are determined mainly by their optimum values, T_{opt}^p and T_{opt}^g (see details in Chapter 2 and Appendix 1). The preceding results were based on the default values $T_{opt}^p = 27^\circ\text{C}$ and $T_{opt}^g = 22^\circ\text{C}$. We now vary these values to test our hypothesis and check if these results apply to communities with other thermal responses. Therefore, we test T_{opt}^p values of 24, 27 and 30°C and T_{opt}^g values of 19, 22 and 25°C.

Figures 4-4 show that, without grazers (BFF= 0 ind./m²), increasing T_{opt}^p shifts the zone of the highest Pout-values to higher temperatures and lowers the increase of Pout with Pin in cold waters. Moreover, the ranges of tolerable Pin-values are almost insensitive to changes in T_{opt}^p , increasing only slightly at cold waters. Therefore, compliance with the quality threshold is only achieved in cold waters (below 10°C) with strong source control. In contrast, with grazers (300 ind./m²), $P_{in}^{tol,max}$ values, i.e. the ranges of tolerable Pin-values, change substantially when altering T_{opt}^p and T_{opt}^g (Figs. 4-4, left panels). $P_{in}^{tol,max}$

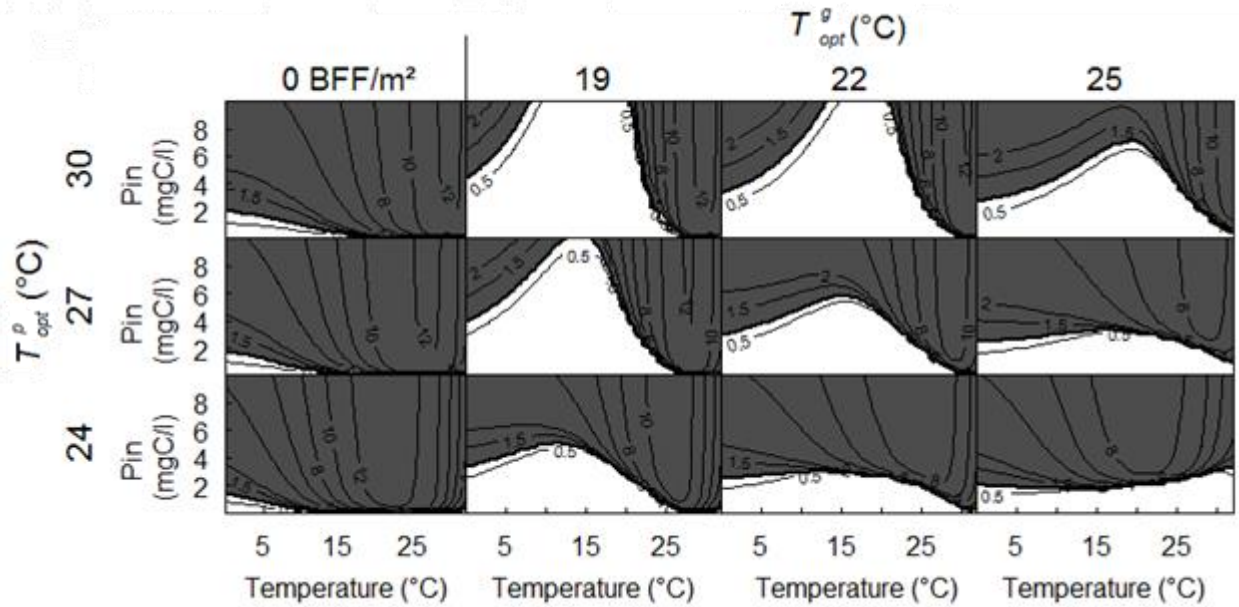


Figure 4-4. Contour plots of the phytoplankton concentration at the outlet, P_{out} , as a function of both phytoplankton concentration at the source, P_{in} , and water temperature for different values of the optimum temperatures (T_{opt}^p and T_{opt}^g) governing the thermal responses of phytoplankton growth and BFF grazing, respectively. The white (black) zone shows when P_{out} is below (above) the quality threshold of 0.87 mgC/l and, thus ‘non-eutrophic’ (‘eutrophic’) (estimated following Mischke *et al.*, 2011; see Methods section in this chapter). BFF density is 0 (first column) and 300 ind./m² (in all other columns).

values increase with T_{opt}^p at moderate temperatures, but decrease with T_{opt}^p at hot temperatures. However, the response of $P_{in}^{tol,max}$ to T_{opt}^g is the opposite. Therefore, increasing T_{opt}^p strengthens the unimodal shape of the $P_{in}^{tol,max}$ vs. temperature curve, while increasing T_{opt}^g flattens it.

Moreover, Figure 4-4 shows that, for certain (T_{opt}^p, T_{opt}^g)-combinations, the pattern of the $P_{in}^{tol,max}$ vs. temperature curve (i.e. the shape of the ‘white zones’) is similar. This is true for combinations (27, 19) and (30, 22) as well as for (24, 19), (27, 22) and (30, 25). Consequently, the difference between T_{opt}^p and T_{opt}^g determines to a large extent the $P_{in}^{tol,max}$ pattern and thereby the influence of warming on the effectiveness of grazer control in mediating compliance with the quality threshold at the outlet. A small difference between thermal responses, e.g. combination (24, 25), results in a flat but wide “white zone” indicating almost independence of $P_{in}^{tol,max}$ of temperature. Increasing the thermal response difference, however,

fosters the formation of a unimodal response of $P_{in}^{tol,max}$ to temperature and the appearance of a temperature threshold above which compliance with the quality threshold is impossible.

4.4 DISCUSSION

The main focus of this study was on exploring the performance of source and grazer control of phytoplankton in large rivers and its sensitivity to warming. Throughout the study, eutrophication assessment was based on the phytoplankton concentration at the outlet (Pout) which depends on the phytoplankton concentration at the source (Pin) and on certain environmental characteristics of the river. Therefore, we systematically analyzed the shapes of the Pout vs. Pin relationships and their dependence on BFF density, river depth and water temperature using the grazer-controlled phytoplankton model developed in Chapter 2. This reveals the requirements at the source needed to control eutrophication, the benefits that can be gained from grazer control, and how warming can change the outcomes. Our results allowed us to derive rules of thumb for the three criteria of success (defined above) used for assessing the performance of phytoplankton control:

- (i) Compliance with a quality threshold (i.e. $P_{out} < 0.87\text{mgC/l}$);
- (ii) Net phytoplankton decline (i.e. $P_{out} < P_{in}$);
- (iii) Substantial Pout reduction (i.e. $P_{out,a} \ll P_{out,b}$: where b and a refer to ‘before’ and ‘after’ a management intervention, i.e. source or grazer control).

To cover all three criteria of success is useful as, first, understanding the effect of warming on the performance of source and grazer control of phytoplankton in large rivers is globally relevant while criteria of success, which influence the evaluation of the performance of any control strategy, can vary between regions and systems (see Table 4-1). Second, some criteria may be unachievable. In this case, considering the next less ambitious criterion of success can be a way to achieve at least some realistic improvement. But also here, being aware about implications of warming is important.

For all three criteria of success, the performance of source and grazer control was found to depend on water temperature and river depth, but also on the ecological traits of phytoplankton and BFF grazers (Table 4-1; for the mechanism of such effects see next section). This indicates that warming effects on the performance of phytoplankton control (i) depend on river attributes and (ii) can interact with other effects of climate change and land use change. Knowing the key factors counteracting or amplifying these warming effects also helps assessing management practices, e.g. identifying chances and risks of (recent

or planned) land use practices to an effective phytoplankton control under predicted warming, and avoiding counterproductive conclusions.

4.4.1 Rules of thumb on the performance of source and grazer control and its sensitivity to warming

4.4.1.1 Criterion 1 - Compliance with a quality threshold

This refers to the ability of source and grazer control to comply with a water quality threshold at the outlet such as that suggested by Mischke *et al.*, 2011 (i.e. 0.87 mgC/l, for evaluating large German rivers regarding the WFD. Accordingly, the outlet is classified as ‘non-eutrophic’ (‘eutrophic’) if the P_{out} value is below (above) this quality threshold value.

In all scenarios and for each temperature value, we were able to identify the range of tolerable P_{in} values which keep the P_{out} values below the quality threshold and assure a ‘non-eutrophic’ outlet (‘white zones’ in Figs. 4-3 and 4-4). The related maximum tolerable P_{in} -value $P_{in}^{tol,max}$ (the frontier of the ‘white zone’) indicates how much source control is needed to meet the quality threshold at the outlet, i.e. how low should P_{in} be. We found that, depending on the river attributes, grazing can markedly enlarge the $P_{in}^{tol,max}$ value so that less source control is needed. This indicated that grazing enhances source control and this enhancement can be measured as the difference in the $P_{in}^{tol,max}$ values for the scenarios with and without grazing. To understand warming effects on source and grazer control, we explored the $P_{in}^{tol,max}$ values and $P_{in}^{tol,max}$ -differences over a wide range of temperatures and found that both vary with river depth and with the thermal responses of phytoplankton growth and BFF grazing.

RULE OF THUMB 1: COMPLIANCE WITH A QUALITY THRESHOLD IN DEEP RIVERS

In deep rivers, grazer control is ineffective. Compliance with the quality threshold, i.e. a ‘non-eutrophic’ outlet, can only be achieved if the source itself is nearly ‘non-eutrophic’. Hence, a stringent source control is needed. The findings are independent of water temperature.

Justification.- Our model results have revealed for this river type that the range of tolerable P_{in} -values is relatively narrow, independent of grazer density and water temperature. The reason is that, although grazers are weak, nearly non-eutrophic sources (i.e. $P_{in} < 1.5\text{mgC/l}$) can be converted to non-eutrophic outlets as there is net phytoplankton decline.

This net phytoplankton decline results from low light availability in deep rivers, which limits phytoplankton growth, regardless of water temperature (see also Lucas & Thompson, 2012). Additionally, in deep rivers, residence time relatively low, reducing the time available for BFF grazing. This reduction, together with the larger water volume (per area of river surface) diminishes BFF grazing effects in deep rivers (even if BFF grazing rates were high due to temperature). The depth effect on BFF grazing is, unlike that on phytoplankton growth, only indirect; see also Fig. 4-1).

RULE OF THUMB 2: COMPLIANCE WITH A QUALITY THRESHOLD IN SHALLOW RIVERS

In shallow rivers, source control alone is unable to yield a ‘non-eutrophic’ outlet, except in case of cold waters where a stringent source control is effective. Thus, grazer control is crucial to comply with the quality threshold at the outlet, but it is affected by temperature. Temperature effects on grazing depend on the matching of the thermal responses of the rates of phytoplankton growth and BFF grazing.

In case of close matching, the effectiveness of grazer control is substantial and insensitive to warming.

In case of mismatch, in contrast, there is a critical temperature threshold (here: approx. 25°C). Below this temperature threshold, the effectiveness of grazer control shows a unimodal thermal response, i.e. it first benefits and then suffers from warming. Above the temperature threshold, even slight further warming can abruptly turn a formerly ‘non-eutrophic’ to a ‘eutrophic’ outlet. Here, neither source nor grazer control is able to ensure compliance with the quality threshold anymore.

Justification.- For shallow rivers without grazers, the maximum tolerable P_{in} -value, $P_{in}^{tol,max}$, is marginal, while, with raising grazer density, it can markedly increase. We also found that $P_{in}^{tol,max}$ can vary strongly with water temperature, depending on the degree of matching of the thermal responses of phytoplankton growth and BFF grazing (Fig. 4-4). The degree of matching was measured as the difference between the optimum temperatures of phytoplankton growth (T_{opt}^p) and BFF grazing (T_{opt}^g) (although other variables differ as well, see details in Chapter 2 and Appendix 1). In case of close matching (i.e. $T_{opt}^p \approx T_{opt}^g$), $P_{in}^{tol,max}$ was found to be only slightly affected by water temperature (see the constant height of the ‘white zone’ in the (24,25)-scenario in Fig. 4-4) and always above the quality threshold (0.87 mgC/l). This indicates that grazers can sufficiently decrease phytoplankton concentration during their travel from the source to the outlet and turn ‘eutrophic’ P_{in} values into ‘non-eutrophic’ P_{out} values. In the case of

mismatched thermal responses of phytoplankton growth and BFF grazing, a temperature threshold (here: approx. 25°C) appeared, and separated two temperature ranges differing its compliance with the quality threshold at the outlet (see Fig. 4-3; BFF= 300 or 500 ind./m²). Below the temperature threshold, $P_{in}^{tol,max}$ showed a unimodal response to warming. Above it, in contrast, $P_{in}^{tol,max}$ was close to zero and P_{out} remained high with further warming. In this last temperature range, grazing pressure was critically reduced, while phytoplankton growth was still remarkable. This temperature threshold is suggested by experimental data, which showed a mismatch in the ingestion rates of the clam *Corbicula fluminea* and the growth rate of its unicellular plankton prey above 25°C (Viergutz *et al.*, 2007).

In shallow rivers, the relatively high light availability promotes phytoplankton growth. This together with the long water residence time of these waters fosters high phytoplankton concentrations. Therefore, under grazer absence, phytoplankton can strongly develop at warm and hot waters (see Figs. 4-4; BFF= 0) that is in line with the reported net phytoplankton growth in this temperature range. The long residence time and low water volume (in relation to river surface area) also amplify the impact of grazing (see also Weitere & Arndt, 2002 and Lucas & Thompson, 2012). Therefore, temperature effects on the rates of phytoplankton growth and BFF grazing are higher than in deep rivers. In case of full matching, phytoplankton growth and BFF grazing synchronously respond to warming. Consequently, the effect of an increasing phytoplankton growth is counterbalanced by an increasing grazing pressure (even when grazing effects on phytoplankton are reduced at cold waters; Fig. 4-4). This synchronization explains the relatively insensitive response of $P_{in}^{tol,max}$ to temperature and thus of the demand for source control to warming (see the (24,25)-scenario in Fig. 4-4). In the case of mismatch, the grazing pressure increases faster (because we assume T_{opt}^g is usually below T_{opt}^p) with warming than phytoplankton growth. This causes large differences in the rates of phytoplankton growth and BFF grazing at several temperatures. These differences cause, in turn, changes in the effectiveness of source and grazer control under warming.

The existence of maximum tolerable P_{in} -values, $P_{in}^{tol,max}$, is in line with a well-known finding from complex adaptive systems theory, namely that ecological systems have a certain capacity to cope with environmental change. In our case, this concerns the capacity to cope with certain phytoplankton concentration at the source, P_{in} , when complying with the quality threshold at the outlet. This coping capacity, however, is evidently dependent on grazer density and water temperature in many cases.

4.4.1.2 Criterion 2 - Net phytoplankton decline

A relatively modest management goal is net phytoplankton decline: $P_{out} < P_{in}$, i.e. to achieve a reduction of phytoplankton concentration while it travels from source to outlet. Our model results revealed that net phytoplankton decline and its response to warming depend on river depth and grazer density (Figs. 4-2).

RULE OF THUMB 3: NET PHYTOPLANKTON DECLINE IN DEEP RIVERS

In deep rivers, there is net phytoplankton decline in most cases, independent of P_{in} value, grazer density and, water temperature. Thus, source and grazer control are unnecessary in most cases to achieve such decline.

Justification.- The net phytoplankton decline in deep rivers is due to hindrance of phytoplankton growth (due to lower light and to the lower water residence time of these rivers). This reduces the carrying capacity of the river, K . Consequently, phytoplankton concentration decreases by density regulation during its travel from the source to the outlet. Hence, source control and grazer control are unnecessary for net phytoplankton decline in deep rivers.

RULE OF THUMB 4: NET PHYTOPLANKTON DECLINE IN SHALLOW RIVERS

In shallow waters, net phytoplankton decline and the importance of source and grazer control for achieving such decline depend on water temperature.

In *cold waters* (6°C), net phytoplankton decline always occurs, independent of source and grazer control.

In *warm waters* ($10\text{-}22^{\circ}\text{C}$), net phytoplankton decline only occurs at high or sufficiently low P_{in} values (i.e., high values above the carrying capacity, K , where density regulation is dominant or low values where grazing is able to reduce phytoplankton). Increasing grazer density enlarges these two P_{in} ranges. Thus, grazer control always promotes net phytoplankton decline, while source control is only beneficial if large P_{in} values are reduced to range of the grazer-mediated net phytoplankton decline.

In *hot waters* (above 25°C), neither source nor grazer control can produce a net phytoplankton decline. Net phytoplankton decline can only occur above the carrying capacity, K . Source control, which reduces P_{in} below K , even becomes counterproductive as it fosters net phytoplankton growth.

To summarize, control measures can be *unnecessary* (source and grazer control at cold waters), *crucial* (grazer control at warm waters), *ineffective* (grazer control at hot waters) or *counterproductive* (source control at warm waters) for achieving net phytoplankton decline. Therefore, warming can substantially alter the relevance of source and grazer control to achieve this success criterion. Moreover, warming can cause a shift from net phytoplankton decline to net phytoplankton growth.

Justification.- Our results revealed that in shallow warm rivers and all scenario considered (see Fig. 4-2) that there is a range of (intermediate) P_{in} values which result in net phytoplankton growth and that the extent of this range shrinks with grazer density but expands with warming. Hence, there is a counteracting effect between grazing and warming on the emergence of net phytoplankton growth. The P_{in} range of net growth is responsible for the separation into the two P_{in} ranges where net phytoplankton decline occurs for different reasons: in the lower P_{in} range, net decline is due to grazer control, while in the upper P_{in} range, which is above the carrying capacity of the river (K), net decline is due to density regulation.

The counteracting effect of grazer density and water temperature on net phytoplankton growth results from several factors: (i) the grazing pressure, which increases with grazer density, (ii) the fact that shallow rivers promote both phytoplankton growth and grazing pressure, (the first because of the high light availability and the long water residence time and the second because of such long residence time) and thus long time of exposure to the grazers as well as the low water volume to be filtered, and (iii) the thermal responses of phytoplankton growth and BFF grazing which both show a unimodal dependence on water temperature. This explains why it depends on P_{in} and BFF density whether phytoplankton growth (promoting net growth) or BFF grazing (promoting net decline) dominate the development of phytoplankton during its travel from the source to the outlet and so the likelihood of net phytoplankton decline.

Remember, that under warm waters and moderate BFF densities, the existence of a range of P_{in} values yielded net phytoplankton growth was reported. This has serious implications: slight increases in P_{in} from below this range (e.g. as a result of inappropriate land use change) can convert net decline to net growth. At first view, this is surprising as enlarging P_{in} relaxes the condition $P_{out} < P_{in}$ (less restriction on P_{out}).

However, Pout increases nonlinearly with Pin. The same is true for slight reductions of Pin values (e.g. through source control), which were originally above the carrying capacity K of the river, which can also convert net decline to net growth. This is in line with classical population ecology which indicates that net population growth is highest markedly below the carrying capacity K because of reduced density regulation. Thus, assuring net phytoplankton decline requires an adequate source control that accounts for the nonlinearity of the system.

4.4.1.3 Criterion 3 - Substantial Pout-reduction after management intervention

The preceding success criteria assessed whether Pout can be kept *below a certain value*, either a quality threshold or the Pin value. Another success criterion assesses whether Pout substantially *declines* in response to a management intervention. In this case, a Pout reduction is considered as ‘substantial’ if $P_{out,a} \ll P_{out,b}$; where *b* and *a* refer to before and after an intervention (i.e. source or grazer control).

RULE OF THUMB 5: SUBSTANTIAL POUT REDUCTION IN DEEP RIVERS

In *deep* rivers source control can constantly diminish Pout, while grazer control is ineffective, independent of the Pin value.

Justification.- Our results for deep rivers (Figs. 4-2) have shown that the Pout-Pin-curves have an *almost linear* shape because of the low rates of phytoplankton growth and BFF grazing. In such rivers, reducing Pin can constantly diminish Pout, while increasing grazer density is ineffective.

RULE OF THUMB 6: SUBSTANTIAL POUT REDUCTION IN SHALLOW RIVERS

In shallow rivers the performance of source and grazer control depends on water temperature.

In cold waters, source control can constantly diminish Pout, independent of the Pin value. In contrast, in warm or hot waters, source control is only beneficial if the Pin reduction takes place in the transition zone. Grazer control is only effective in warm waters.

Justification.- In shallow rivers, the shape of the Pout-Pin-curves depends on water temperature. This shape was similar in shallow cold rivers to that in deep rivers, i.e. relatively linear (Fig. 4-2).

In contrast, in warm waters, such shape was found to be *nonlinear* and formed by three Pin-zones: a Pin-zone of full Pout-control, a transition zone, and a Pin-zone of Pout-saturation. Accordingly, Pin reductions can diminish Pout substantially only if they take place in the transition zone. The position and extent of the Pin transition zone depends on grazer density as increasing grazer density enlarges the zone of full Pout-control and reduces the Pout-saturation value. Hence, grazer control is effective in warm waters.

In hot waters, a Pin zone of full Pout control is missing and the transition zone is, thus, found at very low Pin values. Moreover, Pout-saturation and the location of the transition zone are independent of grazer density. Hence, grazer control is ineffective.

Table 4-1 summarizes the previously described rules of thumb on the effectiveness of source and grazer control of phytoplankton and its sensitivity to temperature and depth for the three criteria of success.

4.4.2 Evidence for combined effects of global warming with other impacts of environmental change on eutrophication control

Major focus of this study was on warming effects on the effectiveness of source and grazer control of phytoplankton in large rivers. So far, however, we merely considered direct effects on the demographic rates which result from changes in water temperature in isolation. A closer look, however, reveals that warming can also have numerous *indirect* effects as it can alter all the other factors influencing the effectiveness of phytoplankton control such as Pin, river and water depth, or the species traits. This can occur *in combination* of warming with other impacts of climate change or impacts of land use change.

Table 4-1. Need of source control and benefit from grazing to achieve three success criteria under three river types. 0: no or low benefit, +: medium or large benefit, -: negative effect (counterproductive). Notes: 1) Complying with the quality threshold needs Pin values very close to such a threshold (for a threshold of 0.87mgC/l); 2) Pin value needs to be much lower than 0.87mgC/l for this threshold to be achieved (the need for source control will thus depend on the original Pin value of the river); 3) without match of the thermal responses of phytoplankton growth and grazing; 4) under matching of such thermal responses; 5) although net phytoplankton decline is achieved at all or almost all Pin values in most deep waters, it is stronger at higher Pin values; 6) except at the transition zone.

	Deep rivers		Shallow cold rivers		Shallow warm rivers		Shallow hot rivers	
Approach Criterion of success	<i>Benefit from source control</i> §	<i>Benefit from grazing</i>	<i>Benefit from source control</i> §	<i>Benefit from grazing</i>	<i>Benefit from control</i> §	<i>Benefit from grazing</i>	<i>Benefit from source control</i> §	<i>Benefit from grazing</i>
Compliance with quality threshold (Pout < 0.87mgC/l)	0 ¹	0	0 (BFF=0) + (BFF>0)	+	0 (BFF=0) + (BFF>0) ₂	+	0 ²	0 ³ + ⁴
Net phytoplankton decline (Pout < Pin)	0 ⁵	0	0 ⁵	0	0 (<K) - (>K)	+	0 (<K) - (>K)	0
Substantial Pout reduction (Pout,a << Pout,b)	+	0	+	+	0 ⁶	+	0 ⁶	0 ⁶

4.4.2.1 Combined effects of warming with other dimensions of climate change

Warming, for instance, can also alter phytoplankton growth at the source. This makes Pin a function of water temperature with implications for the requirements on the effectiveness of source control. This is particularly important if the source has a long water residence time such as a lake or reservoir (for details on how residence time affects phytoplankton growth and benthic grazing see Lucas & Thompson, 2012). In lakes, several effects of global warming on both phytoplankton quality and quantity were reported. With respect to Pin from lake outlets, global change will probably lead to an earlier appearance of significant phytoplankton densities in the annual succession (e.g., Gerten & Adrian, 2000). Furthermore, global warming could even increase the absolute phytoplankton biomass (Kraemer *et al.*, 2017) and might even impede success of nutrient reductions (Horn *et al.*, 2015).

