The ecological carrying capacity of a lowland river section for boating tourism

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Summary

Freshwater ecosystems constitute one of the most important resources for human civilization. Thereby, self-purification capacity constitutes one of the key ecosystem services provided by those systems which is particularly relevant in polluted water bodies serving multiple societal uses. Especially in lowland rivers, a significant proportion of this self-purification capacity can be contributed by the filter feeding activity of freshwater mussels. By the filtration process, organic matter is transferred from the water column to the sediment, and thus gets available to the benthic food web. However, it is hardly known to which extent self-purification activity provided by mussels may be influenced by human uses of the water body, such as recreational boating activities. Within this thesis, I studied the eutrophic lowland river section Krumme Spree (Brandenburg, Germany) that is substantially used for recreational purposes, and aimed to identify the maximal sustainable extent of human use that does not affect self-purification activity provided by mussels. I recorded the filtration activity of native mussel species (*Anodonta anatina*, *Unio tumidus*, and *Unio pictorum*) in field experiments under various boating impact situations, and modeled the disturbance to mussels caused by wave action induced from recreational boating. Moreover, laboratory experiments with invasive species (*Dreissena polymorpha*, *Dreissena bugensis*, and *Corbicula fluminea*) were performed in a wave tank in order to determine their susceptibility to wave disturbances.

In all studied mussel species, filtration activity was significantly affected by shear stress produced by wave disturbance. Increasing shear stress caused interruption of filtration activity, following sigmoid response patterns for both the duration and the degree of shell closing. The sigmoid response curves allowed threshold values for shear stress to be derived, indicating zero to moderate effects on filtration activity. Thereby, the native species showed relatively low threshold values for the starting of shell closing in combination with either the longest duration of shell closing (*A. anatina*) or the highest degree of shell closing (*U. tumidus* and *U. pictorum*), and thus turned out to be more susceptible to wave disturbance than two invasive species. The invasive species *D. bugensis* and *C. fluminea* were still able to filtrate under wave impacts while *D. polymorpha* did not differ significantly in any of the studied susceptibility parameters from the respective range covered by native species. Thus, *D. bugensis* and *C. fluminea* seem to be pre-adapted to hydraulic or morphological disturbance and may compensate other losses of this important ecosystem function in rivers intensively used for inland navigation.

The coupled hydraulic-ecological modeling approach presented in this thesis showed that typical boating activity on the Krumme Spree river section may reduce self-purification activity by mussels, with the extent of disturbance depending on mussel species, river depth, boating frequency, and cruising speed. However, self-purification activity of this lowland river section is not significantly affected under present day conditions, while substantial effects are to be expected under reduced river flow conditions. The developed coupled hydraulic-ecological modeling approach also enables the estimation of the ecological carrying capacity of this river section for sustainable boating tourism which still allows the preservation of water quality. This estimated ecological carrying capacity significantly decreases with lower river discharge during summer. A comparison of the estimated ecological carrying capacity with the social carrying capacity revealed that at water levels of more than 170 cm, boating tourism is limited first by social and spatial aspects, while at water levels of less than 170 cm boating tourism is limited first by ecological values. Thus, the coupled hydraulic-ecological modeling developed here enables to identify mitigation strategies that may contribute to the preservation of surface waters.

Zusammenfassung

Süßwasser-Ökosysteme stellen eine der bedeutendsten Ressourcen auf der Erde dar. Die Selbstreinigungsfähigkeit dieser Systeme ist dabei eine der wichtigsten Ökosystem-Dienstleistungen, die vor allem in verunreinigten und vielfach genutzten Gewässern von Bedeutung ist. Ein erheblicher Anteil dieser Selbstreinigungsfähigkeit wird in Tieflandflüssen über die Filtrationsaktivität von Muscheln erbracht. Während der Filtration wird organisches Material aus der Wassersäule entfernt und dem Sediment zugeführt, wo es dann dem benthischen Nahrungsnetz zur Verfügung steht. Es ist jedoch bisher kaum bekannt, in welchem Ausmaß die Selbstreinigungsaktivität von Muscheln durch Nutzungen der Gewässer wie z.B. den Bootstourismus beeinflusst wird. In der vorliegenden Arbeit habe ich daher einen touristisch genutzten Flussabschnitt der Krummen Spree (Brandenburg, Deutschland) untersucht, um die maximale touristische Nutzung mit Booten zu ermitteln, welche die Filtrationsaktivität von Muscheln noch nicht beeinträchtigt. Dafür habe ich die Filtrationsaktivität heimischer Muschelarten (*Anodonta anatina*, *Unio tumidus*, *Unio pictorum*) in Feldversuchen ermittelt und daraus aufbauend die Störung der Tiere durch bootsbedingten Wellenschlag modelliert. Zusätzlich habe ich Laborversuche mit invasiven Arten (*Dreissena polymorpha*, *Dreissena bugensis*, *Corbicula fluminea*) in einem Wellenbecken durchgeführt, um deren Anfälligkeit gegenüber Wellenstörungen zu ermitteln.

Die Filtrationsaktivität aller untersuchten Muschelarten wurde durch die von Wellen verursachte Sohlschubspannung signifikant beeinflusst. Ansteigende Sohlschubspannungen verursachten Unterbrechungen der Filtration, die sowohl hinsichtlich der Dauer als auch des Grads des Schließens der Schalen mit sigmoiden Reaktionsmustern erklärt werden konnten. Basierend auf den sigmoiden Reaktionssmustern konnten Grenzwerte für die Sohlschub-spannungen ermittelt werden, die keine bzw. nur moderate Auswirkungen auf die Filtration verursachen. Dabei zeigten die heimischen Muschelarten im Verhältnis relativ niedrige Schwellenwerte für den Beginn des Schalenschließens in Kombination mit entweder der höchsten Schließdauer der Schalen (*A. anatina*) oder dem höchsten Schließgrad der Schalen (*U. tumidus* und *U. pictorum*). Diese Arten sind somit empfindlicher gegenüber Wellenbelastung als die invasiven Arten *D. bugensis* und *C. fluminea*. Diese waren auch unter Wellenbelastung noch in der Lage zu filtrieren, während *D. polymorpha* sich nicht signifikant von den heimischen Arten unterschied. *D. bugenis* und *C. fluminea* scheinen daher an

hydraulische Störungen adaptiert zu sein und können durch ihre Präsenz die Verringerung der Selbstreinigungsaktivität in für die Schifffahrt genutzten Gewässern kompensieren.

Mittels des hier erstellten hydro-ökologischen Modellierungsansatzes konnte gezeigt werden, dass durch das typische Bootsaufkommen in der Krummen Spree die Selbstreinigungsaktivität in Abhängigkeit von der Muschelart, der Gewässertiefe, Häufigkeit von Bootspassagen und der Fahrgeschwindigkeit reduziert wird. Unter den aktuell herrschenden Umwelt- und Nutzungsbedingungen fällt diese Minderung nur gering aus, allerdings können bei einer Verringerung der Wasserführung im Sommer, etwa durch Klimawandel, oder einer Zunahme des Bootsaufkommens wesentliche Auswirkungen auf die Selbstreinigungskapazität entstehen. Mittels der hydro-ökologischen Modellierung konnte außerdem die ökologische Tragfähigkeit dieses Flussabschnittes für den Bootstourismus berechnet werden. Diese ökologische Tragfähigkeit nahm mit sinkenden Wasserständen signifikant ab. Ein Vergleich mit der ebenfalls berechneten sozialen Tragfähigkeit des Flussabschnitts hat gezeigt, dass ab Wasserständen unter 170 cm die ökologische Tragfähigkeit gegenüber sozialen Aspekten an Bedeutung gewinnt. In solchen Fällen können über die hydro-ökologische Modellierung Anpassungsstrategien identifiziert werden, die sowohl den Bootstyp, Uferabstand als auch die Geschwindigkeit der fahrenden Boote berücksichtigen.

Thesis Outline

This thesis is a cumulative work composed of three manuscripts that are either published in peer-reviewed journals, or currently under review. Each manuscript forms a separate chapter including its own introduction, methodology, results and discussion section and is therefore independently readable from the other chapters. The general context of this thesis is provided by a general introduction section and all findings are discussed coherently in an overall discussion section. As a result of this structure, these sections overlap to some extent with the content of the different chapters.

All manuscripts have been reprinted with the kind permission of the respective publishing house. However, the layout of the published or currently-under-review manuscripts has been modified to ensure a consistent layout throughout the entire thesis. Figures and tables were renumbered throughout the text and referring lists of tables and figures are presented. The references of each manuscript, general introduction and overall discussion were included in an overall reference section that is presented at the end of the overall discussion.

Chapter 1

Lorenz, S., Gabel, F., Dobra, N., Pusch, M. T. 2012. Modeling the impacts of recreational boating on self-purification activity provided by bivalve mollusks in a lowland river. *Freshwater Science*. Accepted for issue 32(1).

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Author contributions

S. Lorenz designed the study, organized and performed field experiments, analyzed data, performed statistics and compiled the manuscript. F. Gabel co-performed field experiments and contributed to the text. N. Dobra co-performed field experiments and contributed to data analysis and statistics. M. T. Pusch co-designed the study and contributed to the text.

Chapter 2

Lorenz, S., Pusch, M. T. 2012. Higher filtration activity of invasive versus native mussel species under wave disturbance conditions. *Biological Invasions*. Submitted.

Author contributions

S. Lorenz designed the study, organized and performed laboratory experiments, analyzed data, performed statistics and compiled the manuscript. M. T. Pusch co-designed the study and contributed to the text.

Chapter 3

Lorenz, S., Pusch, M. T. 2012. Estimating the recreational carrying capacity of a lowland river section. *Water Science & Technology 66: 2033-2039*.

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Author contributions

S. Lorenz designed the study, analyzed data, performed statistics and compiled the manuscript. M. T. Pusch co-designed the study and contributed to the text.

General Introduction

Ecosystem health

Since the 1950s about 60% of the world's ecosystems have been damaged or overexploited by humans (Millennium Ecosystem Assessment 2005) and consequently, much research has focused on assessing ecosystem health. The tremendous interference of mankind is spread over all kinds of systems and promoted ecosystem health studies in terrestrial (Rapport et al. 1997; Yazvenko and Rapport 1997), marine (Bockstael et al. 1989; Mageau et al. 1995) and freshwater ecosystems (Wichert and Rapport 1998). The term ecosystem health describes the conditions of essential functions and services within a given ecosystem. This general description does not only focus on quantitative information of ecosystem parameters, but includes qualitative information as well. Depending on the scientific approach definitions of ecosystem health vary considerably (Costanza 1992; Peng et al. 2007; Rapport et al. 1998). Actually, the definition of Rapport et al. (1998) is mostly used in current literature. It focuses on the ecological aspects of ecosystems human and economic needs, and raises the concept of ecosystem health on a transdisciplinary and integrated level. While ecologically based definitions state that ecosystem health is described as a stable and sustainable status that can be characterized by vigor, system organization and resilience (Costanza 1992), Rapport et al. (1998) additionally require the '*analysis of linkages between human pressures on ecosystems and landscapes, altered ecosystem structure and function, alteration in ecosystem services, and societal response*'. By including these multiple and transdisciplinary aspects into the term of ecosystem health, the requirements for preserving this status are difficult to reach.

Among the various characteristics of ecosystem health, resilience is the most challenging to be assessed, as it is difficult to define and to measure (Karr and Thomas 1996). The best available, general definition states resilience as the ability of a system to absorb changes of state variables, driving variables and parameters, and still persists (Holling 1973). Nevertheless, the strength of resilience naturally varies among systems and depends on the kind of disturbance (Arrow et al. 1996) and subsequent impacts on ecosystem services might occur if a system loses resilience (Elmqvist et al. 2003). This value of the capability of a system to maintain functioning under stress conditions allows integrating human uses, pressures and alterations in the concept of ecosystem health. Even though resilience is, beside vigor and system organization, an ecologically based characteristic, these properties are able to extent ecosystem health to human and societal impacts (Costanza et al. 1998; Munoz-Erickson et al. 2007). Ecosystem services can be grouped into the four categories '*provisioning services*' (e.g. fisheries, energy, freshwater), '*regulating services*' (e.g. climate regulation, water purification, disease regulation), '*supporting services*' (e.g. nutrient cycling, primary production) and '*cultural services*' (e.g. recreation, ecotourism) (Millennium Ecosystem Assessment 2005). Within the range of the in total 24 analyzed ecosystem services, the United Nations Environment Programme (2009) identified eleven services as '*priorities, based on the seriousness of the degradation, impacts on human well-being and implications for sustainable development*', pointing out their extremely high societal relevance. This central group includes the services '*freshwater provision*', '*water regulation*', '*water purification*' and '*recreation*', which also form key aspects of this thesis, and thus will be elucidated in more detail in the following sections.

Multiple stressors acting on freshwater ecosystems

Inland waters are manifold used by humans for various reasons at the same time (Food and Agriculture Organization of the United Nations 2008). Due to this extremely high usage freshwater ecosystems are the most threatened systems worldwide. Within the Millennium Ecosystem Assessment (2005), freshwater ecosystems are stated to be in '*worse condition than those of forests, grasslands or coastal systems*'. Similarly, the Global Biodiversity Outlook 3 concluded that '*rivers and their floodplains, lakes and wetlands have undergone more dramatic changes than any other type of ecosystem*' (Secretariat of the Convention on Biological Diversity 2010). In result of these degradations and alterations of ecosystem conditions, the capacity of inland waters to produce essential ecosystem services is '*in decline and is as bad or worse than that of other systems*' (Millennium Ecosystem Assessment 2005). Thereby, five major threats that impact freshwater ecosystems have been identified (Dudgeon et al. 2006). These comprise '*overexploitation*', '*water pollution*', '*flow modification*', '*habitat degradation*' and '*species invasion*' that not only affect ecosystem integrity but also interact with each other. All of these threats tend to impact important ecosystem functions and services, and therefore mutual interactions affecting the same service may be expected. Additional environmental stressors like climate change that are able to shift discharge and precipitation regimes (Gerstengarbe et al. 2003) might amplify stressor effects. The prediction and the understanding of multiple stressors thus constitute one of the most important challenges in future (Tockner et al. 2010).

Under the proposed climate change scenarios, '*virtually all freshwater ecosystems will face ecologically significant climate change impacts by the middle of this century*' (Le Quesne et al. 2010). From the three major variables that will be influenced by climate change, flow regime is described as the primary driver of ecosystem functioning (e.g. Le Quesne et al. 2010; Poff et al. 2010; Wrona et al. 2006). Additionally, changes in water quality affect ecosystem functioning to a similar extent, which are often caused or amplified by decreases in water quantity. Thus, water quality has to be seen as a central indicator of ecosystem health in freshwater ecosystems beside biodiversity (Rapport et al. 1998). Water quality suffers from various types of stressors, being either climate driven (Federal Environmental Agency 2005) or resulting from other anthropogenic pressures, such as land-use changes (Foley et al. 2005), commercial use (Pusch and Hoffmann 2000) or recreational activities (Bockstael et al. 1989). While it is widely accepted that intensive agriculture, deforestation and urbanization are severely degrading water quality (e.g. by nutrient input, water abstraction for irrigation, or wastewater discharge), the effects of recreational activities on water quality represent one stressor within this variety that is underestimated so far.

Surface waters provide various opportunities for multiple recreational activities, like swimming, fishing, sailing or boating (Postel and Carpenter 1997). It can be assumed that these activities affect the ecological integrity of surface waters in several ways. Thereby, boating is one major recreational use that causes a series of adverse impacts on freshwater ecosystems. The main environmental impacts include pollution due to fuel and oil contamination (Burgin and Hardiman 2011), hydromorphological alterations facilitating boat traffic (Tacon 1994) as well as the disturbance of wildlife (Liddle and Scorgie 1980). One of the key pressures of recreational boating is the boat-induced wave action, which disturbs and degrades littoral habitats (Gabel et al. 2008), and resuspends organic sediments (Beachler and Hill 2003; Garrad and Hey 1987). In turn, resuspended sediment can lead to damages by smothering or burying organisms (Morgan et al. 1983; Newcombe and Macdonald 1991) as well as to decreased removal of organic particles from the river by mussels (Schneider et al. 1998).

Self-purification capacity of river ecosystems

The self-purification capacity of inland waters – which describes the potential activity to remove e.g. organic pollution – consists one of the key ecosystem services mainly provided by rivers (Costanza et al. 1997; Everard and Powell 2002; Howard and Cuffey 2006), which is especially important in eutrophicated water bodies serving multiple societal uses. This retention effect improves the opportunities to use polluted or eutrophicated rivers in downstream reaches (e.g. Heberer et al. 2002; Ho et al. 2003). Such multiple uses of water bodies are expected to be intensified in future through population increase, economic development and climate change (Meybeck 2003; Pusch and Hoffmann 2000; Tockner et al. 2010). Thus, water management will continue to rely on the self-purification capacity in order to enable such multiple uses (Kronvang et al. 1999). Within the self-purification process, chemical and biological processes play important roles in maintaining and improving water quality by removing organic matter (Spellmann and Drinan 2001). These processes are linked to nearly all criteria of water quality such as dissolved oxygen, nitrate, ammonium and organic load. Therefore, knowledge about the self-purification capacity of streams and rivers is necessary to assess ecosystem integrity and health.

Especially as nutrient inputs into aquatic ecosystems increased dramatically, the self-purification capacity has gained more attention in the assessment of ecosystem integrity (Markussen et al. 2005; Mitsch and Gosselink 2007). Thereby, the intensity of the self-purification in streams and rivers depends on several factors. These comprise temperature, water level, flow velocity, the concentration of inorganic compounds, and the distribution as well as type of aquatic vegetation (Ifabiyi 2008). In lowland rivers, a significant proportion of self-purification capacity may be contributed by mussels (Bauer 2001; Libois and Hallet-Libois 1987; Pusch and Hoffmann 2000; Pusch et al. 2001b; Welker and Walz 1998), which may efficiently transfer organic matter from the water column to the benthic zone (Howard and Cuffey 2006). This transfer consists a critical step for the self-purification in rivers, as most of the microbial degradation activity of organic matter in rivers is located in the sediments (Fischer and Pusch 2001). In consequence, any significant reduction of filtration activity of freshwater mussels will be followed by whole-system effects in the river. As the value of numerous economic and societal functions of waters is significantly influenced by the available water quality (Thomas et al. 1992), a sustainable use of surface waters is mandatory and should seek to minimize detrimental effects on the self-purification capacity, as these would reduce system resilience (Zeng et al. 2011).

Carrying capacity

In order to avoid devaluating major water resources, the detrimental effects of human water-related activities need to be mitigated and regulated in a sustainable way. Estimations of the carrying capacity of water systems subjected to multiple pressures that consider cumulative effects and interactions of all significant pressures on crucial ecosystem functions are therefore inevitable (Everard and Powell 2002). Thereby, human activities do not only affect the environmental resources of the area they use, but additionally affect their own perception of the environment (Wagar 1964). Previous efforts to estimate recreational carrying capacities of lakes (e.g. ERM Inc. 2004; Jaakson et al. 1990; Rajan et al. 2011) or rivers (Rebellato 2007) have integrated these aspects by, for example, describing the minimum required lake surface area that is needed for the safe operation of a single boat type.

