Human impacts on the structure and ecological function of littoral macroinvertebrate communities in lakes

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Abbreviations

f	Wave friction factor
Ab	maximum bottom wave amplitude
ADV	Acoustic Doppler velocimeter
ANOSIM	Analysis of similarity
ANOVA	Analysis of variance
C	Carbon
C_{Bio}	Biomass of a given species
C_{FM}	Carbon content of a given assimilated food mixture
C_i	Fraction of biomass of species *i* derived from a food resource
CWD	Coarse woody debris
DO	Dissolved oxygen
FD	Fractal dimension
IndVal	Indicator species analysis
IV	Indicator value
l	Wave amplitude
MCA	Multiple classification analysis
N	Nitrogen
N_{FM}	Nitrogen content of a given assimilated food mixture
NMS	Non-metric multidimensional scaling
P	Phosphorus
P_{FM}	Phosphorus content of a given assimilated food mixture
p_i	Relative contribution of food resource *i* to the diet of a macroinvertebrate consumer
POM	Particulate organic matter
Re	Reynolds number

TP	Total phosphorus
u	Maximum wave velocity
U_b	Maximum wave orbital velocity
WFD	EU Water Framework directive
WLF	Water level fluctuations
v	water viscosity
ρ	Density of water
τ	Bottom shear stress

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Summary

Littoral macroinvertebrates are a significant biotic component of lake ecosystems and contribute substantially to whole-lake biodiversity and ecosystem functioning. Humans increasingly alter littoral zones and riparian areas for recreational uses and residential development, but the ecological impacts of these alterations on littoral macroinvertebrates have rarely been quantified. In this thesis, I investigated the relative importance of key environmental factors in determining littoral macroinvertebrate community composition and how alterations of these environmental factors through structural degradation, and hydrological and hydrodynamic alterations impact the structure and function of macroinvertebrate communities. Macroinvertebrate community composition was significantly related to trophic state, littoral structure and the hydrodynamic regime. However, the significantly higher compositional dissimilarities among habitat types than among trophic state suggested that littoral structure was the more important driver of community composition. Structural degradation caused a significant reduction of habitat heterogeneity and complexity and resulted in a significant reduction of species diversity, as well as in a significant altered community composition. This was followed by a significant reduction of macroinvertebrate food web complexity, as well as substantial quantitative and qualitative alterations in the trophic base of the food webs. Alterations of the hydrological regime through climate-change induced water level fluctuations resulted in the loss of root habitats and the specific community associated with this habitat type. Hydrodynamic disturbances caused by ship-induced waves had substantial direct effects, since macroinvertebrates were detached from their habitats by waves even at moderate shear stress levels. However, the adverse effects of hydrological and hydrodynamic alterations were mitigated by the presence of habitats with high structural complexities. This thesis provided a mechanistic understanding of how human activities alter the relationships between environmental factors and biotic communities and how this affects the integrity of the littoral zone. This knowledge can be used in order to develop scientifically sound approaches to assess the persistent human impacts on lake ecosystems.

Zusammenfassung

Das litorale Makrozoobenthos stellt eine wichtige biotische Komponente in Seen dar und hat einen bedeutenden Anteil an der Biodiversität und der Funktion von Seeökosystemen. Das Litoral unterliegt weltweit zunehmenden anthropogenen Nutzungen, deren ökologische Auswirkungen auf das litorale Makrozoobenthos allerdings kaum quantifiziert worden sind. In dieser Doktorarbeit wurde daher untersucht, welche relative Bedeutung maßgebliche Umweltfaktoren auf die Zusammensetzung des litoralen Makrozoobenthos haben, und in welchem Umfang sich durch anthropogene Nutzungen verursachte strukturelle Degradation, hydrologische und hydrodynamische Beeinträchtigungen auf die Zusammensetzung und Funktion des Makrozoobenthos auswirken. Die Zusammensetzung des Makrozoobenthos wurde, neben der Trophie, signifikant durch die Uferstruktur und das hydrodynamische Regime bestimmt. Die faunistische Ähnlichkeit zwischen Habitaten war jedoch signifikant geringer als zwischen Trophiestufen, so dass die Unterschiede in der habitatspezifischen Artenzusammensetzung nur zu einem geringen Anteil durch die Trophie erklärt wurden. Daher wurde festgestellt, dass die Uferstruktur, und nicht die Trophie, einen größeren Einfluss auf die Zusammensetzung des Makrozoobenthos hat. Strukturelle Degradation führte zu einer signifikanten Reduktion der Habitatheterogenität und Habitatkomplexität, was eine signifikante Verringerung der Diversität und eine signifikant veränderte Artenzusammensetzung verursachte. Infolgedessen war die Komplexität der Makrozoobenthos-Nahrungsnetze an stark degradierten Ufern bis zu vierfach geringer war als an natürlichen Ufern und es kam zu erheblichen quantitativen und qualitativen Veränderungen der trophischen Basis der Nahrungsnetze. Veränderungen des hydrologischen Regimes durch erhöhte Wasserstandsschwankungen führten zum Ausfall von Wurzelhabitaten und der daran gebundenen Makrozoobenthos-Gemeinschaft. Hydrodynamische Belastungen infolge schiffsinduzierten Wellenschlags führten zu einer Verdriftung des Makrozoobenthos von ihren Habitaten bereits bei geringen Sohlschubspannungen. Die Effekte der Veränderungen des hydrologischen und hydrodynamischen Regimes wurden jedoch durch das Vorkommen von Habitaten mit hoher struktureller Komplexität verringert. Mit der vorliegenden Doktorarbeit konnte ich ein mechanistisches Verständnis darüber erarbeiten, wie anthropogene Nutzungen die Wirkungsbeziehungen zwischen Umweltfaktoren und Artengemeinschaften verändern und welche ökologischen Auswirkungen dies hat. Diese Kenntnisse können als Basis für ein wissenschaftlich fundiertes Verfahren zur Bewertung von anthropogenen Beeinträchtigungen des Litorals von Seen dienen.

1 General introduction

1.1 Background

1.1.1 The littoral environment

The littoral is a transitional zone between the pelagic and profundal zone and the adjacent riparian area. It extends from the shoreline at high water levels to a depth at which 1% of the photosynthetic active radiation available at the lake surface reaches the lake bottom (Wetzel, 2001). The littoral can be divided into three different sub-zones according to the water depth gradient (Fig. 1). The eulittoral is defined as the area between the highest and the lowest water level and is thus subjected to natural water level fluctuations. The infralittoral is the area containing emerged macrophytes, and the sublittoral that is characterised by the occurrence of floating or submerged vegetation. Particularly in German riverine lakes, the sublittoral can be followed by a transitional zone called the littori-profundal (Fig. 1), which is characterised by the accumulations of mollusc shells. The deepest zone in lakes is referred to as the profundal zone and is free of submerged macrophytes and characterised by fine organic sediments mainly from pelagic plankton sedimentation.

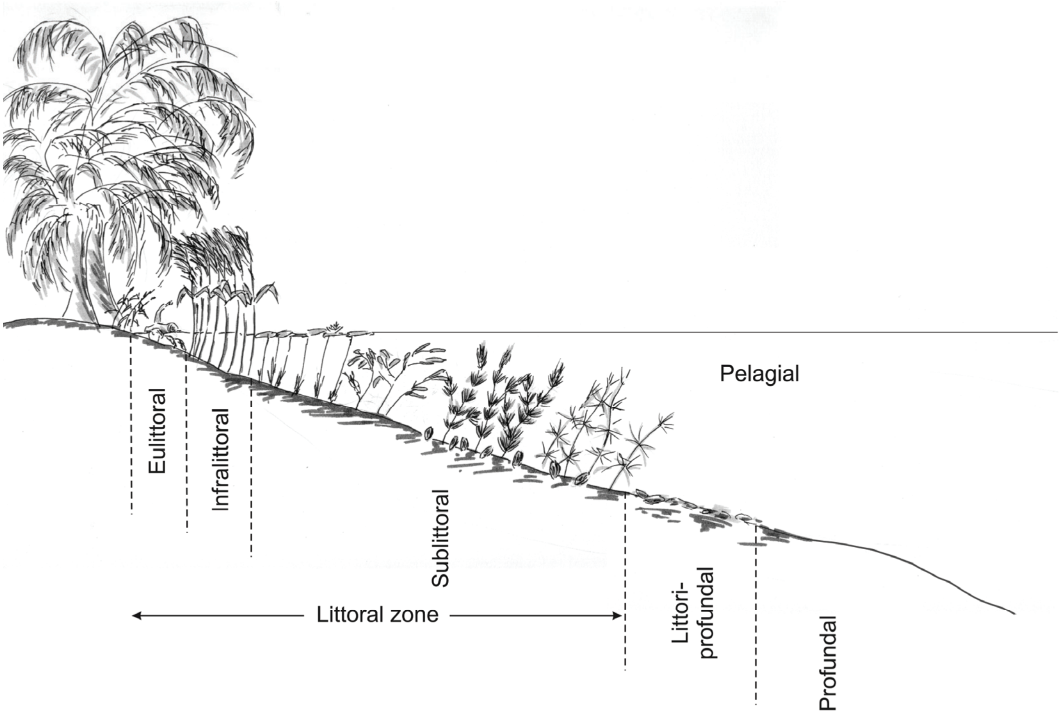

Fig. 1. General zonation scheme in lakes.

One of the inherent properties of the littoral is its high spatial heterogeneity, which is associated with strong lateral and vertical gradients of environmental factors that govern patterns of environmental conditions within this zone (Lodge et al., 1988; Downing and Rath, 1992; Harrison and Hildrew, 2001; Stoffels et al., 2005). For example, the shoreline has different exposure to the main wind direction, which creates a lateral gradient of hydraulic disturbances caused by wind-induced waves where disturbance decreases with decreasing wind exposure. The north-eastern shorelines of larger lakes (ca. > 0.5 km^2) in central Europe are usually exposed to wind-induced waves and are thus subjected to substantial disturbances during storms (Hofmann et al., 2008). Meanwhile, wind-sheltered south-western shorelines are rarely subjected to such disturbances. The level of shear stress produced by wind-induced waves gradually decreases with increasing depth creating a vertical gradient of wave disturbance towards the sublittoral and profundal zone (Rowan et al., 1992). Along with the lateral and vertical wind-exposure gradients, there are gradients of environmental factors, such as sediment particle size composition and organic matter (OM) content. Fine sediment particles and OM are resuspended at wind-exposed shorelines and accumulate either at wind-sheltered shorelines or in deeper littoral areas (Bloesch, 1995; Cyr, 1998).

Interactions between these various environmental gradients result in high spatial heterogeneity that is reflected in the heterogeneity of littoral habitats, such as submerged and emerged macrophytes, stones and sand. At lakes surrounded by forest, riparian trees provide habitats created by coarse woody debris (CWD) and submerged tree root that further increase habitat heterogeneity and reflect a strong spatial coupling between littoral and riparian areas (Schindler and Scheuerell, 2002).

The littoral is not only spatially coupled to the riparian zone but also energetically coupled via allochthonous inputs of dissolved and particulate organic carbon (POC). Especially POC inputs through riparian leaf litter can be substantial and were demonstrated to be as high as 30.3 t DW yr^{-1} at a German lowland lake (Casper et al., 1985). These inputs can play a crucial role in the carbon budget of lake ecosystems, since they often equal or exceed pelagic primary production (Jansson et al., 2007). Moreover, recent studies have demonstrated that 30 to 70% of organismal carbon biomass at all trophic levels was derived from allochthonous resources, making allochthonous carbon a significant trophic subsidy for littoral food webs (Pace et al., 2004; Carpenter et al., 2005; Cole et al., 2006).

The increased availability of nutrients derived from autochthonous or allochthonous sources, combined with the high availability of light and substrates within the littoral, results in an intense periphyton primary production in the littoral benthic zone. Hence, periphyton production can exceed pelagic primary production in large oligotrophic lakes and can contribute up to 95% of whole-lake primary production (Vadeboncoeur et al., 2001; Vadeboncoeur et al., 2002). Furthermore, the increased nutrient availability and higher habitat heterogeneity lead to higher rates of secondary production than in the pelagic or profundal zones (Jonasson, 1992; Paterson, 1993; Sala and Guede, 2006; Babler et al., 2008).

A few studies have indicated that the littoral zone may play an important and dynamic role in the processing and transfer of OM and nutrients for the entire lake. However, current knowledge does not allow for a comprehensive view of the importance of littoral zones within lake ecosystems.

1.1.2 Human impacts

Lakes and their riparian surroundings have always been preferential places for human activities, such as settlement, agriculture, navigation and various recreational activities. The intensity at which humans have modified riparian areas and lakeshores for these purposes has substantially increased during the last decades (Sly, 1991; Schnaiberg et al., 2002; Carpenter et al., 2007). For example, the housing density around U.S. lakes in Wisconsin has increased more than five-fold during the last 60 years (Gonzales-Abraham et al., 2007). Recreational boating has increased by 60 % in this region of Wisconsin during the last 40 years, as indicated by numbers of boat registrations (Engel and Pederson, 1998). Similarly, in central Europe, the housing density at the shores of Lake Constance has more than doubled since 1960 (Schmieder, 2004). It is expected that human use of lakes and lakeshores will increase further and will likely extend to areas that are currently unimpaired (Walz et al., 2002; Peterson et al., 2003; Carpenter et al., 2007).

Human activities impact the structure, hydrology and water quality of lakes in a variety of ways (Table 1). These impacts often occur simultaneously as lakes and their shorelines are developed for human activities. For several decades, the nutrient load and resulting eutrophication of the surface waters have been considered as the most important influences on lake ecosystems. Thus, considerable efforts have been made in developed countries to reduce nutrient loading from waste-water treatment plants. In spite of these efforts, surface run-off from agricultural areas and impervious surfaces within urban areas still constitute a significant source of non-point loadings, which results in eutrophication and its adverse ecological effects (Table 1). More recently, human development of shorelines has been recognised to pose serious threats to the structural integrity of littoral zones. Such human alterations, in particular residential development, tend to simplify the structural heterogeneity of the littoral zone by removing habitats (Table 1).

Moreover, shoreline development is frequently followed by clearcutting of the riparian vegetation, which amplifies the ecological effects of structural degradation in the littoral zone.

Table 1. Common human activities and their most important ecological effects.

Human activity	Type of impact	Ecological effects	References
Nutrient loading	Eutrophication	Increases phytoplankton productivity, resulting in algal blooms that reduce light availability for submerged macrophytes and periphyton; causes reallocation of primary production from the benthic to the pelagic zone; causes hypolimnic dissolved oxygen depletion due to organic matter decomposition	Carpenter et al., 1998; Vadeboncoeur et al., 2003; Moore et al., 2003; Smith, 2003; Egertson et al., 2004; Chandra et al., 2005
Shoreline development	Structural degradation	Reduces littoral habitat heterogeneity through habitat loss or removal especially of structurally complex habitats; disrupts natural connectivity between littoral and riparian area	Bryan and Scarnecchia, 1992; Engel and Pederson, 1998; Radomski and Goeman, 2001; Elias and Meyer, 2003; Francis et al., 2007
Recreational activities	Structural degradation/ Eutrophication	Reduces littoral habitat heterogeneity through habitat loss; affects habitats through mechanical disturbance (e.g. trampling); increases primary production through nutrient loading	Sukopp, 1971; Liddle and Scorgie, 1980; Ostendorp et al., 1995; Ostendorp et al., 2004; Hadwen and Bunn, 2005
Riparian clearcutting	Structural degradation	Reduces the amount of habitats provided by CWD; reduces the amount of allochthonous organic matter supplied by leaf litter, increases the siltation of habitats	Christensen et al., 1996; Francis and Schindler, 2006; Marburg et al., 2006; Sass et al., 2006; Roth et al., 2007; Helmus and Sass, 2008
Regulation of water levels	Alteration of hydrological regime	Alters the seasonal hydrological regime, causes habitat loss through desiccation of eulittoral zones; affects habitat quality by erosion	Wilcox and Meeker, 1992; Hill et al., 1998; Furey et al., 2004; Wilcox et al., 2008; Cott et al., 2008
Commercial and recreational navigation	Alteration of hydrodynamic regime	Causes inputs of contaminants; causes hydraulic disturbance; affects habitat quality by erosion and physical damage; increases turbidity through sediment resuspension	McGee et al., 1995; Ostendorp, 1999; Anthony and Downing, 2003; Asplund, 2003; Beachler and Hill, 2003

Recreational activities at shorelines include walking, angling, swimming, camping and picnicking. In particular the use of lakeshores for recreational beaches causes a variety of ecological effects by combining the adverse effects of shoreline development and nutrient loading (Table 1).

Anthropogenic alterations of the hydrological and hydrodynamic regime most commonly result from navigation and regulation of water levels. Water levels are usually regulated by the construction of weirs at lake outlets, which can prevent flooding of riparian areas in spring and lower water levels in autumn and winter. In part, these dams are designed to increase the seasonal water level dynamics in order to maximise the generation of hydropower (Table 1).

While the regulation of water levels affects the availability of habitats within the littoral (Table 1), navigation mainly creates hydraulic disturbances at shorelines that are otherwise protected from waves, i.e. wind-sheltered shorelines.

1.1.3 The ecological significance of littoral macroinvertebrates

Benthic macroinvertebrates are a systematically diverse group, which include organism of 26 major taxonomic groups (Schmedtje and Colling, 1996) that colonise the benthic zone of freshwater ecosystems for at least a part of their life cycle (Rosenberg and Resh, 1993). Comprehensive surveys of macroinvertebrate biodiversity in lakes are rare but the available data suggest that macroinvertebrates substantially contribute to whole-littoral, as well as to whole-lake biodiversity. For example, a thorough species inventory at Lake Stechlin revealed that macroinvertebrate diversity accounted for 29% of whole-lake biodiversity (Flößner et al., 1985) and contributed to 50% to whole-littoral biodiversity (Casper and Schönborn, 1985).

Littoral macroinvertebrates can have different functional roles in ecosystem nutrient cycling, since they belong to a variety of feeding groups and are thus able to utilise various food resources. For example, shredders process allochthonous coarse particulate organic matter (CPOM), such as riparian leaf litter to fine particulate organic matter (FPOM), thereby making these resources available for other feeding groups such as collector-gatherers (Bjelke et al., 2005) (Fig. 2). Macroinvertebrates also contribute to nutrient cycling within lakes as filterers, such as Bivalvia feed on pelagic phytoplankton and release excess nutrients as faeces into the littoral zone (Vanni, 2002; Vaughn et al., 2008; Gergs and Rothhaupt, 2008). Bivalvia can release substantial amounts of phosphorus (P), which can even exceed the P releases from sediments, thus providing nutrient resources for primary producers, especially if P is limiting (Nalepa et al., 1991). This process is commonly referred to as benthic-pelagic coupling, i.e. the trophic linkage between the pelagic and littoral benthic zone (Fig. 2).

Macroinvertebrates can also regulate primary producer populations through consumption. For example, scraper control periphyton production by grazing, which can alter periphyton nutrient concentration and species composition (Hillebrand and Kahlert, 2001; Bowman et al., 2005; Liess and Kahlert, 2007). In turn, fish predation can regulate macroinvertebrate secondary production because macroinvertebrates can contribute up to 90 % of the biomass of fish (Schindler and Scheuerell, 2002) (Fig. 2). This suggests that macroinvertebrates have an important intermediate trophic position, highlighting the significant role of macroinvertebrates in the benthic pathway during nutrient transfer within lake food webs.

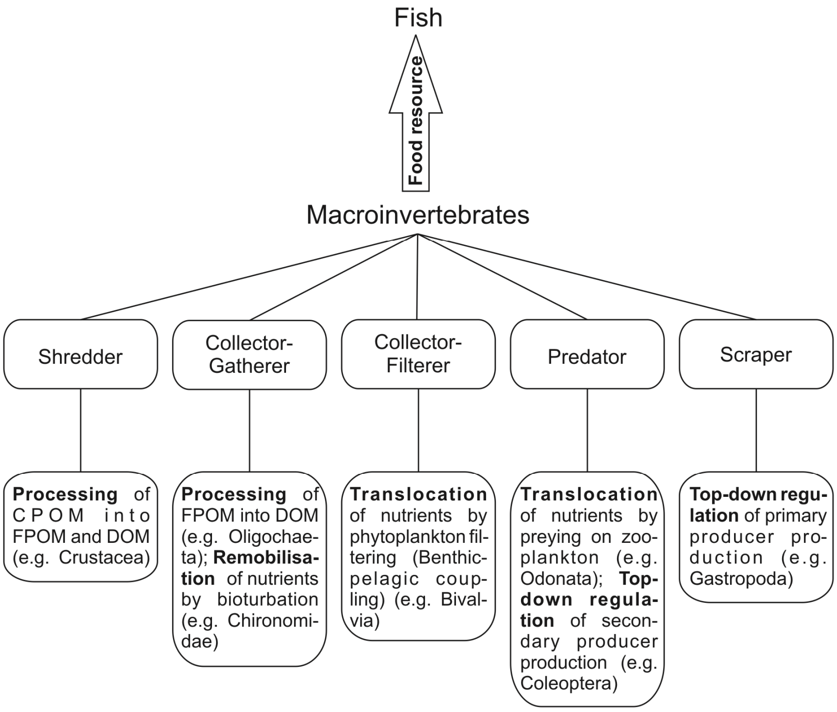

Fig. 2. The functional roles of littoral macroinvertebrates in nutrient cycling (DOM = Dissolved organic matter).

Although the significance of littoral macroinvertebrates for whole-lake biodiversity and function has recently been acknowledged, knowledge about the environmental factors that govern littoral macroinvertebrate community composition is still limited (Weatherhead and James, 2001). This gap in basic knowledge stems from the fact that limnologists have focused their work largely on pelagic or profundal communities and have neglected studying littoral zones and littoral macroinvertebrate communities (Stoffels et al., 2005). This is mainly because of the small- and large-scale heterogeneity within the littoral zone, which leads to a heterogeneous distribution of littoral macroinvertebrate communities (Dall et al., 1990; Death, 1995; Harrison and Hildrew, 2001; Stoffels et al., 2005). Thus, achieving a quantitative and representative sampling of macroinvertebrates across the littoral zone is a difficult task that is further complicated by the fact that researchers currently lack a harmonised sampling method (Solimini et al., 2006).

The few studies that have addressed the relationship between environmental factors and macroinvertebrate community composition have suggested that community composition depends on environmental factors related to hydromorphology, habitat and water chemistry (Dall et al., 1984; Tolonen et al., 2001; Johnson and Goedkoop, 2002; White and Irvine, 2003). Furthermore, the significance of an environmental factor in determining community composition was shown to be inversely related to the spatial scale upon which the factor acts. Thus, small-scaled factors, such as habitat complexity, have been demonstrated to have a greater influence than large-scaled factors, such as the geographical position of the lake (Johnson and Goedkoop, 2002; Stoffels et al., 2005). Nevertheless, the relative importance of environmental factors in determining macroinvertebrate community composition is still poorly understood. In particular, knowledge about the relative importance of trophic state versus habitat structure for littoral macroinvertebrate community composition is still lacking.