Changes in temperature and precipitation can alter the hydrological regime (evaporation, precipitation, water melting) with implications for the water depth in both river channel and source (altering P_{in}). For example, in regions with predicted climate-induced losses/surpluses in precipitation, a reduction/raise of the water depth can be expected. Variation of the hydrological regime can also change the inflow of nutrients to the water body through erosion (de Senerpont Domis *et al.*, 2013) or promotion of internal nutrient release (Beklioglu *et al.*, 2007) which both influence phytoplankton growth in the river.

We have seen that an increasing mismatch in the thermal responses of the rates of phytoplankton growth and benthic grazing restricts the temperature range of effective phytoplankton control and leads to the formation of a temperature threshold above which P_{out} steeply increases with slightly more warming. This is particularly relevant for rivers with periods of high water temperatures such as spring and summer in tropical regions (van Vliet *et al.*, 2013). In these cases, exceeding this threshold ought to be avoided. One way to ensure this can be to avoid any additional warming (e.g. through thermal discharge from energy stations) in phases of hot temperatures (Schiel *et al.*, 2004). Also in moderate climate, summer heat waves in combination with heat emission could lead to critical temperatures above the threshold for the mismatch of phytoplankton growth and BFF grazing around 25°C.

It is also well-known that the ecological traits of a species are not constant but dynamic and can adapt to environmental change to a certain extent. Phytoplankton, for instance, is known to adapt quickly to new or transient conditions due to its short life cycle and its multi-species composition. Accordingly, there is evidence for an increase in the maximum growth rate of several phytoplankton species with temperature (e.g. Eppley, 1972, Bissinger *et al.*, 2008). Benthic grazers, in contrast, adapt slower due to their much longer life cycle (in the range of months or years; e.g. McMahon, 2002). Because of the different time scales of adaptation it can be expected that the thermal responses of phytoplankton growth and benthic grazing change differently under warming promoting short-term mismatch (Viergutz *et al.* 2007, Weitere *et al.*, 2008). As phytoplankton adapts quickly, it does not only respond to long-term increase in the mean river temperature. It also responds to phases of high temperatures appearing only sporadically such as heat waves which are predicted to appear more frequently in the course of climate change (Stott *et al.*, 2004, IPCC, 2013) or result from thermal discharges of power-stations (Schiel *et al.*, 2004). Thus, the degree of matching of the thermal responses of phytoplankton growth and benthic grazing is likely to be variable but can decline in the long term in the course of the ongoing adaptation of the grazers again. Last but not least, warming is also known to cause invasions of species with altered ecological traits (and

probably altered temperature dependencies) with consequences for the composition, functioning and thermal response of the species community.

4.4.2.2 Combined effects of warming and land use change

Simultaneous changes in water temperature and Pin can raise Pout abruptly, in particular, when the thermal responses of phytoplankton and grazers are mismatched (Fig. 4-4). Therefore, the combined effects of warming with the variety of drivers mediating changes in Pin are highly relevant. One of these drivers is land use change, as Pin directly responds to e.g. activities which influence phytoplankton growth at the source (e.g. emissions of nutrients from agriculture, thermal discharge from technical facilities adjacent to the source). Pin can also change with activities which destroy riparian vegetation and thereby cause erosion and sedimentation in the river (Verdonschot *et al.*, 2010) or with those altering the light regime in the water column (through removal of vegetation that intercepts light; e.g. Vannote *et al.*, 1980). Knowing the Pin-values required for meeting a certain criterion of success is helpful for estimating the effectiveness, but also the efforts and affordability of planned measures to reduce Pin.

Benthic grazing was found to be crucial for compliance with a quality threshold at the outlet, esp. in shallow rivers (see 4.4.1.1). This shows the exceptional potential of this ecosystem service which, under certain conditions, even increases under warming. Inappropriate land use change, however, can counteract this benefit by reducing the effectiveness of grazer control through adverse effects on the establishment and activity of benthic grazers. Deepening river channels is particularly critical. In absence of grazers, phytoplankton growth and so phytoplankton concentration are known to decline with river depth (Figs. 4-1,4-2, see also Lucas & Thompson, 2012). In presence of grazers, however, the trend can reverse (depending on the grazer density), i.e. phytoplankton concentration increases with river depth (e.g. Fig. 4-1 at BFF density of 500 ind./m²). Reasons are the enlarged water volume to be filtered and the shortened time of exposure of the phytoplankton to the grazers which both reduce the effectiveness of grazer control to such an extent that it dominates over the reduced phytoplankton growth. This shows the urgency of putting more attention on exploring the functioning of grazer-controlled phytoplankton systems, especially under warming (e.g. Weitere *et al.*, 2009), but also the necessity of mitigating any threats to establishment, survival and activity of benthic grazers such as pollution (e.g. Strayer, 1980), habitat degradation (e.g. Parmalee, 1967, Williams *et al.*, 1993) or deepening of river channels.

Climate change and esp. warming are expected to alter aspects of land use such as location and timing of crop production in a region (Olesen & Bindi, 2002). Contrary, land use can alter the climate by carbon sequestration and vegetation evapotranspiration (e.g. Feddema *et al.*, 2005, Bonan, 2008). Hence, changes of temperature and land use can simultaneously affect a region and cause the described combined effects.

4.4.3 General remarks on the assessment methods

All the results of this study were produced with the grazer-controlled phytoplankton model developed in Chapter 2. This model allowed us to analyze the development of phytoplankton during its travel from the source to the outlet and to explicitly consider water temperature and all the factors influencing the warming effects on phytoplankton control: e.g. river depth and length, grazer density as well as the thermal responses of phytoplankton growth and benthic grazing.

Large parts of the model were parameterized based on data from the river Rhine as case study for large rivers (see Table 2-1 in Chapter 2). Aim of this study was to gain principle understanding of the functional relationships between factors relevant for phytoplankton control. Using a stylized model which is structurally oriented on a case study and performing systematic sensitivity analyses in the sense of a ‘virtual lab approach’ is a useful strategy. In principle, the model can be applied to other rivers by appropriate parameterization. Moreover, comparative model results are usually quite robust to changes in the parameter values. Relative results of core importance for all the conclusions drawn in this study were the shapes of the Pout-Pin-curves, esp. the formation of linear and non-linear shapes. The formation of the shapes was found to depend on the balance between phytoplankton growth and benthic grazing (which determines the river’s carrying capacity) and the water residence time of the phytoplankton in the river. The mentioned balance is influenced by water temperature, whereas the residence time depends on river depth and river length. While water temperature and river depth were systematically varied in this study, river length was kept constant. Note that we focused on large rivers (500km). In this case, the water residence time in shallow rivers is such long that the phytoplankton reaches the river’s carrying capacity during its travel from the source to the outlet. This results in the formation of non-linear Pout-Pin-curves.

In the WFD as important framework of European environmental policy, criteria for water quality based on requirements on phytoplankton concentrations are missing so far. However, the threshold of 0.87mgC/l used in this study as benchmark for the mean phytoplankton concentration at the outlet, Pout, was suggested by Mischke *et al.*, 2011 as criterion for the quality assessment of German rivers. Linking the

outcomes of a study to criteria used in the context of national or international water quality assessments is one way to increase their relevance for policy making as they are better adapted to the structure of the respective decision processes. One can argue that the value of the threshold used is artificial. The assessment methodology used, however, is flexible and can be applied to any other threshold value if needed. If another threshold value than 0.87mgC/l would be used, another contour line in the Pout assessment map (Figs. 4-3 and 4-4) would be relevant. This would not affect the existence of a range of tolerable P_{in} -values, but could alter the temperature dependence of the respective maximum tolerable P_{in} -values $P_{in}^{tol,max}$. This would primarily affect the amount of source control needed for achieving compliance with the new quality threshold at the outlet, but also the enhancement mediated by grazer control and their thermal response. The existence of a temperature threshold would be preserved, esp. when the mismatch between the thermal responses of phytoplankton growth and benthic grazing is large. This is because, in this case, the contour lines are very close at the temperature threshold (Fig. 4-4).

4.5 CONCLUSIONS

This study with its systematic model analyses filled a knowledge gap concerning benthic grazing and its potential to enhance phytoplankton control in large rivers, taking into account prospected implications of climate and land use change, esp. warming. We found that this potential was not universal, but context-dependent. In shallow rivers, benthic grazing was indispensable for avoiding eutrophication at the outlet, especially under warming. Its benefit for phytoplankton control was particularly high in case of mismatched thermal responses of phytoplankton growth and benthic grazing and of water temperatures below the grazers' thermal optimum. In this case, benthic grazing markedly reduced the amount of source control needed for keeping the outlet non-eutrophic. The free ecosystem service of benthic grazing thus helped saving substantial efforts to control the phytoplankton in the river source. This shows the urgency of preserving benthic grazers and their performance and improving the habitat conditions for their establishment, survival and activity in large rivers. These insights ought to be taken into account when elaborating strategies for phytoplankton control and planning future land use activities. Improving habitat suitability for the establishment of benthic grazers, however, requires additional research.

This study assumed spatial homogeneity along the river channel regarding factors such as river width and depth, temperature and BFF density. This was done in order to simplify and avoid hindering understanding through too much complexity. Thus, it is an open question whether the more realistic

assumption of heterogeneity in these factors changes the outcomes and conclusions. As the assessment quantity, P_{out} , subsumes all effects on phytoplankton arising during its travel from the source to the outlet, it can be hypothesized that it averages out the effects of spatial heterogeneity to certain extent. This hypothesis will be tested in the next chapter (focusing on spatial heterogeneity in the BFF distribution).

CHAPTER 5 - RELEVANCE OF THE SPATIAL DISTRIBUTION OF BENTHIC FILTER FEEDERS FOR THE PERFORMANCE OF SOURCE AND GRAZER CONTROL OF PHYTOPLANKTON IN LARGE RIVERS AND ITS RESPONSE TO WARMING

Chapter 4 dealt with the performance of source and grazer control of phytoplankton in large rivers and its response to warming by assuming that the BFFs are homogeneously distributed along the studied river, i.e. their density is constant in all parts of the river. This simplification helped us to study the relevance of grazing and other variables on the eutrophication status at the outlet. In the present chapter, we relax the assumption of homogeneity and investigate the implications of the BFF spatial distribution along the river.

5.1. INTRODUCTION

As stated in Chapters 3 and 4, BFF can reduce phytoplankton in rivers (e.g. Cohen *et al.*, 1984, Effler *et al.*, 1996, Caraco *et al.*, 1997; 2006, Hardenbicker *et al.*, 2015b). Models of BFF effects on phytoplankton usually assume BFF to be homogeneously distributed over aquatic habitats. Such models have been proven to be advantageous to study BFF effects on eutrophication (e.g. Lucas & Thompson, 2012; see also Chapters 3 and 4). However, in nature, the BFF distribution sometimes strongly varies along the course of a river (e.g. Leff *et al.*, 1990, Jantz & Schöll, 1998, Caraco *et al.*, 1997, Hardenbicker *et al.*, 2015b).

Several factors appear to be responsible for the distribution of BFF in rivers, including abiotic conditions such as temperature, (e.g. Mattice & Dye, 1975, Weitere *et al.*, 2009, Müller & Baur, 2011), substrate (Cherry *et al.*, 1980; Leff *et al.*, 1990, Schmidlin & Baur, 2007), current velocity (Schmidlin & Baur, 2007), pH (Kat, 1982 cited in Karatayev *et al.*, 2005) and stream order (Karatayev *et al.*, 2005). In addition, biotic conditions such as food availability and community composition can affect the BFF distribution. Regarding food availability, the gradient in phytoplankton concentration seems to be, together with temperature, responsible for the differences between upstream and downstream BFF in terms of both individual and population size observed in some rivers (e.g. the Rhine; Jantz & Schöll, 1998, Hardenbicker *et al.*, 2015b). With respect to community composition, the presence of competitors can affect the BFF distribution. In fact, even the presence of other BFF can facilitate the occurrence of some benthic grazers (Werner, 2009). Moreover, predation and parasitism have also been proposed to explain BFF distribution (Jantz & Schöll, 1998; see also van Nes *et al.*, 2008). In addition, BFF distribution is

also determined by invasion time and spread speed of invasive species (e.g. Schmidlin & Baur, 2007). It is likely that all these factors together cause the heterogeneous BFF distribution observed in rivers.

It can be hypothesized that the BFFs' spatial distribution along the course of the river also influences their grazing effect on phytoplankton, at least to some extent. This can be concluded from the fact that, during its travel from the source to the outlet, the phytoplankton is constantly growing but from time to time also grazed, depending on the BFF density in the river segment passed. Together with the travel speed, the BFFs' position in the river (distance from the source) influences timing and duration of each grazing event which interrupts the phase of undisturbed phytoplankton growth, determines the strength of the phytoplankton regulation and the time left for phytoplankton recovery during the continued travel to the outlet. Hence, the BFFs' position certainly alters the balance between phytoplankton growth and BFF grazing impact and therefore the phytoplankton concentration at the outlet (Pout). There are few models (e.g. Schöl *et al.*, 2002, Pigneur *et al.*, 2014, Caraco *et al.*, 1997) addressing the relationship between BFF distribution and phytoplankton control in specific case studies, but without performing any systematic assessment. Such a systematic assessment, however, is needed for mechanistically understanding the relevance of the BFFs' spatial distribution for the effectiveness of source and grazer control of eutrophication in the sense of meeting a certain quality threshold at the outlet (e.g. $P_{out} < 0.87 \text{ mgC/l}$ suggested by Mischke *et al.* (2011)) and for answering the question what is more beneficial: early or late grazing. All these issues are not fully understood so far. This is particularly critical if it comes to warming as temperature change is known to alter the dynamic interplay of phytoplankton growth and BFF grazing and, consequently, the effectiveness of source and grazer control at the outlet (see also Chapters 3 and 4). Accordingly, it is an open question whether and how warming also alters the relevance of the BFFs' spatial distribution in this context. To address these issues is aim of the recent chapter, that is, to the best of our knowledge, the first systematic study of this kind. We tackle this task by applying the grazer-controlled phytoplankton model developed in Chapter 2. The approach to assess the effectiveness of the interplay of source and grazer control and its temporal response coincides with that used in Chapter 4. As the only difference, we relax the assumption of BFF homogeneity and assess various scenarios of BFF spatial distribution instead. We finish the study with drawing implications of this spatially explicit perspective for eutrophication assessment and management.

5.2. SPECIFIC METHODS

5.2.1. Overview

We use the simulation-based grazer-controlled phytoplankton model previously developed in this thesis (Chapter 2) and applied to test the effect of BFF grazing on phytoplankton development during the travel from the source to the outlet – so far assuming a homogenous BFF distribution along the river (Chapters 3 and 4). Aim of this chapter is to address the effect of spatial heterogeneity in the BFF distribution along the river on the phytoplankton concentration at the outlet (Pout). Spatial heterogeneity is generated by dividing the river in zones with and without grazers. Different BFF distributions are defined by varying number, length and position of these zones, while keeping the total number of BFF in the river constant.

To investigate the effect of spatial heterogeneity in the BFF distribution on the phytoplankton concentration at the outlet (Pout), we compare various heterogeneous scenarios with the respective homogenous one. Based on this, we can assess whether spatial heterogeneity alters the eutrophication status at the outlet and how relevant the BFF spatial distribution is for the effectiveness of source and grazer control. To meet this goal, control is considered to be successful if the outlet is kept “non-eutrophic”, i.e. the respective phytoplankton concentration remains below the quality threshold $P_{out} < 0.87 \text{ mgC/l}$ set by Mischke et al. (2011). This value was taken as a reference for the eutrophication status of water body and is an example for policy-relevant thresholds used in Germany and all European countries adhering to the Water Framework Directive, for water quality assessments.

As we have seen in Chapter 4, there is a range of phytoplankton concentrations at the source, P_{in} , which can be tolerated in the sense that the respective P_{out} -values are still below the quality threshold. Therefore, the maximum tolerable P_{in} -value can be taken as an indicator for the demand on an effective source control (how strongly must P_{in} be reduced to ensure compliance with the quality threshold). According to Chapter 4, this quantity is highly sensitive to the BFF density. Its enlargement measures the grazer-mediated enhancement of phytoplankton control and can therefore be used as an indicator for the effectiveness of grazer control. Last but not least, Chapter 4 highlighted that the effectiveness of source and grazer control depends on both river depth and water temperature. Therefore, it is highly important to know whether the relevance of the BFF spatial distribution for the effectiveness of source and grazer control also changes with river depth and water temperature.

5.2.2. Simulation experiments

We analyze the response of the phytoplankton concentration at the outlet (P_{out}) to changes in the values for the phytoplankton concentration at the source P_{in} (from 0.02 to 10.02 mgC/l), the mean overall BFF density in the river stretch G (from 0 to 500 ind./m²), the river depth D (1, 2 and 4m) and the water temperature T (from 0 to 32°C). We also explore the effect of varying the optimum temperature for the phytoplankton growth rate (T_{opt}^p) and for BFF grazing rate (T_{opt}^g).

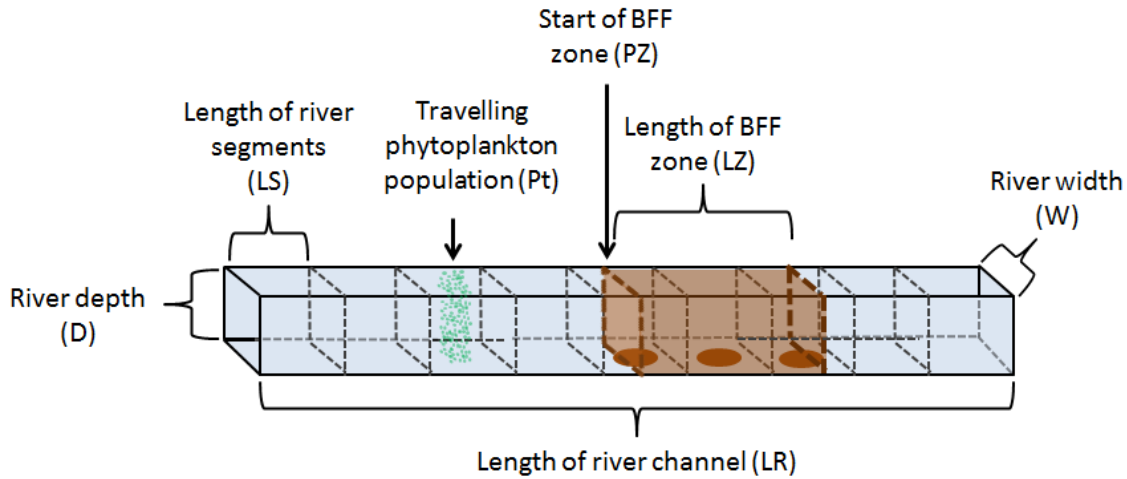


Figure 5-1. Schematic representation of the spatial structure of the modelled river system (lateral view). The river channel (blue rectangle) can contain a zone with BFF (with a length LZ). The phytoplankton population (green dots) travels across the entire river channel (including the zone with BFF), moving in each time step from one segment (of length LS) to the next one. BFF grazing affects the phytoplankton *only* when it is inside the BFF zone (Eq. 18). Note that the depicted proportion between LS and both LR and LZ is much larger than in the model.

5.2.3. Definition of spatial heterogeneity in BFF distribution

In the previous chapters, we assumed that BFF are distributed homogeneously throughout the river stretch of length LR (this homogeneous BFF distribution is depicted in Fig. 5-2d), including the cases without BFF (Fig. 5-2e). In this chapter we simulate heterogeneous BFF distributions throughout the river stretch.

In any heterogeneous distribution, we assume that BFF occupy only a certain zone of the river of length LZ (hereafter called *BFF zone*). To simplify and be able to compare the heterogeneous BFF distributions with the homogeneous one, we preserved the total BFF density in the entire river in all distributions:

$$Eq. 17 \quad G_z = \frac{G * LR}{LZ}$$

where G_z is the density of the BFF population in the BFF zone (ind./m²), G the average BFF density in the whole river stretch (ind./m²), LZ the length of the BFF zone (m), and LR the length of the entire river channel (m). Hence, for a given total BFF density (G), the larger (smaller) the BFF zone (LZ), the lower (higher) the BFF density within such zone (G_z).

The length of the river channel (LR) is divided in quarters of equal length (125m), which could be occupied by BFF (thus forming the BFF zone, LZ) or not according to the BFF distribution. We define nine heterogeneous BFF distributions by placing BFF in zones consisting of one to three quarters and varying the position of such zones along LR (Fig. 5-2a-c). The relationship between LZ and LR is hereafter referred to as the extent (EX ; %): when BFF occupy zones consisting of one, two, three or four quarters the extent is 25, 50, 75 or 100%, respectively. It is important to not confuse the length of the BFF zone (LZ) with that of the river segments (LS) (Fig. 5-1; see Eq. 4 in Chapter 2 for the estimation of LS).

The position (PZ ; unitless) of the BFF zone is defined as the point in the river where the zone starts. Since we divided the river in quarters of 125m PZ was either 0, 125, 250 or 375m (Fig. 5-2).

Whenever the phytoplankton population was inside a BFF zone it was grazed by the BFF, otherwise it was not:

$$\text{Eq. 18} \quad \text{if } ([PP > PZ] \text{ and } [PP < \{PZ + LZ\}]) \text{ then } G_t = G_z$$

$$\text{else } G_t = 0$$

$$\text{Eq. 19} \quad PP = v * 3,600 * t$$

where PP is the position of the travelling phytoplankton population along the river channel (m; all simulations start with a value of zero; Eq. 19), PZ the position where LZ starts, G_t the density of the BFF population (ind./m²) which grazes on phytoplankton at time step t and G_z the BFF density in the BFF zone (ind./m²; Eq. 17).

Note that the BFF zone, LZ , does not exactly fit with the spatial segment structure along which a phytoplankton population travels from time step to time step. Segment length, LS , depends on the water speed (a function of river morphology; Eqs. 1 and 4 in Chapter 2) whereas BFF zone length, LZ , is always a multiple of 125m. Therefore, grazing can be slightly overestimated (or underestimated) during the time steps in which PZ does not coincide with segment boundary. However, this may only happen once (if the

BFF zone is located at the beginning or end of the river channel) or twice (if the *BFF zone* is located elsewhere) in each simulation. Moreover, since time steps are relatively short (one hour), this spatiotemporal discretization is very unlikely to affect substantially the results.

Throughout the text we refer to the nine heterogeneous BFF distributions tested here using the letter *d* followed by a number (Fig. 5-2).