However, existing estimates of the carrying capacity of water systems have primarily focused on human needs, thus neglecting the potential ecological impacts of human recreational activities. For a more comprehensive approach, four components have been recommended to estimate the recreational carrying capacity (Shelby and Heberlein 1986). These comprise (1) the ecological capacity (related to the impacts on ecosystems), (2) the spatial capacity (related to the number of people in a specific area), (3) the facility capacity (related to the use of given services and facilities) and (4) the social capacity (related to visitors perceptions and interactions). Another study (O'Reilly 1986) has similarly identified four major components, namely (1) the physical capacity (related to environmental impacts), (2) the perceptual capacity (related to the quality of recreational experience), (3) the economic capacity (related to the ability to absorb tourist functions) and (4) the social capacity (related to the interaction of the visitors). The key aspects of the overall carrying capacity coincide in both studies, highlighting their relevance.

While the impacts of human use of inland waters are generally well known (Goudie 2006), the specific effects arising from recreational activities, such as the formation of waves from boating, are less understood. Neither the general effects of human development along shores, nor the specific effects of water-based tourism on the ecology of surface waters have been adequately considered in existing studies which have attempted to develop estimates of touristic carrying capacities of lakes and rivers (e.g. Shelby and Colvin 1981). Some studies state that the main reason for this lack of knowledge about the ecological effects of water-based tourism was the absence of background information of its effects on surface water ecosystems (e.g. Confluence Environmental Consulting 2005; Rebellato 2007). The latter study suggested the analysis of potential changes in water quality, which would enable to assess the pollution impacts of recreational watercrafts on freshwater ecosystems. However, natural processes and impacts may also influence various parameters of water quality, including total suspended solids, turbidity, dissolved oxygen, pH and temperature. Thus, it is necessary to identify the specific mechanistic pathways that may lead to environmental impacts resulting from boating, and then specifically focus on the measurement of variables that are primarily impacted by boating.

Impacts of boating and climate change on self-purification activity provided by freshwater mussels

Lowland rivers that suffer both from intense recreational and boating activities and varying framework conditions deserve special attention as their ecological status is threatened by multiple stressors. The river section ‘Krumme Spree’ of the Spree River provides ideal conditions to conduct a case study within this framework. In general, this river section is navigable by all types of motorboats (Hoffmann et al. 2009) and serves as a connection between two lakes of intense touristic use. Therefore, effects of boating on the ecological integrity of the river ecosystem are likely to be shown within this river section.

Furthermore, impacts of water abstraction for refilling large mining pits (Pusch and Hoffmann 2000) occur simultaneously in this river section. Due to the intense lignite mining activities in the times of the German Democratic Republic, the discharge of the River Spree was artificially raised to up to 33 $m^3\ s^{-1}$ (in 1990, see Möbs and Maul 1994) by the discharge of sewage water. After the reunification of both the German Democratic Republic and the Federal Republic of Germany in 1990, the amount of lignite mining was substantially reduced and groundwater extraction for mining activities declined. With the substantial decrease of mining activity in this region, the abandoned lignite pits are now used for the creation of Europe’s largest artificial surface water system. Nowadays, water of the River Spree is abstracted to enable the refilling of both the groundwater aquifers and the lignite pits.

Additionally, the discharge of the river is further reduced by the evaporation of the Spreewald inland delta by up to 7 $m^3\ s^{-1}$ during hot midsummer days. Together with the water abstraction, this may cause extreme minimum discharge values in the ‘Krumme Spree’ river section downstream of the Spreewald during dry summers. These severe reductions of discharge also cause additional consequences for the river ecosystem. Accompanying reductions of flow velocity, times of oxygen depletion and possible thermal layering cause an explicit disturbance of rivers self-regulatory abilities and the ecosystems resilience (Pusch and Köhler 2002).

Hence, the river section Krumme Spree constitutes an ideal study area to investigate both the impacts of water related tourism like boating and of water abstraction proposed by common climate change scenarios. As mutual interactions of both impacts may be expected, a possible amplification of boating impacts on surface water systems by climate change can be studied in this river section under real present-day conditions. Consequently, the river section Krumme Spree was chosen as a case study for the determination of boating impacts on river ecosystems and the subsequent carrying capacity estimations within this thesis.

Aims of this thesis

This thesis aims to determine and analyze the ecological consequences of various types of boating using the Krumme Spree river section as a model region. Thereby, impacts on filtration activity of freshwater mussels (Unionidae and *Dreissena polymorpha*) were chosen to quantify impacts on the self-purification activity of a river section by boating. In order to quantify the impact of boating, the work focuses on the anthropogenic wave disturbance of boats that causes significant detrimental effects on that key ecosystem service. Furthermore, I aimed to identify thresholds for the sustainable use of the river ecosystem. For the first time, coupled hydraulic-ecological modeling enabled estimations of the impact of boating tourism on a socially and ecologically important ecosystem service, as well as calculations of an ecologically based carrying capacity of a river section for boating tourism. By varying several hydrologic, touristic and climatic variables within the developed model, I aimed to predict alterations in this ecologically based carrying capacity that will happen with changing framework conditions.

Chapter 1

The primary goal of this chapter was to identify thresholds for the sustainable use of a river ecosystem subjected to water touristic uses, which also accounted for impacts on system resilience. Hence, I undertook a field study to analyse how hydraulic disturbance by boating activity may affect a river’s self-purification capacity, as represented by the filtration activity of mussels. Moreover, I aimed to quantify the impact of anthropogenic wave disturbance and boating activity on the daily filtration rates of the whole mussel populations within a river section.

Chapter 2

Within this chapter, I aimed to determine the effect of simulated ship waves on the filtration activity of three invasive mussel species in laboratory experiments. The results were compared with the data obtained on native mussel species in Chapter 1. It was hypothesized that (1) the filtration activity of invasive and native mussel species differs if exposed to waves and that (2) there is a difference both in sensitivity and in shell closing behaviour between native and invasive mussel species. I predicted that invasive mussel species are less susceptible to ship-induced waves and that filtration activity under disturbed conditions is higher in invasive than in native mussel species.

Chapter 3

The overall goal of this chapter was to estimate the ecological carrying capacity of a river section used for boating tourism via an integrative approach that included ecosystem health. Here, ecosystem health is measured as potential self-purification, which is a key ecosystem process for the preservation of acceptable water quality for both ecosystem functioning and attractiveness of water tourism. A combination of this ecological approach with spatial and social components is used to develop an integrative concept towards estimating the touristic carrying capacity of rivers. Finally, I aimed to develop recommendations for management options that integrate social, touristic and ecological aspects.

Modelling the impacts of recreational boating on self-purification activity provided by bivalve mollusks in a lowland river

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Abstract

Self-purification is a key ecosystem service provided by riverine biota that is particularly important in polluted water bodies serving multiple societal uses, but the extent to which self-purification may be influenced by human uses is unknown. We studied a eutrophic lowland river used for drinking water and recreation to identify the maximal sustainable extent of human use. We recorded filtration by mussels and modeled the disturbance to mussels caused by wave action induced from recreational boating. Filtration was significantly affected by shear stress produced from boats down to a depth of 2.7 m. Threshold values for the intensity of wave disturbance ranged from 0.21 N/m^2 (*Unio tumidus*) to 0.43 N/m^2 (*Anodonta anatina*) for moderate effects and from 0.02 N/m^2 (*U. tumidus*) to 0.13 N/m^2 (*Dreissena polymorpha*) for no effects on filtration. *Anodonta anatina* and *D. polymorpha* showed a significantly lower degree of shell closing and a higher predicted medium-effect shear stress (the shear stress associated with 50% of the maximum shell closing duration) than *U. tumidus* and *Unio pictorum,* which probably results from differences in the species position in and above the sediment. Coupled hydraulic–ecological modeling showed that typical boating activity may reduce self-purification activity by mussels, with the extent of disturbance depending on mussel species, river depth, boating frequency, and cruising speed. Single passages of boats reduced daily mussel filtration rates by 0.02% for muscle-driven boats, 0.45% for yachts, 0.68% for motor boats, and 0.69% for motorized rafting and rowing boats. Depending on total daily boat traffic and hydrological conditions, a reduction in the daily filtration rate by mussel populations within the studied river section was estimated at 6.9%. We conclude that self-purification activity of this lowland river section is not significantly affected by recreational boating, but might be affected by more intense recreational boating under altered river flow conditions.

Introduction

Self-purification capacity, such as the ability to remove organic pollution, is a key ecosystem service in rivers (Everard and Powell 2002; Howard and Cuffey 2006). This capacity is particularly important in polluted or eutrophic water bodies serving multiple societal uses and greatly improves opportunities to use the downstream reaches of such rivers (e.g., Heberer et al. 2002; Ho et al. 2003). Water managers rely on the self-purification capacity of rivers to facilitate multiple uses (Kronvang et al. 1999), which are expected to intensify because of population growth, economic development, and climate change (Pusch and Hoffmann 2000; Meybeck 2003; Tockner et al. 2010). However, few attempts have been made to identify maximum tolerated loads for sustainable use of river ecosystems subjected to multiple uses, and very few investigators have analyzed effects of multiple pressures, such as eutrophication, morphological alterations, and navigation, and the consequences of integrated management approaches (Wechsung et al. 2005; Ducharne et al. 2007; Hofmann et al. 2010). This lack of knowledge is a serious problem because sustainable management should ensure the resilience of surface waters, which includes persistence of full self-purification capacity (Rapport et al. 1998).

Ecological effects of human pressures on ecosystems are aggravated when ecosystem resilience already has been impaired (Folke et al. 2004). For instance, in lowland rivers, mussels may contribute a significant proportion of self-purification capacity (Libois and Hallet-Libois 1987; Welker and Walz 1998; Pusch and Hoffmann 2000; Bauer 2001; Pusch et al. 2001), which may efficiently transfer organic matter from the water column to the benthic zone (Howard and Cuffey 2006). This transfer is a critical step for self-purification because most microbial degradation of organic matter in rivers occurs in the sediments (Fischer and Pusch 2001). Thus, any reduction in filtration activity by freshwater mussels is likely to be followed by whole-system effects on the river's ecological status, with corresponding consequences for potential human uses of the water body.

Water bodies used for drinking water often are used for recreational purposes, but the effect of boat traffic on self-purification of such water bodies is unknown. Environmental effects of boat traffic include noise, disturbance of wildlife (Liddle and Scorgie 1980), pollution by fuels and oils (Burgin and Hardiman 2011), and hydromorphological alterations undertaken to facilitate boat traffic (Tacon 1994). Boat-induced wave action is an important pressure that causes resuspension of organic sediments (Beachler and Hill 2003) and disturbs and degrades coastal marine habitats (Bishop 2004; 2007) and littoral zones of inland waters (Gabel et al. 2008; 2011b). Wave action may cause mass detachment of macroinvertebrates if critical levels of shear stress are surpassed (Gabel et al. 2008). Furthermore, the resuspension of sediments can smother or bury benthic organisms (Morgan et al. 1983; Newcombe and Macdonald 1991) or affect dissolved O_2 (DO) concentrations via decomposition of organic particles.

We conducted a field study to analyze how hydraulic disturbance by boating activity might affect self-purification capacity based on the filtration activity of mussels. Our goals were to identify maximum tolerance levels of anthropogenic wave disturbance and to estimate the carrying capacity of a water body for recreational boating.

Material & Methods

Study site

The River Spree is a lowland river in northeastern Germany that is subjected to multiple human uses and is the main source of drinking water for Berlin (Köhler 1994). We worked along a straight reach of a 20-km river section called Krumme Spree that connects Lake Neuendorfer See and Lake Schwielochsee, near the village of Kossenblatt (lat 52°6'15.35"N, long 14°4'15.83"E). This river reach supports high densities of mussels (Unionidae and *Dreissena polymorpha*; Pusch et al. 2002) and is used heavily for recreational boating during summer. The section was channelized ~100 y ago, so the Krumme Spree channel has a deep, symmetrical trapezoid cross-section, with a mean width of 25 m and a mean depth of 1.4–2.5 m, depending on discharge level. The mean slope is 0.01%, and the sediments consist mainly of sand with a mean particle size (DC50) of 0.36 ± 0.01 mm. Discharge varied from 0.5–10.4 m^3/s during the study period in June and July 2010.

Field measurements and calculation of shear stress

We collected 8 specimens of each of 3 species of unionid freshwater mussels (Swollen River Mussel *Unio tumidus*, Painter's Mussel *Unio pictorum,* and Duck Mussel *Anodonta anatina*), and zebra mussels *Dreissena polymorpha* attached to stones at the same locations. We quantified filtration activity by measuring the gape width between the tips of both shells of each mussel. Gape width is at its maximum during full filtration activity. We used instant adhesive glue to equip mussels at the sampling site with permanent disk magnets (magnet grade = N52, diameter = 5 mm, thickness = 2 mm) near the tip of 1 shell, and a magnetic sensor (radiometric linear Hall-effect sensor A1321; Allegro Microsystems, Worcester, Massachusetts) near the tip of the other shell. We returned the mussels to the river reach. Stress for the mussels was negligible because they were out of the water for handling for < 1 min. In laboratory experiments, mussel behavior was not significantly affected by handling or measurement equipment (SL, unpublished data). All individuals began to open their shells for filtration activity shortly after resubmersion.

Magnetic sensor systems with Hall-effects sensors have been used by others to investigate valve movements in bivalves (Wilson et al. 2005; Maire et al. 2007; Robson et al. 2009). The magnetic sensors detect the strength of the magnetic field, which we calibrated against the width of opening at the shell tips (gape width, in mm). Measured voltage was converted to gape width, which was converted to relative values (% shell closing relative to maximum gape width). We calibrated the magnet system in a preliminary laboratory experiment with 3 individuals of each species (sizes were similar to those of the individuals used in the larger experiment). The calibration was best fit by a linear inverse polynomial equation. We measured gape width at a 1-kHz recording rate averaged to a 1-Hz sampling rate.

We exposed the experimental mussels at various water depths (25, 50, 75, 100, 125, and 180 cm) in the river from 16 to 29 July 2010. We recorded gape width from 1000 to 1600 h each day, the period with most of the boat traffic. We recorded turbidity and DO with a YSI multiprobe (Yellow Springs Instruments, Yellow Springs, Ohio) installed at the study site at a depth of 1.8 m. We also installed automatic cameras to record boating activity.

During the exposure period, we used a motorboat (8 horsepower [HP]) of the typical size of recreational boats in the study area to produce experimental waves. We ran the boat at various speeds (8, 12, and 18 km/h) and repeated each speed in random order 10 times. We also included waves produced by passing recreational boats. We categorized recreational boats as muscle-driven boats (canoes and kayaks), motor boats (low horsepower open sport boats with outboard motor), yachts (larger boats, including yachts and house boats or barges with inboard motors), and motorized rowing and rafting boats. We measured waves from ≥ 10 passages of boats in each category. We initiated subsequent experimental runs only after turbidity had returned to the predisturbance level and all mussels had fully reopened their shells.

We used an Acoustic Doppler Velocimeter (ADV; Micro ADV 16 MHz, Sontek, San Diego, California) with a recording rate of 50 Hz and the sampling volume positioned 1.5 cm above the river bed to measure bottom orbital velocity (U_w) and wave period (T) near the mussels. In 25-cm-deep water near the shoreline, U_ws created by boat passages were 2.13 ± 0.26 cm/s (SE) (muscle-driven boats), 6.23 ± 0.75 cm/s (motorized rowing and rafting boats), 8.30 ± 0.57 cm/s (yachts), 10.42 ± 2.14 cm/s (motorboats 8 km/h), 14.68 ± 0.63 cm/s (motorboats 10 km/h), 27.19 ± 2.21 cm/s (motorboats 12 km/h), and 30.95 ± 2.51 cm/s (motorboats 18 km/h), which were comparable to values measured by Gabel et al. (2012). We assumed the bottom boundary layer was thinner than the height of the smallest mussel used (cf. Gabel et al. 2008), so our recordings represented the flow velocity acting on the inhalant and exhalant siphons of the mussels.

We obtained wave friction shear stress (τ_w) from U_w of the waves via the wave friction factor (f_w) with the method used by Soulsby (1997) as:

$$\tau_w = 0.5\rho f_w {U_w}^2$$

where ρ is the density of water and f_w reflects laminar or turbulent flow structure. We calculated the smooth wave friction factor (f_{ws}) as

$$f_{ws} = B{R_w}^{-N}$$

where coefficients $B = 2$ and $N = 0.5$ for Reynolds numbers (R_w) $\leq 5 \times 10^5$ (laminar flow) or $B = 0.045$ and $N = 0.175$ for $R_w > 5 \times 10^5$ (smooth turbulent flow). We calculated the rough wave friction (f_{wr}) as

$$f_{wr} = 1.39(A/z_0)^{-0.52}$$

where $A = U_wT/2\pi$, z_0 = DC50/12, and $R_w = U_wA/$kinematic viscosity of water. We took f_w as the maximum of f_{ws} and f_{wr}.

Data analyses

We $\sqrt[4]{x}$-transformed values of τ_w to obtain normal distribution of the data. Relationships between shear stress and duration and % shell closing of all mussel species were best fit by sigmoid regression models. We computed sigmoid regression models and coefficients by minimizing the sum of squared residuals with an iteratively weighted least-squares algorithm to estimate the parameters of the regression model. We used the sigmoid model curves to derive 2 critical levels in the behavioral response of the mussels to increasing shear stress. We defined predicted no-effect shear stress (PNES) as the shear stress at which individuals started closing their shells (10% shell closing). We defined predicted medium-effect shear stress (PMES) as the shear stress associated with 50% of the maximum shell closing duration (inflection point of the sigmoid function of shell closing duration vs τ_w).

We calculated the extent to which mussels were disturbed by boating activity by estimating % reduction of their filtration activity during the 60-s period after boat passage as

$$Remaining\ \ filtration\ activity\ \ [\%] = \int_{0s}^{60s} \frac{100 - intensity\ \ of\ \ shell\, closing\ [\%]}{60s}$$

where remaining filtration activity and intensity of shell closing are expressed as percentages. The vertical pattern of shear stress caused by boating and water depth was best fitted by polynomial cubic regression models. These models accounted for 2 peaks of shear stress, one near the surface that was generated by surface waves and one near maximum depth that was created by the water jet of the propeller from the boat's motor.

We tested for differences in the asymptotic maximum (AMAX), PMES, and PNES of the sigmoid regression models among mussel species as described in Motulsky (1998). We used PASW (version 17.0; SPSS, Chicago, Illinois) and SigmaPlot (version 11.0; Systat Software, Chicago, Illinois) to run all statistical regressions and plots.