Having a thorough understanding of the ecology of littoral macroinvertebrate communities and their responses to natural environmental factors is generally considered as the most important requirement to describe and assess of the effects of human activities (Solimini et al., 2006). Since this basic knowledge is currently lacking, there are almost no published studies assessing whether, and to which extent, human activities affect the structure and functioning of littoral macroinvertebrate communities. Consequently, researchers currently lack methods to assess the ecological status of lakes using on littoral macroinvertebrates which is one reason why the European Water Framework Directive has not been effectively implemented at lakes (Solimini et al., 2006).

1.2 Thesis outline and hypotheses

In the present thesis, I studied the major environmental factors determining littoral macroinvertebrate community composition, as well as the ecological effects of prevalent human activities upon the structure and function of littoral macroinvertebrate communities.

The relationship between littoral macroinvertebrate community composition and environmental factors describing trophic state, morphology, hydrodynamics and water chemistry was studied at 38 German lowland lakes to address the first hypothesis (Chapter 2):

1) Littoral macroinvertebrate community composition is primarily determined by the trophic status of the lake.

Based on knowledge on the effects of natural environmental factors, I aimed to gain a mechanistic understanding of how human alterations of the littoral morphology impact the structure and function of littoral macroinvertebrate communities. Hence, macroinvertebrate diversity and community composition (Chapter 3) and macroinvertebrate food webs (Chapter 4) were investigated along a gradient of structural degradation, which include natural shorelines, shorelines developed by erosion control structures and shorelines developed for recreational activities at German lowland lakes to address the second hypotheses:

2) Structural degradation reduces the complexity and heterogeneity of littoral habitats, thus leading to reduced macroinvertebrate diversity and altered community composition.

Hypothesis 2 is in accordance with the "habitat heterogeneity hypothesis", which assumes that species diversity decreases as habitat heterogeneity decreases (Williams, 1964; Connor and McCoy, 1979; Williamson, 1981). The "habitat heterogeneity hypothesis" has not been thoroughly tested in aquatic ecosystems, and empirical support for this relationship was derived almost exclusively from terrestrial ecosystems (see Tews et al., 2004 and references therein).

Hypothesis 3 is considered an extension of the "habitat heterogeneity hypothesis", since I expected habitat heterogeneity to indirectly determine macroinvertebrate function through its effects on species richness:

3) Reduced habitat heterogeneity following structural degradation results in a loss of trophic links and alters the trophic base of littoral macroinvertebrate food webs.

Human activities can alter the hydrological regime of and hydrodynamic conditions within lakes. The effects that alterations of the hydrological regime following water level fluctuations may have on littoral macroinvertebrates were investigated at six German lowland lakes (Chapter 5). There, macroinvertebrate communities of eulittoral root habitats were compared with communities of four infralittoral habitats, which differed in structural complexity to address the fourth hypotheses:

4) The impact of habitat loss following water level fluctuations can be mitigated by the presence of habitats with high structural complexity.

The effects of hydrodynamic alterations caused by ship-induced waves were studied in mesocosm experiments (Chapter 6). Macroinvertebrate species were experimentally exposed to waves of increasing intensities in habitats with different structural complexities in order to address the fifth hypothesis:

5) High habitat structural complexity increases the resistance of littoral macroinvertebrates against ship-induced waves.

In Chapter 7, a synoptic summary and discussion of the results is presented. Based on a conceptual model, I illustrate the effects of the most important natural environmental factors, as well as the impacts of the human activities studied on the structure and function of littoral macroinvertebrate communities. Finally, I highlight the implications of this thesis towards an approach for the assessment of the ecological status of lakes using littoral macroinvertebrates.

2 Eulittoral macroinvertebrate communities of lowland lakes: discrimination among trophic states

Mario Brauns, Xavier-François Garcia, Martin T. Pusch and Norbert Walz

(Freshwater Biology 52: 1022-1032)

Abstract

1. Nutrient inputs from urban and agricultural land use often result in shifts in species composition of pelagic and profundal invertebrate communities. Here we test if nutrient enrichment affects the composition of eulittoral macroinvertebrate communities, and, if so, if macroinvertebrate communities of five different habitat types reflect differences in trophic state.
2. Macroinvertebrate community composition of 36 lakes was significantly correlated with total phosphorus (TP) concentration, the proportion of coarse woody debris (CWD) and root habitats and the proportion of grassland.
3. However, macroinvertebrate communities of five major habitat types from eight lakes were more dissimilar among habitats than among trophic states. Community composition of reed and stone habitats was significantly correlated with wind exposure but not TP concentration, while macroinvertebrate composition of sand habitats was related to TP concentration and coarse sediments. In CWD and root habitats, both TP concentration and a predominance of invasive species covaried, which made it difficult to relate the observed compositional differences to either trophic state or to the effects of competition between native and invasive species.
4. Trophic state influenced the composition of eulittoral macroinvertebrate communities but to a lesser extent than has been previously reported for profundal habitats. Moreover, the effects of trophic state were nested within habitat type and were partially superseded by biotic interactions and small-scaled habitat complexity. Although eulittoral macroinvertebrate communities were not strong indicators of the trophic state of lowland lakes, they may be used to assess other anthropogenic impacts on lakeshores.

2.1 Introduction

Anthropogenic eutrophication continues to be a major threat to lake ecosystems, despite efforts to reduce nutrient inputs into lakes. The construction of wastewater treatment plants greatly reduced the direct discharge of industrial and/or domestic wastewater, but many lakes still receive substantial inputs of phosphorus (P) and nitrogen (N) from urban and agricultural land use (Behrendt, 1996; Carpenter et al., 1998; Sanyanga and Hlanga, 2004) and atmospheric deposition (Vitousek et al., 1997). Regardless of the source, inputs of nutrients can substantially alter the ecological function of lake ecosystems. For example, increased nutrients, especially P, often result in increased pelagic primary production (Vollenweider, 1968) and algal blooms, which may inhibit the growth of submerged macrophytes (Egertson et al., 2004) and benthic primary production (Vadeboncoeur et al., 2003; Chandra et al., 2005). Moreover, decomposition of algal biomasses may result in anoxic conditions in profundal habitats, adversely affecting community composition. For example, pioneering work by Thienemann (1918; 1928) showed that the composition of profundal macroinvertebrate communities was strongly related to dissolved oxygen (DO) concentrations. This early work inspired the use of profundal macroinvertebrate communities to classify the trophic status of lakes (Thienemann, 1921; Saether, 1979; Brodersen and Lindegaard, 1999; Langdon et al., 2006).

In contrast to a number of studies showing the efficacy of using profundal communities in monitoring the effects of eutrophication on lakes, only a few studies have focused on the use of macroinvertebrate communities of nearshore, stony habitats and fewer still have taken a multihabitat approach. For instance, Macan & Maudsley (1969) studied English lakes along a gradient from oligotrophic to eutrophic conditions and found that macroinvertebrate communities were only partially related to trophic state because wind exposure superseded the compositional differences among trophic states. In Danish lakes, only a few macroinvertebrate species colonising stony shores were significantly related to trophic state, while morphometric variables influenced the majority of species (Brodersen et al., 1998). Similarly, Johnson and Goedkoop (2002) found that environmental factors other than nutrient concentration explained most of the variance of macroinvertebrate communities from wind exposed stony shores of Swedish lakes. However, the applicability of these results to other eulittoral habitats is unknown, and to our knowledge only one study has previously determined if littoral macroinvertebrate communities reflect lake trophic state across multiple habitat types (Tolonen et al., 2001). In a study of a large Finish lake system, Tolonen et al. (2001) showed that macroinvertebrate communities of macrophytes, sand and stone habitats primarily differed among habitat types, while within each habitat type community composition differed among trophic states. However, TP concentrations (range 3-26 µg L^{-1}) did not exceed mesotrophic conditions (Vollenweider and Kerekes, 1982), and habitat types such as coarse woody debris (CWD) and submerged tree roots were not studied.

In the present study, we use macroinvertebrate data from 36 lakes to test the hypothesis that eulittoral macroinvertebrate communities of North-German lowland lakes are related to differences in trophic state. Further, based on habitat-specific macroinvertebrate data from eight lakes, we test if macroinvertebrate communities of CWD, reed, root, sand and stone habitats comparably reflect among-lake differences in trophic state.

2.2 Methods

2.2.1 Sampling

Lake-specific analysis

Macroinvertebrates were collected in autumn 2001 (September-December) and spring 2002 (April-July) from six equidistant sampling sites situated along the shoreline of 36 North-German lowland lakes (Table 2, Fig. 3). A composite macroinvertebrate sample was taken from each sampling site (water depth < 1.2 m) using standardised kick-sampling (10 min. sampling effort, hand net: 250-µm mesh, width 24 cm). In the laboratory, samples were sorted and counted using a stereo-dissecting microscope, and individuals were identified to the lowest taxonomic level possible.

Electric conductivity, dissolved oxygen concentration, pH and water temperature were recorded at each sampling site using a multiparameter probe (HydroLab H20, HydroLab Corporation, Austin, TX, U.S.A.). Habitat availability at the sampling sites was expressed as the proportion of CWD, pebbles, reed (*Phragmites australis*, Cav. Trin. ex Steud.), sand, stones, submerged macrophytes and roots (e.g. if roots were present at three of the six sampling sites they accounted for 50 % availability). Root habitats consisted of submerged roots of riparian alder trees (*Alnus glutinosa*, L.) and constitute an important habitat type in the eulittoral zone of North-German lowland lakes.

Land use within a buffer zone around each lake (from the shoreline to 500 m inland) was estimated by GIS (ArcView, version 3.2, Esri, Redlands, CA, U.S.A.). Data on the lake surface area, TP concentration (annual mean concentrations in 2001), water residence time and trophic state were provided by the Regional Environmental Agency (Landesumweltamt Brandenburg). The 36 lakes were assigned to trophic state classes by the Regional Environmental Agency in 2001 (Länderarbeitsgemeinschaft Wasser, 1998) using TP concentration, chlorophyll a, and water transparency and the classification system of Vollenweider and Kerekes (1982).

Habitat-specific analysis

Eulittoral macroinvertebrate samples were collected from 33 sampling sites in eight lakes in October 2003 and April 2004 (Table 2). At each sampling site (water depth < 1.2 m), the main habitat types (CWD, reed, roots, sand and stones) were sampled. Sampling effort differed among the different habitat types. Macroinvertebrates were brushed from three pieces of CWD (with bark) and sieved through a 250 µm mesh. The length and diameter of the CWD was measured to estimate surface area. For reed habitats, sampling consisted of five 1-m sweeps using a hand net (250-µm mesh, width 24 cm). The area of reed habitats sampled was estimated by multiplying hand net width by the length of the sampled area. In addition, reed stem density was determined by counting stems within a 0.25 m^2 area in each reed habitat.

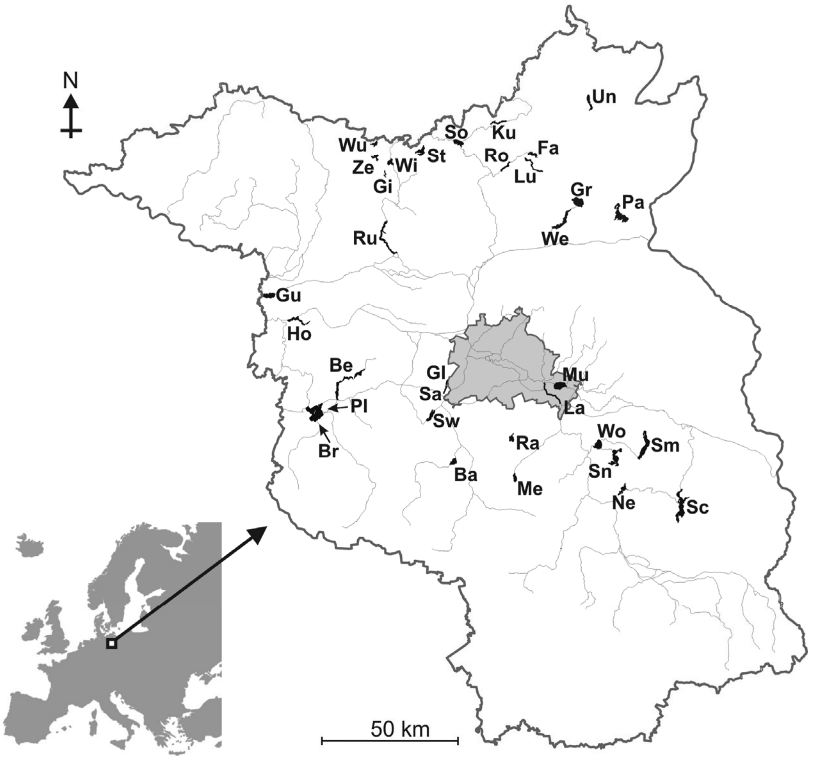

Fig. 3. Map of Europe (lower left), the federal states of Berlin (grey) and Brandenburg showing the location of the 38 study lakes. For lake codes see Table 2.

Five subsamples from root habitats were collected with a hand net (250-µm mesh, width 24 cm), and the area sampled was estimated by multiplying hand net width by the water depth. Although the sampling techniques used for reed and root habitats did not permit the sampled area to be precisely quantified, they assured an efficient sampling of highly mobile species such as Dytiscidae (Coleoptera) that frequently colonise these structurally complex habitats.

Sand habitats were sampled by taking 10 modified Surber samples (area 0.05 m^2, 250-µm mesh). At each site, sediment particle size (three size fractions: fine < 0.03 mm; middle 0.063-1.12 mm and coarse, >2 mm, Analysette 3 Pro, Fritsch, Idar-Oberstein, Germany) was determined on the surficial sediment (top 5 cm) collected with a gravity corer (inner diameter 5 cm, Uwitec, Mondsee, Austria). Stone habitats were sampled by brushing macroinvertebrates from 10 arbitrarily selected stones. The length, height and width of the individual stones were used to calculate surface areas, assuming an ellipsoid shape. Surface areas estimated by ellipsoid surface calculation did not differ from estimations based on the more precise foil wrapping method (paired t-test, $P = 0.760$, $n = 20$). The multiple subsamples for each habitat type were pooled in the field and processed as described above.

Wind exposure of each sampling station was calculated using the formula of Brodersen (1995) that combines data on frequency and velocity of the wind, fetch area and water depth at the sampling site. Wind data from nearby meteorological stations was provided by the German Weather Service.

2.2.2 Statistical analyses

Prior to statistical analyses, species that were recorded from only a single lake were removed from the lake- and habitat-specific datasets. Furthermore, we tested if macroinvertebrate community composition differed between sampling dates using analysis of similarity (ANOSIM, PRIMER, version 5, Primer-E Ltd., Plymouth, U.K.). No differences were noted between seasons for the lake-specific community (R-statistic = 0.036, $P = 0.057$) or for the CWD (R-statistic = 0.047, $P = 0.146$), root (R-statistic = 0.017, $P = 0.325$) and stone (R-statistic = 0.017, $P = 0.579$) habitats. By contrast, communities of reed (R-statistic = 0.205, $P = 0.001$) and sand (R-statistic = 0.071, $P = 0.032$) habitats differed, but, albeit significant, the differences (as shown by the R-statistics) were small between sampling dates. Consequently, data from both sampling dates were pooled for further analyses.

Non-metric multidimensional scaling ordination (NMS) was used to examine relationships between macroinvertebrate community composition, TP concentration and other selected environmental variables. NMS was performed on square root-transformed relative abundances for lake-specific data and on square root-transformed densities (individuals m^{-2}) for habitat-specific data using the PC-ORD software (version 4.25, MjM Software, Gleneden Beach, OR, U.S.A.). Square root transformation was used as it results in a medium down-weighting of common species and allows for a good discrimination of sampling sites (Clarke and Warwick, 2001).

Bray-Curtis distance was used in NMS ordination with the stability criterion set at 0.0001, 100 iterations to evaluate stability and initial step length set at 0.2. The appropriate dimensionality was chosen based on results of a Monte Carlo test (100 runs, $P = 0.01$). The final run was carried out with the optimum dimensionality as the starting configuration and by applying varimax rotation (McCune and Grace, 2002). Pearson correlation (SPSS version 9.0, SPSS Inc., Chicago, IL, U.S.A.) between lake scores from the NMS axes and environmental variables was done to determine the best predictors of the variability in community composition. For correlation analyses, environmental data were tested for deviation from normality and transformed when necessary using arcsine square-root transformation on proportional and Box-Cox transformation (Box and Cox, 1964) on continuous data.

In addition to the habitat-specific analyses, we tested if trophic state or habitat type was the more important driver of macroinvertebrate community composition in lowland lakes. Using pooled macroinvertebrate data for each lake and habitat type, we calculated Bray-Curtis dissimilarities for all combinations with habitat type nested within trophic state ($n = 30$) and with trophic state nested within habitat type ($n = 15$). Between-group differences were tested using a Mann-Whitney test (SPSS version 9.0), assuming that if trophic state was the more important driver of macroinvertebrate community composition then compositional dissimilarities among trophic states within a habitat type would be higher than dissimilarities among habitat types within a given trophic state.

2.3 Results

2.3.1 Lake-specific analysis

TP concentration was significantly correlated with NMS axis 1 and lakes were arranged by trophic state, with oligo- to mesotrophic lakes being grouped in the upper left and eu- to hypertrophic lakes in the lower right part of the NMS plot (Table 2, Fig. 4). However, oligotrophic Lake Wummsee (Wu) as well as several eutrophic and hypertrophic lakes such as Mellensee (Me) and Neuendorfer See (Ne) were positioned closer to the mesotrophic lakes, indicating similarities in community composition (Fig. 2). Only 23 % of all species recorded were significantly correlated with NMS axis 1, among them *Dreissena polymorpha* (Pallas) (Bivalvia) and *Lype phaeopa* McLachlan (Trichoptera) that decreased in abundance along NMS axis 1 (Table 3). On NMS axis 2, lakes were arranged along a gradient of decreasing proportion of CWD and roots and increasing conductivity (Fig. 4, Table 3). Lakes with high proportions of CWD, roots and a low conductivity were characterised by high abundances of *Palpomyia* sp. (Diptera), *Oulimnius* sp. (Coleoptera) and *Gammarus pulex* (L.) (Crustacea), whereas the invasive crustaceans *Dikerogammarus* sp. and *Pontogammarus robustoides* (Sars) were characteristic for the lakes with high conductivity and low proportions of allochthonous habitats (Table 3). Hence, these findings indicate that TP and habitat characteristics were the main factors influencing the composition of the eulittoral macroinvertebrate communities.

2.3.2 Habitat-specific analysis

The relative importance of TP and habitat type was further studied on the habitat-specific level with an initial comparison of dissimilarities. Dissimilarity among trophic states within a given habitat type (median = 77.6, range 68.8 - 89.6) was lower than dissimilarity among habitat types within a given trophic state (median = 84.8, range 51.8 - 93.0) (Mann-Whitney test, *P* = 0.001). Based on this result, we performed NMS analyses on habitat-specific macroinvertebrate communities to test whether discrimination of trophic state by macroinvertebrate communities differed between habitat types.

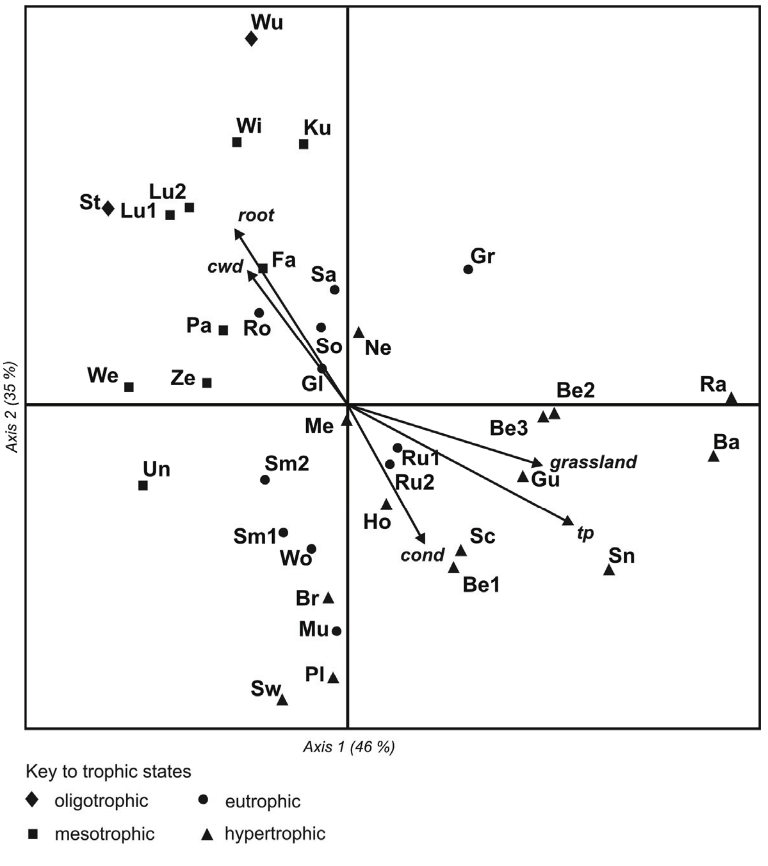

Fig. 4. Non-metric multidimensional scaling (NMS) ordination of 36 lakes of the lake-specific analysis. Only the first two NMS axes are shown as axis 3 explained only 5 % of the variance. The trophic state of each lake is superimposed. The most important environmental variables (italic) (Pearson's *r* to NMS axes > 0.55) are displayed as vectors (*cond* = conductivity, *cwd* = proportion of coarse woody debris habitats, *grassland* = proportion of grassland, *root* = proportion of root habitats, *tp* = total phosphorus). For lake codes see Table 2, for stress, number of axes and cumulative explained variance see Table 3.

Coarse woody debris

NMS and correlation analyses showed that TP concentration was significantly correlated with community composition along NMS axis 1 (Table 5). Furthermore, this axis was correlated with densities of the invasive crustaceans *Dikerogammarus villosus* (Sowinsky) (*r* = -0.90, *P* = 0.000) and *Chelicorophium curvispinum* Sars (*r* = -0.83, *P* = 0.000). For example, mean density (± SE) of *C. curvispinum* increased markedly from 5 ± 3 individuals m^{-2} in mesotrophic to 919 ± 667 individuals m^{-2} in hypertrophic lakes.

Reed

Community composition of reed habitats was significantly correlated with conductivity, wind exposure and water residence time but not TP concentration (Table 5). Furthermore, wind exposure was significantly correlated with stem density (*r* = -0.73, *P* = 0.001). Densities of Ephemeroptera *Cloeon dipterum* (L.) and *Caenis luctuosa* (Burmeister) were highly correlated with NMS axis 1 (both *r* = -0.69, *P* = 0.002).

Roots

Community composition of root habitats was correlated with TP concentration, conductivity, pH, water residence time and DO (Table 5). Similarly, the density of the native *G. pulex* was negatively (*r* = -0.74, *P* = 0.002) and the density of the invasive *P. robustoides* was positively (*r* = 0.76, *P* = 0.002) correlated with NMS axis 1.