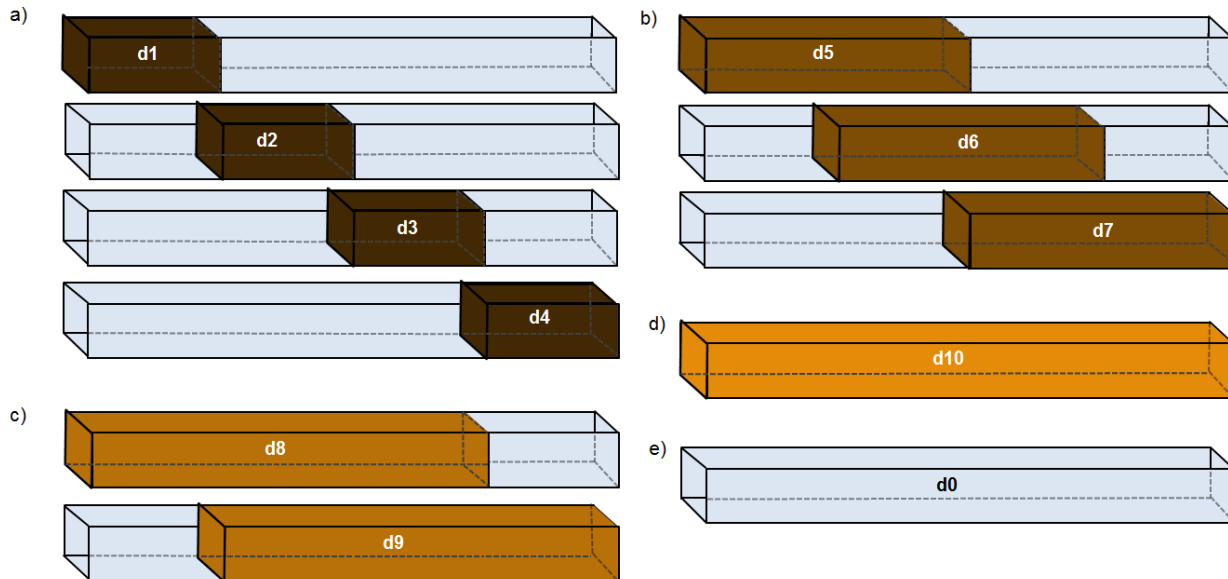


Figure 5-2. Schematic representation of the modelled river system (lateral view) with the eleven BFF distributions tested: a) one fourth of the river is occupied by the BFF zone (EX= 25%), b) one half of the river is occupied (EX= 50%), c) 75% of the river is occupied (EX=75%), d) the entire river length is occupied (EX= 100%; i.e. homogeneous distribution), e) the case without BFF (EX= 0%). We refer to these distributions throughout the text by the letter and number assigned to each of them in this figure.

Symbol	Parameter	Units	Value	References / Notes
<i>Benthic filter feeders (BFF)</i>				
<i>G</i>	Average density of BFF population in the entire river stretch	ind./m ²	0, 100, 300, 500	Although BFF distribution in nature is patchy and, thus, the BFF density in a river stretch is difficult to estimate, our values are roughly within the range of values reported for <i>D. polymorpha</i> and <i>C. fluminea</i> (Appendix 3).
<i>LZ</i>	Length of the zone occupied by BFF	Km	0*, 125, 250, 375 and 500**	*Distribution without BFF (<i>d0</i>). **Homogeneous distribution (<i>d10</i>)
<i>Physical parameters</i>				
<i>D</i>	River depth (i.e. water depth)	M	1, 2 and 4	In the range of values found in some rivers including the Rhine (Admiraal <i>et al.</i> , 1993, Uehlinger <i>et al.</i> , 2009) and the Middle Elbe (Scharfe <i>et al.</i> , 2009)
<i>LR</i>	Length of the river stretch	M	500,000	In the range of long rivers, e.g. the Elbe (1,094km; Scharfe <i>et al.</i> , 2009), the Rhine (ca. 1,250km; Uehlinger <i>et al.</i> , 2009), the Danube (2,780km; WWF, 2002), the Volga (3,531km; WWF, 2002)

Table 5-1. Main parameters of this chapter.

Symbol	Variable	Units	Equation
<i>Benthic filter feeders (BFF)</i>			
<i>EX</i>	Extent of BFF in the river channel	%	-
<i>G_z</i>	Density of the BFF population in the BFF zone	ind./m ²	17
<i>G_t</i>	BFF density that grazes over phytoplankton at time step <i>t</i>	ind./m ²	18
<i>PZ</i>	Position where the BFF zone starts	m	Text below Eq. 17
<i>Physical variables</i>			
PP	Position of the traveling phytoplankton population along the river channel	m	19
<i>t</i>	Simulation time step	hours	-
<i>t_{res}</i>	Water residence time	hours	3 (Chapter 2)
<i>V</i>	Water speed (in downstream direction)	m/s	1 (Chapter 2)

Table 5-2. Main variables of this chapter.

5.3. RESULTS

The aim of this chapter is to analyze the effect of spatial heterogeneity in the BFF distribution along the river on a variety of criteria commonly used in the assessment of eutrophication issues: the phytoplankton concentration at the outlet (P_{out}), the shape of the P_{in} - P_{out} -curves, and the implications for the performance of source and grazer control, by accounting for river depth and water temperature. As we aim to understand the effects of all considered BFF distributions mechanistically, we tracked the temporal development of the phytoplankton bloom during its travel along the river from the source to the outlet, including its passage through BFF zones. Only in this way, we can understand how P_{out} depends on P_{in} , but also on various river conditions such as BFF density and spatial distribution (for the description of the BFF distributions, see Fig. 5-2), river depth (determining water speed), and water temperature.

5.3.1 Effect of BFF spatial distribution on phytoplankton dynamics

To get a first impression of the effect of spatial heterogeneity, we started our investigations with considering the two BFF distributions out of the mentioned variety which are most heterogeneous in the sense that they show the highest spatial concentration of BFF (i.e. $EX=25\%$) and are located at the two ends of the river stretch (i.e. source and outlet): $d1$ and $d4$. These two heterogeneous BFF distributions were compared with the homogenous BFF distribution regarding their effect on the phytoplankton dynamics which evolve during the travel of the bloom from the source to the outlet for four P_{in} -values and three river depths (1, 2, 4m), but fixed values for water temperature ($25^{\circ}C$) and BFF density (300 ind./m^2).

Figure 5-3 shows the temporal development of the phytoplankton concentration, P_t , in the course of the travel from the source to the outlet of the river stretch for the mentioned three BFF distributions (homogenous, $d1$ and $d4$) and the scenario without grazing. Evidently, the extent to which the BFF distributions alter values and shape of the P_t -dynamics depends on both - river depth and P_{in} -values.

In shallow rivers (1m), the P_t -dynamics for the two heterogeneous BFF-distributions ($d1$ and $d4$) substantially deviate from the P_t -dynamics for the homogenous distribution, quantitatively and qualitatively. Under the homogenous BFF-distribution, P_t monotonously decreases or increases in the course of time, depending on the P_{in} -value. For low and very high P_{in} -values, P_t decreases, but for different reasons and with different resulting P_{out} -values: for low P_{in} -values, due to grazing resulting in $P_{out} = 0$ and, for high P_{in} -values above the carrying capacity K of the river, due to density dependence

resulting in $P_{out} = K$. Only in the range of medium P_{in} -values, we see an increase of P_t . In this case, phytoplankton growth counteracts the effect of grazing.

Under the heterogeneous BFF distribution with late grazing (d4), in contrast, the P_t -dynamics show a unimodal shape. At the beginning, P_t follows the dynamics of the non-grazed scenario and increases until it reaches the BFF zone. The strength of the P_t -increase is negatively correlated with P_{in} , whereas the maximum reachable P_t -value before grazing, the decline of P_t during grazing and the resulting P_{out} -value are independent of P_{in} . This independence reflects that P_t can reach the carrying capacity of the river, K , before passing the BFF zone such that the grazer-mediated decline starts from approximately the same level of P_t , regardless of P_{in} . The scenario with early grazing (d1) works differently. As long as P_{in} is small enough, P_t declines to zero, indicating that the grazers in the BFF zone are able to completely remove the phytoplankton without giving it any chance to recover. If P_{in} becomes higher, P_t still declines, but not strongly enough to be completely removed as the time of exposure to the BFF is too short and/or grazing intensity too low. Because of this incomplete control, P_t recovers after leaving the BFF zone and can increase almost up to the level of the (non-grazed) carrying capacity during its travel to the outlet.

Accordingly, the ranking orders among the P_{out} -values resulting for the different BFF distributions depend on the P_{in} -values. Below a critical P_{in} -value, d1 (early grazing) leads to the lowest P_{out} -values and is therefore best, while above it, d4 (late grazing) is best. At most P_{in} -values, at least one of the two heterogeneous BFF distributions is better than the homogenous one. At some P_{in} -values, even both are better than the homogeneous BFF distribution indicating a benefit of concentrated grazing pressure.

In deeper rivers (2 and 4m; Fig. 5-3), the general behavior of the P_t -dynamics for the different BFF distributions is preserved. Major differences due to the increased river depth are that, (i) the water residence time to reach the outlet $t_{res,out}$ is shorter because of the increased water speed, (ii) the maximum reachable P_{out} -values are lower because of a lowered carrying capacity K resulting from the reduced photosynthetically active zone, and (iii) the difference in the P_t -effects of the different BFF distributions is reduced, especially for high P_{in} -values. Early grazing (d1) is found to be best, regardless of the P_{in} -value. However, d1 cannot ensure complete removal anymore such that phytoplankton can recover, even if P_{in} -values are low. Hence, its effectiveness is much lower than in the case of shallow rivers. The deeper the river, the closer are the BFF-mediated P_t -curves to the P_t -curve for the non-grazed case and to each other. This is a reflection of the fact that the grazing pressure is weakened in the deeper rivers such that neither an increase of the BFF density nor a change in the BFF spatial distribution leads to a significant reduction

of Pout. Thus, increasing river depth does not only diminish the carrying capacity K of the river, but also changes the relative performance of the various BFF distributions and the effect of spatial heterogeneity.

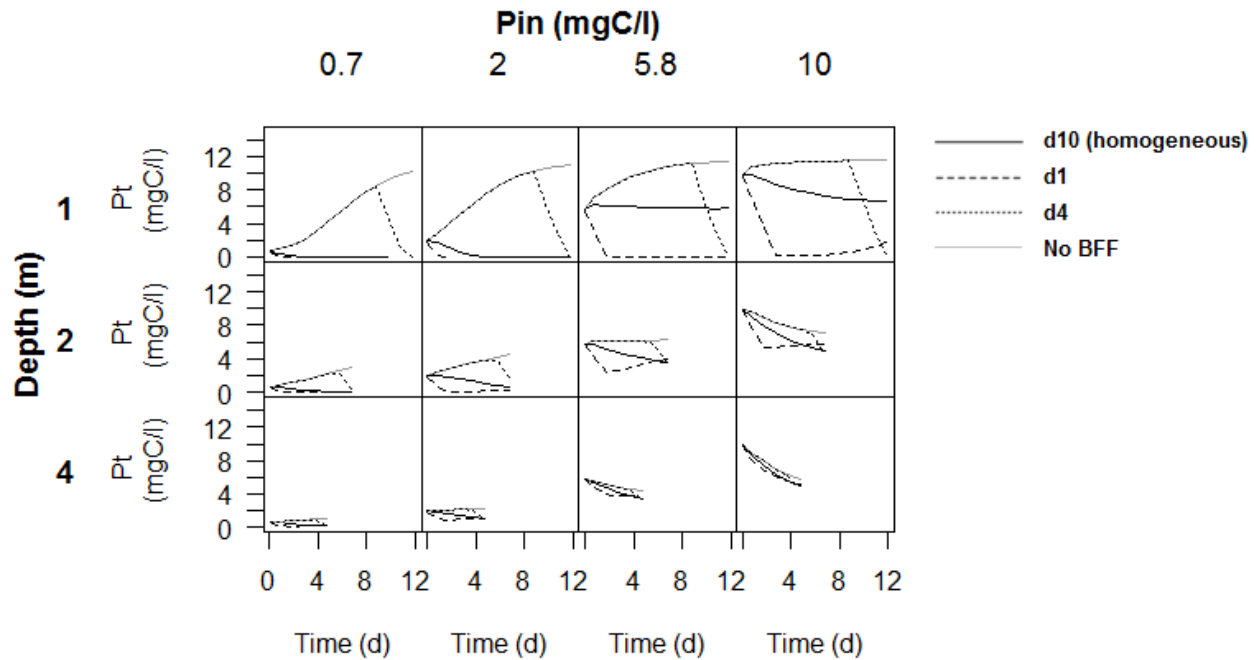


Figure 5-3. Phytoplankton concentration along the river stretch (P_t) as a function of time t for three BFF distributions under different P_{in} values and water depths. Temperature is 25°C and average BFF density in the whole river stretch (G) is 300 ind./m^2 .

5.3.2 Effect of BFF spatial distribution on the P_{in} - P_{out} -curves and its temperature-dependence

So far, we explored the development of P_t from the source to the outlet under different spatial distributions of the BFF by assuming a water temperature of 25°C and got mechanistic understanding. These analyses and previous studies (see Chapter 4) indicated that both P_t and P_{out} strongly depend on the P_{in} -value, but also on river depth and water temperature. As the next step, we therefore want to assess the effect of spatial heterogeneity in the BFF distribution on the shape of the P_{in} - P_{out} -curves and its dependence on the water temperature T (varied from 0 to 32°C).

Previous systematic assessments have indicated that grazing with homogeneously distributed BFF alters the shape of the P_{in} - P_{out} -curves (see Chapter 4). On the one hand, grazing causes the emergence of a critical P_{in} -value below which P_{out} is controlled to zero, i.e. phytoplankton is completely removed by the (homogeneously distributed) BFF grazers during the travel from the source to the outlet. On the other hand,

grazing diminishes the saturation value in the Pin-Pout-curve which reflects a grazer-mediated reduction of the carrying capacity in the river, K . However, Chapter 4 also indicated that water temperature alters the shape of the Pin-Pout-curves and the effect of grazing on it, when BFF are homogeneously distributed, and that small temperature changes can have dramatic effects on Pout under certain circumstances.

Hence, we simulated phytoplankton development for different Pin-values and water temperatures for the same scenarios as before (without BFF, the homogeneous and the two heterogeneous BFF distributions concentrated near to the source (d1) and to the outlet (d4)). Figure 5-4 shows the resulting Pin-Pout-curves for five temperature values, three river depths and an average BFF density of 300 ind/m^2 . It can be seen that water temperature and river depth can change both the magnitude of the difference in the Pout-values of the BFF distributions and the relative performance of the BFF distributions regarding eutrophication control, i.e. the ranking orders in the resulting Pout-values (what distribution does lead to the lowest Pout).

In deeper rivers (Fig. 5-4, 2 and 4m), the Pin-Pout-curves for the two heterogeneous and the homogeneous BFF distributions are close to each other and to the case without BFF. Moreover, the curves are relatively linear, particularly in cold waters (6 and 14°C). For 2m depth, there is a slight advantage of late grazing (d4) and a slight disadvantage of early grazing (d1) for most Pin-values and temperatures. However, for 4m depth, the relative performance of the different BFF distributions concerning Pout is virtually the same for all Pin-values and temperatures.

In shallow rivers (Fig. 5-4, 1m), the situation is different. For very low (6°C) and very high (30°C) temperatures, all curves are very close to each other (no effect of spatial heterogeneity), while the BFF spatial distributions yield very different Pin-Pout-curves which are less linear than in deeper waters under moderate temperatures (14 - 25°C). For 14°C , there is a clear advantage for late grazing (d4) indicating that concentrated grazing near the outlet is able to counteract the effect of undisturbed phytoplankton growth until passing this BFF zone. For 22°C , both heterogeneous distributions (d1 and d4) are much better than the homogeneous one. For 25°C , i.e. the temperature above which the grazing pressure of the BFF strongly declines, the situation is more complex. For high Pin-values, d4 (late grazing) is the best, as early but weak grazing (d1) would insufficiently reduce the phytoplankton which can afterwards recover and grow till the Pout-level from the non-grazed case. In this Pin-range, d1 would be even worse than the homogeneous scenario. For smaller Pin-values, however, scenario d1 (early grazing) is best as Pin is small enough to be completely removed by upstream grazers with their concentrated BFF density. The homogeneous scenario with its lower BFF density, in contrast, would not be able to ensure a complete

removal. This shows that accounting for the spatial BFF distribution is indispensable in shallow rivers of moderate water temperatures, as the homogenous BFF distribution can substantially deviate from the heterogeneous ones and is thus useless as a predictor of the effects of other distributions on Pout in these cases.

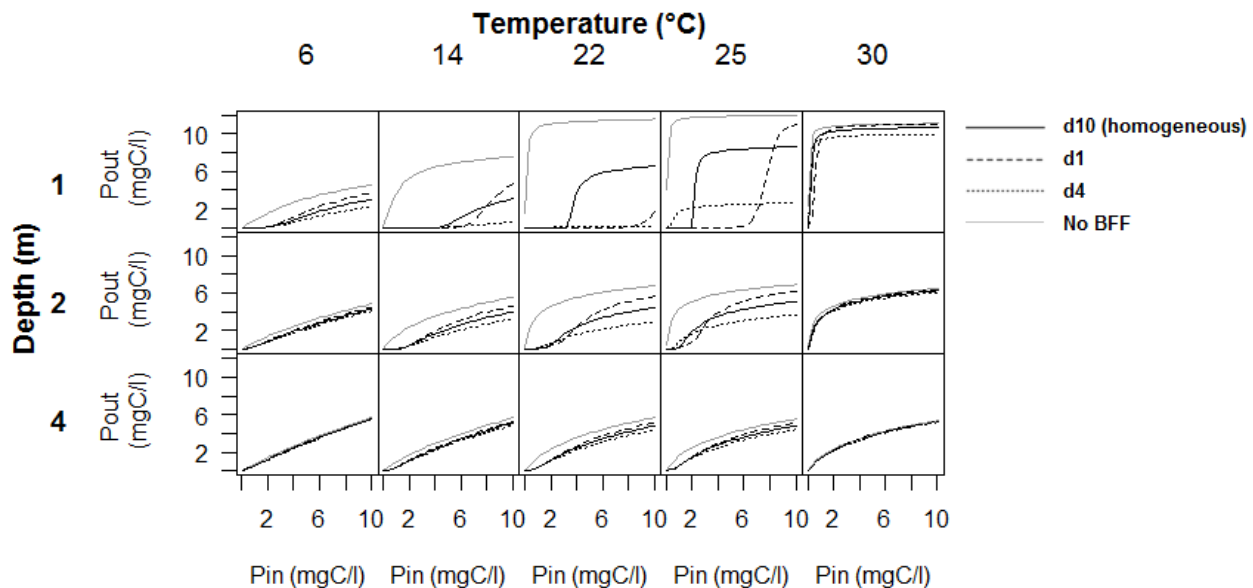


Figure 5-4. Phytoplankton concentration at the end of the river channel (Pout) as a function of Pin value for different temperatures and water depths. BFF density is 300 ind./m².

All these argumentations give rise to various conclusions: First, Pin-values and the river depth are quantitatively and qualitatively influencing the effect of the BFF spatial distribution on Pout, as they can change both the magnitude of difference and the ranking orders among them. Second, river depth and water temperature are constraining the relevance as well. An increasing river depth evidently (i) decreases the difference in both single Pout-values and the shape of entire Pin-Pout-curves yielded by the different BFF distributions, (ii) changes the relative performance of the different BFF distributions and (iii) diminishes the impact of water temperature on them, indicating a combined effect.

5.3.3 Systematic assessment of the relative performance of all ten BFF spatial distributions and their temperature-dependence for different BFF-densities, Pin-values, and river depths

The results from the previous section indicate that both the relative BFF performance (i.e. the ranking order) and magnitude of difference among the Pout-values yielded by the different BFF distributions,

depend on river conditions, i.e. water temperature, river depth and P_{in} -value. However, we assessed the BFF distributions and their temperature-dependence based only on a few selected scenarios (three BFF distributions, five temperature values, one BFF density). Therefore, to study the effect of the spatial BFF distribution and its temperature-dependence more systematically, we now simulate phytoplankton dynamics under different temperatures (from 0 to 32°C at one degree Celsius intervals), ten BFF spatial distributions (see “Methods” for their description) and four average BFF densities (50, 100, 300 and 500 ind./m²). Our assessment consists of three separate analyses: one for the “best” spatial BFF distribution (i.e. the one yielding the lowest P_{out} ; Fig. 5-5), one for the P_{out} -differences between the “best” distribution and the “worst” distribution (i.e. the one yielding the highest P_{out} -value; Fig. 5-6), and one for the P_{out} -differences between $d1$ and $d4$ (Fig. 5-7).

The plot of the “best” BFF distribution (Figure 5-5) with its color code shows that two of the ten BFF distributions were the “best” in most conditions: $d1$ (early grazing, light blue) and $d4$ (late grazing, dark blue). Fig. 5-5 also reveals that, in all cases, there is a certain P_{in} -value (hereafter: “transitional P_{in} value”) above which $d4$ is best. The transitional P_{in} -value is seemingly the value above which the present BFF grazers, even when they are concentrated near the source, are not sufficient to fully remove the phytoplankton which can afterwards recover during its continued travel to the outlet. Under such circumstances, late grazing (i.e. $d4$) is best in minimizing P_{out} . We see that the transitional P_{in} -value shows a unimodal thermal response with a maximum at moderate temperatures. This maximum increases (and the $d4$ -zone accordingly shrinks) with the average BFF density. It markedly decreases (and the $d4$ -zone expands) with river depth, independent of BFF-density and water temperature.

In contrast, below the transitional P_{in} -value (Fig. 5-5), other BFF distributions than $d4$ are “best”, i.e. yield the lowest P_{out} -value. As long as P_{in} is not too low, $d1$ is best in most cases. The $d1$ -zone expands under increasing average BFF-density, esp. in shallow rivers (1m). Under very high average BFF densities (500 ind./m²), however, all spatially concentrated BFF distributions (EX=25%; all “blue” variants) can be “best”, depending on the exact conditions. In deeper rivers (2 and 4m), many BFF distributions can be best below the transitional P_{in} -value. In these rivers, however, the three BFF distributions tested yielded P_{out} -values very close to each other in the previous study (see Fig. 5-4). This explains why the deviation in the respective P_{out} -values is merely minor. Finally, at 32°C, we see a grey stripe indicating that all BFF distributions yield the same P_{out} -value, regardless of P_{in} , BFF density, and river depth, as BFF grazing is zero at this temperature.

The closeness of the Pout-values yielded by the BFF distributions at deeper waters (Fig. 5-4) indicates that knowledge of the relative performance of BFF distributions alone is not enough to conclude on the relevance of the BFF distribution for Pout. The difference in the Pout-values can be significant or minor.

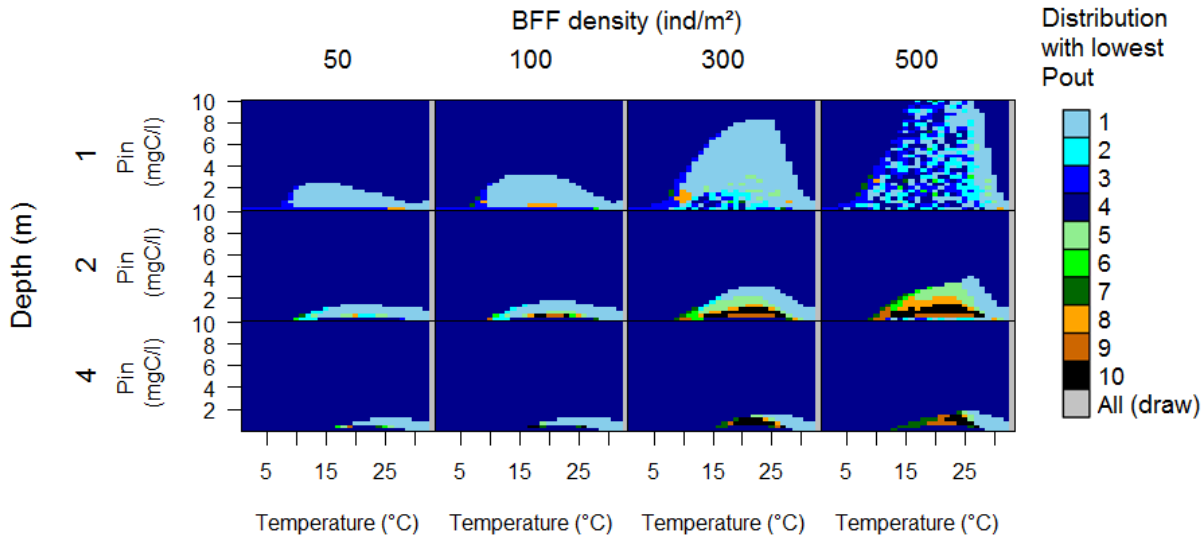


Figure 5-5. The “best” BFF spatial distribution yielding the lowest Pout-value as a function of water temperature and Pin-value under different river depths and average BFF densities. Each color in the subplots represents one BFF distribution: blue colors BFF distributions occupying only one fourth of the river length (EX= 25%), green colors those occupying half of the length (EX= 50%), orange colors those occupying 75% of it (EX= 75%) and black the distribution occupying the entire river (EX= 100% that coincides with the homogeneous distribution). The number to the right of the color legend corresponds to the ID of the BFF distributions in Fig. 5-2: 1 for $d1$, 2 for $d2$ and so on. The grey color represents those conditions where all BFF distributions yield the same Pout.