Results

Water quality

The river section was heavily loaded with organic particles that consisted primarily of planktonic algae and suspended detritus. Organic seston ranged from 6.22 to 10.57 g/L over the study period (mean ± SE: 7.94 ± 0.43 g/L). At high water temperatures, microbial degradation of this organic load resulted in low minimum concentrations of DO during early morning hours (range: 2.22–7.78 mg/L, mean ± SE: 4.06 ± 0.45). For most of the study period, daily minimum DO concentrations were < 4 mg/L.

Wave impact on shell closing

All species responded to boat-induced shear stress by partially or fully closing their shells (Fig. 1). Percent shell closing at times without boat passages when mussels were filtering was estimated as 73 ± 5 (*U. tumidus*), 64 ± 5 (*U. pictorum*), 78 ± 6 (*A. anatina*), and 78 ± 13% (*D. polymorpha*). Duration and % shell closing gradually increased with higher shear stress produced by boat passages (Fig. 2A–H). All responses were best described by sigmoid regression models (Table 1). *Unio tumidus* had the shortest AMAX (~54 ± 8 s, *n* = 113; Figs 2B, 3A). This time was longer for *U. pictorum* and *D. polymorpha* (~77 ± 7 s, *n* = 123 and ~92 ± 12 s, *n* = 97, respectively; Figs 2C, D, 3A). *Anodonta anatina* had the longest AMAX (~187 ± 19 s, *n* = 128; Figs 2A, 3A). Maximum % shell closing was highest for *U. pictorum* (mean % shell closing = 89 ± 7%; Figs 2G, 3B), followed by similar values for *U. tumidus* (88 ± 5%; Figs 2F, 3B), and lower values for *D. polymorpha* (73 ± 5%; Figs 2H, 3B) and *A. anatina* (68 ± 7%; Figs 2E, 3B). Thus, *A. anatina* had the longest closing duration and lowest % shell closing.

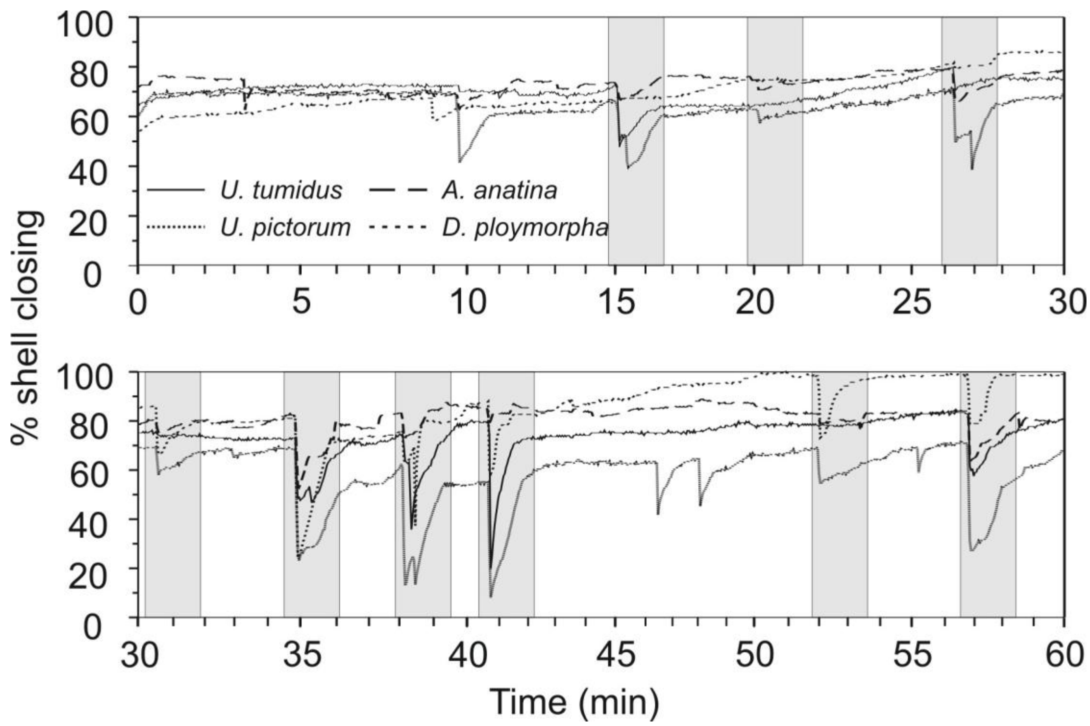

Fig. 1: Percent shell closing for 1 individual of the 4 mussel species *Anodonta anatina*, *Unio tumidus*, *Unio pictorum,* and *Dreissena polymorpha* over 1 h of investigation. Gray boxes indicate boat passages of different velocities and categories.

Unio tumidus had the lowest PNES (0.02 ± 0.029 N/m^2; Figs 2F, 3C), followed by *A. anatina* (0.05 ± 0.015 N/m^2; Figs 2E, 3C), *U. pictorum* (0.10 ± 0.025 N/m^2; Figs 2G, 3C), and *D. polymorpha* (0.13 ± 0.043 N/m^2; Figs 2H, 3C). *Unio tumidus* had the lowest PMES (0.21 ± 0.029 N/m^2; Figs 2B, 3D), followed by *U. pictorum* (0.27 ± 0.025 N/m^2; Fig. 2D), *D. polymorpha* (0.38 ± 0.043 N/m^2; Figs 2D, 3D), and *A. anatina* (0.43 ± 0.015 N/m^2, Figs 2A, 3D).

Table 1: Parameters for the best-fitting sigmoid regression models ($f = a/[1 + e^{-(x - x0)/b}]$) for the dependence of duration and % shell closing on shear stress. The parameters correspond to the asymptotic maximum AMAX (a), the slope (b) and the inflection point (x0) of the respective curves. For each model, the r² value and the corresponding significance levels (*P < 0.05, **P < 0.01, ***P < 0.001) are provided (duration model/degree model).

	a		**b**		**x0**	
	Duration	**Degree**	**Duration**	**Degree**	**Duration**	**Degree**
U. tumidus* (0.29/0.30***)**	54.40	88.39	0.12	0.20	0.68	0.84
U. pictorum* (0.52/0.68***)**	77.02	89.33	0.08	0.10	0.72	0.78
A. anatina* (0.58/0.50***)**	186.54	68.02	0.09	0.10	0.81	0.70
D. polymorpha* (0.54/0.67***)**	91.75	72.69	0.11	0.06	0.79	0.72

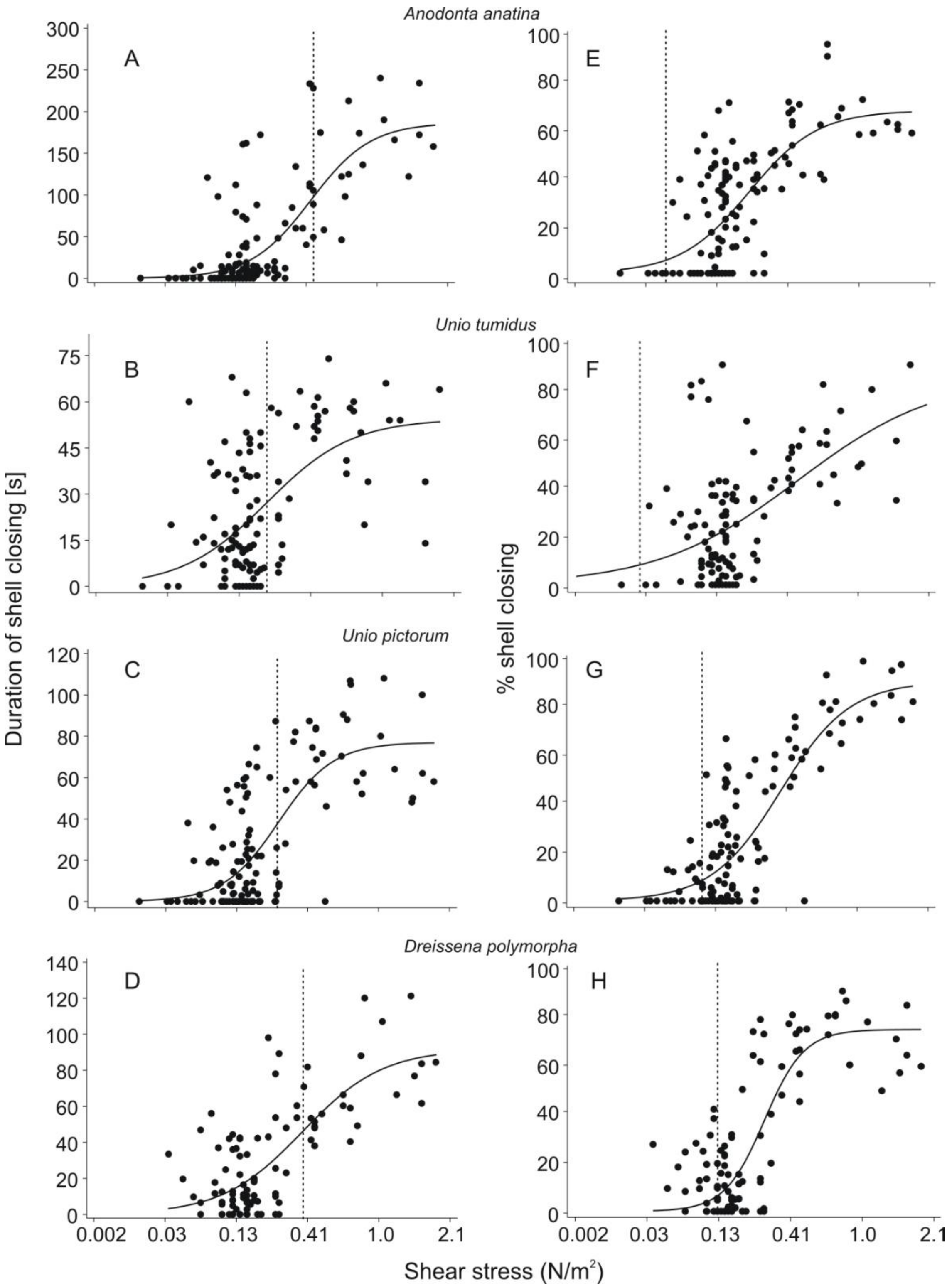

Fig. 2: Duration (A–D) and % shell closing (E–H) as a function of wave-induced shear stress of *Anodonta anatina* (A, E), *Unio tumidus* (B, F), *Unio pictorum* (C, G), and *Dreissena polymorpha* (D, H). Dashed vertical lines in A–D mark the predicted moderate effect shear stress levels (PMES), dashed vertical lines in E–H mark the predicted no-effect shear stress level (PNES).

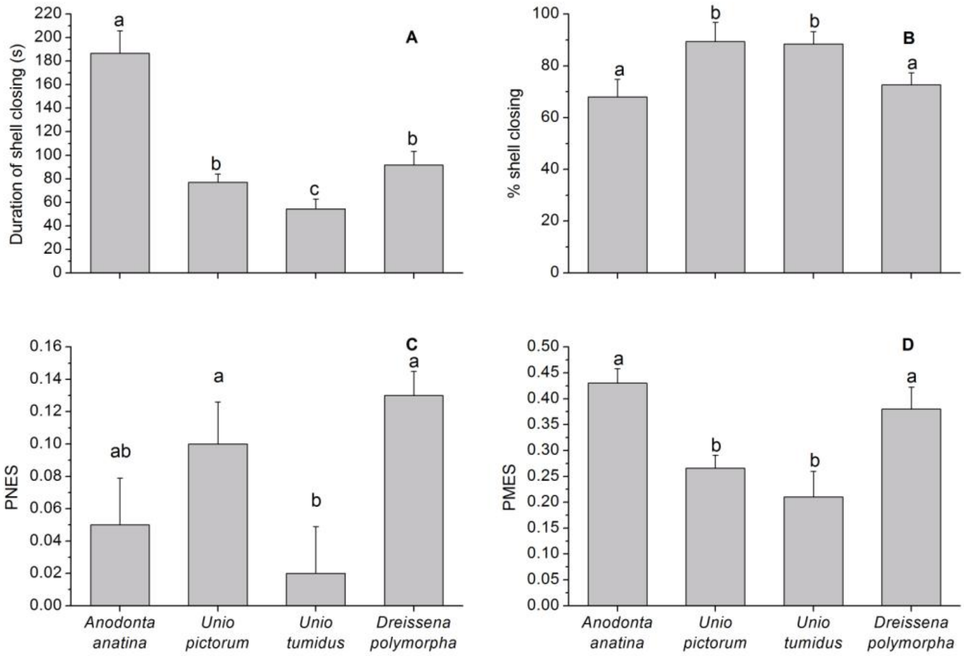

Fig. 3: Mean (+1 SE) duration (A) and % shell closing (B), predicted no-effect shear stress (PNES) (C), and predicted medium-effect shear stress (PMES) (D) for *Anodonta anatina*, *Unio tumidus*, *Unio pictorum,* and *Dreissena polymorpha*. Bars with different letters are significantly different.

Shear stress produced by various boat types and speed levels

Vertical patterns of shear stress varied according to boat type (Table 2). Wave disturbance generally decreased with increasing water depth. The vertical pattern was best described by linear regression models for muscle-driven boats and by cubic regression models for all motorized boat categories (Fig. 4A). The cubic regression was not significant for yachts because of the low number of replicates. Therefore, the maximum depth of boat-induced shear stress varied widely among boat categories. Boat-induced shear stress > PNES occurred at depths ranging from 17 cm (*A. anatina* disturbed by muscle-driven boats) to 270 cm (*U. tumidus* disturbed by yachts) (Table 3). Wave-induced shear stress in the shallow marginal zone more than doubled when motorboat speed increased from low (8 km/h) to medium (12 km/h) (Fig. 4B). A further increase in motorboat speed to 18 km/h did not produce a further increase in shear stress in the shallow marginal zone, but did produce an increase in deeper parts of the river channel because of the stronger action of the propeller jet (Fig. 4B). At deeper locations, depth of motorboat-induced shear stress > PNES increased 21 cm as speed increased from 12 to 18 km/h.

Table 2: Mean (± 1 SE) shear stress produced by various boat types and speeds at various water depths. Where SE could not be calculated (n < 3), calculated values from polynomial cubic regression models are provided with measured means in parentheses.

	Shear Stress [N/m²] ± SE				
	25 cm	**50 cm**	**75 cm**	**125 cm**	**180 cm**
Muscle driven boats	0.06 ± 0.010	0.02 ± 0.005	0.001 ± 0.001	0.00 ± 0.000	0.00 ± 0.000
Motorboats (8 km/h)	0.29 ± 0.030	0.09 ± 0.006	0.08 ± 0.007	0.14 ± 0.010	0.13 ± 0.005
Motorboats (10 km/h)	0.49 ± 0.020	0.18 ± 0.030	0.08 ± 0.020	0.20 (0.16)	0.21 (0.14)
Motorboats (12 km/h)	1.27 ± 0.060	0.49 ± 0.020	0.11 ± 0.004	0.19 ± 0.007	0.15 ± 0.005
Motorboats (18 km/h)	1.23 ± 0.070	0.46 ± 0.020	0.30 ± 0.010	0.19 ± 0.008	0.13 ± 0.004
Yachts (10 km/h)	0.89 (0.89)	0.16 ± 0.004	0.03 (0.09)	0.05 ± 0.030	0.15 ± 0.020
Motorized rowing/rafting boats (10 km/h)	0.20 (0.20)	0.12 ± 0.010	0.14 (0.14)	0.27 (0.27)	0.09 ± 0.001

Table 3: Maximum water depths at which shear stress above the predicted no-effect shear stress PNES was still detectable according to regression models for *Unio tumidus*, *Unio pictorum*, *Anodonta anatina*, and *Dreissena polymorpha* for various boat types and speeds.

	Maximum water depth [cm]			
	Unio tumidus	***Anodonta anatina***	***Unio pictorum***	***Dreissena polymorpha***
Muscle driven boats	57	17	n. d.	n. d.
Motorboats (8 km/h)	202	200	192	189
Motorboats (10 km/h)	187	185	176	172
Motorboats (12 km/h)	181	179	172	169
Motorboats (18 km/h)	191	190	187	185
Yachts (10 km/h)	270	266	258	253
Motorized rowing/rafting boats (10 km/h)	184	181	176	174

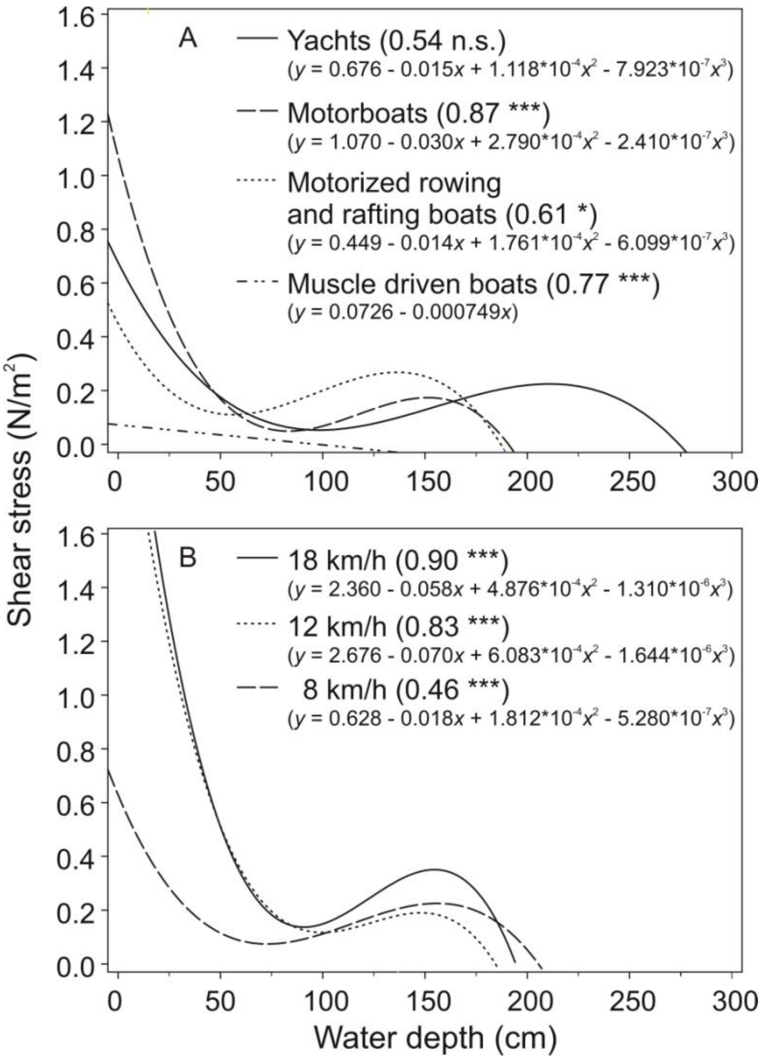

Fig. 4: Polynomial cubic regression models for shear stress measured at 5 water depths for different types of boats (speed of motorized boats = 10 km/h) (A) and for motorboats at 3 speeds (B). For muscle-driven boats, linear regression analysis was done between shear stress and water depth. n.s. = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** $p < 0.001$.

