The impact of shore types on benthic macroinvertebrate community structure and functioning in a large lowland river

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Erklärung des Promovenden

Die Übereinstimmung dieses Exemplars mit dem Original der Dissertation zum Thema:

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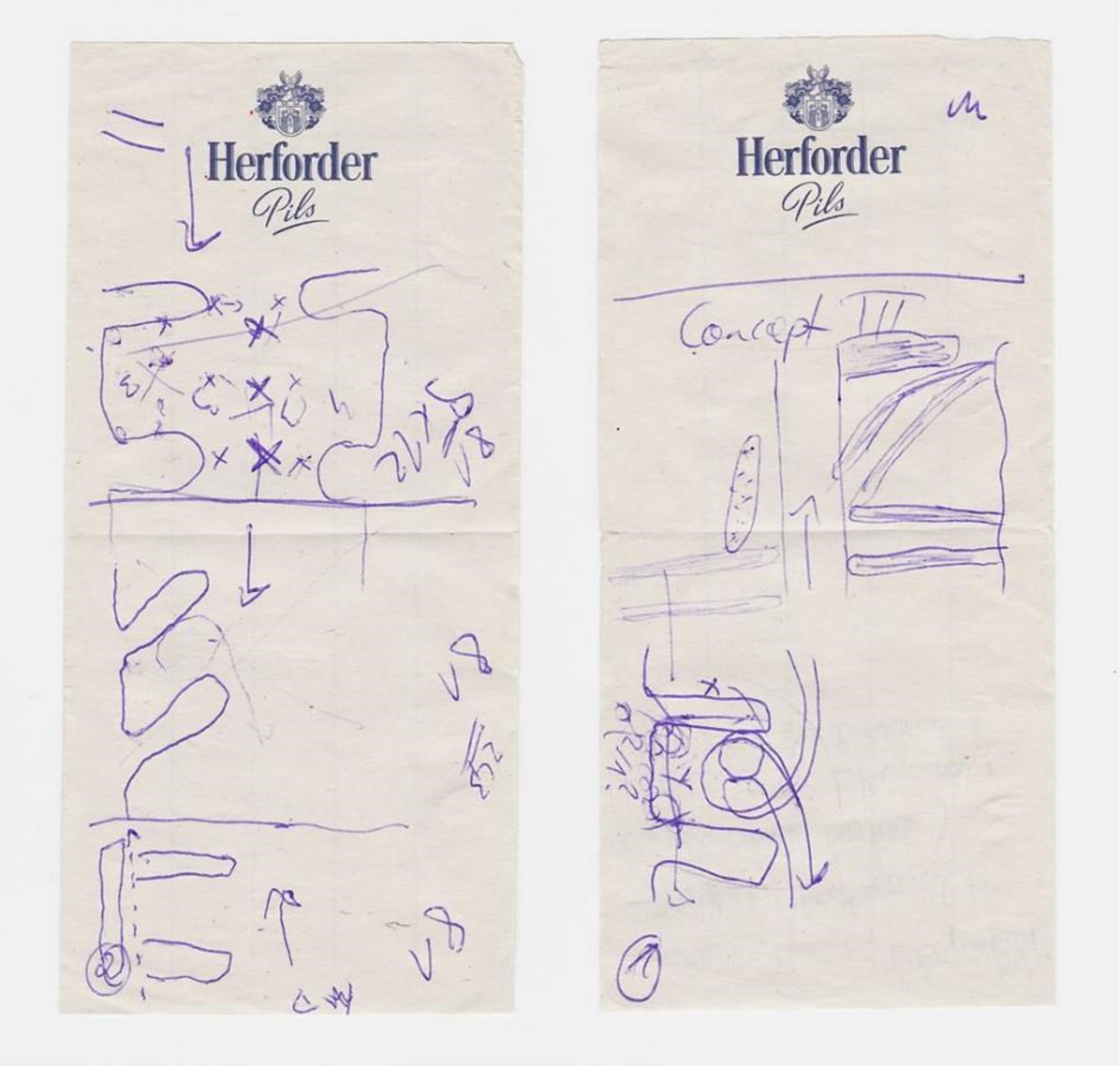

Skizzen des ersten Planungsgespräches für das Dissertationskonzept. Beide Zeichnungen, die linke aus der Feder von Prof. Dr. Markus Weitere, die rechte aus meiner, entstanden in der Stadtfelder Kneipe „Allards“. Trotz dieser künstlerischen Darstellungen wurde das letztendliche Design der Dissertation geringfügig abgewandelt.

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Zusammenfassung

Die Uferbereiche großer Flüsse sind für die Biodiversität und Funktion dieser Ökosysteme von enormer Bedeutung. Uferdegradierung und Kanalisierung gehören zu wichtigen Faktoren, die Flussökosysteme nachhaltig beeinträchtigen. Wie sich anthropogene Umstrukturierungen der Uferbereiche auf die Zusammensetzung benthischer Gemeinschaften und deren Ökosystemfunktion auswirken ist jedoch weitestgehend unbekannt. In dieser Arbeit werden die Effekte von uferspezifischen Habitatfaktoren auf die Komposition des Makrozoobenthos und den Anteil an Neozoen getestet. Zudem wurden die gemeinschaftsassoziierten Ökosystemfunktionen in Bezug auf Sekundärproduktion und Ressourcennutzung erfasst und bewertet. Die benthische Gemeinschaft des Hauptstroms bestand lediglich aus wenigen spezialisierten Arten, welche nur geringfügig zur Gesamtsekundärproduktion des Flusses beitrugen. Dies war vermutlich auf die rauen Bedingungen im Hauptstrom (insbesondere hohe Strömungsgeschwindigkeiten und damit verbundener Sedimenttransport) zurückzuführen. Die Makrozoobenthosgemeinschaften des Hauptroms wurden von den jeweils angrenzenden Ufertypen nicht beeinflusst. Im Gegensatz zum Hauptstrom zeigte jeder der untersuchten Ufertypen hohe Dichten an benthischen Invertebraten wobei sich Zusammensetzung und Funktion der Artengemeinschaften zwischen den Ufertypen stark unterschieden. Dabei brachte das Parallelwerk die diverseste und produktivste Makroinvertebratenfauna hervor, welche enorme Mengen basaler Ressourcen ingestierte (1,323 g DM $m^{-2}y^{-1}$). Hauptfaktoren für eine Erhöhung von Biodiversität, Sekundärproduktion und Ressourcennutzung waren neben variablen Sedimentzusammensetzungen und Makrophytenbeständen sich oft ändernde Fließgeschwindigkeiten mit lentischen Phasen. Allochthone Steinhabitate waren generell anfällig für die Invasion nicht heimischer Arten. Diese Neozoen waren weniger produktiv als viele heimische Taxa und nutzten nur geringe Mengen pelagischer Algen, welche die meist verfügbare Ressource darstellten. Aus dem ökologischen Vergleich der verschiedenen Ufertypen lassen sich Managementempfehlungen zur Verbesserung des ökologischen Zustandes in Bezug auf Biodiversität und Ökosystemfunktionen ableiten, welche für große Flüsse mit degradierter und unveränderbarer Makrostruktur in Betracht gezogen werden können. In ihrer Gesamtheit liefert diese Arbeit ein fundiertes mechanistisches Verständnis über die Effekte von Ufermanipulationen auf benthische Gemeinschaften und deren assoziierte Ökosystemfunktionen in großen Flüssen.

Abstract

Shore zones of large rivers are hot spots of biodiversity and contribute significantly to riverine ecosystem functioning. Today, shore degradation and other structural impairments like river straightening and channelization are strong impact factors on river ecosystem health. However, we still lack a thorough understanding of how structural shore zone degradation affects benthic community composition and their inherent ecosystem functions. In this thesis I tested the influence of training structure induced environmental factors on benthic macroinvertebrate community composition and the share of non-native species. Moreover, I assessed the community-associated ecosystem functions in terms of secondary production and resource utilization. In the main channel, communities were composed of only a few specialized taxa with low abundances, which contributed little to riverine secondary production. This is probably due to the harsh conditions produced by constantly high flow velocities and relocation of the fine sandy sediment. Main channel habitats were hardly affected by the adjacent training structure. Hence, species compositions and productivities were similar at all investigated main channel sites. By contrast, each of the shore communities was diverse, highly abundant and productive in comparison to the main channel. However, variations between shore structure communities and their ecosystem functions were prominent. One particular training structure, i.e. the off-bankline revetment, bore the most diverse and by far most productive benthic community, which utilized vast total amounts of basal resources (1,323 g DM m^{-2} y^{-1}). Varying sediment compositions, availability of macrophytes and diverse flow velocities, including lentic conditions, were revealed as key factors for increasing biodiversity, secondary production and resource utilization. Allochthonous boulder habitats were generally highly prone to non-native species invasion. Neozoa proved less productive than many native community members and consumed minor relative and total amounts of the prevailing resource pelagic algae. The present quantitative comparison of shore type specific effects on biodiversity, biomass and productivity provides managers with a tool to improve the ecological attributes of large river ecosystems with an unchangeable, impaired macrostructure. In its entirety, this thesis constitutes a sound basis to increase the mechanistic understanding of the way in which shore zone manipulation can affect riverine benthic communities and their associated ecosystem functions.

General introduction and aim of the study

Large rivers and human impacts

Large rivers are important freshwater systems that fulfill a variety of functions for human well-being (Postel & Carpenter 1997). They provide freshwater, exhibit both landscapes and diverse possibilities for recreation and represent frequently used waterways (Millenium Ecosystem Assessment 2005). From an ecological point of view, large rivers are important habitats for a magnitude of plants and animals adapted to riverine ecosystems. Particularly the shore zones and flood plains are hot spots of biodiversity and ecosystem processes (Bornette, Amoros & Lamouroux 1998; Strayer & Findlay 2010). River-dwelling organisms accomplish essential ecological functions like the channeling of nutrients and, as in the case of insect larvae, their removal from the river through emergence (Newbold *et al.* 1981; Jackson & Fisher 1986; Arthington *et al.* 2010). Thus, many riverine macroinvertebrates realize the coupling between terrestrial and aquatic environments. Healthy freshwater bodies in general are requisite for human life, but show serious global scarcity and impairment (Vörösmarty *et al.* 2010). It should therefore be a major task to maintain the limited number of intact freshwater bodies and to direct an increasing effort towards the restoration of human-impacted systems.

Despite a far-reaching comprehension of the necessity to preserve and protect our freshwater bodies, the human freshwater demand followed by the utilization of freshwater systems, e.g. as navigation channels, still has severe impacts on their structure and ecological performance. Major anthropogenic threats turned out to be overexploitation, pollution, fragmentation, facilitation of invasion by non-native species and the change or destruction of habitats (Malmqvist & Rundle 2002; Dudgeon *et al.* 2006; Arthington *et al.* 2010). Factors of pollution in terms of eutrophication due to untreated sewage disposal have been considered during the last decades, for instance by installing modern sewage plants in developed countries (Gücker, Brauns & Pusch 2006). Hence, in Europe chemical aspects of water quality are largely improving (Lyche-Solheim *et al.* 2010). However, especially in large navigable rivers, structural degradation persists or is even increasing, so that to date river rehabilitation has to focus more on structural habitat properties (Hering *et al.* 2010). Navigation, flood protection and land use require drastic deviations from the pristine river morphology and hence man-made artificial shore structures dominate the majority of the world's large rivers (Gregory 2006). Constructions like rip raps and standard groynes prevent shore erosion and concentrate the discharge to the main channel to create conditions that allow for a convenient navigation (Sukhodolov, Uijttewaal & Engelhardt 2002). Dikes are installed to protect the civilization from flooding events and to keep drained areas usable. At the same time, valuable habitats that are normally situated in the shallow shore zone become rare (Bis, Zdanowicz & Zalewski 2000; Strayer & Findlay 2010). The concentrated discharge leads to high current velocities and heavy sediment movement (Church 1992). Hence, a deepening of the river bed and a subsequent decrease of the groundwater level occur. Hence, the main river is largely being disconnected from its floodplain and oxbows and temporal lakes are endangered by decreasing water supply (Ward 1998).

Nowadays, structural degradation such as river straightening and channelization as well as general habitat alterations are among the strongest impact factors on river ecosystem health (Hughes *et al.* 1990; Strayer & Findlay 2010). Many ecological niches of specialized species are being altered or destroyed. Previous research has shown that, due to river shore zone degradation, we are facing a severe loss of aquatic species and an increase of invasive taxa at the same time (e.g. Allan & Flecker 1993; Bis *et al.* 2000). At the current state non-native species are frequently the dominating members of benthic communities (Hall, Dybdahl & VanderLoop 2006; Sousa *et al.* 2008b). The primary reason for these invasions is the loss of natural barriers due to shipping, channel connection and other human activities (Hulme *et al.* 2008). Nevertheless, the successful establishment of a neozoa population depends on the local opportunities offered to the invader in its new environment. The physical habitat presents one important factor that can contribute to the success of an invasive species (Moyle & Light 1996). For example, a recent study illustrated that suitable ecological niches for biological invasions are created by morphological and physicochemical degradation of streams and rivers (Frueh, Stoll & Haase 2012). This has also been shown to occur in the River Rhine, where invasive Amphipoda dominated macroinvertebrate communities in artificial stone habitats (Van Riel *et al.* 2006; Van Riel, Van der Velde & De Vaate 2011). However, despite a long-lasting history of studies assessing anthropogenic and non-native species’ impacts on riverine ecosystems, we lack a mechanistic understanding of how structural degradation affects benthic communities and their inherent ecosystem functions (Strayer *et al.* 2012; Cross *et al.* 2013).

Assessment of riverine ecosystems and the role of macroinvertebrates

For decades now, the assessment of an aquatic ecosystem's status has been a strongly considered field of research. Particularly macroinvertebrates have traditionally been used as indicators to assess the ecological status of streams and rivers (Kolkwitz & Marsson 1909; Reynoldson *et al.* 1997; Hering *et al.* 2004). Common assessment procedures are based on the presence and abundance of different taxa that bear a specific tolerance concerning water and/or habitat quality (Birk & Hering 2002). A lack of particular sensitive taxa may thus indicate some kind of impairment. Although those methods provide a fast and convenient type of assessment that furthermore delivers results that allow for a comparison of different systems, biodiversity or indicative taxa alone can only partly give insights into an ecosystem's functional status. Functional aspects may respond to environmental impacts in a different way than biodiversity does (Benke 2010).

One measure of a relevant ecosystem function that went into the focus of ecologists is the production of biomass over a certain time period defined as secondary production (Waters 1977; Huryn, Benke & Ward 1995; Butkas, Vadeboncoeur & Vander Zanden 2010). A prominent reason for the consideration of secondary production in the assessment of ecological conditions is that its reaction to environmental changes is often more pronounced than the effect on biodiversity and abundance (Chung, Wallace & Grubaugh 1993; Whiles & Wallace 1995). As secondary production integrates several components of ecological performance, i.e. biomass, density, growth rate and mortality, it can be applied to investigate effects of ecological stressors on communities (Benke 1993, 2010; Benke & Huryn 2006). However, just like results from diversity studies, secondary production estimates alone can be misleading. High production values do not necessarily indicate a healthy ecosystem as only a few exceptionally productive species can dominate the production of an entire community (Hall *et al.* 2006; Dolbeth *et al.* 2007; Sousa *et al.* 2008b). Studies combining both diversity and production estimates should therefore reveal more meaningful results than studies dealing with only one of these aspects (Benke & Huryn 2010).

Estimates of community structure and productivity provide a powerful tool for the functional assessment of stressors on populations or entire communities inhabiting a particular system. However, these estimates do not allow for the determination and quantification of basal resources that fuel community production and cannot entangle trophic interactions between consumers and their food items. Beyond the assessment of secondary production and biodiversity, estimates of community structure and productivity can be integrated into food web analyses that allow further insights into energy flows within a system or population (Benke & Wallace 2011). According to bioenergetics theory energy is either transferred or lost when it is consumed (Lindeman 1942). This theory has played a major role in ecology for several decades and describes energy flows and energy transformation between species and their resources (Benke 2010). Food webs can mirror how effective basal resources are utilized and channeled through different trophic levels. In addition, food webs enable researchers to detect whether vanished species can be replaced by functionally comparable taxa or if functional gaps remain in a community.

Interactions between consumers and their resources can be revealed either by consumer gut content analyses (Cross *et al.* 2011; Benke & Wallace 2014) or the analyses of stable isotope ratios of consumers and their diet (Peterson & Fry 1987; Layman *et al.* 2012). Gut content analyses detect food items that were ingested at a particular time and hence provide a snapshot of a consumers feeding habit. This procedure requires much laboratory work as many specimens from several sampling dates have to be analyzed under the microscope to allow for temporal differences in ingestion. In contrast, the analysis of stable isotopes detects a consumer's diet that was actually assimilated (Peterson & Fry 1987; Jardine *et al.* 2014). The incorporation of a diet's isotopic signature into a consumer's tissue takes some time and therefore stable isotope analysis mirrors an integrative assimilation picture. Stable isotope analyses require less animal material from only few sampling dates and thus safe both laboratory time and staff. On the other hand, analytical costs can be high and further processing and interpretation of the results demand specific computational skills. However, the outcome of both techniques, the proportions of ingested or assimilated food, can be converted into one another by applying appropriate factors of assimilation and net production efficiencies (Benke & Wallace 1980, 1997; Pandian & Marian 1986). Irrespective of the chosen method, several food web types exist and have advantages and disadvantages for particular research questions. **Connectivity webs** describe interactions among species and their food items and are based on presence/absence determinations by consumer gut analyses (Woodward *et al.* 2005). **Food quantity webs** provide additional information about the proportions of the food items in the guts of examined specimens, but still do not quantify the actual energy flow (Wallace *et al.* 1987). **Assimilation webs** mirror the proportions of food items that actually contributed to a species production in terms of metabolism and growth (Benke & Wallace 2011). Assimilated resource proportions can be combined with secondary production estimates to access the quantified trophic base of secondary production. The most complex type of food web is represented by **flow or ingestion webs**. Flow food webs give information about the ingested amount of food resources (Benke & Wallace 2011). They reveal resource demands of single taxa or entire communities and allow conclusions about top down or bottom up effects and an ecosystem's energetic potential.

Motivation, aims and study site

Today, we are facing severe problems concerning the ecological status of large river systems. However, despite the ongoing methodological advancement for its assessment, surprisingly little progress has been made in linking anthropogenic stressors and large river ecosystem functioning. While the effects of structural alteration on biodiversity and community composition are at least partially documented (Kleinwächter *et al.* 2005; Strayer *et al.* 2012), the implications of altered hydromorphology for the functioning of large river ecosystems are largely unknown.

Studies concerning the patterns of benthic secondary production in large sandy rivers suggest that the secondary production follows patterns of biodiversity with the highest values measured at the shore and riparian zone and the lowest values in the main channel (Benke *et al.* 1984; Zilli 2013). Given this tight relationship between community structure and functioning, secondary production may be sensitive to changes in the hydromorphology as induced by shore constructions (c.f. Elosegi & Sabater 2013). Furthermore, many non-native macroinvertebrate taxa are by now common members of riverine communities. Due to the frequent arrival of ever new invaders in various ecosystems, databases for their assessment and general knowledge on their functional influence on riverine communities are scarce. However, non-native species are often the dominating members of benthic communities that can reach high proportions of a community's biomass (Hall *et al.* 2006; Sousa *et al.* 2008b). As taxa within communities affected by species invasion have not co-evolved, food web structure and energy pathways can be substantially impaired (Vander Zanden, Casselman & Rasmussen 1999; Hobbs *et al.* 2006). Functional analyses like production estimates and food web determination can help in decrypting direct influences of non-native species on native communities' performances and their role in resource utilization and energy channeling. It can be expected that non-native species might further enhance negative effects of structural degradation on native communities by acting as competitors and by disturbing pristine functional patterns.

The objective of this thesis was to gain and improve the mechanistic understanding of how structural shore degradation in large rivers can affect the composition of benthic macroinvertebrate communities and their inherent functional performances in terms of productivity and resource utilization. The thesis aims at detecting relevant differences in environmental factors among already well-established shore types, i.e. a standard groyne, an off-bankline revetment and a rip rap, that may in turn influence the composition and functional performance of the inhabiting fauna. Knowledge on the influences that human-induced stressors have on an aquatic ecosystem's performance is urgently needed. Due to hard socio-economic boundary conditions like navigation or flood protection, large-scaled restructuring in large river systems seems impossible (bij de Vaate, Breukel & van der Velde 2006; Hering *et al.* 2010) and local habitat alteration mostly provides the only possibility to influence the river morphology. This thesis shall provide researchers and managers with fundamental insights on how riverine ecosystem functioning is linked to specific structural impairments and may therefore be useful to help incorporate ecological demands in future restoration activities. Additionally, a collection of data required for functional studies in large European lowland rivers is presented that will facilitate studies in these rarely treated ecosystems and thus contribute to increase the understanding of how anthropogenic stressors in general affect riverine ecosystem functions.

To investigate how shore structure alterations affect riverine community composition and their functional performance, the German River Elbe provides favorable conditions. In former times the river has been heavily polluted by untreated urban and industrial sewage. As a result, the Elbe became one of the most heavily polluted rivers in Germany (Guhr, Dreyer & Spott 1996). At this point in time, navigation did not play an important role yet, so that the river's structure was not as heavily influenced as other large river systems (Thielcke 1999). After the reunion of eastern and western Germany, extensive political and economic changes lead to an improvement of the water quality, but also to an increased navigation activity (Faist & Trabandt 1996). Although the Elbe's structure and morphology were adapted to fulfill demands of navigation, it still provides areas and sections that can be considered at least near-natural, like Europe's largest flood plain forest (Pusch & Fischer 2006). Hence, the River Elbe bears heavily impacted shore types comparable to the majority of large navigable rivers in combination with largely unaffected sites. Those unaffected sites may function as sources of organisms that could theoretically recolonize other, morphologically different sections of the river (Cairns & Dickson 1977; Wallace 1990).

Thesis outline

I present the results of my thesis in four chapters:

For **Chapter 1** new methodological datasets were created that are essential for studies on riverine ecosystem function. It provides the basis for all quantitative functional estimates coming up in the subsequent chapters of my thesis. Newly established head width-body length and length-mass regressions as well as cohort production intervals (CPIs), which constitute indispensable elements for precise and convenient biomass or secondary production estimates, are presented. Already published length-mass regressions and CPIs complete the data-set. As more and more non-native species enter new ecosystems, several allometric regressions had to be developed, most of them for invasive Crustacea. Hence, frequently updated databases like this one are necessary and of great interest. The combination of published and new data led to a comprehensive collection that will facilitate future functional studies in large European lowland rivers.

Chapter 2 detects relevant structural habitat factors that determine benthic macroinvertebrate communities and their associated productivity. I compared mesohabitat-specific macroinvertebrate community structure, secondary production and the share of neozoa between three shore types, i.e. an off-bankline revetment, a standard groyne and a rip rap as well as the adjacent main channel of the Elbe. I tested the hypothesis that benthic diversity and secondary production in the main channel is low and independent from the adjacent shore type. Furthermore, I investigated if the shore construction types systematically differ between one another and whether a particular mesohabitat facilitates the establishment of non-native species. Results from diversity and secondary production estimates provide the basis for the investigations following in chapter 4.

Chapter 3 reports on an unexpected detection of the rare mayfly *Ametropus fragilis* that constitutes the first record for Saxony-Anhalt. The significance of this record for the assessment of riverine recolonization potential is briefly discussed on a theoretical basis.

Beyond diversity and production estimates, **Chapter 4** focuses on quantified ingestion flows at the resource-primary consumer interface. Results from chapter 2 are used to construct quantified flow food webs based on stable isotope analyses of ^{13}C and ^{15}N. I tested the influence of the specific shore structures on the magnitude and effectiveness of basal resource utilization. In addition, taxa-specific organic matter flows are compared between shore types to detect functional key-players and potential missing links in resource utilization. Here, I present the first quantified basal food webs that have ever been constructed for large European river-dwelling benthic communities.

1. Chapter:

Support for the functional assessment of large European rivers: a collection of length-mass relationships and cohort production intervals (CPIs) with new data from the River Elbe, Germany

1.1 Introduction

Estimating biomass and secondary production has increasingly gained importance as a key element in the assessment of ecosystem functioning in various aquatic systems (Schonborn 1987; Buffagni & Comin 2000; Cross *et al.* 2011). Hence, both parameters also constitute a fundamental basis for this thesis. Along with an appropriate sampling strategy and choice of the calculation method, the assessment of reliable biomass data is crucial for the establishment of meaningful secondary production estimates (Johnston & Cunjak 1999; Benke *et al.* 1999). As the direct weighing of fresh or preserved specimens is often technically impossible and time-consuming, applying allometric equations like length-mass regressions turned out to be the most convenient and precise method in biomass determination (Leuven, Brock & van Druten 1985; Burgherr & Meyer 1997). Besides the time-economic advantages, the use of length-mass regressions permit the subsequent use of specimens for further analyses, whereas direct weighing would require a prior, structure-destroying drying step (Burgherr & Meyer 1997).

The most common types of length-mass regressions consider either total body length or head width for the determination of individual weight (Johnston & Cunjak 1999; Benke *et al.* 1999). For the former regression type, specimens are measured from the most anterior part of the head to the posterior part of the last abdominal segment, whereas for the latter type a fixed extension of the head is measured, usually the largest extension perpendicular to the body (Burgherr & Meyer 1997; Poepperl 1998). Although whole body length-mass regressions are in most cases more precise and account for a higher variation than head width-mass regressions (Meyer 1989; Burgherr & Meyer 1997), the application of the latter is essential when gut content biomasses is to be estimated or when specimens are damaged due to a rough sampling procedure or sample treatment (Johnston & Cunjak 1999). Furthermore, if head capsule width has to be measured anyway, as is the case when instar identification is desired, a supplementary body length measurement would be additionally time-consuming.

There are two main types of methods for calculating secondary production, i.e. cohort based methods that calculate the production of a given cohort and non-cohort based methods that in principal calculate the production of a fictive cohort over a given time span (Waters 1977). While the former methods require detection of respective cohorts, the latter can be applied when the life cycle of a population is more complex. An important parameter for accurate secondary production estimates when non-cohort based calculations such as the size frequency method (Hynes & Coleman 1968; Hamilton & Hynes 1969; Benke 1979) are used, is a correction factor that is based on the cohort production interval ($365*CPI^{-1}$; Benke 1979). This factor corrects the calculated annual production value of the single fictive cohort for the development time, which strongly varies between taxa. The cohort production interval is defined as the time span needed from hatching to completion of somatic growth for a given taxa. Compared to fully aquatic organisms, it is easier to detect CPIs for insects as they make a first appearance some day in the year and eventually start emerging at a later point in time. The period between both events can be defined as the CPI. For fully aquatic taxa such as Gastropoda and Crustacea, the detection of one complete life cycle turns out to be more difficult in the field. Thus, CPIs for those taxa are often based on intensive field studies or rather laboratory experiments (Streit 1976; Sousa, Antunes & Guilhermino 2008a). Secondary production is usually estimated for a period of one year and as the vast majority of aquatic benthic organisms complete their somatic growth in a shorter time span, consideration of CPIs mainly prevents underestimation. This is especially true for taxa that can develop within only a few weeks, like, for example, several Chironomidae (Mackey 1977; Nolte & Hoffmann 1992; Walther *et al.* 2006).

Presently, comprehensive reviews of length-mass regressions for many taxa from various systems can be found in literature (Burgherr & Meyer 1997; Poepperl 1998; Johnston & Cunjak 1999; Benke *et al.* 1999). However, a specific collection of length-mass regressions of typical large lowland river dwelling organisms does not exist. A collection of CPI values from large European lowland rivers is, to my knowledge, also lacking. For the best results of biomass estimation it is largely recommended to use equations for the lowest taxonomic level (Burgherr & Meyer 1997; Benke *et al.* 1999). Additionally, it is advisable that they originate from climatic regions and habitats comparable to those that are under study, because these equations explain a greater proportion of variance (Smock 1980; Meyer 1989; Johnston & Cunjak 1999). As the variety of habitats and associated taxa is enormous, so is the respective number of required equations and CPIs for entire community studies in a particular ecosystem. Unfortunately, many authors put a great effort in developing length-mass relationships and determined CPIs for their studies, but do not present their results in the publications (Benke *et al.* 1999). Therefore, the required information is widely scattered in the literature and often difficult to access for the scientific community.

As large rivers are already colonized by high numbers of invasive species, the need for neozoa-specific length-mass regressions in these systems is apparent. However, for invasive taxa regressions derived from studies in large rivers are scarcely available. Two of the few published regressions are available for determining the body mass of *Chelicorophium curvispinum* and *Dikerogammarus villosus* (Rajagopal *et al.* 1999; Bruijs *et al.* 2001). However, they are presented as a linear relationship rather than power equations, which will be presented in this chapter. Taking into account that our aquatic ecosystems will very likely be constantly invaded by new non-native species, updated collections of length-mass equations and CPIs are and will be needed regularly now and in the future.

It has been essential for my studies to conduct a comprehensive literature research combined with new equations from the River Elbe. As results from the following chapters are largely based on reliable biomass and production estimates, data presented in the following collection constitute an essential part of this dissertation. Here, length-mass regressions and CPI values are provided for the lowest taxonomic level possible from climatic regions that are comparable to those in which large European lowland rivers are situated. The collection consists mainly of reviewed data from a wide range of literature. I complete the reviewed collection with self-constructed length-mass equations and CPIs derived from this study, whenever published equations and CPIs failed in applicability or simply did not exist. As often only body length-mass regressions are provided rather than head width-mass regressions, additional self-constructed equations that can be used to convert head width into body length for most Trichoptera, Ephemeroptera and Odonata are presented. These can find applicability whenever solely head measurements are feasible or have to be conducted anyway, though the available regressions for mass conversion are based on body length.

1.2 Material and Methods

New regressions and CPIs for taxa from the River Elbe

Sampling took place in the River Elbe (Germany, river kilometer 250-254; 51.87861045°N, 12.30674744°E). I sampled three different shore types, i.e. a standard groyne, an off-bankline revetment and a rip rap. Additionally, the main channel was sampled in front of each shore type. During the sampling period, the discharge of the river Elbe ranged from 160 to 1,080 m^3 s^{-1} with an average of 339 m^3 s^{-1} (Fig. 1.1). The mean water temperature during the study was 12.2 °C (min. 3.9 °C, max. 21.6 °C; Fig. 1.2). Basic information about abiotic conditions can be gleaned in Table 1.1. For detailed information of abiotic conditions at the shore types see supplement Table S1.

Macroinvertebrates were sampled monthly from April 2011 to March 2012, except for January and February 2012, where high water levels prevented sampling. All available habitats, except boulders, were sampled with a Surber sampler (250 µm mesh). Boulders were sampled by carefully brushing off attached macroinvertebrates.