Therefore, we additionally assessed the difference between the Pout-values yielded by the “best” and the “worst” BFF distributions for the same conditions considered in the preceding analysis. This Pout-difference helps quantifying the effect of spatial heterogeneity in the BFF distribution. Figure 5-6 shows that the Pout-difference can be marginal (i.e. $<0.2\text{mgC/l}$; white color) or substantial (yellow, orange or red color), depending on the conditions. We see that, in deep rivers and in shallow rivers with cold or very hot water (above 30°C), the Pout-difference is merely marginal for the majority of Pin-values and BFF densities. However, in shallow rivers with moderate to hot waters (approx. $10\text{-}30^\circ\text{C}$), the situation is different. Here, the Pout-difference strongly depends on the Pin-value and the BFF-density. Moderate Pout-differences (yellow color in Fig. 5-6) emerge above the transitional Pin-value, i.e. in the Pin-range

favoring *d4* (dark blue in Fig. 5-5), whereas high Pout-differences (orange to red color) only occur in the close vicinity of this transitional Pin-value and under higher temperatures (20-30°C).

The Pout-difference between the “best” and the “worst” BFF distribution does not only reveal the magnitude of the advantage of the “best”, but also the sensitivity of Pout to spatial heterogeneity in the BFF distribution. The term is quantitative, accounts for all BFF-distributions, but is not mechanistic (as we do not know which distribution is “worst”, i.e. yields the highest Pout-value). On the other hand, we have seen that the two spatially opposite distributions, *d1* and *d4*, are of particular importance and “best” under many conditions. Therefore, assessing the Pout-difference between *d1* and *d4* would provide additional information (how strongly do the two distributions actually differ in their effect?). Our results show that their Pout-difference can also be both marginal ($|\Delta Pout| < 0.2\text{mgC/l}$ indicated by the white color in Fig. 5-7) and significant (colorful according to the color code in Fig. 5-7), depending on certain conditions. Not surprisingly, significant positive (yellow to red) and negative (blue) Pout-differences only occur above and below the transitional Pin-value which separates the zone of beneficial *d4* (late grazing) from the zone of beneficial *d1* (early grazing) in the preceding Figure 5-5, respectively. More surprising is the emergence of a range of ‘white constellations’ where the Pout-difference between *d1* and *d4* are merely marginal. Increasing the average BFF density diminishes the percentage of white constellations in the *d4*-beneficial zone (above the critical Pin-value), but increases this percentage in the *d1*-beneficial zone, esp. in shallow rivers. Moreover, the benefits from early grazing (*d1*, blue Pout-difference) are only significant if BFF density is low or water temperature is close to the threshold value (25-27°C) above which the BFF lose their grazing pressure. Around this temperature threshold, the Pout-differences are generally high in shallow waters with high BFF-densities, showing the importance of explicitly accounting for the BFF spatial distribution in these cases. Moreover, under low BFF densities, increasing river depth expands the range of white constellations and reduces the Pout-difference between *d1* and *d4* indicating a decreasing relevance of the BFF spatial distribution for Pout.

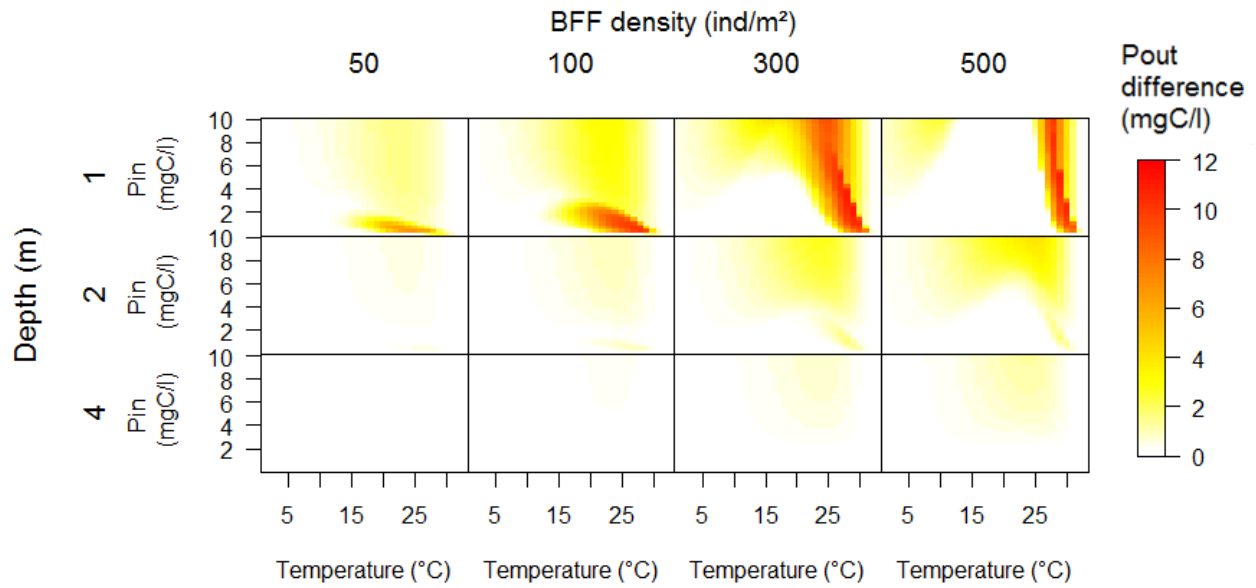


Figure 5-6. Difference between the phytoplankton concentrations at the outlet (Pout) for the best BFF distribution (i.e. that yielding the lowest Pout value), and the worst BFF distribution (i.e. that yielding the highest Pout value) as a function of temperature, Pin value, BFF density and water depth.

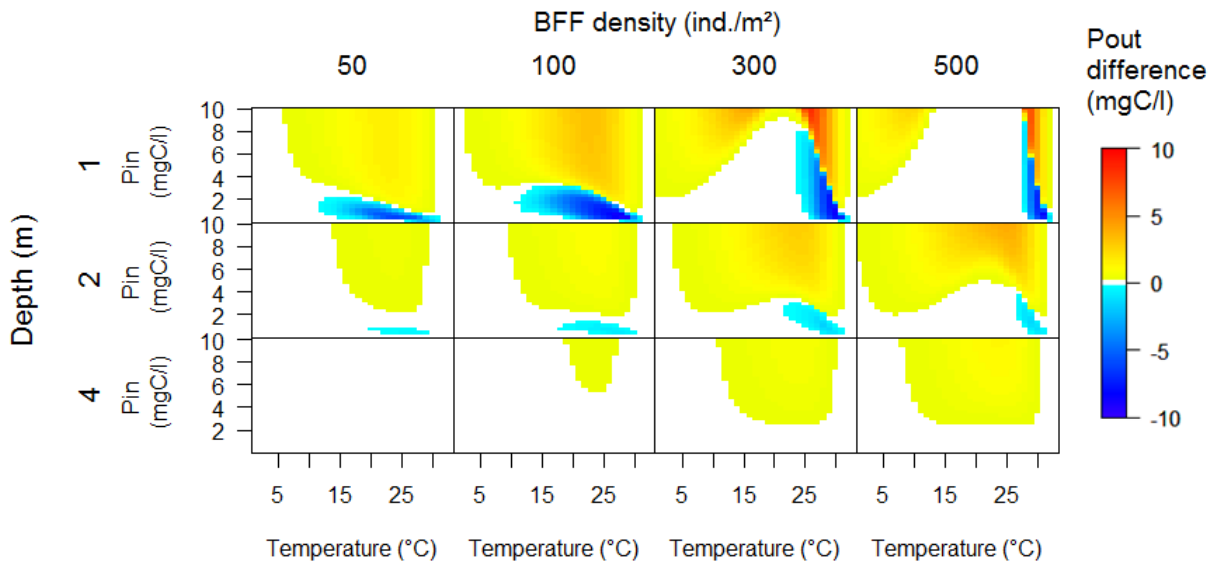


Figure 5-7. Difference in the Pout-values yielded by the BFF distributions *d1* and *d4* as a function of BFF density, Pin value, water temperature and river depth. Warm colors (yellow to red) represent positive differences ($P_{out}(d1) > P_{out}(d4)$), while blue colors represent negative differences ($P_{out}(d1) < P_{out}(d4)$). White means “no difference”.

5.3.4. Relevance of the BFFs' spatial distribution for the effectiveness of source and grazer control in meeting a quality threshold at the outlet of a river stretch and its temperature-dependence

So far, we focused on Pout and its sensitivity to the BFF spatial distribution. We observed that spatial heterogeneity in the BFF distribution can alter the effectiveness of grazing with the consequence that the respective Pout-value can deviate from the value predicted for a homogenous BFF distribution. This directly leads us to the question of the implications for the assessment of the effectiveness of source and grazer control in meeting a certain quality threshold at the outlet (such as that set by Mischke et al. (2011), i.e. $P_{out} < 0.87\text{mgC/l}$). How necessary is it to explicitly account for the BFF spatial distribution when assessing the effectiveness of phytoplankton control? How big would be the failure in the assessment when neglecting spatial heterogeneity and assuming homogeneity instead? Is there any temperature-dependence of the effect of BFF spatial distribution on the effectiveness of source and grazer control?

Figure 4-3 in Chapter 4 showed that there is a critical P_{in} -value below which the resulting Pout-value can be kept below the quality threshold under spatially homogenous conditions. This maximum tolerable P_{in} -value can be interpreted as need of source control (the value until which P_{in} must be reduced to ensure quality compliance at the outlet). This value which increases with BFF density and shows a unimodal thermal response was used as indicator for the effectiveness of phytoplankton control by BFF.

In the following, we repeat the analyses underlying Fig. 4-3 for additional spatially heterogeneous BFF distributions to get insights into their influence on the effectiveness of source and grazer control in meeting the quality threshold of 0.87mgC/l at the outlet. Based on this, we determine the maximum tolerable P_{in} -values for three BFF distributions (the homogenous reference (see the intermediate contour line in Fig. 5-8), but also the optimum/worst BFF distribution with the lowest/highest Pout-value (see the uppermost/lowest contour line in Fig. 5-8)) and compare their thermal responses.

Figure 5-8 shows that the qualitative pattern, i.e. the unimodal shape of the thermal response of the maximum tolerable P_{in} -value with the largest value at intermediate temperatures, observed for the homogeneous BFF distribution (Fig. 4-3) is preserved for the optimum and the worst BFF distribution too (at least for moderate and higher BFF densities). This shows that the benefit from grazing is maximum under moderate water temperatures, regardless of BFF distribution.

The height of the maximum tolerable P_{in} -values, however, can strongly differ between the three BFF distributions under certain circumstances. For deep waters (4m) or low BFF densities (50 and 100

ind./m²), all three contour lines are close to each other and close to the non-grazed case, regardless of water temperature. In these cases, grazing is not effective and the BFF spatial distribution will not change the situation, i.e. the likelihood of meeting the quality threshold at the outlet. Hence, the homogenous distribution is sufficient for the assessments.

In shallow and less deep waters (1 and 2m), the situation is different. Here, the contour lines for the homogenous and the worst BFF distribution are close to each other. However, the contour line for the optimum BFF distribution can strongly deviate from the two other lines markedly expanding the range of tolerable Pin-values – but only under moderate water temperatures at high BFF densities (300 ind./m²) in shallow rivers (1m) or very high BFF densities (500 ind./m²) in moderately deep rivers (2m). In these cases, an appropriate position of the BFF zone in the river can markedly increase the effectiveness of grazer control. Therefore, it is indispensable to account for the BFF spatial distribution in these conditions. In all other cases, the three contour lines are close to each other, i.e. the BFF distribution does not make a difference – but for different reasons: in the case of 2m depth and a BFF density of 300 ind./m² because the grazing pressure of even the optimum BFF distribution is not sufficient to substantially improve the grazer control, while in the case of 1m and a BFF density of 500 ind./m² even the worst BFF distribution is strong enough to reach the quality threshold under many Pin values.

It is also worth noticing that patterns of the three contour lines are similar for the case of 1m depth and a BFF density of 300 ind./m² and the case of 2m depth and a BFF density of 500 ind./m². Moreover, in shallow rivers, the best contour line for the scenario with 300 ind./m² is similar to the homogenous contour line for the scenario of 600 ind./m².

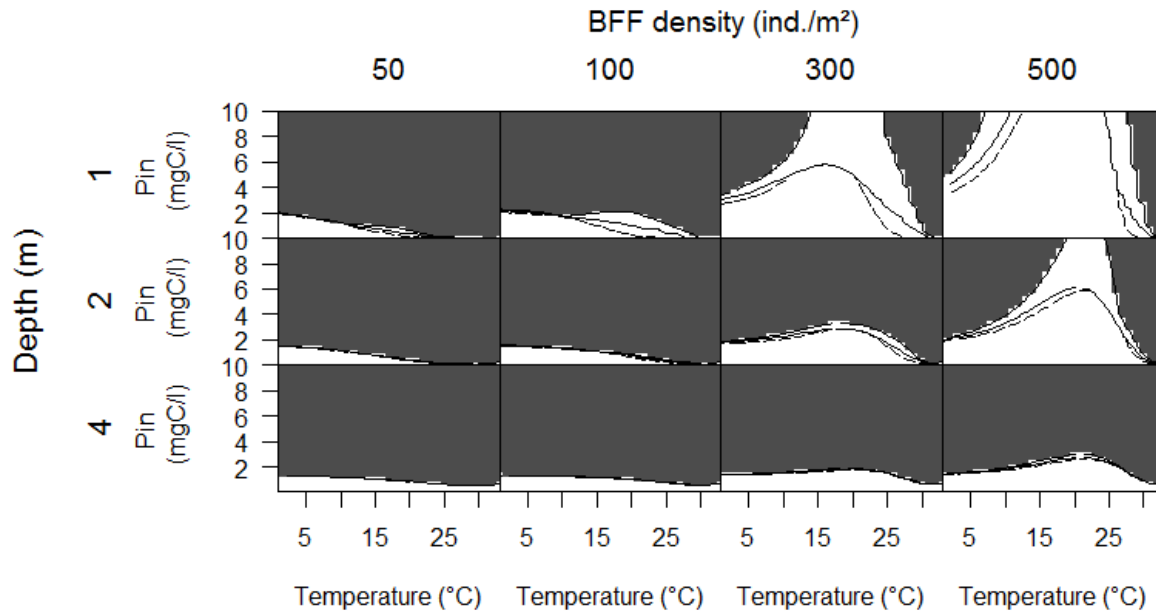


Figure 5-8. Contour lines representing the maximum tolerable P_{in} -values below which the phytoplankton concentration at the outlet, P_{out} , can be kept below the quality threshold of 0.87mgC/l , as a function of water temperature for different values of BFF density and water depth under different BFF spatial distributions. The intermediate contour line belongs to the homogeneous BFF distribution, while the lowest (uppermost) one belongs to BFF distributions with the highest (lowest) P_{out} -value. The white area indicates a ‘non-eutrophic’ (i.e. $P_{out} < 0.87\text{mgC/l}$) and the grey zone a ‘eutrophic’ status ($P_{out} \geq 0.87\text{mgC/l}$) of the outlet for the optimum BFF distribution.

5.4 DISCUSSION

The aim of this chapter was a systematic assessment of the relevance of the spatial BFF distribution in large rivers for both the dynamic behavior of grazer-controlled phytoplankton travelling from the source to the outlet of a river stretch and the performance of its control. The motivation was filling a gap in the study of such distribution: existing models of grazer-controlled phytoplankton either unrealistically assume spatial homogeneity in BFF distribution along rivers (as we did in Chapters 3 and 4) or use the BFF distribution of particular sites (without seeking to understand the impact of BFF distribution but rather to predict phytoplankton development at the sites of interest). Therefore, we wanted to clarify under what conditions it is necessary to account for BFF spatial distribution to reach correct conclusions and to estimate the failure when assuming homogeneity in such distribution.

In this chapter, the relevance of spatial BFF distribution was measured by testing the effect of heterogeneity in such distribution on the phytoplankton concentration at the outlet of a river stretch (Pout), the ability to meet a quality threshold (0.87 mgC/l set following Mischke et al. (2011) for large German rivers), and the shape of the functional relationships of Pt-dynamics and Pin-Pout-curves at different water temperatures. We also determined the difference between the Pout yielded by the heterogeneous BFF distributions and that yielded by the homogenous distribution. Special interest was in the dependence of the outcomes on water temperature to understand possible global warming effects on the impact of BFF spatial distribution. Given the dependence of Pout on various river conditions found in Chapters 3 and 4, we systematically analyzed the dependence of the outcomes on the phytoplankton concentration at the source (Pin), the average BFF density, the river depth and the water temperature.

5.4.1 Conditions under which the spatial BFF distribution is crucial for phytoplankton control

Our results confirm that spatial heterogeneity in the BFF distribution may actually influence the impact of grazing on phytoplankton at the outlet as is indicated by the sometimes substantially differing Pout-values yielded by the various BFF distributions. We also see that the relative BFF performance (i.e. the ranking order among the respective Pout-values) depends on temperature, depth, Pin value and BFF density.

Regarding the effect of spatial heterogeneity in the BFF distribution on the phytoplankton concentration at the outlet, Pout, we found a general pattern: in deep rivers (4m) or under low (ca. 0-10°C) or extremely high (usually above 31°C) temperatures, the vast majority of Pout values yielded by the heterogeneous BFF distributions are close to each other and to that from the homogenous distribution, especially when Pin is small, regardless of BFF density (Figs. 5-4, 5-5 and 5-7). This reflects the weak effect of BFF grazing on phytoplankton under these conditions.

In shallower rivers (1-2m) of moderate to high (approx. 10-30°C) temperatures, the situation differs. Here, the relevance of spatial BFF distribution depends on both Pin-value and average BFF-density. There are two critical Pin-values: a lower and an upper one. Below the lower critical Pin-value, all BFF distributions, homogenous or heterogeneous, are equally able to (almost) fully remove phytoplankton ($P_{out} \approx 0$; see the 'multicolor' zones of the plots in Fig. 5-4 and the 'white' zones below the yellow-red areas in the plots of Fig. 5-6). Hence, even late grazing such as under *d4* can remove all or almost all phytoplankton. This means that phytoplankton can be fully removed by the existing BFF even if it has grown to the carrying capacity, *K*. Hence, spatial heterogeneity does not have any effect in this range.

Above the lower critical P_{in} -value, however, the BFF distributions start differing from each other in their effect and deviating from the homogenous reference. Now only selected BFF distributions are still capable to fully remove P_{out} . The reason is that P_{in} is so high that the timing of grazing (and therefore the position of the BFF zone) becomes important for determining P_{out} . Grazing has to occur early enough before the travelling and thereby further growing phytoplankton reaches the critical concentration at which it cannot be fully removed by the existing BFF anymore (Fig. 5-3). Therefore, all the BFF distributions with too late grazing due to a BFF zone located too distant from the source, fail in fully removing phytoplankton. If P_{in} further increases, it reaches a point where only concentrated early grazing ($d1$) is able either to ensure full phytoplankton removal or at least to yield the lowest P_{out} values ('light blue' zone in Fig. 5-5).

Above the upper critical P_{in} -value, the situation changes again and the BFF distribution in the opposite extreme of the river, i.e. the one concentrated closest to the outlet ($d4$), yields the lowest P_{out} values (dark blue range in Fig. 5-5). Note that in this range, no BFF distribution can fully remove phytoplankton given the average BFF density tested. In this case, phytoplankton recovers after passing the BFF zone (in the worst case, until the carrying capacity, K , of the river), in the remaining time until reaching the outlet. Hence, the distribution with late grazing and the highest local BFF density ($d4$) has an advantage as it gives no time for such recovery. In fact, this distribution is the one yielding the lowest P_{out} values.

This shows that the effect of the spatial BFF distribution changes with P_{in} in a threshold-like way. Evidently, the upper critical P_{in} value does not only separate two zones of 'best' BFF distributions, but also two mechanisms yielding the lowest P_{out} values: below this critical P_{in} -value, (almost) full phytoplankton removal by at least one BFF distribution (upstream grazing); above it, avoidance of phytoplankton recovery through late grazing (downstream grazing). Note that phytoplankton growth in the non-grazed phase of the travel is constrained by the density regulation within the river.

Above the lower critical P_{in} -value, the BFF distributions concentrated in the extremes of the river stretch (i.e. $d1$ and $d4$) are more effective than the homogenous BFF distribution under nearly all conditions (Fig. 5-5). This is due to the locally increased BFF density which helps fully removing phytoplankton. We also see that river depth influences the optimum BFF distribution. While in shallow rivers (1m), the scenario with the highest localized concentration closest to the source ($d1$) is best, in deeper rivers (2m), scenarios with a weaker concentration ($d5$) become as effective. However, the advantage of these scenarios is only marginal because all BFF distributions are almost equally effective in this range (Fig. 5-6). This can be related to the fact, that in deeper rivers, water speed is higher and water residence time shorter. Thus, the

exposure time of phytoplankton to the benthic grazers might become increasingly important and cause a tradeoff between local BFF density and spatial extension of the BFF zone.

Our results also show that the two critical P_{in} -values depend on the average BFF density, water temperature and river depth (within the shallow range, i.e. 1-2m) (Fig. 5-5). As long as the BFF density is low, the lower critical P_{in} -value is negligible and the upper relatively small. Therefore, late grazing (*d4*, dark blue zone) is the best BFF distribution in the vast majority of conditions, except for a few low P_{in} -values where early grazing (*d1*, light blue zone) is best. In both cases (i.e. when BFF density is low and at a few low P_{in} values), the advantage of the best over the worst BFF distribution is moderate over a broad range of temperatures (10-30°C, see the yellow and red zones in Fig. 5-6). When the average BFF density increases, the P_{in} -range of optimum late grazing (*d4*, dark blue zone in Fig. 5-5) shrinks while both the P_{in} -range of optimum early grazing (*d1*, light blue zone in Fig. 5-5) and that of full phytoplankton removal independent of BFF distribution (multi-color zone in Fig. 5-5) substantially expand. While the advantage of the best over the worst BFF distribution is marginal and the effect of spatial heterogeneity is negligible in the last two cases (i.e. optimum early grazing and full phytoplankton removal) (white zone in Fig. 5-6), it is moderate in the first one (i.e. optimum late grazing) (yellow zone in Fig. 5-6). By promoting full removal by all BFF distributions, raising the average BFF density reduces the difference in the grazing performance between the different distributions under most temperatures (ca. 10-20°C) as long as P_{in} is not too high. However, under higher temperatures (ca. 20-30°C) and P_{in} values, increasing BFF density tended to raise the P_{out} difference (Fig. 5-6).