Spatial extension of disturbance

The depth zones with reduced mussel filtration activity gradually extended downward with increasing motorboat speed (Fig. 5A–D) in shallow marginal areas affected by surface waves and in the deeper zone affected by the propulsion jet of the boat motor. Open motorboats moving 8 km/h caused reductions of mussel filtration activity to a depth of 50 cm (Fig. 5A), and an increase in boat speed to 18 km/h extended this depth to 90 cm (Fig. 5D). At 18 km/h, the filtration activity of 3 of the 4 species (*A. anatina, U. pictorum,* and *D. polymorpha*) stopped completely to a depth of 30–50 cm. In deeper water, filtration by all species decreased to a mean of 70% and filtration activity of *A. anatina* decreased to 59% at a depth of ~150 cm when motorboat speed was 18 km/h (Fig. 5D). In contrast, the disturbance level in the intermediate depth zone was mostly stable across all levels of boat speed. *Unio tumidus* appeared to be least affected in the shallow marginal zone and minimally affected in deep water when motorboats passed by with a speed of 18 km/h. *Dreissena polymorpha* in deep water was least affected at all speeds except 18 km/h. *Unio tumidus* was affected most at intermediate water depths, whereas *D. polymorpha* was affected least at these depths.

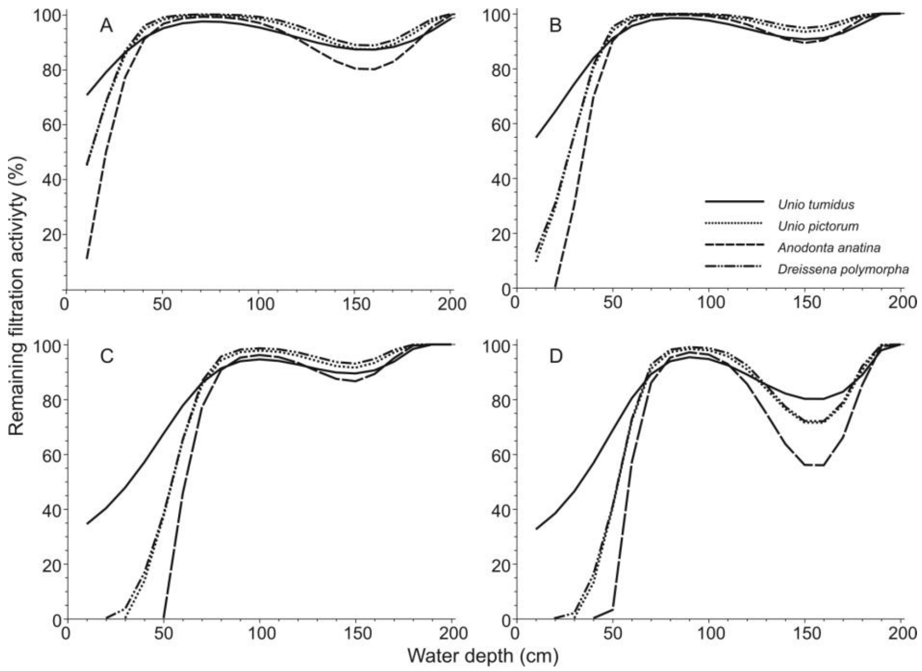

Fig. 5: Remaining filtration activity during the 1-min period after a boat passage vs water depth at locations of experimental *Unio tumidus*, *Unio pictorum*, *Anodonta anatina,* and *Dreissena polymorpha* disturbed by open motorboats navigating at 8 km/h (A), 10 km/h (B), 12 km/h (C), and 18 km/h (D).

Influence of boating on filtration activity

We estimated the community filtration rate of the mussel populations at the sampling site as 5.391 m^3/h based on estimated filtration rates (Pusch and Hoffmann 2000; Pusch et al. 2001) and population size (Graeber 2007). This estimate indicates that the undisturbed mussel community at our study reach could filter 79,507 m^3 of river water/d. Based on an average discharge rate of 3.13 m^3/s (270,432 m^3/d) in July 2010, this value corresponds to filtration of 29.3% of the water in this section of the river by mussels. If we apply the spatial disturbance of shear stress to these estimates, single passages of boats would cause a reduction of the community filtration activity by 0.02% (muscle-driven boats), 0.68% (motorboats), 0.45% (yachts), and 0.69% (motorized rafting and rowing boats) at the sampling site (if all motorized boats were navigating at a speed of 10 km/h). Assuming a mean of 35 boats (as counted by automatic cameras, of which 32% were muscle driven) operating during 9 h of daylight (as indicated by the average operation period of the nearby automatic water gates) during a typical weekend day in July, the reduction in filtration activity would decrease this daily filtration rate by 6.9%, which would reduce the percentage of total river water filtered by mussels to 27.3%.

The effect of boating on the filtration activity of mussels depended strongly on depth (Figs 4A, B, 5A–D), so we calculated the maximum number of motorboats/h that could be present at various water depths until filtration activity of mussels stopped completely (Fig. 6). If the river section is used by 24 to 93 motorboats/h operating at a speed of 10 km/h, filtration activity by mussels could cease entirely, depending on water depth.

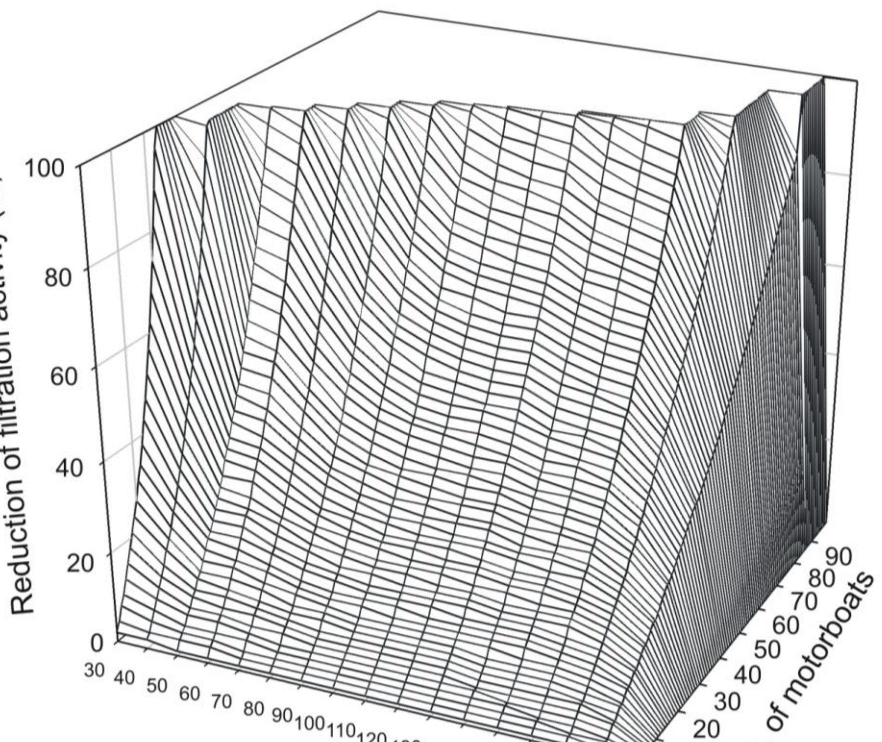

Fig. 6: Mean % reduction of filtration activity in a generalized marginal zone of a water body used for recreational boating during a 1-min period after close boat passage depending on water depth [cm] and the number of open motorboats/h cruising at 10 km/h. Means were calculated across the 4 species *Unio tumidus*, *Unio pictorum*, *Anodonta anatina,* and *Dreissena polymorpha*.

Discussion

Boat-induced increases in shear stress resulted in a highly predictable shell-closing response by mussels. Miller et al. (1999) used magnetic sensors to measure the effects of waves caused by the passage of large work boats or skiffs on mussels and detected shell-closing responses by the North American unionid mussel *Amblema plicata*. However, they did not detect a similar response to recreational crafts, even after multiple passages. Based on our results, we assume that the hydraulic effects of recreational boats did not extend to mussels in the depths of the Mississippi River.

In our study, boat passages caused abrupt shell closing that exceeded natural diurnal fluctuations in shell closing by several times. Freshwater mussels can show a diurnal shell-closing pattern with morning and evening peaks (Englund and Heino 1994; 1996). However, we did not observe such a pattern, possibly because an upstream lake provided a consistent supply of seston or because DO concentrations were low during the study period (Vero and Salanki 1969; Morton 1970; Lorenz and Pusch 2012). Shell-closing responses also can be caused by changes in particle size and concentration (Riisgard et al. 2011) and rapid large changes in water temperature (Salanki et al. 1974). Particle concentration was relatively constant during our study period, and water temperature changed only slightly between measurement days. Thus, we conclude that boating activity was the primary variable influencing filtration activity.

Sigmoid response curves to environmental stressors are widely observed (Calow and Forbes 2003). In our study, % shell closing of all 4 species followed a reproducible sigmoid dose–response curve, and Gabel et al. (2008) observed a similar sigmoid response curve of small benthic invertebrates to wave disturbance. Our sigmoid models explained slightly lower fractions than Gabel's of the total variance (indicated by the r^2 value), especially for *U. tumidus*. The relatively high scatter in response patterns in our study might have been caused by differences in burrowing depths among the unionid species studied. Individuals burrowed deeper in the sediment would experience less wave disturbance than others, and therefore, would show smaller shell-closing responses (discussed further below). Differences in shell position relative to the direction of wave disturbance also could contribute to high variance, especially in *U. tumidus* and *D. polymorpha*.

The sigmoid regression curves facilitated calculation of PMES and PNES thresholds. PMES thresholds discriminated better among species than did PNES thresholds and seem to be more appropriate for detecting differences among mussel species. In contrast, PNES thresholds facilitate identification of conservation requirements for endangered species.

Effect of hydraulic disturbance on freshwater mussel species

The smaller % shell closing and higher PMES for *A. anatina* and *D. polymorpha* compared to *U. tumidus* and *U. pictorum* (Fig. 4A, B) probably were caused by differences in the species' position relative to the sediment surface. Dreissenid mussels live as epifauna attached to hard substrates or to the shells of other mussels. Therefore, *D. polymorpha* might be better adapted to changes in flow or to hydraulic disturbances than endobenthic unionid mussel species, which burrow partially (*A. anatina*) or completely (*U. tumidus*) into the sediment (Mentzen 1926; Arter 1989) so that only the inhalant and exhalant siphons are exposed to the flow occurring near the sediment surface. The partially exposed *A. anatina* had the longest AMAX in our study and, therefore, appears to be less adapted than *D. polymorpha* to hydraulic disturbance. The strong adaptation of the successful invasive species *D. polymorpha* to hydraulic disturbance could be viewed as a preadaptation acquired in its original habitat that suited it for existence in new habitats (Gabel et al. 2011a).

Boating impacts on ecosystem services

Freshwater mussels contribute significantly to the self-purification of surface waters, an extremely important ecosystem service (Everard and Powell 2002; Howard and Cuffey 2006). Mussels filter phytoplankton and detrital organic matter from the water column. In the river section we studied, this benthic–pelagic coupling could lead to removal of most of the phytoplankton in the water column (Welker and Walz 1998). This action improves the ecological status of a water body and increases its utility for other purposes, including recreation and boating (Bockstael et al. 1989). In water bodies that are shallower than the Krumme Spree, boating activities cause significant resuspension of sediments (Beachler and Hill 2003), which can have severe negative effects on mussel filtration activity. The maximum depth of water bodies where outboard motorboats caused resuspension of coarse sandbed material was 1.8 m (Beachler and Hill 2003), which equals the depth measured in our study. However, current boating activity in the Krumme Spree reduces the filtration activity of freshwater mussels by only 6.9% per day, so a severe effect on the self-purification of this river section is not expected.

Management of recreational boating activities

Our modeling approach allows identification of mitigation strategies that might depend on the depth of a given water body or the depth distribution of mussels. Such a model could be used to predict the minimum distance of boat traffic from the shore or maximum boating speed to minimize impacts. We recommend implementation of special restrictions, such as slow no-wake speeds, during times of low flow and low water levels to ensure undiminished ecosystem services. Furthermore, adverse effects of boating might be effectively prevented by restricting access to ecologically vulnerable zones of water bodies to certain vessel types, such as nonmotorized or electric-motor boats, which run at lower speed and often have hulls designed to generate fewer waves. Such restrictions might help protect populations of protected species, water quality, and the resilience of the water body, and thus, enhance its sustainable utility.

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Higher filtration activity of invasive versus native mussel species under wave disturbance conditions

Stefan Lorenz and Martin T. Pusch

The final publication is available at www.springerlink.com

Abstract

Self-purification is one of the most important ecosystem functions of rivers. Multiple human activities regularly impact this ecosystem service, consequently altering river morphology, hydrology, and the composition of biotic assemblages that contribute to self-purification. However, little quantitative information is available about the importance of such impacts. Hence, we tested how invasive mussel species contribute to self-purification under disturbed riverine conditions. In laboratory experiments, invasive mussel species equipped with magnetic sensors that recorded filtration activity were exposed to artificial waves of varying intensity that simulated the hydraulic effects of inland navigation. Shell gape behavior was compared with results obtained for native species in a previous study. Native species were more susceptible to wave disturbance than invasive species, because the threshold values for initiating shell closure in native species were relatively low in combination with the highest duration (*Anodonta anatina*) or the highest degree (*Unio tumidus* and *Unio pictorum*) of shell closing. We demonstrated that the invasive species *Dreissena bugensis* and *Corbicula fluminea* continue filtering during wave impact, whereas no significant difference was found for *Dreissena polymorpha* compared to native species based on the studied susceptibility parameters. Thus, *D. bugensis* and *C. fluminea* appear to be pre-adapted to hydraulic or morphological disturbance, and may compensate against other losses regarding this important ecosystem function in rivers that are intensively used for inland navigation. However, as the dominance of invasive species in river systems may disrupt natural food webs, this compensation of filter-feeding activity may be accompanied by the loss of other ecosystem functions.

Introduction

Human civilization depends, to a certain extent, on ecosystem services provided by rivers; however, these services are often overused (Costanza et al. 1997; Everard and Powell 2002; Kareiva et al. 2007). Among other functions, many river systems worldwide are intensively used for inland navigation and boating activities (Food and Agriculture Organization of the United Nations 2008). Worldwide, 671 886 km of waterways exist for inland navigation (Central Intelligence Agency 2011), many of which use natural rivers and lakes. As many inland waterways are connected to other river systems by canals, inland navigation facilitates or accelerates the spread of invasive invertebrate species to new biogeographic regions. Thereby, species may be actively translocated as a result of being attached to the hull of boats or within the ballast water, or may spread independently along newly built waterways, as documented for the Danube-Main Canal (Leuven et al. 2009; Mills et al. 1993; Pusch et al. 2009). As a consequence, invasive species arriving from various biogeographical regions meet habitat conditions in other river systems that have been modified by humans in many aspects (Tockner et al. 2011; Tockner et al. 2010). This situation often enables non-native species to successfully establish novel ecological niches, and build up large populations (Darrigran 2002). As rivers subjected to multiple human pressures only offer suboptimal habitat conditions to native species, invasive species often replace native species (Byers 2002). Thereby, some invasive species may also benefit from pre-adaptations acquired from their original natural habitats, which result in gaining a superior competitive position relative to native species (Correa and Gross 2008; Gabel et al. 2011a).

Given such profound alterations in physical and biotic structure, there is also a high probability of changes in key ecosystem services, such as self-purification capacity, which includes the removal of organic matter from the water column (Pusch and Hoffmann 2000; Tockner et al. 2011). Recent publications have demonstrated that waves induced by navigation and boating may cause significant hydraulic disturbances to benthic invertebrates and fish (Bishop and Chapman 2004; Gabel et al. 2008; Gabel et al. 2011b), which may also affect the filtration activity of mussel populations (Lorenz et al. 2012; Payne et al. 1999; Widdows et al. 1979). The reduction in mussel filtration rates under wave disturbance may be caused by the resuspension of disturbed inorganic sediment (Moore 1977) or by hydraulic wave pulses (Lorenz et al. 2012).

As freshwater mussels are primary consumers of phytoplankton and seston in aquatic habitats, this group supplies significant food resources to the benthic food web (Howard and Cuffey 2006), in addition to significantly contributing to the self-purification of running waters. Thus, mussels may significantly improve water quality, particularly in eutrophicated surface waters (Welker and Walz 1998). Consequently, anthropogenic impacts on the filtration activity of freshwater mussels are likely to affect the productivity of the benthic food web and decrease ecosystem resilience, in addition to increasing the eutrophication of aquatic ecosystems.

However, in case river systems have been colonized by invasive mussel species, the filtration rate of the benthic community may be even increased, as their filtration capacities and rates are typically higher compared to native species (Atkinson et al. 2011; Leff et al. 1990; Weitere et al. 2008). Aside from the greater capacity to compete for food (Strayer and Smith 1996), invasive species may exhibit other biological characteristics that better fit the habitat conditions of altered river systems, such as substrate preference (as for *Dreissena* spp), temperature preference, or mechanical resistance (as for *Corbicula* spp.) (Tockner et al. 2011). However, there is limited information clarifying which of these multiple modes of anthropogenic disturbance is the most decisive for a given species, or how these modes favor specific invasive species (e.g. Gabel et al. 2011a).

Hence, we conducted a laboratory study to test whether wave disturbance, which represents an anthropogenic disturbance typical to large rivers, affects the filtration activity of three invasive mussel species. The results were compared against similar data obtained from a previous study on native mussel species (Lorenz et al. 2012). We hypothesized that invasive mussels exhibit pre-adaptations to hydraulic disturbance, and are more likely to perform better under wave disturbance than native mussel species. This hypothesis would be supported by obtaining a consistent difference for both wave sensitivity and shell closing behavior between native and invasive species. We predicted that invasive mussel species are less susceptible to ship-induced waves, and that filtration activity is higher under disturbed conditions.

Material & Methods

Experimental settings

We obtained 15 individuals of three invasive mussel species in Germany; specifically (1) the Asian clam *Corbicula fluminea* MÜLLER 1774 from Rhine River, (2) the quagga mussel *Dreissena bugensis* ANDRUSOV 1897 from Main River, and (3) the zebra mussel *Dreissena polymorpha* PALLAS 1771 from the Spree River. The mussels were acclimatized in separate aerated laboratory aquaria to a water temperature of 18 °C. After acclimatization, five individuals of the two *Dreissena* species were placed on ceramic tiles inside the respective aquaria, and were kept for another two weeks at 18 °C in a climate chamber. After all individuals used byssus threads to attach to the tiles, each mussel was equipped with a magnetic sensor (radiometric linear Hall-effect sensor A1321, Allegro Microsystems Inc., Worcester, MA, USA) on one shell, and a disc magnet (magnet grade N48, diameter 2 mm, thickness 2 mm) on the other shell. This equipment was used to record shell gape as a parameter of filtration activity (Hopkins 1933). Subsequently, one tile with five individuals was placed on the sediment inside an experimental wave tank that had three replicate flumes (Fig. 7). For *C. fluminea*, five magnet and sensor equipped individuals were transferred to each replicate section, and individuals were allowed to burrow into the sediment before the experiment. The wave tank was filled with aerated unchlorinated tap water, with a similar temperature of 18 °C. The sediment bed consisted of a 10 cm layer of silica sand, with a grain size of 0.2–0.63 mm. All three species were kept inside this wave tank for an additional 24 h. During all time in laboratory aquaria, individuals were fed with dried *Spirulina sp.* algae.