Sand

Community composition of sand habitats was correlated with TP concentration and sediment particle size (Table 5). In particular, sediment particle size was a strong predictor of macroinvertebrate composition. Densities of almost 45 % of all species recorded from sand habitats were significantly negatively correlated with NMS axis 1, which was explained by an increase in the middle particle fraction (0.063 - 1.12 mm) and a decrease in the coarse particle fraction (> 2 mm). Ordination of sampling sites along NMS axis 2 followed a gradient of increasing TP concentration and decreasing proportion of the fine particle fraction (< 0.03 mm) (Table 5). However, only 9 % of all species recorded were significantly correlated with this axis.

Stones

Community composition of stone habitats was significantly correlated with wind exposure and water residence time but not TP concentration (Table 5); hence community composition responded in a complex pattern to these environmental factors. The density of invasive species was negatively correlated with NMS axis 1. For example, the strongest correlation was shown by *D. polymorpha* (*r* = -0.97, *P* = 0.000); this species increased more than 10-fold from lakes with high water residence times (groundwater supplied lakes) to lakes with low water residence times (riverine lakes). Conversely, densities of lotic species such as *Oulimnius tuberculatus* (Müller) (Coleoptera) (r = 0.56, P = 0.017) and *Theodoxus fluviatilis* (L.) (Gastropoda) (r = 0.64, P = 0.005) increased along NMS axis 1.

2.4 Discussion

2.4.1 Lake-specific analysis

Distinct differences in composition of eulittoral macroinvertebrate communities were found between oligotrophic and hypertrophic lakes. However, similarities between oligotrophic and mesotrophic and between mesotrophic and eutrophic lakes indicated that community composition between these trophic states was less distinct. Even the compositional differences between oligotrophic and hypertrophic lakes were not unequivocally related to differences in TP concentration, since the proportion of grassland was also related to community composition. Grasslands are predominantly used as pasture, and hence it seems unlikely that they constitute a potential source of nutrient inputs. This conjecture was also supported by the lack of a significant relationship between grassland and TP concentration (Pearson's r = 0.23, P = 0.174). However, lakes with a high proportion of grassland in their buffer zones often lacked of riparian trees, as this type of land use usually extended to the lakeshore. Hence, we assume here that grassland may reflect the effects of human-generated shoreline modification and a decrease in the amount of CWD in the littoral zone (Christensen et al., 1996). This is supported by the distribution of the wood-associated L. phaeopa (Hoffmann and Hering, 2000) which decreased in abundance as the proportion of grassland increased. Similarly, the low abundances of D. polymorpha in hypertrophic lakes may not be directly related to trophic state (Ludyanskiy et al., 1993), but may rather indicate a lack of suitable habitat such as CWD. Indeed, macroinvertebrate community composition was strongly related to the presence of CWD and root habitats, both of which contribute to habitat heterogeneity and are known to be good predictors of macroinvertebrate community composition (Nilsson et al., 1994; Heino, 2000; Harrison and Hildrew, 2001).

2.4.2 Habitat-specific analysis

Macroinvertebrate communities were more dissimilar among habitat types than among trophic states, indicating the importance of intrinsic habitat properties in determining community composition. Trophic state was shown to be a good predictor of the community composition of CWD, root and sand habitats, while community composition of sand habitats was also determined by small-scale differences in the structural complexity of sediments. Since more species were related to particle size than to TP concentration, we conclude that trophic state may not be the primary factor determining the shift in community composition observed in sand habitats. For CWD and root habitats, considerably higher densities of invasive crustaceans were related to high trophic state. However, the predominance of invasive species in hypertrophic lakes may not necessarily be related directly to increased TP concentration, but may rather be a result of the low water residence times in these hypertrophic lakes. In the lowland lakes studied here, low water residence times reflect a connection to a larger river system that also serves as a commercial navigation route. Furthermore, since commercial navigation is known to accelerate the dispersal of invasive species (de Vaate et al., 2002; Grigorovich et al., 2003; Duggan et al., 2005), there is a higher probability for these lakes to be colonised by invasive species. As hypertrophic state and the predominance of invasive species coincided, the observed compositional differences among trophic states can not be unambiguously related to differences in TP concentration, as mass occurrences of invasive species might similarly affect community composition (Hall and Mills, 2000; Rahel, 2002). Hence, two alternative explanations are possible for the observed differences in community composition of CWD and root habitats. Eutrophication might have caused an extinction of native species and a subsequent colonisation of the vacant ecological niches by invasive species. Alternatively, invasive species might have outcompeted native species, implying that biotic interactions and not trophic state resulted in the observed differences. At least *D. villosus* might actively displace native species regardless of trophic state, because it exerts a strong predatory impact on native species (Dick et al., 2002; Krisp and Maier, 2005; MacNeil and Platvoet, 2005). Thus, it remains unclear whether the predominance of invasive species in the hypertrophic lakes studied here was the cause or the consequence of the alteration of the macroinvertebrate communities of the CWD and root habitats and whether these communities discriminate among trophic states.

Wind exposure but not TP concentration was significantly correlated to macroinvertebrate community composition of the reed and stone habitats. Moreover, this result was unaffected by the smaller range of TP concentration in the habitat-specific dataset (no oligotrophic lakes), as the correlation coefficient between TP and lake-specific NMS axis 1 decreased only slightly (from $r = 0.76$, $P = 0.000$ to $r = 0.66$, $P = 0.000$) after omitting oligotrophic lakes (TP < 27 µg L^{-1}) from the lake-specific correlation analysis. Assuming that the effect of TP range on statistical results was similar in the habitat-specific dataset, we conclude that the lack of a significant relationship between trophic state and macroinvertebrate community composition of reed and stone habitats was not an artefact of the study design. This finding is also supported by earlier studies that have shown how eulittoral macroinvertebrate communities on stony shores reflect environmental variables other than trophic state (Barton and Carter, 1982; Dall et al., 1984; Johnson and Goedkoop, 2002).

While community composition in stone habitats was directly related to wind exposure, community composition in reed habitats reflected more the effect of wind exposure on stem density. Increasing the density of macrophyte stands has been shown to influence community composition by providing refuges against predation (Diehl, 1992; Tolonen *et al.*, 2003; Warfe & Barmuta, 2004; Rennie & Jackson, 2005). In our study, a high density of reed stands also seemed to favour the sedimentation of organic detritus, which was reflected in higher densities of the detritus collecting mayflies' *C. luctuosa* and *C. dipterum* (Schmedtje and Colling, 1996).

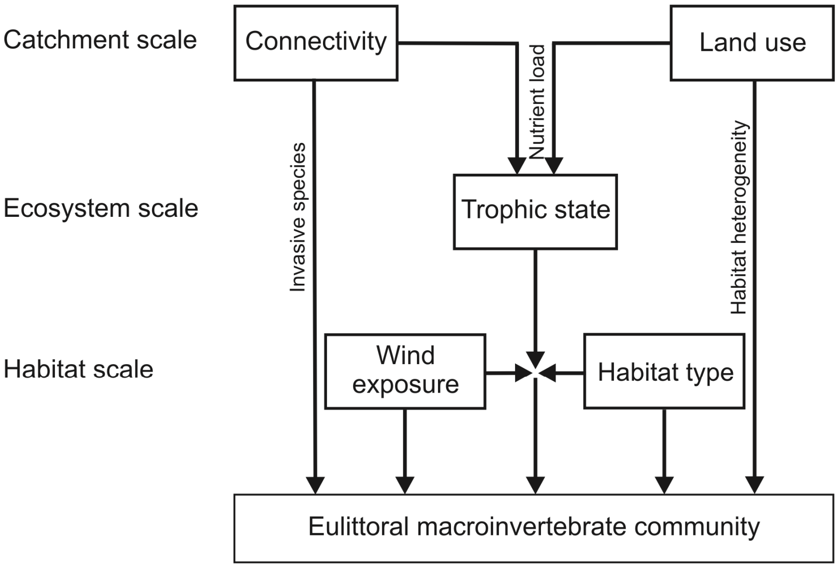

Fig. 5. Conceptual diagram representing the major environmental factors influencing the eulittoral macroinvertebrate communities of lowland lakes. Environmental variables act at different spatial scales, and connectivity of the lake to a larger river system influences macroinvertebrates either directly by accelerating the immigration of invasive species, or indirectly by increasing nutrient loads resulting in eutrophication. Land use influences macroinvertebrates directly through the alteration of littoral habitat structure, and indirectly via nutrient loading. Nutrient load determines the trophic state that in turn influences conditions in habitats in the lake ecosystem. Wind exposure and habitat type influence macroinvertebrates directly and substantially modify the effect of trophic state on the composition of the macroinvertebrate community.

Macroinvertebrate community composition was related to conductivity, pH and DO in the habitat types. However, since these environmental variables exhibited little variability and did not reach extreme values that would directly affect community composition, we conclude that there is no mechanistic relation between conductivity, pH, DO and macroinvertebrate community composition.

In conclusion, trophic state influenced the composition of the macroinvertebrate community of the eulittoral zone, but not as much as has been previously reported for profundal communities (Thienemann, 1921; Saether, 1979; Brodersen and Lindegaard, 1999; Langdon et al., 2006). Furthermore, our study showed that the effects of trophic state were nested within habitat type, and were partially superseded by biotic interactions and small-scaled habitat complexity (Fig. 5). For example, the influence of trophic state on macroinvertebrate communities of stone habitats was seemingly counteracted by wind exposure (Fig. 5), lending support to a number of other studies (Macan and Maudsley, 1969; Brodersen et al., 1998; Johnson and Goedkoop, 2002). Moreover, our results indicate that eulittoral macroinvertebrate communities of the lowland lakes are not a reliable indicator of trophic state, as they were influenced by a number of factors such as lake connectivity, habitat type, land use and wind exposure (Fig. 5). However, our results suggest that eulittoral macroinvertebrates may be useful for assessing other anthropogenic impacts such as human-generated effects on littoral habitats.

3 Effects of human shoreline development on littoral macroinvertebrates in lowland lakes

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Abstract

1. The shores of many lakes have been substantially altered by human developments such as erosion control structures or recreational beaches. Such alterations are likely to increase in the future, yet almost nothing is known about their impacts on the littoral macroinvertebrate community.
2. Macroinvertebrates were studied at seven German lowland lakes exhibiting natural shorelines (reference), retaining walls, ripraps and recreational beaches to examine impacts on eulittoral (0 - 0.2 m water depth) and infralittoral (0.2 - 1.2 m water depth) communities associated with the three types of shoreline development.
3. Among sites, eulittoral species richness and abundance of Coleoptera, Gastropoda, Trichoptera, shredders and xylophagous species were lowest at beaches and retaining walls, but ripraps did not differ significantly from natural shorelines. Retaining walls and ripraps had no significant impact on the infralittoral macroinvertebrate community. Conversely, beaches had significantly lower infralittoral species richness and lower abundance of Bivalvia, Crustacea, Ephemeroptera, Trichoptera and shredders than natural shorelines. Furthermore, species richness was positively correlated with habitat heterogeneity expressed as number of habitat types.
4. Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of developed shorelines due to increasing abundances of Chironomidae. The remaining macroinvertebrate major groups decreased with increasing proportion of shoreline development.
5. The biological impacts of shoreline development in lowland lakes depend on the extent to which structural complexity and heterogeneity of littoral habitats are reduced. Hence, we recommend that management programs focus on the conservation of littoral habitat complexity and habitat heterogeneity. Biological effects of shoreline development may be efficiently assessed by combining an assessment of the morphological status of lakeshores and information on macroinvertebrate indicator species with a defined response to the loss of their preferred habitats.

3.1 Introduction

Lakeshores have always been a preferential place for human settlement and various other human activities (Liddle and Scorgie, 1980; Ostendorp et al., 2004), leading to shoreline development and the discharge of waste water. While the discharge of waste water has been widely reduced, shoreline development represents a current threat to the ecological integrity of lakes worldwide (Stadelmann, 1990; Bryan and Scarnecchia, 1992; Engel and Pederson, 1998; Elias and Meyer, 2003; Toft et al., 2003; Teiber, 2003). Moreover, the intensity of shoreline development is expected to increase in the future (Walz et al., 2002; Schmieder, 2004).

In general, shoreline development is considered to impact the littoral zone through alteration or loss of littoral habitats such macrophyte stands, most prominently the littoral reed belts (Sukopp, 1971; Radomski and Goeman, 2001; Elias and Meyer, 2003) or bottom sediments (Jennings et al., 2003). Also, the amount of coarse woody debris (CWD) in the littoral zone can be substantially reduced in lakes with a high proportion of shoreline development (Christensen et al., 1996; Marburg et al., 2006).

The biological impacts have been quantified mainly for littoral fish communities, particularly impacts on spatial aggregation (Scheuerell and Schindler, 2004), species richness (Jennings et al., 1999) and production (Schindler et al., 2000; Radomski and Goeman, 2001). Impacts on littoral macroinvertebrates are likely, as they exhibit a stronger dependence on littoral habitats and are less mobile than fish. However, we are aware of only one study that examined the impacts of shoreline development on littoral macroinvertebrates. Bänziger (1995) compared macroinvertebrate communities of shorelines subjected to development with those of natural shorelines in the prealpine Lake Geneva and found species diversity and abundance to be lowest at developed shorelines. However, the applicability of these findings to other lake types is unknown, and the impact of recreational use on littoral macroinvertebrates has, to our knowledge, never been examined. An understanding of the ecological impacts of shoreline development on various lake types represents a prerequisite for a scientifically-based ecological management of lakeshores. In particular, this applies to the assessment of their ecological status as well as the identification and implementation of effective restoration measures to improve heavily degraded shores.

In this study, we quantified the impacts of three types of shoreline development on macroinvertebrate communities of seven German lowland lakes differing in trophic status and hydrological regime. We compared two types of erosion control structures (retaining walls, ripraps) and one type of recreational use (beaches) with natural shorelines to test 1) for alterations of the macroinvertebrate communities associated with the three types of shoreline development and 2) whether alterations of the macroinvertebrate communities are also detectable among the studied lakes.

3.2 Methods

3.2.1 Study sites

Seven study lakes were chosen to allow for a sampling design stratified by shoreline type. The lakes are located in North-East Germany (52° 24’ 10” - 53° 18’ 40” N, 12° 52’ 40” - 13° 52’ 40” E) and differ in trophic status and hydrological regime (Table 6). Within the lakes, four different shoreline types, i.e. natural shorelines (reference), beaches (recreational use), retaining walls and ripraps (erosion control structure) were chosen. Local ripraps consisted of layered, rectangular stones and covered the shore from above the water line down to a water depth of about 0.5 m. As beaches and ripraps were not present in all studied lakes, a total of 20 stations were sampled.

3.2.2 Macroinvertebrate sampling

Macroinvertebrates were sampled in autumn (October 2003) and spring (April 2004) at each of the 20 stations both in 0 - 0.2 m water depth (herein after referred to as eulittoral) and in 0.2 - 1.2 m water depth (herein after referred to as infralittoral). Not all infralittoral habitat types were present at all shoreline types preventing a balanced sample design for reed and stone habitats (Table 7). Moreover, CWD habitats were restricted to natural shorelines as developed shorelines were situated in urban areas where riparian trees have been removed.

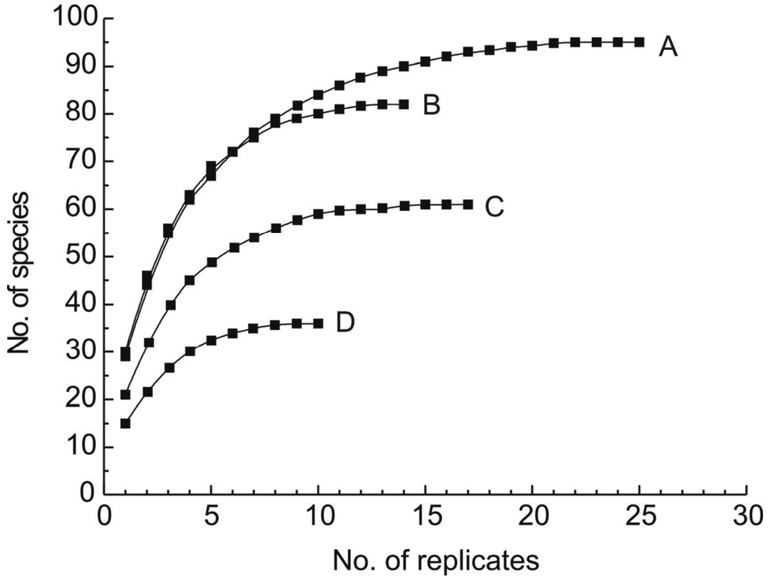

Fig. 6. Species-area curves for (A) natural shoreline, (B) riprap, (C) retaining wall and (D) recreational beach.

We sampled each habitat type separately using sampling techniques that were best adapted to the different degree of spatial complexity of the habitats. This ensured a maximum sampling efficiency and comparability of the samples. Macroinvertebrates from CWD habitats were brushed from three pieces of CWD with comparable states of decay, and subsamples were sieved trough a mesh (250 µm). Subsequently, length and diameter of each piece of CWD was measured, and surface area was calculated assuming a cylindrical shape. Similarly, 10 stones were randomly chosen from each sample point and attached macroinvertebrates were brushed off. From each stone, surface area was calculated based on its length, height and width. We took five 1 m sweeps from reed habitats using a hand net (250-µm mesh, width 24 cm). We estimated the sampled area of reed habitats by multiplying hand net width with length of the sampled area. We took five subsamples from submerged roots of riparian trees with a hand net (250-µm mesh, width 24 cm), and estimated the sampled area by multiplying hand net width with the respective sampling depth. Sand habitats were sampled with 10 subsamples using a modified Surber sampler for lentic conditions (area 0.05 m^2, 250 µm mesh). Retaining walls were sampled with 10 subsamples using a scratch net (250 µm mesh, Hydrobios, Kiel, Germany). Here, sampled area was calculated by multiplying net frame width (13 cm) with the respective sampling depth. Subsequently, subsamples from each habitat type were pooled to create a composite sample per habitat type. Samples were preserved in the field and macroinvertebrates were identified in the laboratory to the lowest taxonomic level possible. Species were assigned to functional feeding groups according to Schmedtje & Colling (1996).

3.2.3 Statistical analysis

Initially, we removed species from the dataset that were recorded in only one lake. Since there were no significant differences in community composition among seasons using analysis of similarity (ANOSIM, PRIMER, version 5, Primer-E Ltd., Plymouth, U.K.) for any of the four shoreline types, we pooled the data from both sampling dates for further analyses.

We constructed species-area curves (PCORD, Version 4.25, MjM Software, Gleneden Beach, OR, U.S.A.) to verify whether species richness was affected by differences in the number of samples at each shoreline type. This analysis revealed that the species-area curve for each shoreline type reached its asymptote indicating that sampling effort was sufficient at all shoreline types (Fig. 6). We converted species densities into relative abundances and calculated relative abundances of the macroinvertebrate major groups, relative abundances of the functional feeding groups and species richness to test for differences between natural and developed shorelines by means of non-parametric Mann-Whitney tests (SPSS, version 9.0, SPPS, Chicago, IL, U.S.A.).

Indicator species analysis (IndVal) (Dufrene and Legendre, 1997) was used to detect macroinvertebrate species that are characteristic for a habitat or shoreline type, respectively (PCORD, version 4.25). We also tested whether species richness was related to the number of habitat types using Spearman correlation analysis (SPSS, version 9.0).

For analyses of the effects of shoreline development among lakes, we estimated whole-lake littoral macroinvertebrate density by calculating the weighted average density based on the proportion of shorelines represented by natural shorelines, shorelines with retaining walls and shorelines with recreational beaches (Table 6). Similarly, we calculated whole-lake relative abundances of the macroinvertebrate major groups. We restricted this analysis to the five lakes (Grienericksee, Langer See, Müggelsee, Unteruckersee, Werbellinsee), which had natural shorelines, shorelines with retaining walls and shorelines with recreational beaches.

3.3 Results

3.3.1 Effects of shoreline development - among sites

Among sites, eulittoral species richness was significantly lower at beaches and at retaining walls than at natural shorelines, but did not significantly differ between ripraps and natural shorelines (Fig. 7a). Relative abundances of Coleoptera, Crustacea, Gastropoda and Trichoptera were significantly lower at beaches than at natural shorelines and relative abundances of Gastropoda and Hirudinea were significantly lower at retaining walls than at natural shorelines (Table 8). IndVal analysis revealed *Bithynia tentaculata* (L.) (Gastropoda) ($IV = 71$, $P = 0.016$), *Ischnura elegans* Vander Linden (Odonata) ($IV = 56$, $P = 0.046$), *Lype phaeopa* McLachlan (Trichoptera) ($IV = 75$, $P = 0.004$), and *Platambus maculatus* (L.) (Coleoptera) ($IV = 60$, $P = 0.038$) as characteristic species for natural shorelines. Moreover, the occurrence of *I. elegans*, *L. phaeopa* and *P. maculatus* was restricted to natural shorelines and relative abundance of *B. tentaculata* was significantly higher at natural shorelines than at beaches or retaining walls (Mann-Whitney test, $P = 0.008$). None of the recorded species was characteristic for beaches or retaining walls, whereas *Dugesia lugubris/polychroa* (Turbellaria) ($IV = 80$, $P = 0.003$), *Cyrnus trimaculatus* (Curtis) (Trichoptera) ($IV = 79$, $P = 0.002$), and *Erpobdella octoculata* (L.) (Hirudinea) ($IV = 72$, $P = 0.020$) were characteristic species for ripraps. Differences between shoreline types were also discernible in the functional feeding group composition. The abundances of piercer, shredder and xylophagous species were significantly lower at beaches than at natural shorelines (Table 9). Similarly, the abundances of predator, shredder and xylophagous species were significantly lower at retaining walls than at natural shorelines. In contrast, we found no significant differences in the abundances of the functional feeding groups between ripraps and natural shorelines.

In contrast to the eulittoral zone, no significant differences were found in species richness (Fig. 7b) nor macroinvertebrate major groups and functional feeding groups (Tables 8, 9) between retaining walls, ripraps and natural shorelines in the infralittoral zone. Conversely, infralittoral species richness, relative abundances of Bivalvia, Crustacea, Ephemeroptera, Trichoptera (Table 8) and relative abundance of shredders (Table 9) were significantly lower at beaches than at natural shorelines. None of the recorded infralittoral species was indicative for natural or developed shorelines.

Spearman correlation analysis revealed that species richness was significantly positively correlated with the number of habitat types (Spearman's $\rho = 0.77$, $P = 0.000$, $n = 20$) and median species richness decreased from 63 species at natural shorelines with all five habitat types present to 17 species at recreational beaches with only one habitat type present.