Figures 5-5 and 5-6 also indicate that the two critical P_{in} -values show a unimodal dependence on water temperature with highest values near the optimum temperature for BFF grazing (T_{opt}^g). This reflects that, below this optimum, the grazing performance benefits from warming (see also Chapters 3 and 4) with the implication that the effect of spatial heterogeneity in the BFF distribution decreases. Warming beyond T_{opt}^g , however, generally reduces the chance of phytoplankton removal as the BFF grazing rate decreases.

To summarize, the effect of spatial heterogeneity in the BFF distribution on P_{out} depends on river conditions. This effect is low or absent at deep rivers and shallow ones with cold or extremely hot temperatures. At shallow rivers with warm to hot temperatures, this effect depends on P_{in} value, BFF density and water temperature. In these rivers, there is a shift in the best BFF distribution from “all equal” over “early grazing” to “late grazing” (Fig. 5-7 serves to visualize these rules of thumb).

5.4.2 Mechanistic explanation of the relevance of the spatial BFF distribution

As long as P_{in} is below the non-grazed carrying capacity K of the river, the effect of a particular spatial BFF distribution on P_{out} is determined by a sequence of processes in three phases:

PHASE 1: Phytoplankton increase from P_{in} during the travel from the source to the BFF zone,

PHASE 2: Phytoplankton reduction during the passage of the BFF zone, and

PHASE 3: Phytoplankton recovery during the remaining travel from the BFF zone to the outlet.

The processes in PHASES 1 and 3 are determined by the phytoplankton gross growth rate and the phytoplankton loss rate non-due to grazing (both constitute the phytoplankton growth rate and the carrying capacity K). The reduction process in PHASE 2 depends on the grazing pressure and on all the determinants of this pressure: average BFF density, grazing rate and the phytoplankton concentration at the time of reaching the BFF zone. Grazing rate depends in turn on water temperature, river depth and phytoplankton concentration. Hence, the effect of the spatial position of a BFF-zone in the river depends on the balance of phytoplankton growth rate and grazing rate (showing the importance of the interplay of density dependent growth and grazing), and the duration of the three phases. The longer PHASE 1 lasts, the more time the phytoplankton has to grow and the higher is the phytoplankton concentration at the time of arrival at the BFF-zone which, however, cannot be higher than K . The shorter PHASE 1 is, in contrast, the higher is the chance to achieve complete phytoplankton removal, but the longer is also PHASE 3 and thus the time available for phytoplankton recovery if such removal is incomplete.

The preceding arguments clarify how river conditions, esp. river depth and water temperature, influence the effect of a particular BFF distribution, namely via their effect on the balance of phytoplankton growth rate and BFF grazing pressure. Regarding depth, as shown in Chapters 3 and 4 and in the work of Lucas & Thompson, 2012), increasing river depth reduces the proportion of the water depth formed by the photosynthetically active zone and therefore the phytoplankton growth rate, but also enlarges the water volume to be filtered and shortens the water residence time until reaching the outlet due to the raised water speed. This enlarged water volume reduces the grazing pressure while the shorter residence time reduces the time available for both phytoplankton growth and BFF grazing. This explains the generally lower effectiveness of grazing and consequently a lower relevance of the BFF distribution observed in deeper waters. Regarding temperature, the mentioned arguments explain why the range of P_{in} -values, for which we found effects of spatial heterogeneity in the BFF distribution, is temperature-dependent and shows a

unimodal thermal response: as in the homogenous reference case (Chapters 3 and 4), this is the result of the unimodal thermal responses of the phytoplankton growth rate and the BFF grazing rate.

Analyzing the duration of the three phases helps to understand the effect of a particular BFF distribution on phytoplankton. For example, upstream grazing near the source (e.g. d1) is characterized by a short (or even lacking) PHASE 1 favoring the chance of completely removing the phytoplankton or of achieving low phytoplankton concentrations (e.g. $P_{out} < 1 \text{ mgC/l}$) if P_{in} is not too high for the given BFF density. On the other hand, d1 has a long PHASE 3 in which phytoplankton can recover if P_{in} is high. In contrast, downstream grazing near the outlet (e.g. d4) is characterized by a long PHASE 1 and a short (or even lacking) PHASE 3. As phytoplankton growth in the river is restricted due to density dependence and cannot exceed the (non-grazed) carrying capacity K , the disadvantages of a long PHASE 1 can be overcome by the advantage of a short or lacking PHASE 3 in form of a short or absent time for phytoplankton recovery, if P_{in} is so high that the existing BFF density cannot completely remove the phytoplankton.

5.4.3 BFF spatial distribution and the compliance with a water quality threshold at the outlet

Our results also provide insights into the effects of the spatial heterogeneity in the BFF distribution on the ability to meet a water quality threshold for the phytoplankton concentration at the outlet (P_{out}) (i.e. the one derived from the study of Mischke et al. (2011) following the WFD, i.e. $P_{out} < 0.87 \text{ mgC/l}$; see methods section in Chapter 2) and their temperature dependence. We applied the analysis used in Chapter 4 for the homogenous BFF distribution also to the heterogeneous distributions.

In our results, contour lines specify the maximum tolerable P_{in} -values, $P_{in}^{tol,max}$, i.e. those which keep P_{out} below the quality threshold and so the outlet “non-eutrophic” as a function of the water temperature (Fig. 5-8). The $P_{in}^{tol,max}$ -values reveal the need of source control. They also provide insight into the effectiveness of grazer control measured as BFF-mediated enhancement of $P_{in}^{tol,max}$ and reduction of the requirements on the source control. We worked with a set of three contour lines of these $P_{in}^{tol,max}$ -values based on P_{out} for the homogenous distribution (intermediate contour line) as well as for the “worst” (lower contour line) and the “best” (higher contour line) BFF distributions (note that the “worst” and the “best” contour lines are extracted from the P_{out} values yielded by different BFF distributions). The contour lines have a unimodal shape with maximum at moderate water temperatures under most water depths and BFF densities (except under low BFF densities and deep waters; Fig. 5-8). This reflects the temperature dependence of grazing (as explained in Chapter 4).

In the P_{in} -zone below the “worst” contour line, all BFF distributions, homogenous or heterogeneous, are able to keep P_{out} below the quality threshold. In the P_{in} -zone above the “best” contour line, in contrast, no BFF distribution can meet this threshold. Hence, the area between the best and the worst contour lines is the only range of P_{in} -values in which BFF spatial distribution can influence the ability to meet the quality threshold.

In deep waters (4m) or under low average BFF densities, the three contour lines are close to each other indicating that spatial heterogeneity in the BFF distribution does not have any effect on the ability of source and grazer control to meet the quality threshold at the outlet.

In shallower rivers (2m) with high average BFF density (500 ind./m²) and shallow rivers (1m) with moderate average BFF density (300 ind./m²), the contour lines of the homogenous and the “worst” BFF distributions are again close to each other. The contour line of the “best” BFF distribution, in contrast, markedly deviates and shows maximum tolerable P_{in} -values which are much higher than those for the two other contour lines under moderate to high temperatures (10-30°C). This indicates that the homogenous BFF distribution is quite ineffective in controlling P_{out} , compared with most of the heterogeneous BFF distributions. The range of P_{in} -values between the “best” and the “worst” contour line covers that addressed in Section 5.4.1 (see also Fig. 5-5) for which we showed that only few BFF distributions are still able to fully remove phytoplankton, namely those enabling early enough grazing. This P_{in} range, like the two contour lines limiting it, shows a unimodal dependence on the water temperature with maximum around the optimum grazing temperature, T_{opt}^g .

For very high average BFF densities (500 ind./m²) in shallow rivers, the three contour lines were very steep and, under cold temperatures, close to each other. In this case, meeting the quality threshold at the outlet is either impossible (under low or very high temperatures) or possible (under moderate temperatures), for the majority of P_{in} -values and all spatial BFF distributions. This shows that warming above a threshold can cause a collapse of the grazer control and a failure to meet the quality threshold at the outlet that is in line with the findings in Chapters 3 and 4. In this chapter, however, we also observed that the temperature threshold can be increased by a few Celsius degrees by the best BFF distribution. From this, it is clear that water temperature strongly determines the outcome. Note that the best contour line for an average BFF density of 300 ind./m² is similar to the homogenous contour line for an average BFF density of 500 ind./m² in Fig. 5-8. This suggests that a favorable BFF distribution can compensate, at

least partly, the deficit of a lower average BFF density, as concentrated localized grazing can as successfully remove phytoplankton as permanent weak grazing.

5.4.4 Distribution besides total number of BFF determines the performance of phytoplankton control

Conclusions from previous studies (e.g. Lucas *et al.*, 2009, Lucas & Thompson, 2012) rely on the assumption of uniform losses of phytoplankton biomass throughout the river such as those caused by homogeneous BFF distributions. These conclusions can be complemented by our findings which consider heterogeneous BFF distributions causing non-uniform losses which can cause other impacts than uniform losses, as was shown in this study. Our study compared these two types of phytoplankton loss under some of the factors studied previously, namely river depth and the related water residence time, both of which are known to alter the growth-loss balance (Lucas & Thompson, 2012). Therefore, our work provides, among other things, a wider, spatially explicit perspective on the effects of BFF, in particular, and losses, in general, under these abiotic factors.

Our findings (from this and the two previous chapters) agree with Lucas *et al.*, 2009 in that the effect of water residence time on phytoplankton concentration at the outlet, Pout, depends on the phytoplankton growth-loss balance. However, unlike Lucas *et al.*, 2009, we did not test the effects of residence time independently but as a part of the effect of river depth. Nevertheless, the effects of residence time became apparent as we compared phytoplankton dynamics with and without grazers for different river depths. However, this chapter also shows that the timing of the phytoplankton losses, which depends on the BFF distribution, determines such growth-loss balance and therefore Pout. This means that the same total amount of BFF (ind.; or overall river density, ind./m²) can have very different effects on the phytoplankton concentration at the outlet Pout, depending on the position and time at which they graze over phytoplankton, e.g. Figs. 5-6 and 5-7.

5.4.5 Implications of the results for water quality management in large rivers

5.4.5.1 Suggestions for water quality management

Although the description of rivers was quite stylized in the model underlying this study as homogeneity was assumed regarding river depth and water temperature, important dimensions of spatial heterogeneity

in the BFF distribution were explicitly addressed. This concerned the spatial extension of the BFF zone (i.e. the degree of BFF agglomeration and thus a proxy for duration and pressure of grazing) and its position in the river (determining the timing of grazing in the phytoplankton's travel from the source to the outlet). Within the BFF zones, however, homogeneity was assumed again. To ensure sound mechanistic understanding of the effects of the spatial BFF distribution and their dependence on the river conditions, we systematically varied the respective model parameters. Despite the stylized nature of the model, several insights on the relevance of the spatial BFF distribution, its temperature dependence and transferability to other rivers were derived which should be useful for quality management in large rivers:

First, we have revealed that, in both deep rivers and shallow rivers with low or very high water temperature, spatial heterogeneity in the BFF distribution does not have any effect on the phytoplankton situation at the outlet. This indicates that assuming a homogenous BFF distribution is adequate and a suitable proxy in this case. At the same time, we found that, in shallow rivers with warm to hot waters, spatial heterogeneity in the BFF distribution makes a difference and can substantially deviate from the effects of the homogenous distribution. In this case, neglecting heterogeneity and assuming homogeneity instead is not adequate anymore and causes a risk of counterproductive conclusions. Additionally, the magnitude of the resulting failure has been quantified in this study (assessment of uncertainty).

Second, we found that the homogenous BFF distribution is either worst or nearly worst concerning the ability to meet the water quality threshold at the outlet (i.e. $P_{out} < 0.87 \text{ mgC/l}$) and is, thus, the worst BFF distribution for phytoplankton control in many cases. As all heterogeneous distributions would lead to better results in these cases, outcomes derived with a homogenous BFF distribution can thus be interpreted as a conservative assessment (what P_{in} -values can be tolerated independent of the spatial BFF distribution). Given the high degree of uncertainty in the available information on the exact spatial BFF distribution, conservative estimations are already valuable.

Third, we revealed that particular heterogeneous BFF distributions can compensate the failure of a homogenous BFF distribution to meet the water quality threshold at a too high P_{in} -value or a too low average BFF density.

Fourth, we have characterized the 'theoretically best' spatial BFF distribution in dependence on various river characteristics. Although BFF densities and distributions cannot be actively influenced, this information can help managers to set spatial priorities for: (i) protecting BFF habitat in case of threats from planned human interventions in the river, or (ii) improving habitat suitability for BFF.

Fifth, we revealed that the effects of spatial BFF distribution have a unimodal dependence on water temperature, which is strongest at moderate temperatures. This is precisely the range where phytoplankton growth would be highest under grazer absence. This shows the importance of considering spatial BFF distribution in large rivers under warming, particularly if they are shallow.

5.4.5.2 Improving phytoplankton control by considering BFF distribution - caveats and challenges

Our results have suggested that, under a wide range of river conditions, either concentrated early (upstream, see *d1*) or concentrated late (downstream, see *d4*) grazing is theoretically best to minimize phytoplankton concentration at the outlet. Admittedly, these two BFF distributions are located completely opposite to each other. However, having only two options to compare for a large range of conditions is likely to simplify decision-making and priority-setting for managers.

In reality, it may be challenging to decide in which part of a river to protect or support BFF habitat because the Pout-differences between *d1* and *d4* can dramatically change and even reverse with small changes in temperature or Pin-value because of the found threshold-like response of Pout (Fig. 5-7). This is especially risky given the ongoing climate change and high variability in Pin-load present in many rivers (e.g. downstream sections of the Rhine, Tubbing *et al.*, 1994). Another factor that may simplify management is that shallow rivers (1m) are the ones with the highest differences in Pout among the various BFF distributions which, however, decrease with depth (Fig. 5-7).

Because in deep rivers, the Pout differences among the BFF distributions are lowest, phytoplankton control by grazers remains a challenge in deep rivers. Here, Pin-control and nutrient-control may be the only effective options. This is concerning given that channelization of rivers for purposes such as navigation usually increases river depth (Brooker, 1985).

5.4.5.3 Active and passive management of BFF distribution: possibilities and limitations

Our findings identify the theoretically optimum locations for BFF to control phytoplankton during its travel from the source to the outlet of a river stretch. However, we know that directly altering BFF density in a significant manner is hardly possible because a large number of individual BFF are required to reach even relatively low densities in rivers. For example, achieving a density of 100 ind./m² in a river of 100m width requires 10 million individuals per km. Moreover, even if that amount of BFF is transplanted to a river, they may not establish successfully (see Cope & Waller, 1995 and Gray & Kreeger, 2014). Thus,

instead of investing in the introduction of huge amounts of BFF in a river with unsuitable conditions, it may be more sensible and sustainable to protect and/or improve the suitability of BFF-habitat.

Riverine habitats are already modified by human activities such as the construction of engineering structures for shipping (Brabender *et al.*, 2016). These modifications can change the abundance of native and non-native macroinvertebrates as well as their relative contribution to ecosystem functions (Brabender *et al.*, 2016). Hence, promoting BFF establishment may not require an extraordinary alteration of (natural) habitats, particularly in rivers where human activities have already modified such habitats (e.g. the Elbe; Brabender *et al.*, 2016). Admittedly, improving habitat for BFF cannot guarantee that a certain BFF density is reached. However, BFF density is likely to be, at least to some extent, proportional to habitat suitability. It is worth noting that habitat suitability and the modifications here mentioned refer mainly to the substrate, which is important for BFF attachment. However, although substrate is likely to promote BFF survival, other factors such as food quantity and quality as well as water quality may limit the long-term establishment of BFF (Gray & Kreeger, 2014).

5.4.5.4 Warning related to invasive BFF species and extrapolation to other BFF species

Like other authors that consider the possibility of managing invasive BFF for their benefits (e.g. Elliott *et al.*, 2008, McLaughlan & Aldridge, 2013), we advocate their use only in sites already invaded by such BFF but consider their introduction to new sites risky. Furthermore, although we parameterized some variables of our model with data from *C. fluminea* because it is found in sites worldwide (e.g. Araujo *et al.*, 1993), the basic mechanisms are the same for all BFF, including native species. Therefore, our model can be easily adapted to simulate other, native or invasive, species. Moreover, the general pattern of our results is likely to be valid for other species (see Appendix 5).

5.5 CONCLUSIONS

The motivation of this study was the fact that, while there is evidence that BFF grazing can be important for phytoplankton control in large rivers and BFF distribution varies along rivers (see Introduction), there is a lack of systematic studies of such BFF distribution effects. This study is, to the best of our knowledge, the first systematic exploration of effects of spatial heterogeneity in the BFF distribution on phytoplankton control by grazers in rivers under various conditions. It identifies the conditions under which the effect of heterogeneity is substantial and assuming homogenous BFF distributions leads to wrong conclusions.

The study reveals the spatial BFF distributions which yield the lowest phytoplankton concentrations at the outlet (Pout) under several variables, including water temperature, river depth, Pin value and BFF density. These distributions are, under the vast majority of conditions, the two located at the extremes of the river, i.e. the one most concentrated upstream (*d1*) and the one most concentrated downstream (*d4*) (Fig. 5-2). Importantly, the performance of phytoplankton control with a homogeneous BFF distribution (used in all simulations with BFF of previous chapters) can, under certain conditions, be substantially surpassed by heterogeneous BFF distributions. In fact, our study shows that, under most conditions, the homogeneous BFF distribution enables a conservative estimation of phytoplankton control by BFF.

Under spatially heterogeneous BFF distributions, the travel of the phytoplankton from the source to the outlet divides into three phases differing in the interplay between phytoplankton growth and BFF grazing: (1) initial phytoplankton growth in absence of BFF, (2) grazing in the presence of BFF and (3) phytoplankton recovery from grazing in absence of BFF. Timing and duration of the three phases evidently depend on the location of the BFF zone in the river. Our study reveals that phytoplankton control with spatially heterogeneous BFF distributions is always characterized by a trade-off between two contrasting mechanisms – avoidance of the first phase (favoring early grazing and upstream BFF distributions) and avoidance of the third phase (favoring late grazing and downstream BFF distributions) – and that the (abiotic and biotic) river conditions determine which of the two mechanism dominates.

In addition, our study shows that the performance of phytoplankton control differs the most among the BFF distributions in shallow rivers with warm to hot waters (depending on BFF density; Fig. 5-6). It indicates that managing the BFF distribution in these rivers by improving habitat quality for BFF grazers in appropriately selected river sections (if it is not possible to do so in the whole river) could yield large benefits (up to almost 10mgC/l). These benefits are important because the mentioned conditions are the same as those where phytoplankton growth is highest in absence of grazers. Our study suggests where to allocate the habitat management optimally. However, warming beyond a threshold temperature usually decreases rapidly the effects of BFF distribution (collapsing the difference between BFF distributions) such that the homogenous distribution is a good proxy for the estimation of grazing effects.

Admittedly, our simulations tackled idealized river systems and the BFF distributions modelled are different from those found in natural rivers (see the introduction for variables determining BFF distribution in nature). We are aware that our results are promising but only a first step towards a realistic assessment of rivers. A next step would be to extend the methodology to more realistic representations of

spatial aspects in rivers by accounting for additional sources of spatial heterogeneity such as river depth, water temperature, or nutrient concentration influencing phytoplankton growth. Nevertheless, the simplifications of our idealized rivers were of great advantage as they allowed us to understand the mechanisms determining BFF distribution effects on phytoplankton control. Moreover, the understanding derived from our model is supported by the robustness of our findings, which gives us confidence that it can be helpful, even if preliminary, to understand and manage phytoplankton control in rivers.

CHAPTER 6 - GENERAL DISCUSSION

This work presents the development and application of a spatially explicit simulation model of grazing control⁵ of eutrophication in large rivers. This model was applied to study the effect on phytoplankton concentration at the outlet of a linear river stretch (Pout), and thereby on eutrophication control by benthic filter feeders (BFF), of potentially important factors: (i) temperature (warming), (ii) water depth, (iii) BFF density, (iv) phytoplankton concentration at the source (Pin), (v) spatial BFF distribution and (vi) thermal responses of BFF grazing (consumer) and phytoplankton growth (resource).

This model is relatively simple. It considers only a few key variables and it greatly simplifies some of them, e.g. river morphology. Hence, my model cannot *predict* eutrophication development in a particular river. Its goal is, nevertheless, to improve our *understanding* of eutrophication (control) by serving as a tool to systematically analyze the effect of key variables on an idealized system, i.e. using a virtual lab approach, VLA. This includes testing large value ranges for some variables (e.g. Pin, temperature and water depth) and analyzing some interactions between them. Although my model is simple, it reveals that the effect of some variables simulated on eutrophication control is complex. This is because the model considers some of the multiple effects of certain variables. For example, my model simulates depth effects on eutrophication control through its impacts on: (i) light availability, (ii) water volume to river surface ratio and (iii) water residence time.

The model applications address some unstudied or poorly studied factors and perform techniques until now seldom applied to our topic (see Table 6-1 for a summary of main novelties of the contributions from this thesis). In particular, they perform what is, to the best of our knowledge, the first systematic study of the effects of Pin value and BFF distribution on eutrophication (control) in a riverlike system. This work is also, to the best of our knowledge, the first study of the effect of varying the *optima of thermal responses*,

⁵ Note that grazer and/or source control are intended to complement, not substitute, eutrophication control by nutrients. Nonetheless, in some cases, the limitations and costs of nutrient control could make these alternatives crucial. Note that grazer control is, unlike source control, a naturally provided ecosystem service and not a management measure. However, both control alternatives can be important (for the importance of both source and grazer control see results and discussion of Chapters 4-5; for that of grazer control see also results and discussion of Chapter 1 and works such as Cohen et al., 1984, Caraco et al., 1997; 2006, Hardenbicker et al., 2015 and Lucas & Thompson, 2012). Moreover, in the future, grazer control might be managed indirectly by controlling habitat properties (Brabender et al., 2016).

T_{opt} (hereafter: thermal optima; see Appendix 1 for details), of resource and consumers on their interaction (Chapters 3-4). Moreover, this is one of the very first studies using a virtual lab approach (VLA) to analyze BFF control of riverine eutrophication⁶. In contrast to other simulations, VLA's main aim is to reveal the effects of certain factors on a process (in this case eutrophication control by BFF), thereby, allowing a mechanistic understanding of such process.

Such mechanistic understanding is shown in the analyses of my model applications (see results and discussion sections of Chapters 3-5). These analyses reveal, in general, pronounced interactions between eutrophication control by BFF and three variables: Pin, temperature and water depth. These interactions cause a non-linear response to those three variables from eutrophication control, which has important implications, i.e. differential eutrophication (control) response to the same changes (incl. management measures) according to initial site conditions (see discussion sections of Chapters 3-4). Moreover, the analyses demonstrate that two factors, rarely considered when modelling BFF effects, i.e. Pin value and spatial BFF distribution, are important for eutrophication control in large rivers (Chapters 4-5).

More particularly, my analyses show, first, that without grazing (Chapter 3) Pout responds unimodally to temperature indicating the temperatures favoring eutrophication. Second, that with grazing, however, eutrophication can be controlled at most temperatures (at least in shallow waters with high BFF densities). Importantly, this study is the first, to the best of our knowledge, reporting a unimodal (first increase, then decrease) response of grazer control performance to temperature. Such unimodal response causes grazing, under moderate-high BFF densities, to reverse phytoplankton response to warming at some temperatures (Chapter 3). This indicates that studies of warming effects, incl. those of climate change, need to consider both grazing and initial temperatures.