After all individuals exhibited filtration activity, waves of different intensity (5 cm s^{-1}, 8 cm s^{-1}, 11 cm s^{-1}, 14 cm s^{-1}, 17 cm s^{-1}, 21 cm s^{-1}, and 24 cm s^{-1}) were produced with a wave paddle driven by a car windshield wiper motor in random order to avoid individual mussels becoming acclimated to the waves. Each type of wave intensity was repeated three times. Data were recorded and processed using own software written in LabVIEW (National Instruments, Germany). Shell gape was calibrated against voltage (mV), and the measured voltage data (x) was then converted into gape opening (in mm) by using the following linear inverse (x) polynomial equation (Lorenz et al. 2012):

$$\text{Distance} = a + \frac{b}{x} + \frac{c}{x^2} + \frac{d}{x^3} + \frac{e}{x^4} + \frac{f}{x^5}$$

Afterwards, data were converted into relative values (percentage of maximum gape opening).

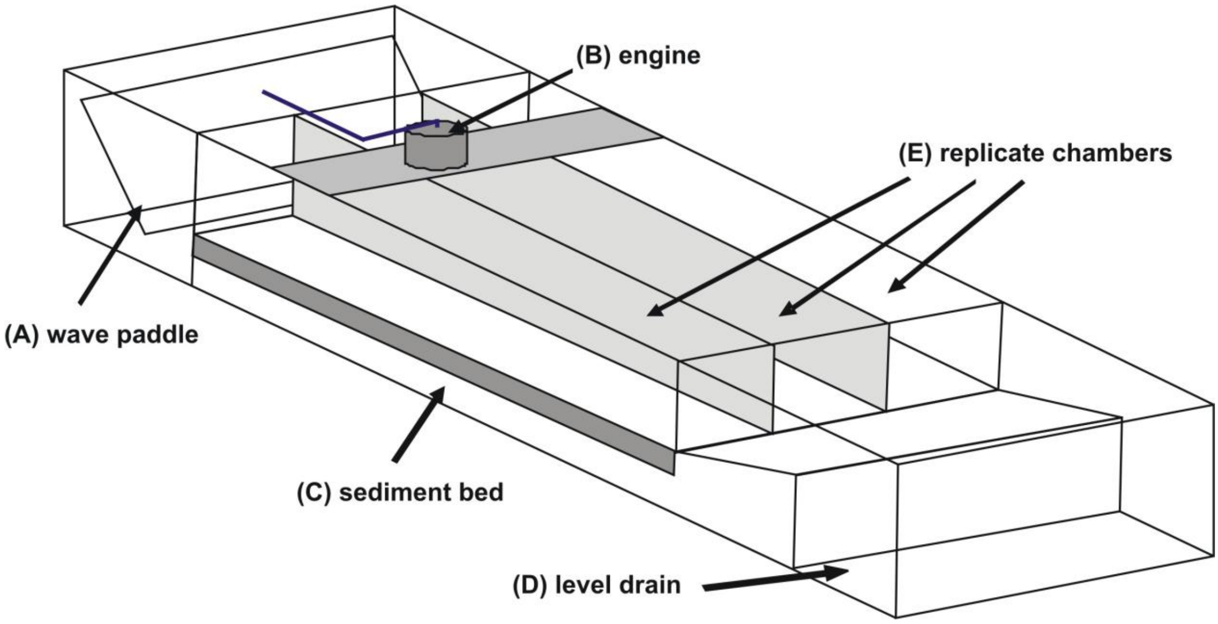

Fig. 7: Experimental wave tank that was used to produce waves of different intensity. The tank consisted of (A) a wave paddle, (B) an engine, (C) a sediment bed, (D) a level drain, and (E) three replicate chambers.

Calculation of shear stress

The bottom flow velocity that was associated with experimental waves was recorded using an Acoustic Doppler Velocimeter (ADV, Micro ADV 16 MHz, Sontek, San Diego, CA, USA), at a rate of 50 Hz. The ADV was placed in the middle section of each wave tank flume, using the same technical set-up as in previous experiments (Gabel et al. 2011a). The three flumes of the wave tank showed no significant differences in orbital velocities (Gabel et al. 2011a). The sampling volume of the ADV probe head was adjusted to 1 cm above the sediment bed. As ADV measurements in clear tap water tend to be subject to high backscatter, one drop of *Lycopodium clavatum* spore suspension was added directly over the probe head before creating each wave to enhance particle concentration, and hence reduce backscatter. Using the bottom orbital velocity U_w and the wave friction factor f_w, wave friction shear stress τ_w was calculated for each wave that was produced, as:

$$\tau_w = \frac{1}{2} \times \rho \times f_w \times U_w^2$$

(see Soulsby (1997) for detailed description).

Data analysis

The recorded shear stress values were double-square-root transformed to obtain a normal distribution, while the other data were left untransformed. Sigmoid regression models of the type

$$f = \frac{a}{1 + e^{\frac{-(x - x0)}{b}}}$$

were calculated for the relationship between shear stress (x) and the duration of shell closure and the degree of shell closure (percent reduction of maximum shell gape) as functions of x. This type of sigmoid regression model explained the highest proportion of mussel response pattern with rising shear stress levels. In the relationships of shear stress versus shell closure duration, the inflection point of the curves (x_0) was determined and re-transformed to an unpotentiated scale. The inflection point x_0 was defined as a threshold value separating tolerable and severe impacts on filtration activity, representing a predicted moderate value for the effect of shear stress, PMES (Lorenz et al. 2012). Accordingly, shear stress levels above this threshold produced less shell gape in all experimental specimens, whereas some specimen were not affected below this threshold. The starting point of any shell closing behavior was defined as the value where 10% of the maximum closing intensity is reached (Lorenz et al. 2012). The value was re-transformed to an unpotentiated scale, and considered as the predicted no-effect shear stress level (PNES).

Sigmoid regression models obtained through these laboratory experiments were statistically compared with field observation data obtained from similar experiments on three native unionid mussel species (Lorenz et al. 2012). We tested differences in the parameter ‘a’ (asymptotic maximum), PMES, and PNES between invasive and native mussel species, as well as for the three invasive species as described in Motulsky (1998). Possible differences arising from field versus laboratory approaches were tested for parameters a, b, and x_0 for *D. polymorpha*, as this species was subjected to both field and laboratory studies. All statistical regressions and plots were performed using PASW (version 17.0, SPSS Inc., Chicago, IL, U.S.A.) and SigmaPlot (version 11.0, Systat Software Inc., Chicago, IL, USA).

Results

Shell closing duration and closing degree

According to the sigmoid regression analysis (Table 4), the longest average closing duration was shown by *D. Polymorpha* (a = 92 s), followed by *D. bugensis* (87 s) and *C. fluminea* (20 s) (Fig. 8). Average closing degree after wave disturbance was strongest in *D. polymorpha* (68%), followed by *C. fluminea* (40%) and *D. bugensis* (39%) (Fig. 8). The statistical differences among these three species are shown in Fig. 10.

Table 4: Parameters of sigmoid regressions [f = a/(1+exp(-(x-x0)/b))] between the duration of shell closing [s] and shear stress [N m^{-2}], and the degree of shell closing [%] and shear stress [N m^{-2}]. For each test, the r^2 value and the corresponding significance levels (*P < 0.05; **P < 0.01; ***P < 0.001) are provided (Duration/Degree).

	a		**b**		**x0**	
	Duration	**Degree**	**Duration**	**Degree**	**Duration**	**Degree**
*Dreissena polymorpha (0.31***/0.59***)*	91.65	67.54	0.11	0.04	0.73	0.77
*Dreissena bugensis (0.74***/0.59***)*	86.77	38.84	0.03	0.10	0.83	0.74
*Corbicula fluminea (0.69***/0.65***)*	19.86	40.18	0.06	0.05	0.61	0.57

Threshold values for inhibition of filtration activity

Predicted moderate effect shear stress (PMES) values were higher in *D. bugensis* (0.47 N m^{-2}) and *D. polymorpha* (0.38 N m^{-2}) compared to *C. fluminea* (0.14 N m^{-2}) (Fig. 10). Similarly, the predicted no-effect shear stress (PNES) value was higher in *D. bugensis* (0.24 N m^{-2}) compared to *D. polymorpha* (0.13 N m^{-2}) and *C. fluminea* (0.04 N m^{-2}) (Fig. 10). The statistical differences among these three species are shown in Fig. 10.

Comparison of field and laboratory studies

The shell closing behavior of *D. polymorpha* followed similar sigmoidal patterns under both field and laboratory conditions (Fig. 9). Respective regressions did not significantly differ between field or laboratory data for the relationship of shear stress and shell closing duration (unpaired t-test, df = 114, p = 0.99 (a), p = 0.85 (b), p = 0.92 (x0)), or the relationship of shear stress and shell closing degree (unpaired t-test, df = 112, p = 0.45 (a), p = 0.94 (b), p = 0.81 (x0)).

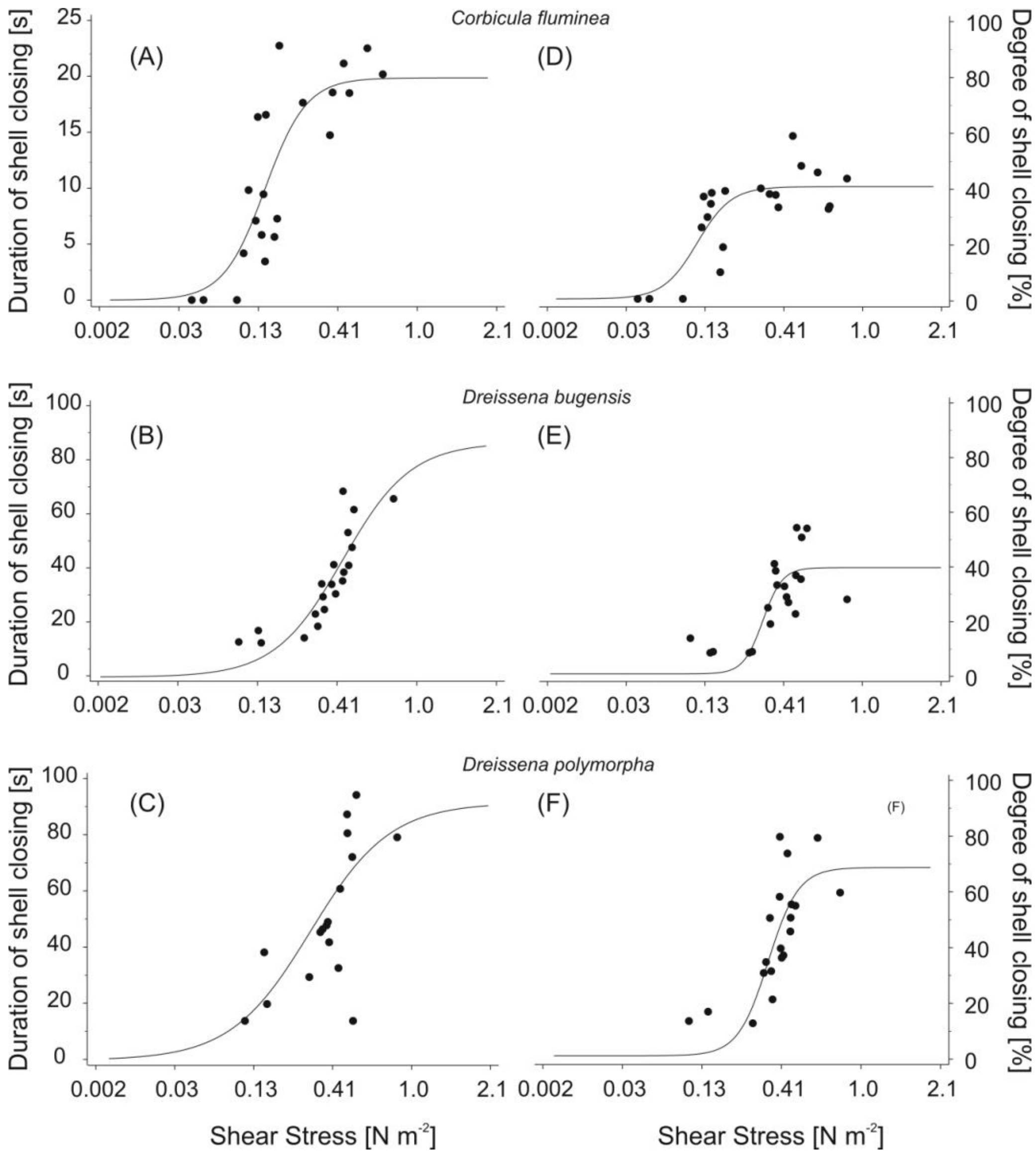

Fig. 8: Duration (A–C) and degree (D–F) of shell closing as functions of shear stress [N m^{-2}] caused by experimental waves of different intensity in the three mussel species *Corbicula fluminea*, *Dreissena bugensis,* and *Dreissena polymorpha*.

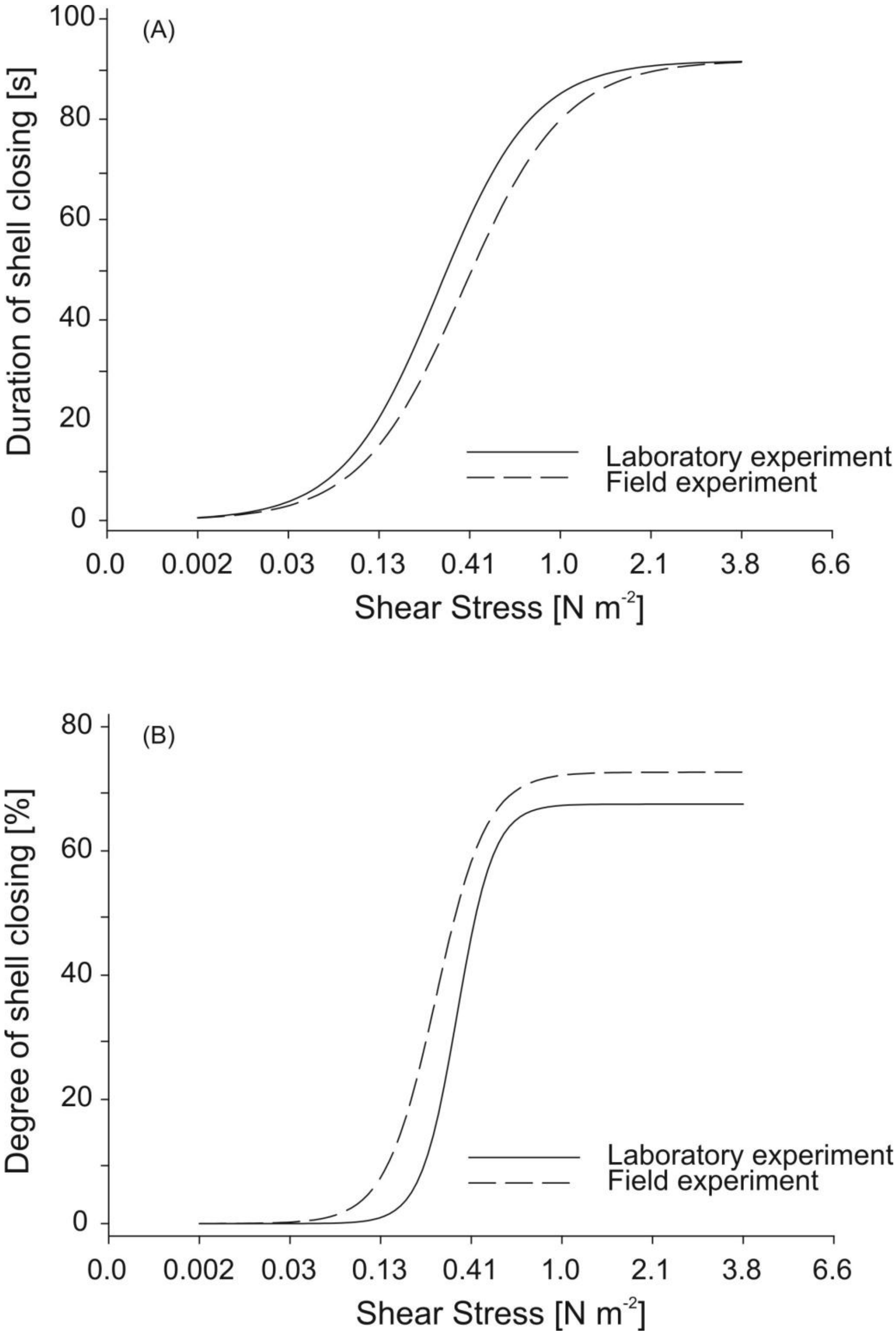

Fig. 9: (A) Duration (in seconds) of shell closing and (B) degree (in percentage) of shell closing as functions of shear stress caused by experimental waves of different intensity in *Dreissena polymorpha* in field (dashed lines, n = 105) and laboratory (solid lines, n = 21) experiments.