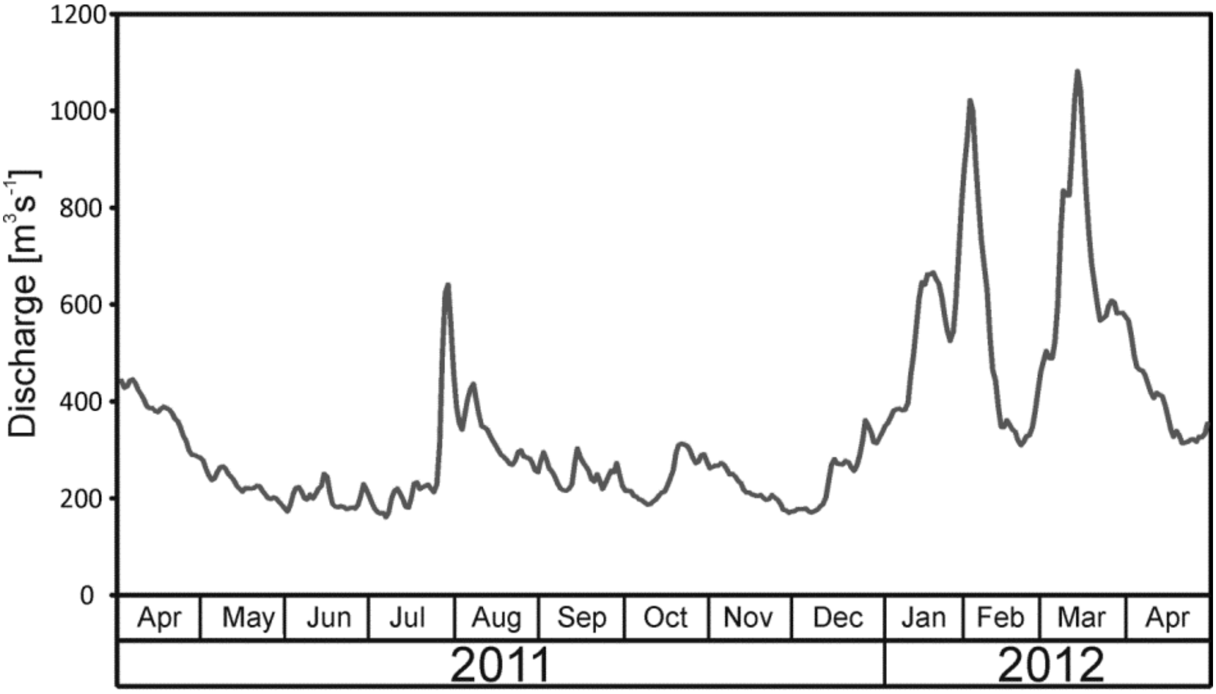

Fig. 1.1 Discharge during the sampling period measured at the gauging station Vockerode 5 km upstream of the study site.

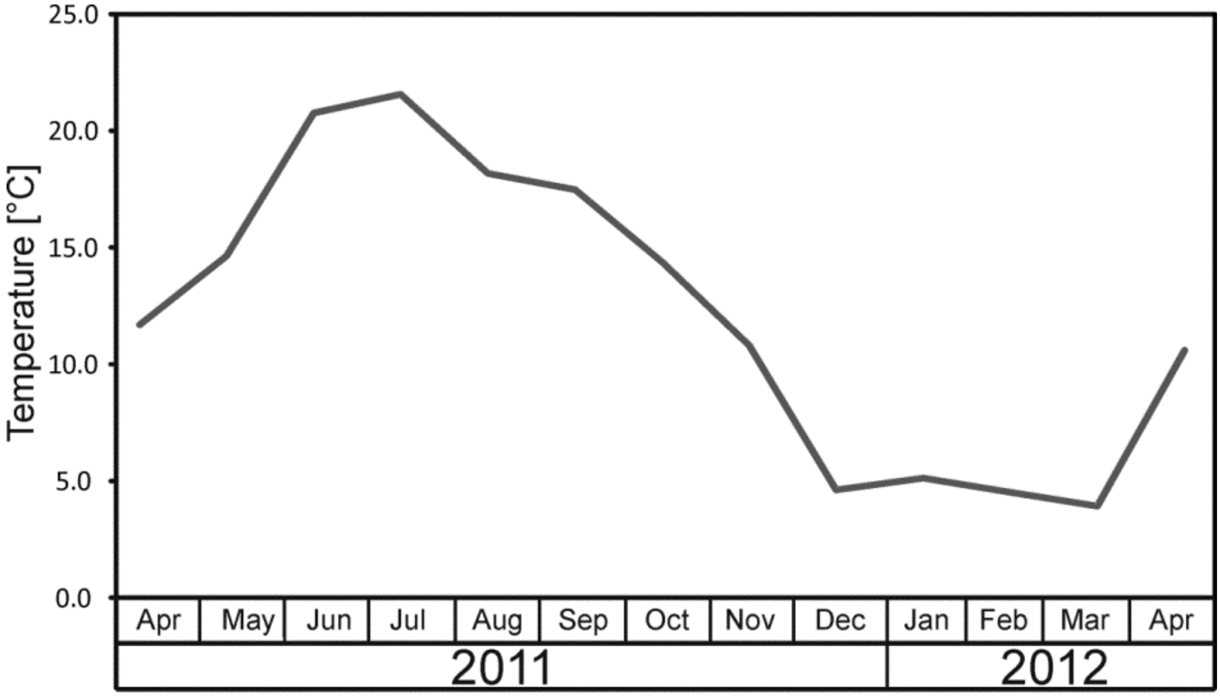

Fig. 1.2 Monthly water temperature measured during the sampling period from April 2011 until March 2012 in the main channel at the gauge Wittenberg, river km 214.1.

Samples from the main channel in front of each shore type were taken by an air-lift-sampler (100 µm mesh, UWITEC, Mondsee, Austria) operated from the research vessel "ALBIS" (Helmholtz-Centre for Environmental Research - UFZ, Magdeburg). All samples were preserved in 70% alcohol in the field. The time of preservation differed between samples. Samples from the main channel, which contained leaching-sensitive *Robackia demeijerei*, were treated after one week. Samples containing insensitive Crustacea were preserved for up to two month. Macroinvertebrates were identified to the lowest taxonomic level possible and measured for body length and/or head width to the nearest 0.01 mm with the digital measurement function of an automated microscope (VHX-1000, Keyence) in the laboratory. Total body length was measured from the most anterior part of the head without antennae to the posterior of the last abdominal segment. Head width was measured at the widest part of the head perpendicular to the body.

After length determination only clean and intact individuals were transferred to pre-weighted tin caps and dried at 60°C for 48h. Large specimens were weighted as single individuals. Small specimens were grouped into size classes to minimize the weighing error. After a cooling step in a desiccator individuals or size classes were determined to the nearest 0.001 mg with a micro balance (ME5, Sartorius, Surrey, UK).

Table 1.1 Mean (± SE) values of habitat and resource variables of the studied shore types and the adjacent main channel. Abbreviations are: AFDW = ash free dry mass, Chl a = chlorophyll a, benthic FPOM = benthic fine particulate organic matter, SPOM = suspended particulate organic matter, - = not present.

	Standard groyne	**Off-bankline revetment**	**Rip rap**	**Main channel**
Habitat variables				
Benthic FPOM (%)	0 ± 0	2 ± 1	0 ± 0	0 ± 0
Gravel (%)	68 ± 9	20 ± 14	17 ± 13	31 ± 6
Macrophytes (%)	1 ± 1	14 ± 8	0 ± 0	-
Oxygen concentration (mg L^{-1})	13 ± 1	13 ± 2	14 ± 2	12 ± 1
Sand (%)	31 ± 9	78 ± 13	83 ± 13	69 ± 6
Resource variables				
Chl *a* from SPOM (µg L^{-1})	45 ± 26	20 ± 14	42 ± 31	38 ± 28
Periphyton standing stock (mg AFDM m^{-2})	8 ± 4	6 ± 5	6 ± 3	-
Sediment organic matter (%)	4 ± 1	9 ± 3	1 ± 0	0 ± 0
SPOM (mg AFDM L^{-1})	9 ± 5	4 ± 3	16 ± 12	12 ± 5

Using sigma plot (Version 12, Systat Software), I calculated length-mass and head width-length regressions on taxon, genus or family level, provided that at least ten useful individuals were at hand. All length-mass equations presented in this paper are of the form

$$M = a \times L^{b} \qquad (1)$$

with M = dry mass [mg], L = body length [mm] and *a* and *b* as fitted constants. This power equation provided the highest values for the coefficient of determination for length-mass relationships in many studies, no matter if whole body length or head capsule width was used (Smock 1980; Burgherr & Meyer 1997; Benke *et al.* 1999). Furthermore, it delivers direct biomass values that can be used without any transformations. The head width-body length regressions are presented as the linear equation

$$BL = a + b \times HW \qquad (2)$$

with BL = total body length [mm], HW = head width [mm] and *a* and *b* as fitted constants. I only present self-constructed regressions that result in a high coefficient of determination ($r^2>0.85$ for length-mass; $r^2>0.7$ for head width-length) and are statistically significant ($p<0.005$).

To determine CPI values for taxa of which no development time was accessible in literature, I applied two methods:

Either, CPI values were derived from maximum body length or maximum instar due to head capsule width. That means, although I was not able to follow entire cohorts, I defined the respective CPI as 365 × number of size maxima^{-1} when clear and temporally well-separated (min. two months) size maxima could be detected in a population over the year. By applying this rather conservative method I made sure to at least account for the minimum number of possible cohorts.

Or, when taxa were not abundant in every campaign, it was sometimes possible to detect the time of hatching and the time of the first occurring size maxima for the respective cohort. This time span between both occurrences was defined as development time. As this happened only either at the beginning or the end of the year when water temperatures were colder and cohorts were not yet overlapping, I can be certain to present a conservative value that is not underestimating the actual CPI.

Published length-mass regressions and CPIs

I conducted an extended online and library search for studies that included length-mass regressions and CPIs. I attempted to find equations and CPIs for the lowest taxonomic level possible. Whenever available, I preferred equations and CPIs from habitats and climatic regions comparable to my study site. If more than one useful equation was available for a certain taxa, I picked the one with higher explained variance (coefficient of determination; r^2). If those values were very close I chose the one with higher number of used individuals (n). Every equation had to be valid for dry mass (DM) calculation. I tried to find regressions that include a coefficient of determination (r^2), the number and size range of used individuals (n; min.-max.) and the constants *a* and *b*, preferably when they included one standard error (SE). For the majority of Chironomidae species I calculated CPIs by applying the formula published in Mackey (1977):

$$\mathrm{CPI} = (a + b \times \mathrm{T})^{-1} \tag{3}$$

with CPI = cohort production interval [d]; T = water temperature [°C] and *a* and *b* as taxa-specific fitted constants. As temperature I used the mean annual temperature of the River Elbe.

1.3 Results

Length-mass regressions

For the development of the new regression equations 3,483 specimens of three invasive Crustacea taxa (*Chelicorophium curvispinum, Dikerogammarus villosus, Jaera istri*), of the family Gomphidae (most likely *Gomphus flavipes* and *Gomphus vulgatissimus*) and of the Chironomidae *Robackia demeijerei* were measured and weighted either as individuals or size classes (Fig. 1.3; Table 1.2). Four of the new regressions were best described by the power function (eq. 1), or at least almost identical to the quadratic form concerning coefficient of determination and residuals.

As an exception, the regression for *Chelicorophium curvispinum* resulted in similar r^2-values and slightly lower residuals when a quadratic or even linear form was applied. As the results concerning coefficients of determination were still almost identical (linear r^2=0.98, quadratic r^2=0.98, power r^2=0.97), I chose the power form for the sake of a comparable and convenient data collection. The significance of all the regressions was very high (p<0.001) and so was the accuracy with coefficients of determination explaining at least r^2=0.97 of variation for *Chelicorophium curvispinum*, *Jaera istr*i and *Robackia demeijerei* (Fig. 1.3 a, c, e). The equations for Gomphidae and *Dikerogammarus villosus* explained more than 86% of variation (r^2=0.86 and r^2=0.88, respectively; Fig. 1.3 b, d). The lowest coefficient of determination (r^2 = 0.86) was calculated for the regression on the family level for Gomphidae and is based entirely on the measurements of single individuals, whereby the lowest number of individuals was used for this regression (n=12; Table 1.2). The highest r^2=0.99 was calculated for the regressions of *Jaera istri* and *Robackia demeijerei*. Both equations are based on size class measurements including a total of n=241 and n=1,311 individuals, respectively. Except for the equation for Gomphidae, which was estimated solely with individuals from a relatively small size range not exceeding 9.76 mm, all equations most likely cover the entire size spectra for the respective taxon (Table 1.2). As the entire body size range of *Jaera istri* was the smallest of the proceeded taxa (0.45 mm - 2.85 mm), only nine size classes were established here. The largest size range could be detected in individuals of *Dikerogammarus villosus*, ranging from 1 mm to 27.23 mm. Here, a measurement of nine size classes and 59 single individuals was conducted (Fig. 1.3 b; Table 1.2).

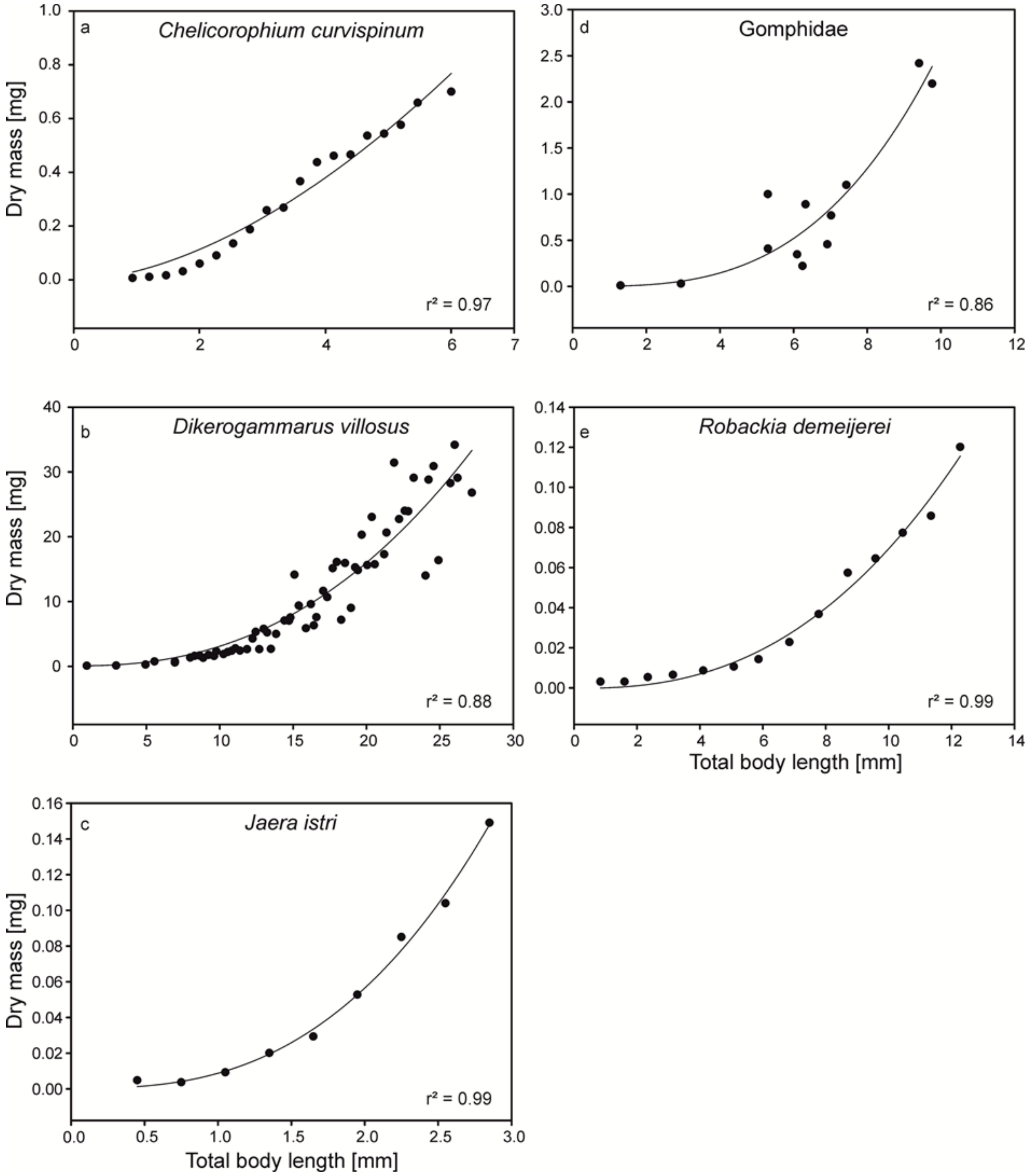

Fig. 1.3 Plots of size classes or single individuals, their respective weight and curves of the regression equations shown for the three invasive Crustacea *Chelicorophium curvispinum, Dikerogammarus villosus* and *Jaera istri* (a-c), Gomphidae (d) and *Robackia demeijerei* (e). The coefficient of determination (r^2) indicates the percentage of explained variation. The form of the equation is M = a × L^b with M = dry mass [mg], L = body length [mm] and a and b as fitted constants. The number of used individuals are presented in Table 1.2.

Together with the regressions from literature, eleven regressions on the species level, 20 on the genus level, eleven on the family level and three on the order level are provided (Table 1.3). Often, it was impossible to retrace the type of aquatic system or habitat from which the regressions originate, but the sampled region and country was always ascertainable. The majority of regressions originate from Germany, Austria or Switzerland (28), while 15 were established in the central US and one in Wales, United Kingdom. I converted logarithmic equations into the power form to provide regressions that can be used for dry mass calculation without a subsequent conversion step. As several studies provided the fitted constant *a* and the respective standard error (SE) in the logarithmic form, it was only possible to convert the constant itself, but not the SE. The fitted constant *a* is stated 20 times together with the respective SE and 25 times without. The SE of the fitted constant *b* was available for almost all taxa except for regressions on the family level for Chironomidae and Empididae (Table 1.3). The chosen regressions show at least a coefficient of determination of r^2=0.67 (Tanytarsini), but in most cases a much higher one. Five of eight coefficients of determination r^2<0.80 are based on regressions from the family- or Chironomidae-clade level. Nine of 13 regressions with a coefficient of determination r^2>0.95 originate from species, three from genus and one from family level. Size ranges are given for all but four regressions and the number of individuals (n) is lacking for one single regression only. The number of used individuals ranges from n=6 to n=1,311 with a mean number of n=195. In the majority of studies (37) individuals were proceeded fresh or frozen. In only six cases scientists used ethanol and in two studies formalin served as a preservative.

Head width-body length regressions

During the study I measured head width and total body length of 1,552 individuals for the development of head width-body length regression equations. In total, 21 head width-body length regressions; nine on the species level, nine on the genus level, two on the family level and one on the sub-order level were established (Table 1.4). The entire set of regressions was best described by the linear function (2).

Table 1.2 Data used for the calculation of the self-constructed length-mass regressions. Number of individuals measured per size class and for length-mass regression equation in total, mean length of size class or total length of individual [mm] and mean dry mass of size class or total dry mass of individual [mg] is shown for three invasive Crustacea taxa *Chelicorophium curvispinum*, *Jaera istri* and *Dikerogammarus villosus*, one Diptera *Robackia demeijerei* and one Odonata family Gomphidae.

Chelicorophium curvispinum			*Jaera istri*			*Robackia demeijerei*			Gomphidae		
Number of individuals/ size class	**Length of Individual or size class [mm]**	**Dry mass [mg]**	**Number of individuals/ size class**	**Length of Individual or size class [mm]**	**Dry mass [mg]**	**Number of individuals/ size class**	**Length of Individual or size class [mm]**	**Dry mass [mg]**	**Number of individuals/ size class**	**Length of Individual or size class [mm]**	**Dry mass [mg]**
13	0.93	0.009	2	0.45	0.005	7	0.84	0.003	1	1.30	0.010
69	1.20	0.013	65	0.75	0.003	110	1.60	0.003	1	2.94	0.030
77	1.47	0.019	54	1.05	0.009	43	2.34	0.006	1	5.30	0.999
72	1.73	0.034	41	1.35	0.020	190	3.14	0.007	1	5.30	0.409
58	2.00	0.063	20	1.65	0.029	165	4.10	0.009	1	6.10	0.347
53	2.27	0.093	14	1.95	0.053	237	5.08	0.011	1	6.25	0.221
49	2.53	0.138	29	2.25	0.085	161	5.86	0.014	1	6.33	0.889
41	2.80	0.190	14	2.55	0.104	54	6.84	0.023	1	6.92	0.456
29	3.07	0.261	2	2.85	0.149	52	7.78	0.037	1	7.02	0.769
29	3.33	0.271	---	---	---	77	8.70	0.058	1	7.43	1.100
20	3.60	0.369	---	---	---	96	9.58	0.065	1	9.41	2.418
18	3.87	0.440	---	---	---	75	10.45	0.078	1	9.76	2.197
24	4.13	0.464	---	---	---	39	11.35	0.086	---	---	---
16	4.40	0.468	---	---	---	5	12.28	0.120	---	---	---
15	4.67	0.539	---	---	---	---	---	---	---	---	---
14	4.93	0.546	---	---	---	---	---	---	---	---	---
10	5.20	0.579	---	---	---	---	---	---	---	---	---
14	5.47	0.661	---	---	---	---	---	---	---	---	---
3	6.00	0.702	---	---	---	---	---	---	---	---	---
Total individuals: 624			**Total individuals: 241**			**Total individuals: 1,311**			**Total individuals: 12**		

Dikerogammarus villosus											
Number of individuals/ size class	**Length of Individual or size class [mm]**	**Dry mass [mg]**	**Number of individuals/ size class**	**Length of Individual or size class [mm]**	**Dry mass [mg]**	**Number of individuals/ size class**	**Length of Individual or size class [mm]**	**Dry mass [mg]**	**Number of individuals/ size class**	**Length of Individual or size class [mm]**	**Dry mass [mg]**
323	1.00	0.017	1	10.87	2.322	1	16.65	7.522	1	22.90	23.880
330	3.00	0.045	1	11.13	2.711	1	17.11	11.579	1	23.28	29.052
305	3.00	0.047	1	11.43	2.353	1	17.38	10.608	1	24.08	13.949
60	5.00	0.210	1	11.92	2.569	1	17.76	15.081	1	24.29	28.761
62	5.00	0.195	1	12.29	4.201	1	18.04	16.053	1	24.62	30.856
67	5.00	0.208	1	12.50	5.258	1	18.33	7.111	1	24.96	16.316
1	5.61	0.681	1	12.75	2.570	1	18.60	15.887	1	25.78	28.223
35	7.00	0.533	1	13.05	5.707	1	19.00	8.943	1	26.06	34.139
25	7.00	0.669	1	13.28	5.162	1	19.29	15.226	1	26.26	29.043
30	7.00	0.505	1	13.54	2.605	1	19.47	14.776	1	27.23	26.758
1	8.04	1.264	1	13.89	4.920	1	19.73	20.251	---	---	---
1	8.34	1.526	1	14.46	6.989	1	20.11	15.568	---	---	---
1	8.68	1.584	1	14.78	6.964	1	20.42	22.999	---	---	---
1	8.93	1.232	1	14.86	7.466	1	20.62	15.700	---	---	---
1	9.30	1.679	1	15.15	14.096	1	21.26	17.249	---	---	---
1	9.67	1.522	1	15.44	9.301	1	21.42	20.596	---	---	---
1	9.82	2.252	1	15.93	5.812	1	21.93	31.385	---	---	---
1	10.31	1.805	1	16.27	9.522	1	22.28	22.680	---	---	---
1	10.60	2.127	1	16.47	6.245	1	22.66	23.969	---	---	---

Total individuals: 1,295

Table 1.3 Length-mass regression equations of the form DM = $a \times L^b$, with DM = dry mass [mg], L = total body length [mm] (unless otherwise stated behind taxon), and a and b as fitted constants. The constants a and b are provided with one standard error if available. HW behind taxon = head width was used for the regression instead of total body length. The regressions are significant with $p<0.05$. Locality/system, country = location or aquatic system and country, range = range of body length or head width measured for the regression [mm], n = number of individuals used, preservative = chemical or type of preservation, source = reference, -- = not stated.

Taxon	Locality/system, country	a ± 1 SE	b ± 1 SE	r²	Range [mm]	n	Preservative	Source
BIVALVIA								
Corbiculiidae								
Corbicula fluminea	North Carolina, USA	0.0141	3.01	0.97	---	21	Fresh or formalin	Lauritsen & Mozley 1983
Dreissenidae								
Dreissena polymorpha	Kiel, Germany	0.2222	2.4683 ± 0.1261	0.98	1.0-33.0	463	Fresh	Poepperl 1998
Sphaeriidae								
Pisidium sp.	Kiel, Germany	0.1066	2.9132 ± 0.0564	1.00	1.0-4.0	1,078	Fresh	Poepperl 1998
Sphaerium sp.	Kiel, Germany	0.0288	3.4024 ± 0.0876	0.99	1.0-12.0	1,071	Fresh	Poepperl 1998
CRUSTACEA								
Corophiidae								
Chelicorophium curvispinum	Elbe, Germany	0.0349 ± 0.0064	1.7264 ± 0.1154	0.97	0.93-6.00	624	70 % ethanol	own study
Gammaridae								
Dikerogammarus villosus	Elbe, Germany	0.0118 ± 0.0061	2.4047 ± 0.1673	0.88	1.00-27.23	1,295	70 % ethanol	own study
Janiridae								
Jaera istri	Elbe, Germany	0.0085 ± 0.0010	2.7335 ± 0.1266	0.99	0.45-2.85	241	70 % ethanol	own study

Taxon	Locality/system, country	a ± 1 SE	b ± 1 SE	r²	Range [mm]	n	Preservative	Source
DIPTERA								
Ceratopogonidae								
Palpomyia spp. *Group*	Virginia, USA	0.0039 ± 0.0007	2.144 ± 0.531	0.71	1.4-7.0	33	Fresh or frozen	Benke et al. 1999
Chironomidae	Wales, UK	0.00113	2.73	0.81	2-19	---	Ethanol	Potter & Learner 1974
Chironominae	Virginia, USA	0.0059 ± 0.0009	2.099 ± 0.235	0.88	1.7-10.8	50	Fresh or frozen	Benke et al. 1999
Orthocladiinae	Virginia, USA	0.0020 ± 0.0006	2.254 ± 0.396	0.74	1.6-5.8	39	Fresh or frozen	Benke et al. 1999
Chironomini	Alabama, USA	0.0007 ± 0.0001	2.952 ± 0.118	0.93	1.0-6.7	51	Fresh or frozen	Benke et al. 1999
Chironomus spp.	Alabama, USA	0.00068 ± 0.00004	2.620 ± 0.112	0.96	2.0-13.7	26	Fresh or frozen	Benke et al. 1999
Dicrotendipes sp.	Alabama, USA	0.00059 ± 0.00005	3.142 ± 0.312	0.87	2.6-6.7	17	Fresh or frozen	Benke et al. 1999
Robackia demeijerei	Elbe, Germany	0.0002 ± 0.0001	2.4834 ± 0.1442	0.99	0.84-12.28	1,311	70 % ethanol	own study
Tanytarsini	Virginia, USA	0.0008 ± 0.0012	2.728 ± 0.197	0.67	1.3-5.3	45	Fresh or frozen	Benke et al. 1999
Tanytarsus spp.	Alabama, USA	0.0012 ± 0.0001	2.294 ± 0.317	0.81	1.6-5.8	14	Fresh or frozen	Benke et al. 1999
Tanypodinae	Virginia, USA	0.0026 ± 0.0005	2.503 ± 0.458	0.81	2.3-8.2	46	Fresh or frozen	Benke et al. 1999
Ablabesmyia sp.	Alabama, USA	0.0010 ± 0.0001	2.884 ± 0.166	0.94	0.8-7.5	20	Fresh or frozen	Benke et al. 1999
Procladius spp.	Alabama, USA	0.00077 ± 0.00006	2.693 ± 0.154	0.91	1.0-9.8	32	Fresh or frozen	Benke et al. 1999
Empididae	Black forest, Germany	0.0047	2.7288	0.72	1.8-6.2	32	Frozen	Meyer 1989
Limoniidae	Kiel, Germany	0.0039	2.4403 ± 0.1530	0.99	6.0-16-0	22	Fresh	Poepperl 1998
Simuliidae	Necker, Switzerland	0.0029	2.49 ± 0.17	0.92	1.2-7.8	20	Frozen	Burgherr & Meyer 1997
Tipulidae								
Pedicia sp.	Black forest, Germany	0.0009	3.1059 ± 0.1667	0.95	6.5-32.0	19	Frozen	Meyer 1989
EPHEMEROPTERA	Lake Constance, Germany	0.0078	2.74 ± 0.11	0.77	---	180	Fresh	Baumgartner & Rothhaupt 2003
Baetidae								
Baetis spp.	Necker, Switzerland	0.0039	2.67 ± 0.13	0.91	1.2-9.5	42	Frozen	Burgherr & Meyer 1997
Caenidae								
Caenis spp.	Lake Constance, Germany	0.0051	2.75 ± 0.16	0.76	1.15-6.30	99	Fresh	Baumgärtner & Rothhaupt 2003
Heptageniidae	Necker, Switzerland	0.0013	3.55 ± 0.10	0.94	2.1-16	73	Frozen	Burgherr & Meyer 1997
GASTROPODA	Lake Constance, Germany	0.0193	3.30 ± 0.18	0.95	---	18	Fresh	Baumgärtner & Rothhaupt 2003
Hydrobiidae								
Potamopyrgus antipodarum	Kiel, Germany	0.1526	2.3761 ± 0.0435	1.00	0.6-5.2	703	Fresh	Poepperl 1998
Planorbidae								
Ancylus fluviatilis	Black forest, Germany	0.0357	3.1403 ± 0.0960	0.98	1.7-7.8	27	Frozen	Meyer 1989

Taxon	Locality/system, country	a ± 1 SE	b ± 1 SE	r²	Range [mm]	n	Preservative	Source
HETEROPTERA								
Corixidae								
Sigara sp.	North Carolina, USA	0.0031 ± 0.0002	2.904 ± 0.157	0.81	3.4-6.8	14	Frozen	Smock 1980
HIRUDINEA	Kiel, Germany	0.0252	1.8413 ± 0.2733	0.73	---	93	Fresh	Poepperl 1998
Erpobdellidae								
Erpobdella octoculata	Kiel, Germany	0.0058	2.2255 ± 0.1190	0.98	2.0-32.0	42	Fresh	Poepperl 1998
Glossiphoniidae								
Helobdella stagnalis	Kiel, Germany	0.0294	1.7525 ± 0.1230	1.00	4.0-10.0	31	Fresh	Poepperl 1998
ODONATA								
Calopterygidae								
Calopteryx sp.	Virginia, USA	0.0050 ± 0.0008	2.742 ± 0.222	0.87	2.0-16.1	25	Fresh or frozen	Benke et al. 1999
Coenagrionidae								
Coenagrion puella	Herzogenburg, Austria	0.02 ± 1.34	1.85 ± 0.16	0.89	1.0-15.4	68	Pres. formalin	Waringer 1982
Gomphidae	Elbe, Germany	0.0019 ± 0.0021	3.1294 ± 0.4991	0.86	1.30-9.76	12	70% ethanol	own study
Gomphus spp.	Virginia, USA	0.0060 ± 0.0008	2.847 ± 0.388	0.90	3.0-37.1	24	Fresh or frozen	Benke et al. 1999
TRICHOPTERA								
Hydropsychidae								
Hydropsyche spp. (HW)	Black forest, Germany	1.2312	2.8606 ± 0.0695	0.827	0.3-2.5	357	Frozen	Meyer 1989
Leptoceridae								
Ceraclea spp.	Lake Constance, Germany	0.0013	4.63 ± 0.55	0.95	2.23-4.56	6	Fresh	Baumgärtner & Rothhaupt 2003
Mystacides sp. (HW)	Kiel, Germany	3.7059	3.5539 ± 0.7503	0.92	0.15-0.65	60	Fresh	Poepperl 1998
Oecetis spp.	Virginia, USA	0.0034 ± 0.0006	3.212 ± 0.251	0.71	1.2-8.0	23	Fresh or frozen	Benke et al. 1999
Limnephilidae	Black forest, Germany	0.0054	2.966 ± 0.0866	0.93	1.3-23.4	93	Frozen	Meyer 1989
Psychomyiidae	Black forest, Germany	0.0018	3.1298 ± 0.2382	0.88	3.1-13.6	26	Frozen	Meyer 1989

Table 1.4 Head width-body length regression equations derived from my study in the River Elbe, Germany. Equations are of the form $BL = a + b \times HW$, with BL = total body length [mm], HW = head width [mm], and *a* and *b* as fitted constants. The regressions are significant with $p<0.0005$. Range HW = range of head width measured for the regression [mm], Range BL = range of total body length measured for the regression [mm], n = number of individuals used.