Third, that, as a part of the unimodal response of grazer performance to temperature, eutrophication control by BFF, decreases rapidly with warming after a temperature threshold (Chapter 3). Hence, after such threshold, even moderate warming strongly affects eutrophication. This study is also the first report revealing the existence of such temperature threshold in *resource control* (despite some similarity, this goes beyond previous findings, which report a threshold in the relationship between temperature and consumer's *attack rate*; Öhlund *et al.*, 2015). This suggests that predictive studies and managers should

⁶ Although other works study eutrophication biocontrol by BFF with observations, experiments and simulations, to the best of our knowledge, there is only one previous study using a VLA to analyze and disentangle the effects of certain factors on riverine EC by BFF (see Introduction).

consider the possibility of encountering strong non-linearities (thresholds) when assessing the potential effects of warming and management measures on ecosystems. Moreover, these results support studies suggesting that abrupt changes are a possible, if not “inevitable”, and challenging response of ecosystems to climate change and other stressors (e.g. NRC, 2013 and references therein).

Fourth, that the (matching of the) thermal responses of phytoplankton growth and BFF grazing determine the temperatures promoting eutrophication (control), as well as the existence, intensity and location of the temperature threshold (Chapters 3-4). This indicates that studies should consider the (evolving) physiology of organisms when evaluating the climate change responses of ecosystems. Moreover, our analyzes, which focused particularly on the thermal optima (T_{opt}) to analyze the effect of the thermal responses, support the predictions of Dell *et al.* (2014) that, if thermal optima differ enough, mismatches in the thermal responses of resource and consumers would be important. Furthermore, being this study, to the best of our knowledge, the first analyzing the effect of varying the *thermal optima* of resource and consumers on their interaction, complements the work of Dell *et al.* (2014), who provided a general framework on the effect of thermal response curves focusing on *the rising part* of them, i.e. the part below the thermal optima. In addition, this finding supports the prediction of Englund *et al.* (2011) that community responses to climate change will reflect the differential thermal optima of species.

In a broader context, these four findings together support studies which indicate the importance of considering species physiological sensitivities and species interactions to assess the effects of climate change and other stressors on ecosystems (e.g., Deutsch *et al.*, 2008, Tewksbury *et al.*, 2008, Bonebrake & Mastrandrea, 2010, Dell *et al.*, 2014). In particular, they highlight that indirect effects of climate change (i.e. through trophic cascading) may be as important as, and sometimes more than, its direct effects on a single trophic level (Suttle *et al.*, 2007; Barton *et al.*, 2009; O'Connor, 2009, Alsterberg *et al.*, 2013). All this agrees with a recent review claiming that among other mechanisms, evolutionary adaptation in physiology (direct responses) and changes in ecological interactions (indirect responses), govern the response of ecological systems to climate change (Urban *et al.*, 2016).

Besides allowing the aforementioned discoveries, our mechanistic model approach helped to explain and synthesize the divergent results of warming effects on resource-consumer interactions, in particular on

resource biomass, from previous studies⁷ (Chapter 3). In particular, our analyses show that what determines the response of resource biomass to temperature is the ratio between grazing (consumer) pressure⁸ and phytoplankton (resource) growth, regardless of their absolute value. This finding supports studies indicating the importance of *relative* consumer efficiency, i.e. how much consumption rate increases in relation to resource growth, when assessing warming effects (e.g. O'Connor, 2009, Eklöf *et al.*, 2012).

In addition, our study shows that both eutrophication and eutrophication control decrease with water depth, confirming the findings of Lucas & Thompson (2012). However, this study is a step forward from the work of Lucas & Thompson (2012) on the effects of BFF on eutrophication control because, in addition to considering depth effects on eutrophication control, it explores the effects of temperature, Pin, BFF distribution and the thermal responses of phytoplankton growth and BFF grazing. This allows exploring the naturally occurring interactions between these factors. For example, our findings reveal that the effect of temperature changes decrease with water depth (Chapter 3). This interaction is important given the dependence of temperature and depth in rivers and because both variables can be affected by climate change and some anthropogenic activities (see details in Chapter 3). In addition, unlike, Lucas & Thompson (2012) this work does not explore separately the effects of water depth and water residence time but instead estimates water residence time as a function of water depth and other factors (Eqs. 1-3, Chapter 2). This contributed to analyzing the interactions between these factors as they naturally occur in rivers. Our simultaneous analyses of the effects of temperature and water depth support the conclusion that changes in temperature and precipitation (in this study through their impacts on water temperature and depth) can have interacting effects on organisms and that climate change impacts are likely to be more complex than what can be predicted based on a single variable such as temperature (e.g. Bonebrake & Mastrandrea, 2010).

Furthermore, our analyses revealed the effect that success criteria selection has on the assessment of (warming effects on) eutrophication control. These effects differ under each criterion and also vary with control type (i.e. grazer or source control) and with river properties (i.e. water depth as well as initial

⁷ This was, at least in part, thanks to our use or consideration of: (1) a wide range of temperatures, (2) unimodal curves to simulate the thermal responses of the rates of phytoplankton growth and BFF grazing and (3) the interplay of temperature with other abiotic variables such as depth.

⁸ Grazing pressure refers to the overall impact of grazing on phytoplankton, i.e. grazing losses. Grazing pressure results, for BFF simulated here, from both grazing rate and water volume (determined by water depth).

temperature and P_{in}) and ecological traits (i.e. thermal response of phytoplankton growth and BFF grazing) (Chapter 4). In particular, the results suggest that warming effects on eutrophication control: (i) depend on regional and/or local environmental properties, (ii) can interact with other effects of climate change and land use change and, (iii) depend on organism physiology (in this case, on the thermal response of phytoplankton growth and BFF grazing) which is, in turn, subject to evolution. Therefore, warming effects can vary with time scale, according to evolutionary processes such as the adaptation (time) of resources (phytoplankton), consumers (BFF) and the difference of these processes between trophic levels (see also Dell *et al.*, 2014).

In addition, our analyses show that BFF distribution, and not only their density, determines how effectively BFF control eutrophication. Note that the effectiveness of a homogeneous BFF distribution, i.e. one in which BFF density is equal throughout the river length, can be substantially surpassed by other BFF distributions in certain conditions (Chapter 5). This suggests that it is worth improving BFF habitats in particular river sections even if it is impossible to do so in the whole river. Moreover, our results show that eutrophication control effectiveness differs mostly between BFF distributions in shallow rivers with warm to hot water (according to BFF density; Fig. 5-6), indicating that managing BFF distribution in these rivers could yield large benefits (up to almost 10 mgC/l). Importantly, in these rivers BFF grazing impact on phytoplankton is high (but not extreme), while in rivers where such impact is extreme (e.g. shallow warm rivers with high BFF density) or low (e.g. deep rivers or cold shallow ones), the effect of BFF distribution is low. Suggesting explanations for such results (see below for mechanistic understanding) and possible effects of variables not tested here.

Our analyses also indicate which BFF distributions yield the lowest eutrophication (P_{out}) throughout relatively large ranges of important variables: temperature, P_{in} , water depth and BFF density. These analyses suggest that under the majority of conditions managers should promote BFF concentration either on the upstream river extreme or on the downstream extreme (as in distributions $d1$ and $d4$ in Fig. 5-2, respectively).

Moreover, our analyses also provided mechanistic understanding of BFF distribution effects on eutrophication control by revealing how the relative performance of BFF is determined by two key factors generally acting in a sequence of three phases during the travel time through the river: (1) initial phytoplankton growth, (2) BFF grazing and (3) phytoplankton recovery from grazing. Timing and

duration of these three phases are given by the particular heterogeneous BFF distribution and determine the optimal spatial distribution, i.e. the one yielding the lowest Pout.

Besides providing the aforesaid knowledge, my model applications can guide further research. In particular, they can promote more realistic, even if more complex, systematic modelling analyses of eutrophication. These further analyses can use my model itself, both its equations and computer code. Regarding my own research, future simulations may include (i) the presence of zooplankton (planktonic grazers), (ii) water stratification (incomplete vertical water mixing) and (iii) spatial heterogeneity in water depth.

Management and prediction: possibilities and caveats

This work, in particular Chapters 4 and 5, is the first addressing the potential of BFF biomanipulation (management) for riverine eutrophication control. It advances the knowledge yielded by previous works, which focus on manipulating fish (pelagic) predators and rely on trophic cascading (see Introduction of Chapter 4) to control either phytoplankton (planktonic algae) in lakes (e.g. Carpenter *et al.*, 1995) or periphyton (benthic algae) in rivers (Winkelmann *et al.*, 2014). In contrast to these works, however, here we rely on benthic consumers (BFF) that directly feed on phytoplankton.

As mentioned above, some of our results could help guiding management. Moreover, they may provide preliminary support for predicting long-term impacts of environmental change in rivers. However, this support for management and prediction require more research and, particularly, long-term experimental studies (e.g. Benndorf, 1995). Moreover, since my work focuses on understanding general principles, its suggestions should be complemented with those of models tailored for particular rivers, especially when river properties deviate strongly from my model assumptions. Nonetheless, my studies can suggest the general conditions of key factors (e.g. temperature and depth) where grazer or source control are adequate (Chapters 4 and 5) and in which certain BFF spatial distribution is more adequate (Chapter 5).

Novelty area	Contribution
Subjects and methods	<ul style="list-style-type: none"> • One of the first works using a VLA to study BFF control of riverine eutrophication* • First study of the effects of varying the <i>thermal optima</i>** on a consumer-resource interaction (Chapters 3 and 4) • First systematic study of the effects of Pin value (Chapters 4 and 5) and BFF distribution in a riverlike system (Chapter 5)
Results	<ul style="list-style-type: none"> • First report of a unimodal (first increase, then decrease) response of the performance of grazer control to temperature • First report of a temperature threshold in resource control • First report describing the distributions yielding the lowest eutrophication (Pout) values and identifying the key factors responsible for the relative BFF performance of different BFF distributions

Table 6-1. Main novelties of the contributions from this work. *The only VLA, i.e. virtual lab approach, study of riverine eutrophication control by BFF previous to this work is Lucas & Thompson, 2012. ** For phytoplankton growth only *thermal optima* (T_{opt}) was varied, while for BFF grazing, maximum grazing temperature (T_{max}) was varied with T_{opt} ($T_{max} = T_{opt} + 10^{\circ}\text{C}$).

APPENDIX 1 - THERMAL RESPONSES OF PHYTOPLANKTON GROWTH AND BENTHIC FILTER FEEDER GRAZING

We have used unimodal functions to describe the thermal responses (also referred to as “thermal response curves” or TRC; see below). Admittedly, it has been argued that within the range of “biologically relevant” temperatures or “normal activity” an exponential function, with some exceptions, describes the thermal response of whole-metabolism in almost all organisms (Gillooly *et al.*, 2001, Brown *et al.*, 2004) and that other biological rates should follow the same form (Brown *et al.*, 2004). However, although using an exponential equation may be justified when thermal optima are indeed above environmental temperatures, this may not always be the case (Englund *et al.*, 2011). Englund *et al.*, 2011 presented two reasons against the use of exponential functions:

First, thermal optima of some species may not be higher than environmental temperatures (even when they are higher than mean annual temperature of the habitat). For example, in some tropical taxa, which experience low temperature variation, thermal optima seem close to the environmental temperature (e.g. tropical insects; Deutsch *et al.*, 2008). Second, laboratory conditions, namely high food availability, may increase thermal optima.

In addition it has been argued that a unimodal model avoids overfitting the data, as exponential functions can do (Bulté & Blouin-Demers, 2006). Finally, using a unimodal function allows to test a larger temperature range, including high temperatures, where the deviations between exponential and unimodal models become larger (Lemoine & Burkepille, 2012).

The thermal responses for phytoplankton growth ($j(T)$; Fig. A1-1) and BFF filtration ($i(T)$; Figs. A1-2 and A1-3) are described by the function in O'Neill *et al.*, 1972 (cited by Schmidt *et al.*, 2010). The value of this equation ranges from zero to one and is defined by the parameters T_{opt} , T_{max} and Q_{10} (in the text and in Table 2-1 parameters for phytoplankton are named with p and those referring to BFF with g before the variables, e.g. T_{opt}^p and T_{max}^g refer to T_{opt} of phytoplankton and to T_{max} of BFF, respectively):

$$Eq. A1 - 1 \quad j(T) = \left(\frac{T_{max} - T}{T_{max} - T_{opt}} \right)^x * e^{\left(\frac{x*(T - T_{opt})}{T_{max} - T_{opt}} \right)}$$

$$x = \frac{w^2 * \left(1 + \sqrt{1 + \frac{40}{w}}\right)^2}{400}$$

$$w = \frac{Q_{10} - 1}{T_{max} - T_{opt}}$$

for values and explanation of the parameters Q_{10} , T_{max} and T_{opt} see Table 2-1 (note that for BFF filtration Eq. A1-1 is also used, simply substituting the term $j(T)$ for $i(T)$.)

The thermal response of phytoplankton growth ($j(T)$); employed to estimate the gross growth rate of phytoplankton (G), Eq. 6) was modelled using data from the literature. The optimum temperature for phytoplankton growth (T_{opt}^p) was set to the values of 24, 27 and 30°C because this is in the range of the mean values of various species of three important phytoplankton groups: diatoms (rarely exceeding 25°C; Lürling *et al.*, 2013), green algae (i.e. chlorophytes: 26.3°C; Lürling *et al.*, 2013) and cyanobacteria (27.2°C, Lürling *et al.*, 2013). We used a T_{max}^p of 36°C because although algae growth for some *individual* species appears to experience a sharp decline above their temperature optimum (e.g. Eppley, 1972, Butterwick *et al.*, 2005) the decrease observed at temperatures above the mean optimum temperature tends to be less steep when several species are grouped together (e.g. Lürling *et al.*, 2013). Moreover, in contrast to BFF where we deal with a single species, here we have chosen to maintain 36°C constant despite the changes in T_{opt}^p . Admittedly, within species, T_{opt}^p is strongly correlated with T_{max}^p (Thomas *et al.*, 2016). However, we chose a conservative value (36°C is low when compared with some datasets, e.g. Lürling *et al.* 2013, Thomas *et al.*, 2016), which is likely to support our results concerning a temperature threshold above which BFF control of phytoplankton is suddenly lost: if using a conservative T_{max}^p value P_{out} is high when BFF are present, P_{out} may be even higher if T_{max}^p is actually higher. Moreover, since our simulations test values only up to 32°C, most of the possible underestimation in P_{out} (which may be higher for phytoplankton communities with high T_{opt}^p , if T_{opt}^p and T_{max}^p are correlated), would be found at values above the range tested here. The Q_{10}^p of 1.88 was chosen because this value fitted a large dataset of laboratory studies of marine phytoplankton ($n=1,501$; Bissinger *et al.*, 2008).

Note that the parameters we varied (T_{opt} and T_{max}) are the ones which appear to be most affected by temperature variation and precipitation, at least for ectotherms, as opposed to mean variations in temperature (Clusella-Trullas *et al.*, 2011). This is important considering that climate change is predicted to increase the frequency of extreme events (IPCC, 2013) and that BFF, like most aquatic organisms, are ectotherms (e.g. Müller & Baur, 2011).

Measurements of the grazing rates of BFF vary in the literature (as stated in the main text) and those of their thermal response vary too. Such is the case with *C. fluminea* (Fig. A1-2). However, we were interested in obtaining a general idea of the grazing rate as a function of temperature (used in Eq. 16). We used as a guide the data from two studies (Mattice, 1979 and Viergutz *et al.*, 2007) and employed three similar but different parameterizations (Fig. A1-2 and A1-3; see parameter values in Table 2-1) which agree with the data but also allow us to account for both measurements errors and the variability between BFF populations and species. (For example, Fig. A1-3 shows measurements from other important BFF, *Dreissena polymorpha*.) Furthermore, to highlight the diversity of filtration rates in different studies (which is likely to reflect, at least to some degree, the diversity between populations) we have included also the filtration rate of *C. fluminea* feeding on a monoalgal culture (*Chlorella*), which shows no decrease at high temperatures in the range tested (Lauritsen, 1986; Fig. A1-2).

Note that it is usually assumed that in nature there is a tradeoff between the width of a TRC (i.e. the range of values at which a rate is feasible) and its height (performance at optimum temperature), reflecting generalists and specialist strategies (Huey & Kingsolver, 1989). Some evidence indeed supports this assumption (e.g. Cooper *et al.*, 2001). However, we assumed the height of TRCs remained the same in our various parameterizations of T_{opt} and T_{max} (Figs. A1-1 and A1-2) and the area below the TRC is not the same for the different parameterizations. However, this is reasonable since we do not test the entire range of temperatures over which such TRC have positive values (we tested values up to 32°C but T_{max} was higher than this value in a TRCs for BFF and in all three TRCs for phytoplankton tested). Moreover, although the tradeoff between the width and height of a TRC seems to be generally valid it does not seem to be universal (e.g. Huey & Hertz, 1984, Bennett & Lenski, 2007).

We digitized the data from the graphs in Viergutz *et al.*, 2007 and Mattice, 1979 using the software *Engauge Digitizer* (Mark Mitchell 2002; version 4.1). Viergutz *et al.* (2007) measured the effect of temperature on the grazing rate of *C. fluminea* feeding on natural communities of heterotrophic flagellates (HF) from the River Rhine. We assumed that the effect of temperature on the grazing rate over HF (which have a size which can be efficiently filtered by BFF; Viergutz *et al.*, 2007) is similar to its effect on the grazing rate over phytoplankton. Mattice (1979) presents the data from Auerbach *et al.* (1977) on the filtration rate of *C. fluminea* on natural seston (see also Buttner & Heidinger, 1981).

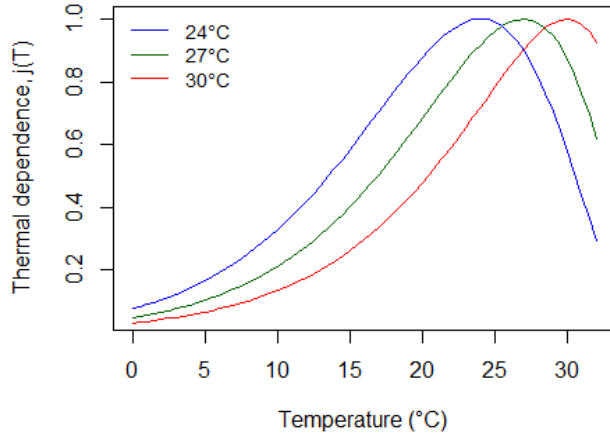


Figure A1-1. Function values for the temperature dependency of phytoplankton growth according the equation presented by O'Neill *et al.* (1972) (Eq. A1-1) with parameter values from Schöl *et al.* (2002) (see Table 2-1).

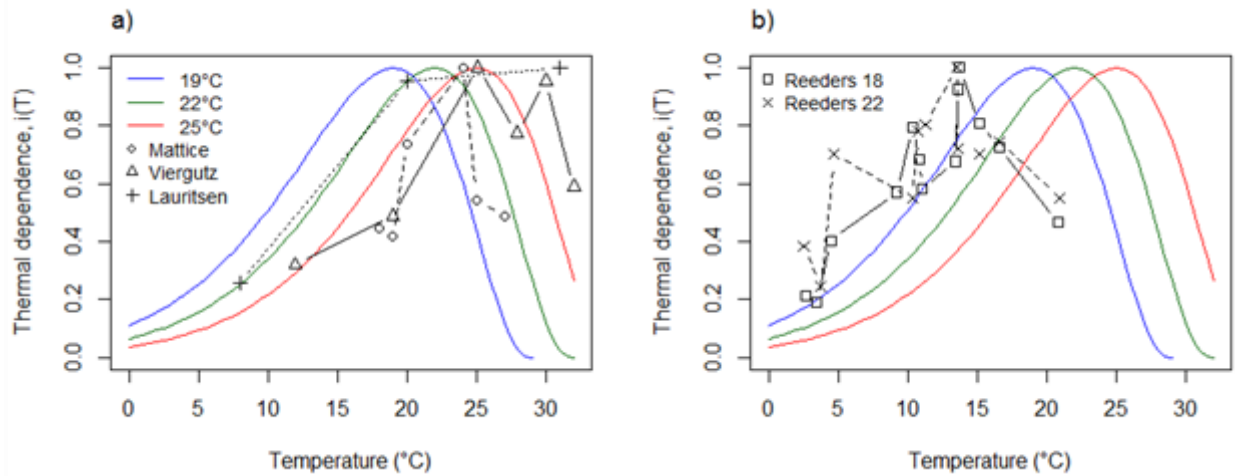


Figure A1-2. Temperature dependence of BFF grazing according the equation presented in O'Neill *et al.*, 1972 (cited by Schmidt *et al.*, 2010; Eq. A1-1) for the three different T_{opt}^g values used in this simulation. For comparison measured data is shown for (a) *C. fluminea* from Viergutz *et al.*, 2007, Mattice, 1979 and Lauritsen, 1986 and (b) *D. polymorpha* from Reiders & Bij de Vaate (1990) for BFF individuals with 18mm and 22mm. All T_{max}^g values shown here are 10°C above T_{opt}^g , e.g. T_{max}^g is 29°C for the function with a T_{opt}^g of 19°C.

APPENDIX 2 - ESTIMATION OF THE GRAZING RATE OF BENTHIC FILTER FEEDERS

We digitized the data on bivalve clearance rate at different phytoplankton concentrations from the River Rhine (Cologne-Marienburg; Figs. 1-2 from Vohmann *et al.*, 2010; Table A2-1) using the software *Engauge Digitizer* (Mark Mitchell 2002; version 4.1). Since this data was measured at different temperatures we estimated their equivalence at optimum temperature using O'Neill *et al.*, 1972 equation (i.e. the same equation used for estimating the BFF ingestion dependence on temperature; Eq. A1-1), assuming a T_{opt}^g of 25°C, a T_{max}^g of 35°C and a Q_{10}^g of 2.0 (see Appendix 1 for the equation and Table A2-2 for the transformed values). As stated in the methods section the grazing rate of BFF depends on the body size of the individuals. The individuals used in Vohmann *et al.*, 2010 had a shell length of 10-11mm, which is in the lower range of sizes exhibited in *C. fluminea*. To simplify we assumed that the BFF in the model have all the body size of those used in Vohmann *et al.*, 2010: 10.5mm.

Note that the fact that field data used were measured at different times of the year (May-October) under different temperatures (Vohmann *et al.*, 2010) means bivalves grazed on different phytoplankton communities (Tubbing *et al.*, 1994, Weitere *et al.*, 2005) which can affect their grazing rate (e.g. Hardenbicker *et al.*, 2015a). However, this is a limitation that studies relying on field data have to face. Even using natural communities and controlling for temperature has limitations of extrapolating results to other times of the year. Moreover, our main concern was to be in the range of values observed in nature.

Note also that filtration rate is not exactly the same as ingestion rate divided by phytoplankton concentration in the digitized data (Table A2-1). This is likely a consequence of the digitization process that we used to estimate all factors (phytoplankton concentration, ingestion and filtration rate and temperature) and, to a lower extent, of rounding of units when transforming them. However, while the largest deviation between the filtration rate digitized from the plots from Vohmann *et al.* and the filtration rate estimated based on the ingestion rate and the phytoplankton concentration digitized from such plots is 47ml/(h*ind.) (before transforming data from Vohmann *et al.*, 2010 to carbon and liters and standardizing to the temperature), the mean deviation is only 11.4 ml/(h*ind.). Since our main concern is to estimate filtration rates in the range of values observed in nature, this small deviation is acceptable.