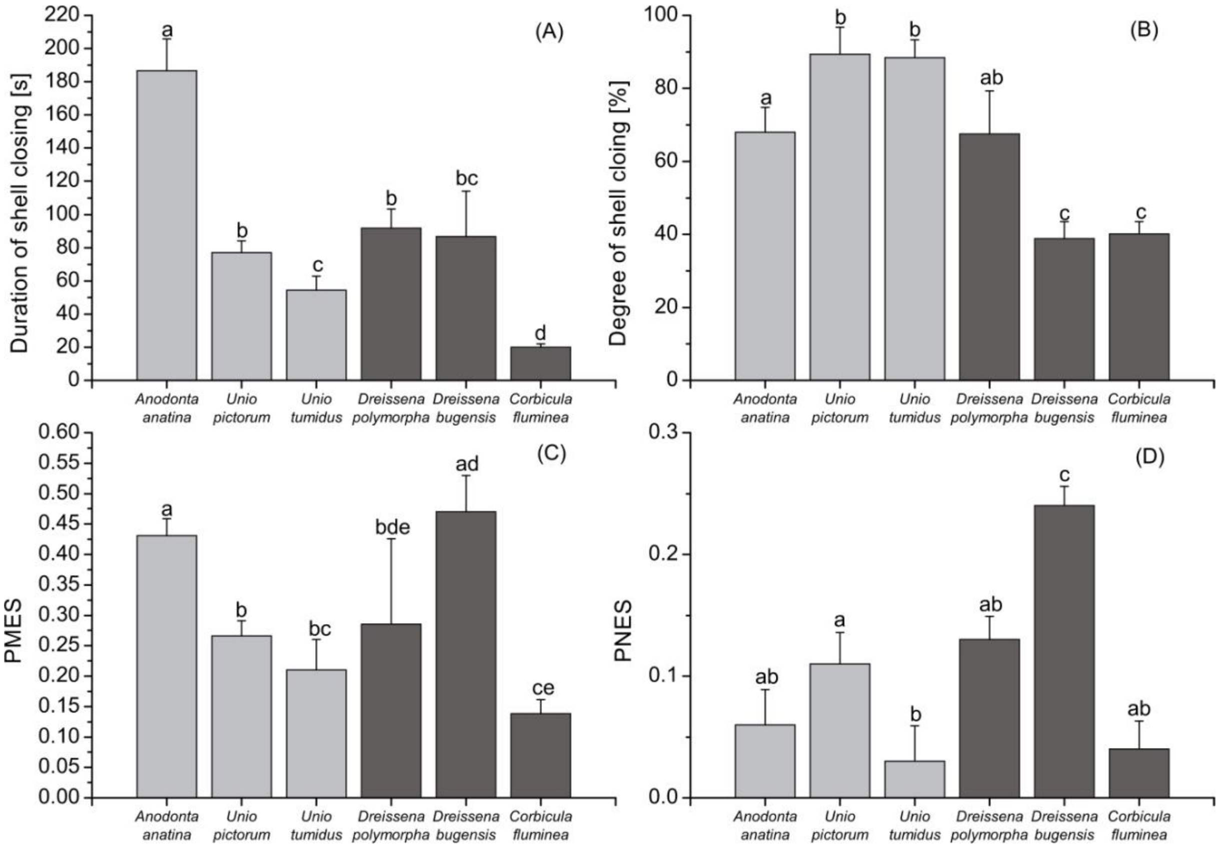

Fig. 10: (A) Duration (in seconds) and (B) degree (in percentage) of shell closing as functions of shear stress [N m-²], and respective (C) PMES and (D) PNES threshold values for the native (three left species) and invasive (three right species) mussel species that were studied. The results for the native species were obtained from Lorenz et al. (2012). Different letters indicate significant statistical differences.

Comparison of native and invasive species

To identify potential differences in the shell closing behavior of native versus invasive mussel species, the results of variables representing susceptibility to wave stress from former field experiments of native mussel species were combined with the results of the current laboratory study (Fig. 10). Closing duration and closing degree of *C. fluminea* was significantly lower compared to the native species *A. anatina*, *U. tumidus,* and *U. pictorum*. Closing duration of *D. polymorpha* did not significantly deviate from that of *U. pictorum,* and its closing degree did not significantly deviate from any of the three native species. Closing duration of *D. bugensis* was significantly lower compared to *A. anatina*, but was similar to that of *U. tumidus* and *U. pictorum*. Closing degree of *D. bugensis* was lower compared to *A. anatina*, *U. tumidus*, and *U. pictorum*.

PMES values of *D. bugensis, D. polymorpha,* and *C. fluminea* differed significantly from each of the three native species. PMES values were significantly lower in *C. fluminea* than in *A. anatina* and *U. pictorum*, significantly higher in *D. bugensis* than in *U. pictorum* and *U. tumidus*, and significantly lower in *D. polymorpha* than in *A. anatina*. The PNES value of *D. bugensis* was higher compared to the three native species, while the PNES values of *D. polymorpha* and *C. fluminea* did not differ significantly from native species.

In summary, the native species showed relatively low PNES values in combination with either the highest duration of shell closing (*A. anatina*) or the highest degree of shell closing (*U. tumidus* and *U. pictorum*); thus, native species were more susceptible to wave disturbance than invasive species. To demonstrate how this varying susceptibility to wave action influenced filtration, the remaining filtration activity was calculated for each mussel species according to equation 2 from Lorenz et al. (2012). By assuming passages of single motorboats at a speed of 18 km/h, mussels living at mean water depth of 1.5 m of the Krumme Spree river section (where the results for the native species were obtained) would show a remaining filtration activity of 80% (*U. tumidus*), 71% (*U. pictorum*), and 56% (*A. anatina*) for native species, while remaining filtration activities of invasive species would be 72% (*D. polymorpha*), 88% (*C. fluminea*), and 98% (*D. bugensis*) compared to undisturbed conditions. In comparison, this means an average reduction in filtration activity of 31% for the studied native species, but just 14% for invasive species.

Discussion

To date, few studies have attempted to link the success of invasive species in newly colonized river systems to the specific habitat conditions that are available, which might reflect the respective biological or ecological traits of particular invasive species (Bij de Vaate et al. 2002; Devin and Beisel 2007; Ricciardi and Rasmussen 1998). In river systems subjected to strong or multiple human pressures, habitat conditions become suboptimal for native species, consequently favoring the establishment of invasive species. Thereby, the successful establishment of invasive species is not only governed by physical habitat conditions, but also by interspecific interactions. Invasive species have been shown to cause a decline in the abundance of native species, such as through competition for food sources

(Strayer and Smith 1996). This exploitative competition may even occur among invasive species, as exemplified by the spread of the quagga mussel *D. bugensis,* which caused a decline in the abundance of *D. polymorpha* (Zhulidov et al. 2010).

Our results indicate that, besides alterations to river hydrology, temperature, water quality, and channel morphology (Rahel and Olden 2008), higher filtration activity under wave exposure provides an additional mechanism to explain the success of invasive species in fresh water habitats used for inland navigation. As invasive invertebrates, such as mussels, in freshwater habitats are mainly spread by ships via navigation channels (Leuven et al. 2009), the benefits of transportation to novel habitats might be twofold. First, their spread is accelerated by the circulation of barges (Byers 2002), and second, they are less susceptible to strong exposure from disturbance by ship-induced waves.

We demonstrated that *D. bugensis* and *C. fluminea* continue to filtrate under wave impacts, which provides a crucial competitive advantage in fresh waters used intensively for navigation. Although both species exhibited similar degrees of shell closing at higher shear stress levels, they exhibited different sensitivity toward this stressor. For instance, *D. bugensis* was the most stress-resistant species, with a minimal degree of shell closing, and maximal PNES and PMES values. Hence, *D. bugensis* seems to be adapted to perform significant filtration activity even in habitats with high hydraulic disturbance.

In comparison, while *C. fluminea* also showed a minimal degree of shell closing, which was even accompanied by a minimal duration of shell closing, this species exhibited minimal PMES and second minimal PNES values among the studied species. This 'opportunistic' pattern to exhibit a minimally sensitive response to hydraulic disturbance may represent an adaptation to life in hydraulically sheltered interstitial spaces within the sediments of fast-flowing rivers (McMahon 1999). In such habitats, disturbance may be mainly produced by relatively coarse particles transported along the river bottom, which pass by quickly. The ingestion of such particles may therefore be avoided by mussels, even by the short and incomplete closure of shells.

During the experiments, we observed that *C. fluminea* individuals exhibited burrowing behavior in response to wave stress, which is a behavioral pattern that has not been previously observed in burrowing unionid species (Lorenz et al. 2012). Thereby, individuals escaped wave disturbances by burrowing into the sediment immediately after the passage of the first wave, leaving just their inhalant and exhalant siphons protruding from the sediment. In other cases, the mussels burrowed completely, without the siphon protruding but the shells remained open. This behavior supports the assumption that filter feeding may not consist the only foraging strategy for *C. fluminea*, as additional pedal feeding has been described for this species (Thorp and Covich 2001).

In contrast, *D. polymorpha* did not differ significantly to native species in any of the studied susceptibility parameters. More specifically, none of the average susceptibility values observed in *D. polymorpha* differed significantly from those observed in *U. pictorum.* Thus, the colonization success of this species (Aldridge et al. 2004; Johnson and Carlton 1996; Johnson and Padilla 1996) cannot be explained (at least for Europe) by invasive species exhibiting lower susceptibility to wave disturbance compared to native species. The underlying mechanism that causes low susceptibility may be based on a pre-adaptation that some invasive species may have acquired through evolution in their original biogeographical region (Correa and Gross 2008), or may reflect adaptive changes in their behavior in newly colonized habitats (Alford et al. 2009), or a combination of both.

Human impacts on aquatic ecosystems, including wave disturbance by navigation, often result in dramatic and well-known reductions in population size or species richness (Tockner et al. 2010), whereas the effects on key ecosystem services remain poorly documented (Chapin et al. 2000). Accordingly, the ecological assessment of fresh water habitats is mostly based on the composition of biotic assemblages, while the status of ecosystem functioning is rarely assessed. The important self-purification mechanism in rivers that is provided by the transport of organic matter from the water column to the benthic food web by the filtration activity of freshwater mussels (Howard and Cuffey 2006; Pusch et al. 2001) is a major process contributing to high water quality (Tockner et al. 2011). Consequently, a reduction in the filtration activity of freshwater mussels by ship waves will result in the loss of the capacity for the self-purification of surface waters. The lower susceptibility of invasive mussel species to wave disturbance indicates that the detrimental effects of ship waves may be compensated by the presence of less susceptible invasive mussel species within this community. As climate change will result in lower minimum water levels of many surface waters, the impact of boat generated waves on mussels is likely to increase (Lorenz et al. 2012). In parallel, the invasion of non-native mussel species, which are also favored by climate change (Rahel and Olden 2008) may ensure that an important component of self-purification in freshwater ecosystems is retained, despite the negative effects of climate change and high boating activities. Accordingly, the ecological carrying capacity of inland waters for boating, as calculated by Lorenz and Pusch (2012), might also benefit from the introduction of mussel species that are less susceptible to the impacts of ship-induced waves. However, as the dominance of invasive species in river systems may disrupt natural food webs, such compensation of filter-feeding activity may be accompanied by important losses in other ecosystem functions, which require identification.

Acknowledgements

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Estimating the recreational carrying capacity of a lowland river section

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Abstract

Recreational boating represents a major human use of inland waters in many regions. However, boating tourism may affect the ecological integrity of surface waters in multiple ways. In particular, surface waves produced by boating may disturb freshwater invertebrates, such as interrupting the filtration activity of benthic mussels. As mussels may significantly contribute to self-purification, disturbance may have crucial impacts on water quality, and thus on water tourism. In this paper we calculate the carrying capacity of a river section for sustainable boating tourism based on the preservation of water quality. This approach is complemented by spatial and social approaches for carrying capacity estimates. The ecological carrying capacity significantly decreases with lower water levels during summer. Hence, the analysis of variables that influence the river's carrying capacity allows the formation of recommendations for management measures that integrate social, touristic and ecological aspects.

Introduction

Rivers and lakes constitute some of the most valuable natural resources for tourism, as they provide opportunities for multiple touristic activities, like swimming, fishing, sailing or boating (Postel and Carpenter 1997). The multiple ways to use the natural resources of lakes and rivers allow the establishment of a broad array of secondary business segments, such as boat rentals, camping grounds, restaurants and hotels (e.g. Colorado Board of State Parks and Outdoor Recreation 2011).

Growing urban development of the shores of inland waters is expected to produce increasing detrimental effects on surface water systems, such as pollution, physical alteration of shoreline areas, and disturbance of aquatic flora and fauna (Gabel et al. 2008). To avoid devaluating major lake resources, the detrimental effects of water-based tourism must be mitigated and regulated. Hence, the carrying capacity of the surface water body under use must be estimated to ensure the sustainable operation of water-related tourism businesses.

The carrying capacity concept was first developed in the field of population ecology and wildlife management, where it was defined as the number of individuals of one species that can be maintained within a given habitat area (Wagar 1964). This concept was also applied to the management of visitor numbers to national parks and wild lands. By applying the concept of carrying capacity to humans, two additional aspects emerged. First, visitors affect the environmental resources of the area they use in a more variable way (as previously hypothesized in wildlife management); and second, visitors affect their own perception of the environment at the same time. Furthermore, crowding or social conflicts also influence a visitor's personal experience and recreational effect (Wagar 1964).

Previous efforts to estimate the carrying capacity of lakes for water-based tourism accounted for these aspects by e.g. estimating the minimum required lake surface area needed for the safe operation of a single boat type (e.g. ERM Inc. 2004; Jaakson et al. 1990; Rajan et al. 2011). The size of this area has mostly been determined based on the social perception of boaters recorded through interviews and surveys. This specification varies greatly between low and high horse power boats, as well as for muscle driven vessels (i.e. kayaks, canoes). An approach to determine the touristic carrying capacity of rivers has been developed, which is based on boat counts and user surveys (Rebellato 2007). However, existing estimates of the touristic carrying capacity of lakes have primarily focused on the human component, thus neglecting the potential ecological impacts of tourism. For a more comprehensive approach, four different components have been recommended to estimate the recreational carrying capacity (O'Reilly 1986; Shelby and Heberlein 1986). These comprise ecological, spatial, economic as well as social aspects. Among these, environmental aspects deserve special attention, as these variables are often regularly monitored but may exhibit considerable variation depending on e.g. season and river discharge.

While the impacts of human use of inland waters are generally well known (Goudie 2006), less is understood about the specific effects arising from recreational activities. Motorized boating activities were found to consist a major source of noise and unburned fuel emissions into surface waters, while the amount of these inputs varies greatly among the engine types (see e.g. Jüttner et al. 1995; Mosisch and Arthington 1998). Thus, it has been suggested to analyze impacts on water quality in order to assess the pollution impacts of recreational watercrafts, which might affect total suspended solids, turbidity, dissolved oxygen, pH and temperature (Rebellato 2007). However, natural processes may also influence these parameters of water quality. In contrast to pollution, the formation of surface waves by all kinds of watercrafts has largely been neglected so far, even though the ecological impacts are strong enough to determine the ecological carrying capacity for boating tourism.

The main pathways of environmental effects that originate from water tourism link boating activities with (1) key variables of ecosystem health, (2) related political goals and (3) respective actions of water management (Fig. 11). Consequently, the major effects originating from water touristic activities, such as sediment resuspension, the disturbance of wildlife and impact of waves, may impact water quality and water ecology. Water quality variables like turbidity, dissolved oxygen and ecosystem processes like the water filtration activity of mussels are negatively influenced by these impacts. This leads to a decline in the visitor's perception of nature experience and quality. Furthermore, impacts on wildlife (such as waterfowl, invertebrates or mussel filtration activity) might also cause conflicts with regulatory requirements, e.g. the European Water Framework Directive (European Parliament and the Council of the European Union 2000). Hence, a sustainability analysis may be developed to establish integrated water tourism management by using the thresholds identified for various types of use and the related carrying capacity for water tourism.

As the success of water tourism is significantly influenced by the available water quality (Bockstael et al. 1989), touristic development should seek to minimize detrimental effects on the self-purification capacity of surface waters, as this would reduce system resilience (Zeng et al. 2011). In an earlier study (Lorenz et al. 2012) we described the impacts of wave formation from boating on freshwater mussels, which transfer organic matter from the water column to the benthic zone by their filter-feeding activity. Therefore, freshwater mussels directly contribute to the self-purification of surface waters, as most of the organic matter is processed by microbial degradation activity associated with the sediments (Fischer and Pusch 2001). Consequently, any impairment of this self-purification potential will produce negative effects on water quality. Decreasing water quality will in turn affect water tourism, as e.g. the attractivity of boat launching sites is strongly determined by water quality (Bockstael et al. 1989).

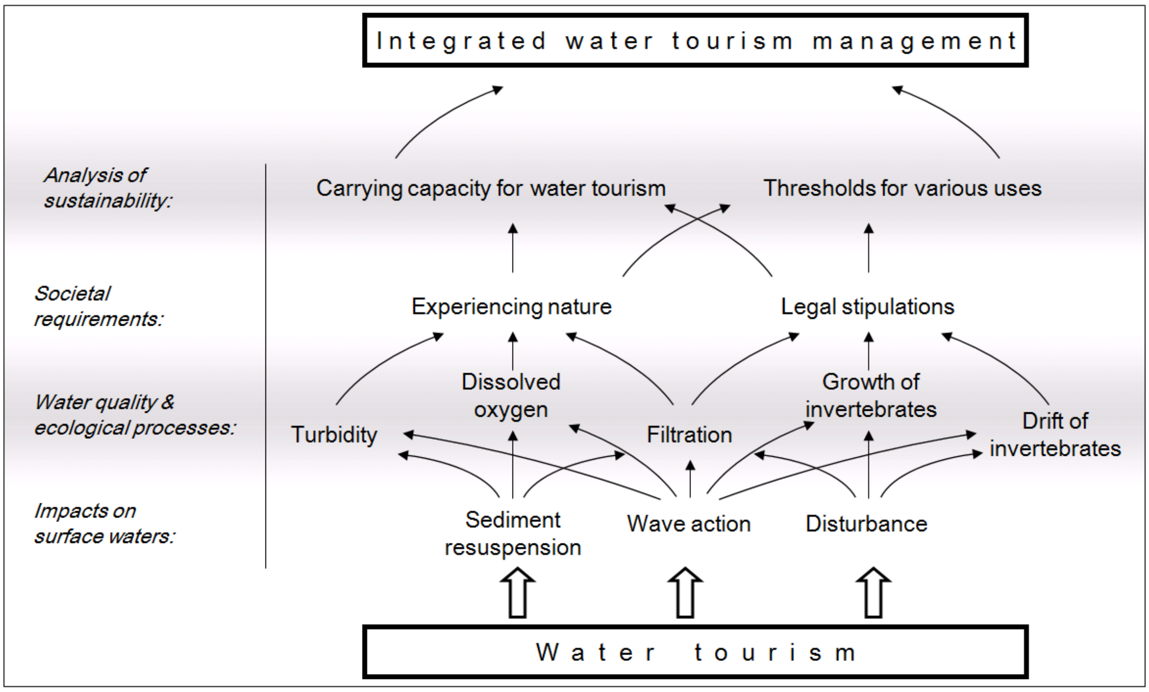

Fig. 11: Conceptual model of the major effects of water tourism on river ecosystems. The effects have impacts on different levels of perception that require consideration in an overall water tourism management strategy. All effects might be additionally impacted if framework conditions, such as water availability, are altered by unswayable events like climate change.

Hence, we aim to estimate the carrying capacity of a river section used for boating tourism based on an ecological approach that considers self-purification as the key ecosystem process for the preservation of acceptable water quality. By comparing this ecological approach with the spatial and social components that are estimated in parallel, integrative concepts to estimate the carrying capacity of surface waters for boating tourism are feasible to be developed.

Methods

Study site

The 21.1 km long river section of the Krumme Spree (Welker and Walz 1998) serves as a connection between two lakes with intensive touristic use, and thus constitutes an ideal area to conduct studies on the impact of boating on water ecosystems. The mean width of this river section is about 25 m, with mean depth ranging from 1.4 to 2.5 m. As calculations of *Usable Lake Areas* suggest the importance of restricted areas (e.g. no-wake areas or shallow water depths) to protect shorelines (Rajan et al. 2011), this concept is not as directly applicable to our study river. Therefore, for our calculations we adopted the notion that the shallower portions of lakes (i.e. of less than 1.5 m deep) are the most susceptible to environmental impacts (Wagner 1991). As the Krumme Spree was straightened due to intense building activities between 1906 and 1911, it now has an almost homogenous trapezoidal cross-section (Pusch and Hoffmann 2000). Hence in this river section, portions of river of less than 1.5 m depth would extend 3 m from the shoreline, reducing the *Total River Area* from 0.528 km^2 to 0.400 km^2 of *Usable River Area*.