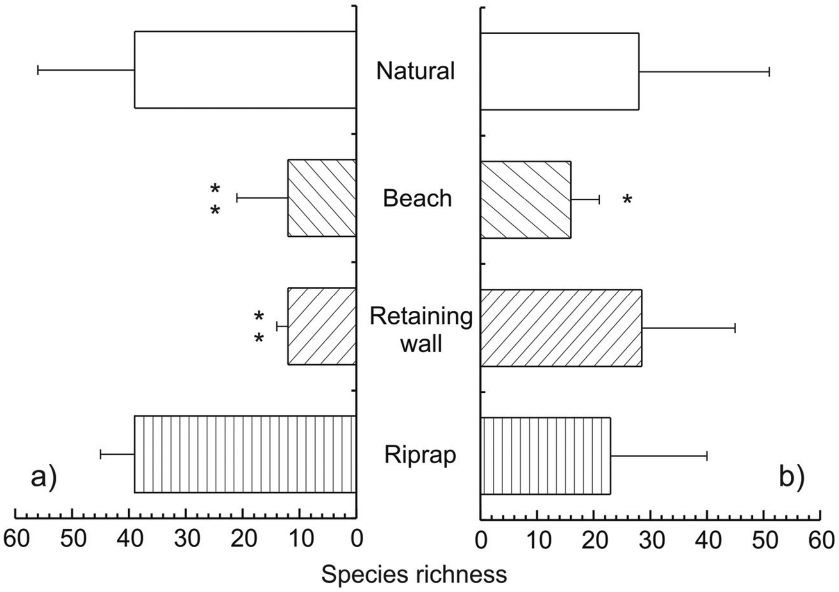

Fig. 7. Median species richness (max) of natural and developed shorelines (beach, retaining wall, riprap) within the (a) eulittoral and the (b) infralittoral zone. Significant differences (Mann-Whitney test) between natural and each type of developed shorelines are indicated by asterisks (** $P < 0.01$, * $P < 0.05$).

3.3.2 Effects of shoreline development - among lakes

Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of developed shorelines and was almost 3-times higher in lakes with high proportions of shoreline development than in lakes with low proportions of shoreline development (Table 10). Similarly, the relative abundance of Chironomidae increased from 73 % in Lake

Unteruckersee with lowest proportions of shoreline development to 96 % in Lake Langer See with the highest proportion of shoreline development. The remaining macroinvertebrate major groups, particularly Coleoptera, Gastropoda and Oligochaeta, decreased in abundance with increasing proportions of retaining walls or recreational beaches (Table 10).

3.4 Discussion

Earlier studies on the impacts of human shoreline development on lakes mainly focused on littoral habitats and littoral fish communities (Christensen et al., 1996; Jennings et al., 1999; Radomski and Goeman, 2001; Elias and Meyer, 2003; Jennings et al., 2003; Scheuerell and Schindler, 2004). Our study demonstrates that, independently of the lake type, shoreline development through erosion control structures and construction of recreational beaches had significant impacts on both eulittoral and infralittoral macroinvertebrate communities. However, the degree and spatial extent of the impacts differed between the types of shoreline development.

Within the eulittoral zone, the impacts of development on macroinvertebrate species richness, major taxonomic groups and functional feeding groups (Tables 8, 9) can be attributed to the reduction of habitat complexity, as roots with their complex 3-dimensional structure at natural shorelines were replaced by habitats with lower complexity at developed shorelines (concrete, sand, cf. Table 7). Habitat complexity is one of the key environmental factors influencing macroinvertebrate communities since complex habitats provide more ecological niches (O'Connor, 1991), decrease the predation risk by limiting the foraging success of predators (Thompson, 1987; Warfe and Barmuta, 2004), and may also provide refuge against wind-induced wave disturbance. Consequently, natural shorelines harboured characteristic species such as *Bithynia tentaculata*, *Ischnura elegans* and *Platambus maculatus* with a strong preference for root habitats. These habitat specialists are highly vulnerable to the loss of their preferred habitat and are those components of the community that are most severely affected from human shoreline development.

In addition to structural properties, complex habitats exhibit a higher available surface for the growth of periphyton (Bowen et al., 1998) and the sedimentation of particulate organic matter (Taniguchi and Tokeshi, 2004). Hence, functional feeding groups such as piercer, shredder and xylophagous species may have benefited from these food resources at natural shorelines.

Due to their low structural complexity, retaining walls and beaches did not have characteristic species in the eulittoral zone, indicating that there is no distinct community associated with these types of shorelines. Interestingly, ripraps had no significant impact on eulittoral macroinvertebrates in the studied lakes, even if ripraps had a distinct community that mainly comprised lithobiontic species. Presumably, the arrangement of stones at ripraps created a structural complexity of big and small crevices that resembled that created by root habitats at natural shorelines. This view is supported by experiments showing that colonisation baskets filled with cement balls to mimic ripraps exhibited higher species richness and macroinvertebrate abundance than baskets with cement blocks that mimic retaining walls (Schmude et al., 1998).

Within the infralittoral zone, erosion control structures had no significant impact on the macroinvertebrate community. Similarly, infralittoral fish species richness and abundance did not differ significantly between natural and developed shorelines in US lakes (Bryan and Scarnecchia, 1992). Our findings may be attributable to the limited spatial extent of retaining walls and ripraps, where impacts hardly extend to the infralittoral zone. However, reed habitats were present at only two of the five sampling stations for ripraps and retaining walls (Table 7). Hence, we can not completely exclude the possibility that erosion control structures may impact infralittoral macroinvertebrate communities due to habitat loss even if we did not find significant impacts during this study.

In contrast, recreational beaches affected the infralittoral macroinvertebrate community which is likely to be attributed to the loss of all but the sand habitats. This conjecture is supported by the significant positive correlation between species richness and number of littoral habitats present at each shoreline type. The reduction of littoral habitat heterogeneity was highest at beaches and thus, macroinvertebrate species richness was lowest there.

As a common effect of all types of shoreline development, CWD was absent either due to removal from the littoral zone or due to the lack of riparian trees that prevented a CWD supply. Consequently, xylophagous species, particularly *L. phaeopa*, were nearly absent from developed shorelines. However, non-xylophagous species such as *Dreissena polymorpha* (Pallas) (Bivalvia), *Radix balthica* (L.) (Gastropoda) and *Tinodes waeneri* (L.) (Trichoptera) occurred on stone habitats at shorelines with erosion control structures in similar abundances to CWD habitats at natural shorelines. For these species, CWD may be substituted by other habitat types exhibiting similar physical characteristics, such as stones. Similarly, France (1997) concluded that most species found on CWD habitats in boreal lakes used CWD as a habitat supplying biofilm or refuge against predation rather than as a direct food resource.

Among lakes, whole-lake littoral macroinvertebrate density increased with increasing proportion of shoreline development, most likely as the result of the increasing abundances of Chironomidae in line with increases in their preferred sand habitats at recreational beaches and concrete habitats at retaining walls (Table 10). The remaining macroinvertebrate major groups decreased with increasing proportion of shoreline development indicating that shoreline development may cause a homogenisation of the macroinvertebrate community. This substantial reduction of whole-lake littoral biodiversity is most likely occurring in those lakes where shorelines have been modified to a large extent.

3.5 Implications for shoreline management

In the littoral zone of lakes, the mosaic of habitat types creates a high spatial heterogeneity which is associated with a high diversity of ecological niches and food resources. Therefore, littoral macroinvertebrate species richness, abundance and biomass are higher than in sublittoral or profundal zone (Särkkä, 1983; Czachorowski, 1993). Hence, human disturbances to the littoral zone affect a crucial biotic component of lake ecosystems whose diversity or biomass may not be substituted by communities from other lake zones. Thus, the strength of the impacts of shoreline development depended upon the extent to which habitat complexity and habitat heterogeneity are altered. Our results across lakes of different trophic state or hydrological regime indicate that the impact of shoreline development may also be applicable to other lake types. We recommend that management efforts to protect the integrity of lake ecosystems should place more emphasis on the morphological status of the littoral zone and that conservation of habitat complexity and habitat heterogeneity within the littoral zone should be a primary aim. In cases where shoreline development is inevitable, our results can be applied to weigh different types of shoreline modification or erosion protection against their biological impacts. Furthermore, our results may serve as the basis for a prediction system using indicator species with a defined response to the loss of their preferred habitat. By linking this approach with methods that focus on the assessment of the morphological status of lakeshores (e.g. Rowan et al., 2006b), lake managers would be enabled to rapidly assess the biological effects of shoreline development. The dependence of macroinvertebrate communities on the presence of certain habitat types may also be used to develop and implement site-adapted simple and cost-effective restoration measures. Specifically, artificial enhancement of habitat complexity may offer a promising strategy in urban lakes that are subjected to several types of human shoreline development.

4 Human lakeshore development alters the structure and trophic basis of littoral macroinvertebrate food webs

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(submitted to Freshwater Biology)

Abstract

The loss of littoral habitats following human lakeshore development constitutes a major threat to the ecological integrity of lake ecosystems. While effects on biodiversity are well documented, almost nothing is known about the effects of shoreline development on the structure and trophic basis of littoral food webs. Here, we compared the structure and trophic basis of macroinvertebrate food webs of natural and developed shorelines at three lowland lakes. Shoreline development was associated with a loss of littoral habitat, causing a reduction in food resource availability, and a decline in primary and secondary consumers species richness. Consequently, trophic links between consumers and food resources were lost and food web complexity was reduced by as much as four-fold at developed shorelines relative to natural shorelines. Concomitantly, the importance of allochthonous particulate organic matter and periphyton as the trophic basis of food webs decreased for developed shorelines, while the contribution of seston increased. Qualitative alterations in the trophic basis of macroinvertebrate food webs were evidenced by higher consumer-resource elemental imbalances at natural shorelines, suggesting better stoichiometric nutrient availability at developed shorelines. However, the biomass of primary consumers at developed shorelines was up to 13-times lower than at natural shorelines, indicating that augmented stoichiometric nutrient availability could not compensate for the substantial reduction in habitat, food resource, and consumer species richness. Future work is needed to elucidate whether the impacts of shoreline development on littoral food webs translate into consequences for the functioning of whole-lake ecosystems.

4.1 Introduction

Human shoreline development accompanying changes in land use and increasing housing density has increased during the last decades and constitutes a major threat to the ecological integrity of lake ecosystems worldwide (Liddle and Scorgie, 1980; Turner et al., 1996; Schindler and Scheuerell, 2002; Jennings et al., 2003; Schmieder, 2004). Shoreline development affects the littoral zone mainly through the alteration and loss of littoral habitats. For example, organic matter content of sand habitats can be substantially lower at developed than at natural shorelines, while macrophyte stands are often absent at developed shorelines (Radomski and Goeman, 2001; Elias and Meyer, 2003; Francis et al., 2007). Such effects on littoral habitat heterogeneity are intensified by clearcutting of the riparian vegetation at developed shorelines, resulting in a reduction in habitat provided by coarse woody debris (CWD) (Christensen et al., 1996; Francis and Schindler, 2006; Marburg et al., 2006). By altering community composition and reducing biodiversity, habitat loss has substantial consequences for littoral biotic communities (Jennings et al., 1999; Bertness et al., 2002; Brauns et al., 2007). However, littoral species are embedded in the lake food web and are linked to other species through trophic interactions. Hence, alterations of littoral biodiversity following human-induced habitat loss may disrupt species interactions with adverse effects on food web structure. Furthermore, the loss of littoral habitats is accompanied by the loss of the food resources they provide. For example, periphyton on CWD might be a nutritionally important food source for consumers and would be lost if CWD were lost from the littoral zone. Moreover, the littoral zone is energetically coupled to the riparian zone via allochthonous inputs of leaf litter. Leaf litter may be a crucial food resource for consumers that are dependent on detrital resources (Schindler and Scheuerell, 2002; Cole et al., 2006; Solomon et al., 2008). However, riparian clearcutting strongly reduces the input of leaf litter into the littoral zone (France et al., 1996).

The reduction of both autochthonous food resources and allochthonous inputs of organic matter may also affect the quality of food available to consumers, as reflected in their different elemental composition. For example, as terrestrial leaves and aquatic macrophytes have high C:N and C:P ratios (Duarte, 1992; Tibbets and Molles, 2005), reduced leaf litter inputs and the loss of macrophyte stands due to shoreline development may reduce C:N and C:P ratios of the detritus pool. On the other hand, the loss of macrophyte stands may be associated with a reduction in the growth of nutrient-rich periphyton and reduced sedimentation of nutrient-rich phytoplankton in the littoral zone (Duarte, 1992), resulting in an increase in the C:N and C:P ratios of available food resources.

Such alterations in the elemental composition of food resources potentially exert strong bottom-up effects on littoral consumers, such as macroinvertebrates, that maintain a fixed elemental composition (Frost et al., 2003). Hence, alterations of the elemental composition of food resources due to shoreline development may constrain the growth and reproduction of consumers when the elemental content of the food no longer matches the consumer's nutritional demand (Frost and Elser, 2002; Stelzer and Lamberti, 2002).

While several studies suggested that human shoreline development may have strong food web implications (Scheuerell and Schindler, 2004; Rosenberger et al., 2008), there are currently no published studies available that directly investigate whether and to which extent shoreline development affects littoral food webs.

In this study, we assessed the effects of shoreline development on the structure and trophic basis of littoral macroinvertebrate food webs of three North German lowland lakes. Specifically, we hypothesized that shoreline development (*i*) causes a loss of trophic links due to the loss of littoral habitats and the associated decrease in macroinvertebrate species richness, (*ii*) alters the trophic base of the macroinvertebrate food web by reducing the availability of food resources, and (*iii*) alters the elemental composition of food resources, thereby leading to a change in consumer-resource imbalances at developed shorelines.

4.2 Material and Methods

4.2.1 Sampling and sample preparation

The three study lakes, Grienericksee, Langer See, and Unteruckersee, located in the North-German lowlands (53°6'18" N, 13°51'52" E) were studied. The lakes are relatively large (surface area: 2.5-10.4 km^2), mesotrophic to hypertrophic (mean annual total phosphorus concentration: 25-168 µg L^{-1}), and have widely differing proportions of developed shorelines (9%-65%). Within each lake, we established a 100-m long sampling site at each of three shoreline types: a natural shoreline, a shoreline with a retaining wall and a recreational beach shoreline. Local beaches are created artificially by beach nourishment and local retaining walls are constructed predominantly of concrete. Sampling sites for shoreline types within each lake were located in close proximity to another to ensure that the effects of natural environmental parameters on macroinvertebrate community composition (e.g. wind exposure) would be comparable among shoreline types.

At each shoreline type within each lake, macroinvertebrates were sampled at a water depth < 1.2m from each of the habitats present in October 2005. At natural shorelines, macroinvertebrate samples were taken from the five habitats - CWD, reed, sand, stones and submerged tree roots -, except for the natural shoreline at the Langer See, which lacks the stone habitat. Macroinvertebrate samples from shorelines developed by retaining walls encompassed the habitats concrete walls, sand and stones. At beaches, macroinvertebrates were sampled from sand habitats only since no other habitats were present at these sites. To account for intra-habitat spatial variability of the macroinvertebrate community at this shoreline type, we collected two macroinvertebrate samples from sand habitats, i.e. one located at a shallow area (0.1-0.5 m water depth) and one at an incrementally deeper area (0.5-1.0 m water depth). The habitat-specific sampling procedure has been described in detail previously (Brauns et al., 2007). Briefly, we collected samples from CWD and stones by brushing off attached macroinvertebrates. Reed and root habitats were sampled using a hand net. Sand habitats were sampled using a modified Surber sampler for lentic conditions (area 0.05 m^2, 250-µm mesh). Concrete walls were sampled using a scratch net (250-µm mesh, Hydrobios, Kiel, Germany). Each habitat was sampled with 3 to 6 subsamples that were pooled in the field to create a habitat-specific composite sample. The sampled area per habitat was fixed to 0.2 m^2, i.e. the total sampled area at a natural shoreline exhibiting five habitats amounted to 1 m^2. In the laboratory, samples from each habitat from each shoreline type and lake were processed separately and macroinvertebrates were sorted, counted, identified, and kept separate for 24 h in filtered lake water to allow for gut clearance. Molluscs were removed from their shells and all macroinvertebrate species were dried at 60°C until constant weight was reached. After drying, macroinvertebrate body weight was determined by weighing 5-100 individuals of each species per habitat-specific sample to the nearest 0.01 mg.

We qualitatively sampled all potential food resources present at the shoreline types. Food resources, such as CWD, decaying leaves from riparian trees, submerged macrophytes and riparian vegetation (such as grass), were collected by hand. Samples were washed in the laboratory to remove detritus and attached invertebrates. Detritus from reed stands and sand was sampled using a sediment corer (6 cm inner diameter, Uwitec, Mondsee, Austria). The upper 1 cm of each core was extracted and stored separately in acid-washed boxes. Detritus samples were examined microscopically and invertebrates were removed from the samples. Seston samples were collected by filtering lake water through precombusted Whatman GF/C filters. Periphyton samples were brushed from solid substrates present at each shoreline type (CWD, concrete, reed and stones) into lake water previously filtered through Whatman GF/F filters.

In the laboratory, periphyton samples were processed by removing detritus and invertebrates under 20x magnification using forceps. We were unable to obtain sufficient amounts of periphyton from submerged tree roots for stable isotope analysis; we therefore used stable isotope values of periphyton from CWD from the same sampling site for root periphyton assuming that root and CWD periphyton have similar signatures. After processing, food resource samples were dried at 60 °C for 48 h.

4.2.2 Stable isotope analysis

Macroinvertebrates and food resources were ground by mortar and pestle, and Crustacea were acid treated to remove inorganic carbon that could confound the carbon isotope signatures of the body (Yamamuro and Kayanne, 1995). Usually, each macroinvertebrate sample for stable isotope analysis consisted of several individuals of the same species from the same habitat at each shoreline type and lake to obtain a sufficient amount of material for analysis and to account for intra-habitat variability. Unionid mussels were the only exception; in this case, samples for isotope analysis corresponded to individuals. The number of individuals pooled for analysis ranged from 1 to 323 (mean = 36). Subsequently, two subsamples of each macroinvertebrate (~500 µg) and food resource (2-21 mg) from each habitat at each shoreline type and lake (a total of 280 macroinvertebrate samples and 118 samples of food resources) were loaded into tin capsules. Organic carbon (C) and nitrogen (N) content and stable isotope ratios of C and N were analyzed on a Carlo Erba NC2500 elemental analyzer connected to a Finnigan MAT Delta Plus mass spectrometer at Cornell University's Stable Isotope Facility. Stable isotope data are expressed as the relative difference between ratios of samples and standard gases:

$$\delta R(‰) = \left[\left(R_{SAMPLE} / R_{STANDARD}\right) - 1\right] \times 10^3 \qquad (1)$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. $\delta^{13}C$ and $\delta^{15}N$ are the deviation (‰) of the sample from the corresponding isotope standards (PeeDee Belemnite for $\delta^{13}C$, atmospheric N for $\delta^{15}N$). Analytical precision (mean SD from in-house standard) of multiple runs was 0.08 ‰ for $\delta^{13}C$ and 0.14 ‰ for $\delta^{15}N$.

4.2.3 Food webs

We determined trophic links between consumers and food resources by estimating the contribution of a given food resource to a given consumer's diet as accurately as possible. Therefore, we did not pool stable isotope data per shoreline type, but rather analyzed the data separately for each habitat at each shoreline type and lake using mixing model analyses. This approach allowed us to constrain the number of food resources potentially assimilated by a species to those that were accessible to it in its habitat and, therefore, rarely exceeded three.

We acknowledge that this habitat-specific analysis of stable isotope data prevented us from determining the degree of error associated with small-scale spatial variability of macroinvertebrate species within a habitat. However, because our macroinvertebrate samples for stable isotope analysis were a composite sample of several individuals from the same habitat, shoreline type and lake, we accounted for intra-habitat variability even if we could not quantify it. Furthermore, several studies have demonstrated that spatial variability in macroinvertebrate $\delta^{13}C$ and $\delta^{15}N$ is smaller within a sampling site than among sampling sites (Jennings et al., 1997; Syväranta et al., 2006; Dubois et al., 2007), indicating that variability decreases with decreasing spatial scale. Consequently, spatial variability within a habitat for a given shoreline type should be small compared to the variability among shoreline types. As our sampling design accounted for both types of variability, our approach should allow for a valid assignment of food resources to macroinvertebrate consumers.

We used the concentration-weighted mixing model, IsoConc (Phillips and Koch, 2002), to estimate the relative contribution of food resources to the diets of the macroinvertebrates. In the two cases in which more than three food resources were accessible to a species, we used IsoSource software (Phillips and Gregg, 2003) with increment set at 1 % and tolerance set at 0.1 % for this purpose. For further analyses, we used the mean relative contribution of the food resources to the consumer's diet. Prior to applying mixing model analysis, macroinvertebrate consumer isotope values were corrected to account for trophic fractionation (i.e. 0.4 ‰for $\delta^{13}C$ and 3.4 ‰for $\delta^{15}N$).

The relative contribution of food resources to the diets of the macroinvertebrates were then used to refine trophic links and to analyze the trophic basis of macroinvertebrate food webs by calculating the fraction of a species' biomass derived from a food resource (C_i in mg C m^{-2}):

$$C_i = p_i \times C_{Bio} \tag{2}$$

where p_i is the relative contribution of food resource i to the diet of a macroinvertebrate species and C_{Bio}, (mg C m^{-2}) is the species-specific biomass. The contribution of a food resource to the biomass of the entire trophic level was calculated as the sum of the C_i values of all species feeding on that food resource divided by the total macroinvertebrate biomass. The trophic position of each macroinvertebrate species was estimated by relating its $\delta^{13}C$ and $\delta^{15}N$ values to a site-specific trophic baseline derived from the $\delta^{13}C$ and $\delta^{15}N$ values of all non-predatory macroinvertebrates (Vander Zanden and Rasmussen, 1999). The nine macroinvertebrate food webs constructed in this way (see Appendix II) encompassed on average 81 % (± 19) of the species and 95 % (± 7) of the biomass recorded at each shoreline type and lake, indicating that the majority of species and their biomass was covered by our food webs, even if not all species could be included.

4.2.4 Elemental imbalances

C and N content of macroinvertebrates and food resources was analyzed prior to stable isotope analyses. For total phosphorus (P) analysis, two subsamples of macroinvertebrates (1-3 mg) and food resources (1-11 mg) from each habitat at each shoreline type and lake were treated with sulphuric acid (5 M) and hydrogen peroxide (30%) at 150°C. Subsequently, total P of the samples was measured as soluble reactive P by the molybdenum-blue method (Murphy and Riley, 1962). We compared the elemental stoichiometry of macroinvertebrates and their food resources, as well as elemental imbalances among shoreline types, using scrapers and collectors, i.e. trophic groups likely to be affected by qualitative alterations of their trophic basis caused by shoreline development. In contrast to approaches that use functional feeding groups to assign a food resource to a macroinvertebrate species, we based our classification of macroinvertebrates to feeding groups on the proportion of the assimilated food resources. Thus, a macroinvertebrate species was regarded to be a scraper or collector if periphyton or detritus, respectively, contributed more than 50% of its diet. Both feeding groups assimilated seston in varying proportions in addition to their main food resource and thus, the elemental composition of the assimilated food mix had to be a weighted combination of the elemental composition of the individual food resources. To calculate the elemental composition of the food mix, we first calculated the C content of the food mix (C_{FM}):

$$C_{FM} = \sum_{i=1}^{n} C_i \tag{3}$$

where C_i is the fraction of a species' biomass derived from a food resource i (mg C m^{-2})

The N content of the food mix (N_{FM}) was calculated as:

$$N_{FM} = \sum_{i=1}^{n} C_i \times (C:N)_i^{-1} \tag{4}$$

where $C{:}N_i$ (g/g) is the C:N ratio of food resource i.