Taxon	**a ± 1 SE**	**b ± 1 SE**	**r^2**	**Range HW [mm]**	**Range BL [mm]**	**n**
DIPTERA						
Simuliidae						
Simulium sp.	-0.5027 ± 0.1330	9.3906 ± 0.3278	0.76	0.162-0.628	0.932-5.823	262
EPHEMEROPTERA						
Baetidae						
Cloeon dipterum	0.1311 ± 0.1358	5.4157 ± 0.1955	0.80	0.182-1.352	1.215-8.875	146
Caenidae						
Caenis sp.	-0.0750 ± 0.0606	4.5544 ± 0.1185	0.83	0.149-1.168	0.833-6.164	315
Caenis luctuosa	0.0250 ± 0.1177	4.2341 ± 0.2161	0.79	0.299-0.871	1.116-4.300	104
Caenis macrura	-0.5749 ± 0.1946	5.5912 ± 0.3745	0.79	0.299-0.941	1.084-5.066	60
Heptageniidae						
Heptagenia sp.	-0.2885 ± 0.1456	3.4267 ± 0.0923	0.95	0.196-4.005	0.587-15.396	75
Heptagenia flava	-1.2445 ± 0.5735	3.8398 ± 0.2614	0.90	0.341-4.005	1.387-15.396	26
ODONATA						
Anisoptera						
Gomphidae	0.1949 ± 0.1632	4.8805 ± 0.0853	0.99	0.179-6.103	0.936-30.374	45
Gomphus sp.	0.8102 ± 0.2674	4.7555 ± 0.1056	0.99	0.179-6.103	0.936-30.374	24
Gomphus vulgatissimus	1.0220 ± 0.4121	4.6760 ± 0.1174	0.99	0.910-6.103	5.303-30.374	12
Ophiogomphus sp.	-0.2563 ± 0.1205	4.8592 ± 0.1573	0.98	0.350-2.135	1.193-9.763	18
Zygoptera	-0.7763 ± 0.2593	5.1245 ± 0.1543	0.91	0.284-4.131	1.805-21.218	114
Coenagrionidae						
Coenagrion sp.	-0.7558 ± 0.2660	5.0898 ± 0.1623	0.92	0.284-4.131	2.012-21.218	87
Platycnemididae						
Platycnemis pennipes	0.2005 ± 0.5889	4.1275 ± 0.3203	0.92	0.784-2.641	3.387-12.123	16
TRICHOPTERA						
Leptoceridae						
Mystacides sp.	-1.0042 ± 0.4564	16.4872 ± 1.3915	0.93	0.141-0.602	0.879-8.957	12
Oecetis sp.	-0.2550 ± 0.1805	6.9855 ± 0.5417	0.83	0.120-0.632	0.752-4.777	36
Oecetis notata	-0.3561 ± 0.5214	6.9743 ± 1.3806	0.72	0.242-0.548	1.843-3.924	12
Limnephilidae	0.1861 ± 0.3593	8.6398 ± 0.3961	0.88	0.162-2.049	1.270-18.518	70
Limnephilus sp.	0.1184 ± 0.4142	8.6246 ± 0.4311	0.88	0.162-2.049	1.323-18.518	59
Limnephilus lunatus	0.4538 ±0.3616	7.9122 ± 0.4409	0.88	0.162-1.445	1.323-13.389	48
Limnephilus rhombicus	0.9024 ± 2.2970	8.6211 ± 1.6176	0.76	0.422-2.049	3.298-18.518	11

I chose only those regressions that exceeded a coefficient of determination of $r^2>0.70$, which was not the case for e.g. *Ceraclea* sp. or Leptoceridae (data not shown). Only five regressions yielded an $r^2<0.80$, ten reached or exceeded a value of $r^2=0.90$ (Table 1.4). The shortest range of head width was detected for *Oecetis notata* with 0.242-0.548 mm, but it is very likely that there were some smaller-headed individuals missing in the regression that could not unambiguously be determined to the species level (see *Oecetis* sp., which doubtless includes several individuals of *Oecetis notata*). With 0.179-6.103 mm, the by far largest range of head width could be detected for Gomphidae. While the lowest number of measured individuals for the regression construction was applied for *Limnephilus rhombicus* (n=11), the highest number of individuals was used for the regression of *Caenis* sp. (n=315). The mean number of used individuals was n=74.

Cohort production intervals (CPIs)

New cohort production intervals (CPIs) were constructed and the literature was reviewed for all taxa that were highly abundant and frequently found during all sampling campaigns and could thus be processed for secondary production estimates (for details see chapter 2). This collection comprises CPI values for 32 taxa; eleven on the species level, 14 on the genus level, two on the Chironomidae-tribe level and five on the family level (Table 1.5). From the 32 CPI values I derived five on my own, i.e. *Jaera istri*, *Robackia demeijerei*, Tanytarsini, Simuliidae and *Setodes punctatus*.

The slowest development time was found for *Pisidium* sp. (CPI=1,043 d), while the fastest development time was calculated for species of the genus *Rheotanytarsus* (CPI=11 d). The mean value of all CPIs in this study is 222 days. Except for the family Chironomidae, the sources from which the CPI values were extracted differ widely. The majority (14 of 16) of the CPIs for Chironomidae were calculated applying the equation (3) published by Mackey (1977).

Table 1.5 Collection of cohort production intervals (CPI) for several taxa that were sufficiently abundant, frequently found and thus processed in secondary production estimates during my study. CPI values were either extracted from literature or developed during this study (indicated as "own data"). CPI = development time in days, source = reference. [1] Arithmetic mean from all Orthocladiinae, [2] Arithmetic mean from all Chironomini.

Taxon	CPI [d]	Source
BIVALVIA		
Corbiculiidae		
Corbicula fluminea	913	Sousa et al. 2008
Sphaeriidae		
Pisidium sp.	1,043	Holopainen & Hanski 1986
Sphaerium sp.	365	Mitropolskii 1966
CRUSTACEA		
Corophiidae		
Chelicorophium curvispinum	365	Rajagopal et al. 1999
Gammaridae		
Dikerogammarus villosus	365	Pöckl 2009
Janiridae		
Jaera istri	365	Own data
DIPTERA		
Ceratopogonidae	365	(González *et al.* 2001)
Chironomidae		
Chironominae		
Chironomini	40	Mackay 1977 [2]
Camptocladius stercorarius	17	Mackey 1977 [1]
Chironomus sp.	30	Mackay 1977
Cryptochironomus sp.	73	Mackay 1977
Dicrotendipes nervosus	65	Mackay 1977
Polypedilum sp.	29	Mackay 1977
Rheotanytarsus sp.	11	Mackay 1977
Robackia demeijerei	121	Own data
Orthocladiinae.	17	Mackay 1977 [1]
Cricotopus sp.	21	Mackay 1977
Eukiefferiella sp.	17	Mackay 1977 [1]
Tvetenia sp.	17	Mackay 1977 [1]
Tanypodinae		
Procladius sp.	173	Mackay 1977
Tanytarsini	30	Own data
Cladotanytarsus sp.	13	Mackay 1977
Tanytarsus sp.	40	Mackay 1977 [2]
Simuliidae	61	Own data
EPHEMEROPTERA		
Baetidae		
Cloeon dipterum	102	Harker 1997
Caenidae		
Caenis sp.	299	González, Basaguren & Pozo 2001
GASTROPODA		
Hydrobiidae		
Potamopyrgus antipodarum	451	Roth 1987
Physidae	365	Glöer 2002
Planorbidae		
Ancylus fluviatilis	365	Streit 1976
ODONATA		
Coenagrionidae	365	Waringer & Humpesch 1984
TRICHOPTERA		
Hydropsychidae		
Hydropsyche sp.	365	Lecureuil *et al.* 1983
Leptoceridae		
Setodes punctatus	240	Own data

1.4 Discussion

Length-mass regressions and cohort production intervals are crucial elements for a convenient and precise estimation of biomass and secondary production (Benke 1979; Meyer 1989; Poepperl 1998; Benke *et al.* 1999). The literature search and construction of new regression equations resulted in a comprehensive data base for both the following analyses in this thesis and future studies. As former studies were mainly conducted in smaller streams, this is the first time a collection provides selected equations and CPIs for large European lowland river-dwelling organisms including common non-native species.

Application and assessment of length-mass regressions

The predictive quality of the self-constructed length-mass regressions can be assessed as high (c.f. Benke *et al.* 1999). The percentage of explained variation for all length-mass regressions by far exceeds 80%. The *b* values of the regressions for the aquatic insects and also two Crustacea fall into the range of most published data, which is close to 3 (Benke *et al.* 1999). In contrast to the majority of published regressions, which mainly used single individuals for their establishment (e.g. Smock 1980; Poepperl 1998; Johnston & Cunjak 1999; Benke *et al.* 1999), I used size classes, partly with very high numbers of individuals, at least for the very small size ranges. The regressions for which I solely applied size classes resulted in high coefficients of determination ($r^2>0.97$; Fig. 1.3; Table 1.2). The use of size classes has several advantages, though it might also have some drawbacks. On the one hand, the error of the balance is evened out, especially for the smallest individuals. In case of *Robackia demeijerei* an error of only 1 µg would result in a relative weighting error of more than 33% for the first size classes (Table 1.2). Additionally, when using size classes, undesired particles like detritus or dust that may accidently remain on some individuals do not play a significant role. Therefore, it is sufficient to clean individuals roughly with forceps and needles under the microscope instead of using ultrasonic sound as a pre-treatment. On the other hand, an inherent variance due to taxa-specific and mass-influencing sexual dimorphism, as occurring in many Crustacea taxa (e.g. Devin *et al.* 2004), cannot be assessed. The use of high numbers of individuals per size class evens out the variance that would be generated if only single individuals were used for the regression establishment. However, whole community biomass estimates or secondary production calculations require the handling of vast numbers of individuals from several periods of the year (e.g. Georgian & Wallace 1983;

Benke 1998; Cross *et al.* 2011). It is very likely that in this type of studies individuals are used that cover the entire range of possible individual variance concerning length and weight and thus the lack of information on the degree of variance for size class-dependent equations does not play a significant role. Technically seen the use of size classes safes a lot of time and laboratory material while at the same time providing useful results for large data sets.

Apart from the above-mentioned types of biases, several other factors are regularly being discussed to have a profound influence on the quality and applicability of length-mass regressions. One very important factor turns out to be the type of preservative used before the establishment of the regressions. In principle, four types of sample treatments can be found: fresh (Benke & Jacobi 1994), frozen (Meyer 1989), formalin-preserved (Clifford, Hamilton & Killins 1979) and ethanol-preserved (Breitenmoser-Würsten & Sartori 1995). All of these handling techniques, including the use of fresh individuals, result in a certain bias. The fact that many studies accounted for gut clearing or removed the gut contents before processing (e.g. Mason 1977; Dudgeon 1989; Poepperl 1998), while others used individuals that still contained unknown amounts of food items (Meyer 1989; Baumgartner & Rothhaupt 2003), has an influence on dry mass even for fresh or frozen individuals. Chemical preservation can result either in a mentionable mass reduction of dry mass (Howmiller 1972; Ladle, Bass & Jenkins 1972; Iversen 1980; Leuven *et al.* 1985), or, as is the case for large caddisfly larvae, only in negligible changes (Ross & Wallace 1983; Mackay 1984). I preserved samples in 70% ethanol. It is reported that individuals of *Simulium* sp. can lose about 20% of dry mass through conservation in ethanol (Schwoerbel 1994). Being a close relative with a comparable morphology, much the same may apply to the individuals of *Robackia demeijerei* in my study. It was the only handled taxa with a thin and fragile cuticle, a fact that could cause a mass loss through leaching. Lowest losses, however, are reported for the Crustacea *Gammarus fossarum* that only loses about 8% of dry mass after several days of preservation in 70% ethanol (Schwoerbel 1994). It can be assumed that due to the comparably thick exoskeleton the three Crustacea taxa from my study are subjected to similar minor mass losses. Contrary to the mass loss, other authors found that about 4% of dry mass of *Chironomus plumosus* (Chironomidae) could be designated to gut content (Landahl & Nagell 1978) and even higher proportions can be expected for other taxa (Johnston & Cunjak 1999). Hence, there are arguments for both under- and overestimation, so that in total reasonable results with low error can be assumed in this study at least for Crustacea.

Possibly even more important than the chosen preservative is the consideration of the size range for which a regression is constructed. As body mass increase is higher in larger individuals than in smaller ones, applied equations should be constructed from organisms covering the entire size range of the processed individuals (Johnston & Cunjak 1999). This becomes obvious by taking a closer look at the regression plots of *Dikerogammarus villosus* and *Robackia demeijerei* (Fig. 1.3). If only the first 30% of the entire size range were used for the regression calculation, the plane slope at the beginning of the curve would have to be strongly extrapolated for larger organisms and would most likely result in highly deviating estimates in upper size ranges. In the particular case for *D. villosus*, applying a regression that is only based on the first 20 values (Table 1.2) resulted in significantly lower dry mass estimates. Dry weight estimation of an individual that has a length of 25 mm would result in a 26% lower value than if it was calculated by the entire size range-based regression (data not shown). Generally, the quality of the regression equations for the different taxa increases with the sample size and when the samples are equally distributed over the size range (Baumgartner & Rothhaupt 2003). Apart from the equation for Gomphidae, my length-mass regressions most likely cover the entire size spectra that can occur in the respective taxa (Table 1.2), as sampling was conducted over the span of an entire year. Additionally, I used vast numbers of organisms from a narrow size class interval for each of the regressions. Hence, the quality of the newly established regression equations is further consolidated.

A significant part of variation in predictions may not only be attributable to methodological distinctions, but also to regional, climatic and taxonomic differences in mass and length (Johnston & Cunjak 1999). In the majority of cases the equations for a lower taxonomic level explain a greater proportion of variance than equations on higher taxonomic levels do. It is thus recommended to choose equations for the lowest taxonomic level possible whenever a high accuracy is needed (Smock 1980; Meyer 1989). Then again, several authors recommended caution as regressions for the same taxa from different regions or systems can vary significantly (e.g. Smock 1980; Meyer 1989; Wenzel, Meyer & Schwoerbel 1990; Burgherr & Meyer 1997). Besides variation between investigators, regional differences accounted for the largest proportion of variation (1-17%) in a recent study (Méthot *et al.* 2012). This may be mainly due to the physical-chemical environment and the quality and availability of food (Johnston & Cunjak 1999; Benke *et al.* 1999). I tried to account for the climatic region and the system from where length-mass regressions were established. However, especially the latter precondition was hard to fulfill because during my study I also found many lentic species in slow flowing areas of the River Elbe. The remarkable combination of large river and highly specific meso-habitat significantly reduces the chance of finding regressions in literature for exactly those conditions. Thus, some length-mass regressions had to be taken from different systems (e.g. Lake Constance, Baumgartner & Rothhaupt 2003), although the majority of regressions for highly abundant taxa (e.g. *Dikerogammarus villosus*) originated from related systems.

Usefulness of head width-body length regressions

In a variety of situations head width-body length regressions can be useful. If, for instance, in addition to biomass estimation the question of interest is the determination of instars, measurement of head width is the most reasonable strategy (Dermott & Paterson 1974). Another situation can be the dry mass estimation of damaged individuals (e.g. due to rough sampling or partly digestion in stomach analyses), because the heavily sclerotized head capsule is hardly affected by physical or chemical stress and can hence still be used for biomass determination. If in those scenarios available length-mass regressions are based on body length, head width-body length regressions provide support.

The 21 established head width-body length regressions provided here are all of high accuracy (r^2>0.72; Table 1.4). While head capsule width barely changes between instars, body length can do so considerably (Johnston & Cunjak 1999). Hence, one may expect the highest proportion of explained variation in taxa that bear the highest number of larval instars, because the entire final body length is distributed over several, relatively fixed head capsule widths. Although Odonata run through only 15 instars (Corbet 1980), in this study they yielded much higher mean coefficients of determination (mean r^2=96; Table 1.4) than Ephemeroptera, which often run through more than 25 instars (Fink 1980) (mean r^2=0.85). One likely explanation is that the intraspecific head width and length variation of *Caenis luctuosa* is higher than in taxa of the order Zygoptera that were measured. As for both groups a comparable number of individuals were assessed, their coefficients of determination are not influenced by the sample size. Although it seems obvious that if a taxon has more instars, the more precise the head width-body length regression should be, this cannot be confirmed by my data. However, the calculated values for the factor *b* in the presented equations seem to be reasonable and well in range with formerly published regressions (Burgherr & Meyer 1997). The mean value of all Trichoptera (b=9.2) almost precisely matches the value calculated by Burgherr and Meyer (b=8.9), thus supporting the applied methodology.

Like for the dry mass, chemical preservation was also detected to potentially cause significant changes in length (Britt; Kulka & Corey 1982; Lasenby, Yan & Futter 1994). It can be expected that these effects are most prominent in taxa bearing a thin cuticle and having a very large length to width ratio, like Oligochaeta or several Chironomidae taxa. This may also apply to some of the Trichoptera species, especially from the family Leptoceridae, which have only a slightly sclerotized abdomen. However, the above-mentioned *b* value, which is almost perfectly in range with that from other published equations, proves that in this case the changes in length due to preservation are not severe. Species from Ephemeroptera and Odonata are more or less heavily sclerotized and should, if at all, hardly be affected.

The possible shrinking of body length after chemical preservation should be at least taken into account when applying head width-body length regressions for some taxa prone to shrinking. Furthermore, as the growth pattern in head capsules happens stepwise and not continuously, head width often accounts for less variation in length-body mass regressions than total body length does (Meyer 1989; Wenzel *et al.* 1990; Towers, Henderson & Veltman 1994; Burgherr & Meyer 1997; Johnston & Cunjak 1999). Nevertheless, the presented regressions for length conversion are of high accuracy and hence provide support if dry mass cannot be calculated from head width immediately.

Difficulties in cohort production interval (CPI) establishment

Cohort production intervals (CPIs) are even less available than length-mass regressions. Hence, the CPI collection provided in this study is, to my knowledge, the first that includes all highly abundant taxa occurring in a large lowland river.

Many CPIs accessible from literature are based on assumptions or are often roughly defined to be one year (e.g. Waringer & Humpesch 1984; Pöckl 2009), so the applicability had to be tested carefully for the system I worked in. At least, the resulting CPI of 365 days provides a conservative estimate that is, in most cases, not underestimating the real development time. It is easier to detect CPIs for insects than for fully aquatic taxa such as Gastropoda and Crustacea, for which the recognition of one complete life cycle in the field is quite difficult. This is why CPIs for these taxa are often based on intensive field studies or laboratory experiments (e.g. Streit 1976; Sousa *et al.* 2008a). However, the maximum life span that is detected in laboratories does not necessarily reflect the conditions in the field. Organisms may grow much shorter in nature due to frequent harsh conditions or predation.

For this chapter conservative values for the CPI collection that should not underestimate the actual development time were chosen (Table 1.5). If several values were available for one taxon, I calculated the mean. All CPIs in this collection that do not reflect the maximum development time (e.g. *Corbicula fluminea* or *Pisidium* sp.) were carefully checked for convergence with my data nevertheless. Hence, I can be certain to have used and provide CPI values whose application is very unlikely to result in an overestimation of the actual secondary production presented in chapter 2 and of that in future studies.

Conclusion

This study presents carefully chosen and generated data that provide the basis for biomass and secondary production estimates following in the next chapters. All methods and preservatives produce certain kinds of biases. Some result in an over-, others in an underestimation of biomass. Errors by mass losses through leaching in a certain preservative for some taxa might be compensated by gut contents that remained in the individuals. However, other sources of errors (e.g. sampling procedure or interval) may substantially affect final results and will be taken into account for secondary production estimates in chapter 2. The presented collection will facilitate future functional studies in large European lowland rivers and comparable systems. The information given here is crucial for the estimation of whole benthic community biomass and secondary production, especially when non-cohort based calculation methods are used. As non-native species are frequently establishing in new ecosystems, updated data bases already are and regularly will be needed in future. I added three new regressions and one CPI for common and widespread invasive Crustacea that will help to minimize current knowledge gaps.

2. Chapter:

Shore types control diversity and secondary production of macroinvertebrate communities in a large lowland river

2.1 Introduction

The majority of the world's large rivers are characterized by rip raps, groynes, or similar structures that are key components of their shores and riparian zones (Shields 1995; Gregory 2006; Habersack, Jäger & Hauer 2013). Most of these structures are created to confine the river flow to the main channel causing an increase in bed shear stress and incision of the river channel, thus facilitating commercial navigation (McCartney *et al.* 2012). Man-made shore structures also alter the near-shore hydromorphology and sediment dynamics (Sukhodolov *et al.* 2002). Groynes, for example, a common shore type in lowland rivers, are sinks for fine sediments (Ockenfeld & Guhr 2003; Schwartz & Kozerski 2004) and cause an accumulation of particle-bound heavy metals and organic pollutants (Echols *et al.* 2008; Baborowski *et al.* 2012). Furthermore, river channelization alters habitat availability and configuration. The heterogeneous mosaic of various mesohabitats with their different hydraulic regimes is usually replaced by construction materials that are not autochthonous, for example stones or boulders (Battle, Jackson & Sweeney 2007). Alterations of riparian hydromorphology may have serious ecological consequences as the shore and riparian zone are hot spots for riverine biodiversity (Wolter & Bischoff 2001; Strayer & Findlay 2010). Strayer *et al*. (2012) studied macroinvertebrate, fish and terrestrial plant communities in the Hudson River and showed that their diversity was lower at altered than at natural shores. Standard groynes in the River Elbe had a lower abundance of indicator species for natural, sandy riverine habitats compared to ecologically optimized groynes with higher hydromorphological diversity (Kleinwächter *et al.* 2005). On the other hand, rip rap structures have been shown to have a comparable macroinvertebrate diversity and numerical abundance like natural shorelines (Shields, Cooper & Testa 1995). The extent to which shore modification impacts main channel communities has, to my knowledge, not been studied previously.

Besides the direct effects exerted by flow modification and degradation of habitats there is preliminary evidence that anthropogenic shore types may favor the establishment of non-native species (Johnson, Olden & Vander Zanden 2008). The primary reason for such invasions is the loss of natural barriers due to shipping, channel connection and other human activities (Hulme *et al.* 2008). Nevertheless, the successful establishment of a neozoa population depends on the local opportunities an invader is provided with in its new environment. Besides the availability of resources and the ability to act as a predator, the physical habitat presents an important factor that can contribute to the success of an invasive species (Moyle & Light 1996). For example, a recent study illustrated that suitable ecological niches for biological invasions are created by morphological and physicochemical degradation of streams and rivers (Frueh *et al.* 2012). This has also been shown to occur in the River Rhine, where invasive amphipods dominated macroinvertebrate communities in artificial stone habitats (Van Riel *et al.* 2006, 2011). Therefore, neozoa might further enhance negative effects of hydromorphological degradation on native communities by acting as competitors and predators. Given the fact that man-made corridors between formerly isolated catchments are known to support the invasion of new species in a non-controllable way, it is a challenge for river management to create habitat conditions that hamper the establishment of invading neozoa.

While the effects of shore modifications on biodiversity and community composition are at least partially documented, the implications of altered hydromorphology for the functioning of large river ecosystems are largely unknown. Published studies concerning the patterns of benthic secondary production in large sandy rivers suggest that the secondary production follows patterns of biodiversity with the highest values measured at the shore and riparian zone and the lowest values in the main channel (Benke *et al.* 1984; Zilli 2013). Given this tight relationship between community structure and functioning, secondary production may be sensitive to hydromorphological changes induced by artificial shore types (c.f. Elosegi & Sabater 2013).

In the present study, mesohabitat-specific benthic macroinvertebrates from three different shore types as well as the adjacent main channel of the River Elbe (Germany) were sampled over a period of twelve months. First, the hypothesis that both benthic diversity and secondary production in the main channel are low and independent from the adjacent shore type was tested. Second, diversity and production were compared to test if the three shore types have systematically different effects on the benthic community. Third, the share of neozoa to community composition and functioning was compared between the three shore types to test if the establishment of neozoa may be facilitated by a certain construction type.

2.2 Material and Methods

Study site

A 4-km reach of the River Elbe, an 8th order sandy lowland river, upstream from the city of Dessau (river km 250-254; 51°52'53.68"N, 12°17'56.53"E) was studied. The river is used for commercial and private navigation and most sections of the watercourse are modified by standard groynes and other shore constructions (Scholten *et al.* 2005). As study sites the three most abundant shore types, i.e. standard groyne, rip rap and off-bankline revetment, were chosen. The studied standard groyne consists of stone bars installed almost perpendicular to the shore (Fig. 2.1) with a ratio between the length of the groyne to the length of the groyne field of 0.7. The studied off-bankline revetment (terminology following McCartney *et al.* 2012) is a stone bar with a length of approximately 500 m installed 5-30 m in front of the shore, parallel to the flow direction (Fig. 2.1). The shoreline itself is not modified and exhibits a near-natural sediment regime, including erosion. An upstream and a downstream opening created a secondary flow that varied with the river’s water level and also included stagnant pool conditions during low water levels. At each shore type the three prevailing mesohabitats were sampled, i.e., the transition zone, ranging from the water margin to a water depth of up to 30 cm; the groyne field, defined as the area with a water depth of 30 to 150 cm; and stones that constitute the actual construction. These mesohabitats were chosen as they have previously been shown to harbor a distinct macroinvertebrate fauna (Brunke *et al.* 2002). Samples from the main channel in front of each shore type were taken at a distance of 15 m from the top of the respective structure.

The wetted areas of the mesohabitat types from the standard groyne and off-bankline revetment were mapped using a total station equipped with a differential GPS (Leica TPS 1200, Leica Geosystems, Munich, Germany) for all wadable areas and an echosounder (Humminbird 1198c, Johnson Outdoors Marine Electronics, Eufaula, USA) for areas not wadable. Geographical coordinates and height were measured every 2.5 m along transversal transects spaced 6.5 m apart in the standard groyne and every 3.5 m along transversal transects spaced 20 m apart in the off-bankline revetment.

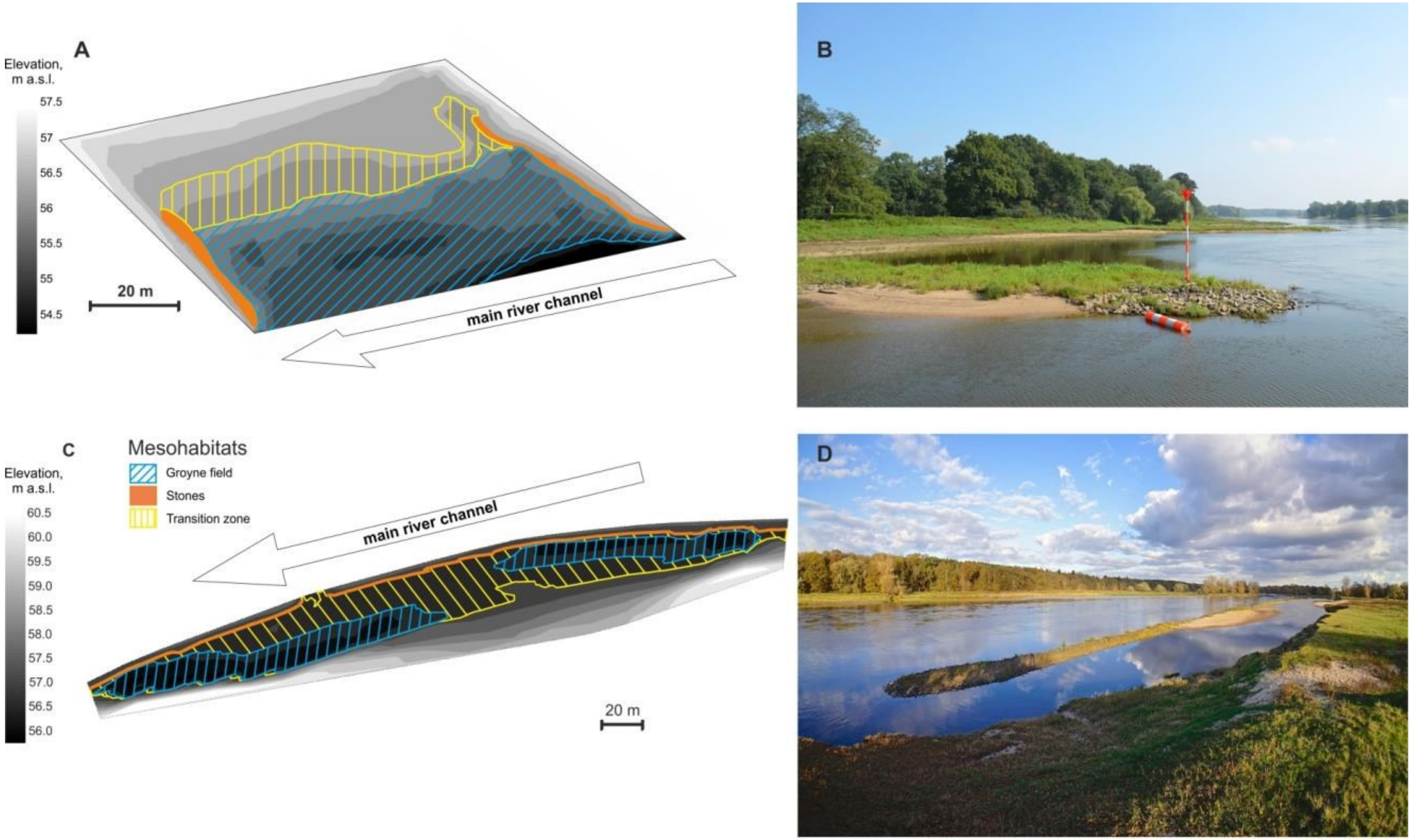

Fig. 2.1 Bathymetric map and photo of the standard groyne (A, B) and the off-bankline revetment (C, D) and the proportions of the mesohabitats for an average water level over the course of the study. The rip rap (not shown) has not been bathymetrically mapped due to its constant inclination of 30°.