Application of the carrying capacity concept to a river section

To apply the current concept of estimating touristic carrying capacity from lakes to rivers, the respective terms and equations required adjustment. The *Optimal Boating Density* describes the recommended space for various boat categories, measured in square metres per boat. We reviewed several carrying capacity studies (Colorado Board of State Parks and Outdoor Recreation 2011; ERM Inc. 2004; Jaakson et al. 1990) to obtain values of *Optimal Boating Densities* that were applicable to the watercraft types that are used for boating tourism on the Spree River. Through collating the various published values, we adopted a density of 5,261 m²/boat for muscle driven boats, 36,422 m²/boat for open motorboats (< 15 HP), 28,328 m²/boat for motorised rowing and rafting boats (< 10 HP), and 60,703 m²/boat for yachts (> 15 HP). The *Optimal Boating Density* for the observed boating mix of the Krumme Spree was defined by the following equation (after Dearlove 2010):

$$\begin{matrix}\textit{Optimal boating density}\\ \textit{of observed boating mix}\end{matrix} = \left(\begin{matrix}\textit{range of optimal}\\ \textit{boating densities}\end{matrix} * \begin{matrix}\textit{proportion of}\\ \textit{motorised boats}\end{matrix}\right) + \begin{matrix}\textit{optimal boating density}\\ \textit{of muscle driven boats}\end{matrix} \qquad (1)$$

The *Range of Optimal Boating Densities* was derived by subtracting the minimum of the *Optimal Boating Densities* for the boat categories from the maximum (60,703 – 5,261 = 55,442), where the proportions of boating at the Krumme Spree correspond to muscle driven boating = 0.39, open motorboats = 0.29, motorized rowing and rafting boats = 0.11 and yachts = 0.21. Therefore, the *Optimal Boating Density* for the observed boating mix on the Krumme Spree amounts to an estimated 39,081 m^2/boat. As the areas that are required per boat describe only the water surface area that is needed for the safe operation of this type of boat, we had to recalculate these values for the straight course of rivers instead of lake areas. Assuming that these areas would enclose a boat like a circle, we can take the radius of these circles as the area in running river meters that is required per boat type between consecutive boats. The results of this calculation for the different boat types are: 41 running river metres for muscle driven boats, 108 m for open motorboats (< 15 HP), 95 m for motorized rowing and rafting boats (< 10 HP), 139 m for yachts (> 15 HP), and 112 m for the observed boating mix. By using the following equation, this leads to an *Estimated Carrying Capacity* of 188 boats of the observed mix that could be present on the river at any one time:

$$\begin{matrix}\textit{Estimated} \\ \textit{carrying capacity}\end{matrix} = \frac{\textit{river length}}{\textit{requested area for observed boating mix}} \qquad (2)$$

At mean peak use on weekends during July, an average of six boats per hour passes the Krumme Spree (Lorenz et al. 2012). To transfer the carrying capacity of 188 boats at the same time on the river into the number of boats per hour, we assume that all boats were moving with a constant velocity of 8 km/h. This leads to a carrying capacity of 257 boats per hour on the whole river section of the Krumme Spree. By using Equation (3), the *Observed Carrying Capacity* of the Krumme Spree is estimated to be 2.3%.

$$\textit{Observed carrying capacity } [\%] = \frac{\textit{total number of boats per hour}}{\textit{estimated capacity per hour}} * 100 \qquad (3)$$

Results and discussion

Hydrology

While the water level exceeds the proposed 1.8 m water depth during most of the boating season at the Krumme Spree (Lorenz et al. 2012), in the summer months this level may drop by about 0.9 m with receding discharge (Fig. 12). An exponential regression model between discharge and water level at the sampling site in the Krumme Spree (Lorenz et al. 2012) revealed that with each 1 m³/s reduction in discharge, the water level falls by about 4.5 cm ($y = 2.061 + 2.027 * (1 - 0.971^x)$, $R^2 = 0.92$, $P < 0.0001$).

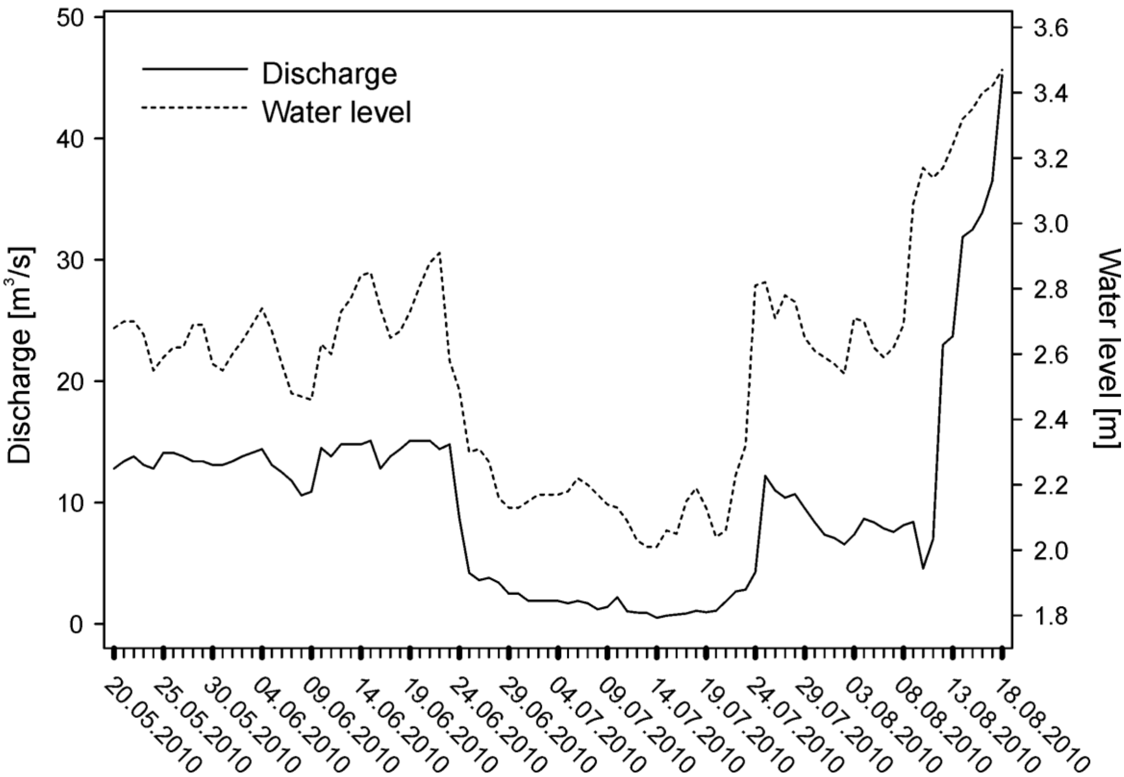

Fig. 12: Dynamics of discharge (records from the nearest gauging station of Leibsch) and related water level fluctuations on the Krumme Spree (Lorenz et al. 2012) during the summer months of 2010.

Estimation of the ecological carrying capacity

As estimated by Lorenz et al. (2012) by use of coupled hydraulic-ecological modeling, motorboats cause the most adverse effects on the filtration activity of freshwater mussels in the shallow marginal zone by their intense wave production, while effects of motorized rafting and rowing boats or yachts were partially significantly smaller. Therefore, we can state that the number of motorboats on the river consists the limiting factor for the estimation of the ecological carrying capacity. This coupled hydraulic–ecological model estimated a number of 93 motorboats passing by within one hour that would be sufficient to prevent all mussel specimens from filtration (with boats navigating at assumed 10 km/h). Using Equation (4), this would correspond to 321 boats per hour for a scenario with the observed boating mix.

$$\begin{matrix}\textit{Ecological} \\ \textit{carrying capacity}\end{matrix} = \sum \frac{\textit{proportion of boat type} * \textit{maximum no. of motorboats}}{\textit{proportion of motorboats}} + \textit{maximum no. of motorboats} \quad (4)$$

Under the hydrological conditions of a summer drought as described in Pusch and Hoffmann (2000) with the water depth reduced to 1.5 m, the estimated maximum number of boats would be 62 motorboats per hour until complete mussel filtration would be inhibited, leading to the calculation of 214 boats per hour of the observed boating mix by using Equation (4). By assuming the observed minimal discharge during the summer of 2010 of 0.49 m^3/s, taking into account the above described accompanying drop in water level, the above number would further be reduced to 203 boats. As the number of boats that are able to pass the river within one hour until mussel filtration completely ceases declines with the lowering of the water level (Lorenz et al. 2012), we consequently calculated the maximum number of boats from the observed boating mix at each water depth by using Equation (4) (Fig. 13). This calculated boating density is further referred to as the *Ecological Carrying Capacity* of the river Krumme Spree.

Estimation of the social carrying capacity

The *Estimated Carrying Capacity* per hour (from now on referred to as the *Social Carrying Capacity*) that is able to pass the river under social and spatial aspects varies by a small number of boats if the water level drops. The almost homogenous, trapezoidal cross-section of the Krumme Spree results in a reduction of the *Usable River Area* with lowered water levels. With a given 26.6° slope of the riprap, the mean river width would be lowered by about 0.44 m each time the water level drops about 10 cm. Therefore, there is an equal reduction in the *Social Carrying Capacity* at each water level drop. Based on this lowered *Usable River Width*, the *Social Carrying Capacity* was calculated by replacing the *Requested Area for the Observed Boating Mix* from Equation (2) with the *Adjusted Area for the Observed Boating Mix* derived from Equation (5). Within this equation, the loss of river area (in square metres) over one section of the *Requested Area for the Observed Boating Mix* was calculated from the lowered river width. Assuming that this area must also be considered for the safe operation of boats when the water level declines, the radius of a circle containing this area must be added to the original *Requested Area for the Observed Boating Mix* for each water level reduction. The dependence of the *Social Carrying Capacity* on varying water levels is also plotted in Fig. 13.

$$\frac{\text{adjusted area for}}{\text{observed boating mix}} = \frac{\text{requested area for}}{\text{observed boating mix}} + \frac{\sqrt{\frac{\text{lower}}{\text{river width}} * \frac{\text{requested area for}}{\text{observed boating mix}}}}{\pi} \quad (5)$$

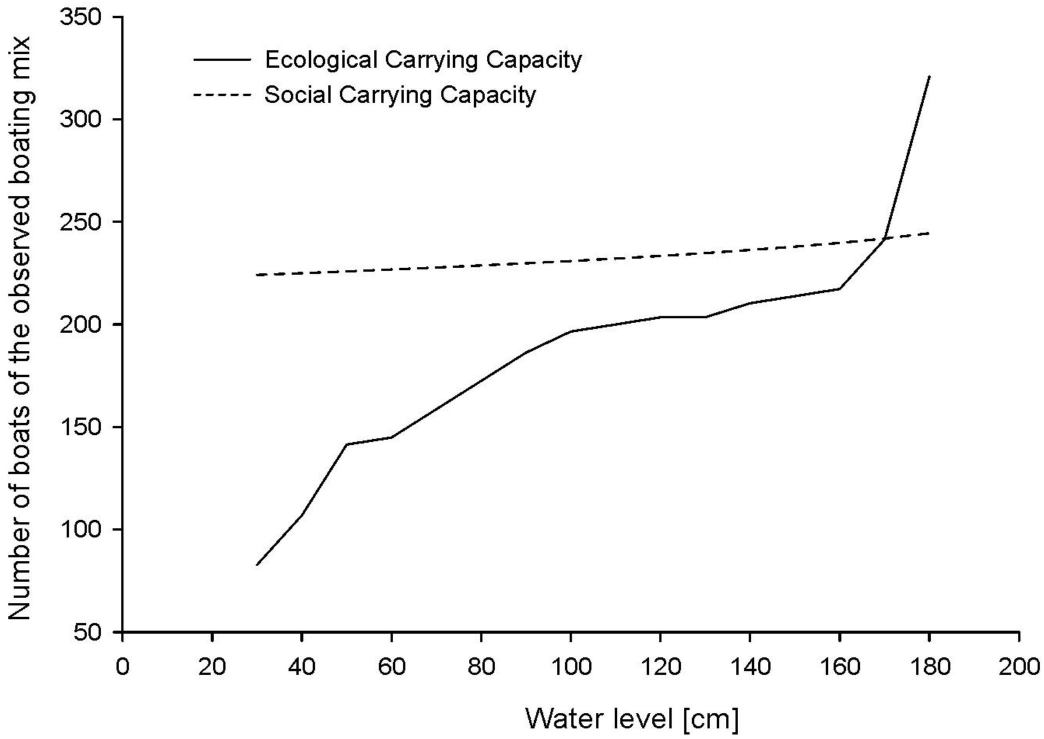

Fig. 13: Dependence of the ecological carrying capacity (black line) and the social carrying capacity (dashed line) of the Krumme Spree on the water level of the river. If the water level drops below 170 cm, the ecological carrying capacity constitutes the limiting component determining the maximum number of boats that is tolerable on the river.

Dependence of the carrying capacity on framework conditions

The *Ecological Carrying Capacity* shows a clearly stronger dependency on river water level than the *Social Carrying Capacity*. At water depths greater than 170 cm, the *Ecological Carrying Capacity* exceeds the *Social Carrying Capacity* several times. As the effects of open motorboats and motorized rowing and rafting boats vanish at water depths exceeding 190 cm (Lorenz et al. 2012), and effects of muscle driven boats only extend down to water depths of about 100 cm, the *Ecological Carrying Capacity* for water depths between 190 and 275 cm only depends on the number of yachts passing the river. Above this water level, the *Ecological Carrying Capacity* of the Krumme Spree is nearly unlimited with respect to the boating tourism of the mentioned boat types concerning the self-purification activity based on mussel filtration. However, at water levels below 170 cm, the *Ecological Carrying Capacity* drops below the line of the *Social Carrying Capacity*. Thus, the *Ecological Carrying Capacity* becomes the more important component during times of low river discharge, and should then be considered instead of social and spatial aspects.

The ecological status of surface waters is influenced by the natural dynamics of framework conditions, such as climatic variation, and by pressures exerted by humans. Consequently, the carrying capacity for a given human use is influenced by this variability and other uses as well. Restoration efforts in the Krumme Spree section could increase flow velocity during drought periods by decreasing channel depth by 0.5–1 m (Pusch and Hoffmann 2000; Pusch et al. 2001a), aiming to compensate the considerable decline in the water levels predicted by the climate change scenarios (Federal Environmental Agency 2005). However, the implementation of these restoration measures would clearly reduce the *Ecological Carrying Capacity* of this river section for boating activities, which in turn might be compensated by a potential change in the actual boat mix (ERM Inc. 2004).

Conclusions

We developed an ecological approach that aims to assure sustainable water tourism in the river section of the Krumme Spree. The approach considers all kinds of watercrafts present in this river section exerting a wave impact on the self-purification activity from freshwater mussels. The ecological carrying capacity showed a marked dependence on the actual water depth of the river, as the self-purification activity of benthic mussels is significantly reduced when shallow river reaches are used for boating. Thus, our approach also allows implications for an integrated water resource management to be derived that might preserve this river section as an area for water tourism. Increased water retention within the catchment area might contribute to maintain water levels above critical thresholds. Alternatively, a shift in the boating mix on the river during times of low flow, involving a smaller proportion of motorboats, would contribute to the preservation of the river's ecological integrity. Consideration of such results could lead to changes in regulatory policies or to an adaptation of business strategies of local boating and tourism industry. Our results suggest that specific concepts for water tourism should be developed for each water body, based on detailed information of respective social and ecological requirements. We could demonstrate that the relative importance of social and environmental aspects towards estimating the overall carrying capacity depends on key framework conditions. Therefore, we recommend the consideration of ecological approaches estimating the carrying capacity for boating tourism in sensitive river or lake ecosystems.

Acknowledgements

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General Discussion

Rationale

Recreational boating consists a major use of surface waters in many regions. Thereby, boat tourism may affect the ecological integrity of surface waters in several ways. On the other hand, the use of surface waters for tourism may also form an important incentive for the development of conservation strategies and their societal acceptance. One of the most important environmental pressures of recreational boating is the formation of boat-induced waves which represent a major hydraulic disturbance for macroinvertebrates in rivers (Bishop 2004, 2007; Bishop and Chapman 2004; Gabel et al. 2008; Gabel et al. 2011a). Ship waves are also known to affect submerged macrophytes (Liddle and Scorgie 1980), and to resuspend organic sediments (Beachler and Hill 2003; Garrad and Hey 1987; Nanson et al. 1994). Thereby, ship waves may reach shorelines that are protected from natural wind-driven waves, and the higher disturbance effect of those anthropogenic generated waves has been well documented (Bhowmik et al. 1982; Hofmann et al. 2011; Schoellhamer 1996).

Many bivalves are especially affected by such hydraulic disturbance due to the exposed position of their sensitive inhalant opening above the sediment bed. Through their ability to transfer organic matter from the water column to the benthic food web via filtration, freshwater mussels represent key species in river ecosystems (Howard and Cuffey 2006). Disturbance of the filtration activity of freshwater mussels therefore impairs the whole river ecosystem. Effects of climate change will presumably amplify the adverse effects of boating. Low river discharge during drought periods will lead to lower filtration activities due to the additional sinking dissolved oxygen concentrations in the water column. Furthermore, critical shear stress levels could appear closer to the sediment beds and the within living mussel populations if river discharge is lowered. However, up until now little is known about potential thresholds in the response of littoral macroinvertebrates in general, and of freshwater mussels in special, to anthropogenic wave disturbances accompanied by increasing shear stress.

In this thesis, I quantified the shear stress produced by waves created by boats of varying size and speed, and its impact on the dominant mussel species in the river section ‘Krumme Spree’. Thereby I considered muscle driven water sports as well as motorised boats of varying size and speed levels. In order to make this knowledge usable to approaches of sustainable water management, I developed a prediction model that links variables characterizing key ecosystem components (i.e. the filtration activity of mussels) with effects induced by boating (Fig. 14). The prediction outcomes of the model are thus determined by the impacts of both natural framework conditions and boating variables on mussel community filtration activity. The model thus enables to estimate the vulnerability of a river ecosystem to touristic use, and to determine thresholds of sustainable use. Based on that, adaptation strategies for both water tourism and environmental management can be developed, which integrate concepts of nature conservation, water management and perspectives in tourism business.