The P content of the food mix was calculated by substituting $(C{:}N)_i$ in Eq. (4) for the C:P ratio of the food resource. Subsequently, we converted C_{FM}, N_{FM} and P_{FM} into molar ratios and calculated the elemental imbalance as the difference between the elemental composition of a consumer and its food mix (Elser and Hassett, 1994).

4.2.5 Statistical analysis

We tested whether the number of food resources and the number of species in the food webs depended on the number of habitats present at each shoreline type by conducting a Spearman's correlation analysis (SPSS, Version 14, SPSS, Chicago, IL, U.S.A.). We tested for differences in the elemental composition of scrapers and collectors, their food resources, and elemental imbalances among natural and developed shorelines using Kruskal-Wallis tests followed by Dunn's multiple comparisons (GraphPad Prism, Version 4). Solid habitats that allow for the growth of periphyton and associated macroinvertebrate scraper were absent at beaches. Thus, the analysis of the elemental composition of scrapers, their food resource and corresponding elemental imbalances are restricted to comparisons of natural shorelines and retaining walls.

4.3 Results

4.3.1 Food web structure

There was a significant decrease in the number of species in the food webs (Spearman's $\rho = 0.84$, $P = 0.005$, $n = 9$), as well as a significant decrease in the number of available food resources (Spearman's $\rho = 0.94$, $P < 0.001$, $n = 9$) with decreasing number of habitats present at the shoreline types (Table 11). Consequently, the number of trophic links was highest at natural shorelines; on average, the number of trophic links was two times lower at retaining walls and four times lower at beaches (Table 11). This substantial reduction in food web complexity was especially apparent at the Langer See, where the beach food web consisted only of Chironominae (Diptera) and *Unio tumidus* Philipson (Bivalvia), which fed on detritus and seston (Fig. 3B; Appendix II). The average number of secondary consumers (trophic level 3) was highest at retaining walls, followed by natural shorelines whereas secondary consumers were absent at beaches (Table 11). Trophic level 3 was mainly represented by predatory *Erpobdella octoculata* (L.) (Hirudinea), which occurred on stone habitats at natural shorelines (Fig. 1A; Appendix II) and at retaining walls (Fig. 2B, C; Appendix II), and by *Platambus maculatus* (L.) (Coleoptera), which was restricted to root habitats at the natural shoreline of the Grienericksee (Fig. 1A; Appendix II).

4.3.2 Trophic basis of food webs

Contributions of food resources to macroinvertebrate biomass at natural shorelines varied substantially among the lakes. For instance, the contribution of seston to trophic level 1 biomass of was more than three times higher at the Langer See and more than two times higher at the Unteruckersee than at the Grienericksee (Table 12). This was mainly due to the invasive filter feeder *Dreissena polymorpha* (Pallas) (Bivalvia), which was absent at the Grienericksee but contributed substantially to biomass at the other lakes, particularly at the Langer See. Hence, to allow for a better comparison among lakes, we removed *D. polymorpha* from this analysis.

At the Grienericksee natural shoreline, trophic level 2 and 3 biomass was mainly derived from periphyton (Fig. 8A, Table 12). Allochthonous POM only marginally contributed to the biomass of trophic level 2 but comprised 29 % of trophic level 3 biomass. At the retaining wall, trophic level 2 biomass was mainly derived from seston, to a lesser extent from periphyton, and allochthonous POM was absent there. The beach food web at the Grienericksee was almost entirely based on seston, which contributed 88 % of the macroinvertebrate biomass. In contrast to natural shorelines, periphyton did not contribute to macroinvertebrate biomass because solid habitats that allow for periphyton growth were absent (Fig. 8A).

At the Langer See natural shoreline, the food web was mainly based on seston and periphyton, which contributed 59 % and 36 %, respectively, to trophic level 2 biomass (Fig. 8B, Table 12). At the retaining wall, the contribution of periphyton to biomass was higher and the contribution of seston was lower than at the natural shoreline. Similar to the Grienericksee, trophic level 2 biomass at the Langer See beach food web was mainly derived from seston, and periphyton did not contribute to biomass (Fig. 8C, Table 12).

At the Unteruckersee natural shoreline, more than 50 % of trophic level 2 biomass was derived from detritus (Fig. 8C, Table 12). There were no apparent differences between the food webs of the natural shoreline and the retaining wall. However, the contribution of detritus to trophic level 2 biomass at the beach at the Unteruckersee was higher than at the natural shoreline (Fig. 8C, Table 12).

The elemental composition of scrapers and collectors did not differ significantly between natural and developed shorelines (Table 13). In contrast, C:N and C:P ratios of the food mix of scrapers were significantly lower at retaining walls than at natural shorelines. Accordingly, C:P and C:N imbalances between scrapers and their food were significantly lower at retaining walls than at natural shorelines. We found significantly lower C:P ratios in the food mix of collectors at developed shorelines than at natural shorelines. Hence, C:P imbalances between collectors and their food were significantly lower at retaining walls and at beaches than at natural shorelines (Table 13).

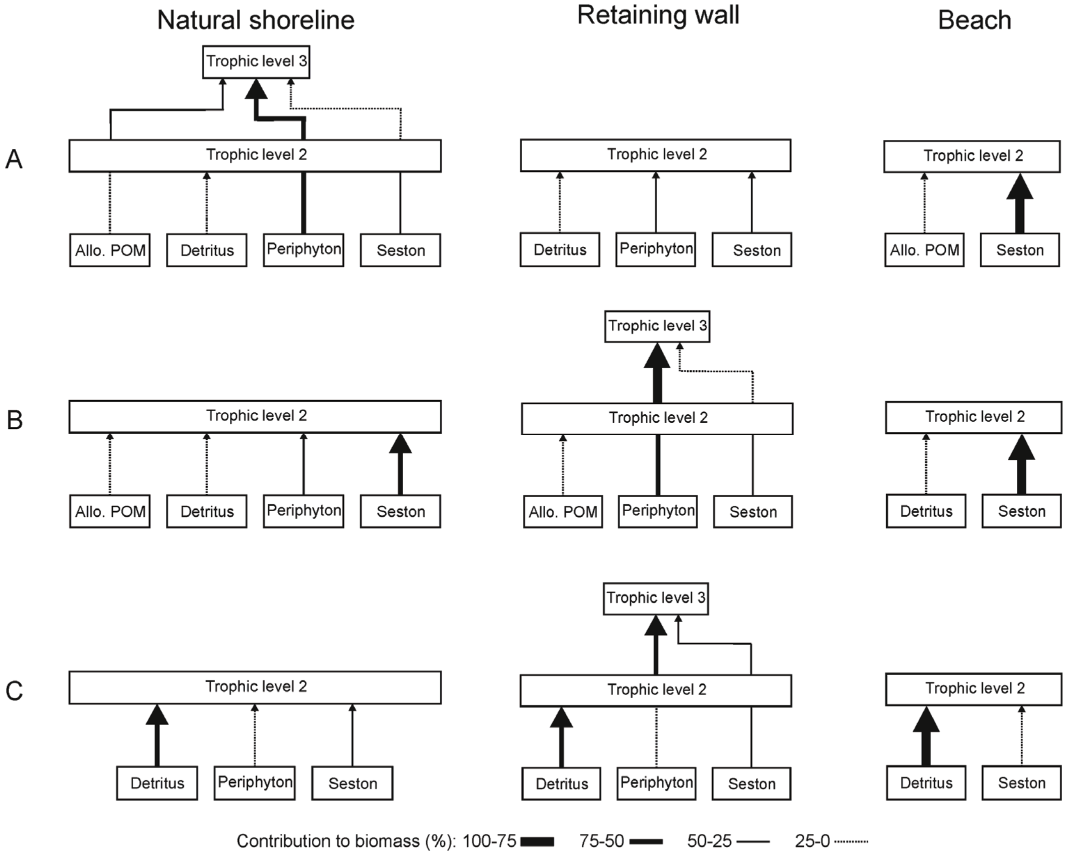

Fig. 8. Summarized food webs of natural shorelines, retaining walls and beaches at the (A) Grienericksee, (B) Langer See and (C) Unteruckersee. Line thickness corresponds to the percentage contribution of the food resources to the biomass of trophic levels. Contributions to biomass were calculated excluding *Dreissena polymorpha* (Bivalvia) to allow for comparisons among lakes. See text for further explanation and Table 12 for contributions to biomass including *D. polymorpha*. Highly resolved food webs are presented in Appendix II.

4.4 Discussion

Our study reveals that anthropogenic development of lakeshores and the associated loss of littoral habitats substantially affect both the structure of littoral macroinvertebrate food webs and the transfer of organic matter through these food webs. In accordance with our first hypothesis, food web complexity declined with decreasing habitat diversity of shoreline types, reflecting a significant relationship between the number of habitats present at a shorelines type and both species richness and number of available food resources. Hence, with decreasing habitat diversity, trophic links between macroinvertebrate consumers and their food resources were lost, leading to simplified macroinvertebrate food webs at developed shorelines.

This relationship was especially apparent at recreational beaches where macroinvertebrate food web complexity, in terms of number of trophic links, was four times lower than at natural shorelines due to the loss of all but the sand habitat. Food web simplification was also apparent at higher trophic levels, as predator species were absent at beaches. Retaining walls did harbour predator populations even though food web complexity was low compared to natural shorelines. This observation contrasts with results from food web models, which show that species at higher trophic levels are among the first to disappear if habitats are lost (Kareiva, 1987; Melian and Bascompte, 2002; Ryall and Fahrig, 2006). In our study, *E. octoculata* and *P. maculatus* were the most common predator species inhabiting natural shorelines and shorelines developed by retaining walls. *P. maculatus* commonly inhabits spatially complex habitats, such as tree roots (Hendrich, 2003) and is indeed among the first species to become extinct if such habitats are lost from the littoral zone. In contrast, *E. octoculata* can inhabit any kind of solid habitat (Mann, 1953) and persists as long as such habitats remain, suggesting that the extinction threshold of macroinvertebrate predators in lakes is determined by the degree of species-specific specialization to a habitat.

The loss of food resources following habitat loss was also reflected in alterations of the trophic basis of macroinvertebrate food webs. Although resource use by macroinvertebrate consumers varied among lakes, seston and periphyton were consistently the most important trophic resources at natural shorelines while the contribution of allochthonous POM to the biomass of primary consumers was comparatively small. This minor contribution was surprising given that allochthonous carbon can contribute up to 85 % to macroinvertebrate secondary production in small lakes (Cole et al., 2006). The low contribution of allochthonous POM can be attributed to the fact that most trophic links from allochthonous POM were to species with low biomass (Fig 1A; Appendix II). For instance, at the natural shoreline at the Grienericksee, 11 % of the biomass was derived from allochthonous POM through 12 links to ten species. However, these ten species accounted for only 20 % of total biomass at this site, hence the low contribution of allochthonous POM to the biomass of primary consumers. Allochthonous POM did not contribute to macroinvertebrate biomass at the Unteruckersee natural shoreline, despite evidence for sufficient entry of allochthonous POM (e.g. terrestrial leaves) at this site. However, the natural shoreline at the Unteruckersee is highly exposed to wind, so it is possible that these allochthonous POM entries are exported from that site before an efficient processing by macroinvertebrate consumers takes places.

In contrast to its contribution at natural shorelines, allochthonous POM did not contribute to primary consumer biomass at retaining walls, thus; trophic links from allochthonous POM to secondary consumers at retaining walls were absent. Here, the removal of the riparian vegetation prevented a sufficient supply of allochthonous POM to the littoral zone. Conversely, allochthonous POM at the natural shoreline at the Grienericksee propagated up the food web and contributed 29 % to the biomass of secondary consumers. The complex root habitat present at his site provided refuge for *P. maculatus* against predation by fish and concurrently allowed opportunities to prey upon macroinvertebrates that were themselves reliant on allochthonous POM.

The alteration of the trophic base of macroinvertebrate food webs was particularly apparent at beaches. Beaches lack solid habitats that enable periphyton growth, and thus, periphyton did not contribute to macroinvertebrate biomass. Instead, two of the three studied food webs at beaches derived their carbon almost entirely from seston, while autochthonous detritus was the primary source of carbon for the beach food web at the Unteruckersee.

No significant differences were found in the elemental composition of scrapers and collectors among shoreline with respect to their elemental stoichiometry (Frost et al., 2003). However, C:P elemental imbalances between scrapers and their food were significantly lower at retaining walls due to significantly lower food C:P ratios at retaining walls than at natural shorelines. Because periphyton comprised the largest proportion of the food mix of scraper, the lower food C:P ratios at retaining walls are likely attributable to lower periphyton C:P at retaining walls than at natural shorelines (Table 1; Appendix I). Lower periphyton C:P at retaining walls could be the result of P inputs associated with lawn fertilization or surface run-off from impervious surfaces at retaining walls. Alternatively, the loss of CWD and reed and their replacement by concrete and stones as surfaces for periphyton growth at retaining walls could also have lead to an alteration of periphyton community composition and an associated decrease in periphyton C:P relative to natural shorelines. Periphyton communities on organic substrates may have higher bacterial biomasses, which could explain the high C:P ratio of periphyton at natural shorelines (Frost et al., 2005).

A similar pattern was observed for collectors, which showed significantly lower C:P imbalances at developed shorelines than at natural shorelines. The overall higher C:P imbalances at natural shorelines suggest that stoichiometric P availability was lower at natural shorelines than at developed shorelines. Conversely, better stoichiometric P availability at developed shorelines should have led to higher consumer biomass, especially as fast growing species with a high P demand may benefit from better nutrient availability (Elser et al., 2003; Fink and Von Elert, 2006). Arguing against this supposition is the fact that, on average, the biomass of primary consumer was three-times lower at retaining walls and seven-times lower at beaches than at natural shorelines (Table 11). Coincident with the low macroinvertebrate biomass at developed shorelines, potentially fast-growing primary consumers, such as *A. lacustris* and *R. balthica*, were largely absent, while other taxa, such as Chironominae, exhibited little increase in biomass (Figs. 2, 3; Appendix II). Thus, the beneficial effects of better nutrient availability on macroinvertebrate consumer biomass were counteracted by the reduction in consumer species richness, suggesting that nutrient-rich food resources at developed shorelines may have been largely unutilized.

In conclusion, we demonstrated that shoreline development substantially reduced the diversity of littoral habitats, with subsequent effects on the availability of food resources and species diversity. This caused a substantial loss of trophic links between macroinvertebrate consumers and food resources, resulting in food webs with up to four times lower complexity. The restricted availability of food resources at developed shorelines also resulted in an alteration of the trophic basis of the studied food webs with substantially more biomass derived from seston at developed shorelines than at natural shorelines. Qualitative alterations in the trophic basis of the studied food webs were apparent in consumer-resource imbalances, which were highest at natural shorelines, suggesting better stoichiometric nutrient availability at developed shorelines. However, consumer biomass at developed shorelines was up to 13 times lower, indicating that better stoichiometric nutrient availability could not compensate for the substantial reduction in habitats and food resources, and the associated reduction in consumer species richness.

Our results do not allow for a precise quantification of the consequences that shoreline development may have on larger, ecosystem-wide scales. However, most developed lakes are situated in densely populated regions where retaining walls and beaches often represent the dominant shoreline type (Ostendorp et al., 1995; Schindler et al., 2000; Ostendorp et al., 2004). Hence, it seems very likely that whole-lake macroinvertebrate biomass may be substantially reduced in such lakes. Given that benthic pathways play a crucial role in the transfer of organic matter within lake food webs (Vadeboncoeur et al., 2002; Vander Zanden et al., 2005; Vander Zanden et al., 2006), anthropogenic alterations of littoral macroinvertebrate food webs can be expected to have substantial ecosystem-wide consequences. Future studies on the effects of lakeshore development should adopt a holistic approach by including estimates of effects on fish and macroinvertebrate community production, as well as a quantification of matter fluxes between trophic compartments under different development scenarios. Such ecosystem-functioning orientated approaches would allow for the identification of trophic keystone species whose loss might have substantial effects on the transfer of organic matter through food webs. Hence, such analyses could be used to forecast functional consequences and could serve as a tool for developing appropriate conservation measures to prevent or mitigate impacts of human shoreline development on the functioning of lake ecosystems. Even without these more extensive studies, our current results suggest that the restoration of habitat diversity may be the most promising strategy for mitigating the adverse effects of human shoreline development on lake ecosystem function.

5 Potential effects of water level fluctuations on littoral invertebrates in lowland lakes

Mario Brauns, Xavier-François Garcia & Martin T. Pusch

(Hydrobiologia 613: 5-12)

Abstract

East-German lowland lakes are highly susceptible to climatic changes, as most lakes are groundwater fed and strongly depend on the balance of precipitation and evapotranspiration in their catchments. As a significant decrease of precipitation at least during summer is forecasted, a substantial and permanent reduction of lake water levels can be expected. Water level fluctuations will predominantly affect the eulittoral zone where submerged tree roots form an important habitat type in lowland lakes that will become unavailable for eulittoral invertebrates. Hence, we compared the invertebrate community from eulittoral root habitats with those of infralittoral habitats to test which components of the invertebrate community would be potentially affected by the loss of root habitats, and whether infralittoral habitat types could mitigate these effects. Species richness did not significantly differ between eulittoral roots and the infralittoral habitat types. Community composition of roots significantly differed from that of coarse woody debris (CWD), sand and stones but not from reed habitats. Abundances of Coleoptera, Trichoptera, and abundances of piercer, predator, shredder and xylophagous species were significantly lower on sand than on roots. Conversely, there were no significant differences in community measures between reed and root habitats except abundances of Coleoptera. Our results suggest that the loss of eulittoral root habitats will cause a significant alteration of the littoral invertebrate community. This could be mitigated if unimpaired reed habitats are available in the infralittoral zone which may serve as a refuge for most species typical for root habitats. Our results need to be verified by direct observations especially as the extent of future water level fluctuations is currently not assessable and might be more severe than assumed.

5.1 Introduction

According to current knowledge, the average air temperature in central Europe will increase by 3 to 5 C within the next century, depending on the future emissions of greenhouse gases (Intergovernmental Panel on Climate Change, 2001). Air temperature has already increased by up to 1°C in the time period 1891-1990 in East Germany (Belke et al., 2003). Concomitantly, annual precipitation has slightly decreased by 50 mm/year in major parts of East Germany within the time period from 1961 to 1990 (Belke et al., 2003). For the Federal state of Brandenburg, a rise in air temperature of 1.4°C by the year 2055 and a reduction of annual precipitation of up to 200 mm is predicted, which will mainly occur during summer (Potsdam Institut für Klimafolgeforschung, 2003). Thus, the sub-continental features of the climate will get more prominent. This will cause dramatic changes in regional hydrological budgets, with associated consequences for agriculture, forestry and water management (Potsdam Institut für Klimafolgeforschung, 2003). The expected alteration of the hydrological regime may severely affect lowland lakes in the eastern part of Central Europe as their water level is strongly dependent on the groundwater level that in turn shows sensitive response to the precipitation regime. Hence, the forecasted reduction of annual precipitation and increasing of air temperatures may lead to a substantial reduction of mean water levels in groundwater supplied lakes. Moreover, the increased evapotranspiration in the catchments and a relative shift in precipitation towards winter may lead to higher amplitudes of seasonal water level fluctuations. Hence, water level fluctuations are expected to become a strong anthropogenic component in the function of lowland lakes in the Eastern part of Central Europe. Most of the existing knowledge on the effects of human altered hydrological regimes is derived from studies on reservoirs or regulated lakes, where water level fluctuations up to 20 m can occur (e.g. Smith et al., 1987). There, water level fluctuations were demonstrated to affect the shore zone of reservoirs directly by desiccation and bottom freezing (Hynes, 1961; Palomaki and Koskenniemi, 1993) but also to affect the littoral food web by the loss of food resources such as macrophytes (Wilcox and Meeker, 1991; Wilcox and Meeker, 1992; Hill et al., 1998). Benthic invertebrates are the biotic component of lake shores that are most severely affected by these alterations since their low mobility restricts their ability to follow the receding water. Consequently, in reservoirs and regulated lakes, invertebrate richness and abundance was lowest in the eulittoral zone and highest within the sublittoral zone below the drawdown limit (Smith et al., 1987; Koskenniemi, 1994; Palomaki, 1994). In lakes characterised by natural water level fluctuations, the amplitude of the fluctuation is smaller and follows a more regular seasonal pattern. There, the highest invertebrate diversity and biomass is found in eulittoral and infralittoral zones of lakes (Czachorowski, 1989; Czachorowski, 1993). Thus, increasing water level fluctuations would cause a loss of eulittoral habitats with associated impacts on eulittoral invertebrates as a crucial biotic component of lake ecosystems. In this study, we examined the potential effects of water level fluctuation on the eulittoral invertebrate community of six East-German lowland lakes. We compared invertebrate communities from eulittoral root habitats with those from four infralittoral habitats to test which components of the invertebrate community would be affected by the loss of the root habitats, and whether the infralittoral habitat types could mitigate these effects.

5.2 Methods

5.2.1 Invertebrate sampling

The six studied lakes are located in East Germany and cover different lake types, i.e. hypertrophic riverine lakes and groundwater supplied mesotrophic lakes (Table 14). Invertebrates samples were taken from the five major habitat types in East-German lowland lakes, i.e. roots within the eulittoral zone (0 - 0.2 m water depth) and coarse woody debris (CWD), reed, sand and stones within the infralittoral zone (0.2 - 1.2 m water depth). Sampling was conducted in October 2003 and in April 2004 on a total of 40 sampling stations (eight per habitat type). Each habitat type was sampled separately using the sampling technique best adapted to the degree of structural complexity of the habitat. This should ensure a maximum of sampling efficiency and allows for a comparison of samples from different habitat types. We took five subsamples from submerged roots of riparian alder trees (*Alnus glutinosa*) with a hand net (250-µm mesh, 24 cm width), and estimated the sampled area by multiplying hand net width with the respective sampling depth. Invertebrates from CWD habitats were brushed from three pieces of CWD with comparable states of decay, and subsamples were sieved trough a mesh (250 µm). Subsequently, length and diameter of each piece of CWD was measured, and surface area was calculated assuming a cylindrical shape. We took five 1 m sweeps from reed habitats using a hand net (250-µm mesh, 24 cm width). We estimated the sampled area of reed habitats by multiplying hand net width with length of the sampled area. Sand habitats were sampled with 10 subsamples using a modified Surber sampler for lentic conditions (area 0.05 m², 250 µm mesh). For stone habitats, we randomly chose ten stones from each sampling station and brushed off attached invertebrates. From each stone, surface area was calculated based on its length, height and width assuming an ellipsoid shape. Subsequently, subsamples from each habitat type were pooled to create a composite sample per habitat type. Samples were preserved in the field and invertebrates were identified in the laboratory to species level.