Subsequently, after creating a regularly spaced grid with a grid cell area of approximately 0.2 m^2, a linear interpolation was conducted using Matlab (Version 8.0, MathWorks Inc., USA). Daily water levels for the sampling sites were calculated by linearly interpolating mean daily values from the two nearest gauging stations (Vockerode at km 246, Rosslau at km 258). Finally, the wetted area of each shore type and mesohabitat on each day was calculated as the number of grid cells covered at a given water level multiplied by the grid cell area. The wetted area of stones was visually estimated in the field during sampling. I did not map mesohabitat areal extensions of the rip rap as it has a constant inclination of 30° and the proportions of the mesohabitats were constant, irrespective of the water level. Here, transition zone and groyne field theoretically contributed 20 and 80%, respectively, to the shore type, but were corrected for the contribution of stones in each campaign.

Macroinvertebrate sampling and processing

Macroinvertebrates were sampled monthly from April 2011 to March 2012, except for January and February 2012, where a flood prevented sampling (Fig. 1.1). The mesohabitats transition zone and groyne field were sampled with a Surber sampler (250 µm mesh). Five replicates were taken in both mesohabitats at each structure (sampled area: 0.31 m^2). The mesohabitat stones was sampled by randomly selecting three to five boulders (sampled area: approx. 0.3 m^2) and brushing off attached macroinvertebrates. The sampled area was calculated by measuring length, height and width of each boulder. Samples from the main channel in front of each shore type (total sampled area: 0.21 m^2) were taken by an air-lift-sampler (100 µm mesh, UWITEC, Mondsee, Austria), operated from the research vessel “ALBIS” (Helmholtz-Centre for Environmental Research - UFZ, Magdeburg). Samples were preserved in 70% alcohol and macroinvertebrates were sorted, counted and identified to species or genus, except for Oligochaeta (order level) and Diptera (family level) excl. Chironomidae (species or genus level, identified by **Dr. Emmanuel Gaulme** (Arles, France) und **Dr. Xavier-Francois Garcia** (Berlin, Germany)). The first 200 individuals of each taxon were measured for body length to the nearest 0.01 mm with a microscope (Keyence VHX-1000, Keyence Corporation, Osaka, Japan). Individual weight was calculated using the length-mass relationships from chapter 2.

Secondary production

Secondary production was calculated for all taxa except Oligochaeta (see below) that were sufficiently abundant (N > 100) in each mesohabitat and shore type using the size-frequency method. The size-frequency method was chosen as taxa encountered in this study had either overlapping or undiscernible cohorts. Secondary production at the species level could not be estimated if identification of early instars was impossible. In such cases, production estimates were made at the genus or family level. I corrected for cohort production intervals (CPI) using the values from chapter 2. For rare taxa having a total abundance of <100 individuals per mesohabitat at a given shore type, but >100 individuals at the entire shore type, shore type-specific production and P/B ratios were calculated. The P/B ratio was subsequently multiplied by the mesohabitat-specific mean annual biomass of the respective taxa to estimate the mesohabitat-specific production. Secondary production for Oligochaeta was estimated using a P/B ratio of 5 (Benke & Huryn 2010), because the high taxonomic level and the poor condition after sample treatment and preservation prevented the determination of individual weights.

Uncertainties in the estimates of secondary production were quantified using non-parametric bootstrap analysis (Efron & Tibshirani 1994). Briefly, size-specific abundance data from replicate samples in each mesohabitat on each date were resampled a 1,000 times to generate vectors of mean size-specific abundance and individual weights. These values were subsequently used to calculate means and 95% confidence intervals for each taxon and mesohabitat combination. When comparing secondary production between shore types, non-overlapping confidence intervals were interpreted as evidence for a significant difference (Babler, Solomon & Schilke 2008).

Habitat and resource variables

Variables related to habitat conditions and food resource availability were measured to explain potential differences between the main channel and the shore as well as between the three shore types. Percentages of gravel, sand and benthic fine particulate organic matter (FPOM) were determined from five sediment cores taken at equidistance across each shore type. The percentages of semi-terrestrial macrophytes and boulders at each site were estimated visually during each campaign. Flow velocity at each shore type and campaign was visually classified as 0 = no flow, 1 = low flow, 2 = medium flow, 3 = high flow. Water temperature and oxygen concentration were measured with a multi-parameter probe (YSI 6920 V2, YSI, Yellow Springs, USA).

Resources were quantified as concentrations of chlorophyll a and suspended particulate organic matter (SPOM) in water samples from each shoreline type and adjacent main channel using standard methods. Standing stock of periphyton was quantified from three randomly collected boulders at each site. Attached periphyton was scraped off, dried, combusted at 550°C, and reweighed to determine ash-free dry mass (AFDM) per m^2. Organic matter content from bottom sediments was measured as loss of ignition from subsamples taken for particle size analysis.

Statistical analyses

For statistical analysis at the spatial scale of the shore type, biomass and secondary production were weighted by the wetted area of the mesohabitats for a given shore type. I compared community composition by principal coordinate analyses (PCO) and permutational multivariate analysis of variance in PRIMER (PRIMER-E Ltd., Plymouth, U.K.). Prior to analysis, I removed all taxa that were found only once during all campaigns and square root-transformed abundances.

Differences in compositional, functional and environmental variables were tested by repeated measure (RM) ANOVA and followed by Holm-Sidak tests, except for categories of flow velocity that were compared using a Friedman test followed by Tukey posthoc tests. All other variables were tested for normality and homogeneity of variances and were appropriately transformed if necessary (Sigma plot, Version 12, Systat Software, San Jose, USA).

2.3 Results

Comparison of main channel and shore

Species richness in the main channel differed significantly among shore types ($P < 0.001$). The main channel community adjacent to the off-bankline revetment had a significantly higher species richness (5 ± 3) than communities adjacent to standard groyne (2 ± 1) and rip rap (3 ± 1). Biomass ($P = 0.881$) and composition of the main channel communities ($P = 0.209$), however, did not differ significantly between associated shore types. Secondary production of the main channel differed only marginally among shore types (Table S3) and thus, I did not differentiate the main channel by shore type in subsequent analyses.

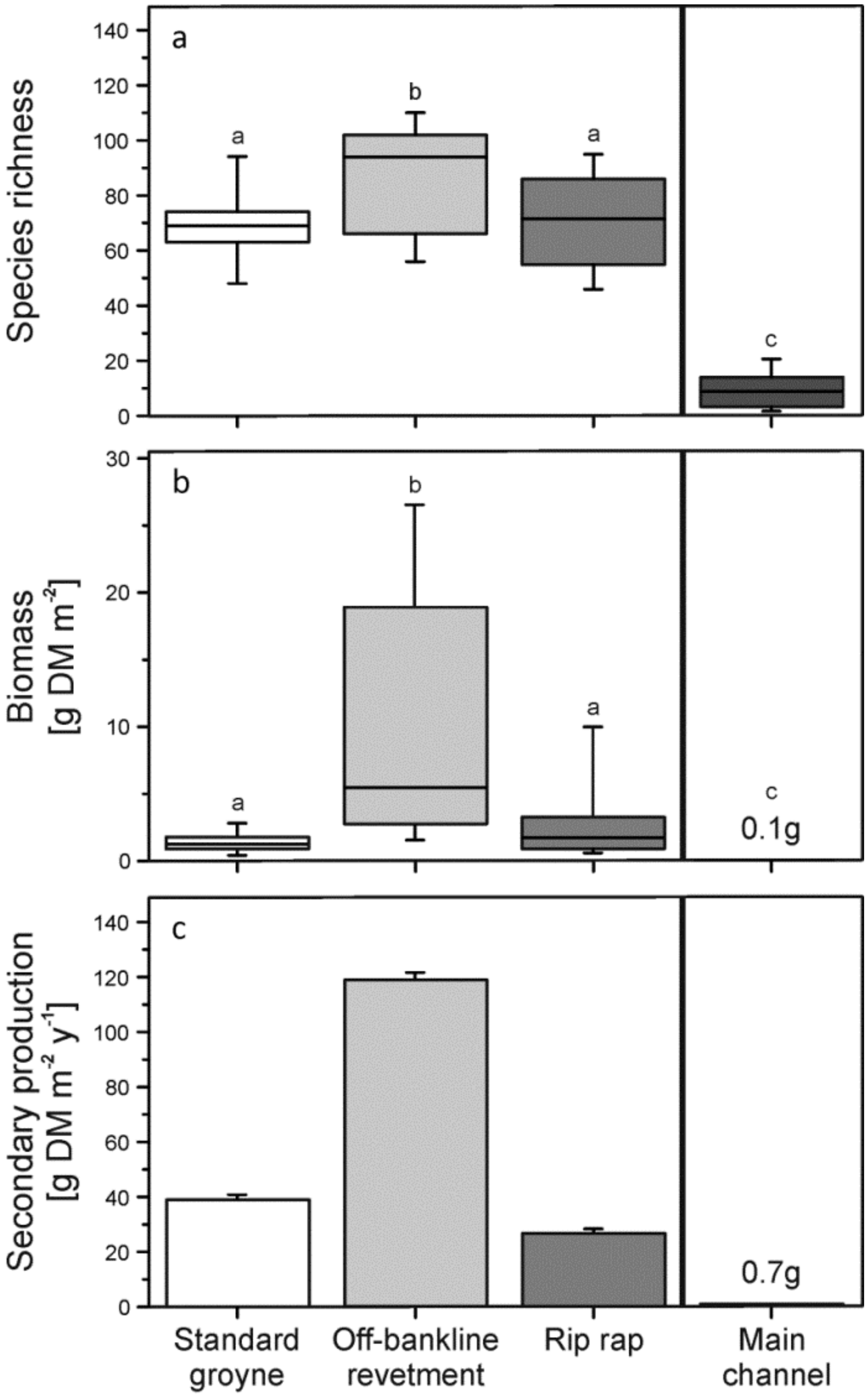

Fig. 2.2 Species richness (a), weighted biomass (b), total weighted secondary production (+ 95% CI) (c) at the studied shore types and the adjacent main channel. Significant differences ($P < 0.05$, RM ANOVA and Holm-Sidak pairwise comparisons) are indicated by different letters. The box-whisker plots represent the data from the different samplings. The horizontal line within each box indicates the median, bottom and top of the box indicate the 25th and 75th percentiles, and whiskers indicate min. and max.

In contrast to the marginal differences between the main channel communities, they all differed significantly from the adjacent shore communities (P < 0.001). Furthermore, main channel communities had significantly lower species richness and biomass than shore communities (Fig. 2.2 a,b). Secondary production was more than two orders of magnitude lower in the main channel than at the shores sites (Fig. 2.2c), with Chironomidae, Oligochaeta and Bivalvia being the only producers (Table S3). *Robackia demeijerei* (Chironomidae) alone contributed more than 50% to the total secondary production of the main channel.

Comparison of shore types

Macroinvertebrate communities grouped by shore type in the PCO ordination (Fig. 2.3) and permutational analysis of variance (PERMANOVA) revealed significant compositional differences for all pairwise comparisons (P < 0.01).

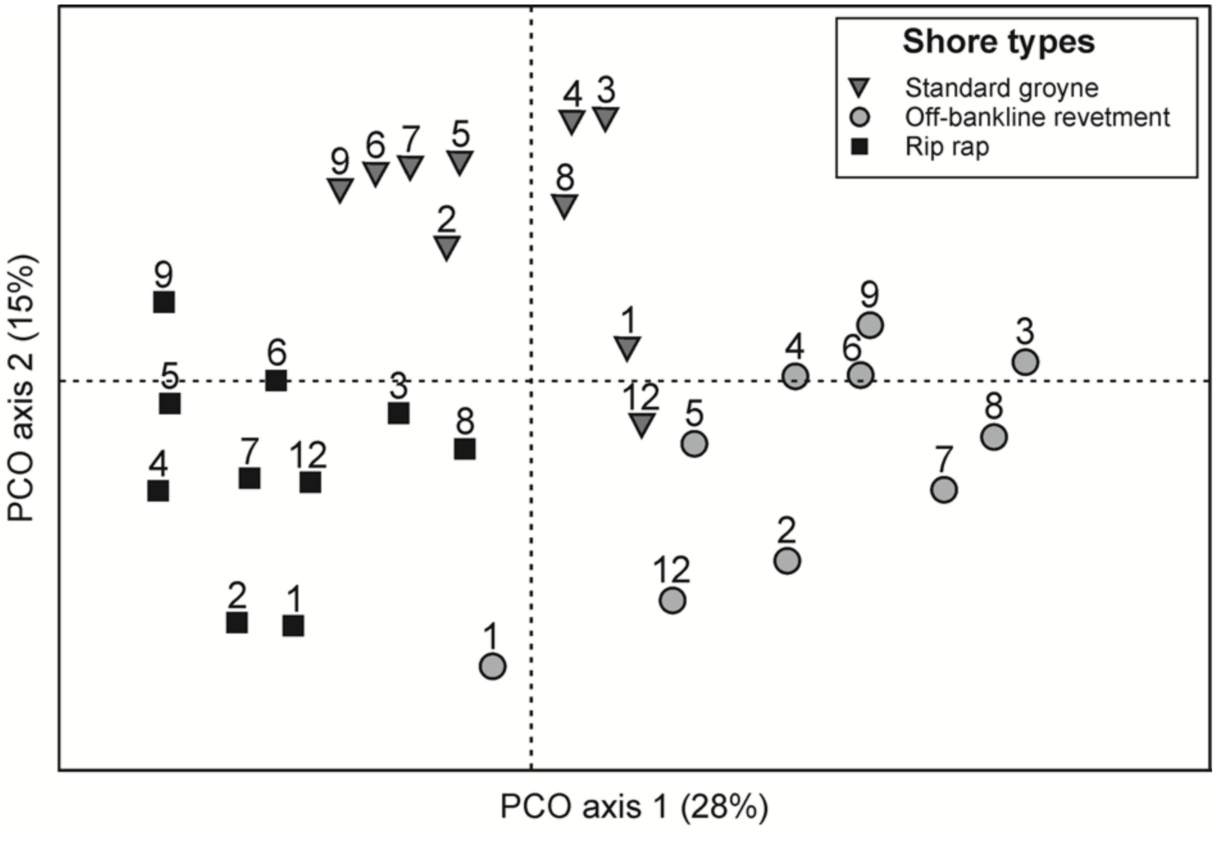

Fig. 2.3 Principal coordinate analysis of macroinvertebrate communities at the three studied shore types. Numbers refer to sample campaigns from April 2011 (1) to March 2012 (12). Campaigns January (10) and February (11) are missing due to flood events.

Species richness was significantly higher at the off-bankline revetment than at the standard groyne and the rip rap, but did not differ between the latter two shore types

(Fig. 2.2a). Similarly, biomass was significantly highest at the off-bankline revetment, but did not differ between standard groyne and rip rap (Fig. 2.2b). Secondary production was highest at the off-bankline revetment, threefold lower at the standard groyne and more than fourfold lower at the rip rap. The non-overlapping 95% CI indicate that the shore types differed significantly with respect to total secondary production.

Contribution of neozoa

The percentage contribution of neozoa to biomass did not differ significantly between shore types ($P = 0.063$). However, the contribution of invasive Crustacea to biomass at the rip rap site was significantly higher than at the other two shore types (Fig. 2.4a, $P < 0.001$). Conversely, the contribution of invasive Gastropoda to biomass was significantly higher at the off-bankline revetment than at the standard groyne and the rip rap (Fig. 2.4a, $P < 0.001$). The contribution of invasive Bivalvia to biomass did not differ between shore types ($P=0.082$). Within one and the same shore type, the contribution of neozoa to secondary production was distinctly lower than their contribution to biomass. This pattern was most obvious at the off-bankline revetment, where neozoa contributed to total biomass with an average of 67%, but less than 21% to secondary production (Fig. 2.4 a, b). However, at the rip rap site, neozoa were the most productive group with a contribution of 50% to total secondary production.

On the mesohabitat scale I tested whether a particular mesohabitat favors the contribution of neozoa to ecosystem structure and function irrespective of the shore type. The contribution of neozoa to species richness did not differ between mesohabitats (Fig. 2.5) and amounted to approximately 10%. However, stone mesohabitats had significantly higher contributions of neozoa to mesohabitat-specific biomass than transition zone and groyne field (Fig. 2.5). Similarly, stone mesohabitats exhibited higher contributions of neozoa to secondary production than the other mesohabitat types. Differences in contributions of neozoa to secondary production between the transition zone and the groyne field were less pronounced and overlapping bootstrapped 95% CI indicate no significant difference at the 0.05 level.

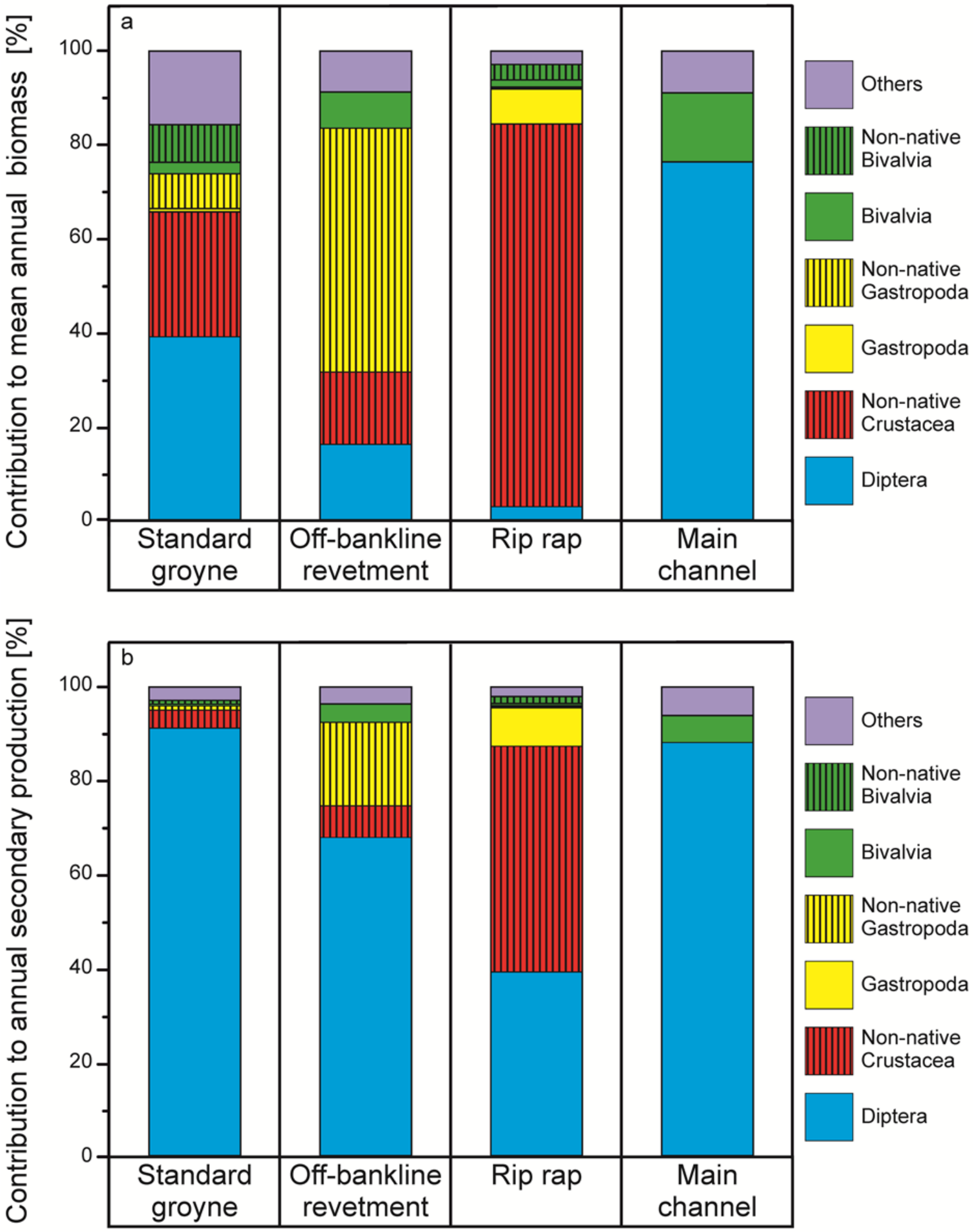

Fig. 2.4 Percentage contribution of the major taxonomic groups, separated into native and non-native taxa, to weighted biomass (a) and total weighted secondary production (b).

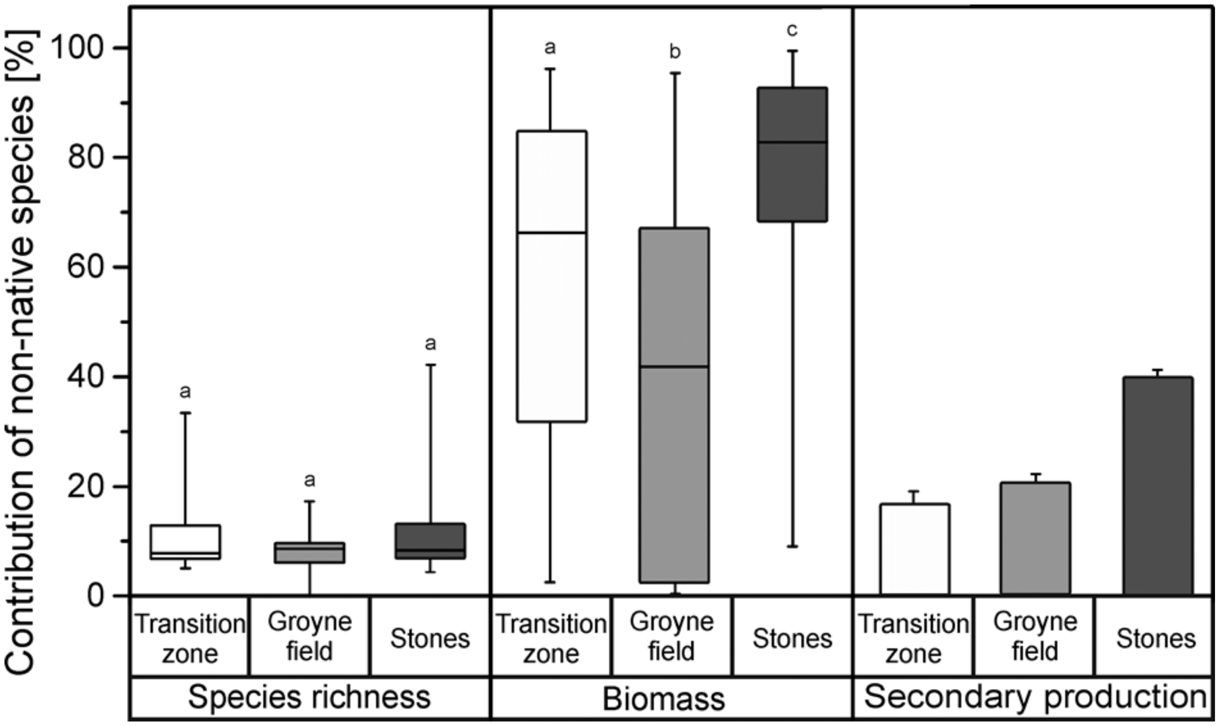

Fig. 2.5 Percentage contribution of non-native species to species richness, biomass, and total secondary production (+95% CI) in the mesohabitats found at the shore types. Significant differences ($P < 0.05$, RM ANOVA and Holm-Sidak pairwise comparisons) are indicated by different letters. The box-whisker plots represent the data from the different shore types and samplings of each mesohabitat (whiskers = min. and max.).

Habitat and resource variables

Macrophytes and boulders were not to be found in the main channel and proportions of sand were significantly higher in the main channel than at the standard groyne (Table 2.1). Categories of flow velocity did not differ between main channel and rip rap, but were significantly higher than at the standard groyne or the off-bankline revetment. Resource variables differed only marginally between main channel and the shore sites, except for sediment organic matter content, which was significantly lower in the main channel than at the standard groyne and the off-bankline revetment.

Differences between shore types were more pronounced; especially the variables describing microhabitat structure differed significantly. For example, contribution of boulders and flow velocity were significantly higher at the rip rap than the other two shore types (Table 2.1). The contribution of macrophytes and FPOM was significantly higher at the off-bankline revetment than at the other two shore types. Surprisingly, variables related to food resource availability showed only minor differences between shore types. Only sediment organic matter content differed between all three shore types (Table 2.1).

Table 2.1 Mean (± SE) values of habitat and resource variables of the studied shore types and the adjacent main channel. Significant differences ($P<0.05$) (RM ANOVA and Holm-Sidak pairwise comparisons) are indicated by different letters. Flow velocity is presented as median categories (± mean deviation from the median) and was compared using a Friedman test followed by Tukey post-hoc tests. Abbreviations are: AFDW = ash free dry mass, Chl a = chlorophyll a, FPOM = fine particulate organic matter, SPOM = Suspended particulate organic matter, - = not present.

	Standard groyne	**Off-bankline revetment**	**Rip rap**	**Main channel**
Habitat variables				
Boulder (%)	2 ± 1^{a}	7 ± 6^{a}	80 ± 12^{b}	-
Flow velocity	2 ± 0^{a}	1 ± 1^{a}	3 ± 0^{b}	3 ± 0^{b}
FPOM (%)	0 ± 0^{a}	2 ± 1^{b}	0 ± 0^{a}	0 ± 0^{a}
Gravel (%)	68 ± 9^{a}	20 ± 14^{b}	17 ± 13^{b}	31 ± 6^{a,b}
Macrophytes (%)	1 ± 1^{a}	14 ± 8^{b}	0 ± 0^{a}	-
Oxygen concentration (mg L^{-1})	13 ± 1^{a}	13 ± 2^{a}	14 ± 2^{a}	12 ± 1^{a}
Sand (%)	31 ± 9^{a}	78 ± 13^{b}	83 ± 13^{b}	69 ± 6^{b}
Water temperature (°C)	15 ± 5^{a}	15 ± 6^{a}	15 ± 5^{a}	14 ± 6^{a}
Resource variables				
Chl *a* from SPOM (µg L^{-1})	45 ± 26^{a}	20 ± 14^{a}	42 ± 31^{a}	38 ± 28^{a}
Periphyton standing stock (mg AFDM m^{-2})	8 ± 4^{a}	6 ± 5^{a}	6 ± 3^{a}	-
Sediment organic matter (%)	4 ± 1^{a}	9 ± 3^{b}	1 ± 0^{c}	0 ± 0^{c}
SPOM (mg AFDM L^{-1})	9 ± 5^{a}	4 ± 3^{b}	16 ± 12^{a}	12 ± 5^{a}

2.4 Discussion

Shores are hotspots of riverine diversity and function

This is to my knowledge the first comprehensive study that relates both the structure and functioning of macroinvertebrate communities from all relevant mesohabitats in a large river to common types of shore types. The data show that the main channel of a large sandy lowland river was colonized by a distinct community consisting of only a few specialized species. Thus, diversity and biomass were significantly lower than at any of the studied shore types. This is in line with previous studies showing that sand-dominated main channels are inhabited by very few specialized species with low numerical abundances and biomasses (Simpson *et al.* 1986; Nakano & Nakamura 2006). Moreover, the results show that the low diversity and biomass also have functional consequences as total secondary production was more than two orders of magnitude lower in the main channel than at the shore zone.

The structure and functioning of main channel communities did not systematically vary with the adjacent shore type, suggesting that all of these structures have similar effects on main channel communities. Most habitat and resource variables did barely differ between main channel and shore zone and were probably not the primary reasons for the observed differences. However, all shore types were characterized by a steep gradient of flow velocity from the shore towards the main channel, which was generated by the structure. I did not measure flow velocity or turbulences directly, but another study conducted at the River Elbe at standard groynes similar to the one studied here showed that current velocity could be as low as 0.2 m sec^{-1} in the groyne field and increased up to 1.3 m sec^{-1} in the main channel during mean discharge (Henning & Hentschel 2013). The corresponding hydraulic stress, along with the mobility of the prevailing sediments, causes the formation of mobile sand dunes (Aberle *et al.* 2010) that may additionally contribute to the high environmental disturbance and thus to the low diversity and productivity of the main channel habitat. It remains unclear whether the difference between the shore and main channel is solely the result of the flow alteration caused by the shore types, as unchannelized reference sites are not present in the River Elbe. However, gradients in flow velocity could be expected to be less steep and the biological difference between the shore zone and main channel might be less pronounced if shores were unaltered.

Effects of shore types depend on habitat

In contrast to the main channel, the studied shore sites were hot spots of diversity, biomass and secondary production, even though the shore types differed from one another. Compared to the other shore types, the off-bankline revetment had significantly higher diversity, biomass and secondary production. The differences between the shore types concerning secondary production may, to a small extent, be related to differences in variables describing resource availability. This is because differences were either not significant or too small to have an ecological effect. Contrastingly, I found that variables describing habitat structure such as proportions of macrophytes and FPOM, as well as variation in flow velocity were significantly higher in the off-bankline revetment than in the other shore types (Table 2.1). The higher variation of flow velocity and the occurrence of lentic conditions and pool phases during low discharges are known to favor diverse communities in large rivers (Arthington *et al.* 2006; Garcia, Schnauder & Pusch 2012). Thus, I detected taxa that are either related to slow or no flow (e.g. *Dicrotendipes nervosus* (Diptera) and Physidae (Gastropoda)), or related to macrophytes (e.g. *Cricotopus* sp. (Diptera), *Cloeon dipterum* (Ephemeroptera)) and several taxa that are strongly related to fine sediments (e.g. *Camptocladius stercorarius* and *Chironomus* sp. (Diptera)) in the off-bankline revetment (Table S2). With 50%, particularly the latter taxa contributed strongly to total secondary production. The rip rap, however, had a significantly higher and less variable flow velocity in combination with a significantly higher proportion of boulders. As a result, this structure was dominated by rheophilic species associated with hard-bottom, lital habitats, e.g. *Ancylus fluviatilis* (Gastropoda), the invasive *Dikerogammarus villosus* (Crustacea) and *Hydropsyche* sp. (Trichoptera). These taxa had a lower productivity compared to the highly productive Chironomidae community at the standard groyne or the off-bankline revetment (Table S3), explaining the relatively low secondary production at the rip rap despite slightly higher community biomasses compared to the standard groyne.