We used a linear regression method to estimate the two parameters in eq. (16), the maximum BFF ingestion (i_{max} ; mgC/(ind.*d)) and the coefficient for BFF ingestion (k_g ; mgC/l). For this we plotted the

ratio of the phytoplankton concentration to the ingestion rate at optimum temperature as a function of phytoplankton concentration and fitted a linear regression to the data (Haldane, 1957; Fig. A2-1; data from Table A2-2; the linear regression was performed using the “*lm*” function from the “*stats*” package version 3.2.2 in R version 3.2.2). Using the intercept and slope of this regression we estimated the parameters (Table A2-3) as follows (Haldane, 1957):

$$Eq.A2 - 1 \quad i_{max} = \frac{1}{\text{slope}}$$

$$Eq.A2 - 2 \quad k_g = i_{max} * \text{intercept}$$

where *slope* and *intercept* are the slope and the intercept of the linear regression fitted to the plot of the phytoplankton concentration (P; mgC/l) divided by the ingestion rate at optimum temperature (I; mgC/(ind.*day)) as a function of the phytoplankton concentration (P; mgC/l), i.e. plot of *P/I* vs *P* (Fig. A2-1).

However, this linear regression method tends to give excessive weight to smaller observations and the plot of *P/I* vs *P* is subject to “inevitable correlation” (other linear methods have limitations too; Dowd & Riggs, 1965). Nevertheless, most the observations from Vohmann *et al.* (2010) have similar ingestion values (Table A2-1).

In addition, we used a non-linear model to estimate the parameters i_{max} and k_g of eq. (16). This was performed with the *nls2* function (from *nls2* package version 0.2; in R version 3.2.2). The *start* parameters were i_{max} of 0.1 and 40, and k_g of 0.01 and 10. The *algorithm* parameter was *brute-force* (alternatively called *grid search*) (Table A2-3). (Note that we used this function and algorithm because the *nls* function with the *default* algorithm cannot fit the data due to a “Singular gradient” error. Such error occurred using both datasets and with several *start* parameter values).

Neither using the whole dataset nor the *dataset without outlier* (i.e. removing measurement 2 from tables A2-1 and A2-2) provided a fit with a significant p-value (Figs. A2-1, Table A2-3). Moreover, the curve fitted to the whole dataset had negative values at high phytoplankton concentrations (Fig. A2-2). In addition, the non-linear regression methods also failed to provide a good fit to both datasets (Table A2-3). This suggests that the data does not follow the proposed Michaelis-Menten equation for ingestion (Fig. A2-2). This is probably due to the fact that, excluding one observation, all measurements from Vohmann *et al.* (2010) include only low phytoplankton concentrations.

We considered the Michaelis-Menten equation reflecting the widely observed saturation of ingestion rates (which in turn causes a decrease in filtration rates) of several bivalves species at high phytoplankton concentrations (see “Phytoplankton losses due to benthic grazing” in Chapter 2). Moreover, by fitting the equation to the data we ensured to be in the range of values observed in the field, which is our main concern. In addition, to be conservative, we have restricted our values with the relatively low maximum filtration rate (f_{max}) of 5l/(ind.*d) (see “Phytoplankton losses due to benthic grazing” section in Chapter 2 for justification of such value). At low P_{in} values, this value is lower than the values obtained by any of the methods we used (Fig. A2-3).

We selected the linear model fitted to the *dataset without outlier*, which yields the lowest rates of ingestion, filtration and grazing (Figs. A2-2, A2-3 and A2-4, light green curves), to be conservative. Note that this curve yields for most of the phytoplankton concentrations tested here, filtration rates below 3l/(ind.*d). This is a relatively low value when compared with observations from the literature (see “Phytoplankton losses due to benthic grazing” section in Chapter 2).

Measurement number	Phytoplankton concentration ($\mu\text{gchl-a/l}$)	Ingestion rate ($\mu\text{gchl-a} / (\text{ind} * \text{h})$)	Filtration rate ($\text{ml} / (\text{ind} * \text{h})$)	Temperature ($^{\circ}\text{C}$)
1	5.80	2.22	381,76	14.42
2 ²	34.40	14.25	415,54	17.75
3	3.86	2.34	601,35	20.07
4	5.80	2.16	364,87	19.91
5	3.86	1.64	415,54	19.46
6	4.64	1.69	371,62	23.23
7	2.71	2.16	750,00	24.67
8	4.64	0.41	94,59	20.71
9	2.71	0.35	111,49	14.57

Table A2-1. Field data from Vohmann *et al.*, 2010. Notes: 1) Assuming a carbon to chlorophyll *a* ratio of 25 (Table 2-1); 2) Measurement number two was excluded from the *dataset without outlier* because it was too large compared with other values.

Measurement number	Phytoplankton concentration (mgC/l) ¹	Relative proportion of optimum temperature (RPT; unitless) ²	Temperature factor ³ (unitless)	Ingestion rate at optimum temperature (mgC / (ind.*d)) ¹	Filtration rate at optimum temperature (l / (ind.*d))
1	0.15	0.41	2.41	3.21	22.09
2 ⁴	0.86	0.62	1.60	13.69	15.96
3	0.10	0.79	1.27	1.79	18.37
4	0.15	0.77	1.29	1.67	11.31
5	0.10	0.74	1.34	1.32	13.41
6	0.12	0.96	1.04	1.05	9.25
7	0.07	1.00	1.00	1.30	18.03
8	0.12	0.83	1.21	0.30	2.74
9	0.07	0.42	2.36	0.50	6.33

Table A2-2. Transformation of data from Vohmann *et al.*, 2010 (Table A2-1). Notes: 1) Assuming a carbon to chlorophyll *a* ratio of 25 (Table 2-1); 2) the relative proportion of the optimum temperature (i.e. 25°C); 3) temperature factor by which the ingestion measurements were multiplied to transform the data to ingestion at optimum temperature (this temperature factor (TF) is equal to the inverse of the relative proportion (RP) of a certain temperature to the optimum temperature: TF= 1/RP); 4) Measure number two was excluded from the *dataset without outlier* because it was much larger than other values.

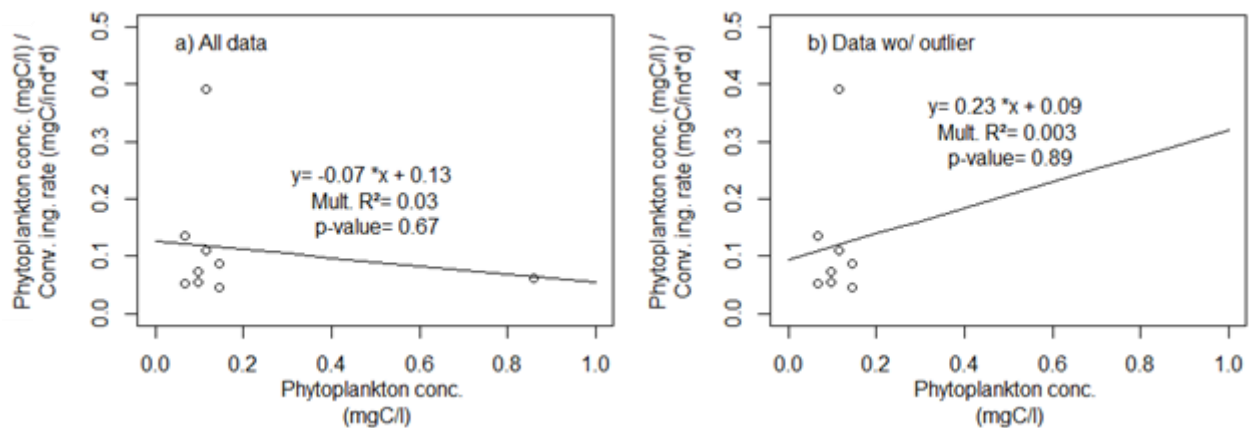


Figure A2-1. Linear regression to estimate parameters for BFF ingestion i_{max} and k_g of eq. 16 (Chapter 2) using data from Vohmann *et al.*, 2010 transformed to account for temperature (see text) for two datasets: a) all data and b) dataset without outlier. Although R^2 is presented, this measure of goodness of fit is not really valid since both axes depend on phytoplankton concentration, a limitation of the linear method used (Dowd & Riggs, 1965).

Parameter	Units	Linear regression method estimates		Nonlinear regression method estimates	
		All data ¹	Data without outlier ²	All data ³ (p-value)	Data without outlier ⁴ (p-value)
i_{\max}	$mgC / ind * day$	-14.29	4.35	34.30 (0.09)	40.00 (0.97)
k_g	mgC / l	-1.86	0.39	1.44 (0.22)	2.86 (0.97)

Table A2-3. Parameters of the linear regression model fitted to data from Vohmann *et al.*, 2010 transformed to account for temperature. Notes: 1) residual standard error: 0.11 (see other values in Fig. A2-1); 2) residual standard error: 0.12 (see other values in Fig. A2-1); 3) residual standard error: 1.33 (7 degrees of freedom), residual sum of squares: 12.29; 4) residual standard error: 0.83 (6 degrees of freedom), residual sum of squares: 4.12.

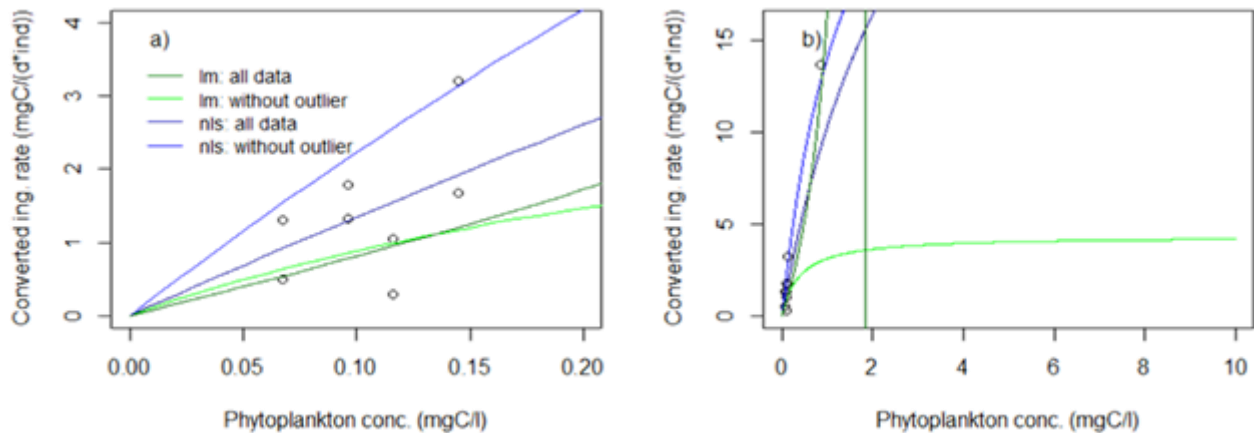


Figure A2-2. Michaelis-Menten curves fitted to the ingestion rate data in Vohmann *et al.*, 2010 transformed to account for temperature (Table A22) for a small (a) and a large (b) range of phytoplankton concentrations, using a linear (lm) and a non-linear model (nls) to fit two datasets: all measurements (*all data*) and measurements excluding an outlier (*without outlier*). See parameter values of the fitted curves in Table A2-3.

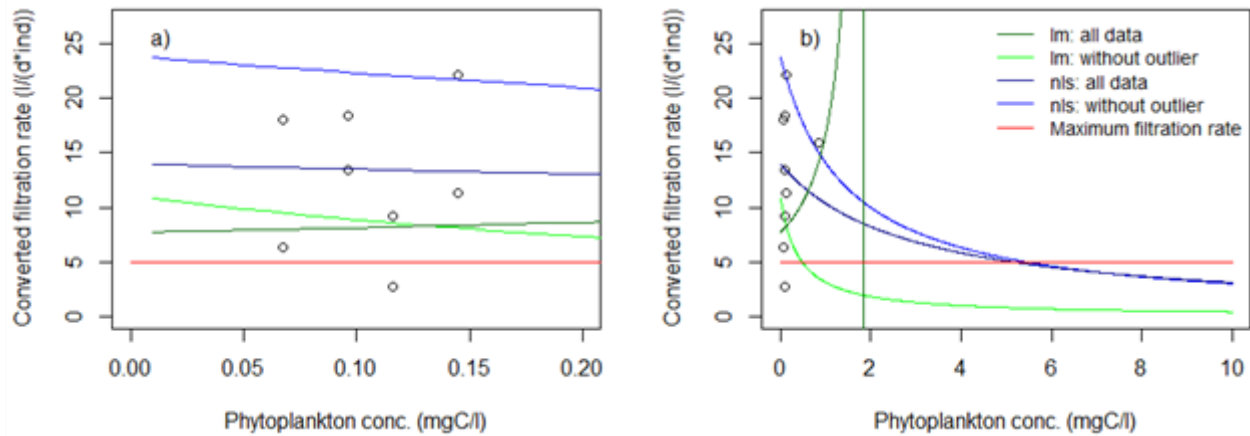


Figure A2-3. Filtration rate curves estimated from the ingestion rate (Fig. A2-2) fitted to the data in Vohmann *et al.*, 2010 for a small (a) and a large (b) range of phytoplankton concentrations, using a linear (lm) and a non-linear model (nls) to fit two datasets: all measurements (*all data*) and measurements excluding an outlier (*without outlier*). Filtration rates are estimated as: $f(P) = i/P$; where $f(P)$: filtration rate (l/(d*ind.)), i : ingestion rate (mgC/(d*ind.)); Fig. A2-2) and P : phytoplankton concentration (mgC/l) (see also Eq. 16). See parameter values of the fitted curves in Table A2-3. The dark green line (lm with all data) indicates a strong (vertical) decline of the filtration rate at certain phytoplankton concentration, reaching even negative values. Due to this unrealistic pattern it was excluded. Among the other curves, we chose the lm without the outlier, light green curve; see text for justification).

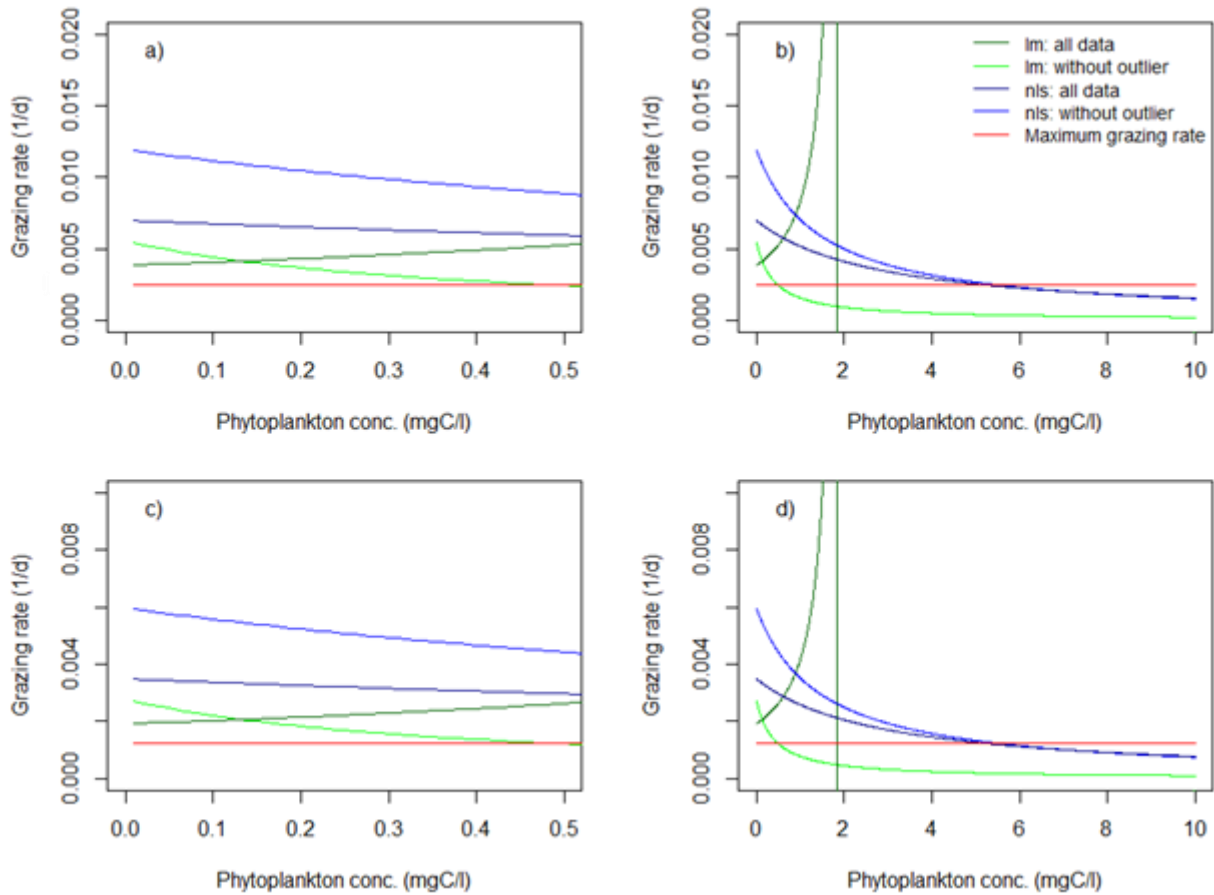


Figure A2-4. Grazing rate (1/d) at a BFF density of 1 ind./m² for two river depths (D): 2m (a,b) and 4m (c,d) for a small (a,c) and a large (b,d) range of phytoplankton concentrations. Grazing rate is calculated by Eq. 15 using the derived filtration rates from the linear (lm) and non-linear model (nls) to fit two datasets: all measurements (*all data*) and measurements excluding an outlier (*without outlier*) (Table A22; Fig. A2-3) The maximum grazing rate (assuming a filtration rate of 5l/d) is also shown (red line); note that such maximum rate only limits grazing at low phytoplankton concentrations (< ca. 0.5 mgC/l, where it has lower values than the light green curve of the model we used in our simulations). Although grazing rate, unlike ingestion rate and filtration rate, strongly depends on water depth (see “Phytoplankton losses due to benthic grazing” section in Chapter 2), the shape of the grazing rate vs phytoplankton concentration curves remains unchanged, even when its value does change. The dark green line (lm with all data) exhibits an unrealistic vertical pattern and was therefore excluded. Among the other curves, we chose the lm model without the outlier fit for the simulations (light green curve). Although the two nls models, with all data and without the outlier, also provided realistic patterns, the lm without the outlier was chosen to have more conservative estimates of grazing rate.

APPENDIX 3 - PARAMETERIZATION OF VARIABLES: CHANNEL SLOPE AND ROUGHNESS, INITIAL PHYTOPLANKTON CONCENTRATION (PIN), BENTHIC FILTER FEEDER DENSITY, WATER TEMPERATURE, AVERAGE DAILY RADIATION (DR) AND DAY LENGTH (DL)

A3.1 CHANNEL SLOPE AND ROUGHNESS – RELATIONSHIP OF WATER DEPTH WITH WATER SPEED AND RESIDENCE TIME

The value of channel roughness ($n= 0.055$) chosen here is near the middle of the range of that found in nature for major streams. For major streams, i.e. those with a top width at flood stage of more than 100 feet (ca. 30m), the minimum and maximum roughness values for a regular section with no boulders or brush are 0.025 and 0.060, respectively, while those for an irregular and rough section are 0.035 and 0.1, respectively (Chow, 1959; cited by Coon, 1995). Moreover, the value of channel slope chosen here ($S= 0.001$) is also in near the middle of the range of those found in the stretches of large order in several streams (see Table A3-1).

As mentioned in the methods, employing the parameter values chosen for our simulations we observe that increasing water depth (D) leads to a fast but relatively constant increase in water speed (v) but to a dramatically decrease in water residence time (t_{res}) in shallow waters followed by a much slower decrease at deeper waters (Fig. A3-1).

We have performed a sensitivity analysis for the values of channel roughness (n) and slope (S) to observe the effect that varying these parameters (and thereby, water speed (v) and water residence time (t_{res}) has on the results (Figs. A3-2 and A3-3). It can be seen that increasing water residence time increase the effects of the net growth rate of phytoplankton on Pout, regardless of if its value is positive or negative. In other words, in those parameter values where grazing was strong enough to decrease phytoplankton Pout became lower, while in those values where phytoplankton growth surpassed grazing Pout became even higher. This lead to higher changes in Pout within small ranges of depth and temperature. However, the main pattern of our results (Fig. A3-2) remained unchanged.

River	Average bed slope (S; ‰)*	Source
River Rhine segment approximately in Rhine-km 0-400	0.52 - 0.89	1
River Rhine segment approximately in Rhine-km 400-900	0.09 - 0.27	1
Rhine segment from Speyer to Worms; i.e. Rhine-km 400.6 – 443.4)	0.15	2
Upper River Danube (from ca. km 2600-1800)	0.2 - 1.1	3
Middle and Lower River Danube (from ca. 1800-0, excluding the Iron Gate)	0.01 - 0.06	3
River Rhine above Lake Constance	>10	1
Several US rivers (data from 16 gauging stations including several topographic and climatic conditions and catchment sizes between Florida and Alaska. Determined for each cell of a global 0.5°)	Mean: 0.45 (range: 0.1- 1.1)	4
Schoal Creek (stream order 6)	1.08	5
Center Creek (stream order 6)	0.99	5
North Folk (stream order 6)	0.36	5
Spring river (stream order 7)	4.2	5
Western Ialomicioara at confluence w/ Ialomita (stream order 5)	26	6
Strimbu at confluence w/ Tisa (stream order 5)	3.3	6
Ursei at confluence w/ Cricovu Dulce (stream order 5)	6.8	6
Ialomita at confluence w/ Cricovu Dulce (stream order 6)	5.7	6
Purcaru at confluence w/ Doftana (stream order 5)	15	6
Doftana at confluence w/ Prahova (stream order 6)	10.8	6
Vărbilău at confluence w/ Teleajen (stream order 6)	8.6	6
Cosmina at confluence w/ Mislea (stream order 5)	5.6	6

Table A3-1. Average channel slope in different river stretches. * Equivalent to $m/m * 10^3$. Sources: 1) Mangelsdorf *et al.*, 1990; 2) Bleninger *et al.*, 2006; 3) WWF, 2002; 4) Schulze *et al.*, 2005; 5) MDC, 2015; 6) Zăvoianu, 1985.

River	Average or range of Manning roughness coefficient (n; $s/m^{1/3}$)	Source
Average European (estimated using physiographic parameters for 5 arc min grid cells)	0.0358	1
European mountains (estimated using physiographic parameters for 5 arc min grid cells)	0.04 - 0.06	1
Several US rivers (data from 16 gauging stations including several topographic and climatic conditions and catchment sizes between Florida and Alaska. Values calibrated for each station.)	mean: 0.0435 (Range: 0.016 – 0.077)	2

Table A3-2. Average Manning coefficients in different river stretches. Sources: 1) Verzano *et al.*, 2012; 2) Schulze *et al.*, 2005

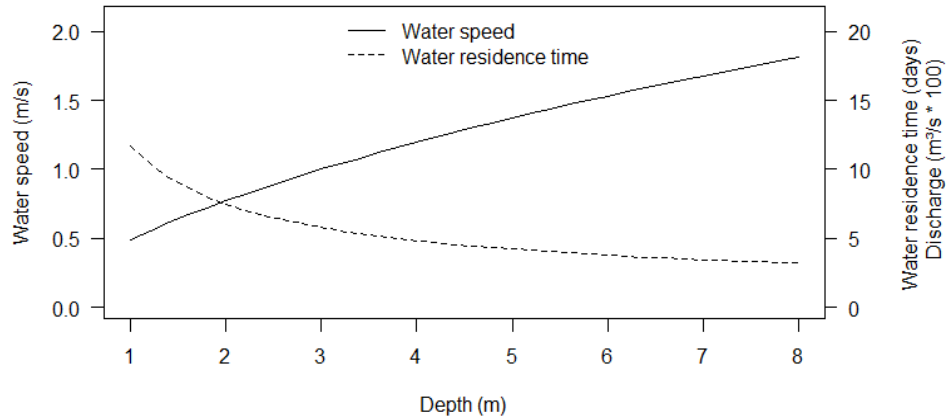


Figure A3-1. Water speed (v) and water residence time (t_{res}) as a function of water depth (D) using the parameters employed in the simulations: slope (S)= 0.0004 m/m, channel roughness (n)= 0.04, channel width (W)= 100m, river length (LR)= 500,000m.