Chironomidae and Oligochaeta could only be determined to family or order level, respectively, and were omitted from further analyses because information on their ecological traits, e.g. functional feeding groups, are imprecise on these taxonomic levels (Lenat and Resh, 2001). Similarly, non-indigenous species *Dreissena polymorpha* (Pallas, 1771) Bivalvia, *Atyaephyra desmaresti* (Millet, 1831), *Chelicorophium curvispinum* (Sars, 1895), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Dikerogammarus villosus* (Sowinsky, 1894), *Echinogammarus ischnus* (Stebbing, 1906), *Gammarus tigrinus* Sexton, 1939, *Pontogammarus robustoides* (Sars, 1894) (Crustacea), and *Potamopyrgus antipodarum* (Gray, 1843) (Gastropoda) were excluded from further analyses as their occurrence is mainly independent from habitat type (Van den Brink et al., 1993; Devin et al., 2003) and their dominance could supersede compositional differences among habitats that are related to native species. Information on invertebrate functional feeding groups was taken from Schmedtje and Colling (1996).

5.2.2 Statistical analysis

Since sampling techniques for the different habitat types were not fully comparable, we converted species densities into relative abundances. Prior to analyses, we tested whether there are differences in the invertebrate community measures from autumn and spring using non-parametric Mann-Whitney test (SPSS, Version 9.0, SPPS Inc., Chicago, U.S.A.). Since from 19 community measures only percentages of Gastropoda, Heteroptera, Scrapers, and Parasites were significantly different between seasons, we pooled the data from autumn and spring. We used non-metric multidimensional scaling (NMS) and analysis of similarity (ANOSIM, PRIMER, Version 5, Primer-E Ltd., Plymouth, U.K.) to test for differences in community composition between eulittoral root and the four infralittoral habitat types using Bray-Curtis similarity as the distance measure. ANOSIM is based on the assumption that if the community composition of two habitat types significantly differs, the similarities between habitats should be lower than the similarities within a habitat. This is expressed by the R-statistic, which ranges from zero to one, where $R = 1$ if all replicates of a habitat type are more similar to each other than to any replicate from the other habitat type. Indicator species for each habitat type were defined using the indicator species analysis (Dufrene and Legendre, 1997) (PcOrd, Version 4.25, MjM Software, Gleneden Beach, OR, U.S.A.) where indicator values close to zero means no indication and indicator values close to 100 means perfect indication of a habitat type by a species (Dufrene and Legendre, 1997). Differences in species richness, relative abundance of major taxonomic and functional feeding groups between roots and the four infralittoral habitat types were tested with non-parametric Mann-Whitney tests (SPSS, Version 9.0) using Bonferroni correction to adjust the level of significance of the pairwise comparisons.

5.3 Results

Non-metric multidimensional scaling (NMS) ordination of the invertebrate community of root and the four infralittoral habitats revealed strong compositional differences (Fig. 9). NMS ordination of root and CWD samples showed that both habitat types were colonised by distinct communities (Fig. 9A) that significantly differ from each other (ANOSIM: R-statistic = 0.37, $P = 0.001$). Similarly, invertebrate communities significantly differed between root and sand (ANOSIM: R-statistic = 0.65, $P = 0.001$, Fig. 9C), and between root and stones (ANOSIM: R-statistic = 0.49, $P = 0.001$, Fig. 9D). NMS ordination of the invertebrate communities of root and reed revealed that samples from both habitat types strongly overlap (Fig. 9B). Consequently, ANOSIM did not detect significant differences between communities of both habitat types (R-statistic = 0.05, $P = 0.241$). Median invertebrate richness (range) ranged from 22 (9-37) on sand habitats to 15 (13-28) on stone habitats, but did not significantly differ between roots (21, 14-52) and any of the infralittoral habitat types (Mann Whitney test, $P > 0.05$). Conversely, differences between eulittoral root and the four infralittoral habitats were apparent in the abundances of the major taxonomic groups. Here, the strongest differences were found for Coleoptera as well as for Odonata, Ephemeroptera and Trichoptera (Table 15). For example, the abundance of Coleoptera was highest in the root habitat and significantly lower in reed, sand and stone habitats. Abundances of Odonata were highest in root habitats but they were absent within the infralittoral zone from all but the reed habitats (Table 15). The abundance of Ephemeroptera was significantly lower on CWD than on roots, and abundance of Trichoptera was significantly lower on sand than on root habitats. Distinct indicator species were found in roots, CWD, sand and stones (Table 16). For example, the dragonfly *Ischnura elegans* Vander Linden, 1820 and the water beetle *Haliplus flavicollis* Sturm, 1834 were highly indicative for root habitats while sand habitats were particularly characterised by species of the genus *Pisidium* (Bivalvia) (Table 16). No indicator species were found for reed habitats.

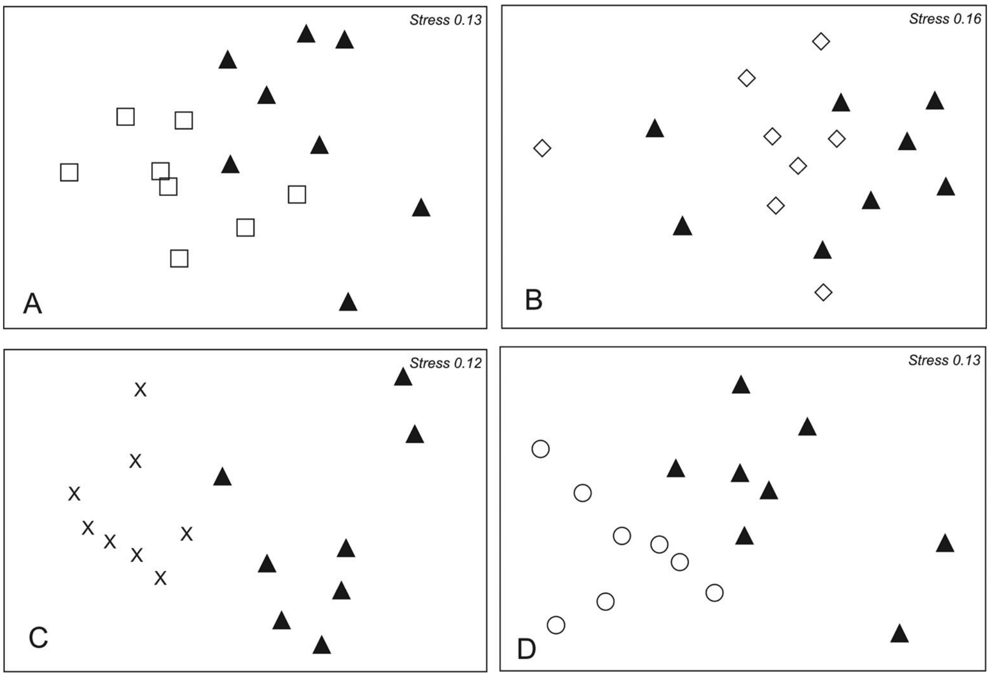

Fig. 9. Non metric multidimensional scaling (NMS) ordination of the invertebrate community of roots (triangles) together with the invertebrate community of (A) coarse woody debris (squares), (B) reed (diamonds), (C) sand (crosses) and (D) stone habitats (circles).

Major differences in the functional feeding group composition between eulittoral roots and the four infralittoral habitat types were found for sand habitats (Table 17). Here, relative abundances of piercer, predator, shredder and xylophagous species were significantly lower than on the roots habitats. Furthermore, abundances of shredder were significantly lower on all but the reed habitats (Table 17).

5.4 Discussion

Species richness did not differ between the five studied habitat types, indicating that all habitat types similarly contributed to the local biodiversity. However, invertebrate community composition differed significantly between roots and all but the reed habitat. Particularly, Coleoptera and Odonata were found in high abundances in roots, while their abundances were lower in the infralittoral habitats. This suggests that Coleoptera and Odonata are the components of the invertebrate community that will be most severely affected by increasing water level fluctuations and that a loss of root habitats may lead to the disappearance of species in both taxonomic groups.

The strongest differences in the examined community parameters were found between root and sand habitats. Despite a similar level of species richness, both communities differed significantly and were characterised by indicator species that primarily reflect the physical properties of the habitat types. For example, roots constitute a 3-dimensional structured habitat that provides niches for large bodied species of Coleoptera and Odonata, while structurally uniform sand habitats were dominated by small Bivalvia such as *Pisidium*. Furthermore, root habitats provided various food resources such as periphyton or CPOM as indicated by the dominance of scrapers and collector/gatherers while functional feeding group composition on sand was dominated by filter feeders that rely on seston. In the littoral zone of several U.S. lakes, periphyton production accounted for 98 % of the whole lake primary production (Vadeboncoeur et al., 2003), and carbon derived from this food resource was used by species of subsequent trophic levels. Hence, an extreme drawdown of the water level that would be paralleled by the loss of all but the sand habitats would disrupt a major pathway of carbon in the littoral zone of lakes. This conjecture is supported by studies on an U.S. reservoir, where strong water level fluctuations caused a shift of food resources of invertebrates from benthic derived carbon to pelagic derived carbon (Black et al., 2003). Hence, sand habitats may not substitute root habitats if an alteration of the hydrological regimes would cause a receding water level within the studied lakes. In contrast to sand habitats, community composition of reed did not significantly differ from that of root habitats. Despite differences in the abundance of Coleoptera, none of the major taxonomic groups found in the root habitats was completely absent in the reed habitat, most likely as the result of a comparable degree of habitat complexity compared. Hence, dense reed habitats may substitute the loss of the root habitats. However, reed stands are subjected to various kinds of human impairments such as wave disturbance or eutrophication that reduces their stem density (Ostendorp et al., 1995). Consequently, the ability of reed habitats to substitute the loss of root habitats could be limited in lakes with significant human impacts on the lake shore.

In summary, we demonstrated that submerged roots of riparian trees constitute an important habitat in the littoral zone colonised by a distinct invertebrate community. However, eulittoral root habitat may fall dry for extended time periods if water level fluctuations increase as predicted for East and Central Europe. The loss of root habitats could partially be substituted by a dense infralittoral reed stand, which seems to offer similar habitat conditions. However, total habitat area available for the species found in root and reed habitats will be clearly reduced at lowered water levels. Conversely, CWD, stone and especially sand habitats may not provide an appropriate substitute habitat due to their limited habitat complexity. Our results on the potential effects of water level fluctuations on littoral invertebrates have to be verified by further studies, especially as the amplitude of future water level fluctuations is currently not assessable and might more be severe than assumed.

6 Resistance to ship-induced waves of benthic invertebrates in various littoral habitats

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(Freshwater Biology 53: 1567-1578)

Abstract

1. Ship-induced waves disturb benthic invertebrate assemblages colonising littoral zones of lakes and rivers. However, the impact of ship-induced waves on invertebrates has rarely been quantified, and the influencing factors have not been addressed.
2. In an experimental wave tank, five benthic invertebrate species, *Bithynia tentaculata, Calopteryx splendens*, *Dikerogammarus villosus, Gammarus roeseli* and *Laccophilus hyalinus*, were exposed to waves of increasing shear stress (0.43 to 2.19 N m^{-2}). Mean number of detached individuals was recorded for five littoral habitats [coarse woody debris (CWD), reeds, sand, stones, and tree roots), representing different levels of structural complexity as quantified by their fractal dimensions.
3. Results showed that detachment of invertebrates was significantly related to shear stress in all habitats except tree roots. Detachments averaged for the five species were significantly lower in habitats with a high degree of structural complexity, decreasing in the habitat sequence: sand, coarse woody debris, stones, reeds and tree roots.
4. Consistent with their different morphologies and methods of attachment to substrates, the five species displayed difference in their responses to hydraulic stress that were dependent on habitat.
5. The increasing sheltering effect of structural habitat complexity was mirrored by increasing dissipation of the kinetic energy of waves; i.e. the fractal dimension of the habitat was positively correlated with shear stress reduction due to the flow resistance of the habitat.
6. Network habitats such as tree roots provided the best sheltering conditions against hydraulic disturbance, because they combined good refuge availability for all studied invertebrate species and maximal dissipation of kinetic wave energy. Consequently, persistent anthropogenic impacts, such as lakeshore modification or long-term exposure to ship-induced waves, which cause disappearance of complex littoral habitats such as tree

roots or dense reed belts, will drastically increase the adverse effects of boating and ship traffic on littoral invertebrate assemblages.

6.1 Introduction

Wind-induced waves are a key determinant of habitat conditions at wind-exposed shores of lakes. Wind exposure maintains stony bottoms by preventing sediment accumulation (Brodersen, 1995; James et al., 1998; Tolonen et al., 2001), which generally favours high diversity and abundance of benthic invertebrates (Cardinale et al., 1997; Abdallah and Barton, 2003). Ship-induced waves produced by freight barges, passenger ships and recreational boats constitute a major additional hydraulic disturbance for invertebrates in the littoral zones of lakes, rivers and canals used as inland waterways. Although organisms at wind-exposed shores may be adapted to a regime of strong hydrodynamic forces, ship-induced waves are characterised by strong amplitudes and short-term increase of flow velocity (Bhowmik and Mazumder, 1990; Rodriguez et al., 2002) and boat wakes can introduce waves to otherwise sheltered habitats where organisms are poorly adapted to hydrodynamic forces.

Very few published studies have documented the impact of ship-induced waves on shore assemblages. Studies of estuarine invertebrates have indicated that hydrodynamics regime and not sediment characteristics drive differences between invertebrate assemblages of wash and no-wash zones (Bishop and Chapman, 2004; Bishop, 2004; Bishop, 2007). Bishop (2003; 2005) found lower abundances of gastropods and amphipods on sea grass blades exposed to ship-induced waves, and suggested that invertebrates were detached by the flapping of the blades as wave propagates. In the littoral zone of navigable rivers, ship-induced waves evidently constitute a major impact on macroinvertebrate communities (Brunke et al., 2002; Garcia et al., 2006) and on young fish (Holland, 1986; Wolter and Vilcinskas, 1997; Arlinghaus et al., 2002; Wolter and Arlinghaus, 2003). Mainly, organisms are expected to be relocated, but also to suffer from mechanical injuries caused by shear stress, increased expenditure of metabolic energy for swimming, oxygen depletion due to sediment resuspension and increased risk of predation.

However, little is known about potential thresholds in the response of littoral invertebrates to anthropogenic wave disturbances of increasing shear stress, or about the interaction with habitat properties. In particular, the factors influencing the extent to which invertebrates are detached by waves in specific littoral habitats have never been addressed. The only published evidence comes from a related case with stream invertebrates exposed to continuous flow in flume experiments, which demonstrated that current-induced drift of lotic invertebrate species increased with increasing flow velocities (Borchardt, 1993; Imbert and Perry, 1999), and that the proportion of drifting individuals decreased when woody debris was added to a sand habitat (Borchardt, 1993).

As the global navigation network constantly expands (see Revenga et al., 2000), and recreational boating increases, quantitative information about the impacts of ship-induced waves is urgently needed to develop scientifically-based recommendations for shoreline management in navigable water bodies. We therefore investigated the resistance of invertebrates to ship-induced waves in relation to the structural complexity of littoral habitats. Five benthic macroinvertebrate species, representing a spectrum of body morphologies and attachment strategies, were successively exposed to waves of increasing shear stress in five habitats exhibiting different structural complexity. We hypothesized that (i) the proportion of detached individuals depends on the level of shear stress associated with the wave; (ii) the proportion of detached individuals also depends on species-specific adaptations to certain habitats, and (iii) the number of detached individuals decreases with greater habitat structural complexity.

6.2 Material and Methods

6.2.1 Experimental system

Experiments were conducted in an experimental wave tank 3.0 m long, 0.80 m wide and 0.60 m deep made of 10 mm thick Perspex panels (Fig. 10). Waves of different shear stress were produced with a flap wave maker (Dean and Dalrymple, 1984), by varying the water level in the wave tank and the weights used to move the flap-plate.

In the observation area, two removable plastic trays each of 0.115 m² area and filled with sand, were placed side by side, in which the various habitats were exposed to waves. At the far end of the tank a slope with an angle of 20° and a discharge basin covered by a net were added to prevent reflection of the waves against the tank wall. The net collected invertebrates that were flushed from the observation area by the wave. Sand was glued on the plates 40 cm in front and behind the habitat trays to avoid any hydraulic perturbations in the study area due to changes in roughness along the wave route.

Hydrodynamic characteristics of the waves were measured by electronic devices installed in front of the habitat trays on the right side of the tank. Wave height was recorded with an acoustic wave sensor (UltraLab USS2001300, General Acoustics, 20 Hz recording, Kiel, Germany) located 50 cm above the water level. Flow velocity was recorded using an Acoustic Doppler velocimeter (Micro ADV 16 MHz, Sontek, 50 Hz recording, San Diego, CA, U.S.A.) with the sampling volume positioned 1 cm above the flow bed. This location was the closest location to the bottom allowed by the technical characteristics of the ADV for measurements of flow velocities faced by invertebrate species. We assumed that bottom boundary layer is thinner than the body height of the flattest invertebrate species studied so that flow velocities measured by the ADV are those really faced by invertebrates. The proportion of benthic invertebrates disturbed by the experimental waves was assessed by counting the number of individuals detached from the habitat, using video records from two cameras located on the top and on the right side of the study area (Fig. 10).

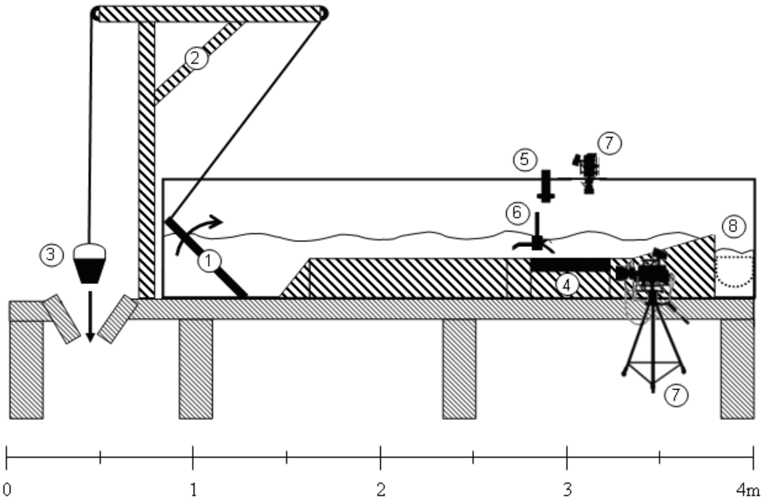

Fig. 10. Sketch of the experimental wave tank. Wave maker system: flap-plate (1), gibbet (2), bucket with varying-weight (3). Observation area: removable habitat trays (4), acoustic wave sensor (5), acoustic Doppler velocimeter (6), video camera (7), discharge basin with net (8)

6.2.2 Shear stress calculation

The bottom shear stress τ (N m^{-2}) caused by the wave at the location of the habitat trays was calculated as:

$$\tau = 0.5 f \rho U_b^2 / 10$$

where ρ is the density of water (1 g cm^{-3}), U_b (cm/s) is maximum wave orbital velocity (measured by the ADV) and f is the wave friction factor. The null values recorded for the vertical and lateral components of the maximum wave orbital velocity indicated that the flow in the wave tank was unidirectional.

In addition, Reynolds numbers for the experimental flow calculated as

$$\mathrm{Re} = \frac{ul}{v}$$

where u is the maximum wave velocity behind the different habitats (maximum 43 cm s^{-1}), l is defined as the wave amplitude (Dyer, 1986) (maximum 4 cm) and ν is water viscosity (~0.01 cm^2 s^{-1}), were about 10^4, which is one order of magnitude lower than the critical value reported by Jensen (1989) for turbulent flows on smooth beds. Hence, shear stress at the front of the habitat tray was mainly produced by mean flow since according to calculated Reynolds numbers, no significant turbulences were generated. Consequently, the wave friction factor was calculated according to the formula given by Dyer (1986) for laminar flow:

$$f = 2\sqrt{\frac{\nu}{U_b A_b}}$$

where A_b (cm) is the maximum bottom wave amplitude (measured by the acoustic wave sensor).

6.2.3 Flow conditions in the wave tank

Single waves (soliton) were generated in the wave tank in order to simulate the first wave of a characteristic ship-induced wave train hitting the habitats. In natural conditions, the first wave of a characteristic ship-induced wave train is expected to have the greatest effects on invertebrates because of its highest amplitude and sudden appearance. We thus used solitons since they are technically easier to produce in an experimental wave tank than a wave train. Using combinations of eight different weights and two water levels, waves of 10 different shear stress levels were produced in the experimental wave tank. Resulting shear stress values at the location of the habitat trays ranged from 0.45 to 2.19 N m^{-2} (Table 18), and were significantly different from each other (ANOVA with Scheffé's Post-Hoc test, n = 100, lowest significance level: P = 0.023; Table 18). The observed coefficient of variation for all combinations was low, ranging from 0.36% to 2.17% (Table 18), indicating that a given combination of weight and water level generated waves with similar hydraulic characteristics.

The waves produced in the wave tank (wave heights ranging from 1.5 to 8 cm and maximum orbital velocities from 11 to 50 cm s^{-1}) were comparable with wave characteristics induced by small private boats (wave heights 4.5-8.8 cm, maximum orbital velocities of 21- 44 cm s^{-1}) as measured on Lake Langer See and the River Spree, Berlin, Germany (Franke, unpublished data).

To assess the spatial homogeneity of the hydraulic conditions at location of the habitat trays, 10 repeated measurements of wave characteristics were conducted on both the left and right sides of the tank for two different shear stress levels (0.43 and 1.37 N m^{-2}). No significant differences in maximum wave orbital velocities, wave heights or calculated shear stress values were found between the two sides (ANOVA, n = 10 per test, $P > 0.05$ for all tests). Consequently, all experiments were conducted with the electronic devices fixed on the right side of the wave tank. Similarly, no significant differences in flow velocities were found at different depths along the vertical profile (measured each subsequent centimetre from 1.0 to 8.0 cm above the flow bed for 10 replicated waves of 1.37 N m^{-2}, ANOVA with Scheffé's Post-Hoc test, $n = 90$, $P > 0.05$), indicating that the flow generated by the waves in the experimental wave tank was vertically uniform above bottom boundary layer and that the measurement point of 1 cm distance to the bottom is representative for the flow.

6.2.4 Habitat trays

Five habitats [coarse woody debris (CWD), reeds, sand, stones and tree roots] commonly found in the littoral zone of north-east German lakes were used for the experiments. Structural elements used in the simulations of the five habitats were collected from regional lakes, and arranged in the removable trays on a 2 cm thick layer of sand, respecting design and densities observed under natural conditions. The CWD habitat tray consisted of two flat pieces of ridged bark of about 400 cm² each. The reed (*Phragmites australis* (Cav.) ex. Trin. Steud.) habitat tray comprised 21 vertical, living reed stems, randomly distributed over the tray bottom with their intact roots underneath. In each tray, the stems density of 175 stems m^{-2} corresponded to the mean reed density observed in 30 north-east German lakes (Brauns, unpublished data). The root habitat tray contained a bunch of willow roots of about 120 cm³, fixed in the tray by a stick. The sand habitat tray simply consisted of the 2 cm layer of sand. The stone habitat tray contained six angular basaltic stones of about 60 cm^3 each, and spaced at 5 cm distances.