Configuration of shore type determines neozoa contribution

The contribution of non-native species to the structure and functioning of the macroinvertebrate community varied systematically with shore type. Contributions to biomass and secondary production were highest at the rip rap, intermediate at the off-bankline revetment and lowest at the standard groyne (Fig. 2.4). This result coincides with the proportion of boulders that contributed on average 80% to total area at the rip rap but only 7% and 2% at off-bankline revetment and standard groyne, respectively (Table 2.1). The mesohabitat specific analysis underlined this relation, as the mesohabitat stone had a significantly higher contribution of non-native species to biomass and production than transition zone or groyne field (Fig. 2.5). In fact, several neozoa found at the rip rap, like *Dikerogammarus villosus*, are typical colonizers of hard substrates. A high share of neozoa on boulders used for artificial shore constructions has also been found in other riverine systems (MacNeil *et al.* 2010; Boets *et al.* 2013). Hence, the local and habitat-specific results suggest that the shore type may drive the establishment success of neozoa and provides evidence that even though invasions of non-native species are omnipresent in navigable rivers, their standings stocks and secondary production could most likely be regulated by mesohabitat structure.

It could also be shown that the contribution of neozoa to secondary production was substantially lower than their contribution to biomass at a given shore type. For example, non-native *Potamopyrgus antipodarum* (Gastropoda) contributed on average 40% to total weighted biomass but only 9% to total production at the off-bankline revetment (Fig. 2.4). This suggests that the importance of *P. antipodarum* would be overestimated if the impact on the local community was assessed by its dominance in terms of biomass (Hall et al. 2006). The low contribution to secondary production indicates that the local functional impact of *P. antipodarum* is rather small and suggests that parameters describing contribution to ecosystem functioning may provide a better indication for the ecological significance of non-native species than structural indicators.

Implications for large river management

The contemporary management of large rivers has to deal with the trade-off between maintaining the usability for navigation and maintaining or restoring the ecological integrity, i.e. biodiversity and ecosystem functioning (Gore & Petts 1989; Kotenko 2005). This trade-off is exacerbated by the fact that restoration of a natural riverine hydromorphology on larger spatial scales is virtually impossible under a given human use regime like navigation (Gore & Shields 1995). Hence, scientific knowledge on structural and functional aspects associated with different shore types is important to be able to determine the type and location of management measures on local scales (Large, Boon & Raven 2012). Based on the presented results that combine biodiversity, impact of neozoa measured by their dominance and macroinvertebrate secondary production as independent measures of ecosystem integrity, three management recommendations can be derived. First, river management should allow for sufficient space for shallow shore zones, because these sites provide physical habitat for macroinvertebrate communities with a substantially higher diversity and productivity compared to the main channel. River sections altered by confined shore constructions such as rip raps contribute little to secondary production and biodiversity and should thus be avoided whenever possible. Given that most of the secondary production takes place at the shore zone and secondary production itself represents patterns of larger scaled energy fluxes (Benke & Huryn 2010), the shore type is likely to also have implications for whole-river ecosystem functioning. Secondly, a high diversity of flow patterns should be supported, in particular through the establishment of shore types that create stagnant, backwater-like conditions during periods of low water levels. It was shown that those sections are colonized by lentic communities that contribute to the diversity and production of the entire river. Off-bankline revetments are a promising strategy to maintain navigation in the main channel while simultaneously protecting the near shore zone from the associated adverse effects. Lastly, the restricted use of shore types constructed of non-autochthonous substrates such as stones or boulders in sandy rivers is recommended to limit niche opportunities for non-native species. Given that already established invasive species facilitate the establishment of other neozoa (Simberloff & Von Holle 1999; Green *et al.* 2011), any significant reduction of the numerical abundance or standing stock of neozoa through local management measures is useful in case large-scale measures to prevent invasion are not feasible. In conclusion, the study showed the great potential of appropriate shore types to improve macroinvertebrate community diversity and functioning in a large lowland river. Nonetheless, more studies that adopt other measures of ecosystem functioning are needed to derive ecologically sound management recommendations for large rivers.

3. Chapter:

First record of *Ametropus fragilis* Albarda, 1878 (Insecta: Ephemeroptera, Ametropodidae) in Saxony-Anhalt (Germany): Implications for the recolonization potential of large lowland rivers[1]

3.1 Introduction

Ametropus fragilis is a typical psammophilous mayfly in large lowland rivers. The first record for Germany was made by Berger and Rothe in 1998 in the Lusatian Neisse. To that date this marked the most western record in Europe, apart from the detection of the type species in the Netherlands. This has, however, been the only record of *A. fragilis* in the Netherlands (Mol 1985). Surprisingly, Cozilis and Chovet recorded a single larva in the River Loire in France in 2010. Despite this recent record, *A. fragilis* still belongs to the rarest and probably also most endangered European mayflies (Landa & Soldán 1985; Russev 1992; Sowa 1992; Berger & Rothe 1999).

A large body of management activities is directed towards the recolonization of impaired sites by rare species in order to improve their biodiversity (Ward 1998; Dudgeon *et al.* 2006). Actually, to the current state only few large river management activities resulted in detectable biodiversity increases (Palmer, Menninger & Bernhardt 2010; Haase *et al.* 2012). One prominent reason may be the fact that the recolonization success does not only depend on the constitution of the habitat that is to be colonized itself, but also largely on the surrounding catchment (Lake, Bond & Reich 2007; Sundermann, Stoll & Haase 2011). Appropriate sources of desired species like tributaries or wetlands have to be present in close proximity to the restored site. Furthermore, suitable shore types within a riverine system of interest may be valuable habitats that function as stepping stones for recolonizing taxa. Former studies showed that the maximum distance from a putative source to the location of interest approximates 5,000 m for a successful inoculation, but at a distance larger than 1,000 m the recolonization success already declined markedly (Sundermann *et al.* 2011; Tonkin *et al.* 2014). However,

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[1] Main results of this chapter were published in Brabender, M. & M. Brauns (2013): First record of *Ametropus fragilis* Albarda, 1878 (Insecta: Ephemeroptera, Ametropodidae) in the River Elbe in Saxony-Anhalt, Germany.- Lauterbornia ***76****: 1-3*

appropriate assessment of potential sources is difficult and requires much effort and large datasets of the surrounding catchment.

In the course of this study, two individuals of *A. fragilis* were recorded in the River Elbe. Here, I will report on these findings and put them into the broader context of the recolonization potential of a large river.

3.2 Material and Methods

The study area at the River Elbe is situated in the biosphere reserve “Mittelelbe” near Dessau (German river kilometer 252) in Saxony-Anhalt. Here, monthly samplings of benthic macroinvertebrates at different types of shore structures (standard groyne, off-bankline revetment and rip rap) were conducted between April 2011 and April 2012. All mesohabitats present at each shore structure were sampled quantitatively using hand nets or a Surber sampler. For details see chapters 1 and 2.

3.3 Results

In October 2011, a larva of *Ametropus fragilis* was collected at the downstream opening of the off-bankline revetment (51.884082° N, 12.308082° E; WGS 84). The specimen was 10.1 mm long (without cerci) and had a thoracic width of 1.9 mm (Fig. 3.1).

Fig. 3.1 *Ametropus fragilis*, dorsal view

A second record was made in April 2012 in close proximity to the first location. In April the mayfly had reached a total length of 17.4 mm (without cerci) and a thoracic width of 3.8 mm. Both individuals had normally developed forelegs (Fig. 3.1). Numerous bristles insert at the coxae of the forelegs and form a kind of bow net (Fig. 3.2). The labial palps resemble pincer-like structures.

Fig. 3.2 *Ametropus fragilis*, ventral view, showing the bristles at the coxae of the foreleg

The location in which the specimens were found is situated directly behind the downstream opening of the off-bankline revetment in a water depth of 70-90 cm (Fig. 3.3). The bottom sediment was dominated by sand (97%) with only a minor amount of organic material (0.7%), which is due to the from time to time high flow velocities of up to 0.8 m s^{-1}, depending on the water level (Table S1). The water column was characterized by high chlorophyll a concentrations of up to 144 µg L^{-1}, which reduced the water transparency to less than 40 cm at some dates of the year (Table S1).

3.4 Discussion

Overall, the environmental conditions at the locality at the River Elbe largely match those described from the River Neisse, where flow velocities amounted to 0.6 to 1.0 m s^{-1}

and the sediment was also dominated by sand (Berger & Rothe 1999). The fact that both individuals showed normally developed forelegs support Jacob (2006), who suggests that the often described reduction of the forelegs (Bauernfeind & Humpesch 2001; Eiseler 2005) is due to an aberration of single specimens.

Fig. 3.3 Location in which *Ametropus fragilis* was detected. The image shows the downstream outflow of the off-bankline revetment. The sandy structure at the end of the technical groyne construction continues under the water surface. This picture was taken at a water level considerably lower than the mean.

Ecological traits and required habitat conditions

Information on the feeding mode of *A. fragilis* is inconsistent. The numerous bristles inserting at the coxae of the forelegs form a kind of bow net that enables *A. fragilis* to filter suspended particulate material (Fig. 3.2). The labial palps that resemble pincers may be used to strip off particles entangled in the bristles (Berger & Rothe 1999). While Kazlauskas (1962) assumed that *A. fragilis* passively feeds on detritus, Edmunds et al. (1976) supposed that they consume microbial food, mainly algae, that is collected from the interstitial. At my sampling location, both feeding modes are possible and further investigations are needed to clarify whether detritus or algae are being preferred. The stable isotope analysis of the recently found specimen indicates that pelagic algae contributed more to *A. fragilis*' diet than benthic FPOM (data not shown, for details of stable isotope analyses see chapter 4).

It can be assumed that *A. fragilis* has disappeared from most European streams as a result of both discharging untreated waste water into riverine systems (Soldan 1978; Klausnitzer, Jacob & Joost 1982) and, like several other sensitive taxa, the widespread structural river degradations (Arthington *et al.* 2010). An improvement of the water quality as well as favorable shore structures that include well flown-through, sandy habitats in some localities of the River Elbe may have facilitated the dispersal of *A. fragilis*. The recent discovery in France (Cozilis & Chovet 2010) suggests that recolonization sources might also to be found in other parts of middle Europe. The locality described here is characterized by natural, moderate and thus not destructive sediment dynamics. These are, however, no longer to be found in most large lowland rivers. The main channel may provide sediment with an appropriate grain size, but the constantly high flow velocities lead to harsh sediment movements (Aberle *et al.* 2010). The majority of large river shore zones are either dominated by rip raps or standard groynes, while natural shore zones or off-bankline revetments are still the exception. Both of the former shore types lack the required habitat conditions for *A. fragilis* and hinder its establishment at the banks of most European rivers that are used as waterways. In addition, potential sources for the recolonization are still rare or at least unknown. Hence, based on the only two German records, the classification as "Critically Endangered" on both the Red Lists of Saxony-Anhalt and Germany is suggested for *A. fragilis*.

Recolonization potential of large rivers

Taking into account the fact that this record of *A. fragilis* is the first for Germany since more than a decade, it becomes clear that potential recolonization sources are presently unknown. One potential source for the recolonization of the investigated study site may have been the sand-dominated River Mulde, which provides suitable habitat conditions for *A. fragilis*. However, it is situated approximately 4.5 km to the west of the study location and may therefore be too far away to serve as a direct recolonization source (Sundermann *et al.* 2011; Tonkin *et al.* 2014). Although a minor factor, the potential path for a compensatory flight is strongly interrupted by a flood plain forest that may further impede a successful arrival at the respective site (Tonkin *et al.* 2014). It is conceivable that *A. fragilis'* distribution took place within the River Elbe itself. Hence, favorable shore structures in large rivers that are in close proximity to each other seem appropriate to partly compensate for missing tributaries or flood plains in the surroundings. In contrast to other large navigable rivers, shore constructions at the River Elbe are often in technically poor conditions, so that groyne stone bars are perforated or clogged with sand and can thus form valuable habitats. Moreover, in the course of recent restoration activities in the nature reserve catchment, entire shore constructions at several locations have been removed. These, in other large rivers rare habitats, may have functioned as stepping stones for the arrival of *A. fragilis* at the study site from either downstream or upstream. Although their recolonization may take many years (Langford *et al.* 2009), implementing many small projects as stepping stones has already been suggested by others (Rouquette & Thompson 2007; Jähnig, Lorenz & Hering 2008). The valuable and unexpected double record of *A. fragilis* at an off-bankline revetment of the River Elbe indicates that the chemical requirements for the reestablishment of rare taxa may largely be met nowadays, but that riverine systems mostly do not provide sufficiently well-structured shore zones. In accordance with the former recommendations (Rouquette & Thompson 2007; Jähnig *et al.* 2008), it can be further assumed that sites far away from putative recolonization sources can still be reached by desired taxa via the construction of suitable habitat islands in close proximity to each other. These may serve as stepping stones from an inoculating source to large river sections further away. The detection of *A. fragilis* is welcome news for the improvement of biodiversity in German aquatic ecosystems. It is encouraging for renaturation activities that even a species that was long thought to have vanished from Germany has reappeared in a large navigable river.

4. Chapter:

Shore structure alters connectivity patterns and interaction strength among basal resources and primary consumers in benthic large river food webs

4.1 Introduction

Rivers are important habitats for many specialized plants and animals (Allan & Flecker 1993). Those ecosystems and the inhabiting species perform a variety of crucial ecosystem services like the exchange of substances between aquatic and terrestrial areas or the channelization and transformation of nutrients (Postel & Carpenter 1997; Millenium Ecosystem Assessment 2005). As most rivers have been structurally altered by human use, these valuable habitats are increasingly threatened. Nowadays, the impaired hydromorphology is one of the main stressors for riverine ecosystems (Hughes *et al.* 1990; Allan & Flecker 1993). Habitat-induced alterations in hydromorphology and community composition can lead to functional changes like the availability of basal resources and the flow of energy in benthic macroinvertebrate food webs (Chapin *et al.* 2000; Cross *et al.* 2013). Modifications in resource utilization may have long-range consequences for the river itself in terms of eutrophication, nutrient channelization and loads of particulate matter, but also for adjacent ecosystems (Sabo & Hagen 2012).

Determining the origin and flow of energy that fuels aquatic secondary production has been a main effort in ecological research (Lindeman 1942; Benke & Wallace 1980; Pingram *et al.* 2012). The majority of studies determining food web structure and the trophic basis of secondary production in large rivers revealed autochthonous algal production as the main basal resource (Roach 2013). Some rare exceptions are known in which secondary production was mainly fueled by detrital organic matter, but those were derived from systems with high turbidity and sediment loads (Roach 2013; Wellard Kelly *et al.* 2013). Not only the availability, but also the quality of resources is an important factor for their utilization by benthic communities (Marcarelli *et al.* 2011). In addition, community composition and the inherent species traits play a crucial role for resource uptake and energy channeling through the food web (Vaughn 2010; Vandewalle *et al.* 2010). Structural changes in communities can strongly influence both the use of resources and the effectiveness of energy transfer through food webs, e.g. due to missing or newly established links (Vander Zanden *et al.* 1999; Chapin III *et al.* 2000). Individual species can act as functional key players that dominate energy flow or shift resource utilization away from pristine patterns (Hall *et al.* 2006; Vaughn 2010). Particular resources may thus be inadequately incorporated into food webs or even remain entirely untouched.

As earlier studies revealed profound impacts of the shore morphology on species composition and secondary production (see chapter 2), effects on the food web structure and interaction strength are likely. Given that most of the secondary production takes place at the shore zone and secondary production itself represents patterns of larger scaled energy fluxes (Benke & Huryn 2010), the shore type can be expected to have implications for whole-river ecosystem functioning. Additionally, the shore type specific communities differed substantially concerning their contributions of non-native species (chapter 2). This may be one particular important element that influences shore type specific food web attributes as interacting species have not co-evolved (Hobbs et al. 2006). These potential changes in community-resource interactions can best be described by the use of flow food webs rather than simple connectivity food webs, which lack information about interaction strength (Benke & Wallace 2011). As new methods were established and the descriptive power of flow food webs was approved, studies on the quantified trophic base of secondary production and the energy transfer from one trophic level to another gained importance in recent research (Benke & Huryn 2010). Flow food webs can provide a powerful tool to describe impacts that human alterations like river damming, the degree of land use or habitat degradation have on the functional performance of aquatic ecosystems (Woodward & Hildrew 2002; Benke & Wallace 2011; Cross *et al.* 2013).

However, despite a long-lasting history of studies assessing human impacts on ecosystems and the ongoing methodological progress, our understanding of food webs and energy flow in large riverine systems is still limited (Johnson, Richardson & Naimo 1995; Cross *et al.* 2013). The majority of food web analyses have been conducted in smaller streams (e.g. Hall Jr, Wallace & Eggert 2000; Peipoch, Martí & Gacia 2012; Whiting *et al.* 2014). While some qualitative information on large river food webs from several locations exist (Herwig *et al.* 2007; Pingram *et al.* 2012), quantified organic matter fluxes from temperate lowland rivers do not (but see Lewis et al. 2001 for a tropical river analysis). Most of the few large river food web studies were conducted to detect the origin of basal resources to test energetic concepts (Thorp & Delong 2002; Roach 2013), rather than to quantify energy transfer in relation to anthropogenic stressors.

As the majority of large river systems are morphologically impaired, mechanistic understanding of how this degradation may affect the structure and magnitude of energy flow is essential to assess widespread human impacts on aquatic ecosystem functioning. Especially in navigable rivers, shore construction types mostly provide the only possibility for structural improvement within a fixed, large river macrostructure (Gore & Shields 1995; Large *et al.* 2012). Therefore, it is this particular knowledge that is needed to provide guidelines for functional management in these seemingly unchangeable systems. Managers and researchers can apply the results in attempts to influence the food web attributes and in turn produce desired outcomes (Cross *et al.* 2013).

In this study I used annual secondary production estimates and mean annual resource assimilation rates from three seasonal campaigns to construct fully quantified basal ingestion flow food webs for three different shore types. The objectives were twofold. First (i), I sought to determine the influence of different shore type morphologies on the basis of secondary production and the quantity of matter fluxes from basal resources to benthic primary consumer communities. As the River Elbe provides high amounts of pelagic algae and this type of high quality food was shown to fuel food webs in several large river systems (Roach 2013), I predicted that pelagic algae constitute the main basal resource for all benthic communities in the Elbe irrespective of the shore type. In contrast, I expected a shore type dependent effect concerning the relative importance of benthic FPOM and periphyton. I predicted that FPOM is of higher relative importance in the off-bankline revetment because previous analyses revealed higher standing stocks there (Table 2.1). At the same time, I hypothesized that due to the higher proportion of boulders at the rip rap, which should function as a preferential substrate for scrapers, the relative importance of periphyton is highest there. My second main objective (ii) was to test the effect of shore types on patterns and magnitudes of basal trophic interactions including the detection of energy flow key players, potential missing links and resource utilization efficiencies in terms of resource ingestion/availability relationships.

4.2 Material and Methods

Sampling of food web components

Sampling for stable isotope analyses (SIA) material (except for suspended fine particulate organic matter) was conducted in early summer (end of May) in autumn (October) 2011, and in early spring (end of March) 2012 to account for inter annual variation in $\delta^{13}C$ and $\delta^{15}N$ signatures (Walters & Post 2008; Sabo *et al.* 2010). All available taxa of macroinvertebrates were qualitatively sampled at the three shore types described above, i.e. off-bankline revetment, standard groyne and rip rap (see chapter 1 and 2 for details). When possible, several replicates for each taxon were collected, but some taxa were only represented by a single sample due to limited material. Sampling devices were used as described above (see chapter 2). Individuals were immediately sorted and determined to species or genus, except for Oligochaeta (order level) and Diptera (family level). Living animals were transferred to filtered river water for several hours to allow for gut clearance.

Benthic macroinvertebrates have access to four potential basal resources, i.e. suspended fine particulate organic matter (SPOM), periphyton, benthic fine particulate organic matter (FPOM) and terrestrial coarse particulate organic matter (terrestrial CPOM). SPOM was sampled monthly from April 2011 until March 2012 as the contained algae may exhibit high temporal variability in $\delta^{13}C$ and $\delta^{15}N$ signatures (Singer *et al.* 2005; Rasmussen & Trudeau 2007). In each of the shore types and the adjacent main channel, 40 l of river water, pre-filtered through a 100 µm gaze net to remove coarse particles, were concentrated by cross flow filtration (0.1 µm cassette filter, Millipore, Merck, Darmstadt) to gain sufficient quantities for stable isotope analyses. Periphyton was sampled once per season by brushing at least three stones per site with a plastic nail brush that was subsequently rinsed with filtered river water. In most cases samples from different stones were combined to one composite sample. Benthic fine particulate organic matter (FPOM) was sampled by combining the uppermost centimeter-part from five sediment cores taken at equidistance across each shore type. In order to prevent contamination, FPOM was carefully checked for macroinvertebrates, which were then removed from the sample. Leaves and shoots from all available terrestrial plants near the sampling site, i.e. poplar (*Populus*), willow (*Salix*), elm (*Ulmus*) and semi terrestrial grasses (*Phalaris*) were sampled by hand to represent terrestrial coarse particulate organic matter inputs (terrestrial CPOM). Different plant taxa were treated as separate samples.

Sample preparation and stable isotope analyses (SIA)

In the laboratory, single individuals of consumers were transferred to glass vials if they provided enough mass to meet the required minimum dry weight for sample analyses (min. 300 µg). Otherwise several individuals from one taxon were pooled. Snails and mussels were separated from their shells and only the soft body was used for analyses, because shell material is enriched in $\delta^{13}C$ and does not reflect the $\delta^{13}C$ signature of consumed food (Mitchell *et al.* 1996).

A major problem in analyzing the stable isotope composition of SPOM is the contamination of algal seston, which can easily be assimilated, with recalcitrant detritus (Jardine *et al.* 2014). Inclusion of the detrital signal in the food web analyses may result in misleading signatures if consumers just excrete this material rather than assimilating it (Trakimas *et al.* 2011). I accounted for this problem by separating pelagic algae from detritus by density gradient centrifugation through a colloidal silica matrix following the manual provided by Hamilton et al. (1992). Briefly, I transferred 20 ml (5 ml per tube) of highly concentrated SPOM from each sample to four 50 ml Falcon tubes (Sarstedt, Nümbrecht) containing a colloidal silica matrix (1.16 specific gravity at 25°C). After 10 minutes of centrifugation (1,000 rpm), the supernatants that contained the algal fraction were carefully removed with a pipette. Although the supernatant may contain minor amounts of heterotrophic organisms like flagellates or ciliates, it is much more likely to reflect the true algal isotopic signature than the bulk SPOM would do. To remove accidentally transferred colloidal silica matrix, the supernatants were resuspended with particle-free river water and filtered onto a pre-ashed glass fiber filter (Whatman GF/F, nominal pore size 0.7 mm; Whatman, Clifton, New Jersey, USA). The filter cake was scraped off with a spatula and transferred into a glass vial. This procedure was also applied to the detrital fraction that was situated at the bottom of the tube. Additionally, from each site a sample of the concentrated bulk SPOM was kept to evaluate the separation success. I also applied the colloidal silica separation technique to separate light and heavy fractions of periphyton as high ash-contents indicated that it is strongly contaminated by detritus in the River Elbe (data not shown). Due to technical problems in the summer campaign, only the bulk sample of periphyton exists. FPOM and terrestrial CPOM samples were transferred into large aluminum bowls (22*13 cm) to accelerate the drying process. All samples were dried at 60°C until they reached a constant dry weight and were subsequently stored in a desiccator. To prepare samples for SIA they were ground to fine powder using a mortar or, for fibered resources, a ball mill. Consumers (ca. 500 µg) and resources (1-25 mg, depending on expected C and N content) were weighed in tin capsules to the nearest 0.001 mg with a micro balance (ME5, Sartorius, Surrey, UK). Isotope ratios were measured using a Delta Advantage isotope ratio mass spectrometer connected to a Flash HT Elemental Analyzer (Thermo Finnigan, Bremen, Germany). Stable isotope ratios of samples ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) are expressed as delta (δ) and defined as parts per thousand (‰) relative to international standards (PeeDee Belemnite for $\delta^{13}C$, atmospheric N_2 for $\delta^{15}N$; Peterson & Fry 1987). Repeated analyses of an internal standard resulted in a typical accuracy (±1 SD) of 0.12 and 0.05‰ for carbon and nitrogen, respectively.

Food web analyses

Annual organic matter flow food webs were constructed for each shore type. As the objective was to quantify the organic matter flux that fuels benthic secondary production, only primary consumers were included into the model, so no feeding interaction between species will be shown. Conclusions about interaction strength and effectiveness of resource utilization can be drawn by calculating the relation between the potential availability of food resources and total ingested food quantities. These outcomes are based on benthic secondary production estimates (see chapter 2), composition of assimilated diet, assimilation and production efficiencies, and estimates of annual potential availability of food resources.

Relative composition of assimilated diet for each taxon of the benthic community was modelled based on the natural stable isotope signatures of ^{13}C and ^{15}N. Three seasonal proportions of assimilated diet per site were modelled. Finally, the annual mean assimilated diet proportions were used to construct site-specific food webs. Only primary consumers representing the key players of secondary production in my study (chapter 2), were chosen as food web members. *Dikerogammarus villosus* and *Hydropsyche* sp. were formerly revealed as potentially omnivorous (e.g. Benke & Wallace 1980; Dick, Platvoet & Kelly 2002; van Riel *et al.* 2006). I accounted for potential omnivory in the studied system by estimating consumers' trophic positions relative to a site-specific baseline (primary producers as trophic position 1). Trophic positions higher than 2.6 indicate that some biomass has been derived from consuming animal material and leads to the exclusion of the respective taxa from the analyses. A common indirect procedure in trophic baseline estimation is the use of long-living primary producers, e.g. suspension-feeding Bivalvia, as they integrate the variable isotopic signature of the microalgal food resource (Post 2002; Howard, Cuffey & Solomon 2005; Gustafson *et al.* 2007). As Bivalvia also consume significant amounts of fine particulate organic matter (Raikow & Hamilton 2001; Atkinson *et al.* 2009), they are useful baseline organisms representing the average baseline $\delta^{15}N$ from two prevailing basal resources of food webs (Jardine *et al.* 2014). Rather than applying an indirect method for baseline determination, I was able to use temporally resolved isotope signatures of pelagic algae and benthic FPOM as baseline representatives. It may be useful to include the entire set of basal resources (including terrestrial CPOM and periphyton) into baseline estimates when trophic positions from all food web members and food chain length are of interest. Here, trophic position estimates only served as criteria for omnivory exclusion. Hence, I chose the two lowest basal resources in terms of $\delta^{15}N$ concentration to produce the most conservative baseline that prevents underestimation of trophic positions. The $\delta^{15}N$ signatures from pelagic algae from May until August 2011 and from March 2012 were chosen, as high chlorophyll a values of water samples indicated strong algal dominance of the entire SPOM pool. The potential amount of heterotrophic organisms in the algal fraction can thus be assumed to be negligible. Additionally, the seasonal $\delta^{15}N$ values of benthic FPOM were included. The site-specific annual trophic baseline is reflected by the mean $\delta^{15}N$ value from mean benthic FPOM and mean pelagic algae signatures. I assumed evenly assimilated proportions of benthic FPOM and pelagic algae and an enrichment of +3.4‰ $\delta^{15}N$ per trophic transfer (Post 2002), so that the actual trophic position (TP) of a consumer (con) was calculated using the equation:

$$TP_{con} = 1 + (\delta^{15}N_{con} - \delta^{15}N_{base}) \times 3.4^{-1} \qquad (4)$$

where $\delta^{15}N_{con}$ = $\delta^{15}N$ of consumer; $\delta^{15}N_{base}$ = $\delta^{15}N$ of baseline; 3.4 = one trophic level increment in $\delta^{15}N$. The final annual trophic position of a consumer was calculated as the mean of the trophic positions from the three seasonal campaigns.

Before modelling, resources were also examined for reasonable applicability. Statistical analyses (repeated measures ANOVA followed by Holm-Sidak tests or, if not normally distributed, Friedman repeated measures ANOVA on ranks followed by Tukey post-hoc tests) of the algal isotopic signatures between shore type and the adjacent main channel revealed only significant differences for the off-bankline revetment and the respective main channel. Main channel signatures did not differ among each other. To reach the highest number of possible replicates, I used the mean algal isotopic values and the respective standard deviations from the main channel samples for food web modelling in standard groyne and rip rap, as they were statistically identical. For off-bankline revetment food webs, the pelagic algal signature from the respective shore type was applied. Signatures of pelagic detritus and benthic FPOM were not sufficiently distinct (overlapping standard deviations) to be simultaneously included in the models. However, benthic FPOM can be expected to exhibit a slightly integrated signature of pelagic detritus due to precipitation. Therefore, pelagic detritus was excluded from the model. All different samples of terrestrial CPOM should be available at each site as leaves can be spread by wind or downstream by river flow. Thus, for each site the mean signatures and respective standard deviations from all seasonal sampled plants were applied.

Consumers can show considerable time lags (some days to several months) in tissue turnover, so that incorporation of the resource signature does not take place immediately after consumption (Hamilton *et al.* 2004). Due to the reaction rate temperature rule, the reaction rate doubles or quadruples as a consequence of a temperature increase by 10°. It is thus obvious that tissue turnover time strongly depends on season and/or water temperature. The so-called "Q10" factor of acceleration has been applied in former studies (e.g. Cross *et al.* 2013). I accounted for temperature-influenced tissue turnover rates in each seasonal food web by including pelagic algal signatures from a reasonable time interval (see also Choy *et al.* 2009). For summer food webs, when water temperature reached about 20°C (Fig. 1.2), tissue turnover rates were assumed to be high and only the pelagic algae signatures of the summer campaign itself were included. In autumn, water temperature dropped below 15°C, so that an intermediate tissue turnover rate was assumed and pelagic algae signatures from the autumn campaign and the previous month were included. During winter, water temperature barely reached 5°C and did not rise above 10° C during spring campaigns. Hence, signatures from spring and the two earlier months were applied. For the remaining resources, isotopic signatures from the respective campaigns were used. If resource replicates were missing due to sampling design or technical problems, standard deviations from comparably variable resources and the same campaign were used to provide reasonable errors for food web modelling (pelagic detritus SD applied on FPOM). Furthermore, periphyton can be expected to exhibit a comparable temporal variability like SPOM (Singer *et al.* 2005). Consequently, I assumed the standard deviation of both resources to be similar and transferable from the SPOM fractions to the periphyton fractions.

As Bayesian mixing models, such as the one applied here, calculate resource contributions even when a certain resource is out of a reasonable range of a consumers diet (Parnell *et al.* 2010), pre-evaluation of the data is essential. I used simulated mixing polygons for the evaluation of consumer data (Smith *et al.* 2013). In summary, this method generates 1,000 possible mixing polygons based on resource data (mean values and standard deviations) with a Monte Carlo simulation and tests if consumers lie inside these polygons (point-in-polygon, e.g. Benstead *et al.* 2006). For each consumer the proportion of iterated polygons containing the respective consumer is calculated. Consumers that were inherent in less than 5% of the iterations were discarded from the final model. For the simulation of mixing polygons the same data and uncertainties incorporated in the final Bayesian mixing model were used. For data evaluation and the final model I assumed a trophic enrichment of +0.4 ± 1.3‰ δ^{13}C and +3.4 ± 1.0‰ δ^{15}N per trophic transfer (Post 2002). The final assimilation food webs were modelled using the R-based software package MixSIAR (Stock & Semmens 2013). The model estimates the probability distributions of each resource to a consumer's tissue (5th, 25th, 50th, 75th and 95th percentiles) and considers uncertainty associated with multiple sources and isotope signatures (SD). Within MixSIAR Gibbs sampling was performed for three chains. The model was run for 100,000 iterations using a burn-in-phase of 50,000 and every 50th draw was retained. From the resulting 1,000 taxa-specific relative assimilated dietary proportions for each site and season, the mean and variance for the final 95% confidence interval determination were calculated.