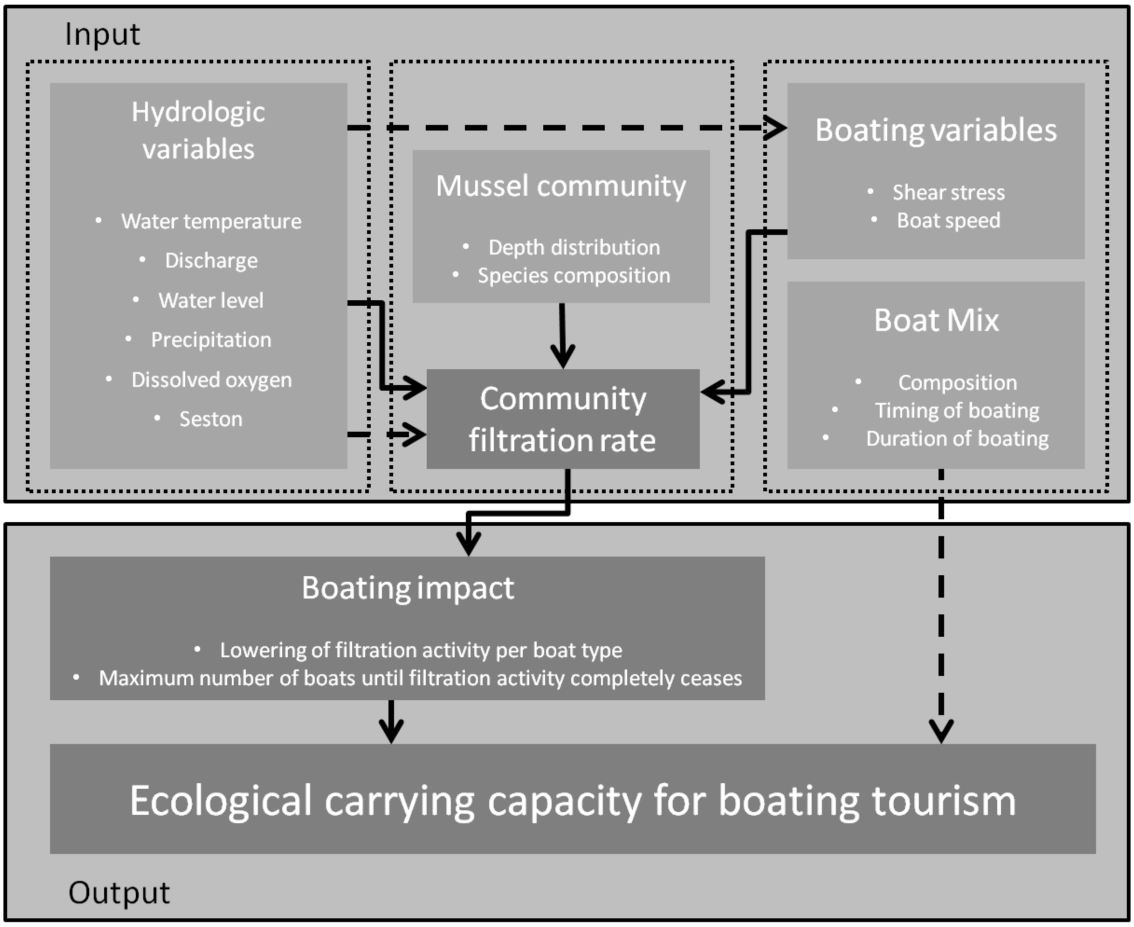

Fig. 14: Structure of the coupled hydro-ecological model SIMBoaT (**S**ocio-ecologic **I**ntegrated **M**odel for **Boa**t **T**ourism). This model consists of a modular composition including natural hydrological input variables, a freshwater mussel population component considering community composition and depth distribution, and a boating model describing shear stress production by different boat types and speeds in various water depths.

Impact of ship waves on freshwater mussels

In several studies, magnetic sensor systems fixed to bivalves have been used for the investigation of valve movements. Most of them have used the output of such sensors as an indicator of water quality in biological early warning systems (Allen et al. 1996; Borcherding 2006; Englund et al. 1994; Gnyubkin 2009; Kramer et al. 1989). Others investigated circadian rhythms and activities of marine and freshwater mussels (Englund and Heino 1994b; Gnyubkin 2010; Vero and Salanki 1969). All of them stated the reliable interpretation of the mussel reactions. In more recent investigations, magnetic sensor systems with Hall-effects sensors have been successfully used in bivalves to investigate valve movements under near natural conditions (e.g. Maire et al. 2007; Robson et al. 2009; Wilson et al. 2005).

Despite the large amount of studies concerning mussel shell gape response patterns, the only application of a magnetic sensor system for the determination of ship wave effects was done by Miller et al. (1999) in the Mississippi River. In this study, no effects were found in the shell gape response of *Amblema plicata* to multiple passages of recreational crafts, but six passages of greater work boats or skiffs caused measurable responses in the shell gape. The results of this thesis show that the hydraulic effects of recreational crafts vanish at larger water depths, which might have been the case in the previous mentioned study (**Chapter 1**). I could demonstrate that in shallower water depths up to 2.7 m, the relationships between ship-induced shear stress and shell closing behavior follows a sigmoid progression with clear threshold values for each species (**Chapter 1**).

The results of this thesis also confirm the suggestion that closure of the shell valves of mussel species is mainly related to ship-induced changes in shear stress and not to resuspended sediment. Mitchener and Torfs (1996) provided a formula to estimate the critical shear stress for the resuspension and erosion of sandy-mud sediments. The estimate of 0.77 N/m^2 at the study site of this thesis is several times higher than the calculated predicted medium (PMES) and no (PNES) effect shear stress threshold values of the investigated mussel species. Therefore, the occurring transport of resuspended sediments in larger water depths via compensating flows does not represent a major mechanism for the starting of shell closing, as shell closing is likely to start at lower shear stress values. However, filtration activity might be impacted by resuspended sediment in the water column when the mussels start to re-open after the boat passage (Summers et al. 1996).

Influence of species composition on self-purification activity

Transportation via navigational waterways favours the invasion of non-native mussel species in freshwater ecosystems (Leuven et al. 2009; Mills et al. 1993). During and after this immigration process, non-native mussel species are frequently exposed to the waves created in navigation channels by ship waves. As native species only find suboptimal habitat conditions in these environments, invasive species might successfully colonize these habitats (Byers 2002). In such disturbed systems invasive species may either fill the ecological niche that is left by the decline of native species, or use a novel niche offered by altered habitat conditions (Darrigran 2002).

As outlined before, the results of this thesis indicate that the main effect of ship traffic on freshwater mussels consists in a reduction of filtration rate of these organisms by hydraulic wave pulses (**Chapter 1**). Thereby, highly invasive species such as *Dreissena bugensis* and *Corbicula fluminea* are able to filtrate under wave impacts even under disturbed conditions when native mussel species already stop filtrating (**Chapter 2**). This ability might give a crucial advantage during spreading into novel habitats to outcompete the native species there.

Additional to translocation into novel habitat conditions, ship traffic also modifies the dominance structure in macroinvertebrate assemblages. There is evidence from responses of single macroinvertebrate taxa in laboratory experiments that invasive species could outcompete natives at sites exposed to ship-induced waves (Gabel et al. 2011a). Ship waves were found to affect total abundance of benthic invertebrates (Bishop and Chapman 2004; Gabel et al. 2008) as well as the physiology and behaviour of single species of amphipods and gastropods (Gabel et al. 2011a) and therefore represent one major driver of the composition of macroinvertebrate assemblages. Furthermore, wave impacts on filtering organisms such as freshwater mussels have been described (Payne et al. 1999; Widdows et al. 1979).

The reduction of species abundances or a loss of species caused by anthropogenic impacts (such as wave disturbance by boating) is dramatic and well reported (Tockner et al. 2010), but it does not necessarily lead to a deterioration of important key ecosystem functions and services (Chapin et al. 2000). The invasion of non-native mussel species may help to assure an important portion of self-purification by maintaining filtration activity under disturbed conditions (**Chapter 2**). As this invasion process is also driven by climate change (Rahel and Olden 2008), a compensation of self-purification losses might occur in freshwater ecosystems which suffer both from climate change and high boating activities.

Dependence of the ecological carrying capacity on framework conditions

The carrying capacity for a given human use is influenced by other uses of the same surface water body, in addition to climatic variations. For example, the status of aquatic and riparian vegetation and aquatic fauna is influenced by variations in water level and discharge (Bunn and Arthington 2002). In parallel, economic uses, such as hydropower generation and the provision of drinking water (Pusch and Hoffmann 2000) are also affected by periods of drought. Similarly, boat navigation and boating tourism (Eiswerth et al. 2000) also suffer.

Estimations of ecological carrying capacities of surface waters for water tourism use are thereby highly influenced by the variability of natural framework conditions and human pressures (**Chapter 3**). Previous studies estimating minimal flow requirements to ensure the ecological functions for the river/floodplain system of the Krumme Spree (Pusch and Hoffmann 2000) have indicated that the minimal flow requirements of the Krumme Spree section would be lower after restoration of the original river channel profile, which would have a smaller channel cross-sectional area and water depths of 0.5 – 1 m. Such restoration efforts would increase discharge and flow velocity during drought periods (Pusch and Hoffmann 2000; Pusch and Köhler 2002). However, the implementation of these restoration measures would clearly reduce the ecological carrying capacity of this river section for boating (**Chapter 3**). Consequently, boating tourism would only be possible with smaller boats, if significant disturbance of the aquatic fauna and flora should be avoided.

A change in the actual boating mix towards muscle driven boats or new boat types that produce less waves and turbulence would positively influence the carrying capacity (ERM Inc. 2004) and might preserve this river section as an area for water tourism, if the suggested restoration concepts are realised. River restoration would probably increase the quality of the boating experience, and thus touristic attractiveness of the river section.

According to published scenarios of climate change, periods of drought are expected to become more frequent (Gerstengarbe et al. 2003). As a result, the decrease in groundwater discharge would cause a considerable decline in the water levels of surface waters and water quality (Zebisch et al. 2005). Primarily, shallower water systems are expected to be subjected to a higher risk of eutrophication as a result of lowered water levels, causing longer water retention times, increasing temperature and increasing phytoplankton growth (Nõges and Nõges 1999). As a consequence, the water level of the Krumme Spree would fall more frequently below the 170 cm level, at which point the ecological carrying capacity would limit boating tourism (**Chapter 3**). In addition, the river would have higher loads of phytoplankton, which would clearly reduce its attractiveness for boating tourism.

Despite this high variability in the natural variables which form the basis for calculations, the resulting carrying capacity estimation is often based on a given moment in time. The results of this thesis show, that variation in one single variable, such as water level, could lead to dramatic changes in the estimation of the carrying capacity for touristic use (**Chapter 3**). Therefore, estimations of ecological carrying capacities need to be adaptive to changing framework conditions, and should especially comprise various scenarios coping with this high variability.

Sustainable use of surface waters subjected to multiple human uses

Human use of natural resources aims to maximize a few ecosystem services while reducing others (Foley et al. 2005). The results of this thesis show that boating activity may produce immediate effects on the water quality, and on the aesthetic value, too, as organic sediments might be resuspended (Beachler and Hill 2003; Garrad and Hey 1987) and filtration activity of freshwater mussels decreases (**Chapter 1**). Consequently, exactly those ecosystem features are directly affected that form preconditions for recreational boating. In addition, boating activity also reduces the self-purification capacity of rivers, which is considered to significantly contribute to ecosystem resilience (Fig. 15). Direct and indirect effects together result in a significantly increased risk of algal blooms, which would greatly decrease the ecological status and availability of required ecosystem services.

Based on the coupled hydraulic-ecological modeling approach presented in this thesis, I was able to provide the first quantification of the relationship between the intensity of use of the recreational potential and the impact on self-purification capacity (**Chapter 3**). This calculation allowed to show that the ecological value of the Krumme Spree for recreational boating would decrease if a certain threshold of boat density is surpassed. Exceeding this carrying capacity may eventually lead to reduced economic benefits for water-dependent tourism (Bockstael et al. 1989).

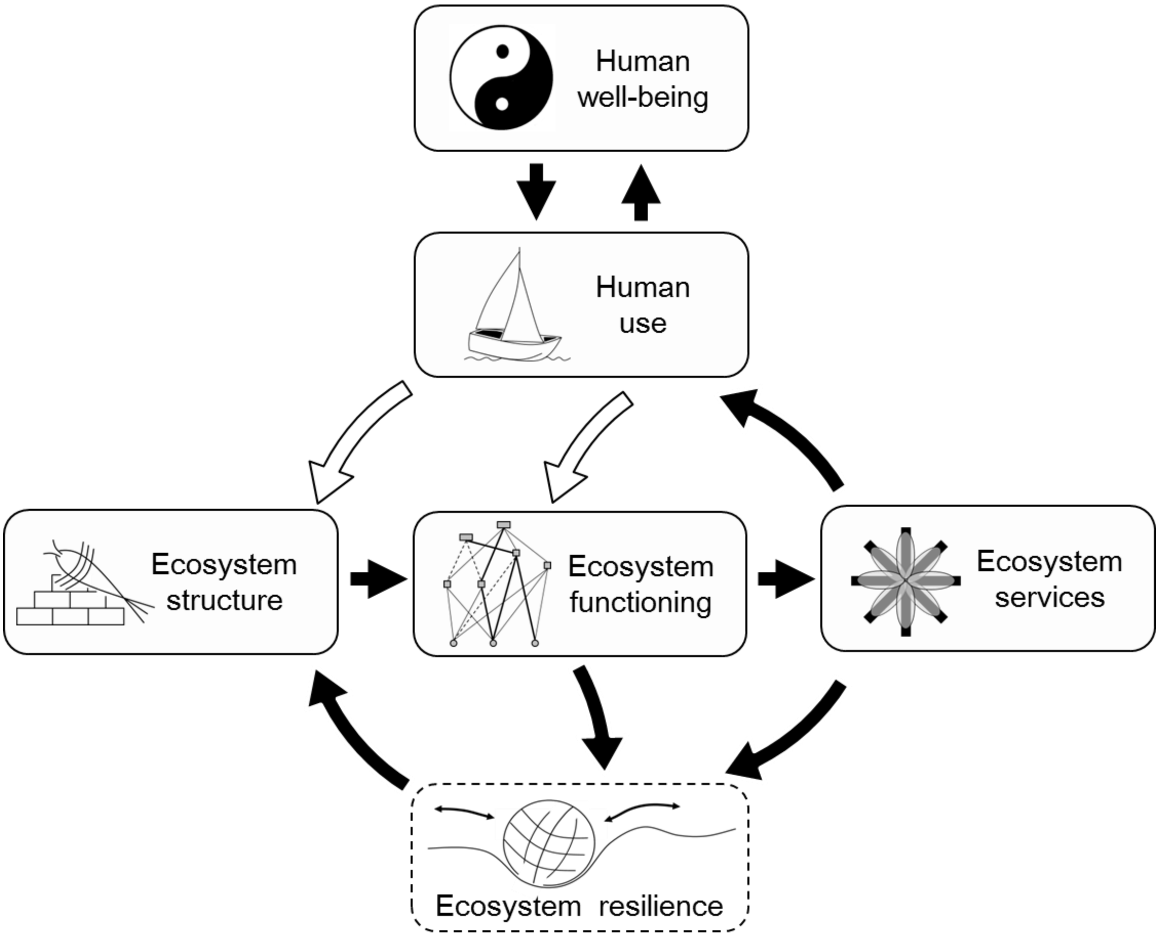

Fig. 15: Conceptual model of the effects of human uses on the structure, functioning, and resilience of aquatic ecosystems, reflecting causal relationships that were documented in the present thesis. Black arrows represent positive effects, while white arrows represent negative effects. Ecosystem functioning supports both ecosystem resilience and ecosystem services; hence, human uses that modify ecosystem functioning, such as recreational boating near shorelines, will affect both variables, and should be avoided if sustainable use is sought. Human uses that modify ecosystem structure will have less impact, as long as resilience is not affected. Symbol for ecosystem services after Foley et al. (2005).

I could demonstrate in this thesis that human use of an ecosystem service, such as the recreational potential of the river, may not only reduce the immediate availability of another ecosystem service such as self-purifcation, but may also weaken ecosystem resilience (Folke et al. 2004), thus reducing the availability of other services provided by the ecosystem (Fig. 15). Hence, the sustainable use of surface waters for recreational boating should be managed to minimize the effects on the self-purification capacity of rivers.

Conclusions

Within this thesis, I developed a coupled hydrological-ecological approach that may be used to establish sustainable water tourism in surface waters such as the Krumme Spree river section. The ecological carrying capacity showed a marked dependence on the water level dynamics of the river, as the self-purification activity of benthic mussels is significantly reduced when shallow river reaches are used for boating. Thus, the following options for water management, nature conservation and the boating industry were developed, which stabilise or increase the ecological carrying capacity of this river section.

First, increased water retention within the catchment area might help reduce the effects of droughts on the water level, and maintain the water level above critical thresholds. This could be accomplished by water retention behind new dams or weirs; however, such approach would significantly affect the river system and its touristic usability, as well as conflict with the legal stipulations of the European Water Framework Directive (European Parliament and the Council of the European Union 2000). Alternatively, the river cross-section could be reduced to its original size through restoration effort. This would increase the attractiveness of the river section for boating tourism, but would restrict boating to the use of smaller vessels.

Second, the results suggest that a shift in the boating mix on the river during times of low flow and low water levels could clearly contribute to the preservation of the river's ecological integrity. Such a change could be accomplished by regulatory policies, such as the selective restriction of boating to specific boat types, or by speed limits at certain times of the year. Alternatively, selective advertising of the boating and tourism industry (e.g. provision of appropriate offers) would also comprise a suitable tool to implement this shift. Third, the use of boat types with improved hull forms should be supported, as such craft exhibit a minimised draught and wave production due to the hydraulically optimised shape of the underwater hull.

Finally, specific concepts for water tourism should be developed for each water body, based on detailed information of respective social and ecological requirements. I could demonstrate that the relative importance of social and environmental aspects towards estimating the overall carrying capacity is subjected to variation and depends on decisive co-variables. Therefore, I recommend the inclusion of such integrative approaches for the estimation of the touristic carrying capacity of surface waters, which may be implemented as an adaptive element within business and management plans of touristic facilities marketing the sensible recreational use of river or lake ecosystems.

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Statement of academic integrity

I hereby certify that the submitted thesis "The ecological carrying capacity of a lowland river section for boating tourism" is my own work, and that all published or other sources of material consulted in its preparation have been indicated. All collaboration that has taken place with other researchers is indicated and I have clearly stated my own personal share in those investigations in the Thesis Outline. I confirm that this work has not been submitted to any other university or examining body in an earlier doctoral procedure in the same or a similar form, or has been judged to be insufficient.

Berlin, 31.10.2012

Stefan Lorenz

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List of included publications

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Author contributions

S. Lorenz designed the study, organized and performed field experiments, analyzed data, performed statistics and compiled the manuscript. F. Gabel co-performed field experiments and contributed to the text. N. Dobra co-performed field experiments and contributed to data analysis and statistics. M. T. Pusch co-designed the study and contributed to the text.

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Author contributions

S. Lorenz designed the study, organized and performed laboratory experiments, analyzed data, performed statistics and compiled the manuscript. M. T. Pusch co-designed the study and contributed to the text.

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Author contributions

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Curriculum vitae

For reasons of data protection, the Curriculum vitae is not published in the online version.