The habitat trays each had a comparable surface area of 0.115 m². The structural complexity of the five habitats was quantified by their fractal dimension (FD). FD represents habitat complexity across all spatial scales, from surface roughness of single habitat elements to distances between these elements, of the five habitats arranged in the habitat tray. In this sense, structural complexity of the habitat at high resolution levels, like for example roughness of the stones or CWD surfaces could not be captured separately. However, although structural complexity at such high resolution level also influences the ability of invertebrate to withstand wave action (i.e. by providing anchorage points), none of the invertebrate species used in the experiments exhibited a body size matching the size of habitat surface crevices, so that they could have used them to fully escape from waves. FD was calculated following Frontier's grid method (Frontier, 1987) on size-comparable top-view digital pictures of the habitat trays. The frame of the habitat tray was taken as the first square of the grid, which was progressively split into finer grids until reaching a level of 4,096 squares. The structural complexity of the five habitats increased in the sequence sand (FD=1), CWD (FD=1.29), stones (FD=1.34), reeds (FD=1.39) and tree roots (FD=1.80).

The reduction of wave kinetic energy when the wave was passing through the habitats was quantified as the difference in shear stress in front of and behind the habitat tray. Ten replicated waves were produced for four different levels of shear stress, i.e. 0.43, 1.37, 1.64 and 2.19 N m^{-2}. Differences in shear stress values calculated in front and behind the habitat tray were tested using paired t-tests, and between-habitat differences using ANOVA with associated Post-Hoc test (Scheffé's procedure).

6.2.5 Invertebrate species

Five epibenthic invertebrate species (*Bithynia tentaculata* L. [Gastropoda], *Calopteryx splendens* Harris [Odonata], *Dikerogammarus villosus* Sowinsky [Crustacea], *Gammarus roeseli* Gervais [Crustacea] and *Laccophilus hyalinus* DeGeer [Coleoptera]), which are all common in the littoral habitats of German lowland lakes, were used for the experiments. All these species occur in the tested habitats, although *B. tentaculata* and *D. villosus* are eurytopic, *C. splendens* is more abundant in CWD, reed and tree roots, *G. roeseli* generally occurs in tree roots and CWD, and *L. hyalinus* is mainly found in tree roots as well as between stones.

Moreover, these species were selected because they differ considerably in body shape, locomotion behaviour and attachment strategies, all of which should influence their sensitivity to wave impact. Thus, conically shaped *B. tentaculata* attaches by its foot. *C. splendens* has an elongated body and long legs bearing strong claws, which allow it to firmly grip a wide range of habitat types. *D. villosus* and *G. roeseli* are laterally compressed organisms and actively swim lying on their side, reducing their exposure to flow. *D. villosus* is also known to fix itself strongly in crevices with its two anterior large claws. *L. hyalinus* exhibits an oval outline and is a highly mobile organism.

B. tentaculata, *C. splendens, G. roeseli* and *L. hyalinus* were collected in the River Spree upstream of Berlin, and *D. villosus* in Lake Müggelsee (Berlin, Germany). New individuals were taken for each experimental series using one of the habitats, in order to avoid individual adaptation to disturbance, or decreasing fitness of individuals. For better visibility on the videos, only large specimens were used (mean body length ± SE, n = 100 for each species: *B. tentaculata* 9.4 ± 0.07 mm, *C. splendens* 15.8 ± 0.3 mm*, D. villosus* 15.3 ± 0.2 mm, *G. roeseli* 13.9 ± 0.1 mm, *L. hyalinus* 4.8 ± 0.04 mm). Individuals were kept in oxygen-saturated water in separate aquaria and fed with appropriate food when not used for experiments.

6.2.6 Experimental design

Experiments followed a crossed design with the five habitats and the five invertebrate species. After twelve hours adaptation to habitat conditions in the wave tank, 20 individuals were exposed to single waves of increasing shear stress for each habitat-species combination. The corresponding invertebrate density of 71 individuals m^{-2} represents the lower end of the density range observed in north-east German lakes (Brauns and Leszinski, unpublished data), so that no artefacts in the responses of the species to hydraulic disturbance could be generated due to strong competition for living space. During the adaptation period, water was oxygenated and the habitat trays were caged in order to prevent dispersal of the individuals. Cages were removed shortly before each single wave was produced and replaced immediately after. Three replicated single waves per shear stress level were produced, with a time interval of 15 minutes, which allowed the individuals that had been detached by the previous wave to fix or hide themselves again. Since each of the three replicated waves corresponded to a distinct experiment and no consistent trend towards increasing or decreasing detachments comparing the three replicates was detected, the numbers of detached individuals resulting from each single wave were used as replicates.

For each wave produced, wave velocity and wave amplitude were recorded to calculate the bottom shear stress. After each wave, the top and side video records were analysed to count the number of individuals detached from the habitat. The shear stress was increased until 100% of the individuals were detached or the maximum applicable shear stress was reached. Mean number of detached individuals for each habitat-species combination, in the following referred to as detachment, was calculated as the overall number of detached individuals divided by the total number of generated waves.

6.2.7 Statistical analysis

Relationships between the proportion of detached individuals and shear stress were explained using sigmoid regression analysis ($\ln y = b_0 + b_1/t$). The sigmoid curve best fitted the observed response of the individuals to hydraulic disturbance since there is a critical shear stress threshold at the lower end of the curve at which individuals started to become detached. Detachments averaged for the five species studied were compared among habitats using an ANOVA with associated Post-Hoc test (Scheffé's procedure). In order to determine the extent to which the selection of species for the study influenced the detachment observed in specific habitats, the proportions of variance explained by species and habitats were calculated separately using multiple classification analysis (MCA, Andrews et al., 1973). MCA is a parametric statistical technique for examining the interrelationship between several predictor variables and one dependent variable in the context of an additive model. It provides the part of explained variance by each predictor, both before and after taking the effects of all other predictors into account. The predictor with the higher explained variance has the greater influence on the dependent variable.

Relationships between the structural complexity of the habitats (expressed by their fractal dimension) and the detachment were explored using Spearman rank correlations. Similarly, Spearman rank correlations were also used to explore relationships between structural complexity of the habitats with habitat-specific reduction of shear stress. Deviation of the data from normality and homogeneity of variances were tested using Shapiro-Wilk and Levenè tests before statistical analyses. All statistical tests and regressions were performed using SPSS (Version 9.0, SPSS Inc., Chicago, IL, U.S.A.).

6.3 Results

6.3.1 Impact of wave-induced disturbance on benthic invertebrates

The five species exposed to waves showed a similar response to increasing shear stress in four (sand, coarse woody debris, stones and reeds) of the five habitats studied. In these four habitats, the number of detached individuals generally increased with increasing shear stress (Fig. 11). These disturbance-response relationships could be well described by sigmoid regression models (Table 19), except for *B. tentaculata* on stones, where the relationship was not significant ($P > 0.05$). Conversely, such a pattern was not observed in tree root habitat where only a few individuals of each species were detached even by the strongest waves (Fig. 11). Here, a significant regression ($R^2 = 0.52$, $P = 0.01$) could only be found for *B. tentaculata*.

6.3.2 Role of habitat structural complexity

Detachments averaged for the five species (mean ± SE) varied among habitats. More individuals were detached on sand (20 ± 0) than on CWD (11.9 ± 1.7), stones (10.4 ± 1.9), reeds (7.9 ± 1.9) and tree roots (1.3 ± 0.5). The detachments were significantly higher (ANOVA, Scheffé's Post-Hoc test, n = 75) on sand than on all other habitats ($P < 0.001$, n = 75), and significantly lower on tree roots than on all other habitats ($P = 0.022$ at the lowest, $n = 75$). Conversely, no significant differences in detachments were observed between CWD, stones and reeds ($P > 0.05$, $n = 75$).

Comparison of the detachments of each species showed species-specific responses to wave-induced hydraulic disturbance according to habitats (Table 20). On CWD, more individuals of *B. tentaculata*, *G. roeseli* and *L. hyalinus* were detached than individuals of *C. splendens* and *D. villosus*. On reed, more individuals of *D. villosus*, *G. roeseli* and especially *L. hyalinus* were detached than individuals of *B. tentaculata* and *C. splendens*. On stones, more individuals of *C. splendens*, *G. roeseli* and *L. hyalinus* were detached than individuals of *B. tentaculata* and *D. villosus*. Even on sand and tree root habitats, differences in detachments among species were recorded (Table 20).

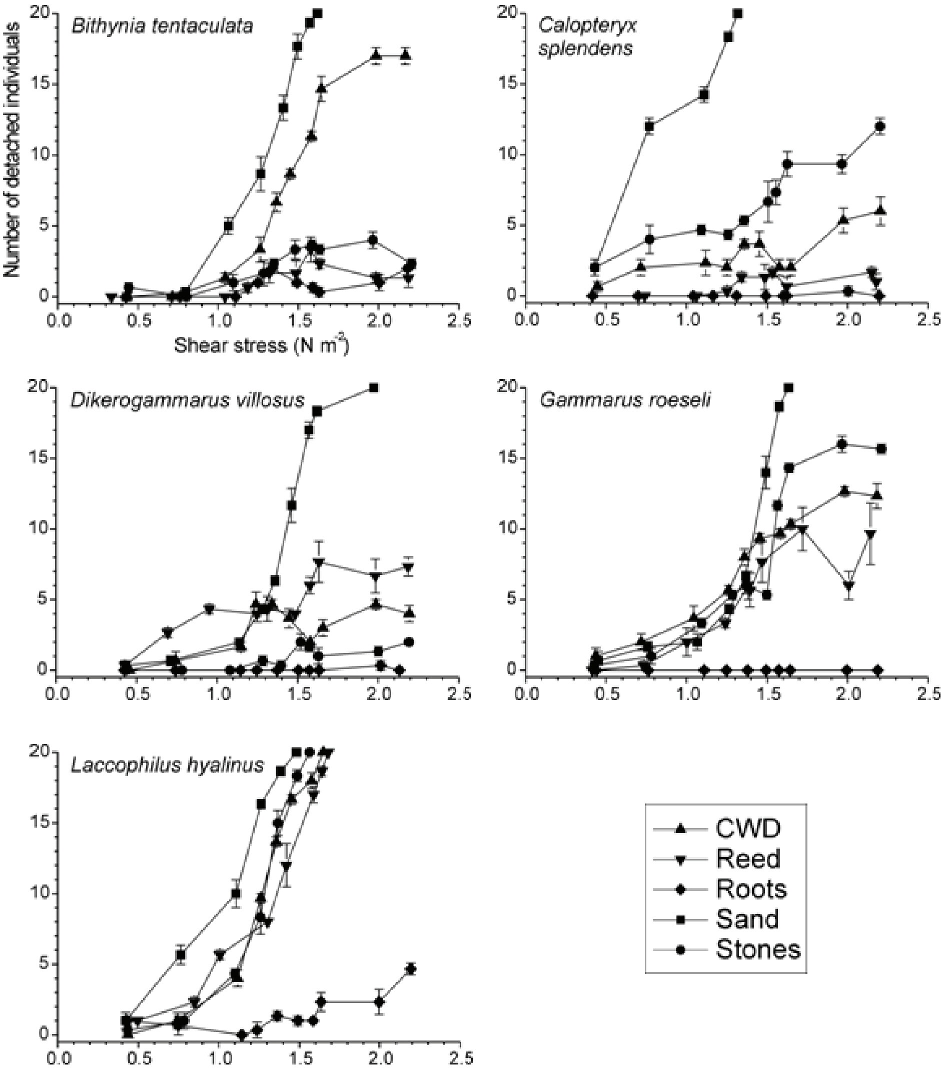

Fig. 11. Number of detached individuals from a maximum possible 20 in each habitat for the five species studied as a function of the shear stress caused by experimental waves. Plotted values represent the mean number of detached individuals (± SE) for three replicated waves. Results for each habitat are connected by lines. CWD: coarse woody debris.

To determine the extent to which these species-specific responses might influence observed differences in the detachments among habitats, we conducted a Multiple Classification Analysis (MCA). Results showed that 77% of the variance in detachments was explained by habitat type (value corrected from the influence of the species factor) versus 47% by species (value corrected from the influence of the habitat factor - full model: $R^2 = 0.81$, $P < 0.001$, $n = 75$).

Hence, the choice of the five species did not compromise the conclusion that the habitat had the strongest influence on detachment in wave experiments.

The impact of the wave-induced hydraulic disturbance on invertebrates was found to decrease along the gradient of habitat structural complexity parameterised by the fractal dimension (Fig. 12A). Detachments averaged for the five species were significantly negatively correlated to the fractal dimension of the habitats (Spearman's $\rho = -0.99$, $P < 0.001$, $n = 5$). Considering each species separately, significant negative correlations were found for *B. tentaculata* (Spearman's $\rho = -0.99$, $P < 0.001$), *C. splendens* ($\rho = -0.90$, $P < 0.05$), and *G. roeseli* ($\rho = -0.90$, $P < 0.05$).

6.3.3 Shear stress in front of and behind the habitat

Shear stress measured in front of and behind the habitat trays differed significantly for all habitats ($P < 0.001$ for all tests, $n = 10$ per test). Shear stress reduction tended to increase in the sequence: sand, CWD, stones, reeds and tree roots (Fig. 13). Only waves of low initial shear stress (0.43 N m^{-2}) showed no significant differences in reduction of shear stress among habitats ($P > 0.05$, $n = 50$). For stronger waves (1.37, 1.64 and 2.19 N m^{-2}), shear stress reduction was significantly different between sand and stones ($P = 0.014$ at the lowest, $n = 50$), sand and reed ($P = 0.001$ at the lowest, $n = 50$) except for waves of 1.37 N m^{-2}, as well as between roots and the other habitats ($P = 0.012$ at the lowest, $n = 50$). No significant differences were recorded between CWD, stones and reed habitats, except for waves of 2.19 N m^{-2}, where shear stress reduction in stones was significantly higher ($P < 0.001$, $n = 50$) than in CWD (Fig. 13).

The reduction of shear stress caused by the habitat was correlated with the structural complexity of the habitat (Fig. 13B), as shown by the significant positive correlations found between habitat-specific shear stress reductions and habitat fractal dimensions for three of the four shear stress levels tested (1.37 N m^{-2}: Spearman's $\rho = 0.90$, $P < 0.05$; 1.64 and 2.19 N m^{-2}: both $\rho = 0.99$, $P < 0.001$).

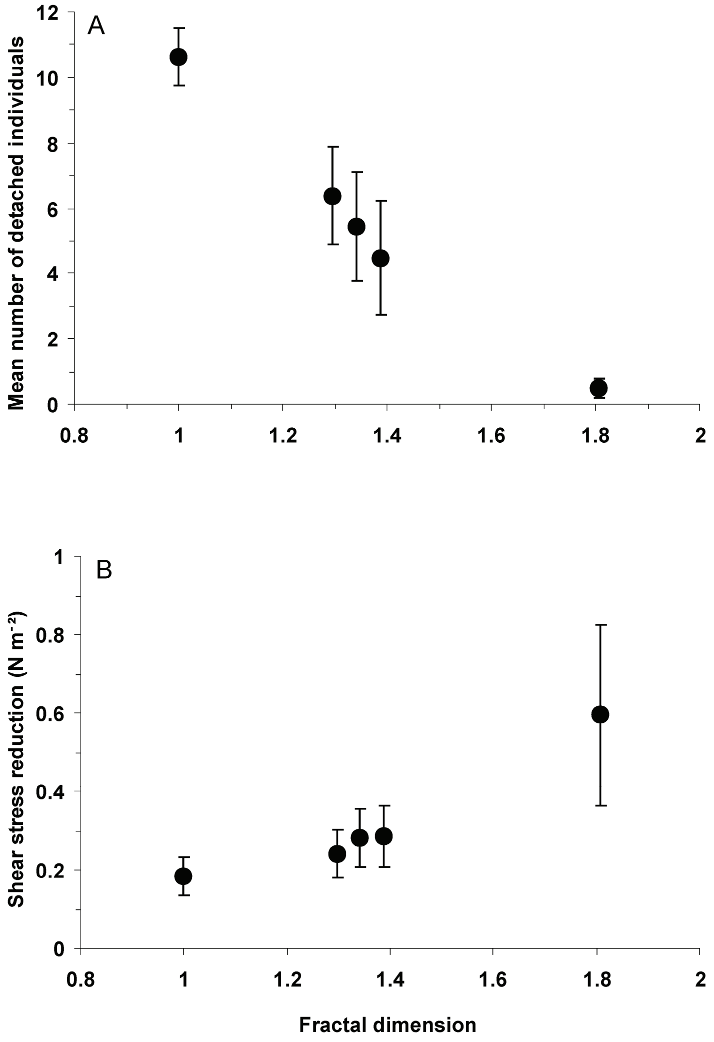

Fig. 12. Relationships to the fractal dimension of the habitats of (A) the mean number (average for the five species ± SE, n = 15) of detached individuals, and (B) the shear stress reduction (mean ± SE for four initial shear stress levels: 0.43, 1.37, 1.64 and 2.19 N m-2, n = 10 each) caused by the habitats.

6.4 Discussion

6.4.1 Impact of wave-induced hydraulic disturbance on benthic invertebrates

In our experiments, clear relationships were found between wave-induced shear stress and invertebrate detachment for all habitats except roots, and for each species studied. Our observations were best described by a sigmoid regression model, which revealed a threshold of shear stress corresponding to the beginning of mass detachment of invertebrates. This threshold varied according to the habitat-species combination considered, but was mainly observed to be at 1.0-1.2 N m^{-2}. Furthermore, 50% of individuals were already detached at shear stress values from 1.5 N m^{-2}. Such shear stress values were produced in the wave tank by waves with an orbital velocity of 19 to 42 cm s^{-1}, and bottom shear stresses produced under natural conditions by boats are generally higher.

For example, maximum orbital velocities measured in the littoral zones of Lake Langer See and the River Spree ranged from 21 to 44 cm s^{-1} for small private boats, up to 54 cm s^{-1} for freight barges and up to 65 cm s^{-1} for passenger ships (Franke, unpublished data), which indicates that hydraulic disturbance created in the wave tank corresponded to the lowest disturbance experienced by benthic invertebrates in natural conditions. Moreover, due to their large dimensions, passenger ships or commercial barges create waves that tend to break before they reach the shoreline. Such breaking waves produce even more severe hydraulic conditions and the detachment of invertebrates is likely to be higher under those conditions than in the wave tank. Hence, detachment of invertebrates by waves should also occur under field conditions and is probably a widespread phenomenon in the littoral zones of navigable waterways.

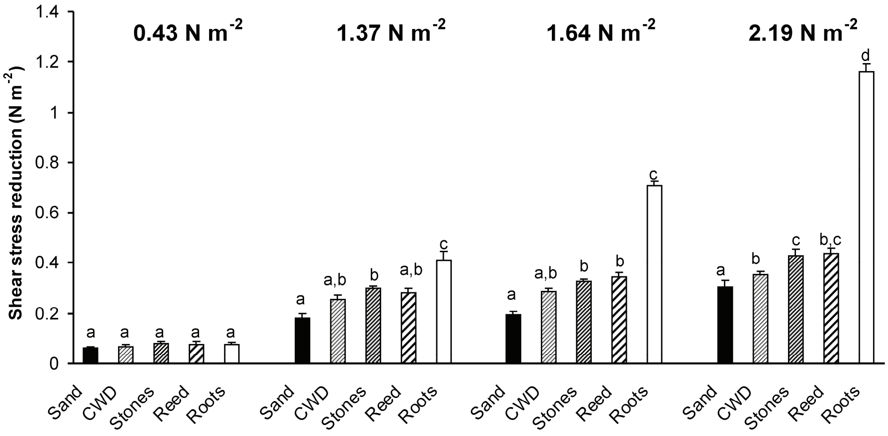

Fig. 13. Reduction of shear stress (mean ± SE, n = 10 each) caused by the five habitats studied under the four different shear stress levels indicated. Shear stress reduction was calculated as the difference between shear stress values measured in front of and behind the habitat tray. Bars with different letters indicate significant differences among habitats for a given shear stress level (ANOVA, Scheffé's Post-Hoc test, n = 50). CWD: coarse woody debris.

6.4.2 Complex habitats provide refuge for invertebrates

The detachment of invertebrates by wave-induced hydraulic disturbance was found to be significantly reduced in complex habitats that provide numerous refuges and anchorage points enabling individuals to resist drag forces imposed by peaks in flow velocity. Sand did not offer suitable hiding or fixing options for any of the five species and as a result, mass detachment of individuals started here at low stress values (0.4-0.8 N m^{-2}). In contrast, root habitats offered maximal sheltering conditions for all the studied species, and the dense network of tiny, flexible branches of the root network allowed every species, irrespective of its size or gripping abilities, to enter the network and fix itself. Even *B. tentaculata*, for which the tiny root branches do not offer optimal surfaces for efficient foot adhesion, showed a low detachment here.

Slightly fewer individuals were detached in reed than in stones or coarse woody debris (CWD) habitats. However, since no significant differences were recorded between these three habitats in the detachments of all five species combined, these habitats evidently offered a similar level of protection against detachment despite their differing fractal dimensions. Nevertheless, the five species showed differences in detachments among these three habitats, and species-specific differences in detachments were also observed for a given habitat. Furthermore, significant negative correlations between detachment and habitat fractal dimension were found for only three of the five species studied. Thus, detachment did not only depend on habitat complexity, but also partially on the extent to which species-specific fixing or hiding capabilities matched the physical habitat characteristics. For example, the rough ridges of CWD provided good anchorage points for species fixing themselves with big claws, such as *C. splendens* and *D. villosus*, but not for either *B. tentaculata*, which needs smoother surfaces for efficient attachment, or for *G. roeseli* and *L. hyalinus*, which possess smaller claws. Similarly, reeds provided better sheltering conditions against waves for *B. tentaculata* and *C. splendens* than for *L. hyalinus* and the two crustaceans. Reed stems provided an ideal smooth surface for *B. tentaculata*, while *C. splendens* was able to fix itself by gripping the reed stems between its long legs. In contrast, the claws and legs of *L. hyalinus, D. villosus* and *G. roeseli* were far too small to grip reed stems firmly. Species such as *L. hyalinus* and *G. roeseli*, which do not exhibit morphological or behavioural characteristics matching the structural characteristics of the CWD, stone or reed habitats used in the experimental wave tank, were strongly detached.