Relative annual incorporated diet proportions were multiplied by absolute taxa-specific secondary production values (see chapter 2) to gain absolute amounts of incorporated resources. The absolute amount of consumer *j*'s production attributed to resource *i* (PR_{ji} measured in g DM m^{-2} y^{-1}) is

$$PR_{ji} = P_j \times R_i \tag{5}$$

where P_j = annual secondary production of consumer *j* (g DM m^{-2} y^{-1}), R_i = relative proportion of secondary production attributed to resource *i*.

I calculated assimilation efficiencies (AE) for consumers based on the nitrogen content of the basal resources after Pandian and Marian (1986; Table 4.1). The applied formula for the calculation of AE (%) of resource *i* is

$$AE_i = 9.29 + 8.82 \times N_i \qquad (6)$$

where N_i = Nitrogen concentration of resource *i* (%).

Table 4.1 Shore type specific assimilation efficiencies and nitrogen contents for each resource in percent.

	Rip rap		Standard groyne		Off-bankline revetment	
Resource	Assimilation efficiency [%]	Nitrogen content [%]	Assimilation efficiency [%]	Nitrogen content [%]	Assimilation efficiency [%]	Nitrogen content [%]
Benthic FPOM	16.8	0.9	16.1	0.8	17.2	0.9
Pelagic algae	31.7	2.5	31.7	2.5	34.9	2.9
Periphyton	20.9	1.3	21.1	1.3	23.4	1.6
Terrestrial CPOM	32.6	2.6	32.6	2.6	32.6	2.6

The absolute amount of ingested resource *i* by consumer *j* (CR_{ji} measured in g DM m^{-2} y^{-1}) was calculated as

$$CR_{ji} = PR_{ji} \times (AE_i \times NPE)^{-1} \qquad (7)$$

where PR_{ji} = the absolute amount of consumer *j*'s production attributed to resource *i*, AE_i = assimilation efficiency of resource *i*, NPE = net production efficiency (Benke & Wallace 1980; Cross *et al.* 2013). NPE was assumed to be 0.4 (Wallace *et al.* 1987).

I accounted for uncertainties in consumption estimates by combining the errors (95% bootstrapped confidence intervals) of secondary production and diet assimilation estimates and applying this error on the absolute mean amounts of ingested resources. Means without overlapping 95% confidence intervals were interpreted as significantly different. Errors associated with AEs or NPE were not incorporated, but this source of error is far outweighed by accounting for uncertainties in secondary production estimates and diet assimilation proportions (Cross *et al.* 2013).

Potentially available amounts of resources

Site-specific potentially available annual amounts of resources were calculated based on data accessed in this study and from literature. For pelagic algae availability (i.e. transported load), I used mean annual chlorophyll a values (Table 2.1), site-specific mean water depth and assumed mean flow velocities (compare seston availability estimates by Benke and Wallace 2014). The mean of published carbon to chlorophyll a ratios for pelagic algae was approximately 100:1 (Garnier & Mourelatos 1991; Erikson *et al.* 1998) and the amount of algal carbon was assumed to be 50% of their dry mass (McCutchan & Lewis 2002). From these factors I calculated the annual mean algal dry mass (Al measured as g DM L^{-1}):

$$Al = 100 \times Chla \times 0.5^{-1} \qquad (8)$$

where Chla = mean chlorophyll a concentration (g L^{-1}).

With the help of the mapping data (see chapter 2), I was able to estimate the mean annual site-specific water depth (0.091 m at the off-bankline revetment, 0.91 m at the standard groyne and 0.75 m at the rip rap) and therefore the mean annual water volume of the water column above $1m^2$ (Vol measured as L m^{-2}):

$$Vol = dep \times 1{,}000 \qquad (9)$$

where dep = mean annual depth (m) and 1,000 = liters per m^3.

Mean annual flow velocities were derived from literature (0.55 m s^{-1} at the off-bankline revetment, 0.8 m s^{-1} at the standard groyne and 1.1 m s^{-1} at the rip rap; Pusch & Fischer 2006). Finally, annual potential available amounts of algae were calculated with the equation (Ay measured as g DM m^{-2} y^{-1}):

$$Ay = Al \times Vol \times v \times 31{,}536{,}000 \qquad (10)$$

where v = flow velocity (m s^{-1}) and 31,536,000 = seconds per year.

Mean annual availability of FPOM is estimated with the help of sedimentation rates published for the River Elbe. Mean daily sedimentation in a standard groyne field was 67 g DM m^{-2} d^{-1} (Ockenfeld & Guhr 2003). In spite of the slightly higher mean flow velocity at the standard groyne, I assumed the same precipitation rate at the off-bankline revetment. Sedimentation rates at the rip rap were related to flow velocity dependent sedimentation estimates for the Elbe (Schwartz & Kozerski 2004). I assumed sedimentation to be 2.5 g DM m^{-2} d^{-1}.

Concerning periphyton I accounted only for bacterial production because, turbidity in the Elbe is very high and therefore benthic algal growth can be assumed to be strongly reduced in zones deeper than 50 cm (Fischer, Hardenbicker & Schöl 2012). As a mean value from literature I assumed bacterial production to be 0.12 g C m^{-2} d^{-1} (Carr, Morin & Chambers 2005; Fukuda *et al.* 2006). The potential annual available periphyton dry mass was calculated as (Py measured as g DM m^{-2} y^{-1}):

$$Py = Pd \times Cp^{-1} \times 365 \qquad (11)$$

where Pd = daily periphyton carbon production (g C m^{-2} d^{-1}), Cp = site-specific relative carbon concentration in periphyton and 365 = days per year.

For the amount of annual available terrestrial CPOM 80 g DM m^{-2} y^{-1} were chosen, because this is the mean value from 6th, 7th and 9th order streams (Benfield 1997).

Consumer-resource interaction strength

To quantify which site-specific proportion of the potentially available basal resources is actually consumed by benthic primary consumers ("resource utilization efficiency"; Rue), the annually consumed amount of resource *i* is divided by its potentially available dry mass (e.g. Benke & Wallace 2014; c.f. Christensen & Pauly 1992; Benke & Wallace 2011; Cross *et al.* 2013):

$$Rue = CR_i \times AR_i^{-1} \qquad (12)$$

where CR_i = consumed amount of resource *i* (g DM m^{-2} y^{-1}), AR_i = potentially available amount of resource *i* (g DM m^{-2} y^{-1}). A value of 1 indicates effective utilization of a resource in terms of its total consumption by benthic primary consumers and thus a high interaction strength.

4.3 Results

Trophic basis of secondary production

The main ingested resource at all sites was benthic FPOM with proportions reaching from 32% at the rip rap to 60 % at the off-bankline revetment (Fig. 4.1 a). Relative proportions of all resources were almost identical at rip rap and standard groyne. This was also the case for the proportions of periphyton and pelagic algae from the off-bankline revetment when compared to the other shore types, whereas FPOM was ingested in mentionable higher (60%) and terrestrial CPOM in significantly lower (4%) proportions

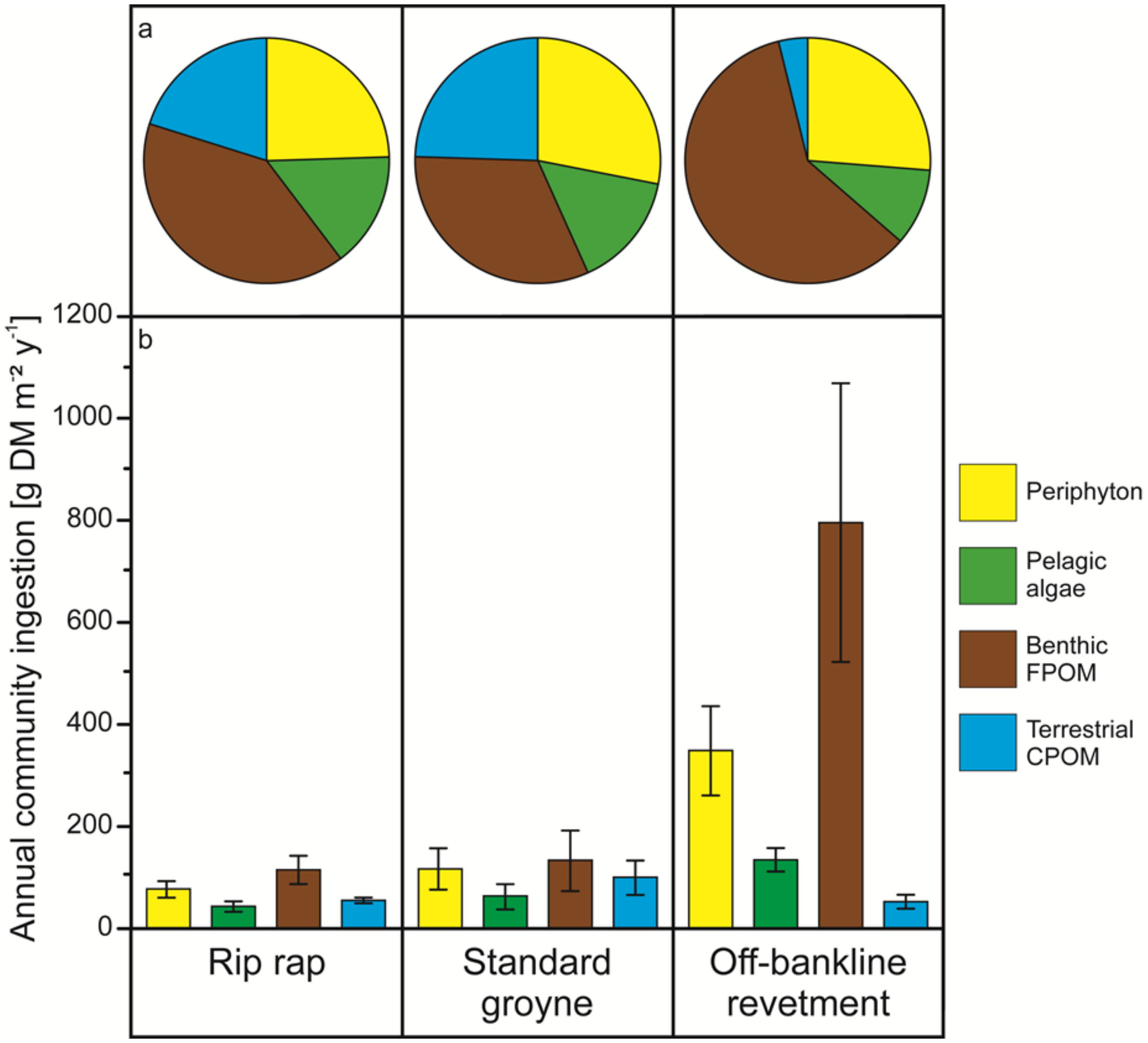

Fig. 4.1 Mean relative (a) and absolute (b) annual community ingestion of the basal resources periphyton (yellow), pelagic algae (green), benthic fine particulate organic matter (brown) and terrestrial coarse particulate organic matter (blue) at each shore type. Error bars show 95% confidence intervals.

when comparing 95% confidence intervals (errors not shown). Absolute mean ingestion rates differed between shore types (Fig. 4.1 b). The prevailing utilized resource FPOM was ingested in high rates ranging from 115 g DM m^{-2} y^{-1} at the rip rap to 794 g DM m^{-2} y^{-1} at the off-bankline revetment. Periphyton constituted the second-most ingested resource with 69 g DM m^{-2} y^{-1} at the rip rap, 116 g DM m^{-2} y^{-1} at the standard groyne and 348 g DM m^{-2} y^{-1} at the off-bankline revetment. Pelagic algae were the least ingested resource at rip rap and standard groyne, while at the off-bankline revetment terrestrial CPOM was ingested in minor amounts. In the latter shore type higher absolute ingested amounts of all resources, except for terrestrial CPOM, were significant when compared to ingestions at the other shore types. The only significant difference of resource ingestions between rip rap and standard groyne could be revealed for terrestrial CPOM. With 101 g DM m^{-2} y^{-1} it was consumed in significantly higher rates at the standard groyne compared to the rip rap (55 g DM m^{-2} y^{-1}).

Patterns of food web attributes

Basal food webs substantially differed between shore types concerning their complexity, key players and magnitudes of flows. The least complex food web in terms of basal trophic links was detected at the rip rap bearing a total of 32 connections (Fig. 4.2 a). I found highest complexity at the off-bankline revetment with a total of 44 links from basal resources to the main groups or taxa, respectively (Fig. 4.2 c). Strongest flows at the rip rap were detected for non-native *Dikerogammarus villosus* consuming the majority of entire community ingested FPOM (72 g DM m^{-2} y^{-1}; Table S4). Except for Chironominae, Orthocladiinae and *Ancylus fluviatilis*, matter flows to the remaining taxa did not exceed 1.5 g DM m^{-2} y^{-1}. At the standard groyne, organic matter flow was strongly dominated by Chironominae that consumed 118 g DM m^{-2} y^{-1} of total community ingested FPOM and 104 g DM m^{-2} y^{-1} of total community ingested periphyton (Fig. 4.2 a; Table S4). The remainder of organic matter flows was relatively evenly distributed among the community, which included two more invasive taxa (*Potamopyrgus antipodarum* and *Corbicula fluminea*). Magnitudes of the remaining flows were mostly below 3.5 g DM m^{-2} y^{-1} except for *D. villosus*, which ingested 6.3 g DM m^{-2} y^{-1} of FPOM and 4 g DM m^{-2} y^{-1} of periphyton at the standard groyne. In contrast, the off-bankline revetment food web showed several strong links (above 10 g DM m^{-2} y^{-1}) to each of the main taxonomic groups (Diptera, Gastropoda, Bivalvia, Crustacea and Others; Fig. 4.2 c). The by far largest flow of organic matter is represented by Chironominae that were consuming 633 g DM m^{-2} y^{-1} of total community ingested FPOM. It is important that the number of species included in the group Chironominae can be expected to be much higher here than at the standard groyne and especially at the rip rap (Table S2). The off-bankline revetment food web was the only one bearing a significant contribution to organic matter flows by native Bivalvia (*Sphaerium* sp.). This taxon covered its need of resources mainly by pelagic algae (17 g DM m^{-2} y^{-1}; Fig. 4.2, Table S4). While terrestrial CPOM constituted 15-21% of *Dikerogammarus villosus'* total ingested resources at rip rap and standard groyne, respectively, at the off-bankline revetment the invasive Crustacea did not ingest terrestrial CPOM at all (Fig. 4.2 c).

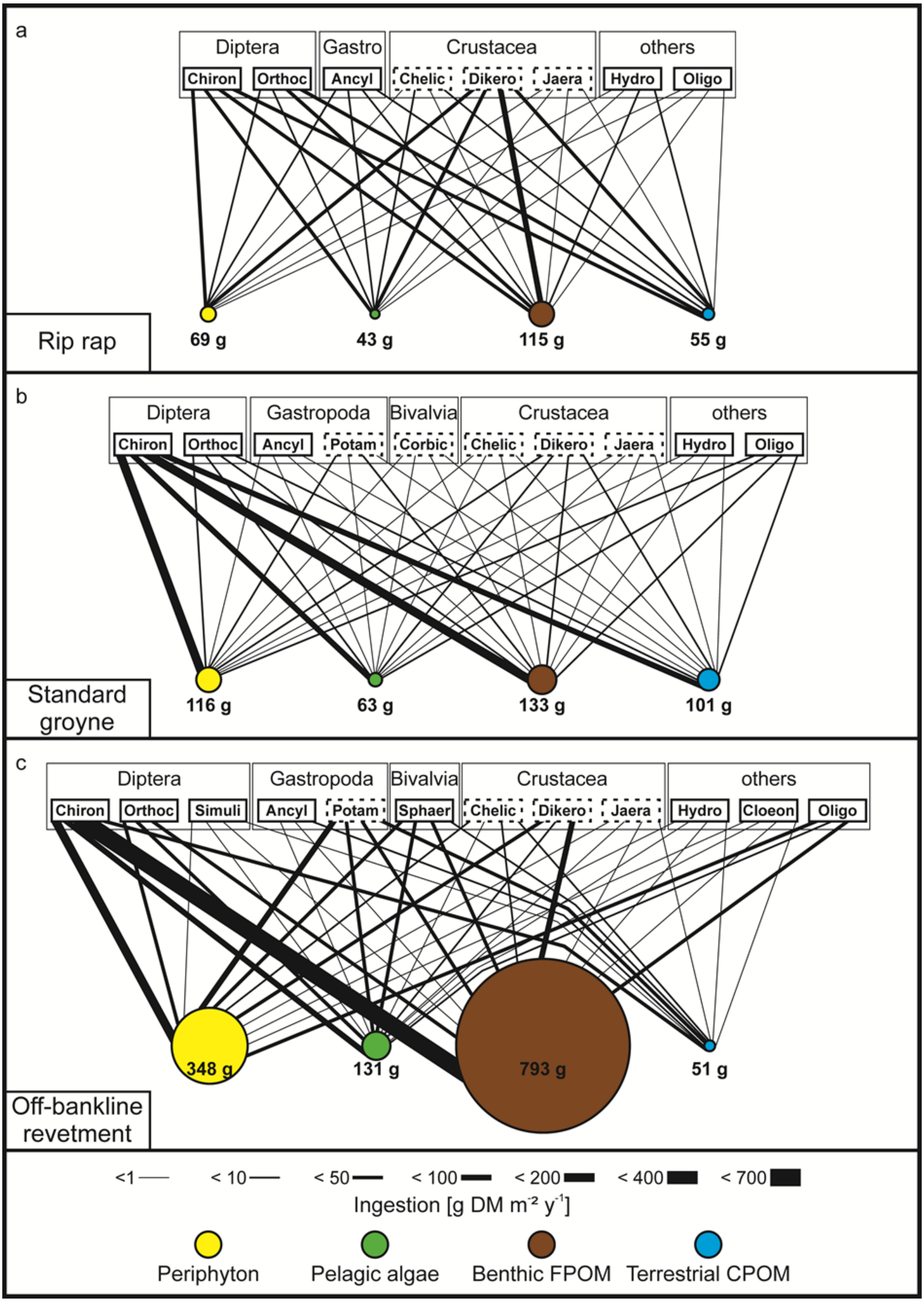

Fig. 4.2 Averaged ingestion flow food webs from rip rap (a), standard groyne (b) and off-bankline revetment (c). Line widths correspond to the magnitude of flows. Sizes of the resource dots and the internal values show mean absolute annual community ingestions in g DM m^{-2}. Ba-

sal resources are periphyton (yellow), pelagic algae (green), benthic fine particulate organic matter (brown) and terrestrial coarse particulate organic matter (blue). Consumer taxa are: Chironominae, Orthocladiinae, Simuliidae (Diptera), *Ancylus fluviatilis*, *Potamopyrgus antipodarum* (Gastropoda), *Corbicula fluminea*, *Sphaerium* sp. (Bivalvia), *Chelicorophium curvispinum*, *Dikerogammarus villosus*, *Jaera istri* (Crustacea), *Hydropsyche* sp., *Cloeon dipterum* and Oligochaeta (Others). Native taxa are surrounded by solid lines, invasive taxa by dotted lines.

Resource utilization efficiencies

The four basal resources in the river Elbe differed widely with respect to their potential availability (Table 4.2). The smallest amount of potential annual dry mass was that of terrestrial CPOM with 0.08 kg DM m^{-2} y^{-1}, a mean value of several large rivers. Potential sink areas for terrestrial CPOM were not detected and thus not accounted for. Although I assumed periphyton to grow at the same rates, availability differed between shore types (0.37-0.41 kg DM m^{-2} y^{-1}) due to varying C-concentrations.

Table 4.2 Annual potentially available basal resources in each shore type based on literature and empirical data from this study.

Resource [kg DM m^{-2} y^{-1}]	**Rip rap**	**Standard groyne**	**Off-bankline revetment**
Periphyton	0.37	0.41	0.34
Pelagic algae	191,226	168,743	5,540
Benthic FPOM	0.9	24.5	24.5
Terrestrial CPOM	0.08	0.08	0.08

Much higher amounts of available dry mass were calculated for benthic FPOM at standard groyne or off-bankline revetment, respectively (24.5 kg DM m^{-2} y^{-1}). Higher flow velocities and thus reduced precipitation lead to much smaller amounts of FPOM at the rip rap (0.9 kg DM m^{-2} y^{-1}). The by far highest amounts of potential available dry mass were calculated for pelagic algae. This resource was available from 5,540 kg DM m^{-2} y^{-1} at the off-bankline revetment to 191,226 kg DM m^{-2} y^{-1} at the rip rap. It is important to keep in mind that pelagic algae availability does not constitute a production or precipitation rate, but the load of dry mass in the water column flowing above one m^2 within one year. Resource utilization efficiencies differed between resources and shore types due to the highly variable amounts of availability and utilization rates.

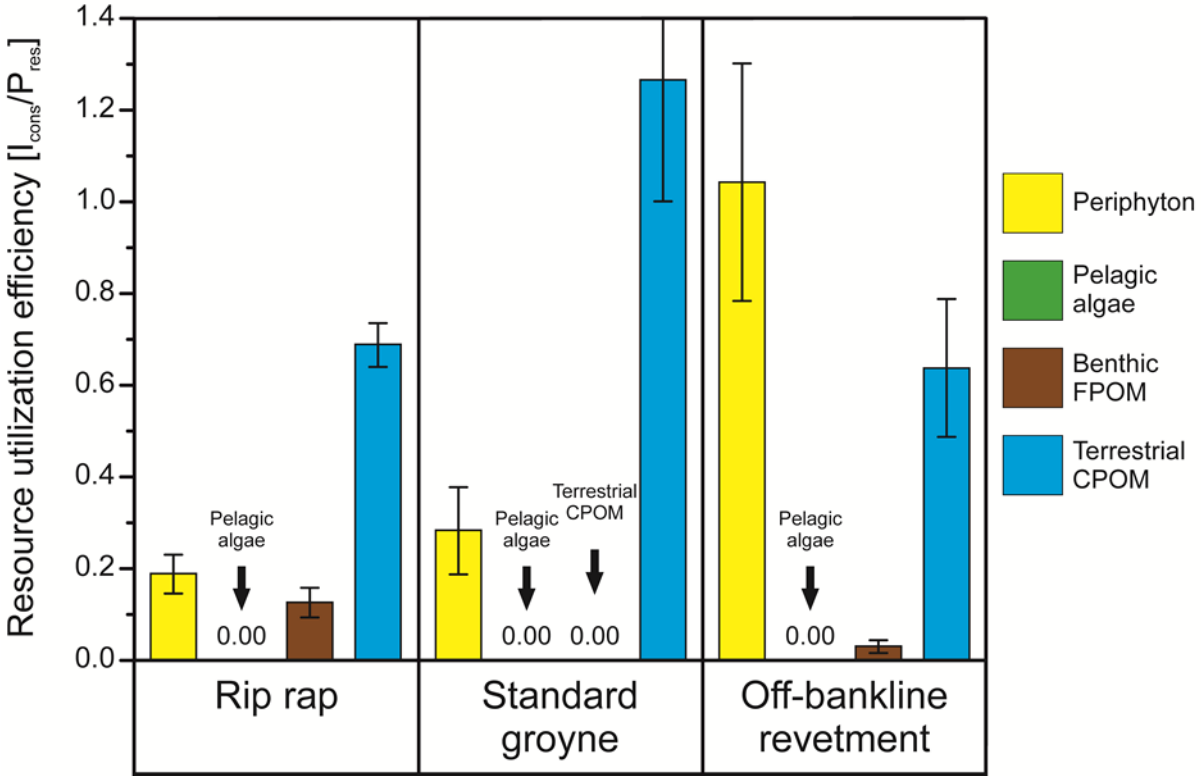

Fig. 4.3 Resource utilization efficiencies per m^2 and year expressed as the total community ingestion (I_{cons}) relative to the potential availability (P_{res}) of the basal resources periphyton (yellow), pelagic algae (green), benthic fine particulate organic matter (brown) and terrestrial coarse particulate organic matter (blue) at each shore type. Error bars show 95% confidence intervals. Values higher than 1 are actually unrealistic, but appear in this calculation as the potential availability of periphyton is based on bacterial production only and does not include algal production. For terrestrial CPOM values higher than 1 occur, because terrestrial litter input is a total river mean so that sink habitats can have higher availability.

The most effectively utilized resource at all sites was terrestrial CPOM (Fig. 4.3). More than half of the available material is ingested at the rip rap and off-bankline revetment, whereas at the standard groyne it was entirely and significantly more effectively utilized (I/P=1.3). Although resource utilization efficiency values >1 are not possible in reality, terrestrial CPOM may have been more available at the standard groyne. Terrestrial CPOM amounts are whole river means, so that certain sink zones may retain more, and high flow zones less material. The second most effectively utilized resource is periphyton. At the rip rap and standard groyne about 19 and 28% of potentially available periphyton were consumed, respectively (Fig. 4.3). At the off-bankline revetment the entire amount of periphyton is consumed, which leads to a significantly higher resource utilization efficiency (I/P=1.0). The vast amounts of available FPOM and pelagic algae mostly lead to efficiency values below 0.01, except for FPOM consumption at rip rap and off-bankline revetment (0.13 and 0.03, respectively). The relatively high value of 0.13 at the rip rap was the result of a much lower FPOM precipitation (Table 4.2).

4.4 Discussion

This chapter presents quantified flow food webs from a large lowland river. The empirical analysis of basal organic matter flows at different shore types revealed strong site-specific patterns in food web structure, identities of interactions and quantities of utilized basal resources. Benthic FPOM was the prevailing energy source at all sites. In contrast, pelagic algae played only a minor role despite vast available amounts. Total ingestion mostly followed patterns of secondary production and thus was lowest at the rip rap and much higher at the off-bankline revetment, especially concerning benthic FPOM. As also apparent from chapter 2, shore morphology changed ingestion-dominating taxa from native Diptera at standard groyne and off-bankline revetment to non-native Crustacea at the rip rap. Exclusively in the off-bankline revetment, native Bivalvia played a mentionable role in resource utilization. These results demonstrate that man-made shore constructions alter the pattern and magnitude of links at the resource-consumer interface and provide mechanistic understanding for future functional research and implications for management activities.

Trophic basis of benthic macroinvertebrate secondary production

There is an ongoing debate about the type of energy that fuels aquatic secondary production in large rivers (Delong *et al.* 2001; Zeug & Winemiller 2008; Roach 2013). The majority of studies revealed that most large river food webs were qualitatively based on algal production (Thorp *et al.* 1998; Delong *et al.* 2001; Roach 2013). However, at least a few studies examined river food webs that were fueled to only a limited extend by pelagic algae, but mainly by detritus and FPOM instead, e.g. at the Brazos River in Texas (Zeug & Winemiller 2008). This chapter designated benthic FPOM as the main ingested resource in all food webs from the River Elbe (Fig. 4.1). This contradicts with the prediction that pelagic algae constitute the main ingested resource at all sites due to the high loads available in the Elbe. One prominent reason for the increased importance of detritus in aquatic food webs is the high availability in terms of large sediment loads and turbidity (Roach 2013; Cross *et al.* 2013). On the other hand, the most available resource is not necessarily the one that is also consumed most (McCutchan & Lewis 2002), a point that is also evident from this study. It is rather a combination of food resource availability and quality that decides on their utilization by benthic communities (Marcarelli *et al.* 2011). The facts that microalgae typically provide a higher nutritional value than benthic FPOM (Sarkanen & Ludwig 1971; Renaud, Thinh & Parry 1999), and that pelagic algae were available in vast quantities in the studied system, let the Elbe food webs appear somewhat abnormal. Obligatory filter feeders are largely missing and facultative filter feeders seem to use other pathways (Fig. 4.2). One likely explanation is that benthic FPOM in the River Elbe is actually of higher nutritional quality than generally assumed. Chemical analyses of Elbe FPOM indeed uncovered relatively high N-concentrations, which lead to higher assimilation efficiencies (Table 4.1) compared to those usually applied in food web studies (AE=0.1; Benke & Wallace 1980; Cross *et al.* 2013). Nutritional value and N-content of benthic FPOM is often increased by bacterial production, which can be so substantial that it accounts for the majority of the entire riverine bacterial production (Edwards 1987). Additionally, extracellular polymeric substances (EPS) excreted by bacteria, as well as bacterivorous protists can make a substantial contribution to an increase in food quality (Carlough & Meyer 1989; Couch, Meyer & Hall 1996). The potentially higher nutritional value and the accompanied increase in assimilation efficiency of FPOM have already been taken into account in past and recent studies (Benke & Wallace 1997, 2014) and are likely explanations for the dominance of benthic FPOM as basal resource for secondary production in the Elbe.

Shore type specific uptake of basal resources

Chapter 2 showed that shore morphology affects community composition and secondary production patterns. It became clear that it also impacted the organic matter flux. Total community ingestion followed secondary production patterns with total resource ingestion being lowest at the rip rap and highest at the off-bankline revetment (Figs. 2.2c; 4.1b). As quantified trophic base estimations are rare or even lacking from large rivers, no data exist from a system comparable to that I worked in. The only available results from larger rivers (sixth order) do by far not reach consumption rates of FPOM like those found in the off-bankline revetment (794 g DM m^{-2} y^{-1}; Fig 4.1 b). Cross *et al.* 2013 reported total community (macroinvertebrates and fish) ingestion of all resources to be 219 g AFDM m^{-2} y^{-1} and interpreted these results as high. Benke and Wallace (2014) worked in a sixth order subtropical blackwater river and found amorphous detritus ingestion rates of 332 g DM m^{-2} y^{-1}. As they assessed the secondary production rates as "extremely high", so should be the ingestion of the prevailing basal resource. However, FPOM ingestion at the off-bankline revetment was still more than twofold higher than the highest rates formerly reported. Total ingestion of all resources (1,323 g DM m^{-2} y^{-1}) even exceeded the high ingestion rates reported by Cross *et al*. (2013) by six times. Whole community ingestion rates of all resources and in particular ingestion of benthic FPOM can hence so far be designated as extremely high at the off-bankline revetment. Total ingestions at the rip rap and the standard groyne (282 and 413 g DM m^{-2} y^{-1}, respectively) can rather be assessed as moderate or high. Despite these much higher total ingestion rates at the off-bankline revetment, absolute consumption of terrestrial CPOM was in the range of that at the rip rap or even less compared to standard groyne (Fig. 4.1b). Of course, those massive differences in FPOM consumption and the moderate utilization of terrestrial CPOM in the light of vast amounts of total ingested resources affected the relative resource ingestion rates between off-bankline revetment and the other shore types. Relative ingestion rates did not markedly differ between rip rap and standard groyne (Fig. 4.1a). This was also the case for periphyton and pelagic algae at the off-bankline revetment and is thus in contrast to my prediction that periphyton should be relatively more important at the rip rap. Although the rip rap constituted an ineffective sink for FPOM (Table 4.1), this very resource was the main food ingested there. More taxa were expected that could be designated as grazers on the hard substrate, mostly provided by the rip rap, and hence a higher periphyton consumption. My third prediction that FPOM would play a relatively more important role at the off-bankline revetment than at the other shore types was confirmed (Fig. 4.1.a). The main reason, however, cannot really have lain in the larger standing FPOM stock that was revealed in chapter 2 (Table 2.1), because precipitation rates from the seston were too high for FPOM availability to be limiting macroinvertebrate ingestion elsewhere (Table 4.2). It is more likely that besides the nutritional quality of benthic FPOM, the different compositions of shore type specific communities and the inherent traits were responsible for relative differences in resource uptake. This has also been revealed by Vaughn (2010). However, high community diversity does not always lead to high ingestion rates. Many estimates of high production and thus ingestion were shown to be associated with low taxonomic diversity, e.g. from non-native Gastropoda or Bivalvia (Hall *et al.* 2006; Sousa *et al.* 2008b). This did not apply to the community with highest ingestion flows at the off-bankline revetment, as species richness was also highest there (Fig. 2.2 a). The strongest link was to Chironominae, which most likely included a high number of sediment feeding species (Fig. 4.2 c; supplement Table S1). Additionally, several strong links to other community members were detected here. Indeed, at the rip rap the strongest ingestion flows were associated with only a single non-native taxon, *Dikerogammarus villosus*.