A3.2 INITIAL PHYTOPLANKTON CONCENTRATION (PIN)

In Chapter 3 we used a Pin value ($Pin = P_{t=0}$) equal to 1.0 mgC/l. This is in the higher range of the values *usually* found in the Rhine in the last years (Hardenbicker *et al.*, 2014) but is conservative compared to more productive rivers such as the Elbe, which can reach more than five times such quantity (Hardenbicker *et al.*, 2014) and to the values found in the Rhine River in previous years (Friedrich & Pohlmann, 2009). Moreover, even in recent years phytoplankton concentrations much higher than 1.0 mgC/l have been observed in the Rhine (Hardenbicker *et al.*, 2015b).

In Chapter 4 and 5 we test a large range of Pin values (0.02-10.02mgC/l; equivalent to 0.8-400.8 $\mu\text{gchl-}a/l$, assuming a carbon to chlorophyll a ratio of 25. This ratio is used to convert all values from carbon to chlorophyll a and vice versa throughout this text). Although this range is large compared with measurements in some rivers, particularly in upstream stretches (where they are usually between 0-50 $\mu\text{gchl-}a/l$ or 0-1.25mgC/l), values in downstream river sections can be quite high and maximum phytoplankton concentration in rivers appear to be ca. 400 $\mu\text{gchl-}a$ according to Reynolds & Descy (1996). Even in the Rhine, an exceptionally high value of 244 $\mu\text{gchl-}a/l$ or 6.1mgC/l has been observed in recent years (Hardenbicker *et al.*, 2015b).

Certainly, such high phytoplankton concentrations need both optimal growth conditions (including temperature, nutrients and light), and long water residence times to develop and, thus, are more likely to

develop in downstream river stretches than in upstream ones. On the other hand, phytoplankton concentrations in lakes as potential sources can be considerably high, e.g. 360µgchl-*a*/l or 9mgC/l (Brown *et al.*, 1998), and may reach up to ca. 500-1000µgchl-*a*/l or 12.5-25mgC/l in extreme cases (Smith, 2016). However, river (or stream) concentrations at lake outlets tend to be lower, e.g. River Klingavälsån near the outlet of Lake Sövedsjön is on the higher range of phytoplankton concentrations values with ca. 100µgchl-*a*/l (= ca. 2.5mgC/l; Brönmark & Malmqvist, 1984).

However, considering a large Pin range allows us to test the general patterns of phytoplankton development. Furthermore, these main patterns remain unchanged if we exclude the upper part of the Pin range tested and analyze only values up to e.g. 6mgC/l (= 240µgchl-*a*).

A3.3 BFF DENSITY

Although the variation of BFF density within and between rivers can be very large, the BFF concentrations tested here (0-500 ind./m²) are in the lower range of values reported for *D. polymorpha* and *Corbicula fluminea*. Admittedly, the variation of BFF density through a river and their patchy distributions make BFF density in the entire river length is hard to estimate. The following sentences provide examples of BFF densities reported in different rivers to illustrate their variability.

On the lower range, maximum densities of 94.6 ind./m² for *C. fluminea* were observed in Lake Arlington (Aldridge & McMahon, 1978). In contrast, maximum values of 5000-6000 ind./m² and minimum values of 900 ind./m² were observed for *C. fluminea* populations of California, USA (Heinsohn, 1958, as cited by Aldridge & McMahon, 1978). In addition, in rocks of the Cruger Island of the Hudson River (USA) *D. polymorpha* density varied from < 500 ind./m² to almost 4000 ind./m² (Strayer *et al.*, 1999). Furthermore, *C. fluminea* density varied from ca. 100 ind./m² to almost 1400 ind./m² within a few hundred meters in Meyers Branch (a second-order blackwater stream of South Carolina, USA; Leff *et al.*, 1990).

Other example is the Rhine where, while in most segments *Corbicula* spp. (*Corbicula fluminea* and *C. fluminalis*) is absent or present with a density below 300 ind./m², in a few segments density is above 800 ind./m² (Hardenbicker *et al.*, 2015b). Moreover, *Dreissena* spp. (*Dreissena polymorpha* and *D. rostriformis*) is found in the Rhine mostly below 1000 ind./m² but it can reach densities above 5000 ind./m² (Hardenbicker *et al.*, 2015b). In the Elbe the densities for both bivalve genera are lower and they are absent in most segments. However, although *Corbicula* spp. is always below 100 ind./m², *Dreissena*

spp. can reach values ca. 3000 ind./m² (Hardenbicker *et al.*, 2015b). These maximum values for *D. polymorpha* are in the range of those reported for the Moselle, which can reach about 7000 ind./m² (near Metz, France; Descy *et al.*, 2003). A wide variation was also reported in segments located slightly upstream of those explored by Hardenbicker *et al.*, 2015b. *C. fluminea* density of 200-600 ind./m² was observed 7km downstream of Basel, while density decreased to 5-200 ind./m² at Basel and to only 1-20 ind./m² at localities upstream of Basel (Schmidlin & Baur, 2007).

Moreover, density variation with time can be huge within a site. For example, at the Potomac River (USA), *C. fluminea* density was only ca. one ind./m² in 1977 but it increased to almost 1,500 ind./m² by July 1981 (Cohen *et al.*, 1984). However, these large density decreased sharply to 7% of its size by October 1981 (Cohen *et al.*, 1984).

Although some of the above densities are quite large, much larger densities have been reported in rivers, e.g. above 60,000 ind./m² have been reported for a section of the Seneca River, NY (USA; Effler & Siegfried, 1994). It is probable that such higher grazing enables better eutrophication at deeper and colder waters compared with the range used here. However, these high values are exceptionally above usual values, at least in the River Rhine and Elbe, and thus, we consider the range of bivalve densities used here wide enough to see the potential effect of bivalves in most sites. . On the other hand, if some bivalve densities tested here are high when compared with those in some sites (e.g. 500 ind./m²), our estimates of the grazing rate are likely to be conservative because we limited our filtration rate to a relatively low value in three ways: 1) choosing a moderate maximum filtration rate (f_{max}) value, 2) basing our estimations of filtration rate on data from bivalves of a relatively small size (10-11mm; Vohmann *et al.*, 2010) and 3) although no model produced a good fit to the data, we chose the model that yielded the lowest filtration values (see “*Phytoplankton losses due to benthic grazing*” section of the methods and Appendix 2). Given these considerations we believe that our simulated BFF grazing rates are realistic, and probably conservative, in most rivers.

Finally, it is worth noting that grazing by BFF on phytoplankton is not restricted to single bivalve species in nature but usually includes other native or invasive bivalves, sponges and bryozoans, among other organisms (e.g. Ostroumov, 2005). Together these species determine the grazing pressure on phytoplankton. For simplification, however, we model explicitly the grazing rate of a single BFF and aggregated all other grazing impacts, together with other factors that decrease phytoplankton biomass, in a

single mortality term (see “*Phytoplankton losses due to processes other than benthic grazing*” section in the methods chapter).

A3.4 WATER TEMPERATURE

We used a comprehensive temperature range (0-32°C) to include rivers with stretches that reach quite high temperatures in summer or may do so in the future. Although mean water temperature of most rivers in temperate climates is currently below 25°C (van Vliet *et al.*, 2013), tropical and dry areas have higher values (van Vliet *et al.*, 2013). Moreover, higher values may occur in temperate areas as well, at least in some days and river segments. For example, in the Rhine the number of days with temperatures above 25°C was between 9 and 41 in some stretches (Weil am Rhein 2006 and Koblenz 2003, respectively. Although in 2009 these days were zero. ICPR, 2013). Moreover, maximum values for mean daily water temperature in the Middle and Lower Rhine already surpassed 28°C (2003 and 2006; ICPR, 2013).

However, future river temperature is likely to be higher due to the ongoing climate warming. Mean (and high; 95th percentile) global temperature of river water has been predicted to increase by 0.8-1.6°C (1.0-2.2°C) for 2070-2100 relative to 1971-2000 (scenarios B1-A2 from SRES; van Vliet *et al.*, 2013). Concerning the Rhine, although mean *year* temperatures for spring and summer in the lower Rhine are predicted to stay well below 25°C during this century, the number of days with a mean *daily* water temperature above 23°C is predicted to increase between ca. 40 and 60 days by 2100 (scenarios B1 and A2 of the Special Report on Emissions Scenarios (SRES), respectively; van Slobbe *et al.*, 2016).

Therefore, our simulated range seems to be large enough to include both present and future, at least within this century, temperatures of most rivers, particularly those of temperate areas.

A3.5 DAY LENGTH (DL) AND AVERAGE DAILY RADIATION (DR), CONSIDERATION OF DENSITY-DEPENDENT MORTALITY OF PHYTOPLANKTON

The values for the solar irradiation used here (Table 2-1) are taken from Northern Germany (Cologne/Wahn station) for the years 1966-1975 (means of values from April, May and June). This may limit the applicability of our results to areas with similar regimes. The values in this area, however, are usually in the lower range of those found in Europe. For example, while the annual daily global irradiation

in Europe ranges from ca. 2.2 to 4.8 kWh/m² (mean of annual means 1966-1975), in Northern Germany it is ca. 2.8 kWh/m² (visual inspection of contour maps from Palz & Greif, 1996). Thus, our Pout values are likely to serve as conservative estimates for Europe.

Furthermore, the value for day length, *DL* (amount of hours per day with solar radiation), 15.03h, is also intermediate to more extreme values, e.g. in May values are 14.2h in Konitsa, Greece (latitude 40°3'N) and 17.0h in Bergen, Norway (latitude 60°24'N) (Palz & Greif, 1996). However, although these values may apply to different European areas for some part of the year, e.g. spring to autumn, they are likely to be restricted in winter, particularly in Northern regions. However, phytoplankton blooms in rivers usually take place somewhere between spring and autumn so this limitation is probably unimportant for most managers.

Moreover, although our values are likely to change with the light regime of different regions, it is likely that the general result pattern will remain the same as light affect phytoplankton growth but our pattern of results, depends on the differences that temperature and grazing have throughout river depths. Hence, a lower light regime will likely decrease phytoplankton growth in general, producing the same pattern but lower phytoplankton biomass for different temperatures, depths and BFF densities.

Furthermore, note that Pout values also depend on the choice of parameters for phytoplankton mortality (k_m and m_{max}). These parameters may impact on phytoplankton growth more than variations in light regime between sites. Moreover, although these parameters were calibrated to yield realistic phytoplankton concentrations in our idealized river, given the complexity of natural rivers their values may differ depending on the site.

APPENDIX 4 - ADDITIONAL RESULTS FOR CHAPTER 1 – BENTHIC FILTER FEEDER DENSITIES OF 100 AND 500 IND./M²

Simulations for several water depths and temperature values for different temperature optima of grazing and phytoplankton growth were tested under two additional grazer densities 100 (Figure A4-1) and 500 (Figure A4-2) ind./m².

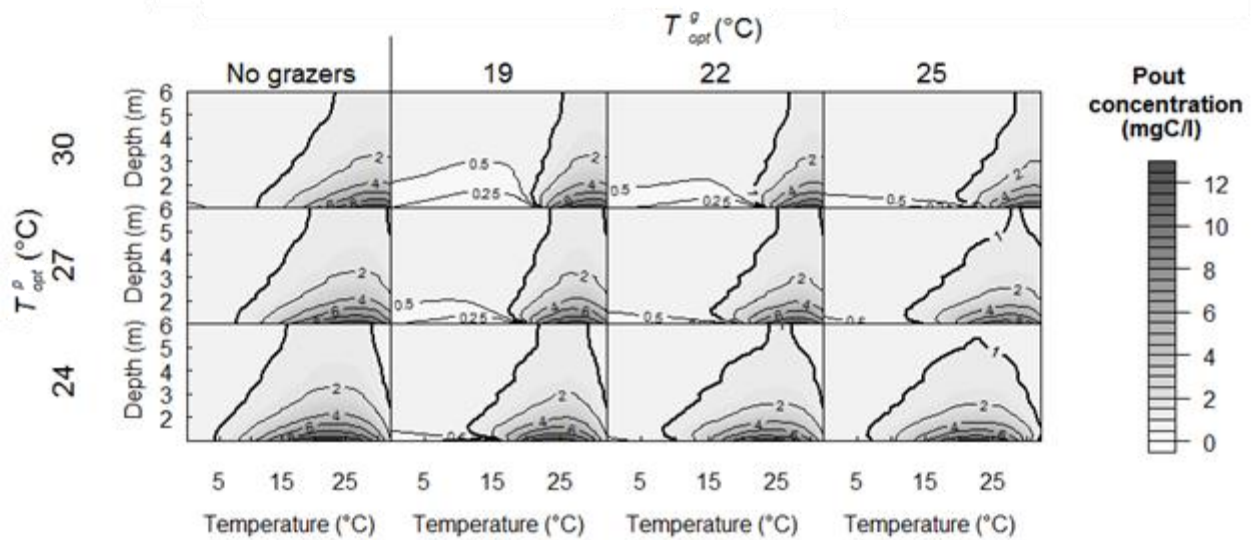


Figure A4-1. Phytoplankton concentration (P_{out}) at various temperatures, depths and different optimum temperatures for phytoplankton growth (T_{opt}^p) and BFF grazing (T_{opt}^g). The three panels in the left show no BFF grazing, while the rest of the panels show BFF grazing at a density of 100 ind./m².

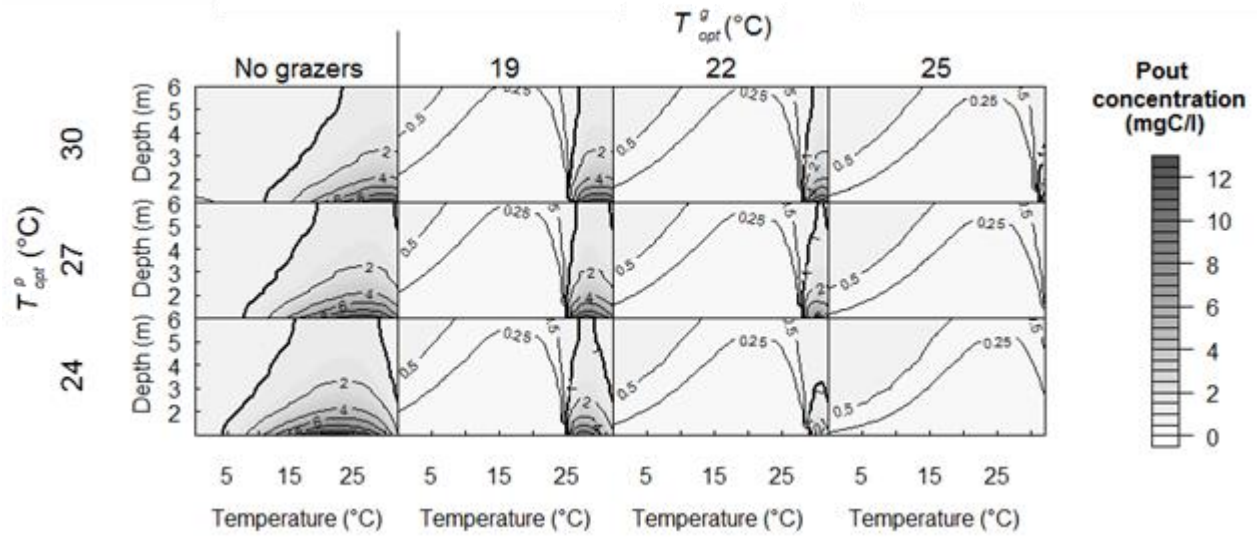


Figure A4-2. Phytoplankton concentration (P_{out}) at various temperatures, depths and different optimum temperatures for phytoplankton growth (T_{opt}^p) and BFF grazing (T_{opt}^g). The three panels in the left show no BFF grazing, while the rest of the panels show BFF grazing at a density of 500 ind./m².

APPENDIX 5 - ADVANTAGES AND DISADVANTAGES OF NATIVE AND INVASIVE BENTHIC FILTER FEEDERS FOR EUTROPHICATION MANAGEMENT

Like other authors that consider managing invasive BFF for their benefits (e.g. Elliott *et al.*, 2008, McLaughlan & Aldridge, 2013) we only advocate their use in some sites already invaded by BFF but consider the introduction of invasive BFF to new sites completely unacceptable. Although some parameters of our model are based on *C. fluminea*, which has already invaded many sites worldwide (e.g. Araujo *et al.*, 1993), our model can serve to simulate other BFF, including native bivalves.

Moreover, the general patterns of our findings are likely to be valid for other species. This is because it is likely that differences in the effect of distinct BFF species on phytoplankton are driven to a large extent by variations in the maximum grazing rate (here a function of i_{max} ; Eqs. 15-16 in Chapter 2) and are therefore represented here by varying BFF density. This is because both individual grazing rate and BFF density increase the total grazing rate of the BFF population; Eq. 15 in Chapter 2). Admittedly, however, other variables may play a role in such effects, e.g. the phytoplankton concentration where maximum filtration is achieved before declining (also called “incipient limiting level”; Marescaux *et al.*, 2016), found here at the point where the maximum filtration rate (f_{max}) intercepts with the daily filtration rate ($f(Pt, T)$; Fig. A2-3).

In the following paragraphs we address the disadvantages of invasive BFF first and then consider the advantages that they have over native bivalves. Again, we do not advocate in any way the introduction of invasive species to new sites and only mention the advantage and disadvantages to highlight the potential risk of BFF management in sites where they are already present.

A5.1 ADVERSE EFFECTS OF INVASIVE BFF

Although grazer control could be a useful strategy to reduce eutrophication in rivers, invasive BFF can also impact ecosystems negatively. BFF like *C. fluminea* and *D. polymorpha* are invasive species with traits like high fecundity, rapid growth and high filtration rates (McMahon, 2002). These traits may favor a relatively fast adaptation to new sites and the ability to quickly reach high densities and recover from disturbances, but they also give invasive BFF competitive advantage over native species. It has been observed that populations of *D. polymorpha* and *C. fluminea* can displace native bivalves (e.g. Darrigran,

2002, Gillis & Mackie, 1994). However, the presence of invasive bivalves does not seem to impact negatively native ones in all sites (e.g. Leff *et al.*, 1990).

Nevertheless, the impact of invasive BFF on biodiversity is an important issue considering that human activity has already affected strongly various populations of native bivalve species some of which are currently endangered or already extinct (e.g. Gillis & Mackie, 1994). Native bivalves are even considered the most endangered group in North America (Ricciardi *et al.*, 1998). Nonetheless, native bivalves are not the only freshwater fauna already threatened (e.g. Allan & Flecker, 1993).

Besides the displacement of native bivalve species, several habitat characteristics are likely altered by invasive bivalves (Strayer *et al.*, 1999): (1) decrease of phytoplankton consumers (e.g. Caraco *et al.*, 1997), (2) increase in populations feeding on bivalves or using their tissues and biodeposits (including fish and bird species preying on BFF and macroinvertebrates using the microhabitats BFF create; Darrigran, 2002), (3) free the resources that were used by phytoplankton and (4) increase the species depending on these resources (including increased water clarity and, thus, macrophytes and its grazers; Phelps, 1994).

Although the importance of these effects may be system specific, it can be substantial. For example, regarding (2), some evidence suggests that invasive BFF can facilitate subsequent invasions of species feeding on them or using their biodeposits as shelter (e.g. Ricciardi, 2001). In addition, bivalves can also settle on other fauna (e.g. Gillis & Mackie, 1994; Darrigran, 2002) and decrease dissolved oxygen due to respiration (Effler & Siegfried, 1994).

It is also well known that species of invasive BFF can foul industrial and agricultural facilities (e.g. electric power plants and water treatment plants) with their shells (e.g. Park & Hushak, 1999, Darrigran, 2002, Connelly *et al.*, 2007). In fact, several efforts have been devoted to investigate and apply methods to get rid of the populations of these species, e.g. chemical biocides (mainly halogenation), mechanical straining, heat treatment, the removal of clam-laden sediment within installations, screen and traps (e.g. Mattice & Dye, 1975, Cherry *et al.*, 1980, Bidwell *et al.*, 1999, Sousa *et al.*, 2014). Such effort is reflected in the high number of publications addressing invasive bivalves (surpassing already 1,500 for *D. polymorpha* and *C. fluminea* together; Sousa *et al.*, 2014). This is not surprising as estimated economic losses range from hundreds thousands to billions of U.S. dollars (Connelly *et al.*, 2007).

A5.2 ADVANTAGES OF INVASIVE BFF OVER NATIVE FAUNA

Although the advantages of using native fauna versus invasive bivalves are potentially manifold (see previous paragraphs), there are some disadvantages of using them instead of invasive bivalves. Such disadvantages include (McLaughlan & Aldridge, 2013): (1) larvae of native unionids need to use fishes as hosts. Thus, these species would need to be cultivated artificially and propagated; (2) native unionids are in worldwide decline; (3) some invasive bivalves are better studied than other species which can also remove seston, e.g. sponges and bryozoans; (4) these other species and, sometimes, even native unionids, occur in low densities in nature so their seston removal capacity is limited. In contrast, invasive species can reach very high densities (see Appendix 3)

Finally, it has been argued that invasive species cannot only provide ecosystem services such as eutrophication control but, in some cases, help conservation (Schlaepfer *et al.*, 2011). For example, some studies show that the invasive BFF species *D. polymorpha* and *Limnoperna fortunei* can favor invertebrate fauna (reviewed in Sousa *et al.*, 2009). However, other studies show the opposite effect (reviewed in Sousa *et al.*, 2009). Therefore, these potential advantages are likely to be species- and site-specific.

In addition, bivalves which are usually considered invasive species may not be so in all sites. For example, it has been argued that the invasive BFF *D. polymorpha*, can be considered native to Northern Germany where it occurred before the last ice age (Stybel *et al.*, 2009). Within such ranges managing such species is likely to face lower ecological and societal challenges.

In conclusion, although, in already invaded sites using invasive BFF may be a way to control eutrophication, managers should be aware of the potential problems they represent and consider that these grazers may cause problems similar to those caused by eutrophication and additional ones. We reiterate that we do not advocate the introduction of invasive BFF but only their use in some of the sites where they are already present. In sites where they are not present, management of native BFF is likely the only alternative for eutrophication control by grazers.

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DECLARATION OF AUTHORSHIP

Erklärung über die Eigenständigkeit der erbrachten wissenschaftlichen Leistung

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet.

Nachfolgend sind die Personen aufgeführt, die mir bei der Auswahl und Auswertung von Material in der jeweils beschriebenen Weise unentgeltlich geholfen haben.

Gesamte Arbeit

- *Kommentare/Sprachliche Korrekturen, Anteil an Idee, Konzept, Interpretation und Analyse* – Karin Frank, Karin Johst, Markus Weitere

Weitere Personen waren an der inhaltlichen materiellen Erstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich hierfür nicht die entgeltliche Hilfe von Vermittlungs- bzw. Beratungsdiensten (Promotionsberater oder andere Personen) in Anspruch genommen. Niemand hat von mir unmittelbar oder mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

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