Chapter 2 revealed the availability of macrophytes, varying flow velocities and the proportion of allochthonous boulder material as main factors that influence a benthic community's assemblage and their productivity. The tight relationship between species composition, secondary production and organic matter flow patterns shows that shore type induced habitat conditions and hydromorphology strongly affect the magnitude and, to a certain degree, also the relative proportions of consumed basal resources as well.

Organic compound retention and ingestion dominating food web members

The direct assessment of mass balances in terms of resource availabilities and their utilization by consumers is essential to detect top down or bottom up effects. If the direct influence of predators like fish on their prey has to be measured, the so-called ecotrophic efficiency is often applied (Christensen & Pauly 1992; Daskalov *et al.* 2007; Cross *et al.* 2013). The ecotrophic efficiency is the relative amount of prey production that is actually consumed by predators. A value of 1 indicates the entire consumption of a predator's prey and thereby a strong top down control. A comparable kind of mass balance assessment is also useful for basal matter flows (e.g. Poepperl 2003; Benke & Wallace 2014). In contrast to ecotrophic efficiency calculations, in this study not only mere production estimates of resources were used, but also their loads which mirror potential availabilities. Resource utilization efficiencies were calculated on the primary consumer level to shed light on the question of which amounts of available basal resources are actually utilized and which parts remain untouched.

Terrestrial CPOM and periphyton were consumed with high efficiency (Fig. 4.3). Most taxa were opportunistic concerning their food resource, so that a switch was possible if needed. *Dikerogammarus villosus* at the off-bankline revetment, for example, shifted diet compositions and did not consume any terrestrial CPOM, whereas at the other shore types it did (Fig. 4.2). Due to the effective utilization of terrestrial CPOM and periphyton, both resources seem irrelevant from a particle load perspective. In contrast, benthic FPOM and pelagic algae consumption could not reach mentionable efficiencies due to the vast amounts available in the Elbe. The only taxa that covered about half their nutritional needs by consuming the most common large river resource, i.e. pelagic algae (Thorp *et al.* 1998; Delong *et al.* 2001; Roach 2013), were *Sphaerium* sp. and Simuliidae (Fig. 4.2 c; Table S4). Both were exclusively present in sufficient numbers for secondary production estimates at the off-bankline revetment. Although in comparison to rip rap and standard groyne, contributions of Bivalvia to total off-bankline revetment community ingestion are relatively high, benthic communities and thus food webs at the River Elbe generally lacked high proportions of mussels and clams (Figs. 2.4; 4.2). In other large river systems, Bivalvia often dominate benthic community biomass and ensure that pelagic algae are utilized in large amounts (Strayer 1999). Why bivalve molluscs did not establish prominent populations in the River Elbe can only be speculated. As, in principle, at the off-bankline revetment mussel populations could establish, growth-repressing factors like food quality and toxic components in the sediment (Byrne & O'Halloran 2001; Wacker & Von Elert 2003) are no likely reasons for low mussel contributions in the River Elbe. One plausible reason for a hampered establishment of large mussel populations may lie in top down pressure due to fish predation (Magoulick & Lewis 2002; Lappalainen, Westerbom & Heikinheimo 2005; Nakano, Kobayashi & Sakaguchi 2010). The access that fish have to benthic macroinvertebrates differed considerably between the different shore types, so that the off-bankline revetment bore the only habitats that could not be reached by larger fish most of the time. However, it is a fact that algal diet proportions of Chironomidae were substantially higher than those of the non-native *Dikerogammarus villosus* (Table S4). The increased contribution of Chironomidae to secondary production did therefore result in higher amounts of utilized pelagic algae, whereas high contributions of *D. villosus* resulted in low amounts of utilized pelagic algae. Hence, productive facultative filter feeding Chironomidae dampen the effect of missing obligatory filter feeders, at least slightly. As amounts of pelagic algae did not mirror the production, but the transported dry mass that is available in the water column, small increases in pelagic algae utilization along the entire river stretch would have an integrative effect and thus potential amounts might substantially decrease downstream (c.f. Benke & Wallace 2014). That means an installation of shore structures such as off-bankline revetments, which enhance pelagic algal retention, in relatively close and regular distances along the river, would most likely achieve drastic reductions of algal charges.

Irrespective of the fact that benthic FPOM constituted the main basal resource for benthic macroinvertebrate secondary production and was ingested in high amounts, due to its more or less recalcitrant character it is continuously re-deposited by excretion (Benke & Wallace 2014). However, excreted FPOM is a food resource for microbes which in turn increase the FPOM's nutritional value again (Wotton & Malmqvist 2001). Hence, even if the FPOM standing stock cannot be effectively decreased by macroinvertebrate consumption, the organic compounds will be channeled and thereby reduced. At the rip rap total FPOM ingestion was lowest and *Dikerogammarus villosus* dominated the local FPOM ingestion flows. The benthic community provided by the off-bankline revetment was dominated by Chironomidae and channeled six to seven times higher amounts of benthic FPOM compared to standard groyne and rip rap, respectively. Thus it did not only play a crucial role for pelagic algae utilization, but also in reducing the organic compounds of FPOM, the second most available resource in the River Elbe.

When matter fluxes through the entire food web were studied on a more than basal level, food webs were assessed as efficient if the majority of invertebrate production was consumed by top predators such as fish (Cross *et al.* 2013). The proportion of invertebrate production that may be consumed by fish remains unclear in this study, but even if large parts of secondary production were not consumed at the off-bankline revetment and thus organic compounds were processed and partly decreased, energy could still be removed by emergent insects (Jackson & Fisher 1986). In terms of organic compound removal emerging insects could be seen as an efficient mechanism in aquatic systems because organic material is directly transported out of the system. The off-bankline revetment bore the highest secondary production of emergent insects (84 g m^{-2} y^{-1}) and hence provided the highest nutrient removal potential (Figs. 2.2c; 2.4b). The rip rap community, however, is dominated by invasive Crustacea that have holoaquatic life cycles and do not remove any nutrients from the riverine system by emergence.

Conclusion

In contrast to the majority of large riverine food webs, secondary production at the River Elbe was mainly fueled by benthic FPOM. Flow food web analyses showed that habitat characteristics and the hydromorphology induced by anthropogenic shore structures do not only determine community composition and productivity (chapter 2), but also strongly affect energy pathways and organic compound retention. The off-bankline revetment led to a community that consumed the highest absolute amounts of pelagic algae and by far the highest amounts of benthic FPOM, the two most abundant resources in the Elbe. Here, the only mentionable population of filter feeding Bivalvia was detected, which, in combination with vast quantities of potentially emergent Chironomidae, contributed significantly to the retention of the most available resource, namely pelagic algae. In contrast, the rip rap community is dominated by non-native Crustacea that utilize only minor proportions of pelagic algae and do not have the potential to directly remove organic compounds due to their holoaquatic life cycle. This study provides mechanistic understanding of how anthropogenic shore constructions impact riverine benthic ecosystem functioning. From a management perspective, creating hydromorphological conditions similar to those at off-bankline revetments seems promising for substantially increasing organic matter channeling and retention in large navigable rivers.

General Discussion

Rationale

Large rivers provide a variety of economical goods and perform several crucial ecosystem services (Millenium Ecosystem Assessment 2005). Nevertheless, those ecosystems are threatened by human-induced stressors like chemical and structural impairment (Allan & Flecker 1993; Vaughn 2010). Structural degradation, as one of the most prominent stressors nowadays (Hughes *et al.* 1990; Allan & Flecker 1993), was formerly shown to influence the composition and diversity of benthic macroinvertebrate communities (Dudgeon *et al.* 2006; Strayer & Findlay 2010). A recent study also detected impacts from damming on the structure and magnitude of matter flow (Cross *et al.* 2013), but studies that determine stressor effects on those ecosystem functions require high efforts. Relatively few attempts have been made to test the direct influence of man-made structural degradation on an ecosystem's performance. However, as there is virtually no large river system free from structural impairment (Hughes *et al.* 1990), it is of fundamental importance to get insights into how this particular stressor affects benthic communities and, as a result of this, influences ecosystematic features like productivity and organic matter fluxes.

The main objective of this study was to improve the mechanistic understanding of how particular shore types in large rivers affect benthic macroinvertebrate communities and their inherent functional performances in terms of productivity and resource utilization. Additionally, it aims at facilitating future studies on ecosystem functioning in large rivers by providing a comprehensive collection of already published and newly established data essential for biomass and secondary production estimates.

Abiotic factors determining macroinvertebrate communities

This study showed that habitat structure and hydromorphology were key elements that affected community compositions and their associated ecosystem functions. Habitat conditions in the main channel differed substantially from those at the shore zones. However, the habitat conditions at the shore types themselves showed characteristic differences between one another.

Constantly high flow velocities and relocation of the fine sandy sediment produced harsh conditions in the main channel, which most probably led to a community composed of only a few taxa. This is in line with previous studies which showed that sand-dominated main channels are inhabited by very few specialized species with low numerical abundances and biomasses (Simpson *et al.* 1986; Nakano & Nakamura 2006). The unfavorable conditions also affected the functional performance of the main channel community, as secondary production was more than two orders of magnitude lower than the shore community productions (Fig. 2.2c). These pronounced negative effects on riverine communities occurred irrespective of the adjacent shore type and thus designate navigable large sand-dominated lowland river main channels as zones of poor ecosystem functioning. However, for some species the sandy substrate seems to be less a problem than the high flow velocity. This is indicated by the detection of *Ametropus fragilis* at the outflow of the off-bankline revetment. It suggests that fine sandy substrates that are mainly overflown by only moderate velocities can indeed be inhabited by species other than the usually to be found Oligochaeta and small Chironomidae.

Differences between shore type communities and their respective ecosystem functions could barely be explained by resource variables or availabilities. Many taxa were able to shift contributions of particular resources to their diet and the availability of the most ingested resource, benthic FPOM, was not limiting at all. Rather, differences in habitat conditions were responsible for shore type specific community assemblages and their associated functions. The sediment composition differed between shore types, as a result of near-bed hydraulic conditions (Statzner, Gore & Resh 1988). Sediment grain size and structure have profound influences on the inhabiting fauna and so does the hydraulic regime itself. High variation of flow velocity and the occurrence of lentic conditions and pool phases during low discharges are known to favor diverse communities in large rivers (Arthington *et al.* 2006; Garcia *et al.* 2012). Additionally, macrophytes which are dependent on particular sediment and flow conditions play a special role as riverine habitats. Lorenz et al. (2009) found a large number of taxa on macrophytes that could not be detected in straightened river regions. As a result of those direct and indirect hydraulic influences, species that are related to slow or no flow (e.g. *Dicrotendipes nervosus* (Diptera) and Physidae (Gastropoda)) or macrophytes (e.g. *Cricotopus* sp. (Diptera) and *Cloeon dipterum* (Ephemeroptera)), as well as several taxa that are strongly related to fine sediments (e.g. *Camptocladius stercorarius* and *Chironomus* sp. (Diptera)) were detected in the off-bankline revetment (Table S2). The latter taxa in particular contributed 50% to the total secondary production and obviously used the FPOM-dominated sediments as habitat and food resource at the same time.

A special type of habitat is provided by allochthonous stones or boulders that are used for building most of the technical shore constructions. The boulder-dwelling macroinvertebrate fauna is apparently hardly affected by the shore type in which it is situated. Communities and secondary production patterns were comparable between the mesohabitat stones of all shore types (data not shown). Similar observations were made by several former studies, which showed the hardened shoreline to produce a largely distinct biota (Chapman 2003; Bulleri, Chapman & Underwood 2005; Moschella *et al.* 2005). The most prominent members of the boulder community concerning biomass and secondary production were non-native species. At the rip rap boulders made up more than 80% of the total habitat and, as a result, non-native species controlled the entire food web and organic matter flow at this shore type. It could thus clearly be shown that boulders provide the key substrate for a successful establishment of invasive species, especially *Dikerogammarus villosus*. This finding is supported by Frueh *et al.* (2012), who in a comprehensive meta-analysis recently detected that physically degraded shore zones face a higher risk of being invaded by neozoa species than non-impacted shores. Furthermore, van Riel *et al.* (2006) found enormous neozoa contributions (up to 95%) to total macroinvertebrates on boulders during field experiments in a large lowland river.

This study highlighted the fundamental importance of the shore type induced hydraulic regime and the associated direct effects on mesohabitat conditions for the establishment of diverse communities and their functional integrity. If the percentage contribution of shallow shore zones with a highly dynamic flow regime was increased in large rivers, the proportion of unproductive main channel area would decrease at the same time. Profound large-scaled positive effects concerning biodiversity improvement and resource utilization increase could thus be expected. Additionally, as allochthonous building material for shore constructions could be designated the main reason for local non-native species establishment, its proportional reduction or replacement by alternative materials like deadwood will most likely result in lower shares of undesired species and an eased influence on the functional performance of native communities.

Shore type dependent functional attributes

Despite the areal dominance of main channel habitat in large navigable rivers, its functional role has been revealed as negligible. Therefore, food web analyses and matter flux determinations in this study focused on the shore zone dwelling communities. Here, community productivity and matter fluxes as well as the food web structure were strongly influenced by the shore construction type. However, in contrast to most large river food webs that were qualitatively based on algal production (Thorp *et al.* 1998; Delong *et al.* 2001; Roach 2013), this study generally revealed benthic FPOM as the main ingested resource in all food webs from the River Elbe (Fig. 4.1). Food webs in which a high fraction of secondary production is derived from detritus are thought to have less secondary production but higher species diversity than food webs that are supported by algae (Rooney & McCann 2012). This applied to the relatively low secondary production at the rip rap, but, deviating from this, species richness was also only moderate here (Fig. 2.2a). At the standard groyne species numbers was comparable to the rip rap, but secondary production was substantially higher. The most prominent contradiction to the statement of Rooney and McCann (2011) was found at the off-bankline revetment, where highest species numbers were found and secondary production estimates could be assessed as very high (Huryn & Wallace 2000). As amounts of ingested resources more or less followed secondary production estimates, basal matter fluxes at the off-bankline revetment could even be designated as extremely high (Cross *et al.* 2013; Benke & Wallace 2014), especially with respect to benthic FPOM.

Differences of secondary production between shore types become particularly apparent when their areal extension in the river's cross section is considered. The rip rap did not only show the least productivity and ingestion flows, but also the lowest suitable area for macroinvertebrates due to its steep inclination. Assuming a maximum suitable depth of two meters, the areal extension of the rip rap towards the main channel would only add up to four to five meters. The mean cross extension of a standard groyne and off-bankline revetment is manifold larger with about 40 and 20 meters, respectively. That means, compared to a rip rap controlled river section, the whole riverine cross section secondary production would be more than ten times higher if standard groynes constituted the shore protection type and more than 16 times higher if off-bankline revetments were installed (cf. Fig. 2.2c). If benthic FPOM ingestions were compared in the same way, differences would be even more pronounced, designating the off-bankline revetment the most productive shore type with highest community ingestion rates. (Entire river cross section ingestion will be dealt with in more detail below.)

The food web at the off-bankline revetment showed the highest values of community ingestions as well as the highest number of basal trophic links. Additionally, whole community ingestion was more evenly distributed between food web components than at standard groyne and rip rap. Although there was a single most prominent link from benthic FPOM to Chironominae, the high resolution in Chironomidae determination showed a large number of single midge taxa inhabiting the off-bankline revetment (Table S2). Hence, it is likely that FPOM matter flows are distributed among many Chironominae taxa. The combination of the enormous amount of benthic FPOM that is utilized at the off-bankline revetment and the more evenly distributed magnitudes of connections allow the assumption that food webs should exhibit high community resistance and resilience to disturbances here (DeAngelis 1992; McCann, Hastings & Huxel 1998). In contrast, the rip rap food web was characterized by only a few links and one taxon dominating the entire matter flow, indicating low food web stability. However, as the dominating taxon *Dikerogammarus villosus* is very tolerant to a variety of stressors (Maazouzi *et al.* 2011; Gabel *et al.* 2011; Bundschuh *et al.* 2013), it is unlikely that rip rap food webs are especially prone to disturbances, at least at the current state of succession. Now, the functional dominance of a single tolerant, non-native taxon accompanied with lower total species richness and community productivity paradoxically seems to bear negative connotations of stability.

It should be mentioned that the presented resource flows were exclusively between the trophic basis of secondary production and primary consumers. Modelling was based on a pre-evaluation of the consumers' trophic positions. Two taxa (*Hydropsyche* sp. and *Dikerogammarus villosus*) that were formerly reported as potentially omnivorous (e.g. Benke & Wallace 1980; Dick *et al.* 2002; van Riel *et al.* 2006), are treated here as primary consumers. All taxa with a mean trophic position >2.6 were discarded to avoid the inclusion of omnivores. Nevertheless, as trophic positions were mean values from several seasonal samples, it may be that few specimens were included that derived some biomass from consuming animal tissue. For *Hydropsyche* sp. such an overestimation of ingested basal organic matter would be negligible at all sites because contributions to whole community ingestion were very low (Fig. 4.2). The consumption of animal prey by *D. villosus* is, in contrast to a widespread opinion, actually unlikely. The vast majority of former studies designating *D. villosus* as a “killer shrimp” were performed under laboratory conditions (Dick *et al.* 2002; MacNeil & Platvoet 2005). Recent results from field studies found no evidence for carnivorous behavior (Koester & Gergs 2014), and so did trophic position estimates from this study. In general, omnivory is often an adaptive response to nutritional limitations, competition and frequent disturbance (Jepsen & Winemiller 2002; Loeuille & Loreau 2005; Wilder & Eubanks 2010). All those factors can be excluded at the rip rap, where ingestion proportions from the potentially omnivorous taxa were highest (Fig. 4.2). For the abovementioned reasons the overestimation of basal resource ingestion due to omnivory can be neglected. Hence, extremely high ingestion rates at the off-bankline revetment and much lower resource utilization rates at the rip rap and standard groyne are further validated.

Potential for particle retention and organic compound removal

One main objective of this thesis was the qualitative and quantitative detection of basal resource ingestion by benthic primary consumers. In contrast to the high number of studies that were directed toward resolving the origin of energy-fueling aquatic secondary production to test energetic concepts (Delong *et al.* 2001; Zeug & Winemiller 2008; Roach 2013), results from this work allow for a quantified direct assessment of resource utilization and retention. One prominent example that mirrors the ecological and economic problems that high organic particle loads in riverine systems can generate is the sedimentation process at estuarine harbors. Here sedimentation leads to massive FPOM layers that regularly have to be removed for the sake of navigation (Owens *et al.* 2005). Furthermore, pelagic freshwater algae entering the brackish water section rapidly die, precipitate in vast amounts, and their microbial degradation leads to oxygen depressions that can even constitute insurmountable barriers for migrating fish (Kerner 2007). This example alone already illustrates the need for a systematic understanding of how organic particle loads in large rivers are influenced by structural degradation.

The mere particle load can be reduced by filter feeding taxa that remove particles from the water column and deposit a certain, assimilation efficiency depended fraction to the benthic environment by excretion (Strayer 1999). The reduction or export of organic compounds from the aquatic system by benthic macroinvertebrates, however, is in principle accomplished by two mechanisms. The first is the ingestion and subsequent processing of a resource. This leads to a reduction of organic compounds through respiration (Benke 2010), which in turn depends on the net production efficiency (Benke & Wallace 1997, 2011). The second mechanism, the direct removal of organic matter, can be achieved by specimens that leave the aquatic environment, e.g. through emergence (Jackson & Fisher 1986; Gratton & Vander Zanden 2009). Resource ingestion and thus benthic FPOM utilization and the retention of pelagic algae were directly quantified in this study.

At the off-bankline revetment enormous amounts of benthic FPOM that were six- to sevenfold higher than at the standard groyne and the rip rap were ingested per m^2. When the river cross section ingestion is compared (see above), FPOM ingestion is more than 27 times higher than at a rip rap-controlled river section and it is still three times higher if standard groynes constitute the shore protection. Irrespective of the fact that benthic FPOM is continuously re-deposited by excretion due to its more or less recalcitrant character (Benke & Wallace 2014), excreted FPOM is a food resource for microbes, which, in turn, increase the FPOMs nutritional value again (Wotton & Malmqvist 2001). Hence, even if the mere benthic FPOM load cannot be decreased effectively by macroinvertebrate consumption, the organic compounds are channeled several times and thereby reduced step by step.

In the River Elbe the annual mean value of pelagic algae concentration is more than six times higher than in the River Rhine (Hardenbicker *et al.* 2014). In contrast to the Rhine, where filter feeding macroinvertebrates cause high losses of pelagic algae (Viergutz *et al.* 2007; Friedrich & Pohlmann 2009), low contributions of obligatory filter feeders and missing links from facultative filter feeders make pelagic algae in Elbe food webs a less important resource, despite vast availabilities (Fig. 4.2; Table 4.2). In the current state algal loads are so high that retention by riverine macroinvertebrates are virtually negligible (Fig. 4.3). However, annual pelagic algae ingestion per m^2 of the benthic community at the off-bankline revetment exceeded that of standard groyne and rip rap by more than two and three times, respectively. Given the fact that due to inoculating impoundments in the upper regions of the River Elbe initial chlorophyll a loads are much higher than in other large rivers (Fischer *et al.* 2012), it can be expected that small increases in pelagic algae utilization, especially at the base of those impoundments, may hamper the rapid algal growth further downstream. In general, the implementation of shore structures that promote the consumption of pelagic algae along the entire river stretch can be expected to have an integrative decreasing effect on potential algal amounts, no matter if they are placed in upper regions or elsewhere (c.f. Benke & Wallace 2014). When pelagic algae consumption is again calculated for the whole river cross section (see above) and compared between shore types, the off-bankline revetment's value is comparable to that of the standard groyne but more than twelve times higher than that of the rip rap. It is impossible to exactly predict how the shore type specific retention rates would impact the total riverine algal load as suitable measurements of algal production have not been conducted yet. Moreover, changes in algal densities would lead to complex cascading effects of growth-controlling factors like self-shading (e.g. Basu & Pick 1996). However, when considering the river cross section, it became obvious that standard groyne and off-bankline revetment communities retain pelagic algae in amounts more than one order of magnitude higher than those at a rip rap. Hence, despite the enormous pelagic algae standing stock, it is likely that a long river stretch entirely framed by standard groynes or off-bankline revetments would result in an integrative effect on the pelagic algal load. This possible effect would of course be even more pronounced if contributions of taxa that preferably consume pelagic algae, like clams or mussels, increased further.

Although emerging biomass was not measured during this study, it has to be considered for organic compound removal nevertheless. Emerging biomass can reach high proportions (about 30%) of a population's secondary production (Jackson & Fisher 1986). The highest absolute production attributed to emerging insects was found at the off-bankline revetment (84 g m^{-2} y^{-1}), the lowest at the rip rap (10 g m^{-2} y^{-1}; Figs. 2.2; 2.4b). It can be assumed that a large part of the benthic secondary production is consumed by fish (Gilinsky 1984; Diehl 1992; Dahl 1998). Food webs could thus be assessed as efficient (e.g. Cross et al. 2013), but organic compounds would largely be channeled within the system instead of being entirely removed. At the off-bankline revetment high proportions of unconsumed benthic secondary production would directly be removed from the aquatic system by emergence, whereas at the rip rap a high proportion of unconsumed macroinvertebrate production would remain in the system as a result of the holo-aquatic life cycle of most taxa (Crustacea, Gastropoda). Shore types displaying habitat conditions that are comparable to those at off-bankline revetments will therefore either contribute significantly to fish biomass production or to an effective organic compound removal from aquatic to terrestrial environments. In addition, they were shown to provide the most productive benthic communities, which utilize vast amounts of the prevailing basal resources and will thus further contribute to organic compound channeling and reduction.

The role of neozoa in riverine ecosystem functioning

Non-native species are often the dominating members of benthic communities and can reach high proportions of a community's production (Hall *et al.* 2006; Sousa *et al.* 2008b). As taxa within communities affected by species invasion have not co-evolved, food web structure and energy pathways can be substantially impaired (Vander Zanden *et al.* 1999; Hobbs *et al.* 2006). This study revealed that the contribution of neozoa to a community's secondary production was in general substantially lower than their contribution to biomass at a given shore type (Fig. 2.4). For example, non-native *Potamopyrgus antipodarum* (Gastropoda) contributed with an average of 40% to total weighted biomass, but only 9% to total production at the off-bankline revetment. In contrast, native Chironomidae were effective biomass producers in such an extent that a contribution to biomass of less than 20% resulted in a contribution of about 70% with respect to secondary production at the off-bankline revetment. The only exception was detected at the rip rap, where invasive Crustacea contributed more than 80% to community biomass and therefore also dominated secondary production (but again in lower proportions compared to the biomass).

In this study, all relevant non-native species were larger than the most productive group of Chironomidae. For instance, the most prominent invader, *Dikerogammarus villosus*, grew to a total body size of about 28 mm (chapter 1) and can reach a total length of 30 mm in some natural environments (Nesemann, Pöckl & Wittmann 1995). Most Chironomidae taxa are considerably smaller, have a lower body weight and can thus reach much higher production values (Mackey 1977; Benke 1998). Former studies indicated that *D. villosus* shows higher growth rates than native amphipods, despite comparable or even larger body size (Devin *et al.* 2004). It can thus be assumed that the detected lower contributions to secondary production by non-native species are mainly based on larger body sizes that in turn lead to lower turnover rates (Brown *et al.* 2004; Woodward *et al.* 2005) and that native communities in principle have higher production rates if Chironomidae are sufficiently present.

Direct pressure of the prominent invader *Dikerogammarus villosus* on native community members as a result of a predatory feeding type could not be detected in this study and has recently been rejected by others (Koester & Gergs 2014). Then again, Gergs *et al.* (2014) found a negative correlation between the density of *D. villosus* and the amount of aquatic emergence and made a predatory feeding type responsible, although *D. villosus*' diet was not assessed. However, the fact that *D. villosus* is capable of reducing the emerging biomass intensifies the already-present poor organic compound-removal-potential of rip raps. Moreover, there are generally no emerging insects among invasive species, so that their shown negative impact on the potential of organic compound removal from aquatic systems is further increased.

The most abundant non-native taxa in this study, *Dikerogammarus villosus* and *Potamopyrgus antipodarum*, meet their nutritional requirements with only minor portions of pelagic algae (Table S4). A functional dominance of those taxa would lead to a further reduction of pelagic algae utilization in a way that is already detectable at the rip rap. Those functional influences of non-native taxa were buffered by native members at the standard groyne and especially at the off bankline revetment, whereas in the boulder habitat of the rip rap the community was not able to dampen the functional dominance of *D. villosus*. This study showed that non-native species can have a profound influence on the functioning of benthic communities. However, it also became apparent that the degree of functional impact strongly depends on the habitat conditions and particularly on the percentage contribution of boulders. It is still under considerable debate if non-native species like *D. villosus* actively replace native inhabitants or if they just benefit from habitat modification that lead to unfavorable conditions for native taxa (Didham *et al.* 2005). My results indicate that at least direct pressure by predation on native taxa is not fundamental for maintaining a stable non-native species-dominated population.

Implications for future management and research

Man-made shore types dominate the riparian zone of the River Elbe. These constructions have a strong influence on the diversity and ecosystem functioning of benthic macroinvertebrate communities and their share of non-native species. As there are virtually no aquatic ecosystems free from structural degradation (Arthington *et al.* 2010; Vörösmarty *et al.* 2010), this situation can be considered the norm. Due to hard socio-economic boundary conditions like navigation or flood protection, large-scaled restructuring in large river systems is virtually impossible (bij de Vaate *et al.* 2006; Hering *et al.* 2010) and local habitat alteration mostly provides the only possibility to influence their morphology (Large *et al.* 2012). Hence, this study provides researchers and managers with fundamental knowledge on how communities respond to specific local structural impairments. I revealed the complex hydromorphology detected at the off-bankline revetment to be essential for diverse and productive benthic communities. As a secondary effect, near-bed hydraulic conditions determine the sediment composition (Statzner & Higler 1986) and lead to different mesohabitats, which is important for the establishment of a diverse fauna. The partly prominent influences of the shore types on biodiversity might be the result of valuable recolonization sources in the surrounding of the sampling sites (although they were not apparent). The detection of the ancient lowland river dwelling mayfly *Ametropus fragilis*, which is now listed as extremely endangered, supports this assumption. Increases of biodiversity after manipulation experiments or management actions can only be expected if sources providing the desired taxonomic pool are in close proximity to the managed site (Sundermann *et al.* 2011). The recolonization potential of the Elbe may present a considerable advantage over many other riverine systems (Jähnig, Lorenz & Hering 2009), in which diversity increases could be hampered or slowed down due to the presence of long sections of monotonous structures that can hardly be overcome by many organisms. However, if structural manipulations are applied at sites with low recolonization potential, at least a shift of dominances within already established benthic communities and the respective functional response is to be expected. In this study, Chironomidae were functional key players of both production and organic matter flow, whereas non-native taxa turned out to be relatively unproductive. Both taxa are ubiquitous in large river systems. As boulders provided habitats highly prone to invasion, a reduction of this allochthonous material would most likely result in lower shares of neozoa. If shore manipulations additionally changed the hydromorphology to conditions comparable to those at the off-bankline revetment, a change of the dominance patterns from e.g. non-native Crustacea towards native Chironomidae and therefore higher production and resource utilization rates could be expected, irrespective of the re-establishment of vanished taxa. Consequently, management activities at sites with low recolonization potential are nonetheless promising to deliver useful results and desired functional outcomes.

In my study three frequently applied scientific methods turned out to be only partly successful for the functional assessment. First, most taxa showed links to each of the resources (Fig. 4.2), so that it seems unlikely that the classical feeding type assignment (Cummins & Klug 1979) is valid for the River Elbe. The use of functional feeding types is still common for several research questions (Rawer-Jost *et al.* 2000; Cummins, Merritt & Andrade 2005). However, the application is restricted. Smock and Roeding (1986) quantified matter flows to an entire macroinvertebrate assemblage and showed that, contrary to their functional group categorization, a high fraction of scraper ingestion originated from consuming fine particulate organic matter and a high fraction of shredder ingestion originated from consuming algae. These findings strengthen my assumption and show that traditional functional feeding groups should be applied with care. Second, it became further apparent that food web complexity alone does not allow predictions about key resources and consumers, insufficient connections or food web stability (Benke & Wallace 2011). The application of flow food webs allowed for such predictions and pointed out strong differences between the different shore construction types. Although the construction of flow food webs demands high efforts, the surplus of analytical power and scientific interpretability outweigh the extra work that has to be invested. And third, the here detected generally higher relative contribution of non-native species to benthic community biomass than to secondary production suggests that their functional importance would be overestimated if the impact on the local community was assessed by its dominance in terms of abundance or biomass (Hall *et al.* 2006). Hence, parameters describing contribution to ecosystem functioning may provide a better indication on the ecological significance of non-native species than structural indicators.

Conclusion

This study demonstrated that shore morphology in large lowland rivers profoundly affects the composition of benthic macroinvertebrate communities, the contribution of non-native species and the communities' functional performance. It was revealed that structural habitat conditions and the hydromorphology in off-bankline revetments support highly valuable benthic communities in terms of biodiversity and organic matter utilization. A diverse flow pattern including lentic conditions and the occurrence of macrophytes have to be emphasized as particularly beneficial. Furthermore, the use of allochthonous building material like boulders turned out to facilitate and support the establishment of non-native species. These insights provide managers with a powerful tool to improve the biodiversity and functional attributes of virtually unchangeable ecosystems. The gained knowledge can help to develop new scientific methods for the assessment of impacts that the ongoing structural impairment of riverine shore zones has on the system's functional status. In its entirety, this thesis constitutes a sound basis to increase the mechanistic understanding of how shore zone manipulation can affect riverine benthic communities and their associated ecosystem functions.

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Appendix

Table S1 Abiotic factors taken every two month in each of the shore types. Mean, minimum and maximum values are shown.

Environmental factor	Standard groyne			Off-bankline revetment			Rip rap		
	mean	min	max	mean	min	max	mean	min	max
Percentage contribution of habitat to total shore and current									
Macrophytes [%]	1.26	0.00	3.71	13.53	1.93	32.31	0.02	0.00	0.20
Boulders [%]	2.44	1.00	5.00	6.67	0.00	30.00	80.09	60.00	98.00
Grain size distribution									
D90/D10	244.54	11.84	931.62	504.35	4.34	2928.97	536.52	3.17	2730.47
Gravel (2-64mm) [%]	68.43	51.07	84.68	19.56	4.61	39.65	16.99	2.66	52.81
Sand (>0.063mm<1mm)[%]	31.35	15.18	48.86	78.11	59.31	93.01	82.73	46.96	97.00
Mud(<0.063mm) [%]	0.22	0.07	0.39	2.33	0.86	6.53	0.28	0.15	0.39
Loss of ignition [%]	3.79	1.90	6.35	8.67	3.30	13.63	0.86	0.68	1.17
Standard parameters from probe measurement									
Temperature [C]	14.84	5.56	21.23	15.11	3.04	24.34	15.17	5.59	21.22
SpKond [µS cm^{-1}]	476.14	430.40	554.00	456.17	421.60	486.00	487.66	437.40	561.20
pH	9.11	8.01	9.60	8.98	8.54	9.53	9.03	8.02	9.56
ODOSat [rel. %]	133.77	93.14	174.64	126.27	110.10	151.44	134.07	93.70	171.64
ODO Conc [mg L^{-1}]	13.50	10.46	15.53	12.89	9.65	15.23	13.37	11.19	15.53
Chemical water analyses									
Chl-A [µg L^{-1}]	45.44	3.64	134.10	20.07	4.29	42.65	41.76	3.78	143.70
DOC [mg L^{-1}]	4.69	4.21	5.47	5.81	3.95	9.04	4.75	4.02	5.59
UV Absorption_254nm	0.13	0.12	0.15	0.17	0.11	0.29	0.14	0.12	0.15
NH4-N [mg L^{-1}]	0.04	0.01	0.09	0.03	0.01	0.09	0.05	0.01	0.09
NO3-N [mg L^{-1}]	3.11	2.11	4.03	2.33	0.09	3.62	3.14	2.09	4.16
POC [mg L^{-1}]	3.43	0.80	7.70	2.78	0.60	8.50	4.51	0.80	14.20
Particulate matter ash content [mg L^{-1}]	9.42	2.40	18.20	3.87	0.50	10.00	15.96	2.00	71.60
SO42- [mg L^{-1}]	75.22	46.10	91.80	65.86	41.60	88.90	79.02	51.00	106.00
Cl- [mg L^{-1}]	34.84	20.70	41.70	30.67	21.20	38.10	36.38	24.40	49.10
SRP [mg L^{-1}]	0.04	0.01	0.07	0.04	0.01	0.08	0.04	0.01	0.08
TP [mg L^{-1}]	0.14	0.11	0.17	0.16	0.08	0.31	0.15	0.09	0.21
TSi [mg L^{-1}]	4.95	3.29	6.21	4.16	2.19	5.47	5.23	3.60	8.13
Chemical sediment analyses									
As [mg Kg^{-1}]	6.44	5.00	9.50	5.29	3.00	11.00	2.31	1.50	3.50
Cr [mg Kg^{-1}]	12.39	0.00	20.00	21.60	6.50	45.50	30.66	16.00	52.00
Cu [mg Kg^{-1}]	6.17	5.50	7.60	10.40	5.00	25.50	5.23	4.00	6.00
Mn [mg Kg^{-1}]	215.79	159.00	280.20	465.04	192.00	1590.50	226.16	118.00	324.50
Zn [mg Kg^{-1}]	53.86	43.00	64.00	84.30	43.40	191.50	39.77	31.00	49.50
Ni [mg Kg^{-1}]	7.11	5.50	9.40	8.07	2.50	15.50	5.98	1.67	10.50
Fe [mg Kg^{-1}]	5419.71	2821.00	6470.00	6686.14	3122.00	14235.00	6040.52	3584.00	11785.00
P [mg Kg^{-1}]	318.43	235.00	582.00	502.14	235.00	1330.00	243.52	176.67	400.00
Pb [mg Kg^{-1}]	16.06	13.50	21.00	44.77	13.20	202.00	13.52	11.33	17.00
Sn [mg Kg^{-1}]	3.16	1.50	4.00	3.87	0.00	6.00	10.35	0.00	26.50

Table S2 List of mean, min and max abundances from all taxa detected during this study. Non-native species are shown with a grey background. Numbers of species that were exclusively found at a particular shore type are shown in bold.

Taxon	Group	Rip rap			Standard groyne			Off-bankline revetment		
		mean	**min**	**max**	**mean**	**min**	**max**	**mean**	**min**	**max**
Corbicula fluminea	Bivalvia	85	1	667	81	2	448	1	0	7
Dreissena polymorpha	Bivalvia	1	0	4	0	0	3	0		
Pisidium sp.	Bivalvia	79	4	506	55	0	222	82	0	262
Sphaerium sp.	Bivalvia	3	0	30	7	0	27	64	6	422
Dryops sp. Lv.	Coleoptera	**0**	**0**	**1**	--	--	--	--	--	--
Hydrophilus piceus Ad.	Coleoptera	--	--	--	--	--	--	**1**	**0**	**3**
Laccophilus hyalinus Ad.	Coleoptera	--	--	--	--	--	--	**4**	**0**	**35**
Asellus aquaticus	Crustacea	**0**	**0**	**1**	--	--	--	--	--	--
Atyaephyra desmaresti	Crustacea	0	0	1	--	--	--	9	0	83
Chelicorophium curvispinum	Crustacea	824	16	4289	151	1	1046	824	0	6024
Dikerogammarus villosus	Crustacea	627	17	2874	136	5	276	508	10	2253
Gammarus roeselii	Crustacea	0	0	1	--	--	--	1	0	3
Jaera istri	Crustacea	706	57	3136	241	25	894	90	2	345
Orconectes limosus	Crustacea	--	--	--	--	--	--	**0**	**0**	**3**
Proasellus sp.	Crustacea	--	--	--	--	--	--	**1**	**0**	**8**
Ablabesmyia sp.	Diptera	0	0	1	1	0	6	63	36	596
Atrichopogon sp.	Diptera	--	--	--	--	--	--	**23**	**0**	**227**
Brillia bifida	Diptera	0	0	2	0	0	0	0	0	1
Bryophaenocladius sp.	Diptera	1	0	3	0	0	2	2	0	6
Camptocladius stercorarius	Diptera	14	2	49	4	0	33	75	1	291
Ceratopogoninae/Palpomyiinae Gen. sp.	Diptera	1	0	2	9	3	41	61	8	196
Chironomus acutiventris acutiventris	Diptera	13	1	76	62	8	194	1594	0	10736
Chironomus agilis	Diptera	26	0	121	700	38	4130	985	1	6355
Chironomus annularius	Diptera	0	0	1	3	0	23	11	0	69
Chironomus bernensis	Diptera	0	0	2	1	0	9	17	0	117
Chironomus commutatus	Diptera	0	0	0	1	0	8	2	0	17
Chironomus plumosus-Gr.	Diptera	3	0	20	6	0	28	556	0	4224
Chironomus riparius-Agg.	Diptera	0	0	1	0	0	1	8	0	62
Chironomus sp.	Diptera	0	0	1	0	0	1	7	0	34
Cladotanytarsus mancus-Gr.	Diptera	1	0	4	527	12	3405	584	2	2038
Cladotanytarsus vanderwulpi-Gr.	Diptera	591	12	2423	1517	18	5090	789	0	5527
Conchapelopia sp.	Diptera	--	--	--	--	--	--	**2**	**0**	**18**
Corynoneura sp.	Diptera	3	0	10	7	0	72	68	17	297
Cricotopus sp.4	Diptera	81	4	213	15	0	84	168	0	694
Cricotopus sp.5	Diptera	35	2	97	16	0	59	520	0	2348
Cricotopus tremulus	Diptera	16	1	70	20	0	175	108	0	606
Cricotopus intersectus-Agg.	Diptera	3	0	11	1	0	8	22	0	131
Cryptochironomus sp.	Diptera	62	1	326	402	16	827	95	3	474
Cryptotendipes sp.	Diptera	0	0	1	13	0	101	1	0	4

Dicrotendipes modestus	Diptera	0	0	0	0	0	0	0	0	1
Dicrotendipes nervosus	Diptera	19	0	97	10	1	65	1411	1	7627
Dicrotendipes notatus	Diptera	0	0	1	0	0	0	15	0	151
Dolichopodidae Gen. sp.	Diptera	--	--	--	--	--	--	**1**	**0**	**5**
Eloeophila sp.	Diptera	1	0	3	1	0	5	--	--	--
Empididae Gen. sp.	Diptera	0	0	3	--	--	--	5	1	35
Ephydridae Gen. sp.	Diptera	--	--	--	1	0	5	5	1	25
Eukiefferiella sp.	Diptera	110	2	765	8	0	34	89	0	391
Glyptotendipes barbipes	Diptera	0	0	1	0	0	0	6	0	54
Glyptotendipes pallens-Agg.	Diptera	1	0	7	0	0	2	106	0	483
Glyptotendipes paripes	Diptera	0	0	1	0	0	0	0	0	1
Hayesomyia tripunctata	Diptera	3	0	20	12	0	69	16	0	140
Limnophyes sp.	Diptera	1	0	2	0	0	1	5	0	39
Limoniidae Gen. sp.	Diptera	0	0	1	--	--	--	1	0	6
Lipiniella moderata	Diptera	10	0	31	5	0	27	119	0	431
Lispe sp.	Diptera	--	--	--	--	--	--	2	0	13
Microchironomus tener	Diptera	2	0	14	0	0	4	135	0	991
Micropsectra apposita	Diptera	0	0	2	7	0	70	11	0	70
Microtendipes pedellus-Gr.	Diptera	0	0	1	0	0	0	16	0	154
Nilotanypus dubius	Diptera	--	--	--	--	--	--	**1**	**0**	**9**
Orthocladiinae sp.B	Diptera	0	0	0	0	0	0	6	0	53
Orthocladiinae sp.C	Diptera	0	0	4	0	0	0	0	0	1
*Orthocladius (*Eu-) sp.	Diptera	79	4	430	10	0	78	135	0	411
Orthocladius consobrinus	Diptera	0	0	0	0	0	0	0	0	1
Orthocladius sp.	Diptera	261	12	605	161	0	1048	1069	15	5804
Parachironomus frequens-Gr.	Diptera	6	0	49	0	0	1	4	0	27
Parachironomus gracilior-Gr.	Diptera	3	0	30	3	0	23	387	0	2617
Paracricotopus sp.	Diptera	--	--	--	--	--	--	**10**	**0**	**100**
Parakiefferiella bathophila	Diptera	32	2	70	13	0	48	60	3	145
Paratanytarsus sp.	Diptera	0	0	4	3	0	23	415	0	2680
Paratendipes albimanus	Diptera	2	0	15	54	0	296	101	0	755
Paratrichocladius sp.	Diptera	**0**	**0**	**3**	--	--	--	--	--	--
Polypedilum acifer	Diptera	129	1	467	71	17	692	180	2	655
Polypedilum albicorne	Diptera	0	0	0	1	0	6	0	0	1
Polypedilum nubeculosum	Diptera	8	0	58	524	3	1974	3158	0	16883
Polypedilum scalaenum	Diptera	1	0	4	37	0	352	3	0	22
Polypedilum uncinatum	Diptera	1	0	4	42	0	422	7	0	40
Procladius sp.	Diptera	--	--	--	10	1	55	542	60	1998
Prodiamesa olivacea	Diptera	--	--	--	6	0	42	2	0	15
Prosimulium sp.	Diptera	--	--	--	--	--	--	**0**	**0**	**1**
Psectrocladius obvius/platypus	Diptera	--	--	--	**13**	**131**	**131**	--	--	--
Psectrocladius sordidellus-Gr.	Diptera	--	--	--	--	--	--	**0**	**0**	**0**
Pseudosmittia sp.	Diptera	1	0	3	0	0	2	7	0	40
Psychodidae Gen. sp.	Diptera	--	--	--	--	--	--	**1**	**0**	**5**
Rheocricotopus sp.	Diptera	1	0	4	1	0	3	3	0	9
Rheotanytarsus sp.	Diptera	730	4	5497	11	0	64	194	0	1858
Rhypholophus sp.	Diptera	1	0	7	1	0	2	5	0	21

Robackia demeijerei	Diptera	86	0	304	36	3	163	40	0	206
Saetheria reissi	Diptera	8	0	50	65	20	202	22	0	76
Simulium sp.	Diptera	2	0	8	0	0	1	20	0	193
Smittia aquatilis-Gr.	Diptera	8	1	28	3	0	22	51	0	236
Stenochironomus gibbus	Diptera	0	0	0	0	0	0	2	0	21
Stictochironomus sp.	Diptera	0	0	1	1	0	8	1	0	5
Synendotendipes dispar-Gr.	Diptera	1	0	3	8	0	37	19	0	114
Tanypodinae sp.1	Diptera	5	0	25	36	19	235	27	8	111
Tanytarsus buchonius-Agg.	Diptera	74	3	501	316	9	1044	253	0	1135
Tanytarsus ejuncidus	Diptera	0	0	0	0	0	2	3	0	21
Tanytarsus heusdensis	Diptera	10	2	75	999	0	8417	103	0	670
Tanytarsus mendax	Diptera	5	1	18	53	0	333	2741	6	25482
Tanytarsus sylvaticus	Diptera	0	0	0	0	0	2	8	0	78
Tanytarsus brundini-Agg.	Diptera	2	0	11	63	0	348	61	0	244
Telopelopia fascigera	Diptera	21	4	158	47	2	274	1	0	9
Thienemanniella flaviforceps	Diptera	1	0	3	0	0	1	1	0	5
Thienemanniella sp.	Diptera	0	0	1	1	0	4	1	0	3
Tipulidae Gen. sp.	Diptera	--	--	--	--	--	--	**1**	**0**	**5**
Tvetenia verralli/discoloripes	Diptera	221	2	1769	12	0	58	68	0	270
Ametropus fragilis	Ephemeroptera	**0**	**0**	**1**	--	--	--	--	--	--
Baetis sp.	Ephemeroptera	0	0	2	--	--	--	1	0	6
Caenis horaria	Ephemeroptera	--	--	--	1	0	3	5	0	20
Caenis luctuosa/macrura	Ephemeroptera	4	0	18	51	6	131	50	2	255
Caenis pseudorivulorum	Ephemeroptera	--	--	--	2	0	8	1	0	4
Cloeon dipterum	Ephemeroptera	--	--	--	0	0	2	60	0	177
Heptagenia flava	Ephemeroptera	4	1	15	1	0	3	4	0	13
Heptagenia sulphurea	Ephemeroptera	2	0	5	0	0	2	0	0	1
Kageronia fuscogrisea	Ephemeroptera	--	--	--	--	--	--	**0**	**0**	**3**
Potamanthus luteus	Ephemeroptera	0	0	1	--	--	--	0	0	0
Procloeon bifidum	Ephemeroptera	--	--	--	--	--	--	**0**	**0**	**3**
Serratella ignita	Ephemeroptera	--	--	--	**0**	**0**	**0**	--	--	--
Ancylus fluviatilis	Gastropoda	95	6	207	2	0	11	8	0	56
Bithynia tentaculata	Gastropoda	--	--	--	0	0	1	13	9	124
Gyraulus albus	Gastropoda	--	--	--	--	--	--	**7**	**0**	**62**
Gyraulus chinensis	Gastropoda	--	--	--	--	--	--	**12**	**0**	**124**
Lymnaea stagnalis	Gastropoda	--	--	--	--	--	--	**3**	**0**	**30**
Physidae Gen. sp.	Gastropoda	0	0	1	--	--	--	234	54	1055
Potamopyrgus antipodarum	Gastropoda	33	1	238	86	1	375	3485	31	14602
Radix auricularia/balthica/labiata	Gastropoda	0	0	2	--	--	--	46	2	372
Valvata piscinalis piscinalis	Gastropoda	--	--	--	--	--	--	**11**	**1**	**94**
Corixidae Gen. sp.	Heteroptera	--	--	--	--	--	--	**2**	**0**	**9**
Micronecta sp.	Heteroptera	0	0	1	--	--	--	1	0	6
Erpobdella octoculata	Hirudinea	--	--	--	0	0	0	1	0	9
Erpobdella vilnensis	Hirudinea	**0**	**0**	**1**	--	--	--	--	--	--
Helobdella stagnalis	Hirudinea	--	--	--	**1**	**0**	**5**	--	--	--
Piscicolidae Gen. sp.	Hirudinea	0	0	2	2	0	11	2	0	14
Calopteryx splendens	Odonata	--	--	--	--	--	--	**1**	**0**	**5**

Coenagrion sp.	Odonata	--	--	--	--	--	--	**41**	**0**	**138**
Enallagma cyathigerum	Odonata	--	--	--	--	--	--	**0**	**0**	**2**
Gomphus sp.	Odonata	0	0	1	8	1	26	1	0	3
Ophiogomphus sp.	Odonata	0	0	2	5	0	15	1	0	5
Platycnemis pennipes	Odonata	--	--	--	--	--	--	**19**	**5**	**106**
Oligochaeta Gen. sp.	Oligochaeta	1266	96	4309	2859	217	9925	16274	2495	50027
Brachyptera braueri	Plecoptera	0	0	2	0	0	1	--	--	--
Leuctra sp.	Plecoptera	**0**	**0**	**1**	--	--	--	--	--	--
Nemoura sp.	Plecoptera	0	0	1	0	0	0	--	--	--
Anabolia furcata/nervosa	Trichoptera	--	--	--	--	--	--	**1**	**0**	**9**
Brachycentrus subnubilus	Trichoptera	**0**	**0**	**3**	--	--	--	--	--	--
Ceraclea dissimilis	Trichoptera	3	0	9	1	0	8	3	0	15
Cheumatopsyche lepida	Trichoptera	0	0	2	0	0	0	0	0	0
Halesus digitatus/tesselatus	Trichoptera	0	0	2	--	--	--	0	0	0
Hydropsyche bulgaromanorum	Trichoptera	132	2	343	1	0	6	2	0	11
Hydropsyche contubernalis contubernalis	Trichoptera	27	0	94	2	0	8	0	0	3
Hydroptila sp.	Trichoptera	1	0	5	0	0	3	1	0	4
Limnephilus lunatus	Trichoptera	--	--	--	--	--	--	**23**	**0**	**106**
Limnephilus rhombicus rhombicus	Trichoptera	--	--	--	--	--	--	**3**	**1**	**31**
Mystacides sp.	Trichoptera	0	0	4	1	0	6	13	0	68
Oecetis ochracea	Trichoptera	1	0	7	1	0	3	1	0	5
Oecetis testacea	Trichoptera	2	0	14	2	0	7	3	0	24
Orthotrichia sp.	Trichoptera	1	0	2	0	0	3	3	0	17
Oxyethira sp.	Trichoptera	1	0	5	0	0	4	4	0	33
Psychomyia pusilla	Trichoptera	12	0	35	0	0	1	0	0	1
Setodes punctatus	Trichoptera	15	1	128	27	1	86	3	0	14
Triaenodes bicolor/unanimis	Trichoptera	0	0	0	0	0	0	2	0	21

Table S3 Weighted biomass (B; mg DM m^{-2}), Weighted secondary production (P; mg DM m^{-2} y^{-1}), and the P/B of macroinvertebrates found at the studied shore types. For each taxon, the cohort production interval correction factor (365/CPI) and its source are given.

	Standard groyne			**Off-bankline revetment**			**Rip rap**			**Main channel**		
	B	**P**	**P/B**	**B**	**P**	**P/B**	**B**	**P**	**P/B**	**B**	**P**	**P/B**
Bivalvia												
Corbicula fluminea	263	321	1.2				298	433	1.5			
Pisidium sp.	181	107	0.6	169	147	0.9	148	112	0.8	164	122	0.7
Sphaerium sp.	7	12	1.7	2,728	4,699	1.7						
Crustacea												
Chelicorophium curvispinum	81	174	2.2	230	554	2.4	218	444	2.0			
Dikerogammarus villosus	621	1,318	2.1	2,343	7,482	3.2	2,633	12,262	4.7			
Jaera istri	9	21	2.2	41	104	2.5	27	80	3.0			
Diptera												
Camptocladius stercorarius				13	461	35.9						
Ceratopogonidae				15	53	3.6						
Chironomini	7	208	29.1	29	159	5.6	19	76	3.9	0	8	27.8
Chironomus sp.	675	21,342	31.6	2,231	58,770	26.3	33	1,284	39.3			
Cladotanytarsus sp.	140	11,515	82.3	86	6,670	77.4	49	3,060	62.7	1	57	54.0
Cricotopus sp.	3	72	25.1	5	153	31.8	4	66	18.4			
Cryptochironomus sp.	107	417	3.9				18	308	16.9			
Dicrotendipes nervosus				128	2,687	21.0						
Eukiefferiella sp.	0	4	31.5				20	618	31.5			
Orthocladiinae.	18	628	34.7	134	6,293	47.0	48	1,560	32.5	0	20	56.2
Polypedilum sp.	45	1,073	24.0	1,007	3,581	3.6	7	217	32.8	27	564	20.7
Procladius sp.				186	718	3.9						
Rheotanytarsus sp.	0	53	110.9	2	174	77.3	28	1,477	53.3			
Robackia demeijerei	5	31	6.9	2	9	4.4	8	42	5.5	144	1,213	8.4
Simuliidae				2	37	16.4						

Table S2 continued

	Standard groyne			Off-bankline revetment			Rip rap			Main channel		
	B	**P**	**P/B**	**B**	**P**	**P/B**	**B**	**P**	**P/B**	**B**	**P**	**P/B**
Tanytarsini Gen. sp.	2	57	27.6	2	55	34.9	0	11	41.9	0	19	41.2
Tanytarsus sp.	38	858	22.4	164	3,151	19.2	4	88	23.8			
Tvetenia sp.	0	6	32.0	1	46	32.0	38	1,589	41.6			
Ephemeroptera												
Caenis sp.	23	70	3.1	8	24	3.1	1	3	3.1			
Cloeon dipterum				22	104	4.8						
Gastropoda												
Ancylus fluviatilis	13	26	2.0	30	196	6.4	580	2,179	3.8			
Physidae				2,898	8,690	3.0						
Potamopyrgus antipodarum	239	338	1.4	5,624	12,851	2.3	18	60	3.3			
Odonata												
Coenagrionidae.				186	409	2.2						
Oligochaeta												
Oligochaeta	198	992	5.0	765	3,827	5.0	38	191	5.0	26	128	5.0
Trichoptera												
Hydropsyche sp.	16	59	3.8	2	6	3.8	89	343	3.9			
Setodes punctatus	8	23	2.9				4	12	2.8			

Table S4 Taxa and shore type specific ingestion rates for each resource (benthic FPOM; pelagic algae; periphyton and terrestrial CPOM in absolute and relative amounts

Taxon/group	Resource	Rip rap		Standard groyne		Off-bankline revetment	
		Absolute [g DM m^{-2} y^{-1}]	Relative [%]	Absolute [g DM m^{-2} y^{-1}]	Relative [%]	Absolute [g DM m^{-2} y^{-1}]	Relative [%]
Ancylus fluviatilis	Benthic FPOM	7.99	35.9	0.07	25.5	0.55	31.2
	Pelagic algae	3.23	14.5	0.05	19.0	0.14	8.0
	Periphyton	4.39	19.8	0.08	30.4	---	---
	Terrestrial CPOM	6.62	29.8	0.07	25.0	1.06	60.8
Chelicorophium curvispinum	Benthic FPOM	0.98	23.8	0.48	28.7	1.58	28.5
	Pelagic algae	1.47	35.8	0.33	20.0	0.43	7.7
	Periphyton	0.50	12.1	0.22	13.4	2.04	36.7
	Terrestrial CPOM	1.16	28.3	0.63	38.0	1.50	27.0
Chironominae	Benthic FPOM	18.40	27.8	117.94	31.8	622.61	68.0
	Pelagic algae	17.04	25.8	57.86	15.6	80.32	8.8
	Periphyton	19.01	28.7	104.02	28.1	175.48	19.2
	Terrestrial CPOM	11.72	17.7	90.52	24.4	37.20	4.1
Cloeon dipterum	Benthic FPOM	---	---	---	---	0.25	23.9
	Pelagic algae	---	---	---	---	0.22	20.9
	Periphyton	---	---	---	---	0.50	48.1
	Terrestrial CPOM	---	---	---	---	0.07	7.1
Corbicula fluminea	Benthic FPOM	---	---	0.70	23.0	---	---
	Pelagic algae	---	---	0.23	7.6	---	---
	Periphyton	---	---	0.65	21.3	---	---
	Terrestrial CPOM	---	---	1.47	48.1	---	---
Dikerogammarus villosus	Benthic FPOM	72.23	50.4	6.26	42.5	64.96	68.2
	Pelagic algae	14.98	10.4	1.33	9.0	4.07	4.3
	Periphyton	34.30	23.9	4.04	27.4	26.20	27.5
	Terrestrial CPOM	21.93	15.3	3.11	21.1		0.0
Hydropsyche sp.	Benthic FPOM	1.02	29.7	0.14	25.7	0.01	17.6
	Pelagic algae	0.53	15.5	0.07	12.9	0.02	31.6
	Periphyton	0.80	23.2	0.04	6.7	0.01	17.9
	Terrestrial CPOM	1.08	31.5	0.29	54.7	0.02	32.8
Jaera istri	Benthic FPOM	0.32	36.5	0.08	38.0	0.69	56.1
	Pelagic algae	0.11	12.4	0.06	27.5	0.05	4.2
	Periphyton	0.29	32.9	0.02	8.5	0.39	31.7
	Terrestrial CPOM	0.16	18.2	0.06	26.0	0.10	8.0
Oligochaeta	Benthic FPOM	0.63	31.5	3.31	31.7	18.02	41.4
	Pelagic algae	0.38	19.4	1.18	11.3	4.33	9.9
	Periphyton	0.57	28.9	3.14	30.1	21.20	48.7
	Terrestrial CPOM	0.40	20.2	2.80	26.8	---	---
Orthocladiinae	Benthic FPOM	13.15	33.3	2.48	33.6	16.03	22.0
	Pelagic algae	5.01	12.7	1.50	20.3	11.67	16.0
	Periphyton	9.12	23.1	1.83	24.8	45.10	62.0
	Terrestrial CPOM	12.21	30.9	1.57	21.3	---	---
Potamopyrgus antipodarum	Benthic FPOM	---	---	1.48	37.0	60.84	42.3
	Pelagic algae	---	---	0.18	4.4	13.06	9.1
	Periphyton	---	---	1.85	46.3	62.18	43.2
	Terrestrial CPOM	---	---	0.49	12.3	7.88	5.5
Simuliidae	Benthic FPOM	---	---	---	---	0.03	9.3
	Pelagic algae	---	---	---	---	0.17	55.6
	Periphyton	---	---	---	---	0.10	30.5
	Terrestrial CPOM	---	---	---	---	0.01	4.5
Sphaerium sp.	Benthic FPOM	---	---	---	---	7.73	18.1
	Pelagic algae	---	---	---	---	16.71	39.1
	Periphyton	---	---	---	---	15.21	35.5
	Terrestrial CPOM	---	---	---	---	3.13	7.3

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Erklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne zulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als diese kenntlich gemacht worden. Fachlich begleitet wurde die Arbeit von **Prof. Dr. Markus Weitere** und **Dr. Mario Brauns** (Helmholtz-Zentrum für Umweltforschung – UFZ), was Hilfestellungen bei Konzeptentwicklung, Probenahmestrategie, Auswertung und Manuskriptanfertigung umfasst. Beiträge Dritter sind zudem in Kapitel 2 eingegangen: Frau **Christine Anlanger** (Helmholtz-Zentrum für Umweltforschung – UFZ) hat die topographische Vermessung der Ufertypen und Modellierung in Matlab durchgeführt. Die Chironomiden-Bestimmung auf Art- bzw. Gattungsniveau aus dem von mir vorsortierten Material wurde durch **Dr. Emmanuel Gaulme** (Arles, Frankreich) und **Dr. Xavier-Francois Garcia** (Berlin)geleistet.

Weitere Personen waren an der geistigen Herstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich nicht die Hilfe eines oder mehrerer Promotionsberater(s) in Anspruch genommen. Dritte haben von mir weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Die Arbeit wurde bisher weder im Ausland noch im Inland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde zum Zweck der Promotion vorgelegt.

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