Despite specific habitat-species relationships, the structural complexity of the habitat has proved to influence the degree of protection of benthic invertebrates against wave-induced hydraulic disturbance. The higher proportion of variance in detachments explained by habitat features alone, in comparison to the influence of the species used, supports the conclusion that there is a strong causal relationship between detachment and the structural complexity of the habitat. Comparable influences of habitat complexity in sheltering benthic invertebrates against hydraulic disturbance have been demonstrated for *Seratella ignita* and *Gammarus pulex* exposed to high currents (Borchardt, 1993). In that study, the proportion of drifting individuals decreased as more and more woody debris was added to the sandy bottom of a circular flume. *S. ignita* started to drift at lower shear stress values (1.1 N m^{-2}) than *G. pulex* (3.1

N m^{-2}), a fact attributed to behavioural differences between the swiftly swimming *G. pulex* and the slowly crawling *S. ignita*.

6.4.3 Habitat complexity dissipates wave kinetic energy

Besides providing refuges for the organisms, the spatial structure of benthic habitats also influences the hydrodynamics in their surroundings (Grass, 1971). From the perspective of flow mechanics, the structure of the habitat provides obstructions to the unidirectional flow, transforming some portion of the mean flow into turbulent components. In turbulent flows, the kinetic energy is extracted by larger vortices from the mean flow, transferred by the cascade of turbulences towards smaller scales, where it finally dissipates into heat due to molecular viscosity (Tennekes and Lumley, 1972; Townsend, 1976). Correspondingly, higher structural complexity provides more obstacles to flow and dissipates a larger portion of kinetic energy. Notably, with almost 1.2 N m^{-2} of shear stress reduction, which corresponds to 54% of the shear stress caused by the strongest wave produced in the wave tank, roots were three to four times more efficient in dissipating kinetic energy than any other habitat studied. A direct implication for invertebrates is that in more complex habitats, hydraulic disturbance is attenuated after a short distance inside the habitat patch, so that even small patches of complex habitats may serve as effective refuges.

On the other hand, generated turbulences may potentially increase detachment of individuals since the erratic flow pattern creates drag forces constantly varying in direction. Shear-stress distribution depends on the spatial arrangement of the habitat elements providing obstacles to flow and is even more complex in presence of turbulences, so that the relative influences of refuges, dissipation of wave kinetic energy or turbulences on invertebrate detachment are difficult to assess separately. As a general pattern, habitat efficiency to dissipate wave energy was found to increase following the habitat sequence CWD, stones and reeds. In parallel, for species whose specific fixing capabilities do not strongly match fixing options of a specific habitat (i.e. *C. splendens* and reeds), intensity of detachment was found to follow a reverse habitat sequence. For example, *C. splendens* and *G. roeseli* were more detached in stone habitat than in CWD habitat. Similarly, *D. villosus* was more detached in reed habitat than in CWD or stone habitats. Hence, it is likely that refuges provided by complex habitats as well as how habitat structure matches species fixing capabilities, act as the main factor in sheltering invertebrates. Concomitantly, in more complex habitats, waves are attenuated after a shorter distance, improving sheltering conditions for invertebrates.

6.5 Implications for shoreline management

We could show that the effect of wave disturbance resulted in significant detachment of invertebrates even at moderate shear stress levels. Since ship-induced waves occur stochastically and create harsh hydraulic conditions, they constitute a major hydraulic disturbance for invertebrate inhabiting shoreline habitats. The threshold values at which invertebrates started to be detached were lowest in the sand habitat (0.4-0.8 N m^{-2}), intermediate in the other habitats (1.4-1.6 N m^{-2}) and not reached for roots even at the maximum shear stress levels produced in the wave tank (2.19 N m^{-2}). It can be concluded that network habitats such as tree roots, and to a certain extent also dense reed belts, provide efficient protection of invertebrates against wave-induced disturbance. Mechanistic explanations are that complex three-dimensional habitats provide both the best options for all species to hide or to fix themselves, and also the strongest dissipation of kinetic wave energy.

Consequently, complex habitats such as tree roots and dense reed belts should be protected to preserve a diverse and natural fauna in the littoral zone of inland waterways, as required by water policies. These habitats are often removed during shoreline stabilisation, which in urban areas results in two additive constraints on the littoral fauna, i.e. simplification of habitat structure and increase of hydraulic stress. Also, tree root habitats and reed stands may be heavily damaged if ship-induced waves occur repeatedly over the long-term (Ostendorp, 1989; Ostendorp, 1999), amplifying the short-term ecological effects of ships passing by. These factors lead to a reduction in species richness and decreased abundances of the benthic communities (Bishop, 2003; 2004; 2005) in wash-zones. Thus, water managers should be able to reduce ship-induced disturbance in the littoral zone to a level lower than the detachment threshold for typical species, so that invertebrate assemblages in wash-zones maintain similar structure and abundance patterns as in non-wash zones.

7 General discussion

7.1 Rationale

In its pristine state, the littoral zone of lakes is characterised by a mosaic of habitat types creating a high spatial heterogeneity that results in an immense diversity of ecological niches and food resources (Heino, 2000; Harrison and Hildrew, 2001; Heino, 2008). Hence, macroinvertebrate diversity, abundance and production are higher in the littoral zone than in the sublittoral or profundal zone (Tolonen et al., 2001; Babler et al., 2008). However, humans increasingly alter riparian areas and littoral zones for recreation use or residential development, which impacts the structure, hydrology and water quality of lakes. The ecological impacts of these human alterations have rarely been quantified as the littoral zone and especially their macroinvertebrate communities have been largely neglected from previous studies. Hence, the ecology of littoral macroinvertebrate communities, in particular their response to natural environmental factors, is still poorly understood. This knowledge constitutes an essential prerequisite to mechanistically understand and assess how human alterations of the littoral zone impact the structure and function of macroinvertebrate communities.

In this thesis, I investigated *i*) the key environmental factors that determine littoral macroinvertebrate community composition, *ii*) whether and to which extent common human activities alter these environmental factors, and *iii*) how these alterations impact the structure and function of macroinvertebrate communities. Thus, five hypotheses were tested (see Chapter 1) using data derived from extensive field surveys at 38 German lowland lakes, as well as data derived from mesocosm experiments. The material studied included a total of 837,223 individuals corresponding to 382 taxa, which were collected over a total area of 356 m^2.

7.2 Environmental factors determining macroinvertebrate communities

The few studies that have addressed the relationships between environmental factors and littoral macroinvertebrate communities have suggested that community composition is governed by hydromorphology, habitat characteristics and water chemistry (Brodersen, 1995; Brodersen et al., 1998; Tolonen et al., 2001; Johnson and Goedkoop, 2002). However, no study has investigated these key environmental factors at the same time, and thus, the relative importance of trophic state versus shoreline structure is poorly understood. Thus, the relationship between littoral macroinvertebrate community composition and major environmental factors was examined in this study based on the hypothesis that community composition is primarily determined by the trophic state of the lake (Chapter 2).

In the 38 lowland lakes studied, differences in trophic state only partially explained the compositional differences because community composition was also significantly related to riparian land use, habitat structure and wind exposure. Moreover, macroinvertebrate communities were significantly more dissimilar among habitat types than among trophic states, suggesting that community composition was primarily determined by the intrinsic properties of the habitats (Fig. 14). Therefore, habitat complexity and wind exposure but not trophic state, were significantly related to community composition on reed, sand and stone habitats (Fig. 14). A significant relationship between trophic state and community composition was only found for coarse woody debris (CWD) and root habitats, where polytrophic states coincided with predominance of invasive species. Since both trophic state and mass occurrences of invasive species may have affected community composition, it remains unclear as to whether community composition on CWD and roots is determined by trophic state.

In conclusion, hypothesis 1 was rejected, since structural and partially hydrodynamic properties of the littoral zone of the studied lakes constituted the more important driver of macroinvertebrate community composition than trophic state. Our results confirmed the hierarchy of the effects of environmental factors according to the spatial scale, where habitat properties acting on small spatial scales have a greater influence on community composition than ecosystem-scaled factors such as trophic state (Fig. 14).

7.3 Impacts of structural degradation

The intensity at which humans alter the structure of riparian areas and littoral zones has increased during the last decades and constitutes a serious threat to the integrity of lake ecosystems worldwide (Sly, 1991; Schnaiberg et al., 2002; Schmieder, 2004). Such alterations will probably increase in the future, yet almost nothing is known about their impacts on littoral macroinvertebrates. In order to gain a mechanistic understanding of how structural degradation impacts the structure and function of macroinvertebrate communities, community composition and benthic food webs were investigated along a gradient of increasing structural degradation (Chapters 3 and 4).

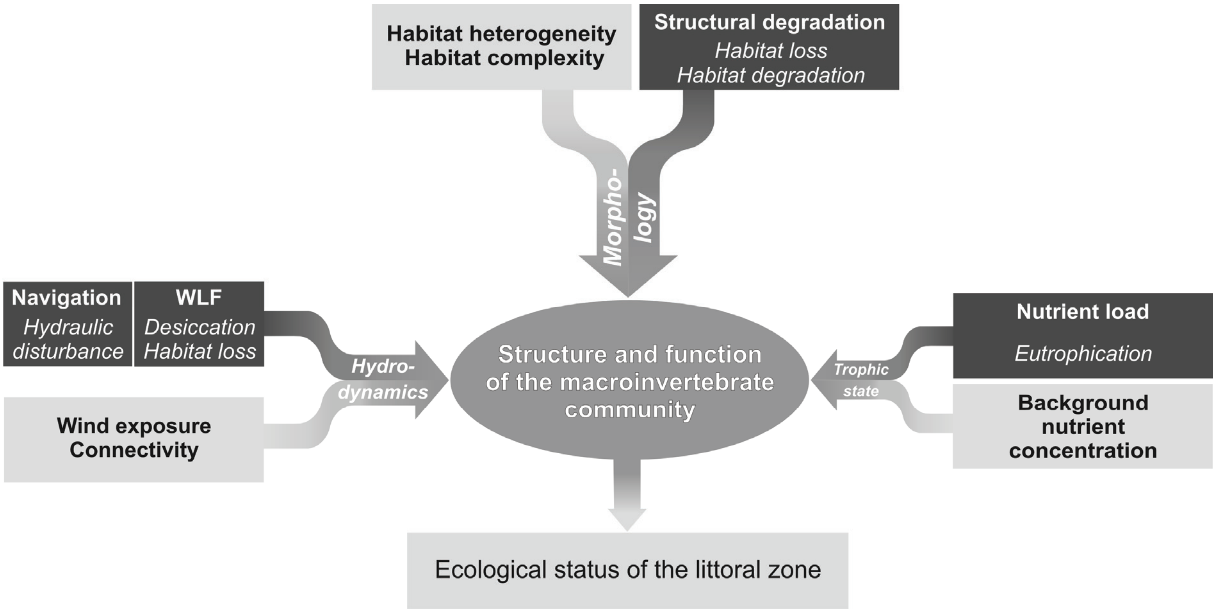

Fig. 14. Conceptual model of human activities (dark grey) that alter key environmental factors (light grey) thereby impacting the structure and function of macroinvertebrate communities in lowland lakes. The width of the arrows represents the extent to which the environmental factor determines, and consequently the human activity impacts, macroinvertebrate communities. Macroinvertebrates are highly susceptible to these alterations in the littoral environment, which makes them suitable for use in an integrative ecological assessment of the littoral zone (WLF = water level fluctuations).

In accordance with hypothesis 2, structural degradation due to erosion control structures, recreational beaches and riparian clearcutting substantially reduced habitat heterogeneity as a result of habitat loss at highly developed shorelines. Furthermore, structural degradation was followed by a reduction in habitat complexity, since complex three-dimensional root habitats at natural shorelines were replaced by spatially homogenous, concrete habitats at developed shorelines. Hence, the abundance of Coleoptera, Ephemeroptera and Trichoptera was significantly lower at erosion control structures and beaches than at natural shorelines. There was a significant positive correlation between species richness and habitat heterogeneity. Hence, species richness was highest at natural shorelines and was more than four-fold lower at beaches where all but the sand habitats were absent. This strong relationship provides evidence that the concept described by the "habitat heterogeneity hypothesis" (Williams, 1964; Connor and McCoy, 1979; Williamson, 1981) also applies to littoral communities.

To evaluate whether structural degradation impacts macroinvertebrate function, the structure and trophic base of macroinvertebrate food webs was compared among natural shorelines, shorelines developed by erosion control structures and recreational beaches. For that, macroinvertebrate food webs were constructed by analysing carbon and nitrogen stable isotopes of consumer and potential food resources, as well as by applying mixing model analyses. Habitat heterogeneity was significantly correlated to both species richness and number of available food resources. Hence, with decreasing habitat heterogeneity, trophic links between macroinvertebrate consumers and food resources were lost. Thus, food webs had up to four times less complexity at highly degraded shoreline than at natural shorelines. As predicted by hypothesis 3, the loss of food resources led to a shift in the trophic basis of macroinvertebrate food webs. For example, the biomass of primary and secondary consumers at natural shorelines was derived from seston, periphyton and allochthonous particulate organic matter (POM). At shorelines developed by erosion control structures, riparian trees were absent due to riparian clear-cutting and thus, allochthonous POM did not contribute to consumer biomass. At recreational beaches, substantially more biomass was derived from seston than at natural shorelines, since solid habitats that enable periphyton growth were absent on recreational beaches. Qualitative alterations in the trophic basis of the studied food webs were apparent in consumer-resource imbalances, which were highest at natural shorelines, suggesting better stoichiometric nutrient availability at developed shorelines. However, consumer biomass at developed shorelines was up to 13 times lower, indicating that better stoichiometric nutrient availability could not compensate for the substantial reduction in habitats and food resources, and the associated reduction in consumer species richness.

These results can be mechanistically explained by the strong relationship between the littoral macroinvertebrate community and the morphology of the littoral zone. By altering this key environmental factor of community composition, structural degradation caused a significantly altered macroinvertebrate community that directly translated into substantial impacts on macroinvertebrate function (Fig. 14). These results were observed across lakes with different trophic state and hydrological regime, which indicates that structural degradation may have similar impacts on other lake types. Indeed, recent studies have corroborated this conjecture suggesting that structural degradation and its ecological impacts are a major threat to lake ecosystems worldwide (Francis et al., 2007; Rosenberger et al., 2008; Butler and DeMaynadier, 2008).

7.4 Impacts of hydrological and hydrodynamic alterations

Especially at wind-exposed shorelines of large lakes, the littoral zone is exposed to natural wave regimes (Fig. 14). In lakes subjected to human activities, the littoral zone may also be affected by hydrological alterations caused by climate change-induced water level fluctuations (WLF) and by hydrodynamic alterations caused by ship-induced waves. However, the effects of hydrological and hydrodynamic changes on littoral macroinvertebrates have rarely been studied. To evaluate the ecological effects of WLF and ship-induced waves, field (Chapter 5) and mesocosm (Chapter 6) studies were conducted to evaluate the hypotheses that the impacts of hydrological and hydrodynamic alterations on littoral macroinvertebrates can be mitigated by habitats with high structural complexity.

Seasonal water level fluctuations that are augmented by climate change may affect the littoral zone primarily through the loss of structurally complex root habitats. This may lead to the disappearance of the distinct macroinvertebrate community associated with this habitat type. Thus, macroinvertebrate communities from root habitats were compared to those from four infralittoral habitats in order to test whether the infralittoral habitat types could mitigate the loss of root habitats by serving as a substitute structure (Chapter 5).

Macroinvertebrate community composition differed significantly between root and CWD, sand and stone habitats. The strongest compositional difference was found between root and sand habitats. Despite having a similar level of species richness, root and sand communities were characterised by indicator species that primarily reflected the structural properties of the habitat. For example, structurally complex root habitats provided niches for large-bodied species of Coleoptera and Odonata, while structurally uniform sand habitats were dominated by small-bodied species of Bivalvia. Furthermore, root habitats provided food resources, such as periphyton or CPOM, as indicated by the dominance of functional feeding groups such as scrapers and collector/gatherers. The functional feeding group composition in sand habitats was dominated by filter feeders that feed on seston. In contrast to sand habitats, community composition of reed did not significantly differ from that of root habitats and all major taxonomic groups found in root habitats also occurred in reed habitats. The compositional similarity between these habitats likely reflects the similarity of structural complexity, since both habitats exhibit a complex three-dimensional structure. Hence, hypothesis 4 was accepted, since the results suggest that the adverse effects of WLF can be mitigated provided that habitats with similar structural complexities are present in the infralittoral zone.

The effects of ship-induced waves were studied in mesocosm experiments where macroinvertebrates were exposed to experimental waves with increasing shear stress in five littoral habitats differing in structural complexity (Chapter 6). Macroinvertebrates were detached from their habitats by waves even at moderate shear stress levels, suggesting that ship-induced waves have substantial direct effects on macroinvertebrates (Fig. 14). However, macroinvertebrate detachment rates significantly differed among habitats. The detachment rates were significantly highest at sand habitats, where more than 90% of the individuals were detached at shear stress levels as low as 0.4 N m^{-2}. Conversely, even at the maximum shear stress levels producible by the experimental setup (2.19 N m^{-2}), only 40 % of all individuals were detached from reed habitats and only 25 % of all individuals were detached from root habitats. The observed differences in detachment rates among habitats can be explained by the significantly positive correlation of habitat complexity and reduction of shear stress. Furthermore, complex habitats offered better sheltering conditions by providing small-scaled refuges for the studied macroinvertebrate species against hydraulic disturbances. Hence, hypothesis 5 was accepted, since structural complexity of littoral habitats increased the resistance of macroinvertebrates against ship-induced waves.

In conclusion, hydrodynamic and hydrological alterations impacted littoral macroinvertebrates either by directly exerting a substantial hydraulic disturbance or indirectly by reducing littoral habitat heterogeneity (Fig. 14). However, both studies demonstrated that the presence of habitats with high structural complexity counteracts the adverse ecological effects of ship-induced waves and water level fluctuations on littoral macroinvertebrate communities. Given that complex habitats are among the first to be lost from the littoral zone as a result of structural degradation (Chapters 3 and 4), lake management should focus on protecting habitat complexity, especially at urban lakes that are subjected to several types of human activities.

7.5 Littoral macroinvertebrates as ecological indicators

Macroinvertebrates have traditionally been used to assess the ecological status of streams and rivers (Kolkwitz and Marsson, 1909; Fore et al., 1996; Reynoldson et al., 1997; Hering et al., 2004) but the suitability of using littoral macroinvertebrate communities to assess the ecological status of lakes has received less attention.

Previous studies have demonstrated that profundal macroinvertebrates can indicate eutrophication (Thienemann, 1918; Langdon et al., 2006). The results of this thesis suggest that the suitability of littoral macroinvertebrates for indicating eutrophication is restricted. However, littoral macroinvertebrates responded sensitively and predictably to the human alterations of the morphology, hydrology and hydrodynamics of the studied lakes. This suggests that littoral macroinvertebrates in lowland lakes may be a suitable integrative indicator of such impacts (Fig. 14).

Several macroinvertebrate species were strongly linked to a habitat type and disappeared when their preferred habitat was lost from the littoral zone as a result of human activities (Chapters 3 and 5). These clear response patterns may be used as an integral part of an EU Water Framework Directive (WFD) compliant assessment method for the ecological status of lakes, since the integration of metrics describing the ratio of sensitive to robust species is compulsory (European Parliament and Council, 2000). Furthermore, indicator approaches can be successfully combined with methods developed to assess the morphological status of littoral zones (e.g. Lake habitat survey; Rowan et al., 2006a). In combination, both methods could be used to rapidly assess the ecological effects of structural degradation in the littoral zone.

Human activities exert impacts not only indirectly by affecting habitat heterogeneity but also by causing direct hydrodynamic disturbances (Chapter 6). The latter impacts cannot be addressed by merely describing the morphological state of the littoral zone because macroinvertebrate communities may be significantly impacted by navigation even if the physical structure of the littoral is unaffected. Moreover, future methods used to assess the ecological state of littoral zones must be consistent with the WFD requirements. Therefore, assessment approaches have to consider the current state of the macroinvertebrate community compared to the normative descriptions for the respective ecological status given there. These are generally derived from communities observed under reference conditions.

Considering the results of this thesis and the WFD requirements, a future assessment method may consist of a structural and a biocoenotic component in order to assess the ecological effects of hydro-morphological degradations. The structural component may be based on a predefined biocoenotic quality for each of the habitats based on macroinvertebrate community metrics. That is, the habitat quality would reflect the ecological value of each habitat for the macroinvertebrate community. Hence, mapping of the habitats present on a given shoreline results in a biocoenotically weighed assessment of the structural state. The biocoenotic component may be based on the same predefined biocoenotic habitat qualities that constitute the reference conditions. The ratio between biocoenotic reference conditions and the current state of the macroinvertebrate community corresponds to a biocoenotic state class and allows for a WFD compliant ecological assessment of human impacts that directly affect the macroinvertebrate community. The combination of the results of both components into a single index would reflect the current structural-biocoenotic state and allows the ecological status of the littoral zone to be interactively assessed.

In conclusion, I demonstrated that littoral macroinvertebrate communities in German lowland lakes are more dependent on structural and hydrodynamic properties of the littoral zone than on the trophic status of the lake. Hence, human activities in the littoral zone and the riparian area, which modify hydrodynamic and morphological conditions, significantly affect the structure and diversity of the littoral macroinvertebrate community, as well as the flows of organic carbon through its food web. This thesis provided a mechanistic understanding of how human activities alter the relationships between environmental factors and biotic communities and how this affects the integrity of the littoral zone. This knowledge can be used in order to develop scientifically sound approaches to assess the persistent human impacts on lake ecosystems.

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Tables

Table. 2. Lake area (Area, km^2), residence time (RT, year), trophic state and total phosphorus concentration (TP, mean annual concentration of 2001, µg L^{-1}) of 38 lakes. Underlined codes represent lakes sampled for habitat-specific analysis.

Code	Lake	Area	RT	Trophic state	TP
Ba	Blankensee	2.9	1.2	hypertrophic	366
Be1	Beetzsee, southern basin	4.0	1.5	hypertrophic	97
Be2	Beetzsee, middle basin	1.9	1.5	hypertrophic	97
Be3	Beetzsee, northern basin	2.6	1.5	hypertrophic	97
Br	Breitlingsee	5.1	2.8	hypertrophic	121
Fa	Fährsee	2.1	4.0	mesotrophic	43
Gi	Grienericksee	0.7	4.2	eutrophic	37
Gl	Glienicker See	0.7	6.8	eutrophic	29
Gr	Grimnitzsee	7.8	4.6	eutrophic	50
Gu	Gülper See	4.4	0.6	hypertrophic	278
Ho	Hohennauener See	3.6	3.4	hypertrophic	104
Ku	Küstrinsee	2.2	6.0	mesotrophic	27
La	Langer See	2.5	0.1	hypertrophic	168
Lu1	Lübbesee, southern basin	2.1	5.0	mesotrophic	22
Lu2	Lübbesee, northern basin	0.9	5.0	mesotrophic	22
Me	Mellensee	2.2	3.3	hypertrophic	96
Mu	Müggelsee	7.3	4.8	eutrophic	108
Ne	Neuendorfer See	3.0	2.4	hypertrophic	86
Pa	Parsteiner See	8.9	7.7	mesotrophic	31
Pl	Plauer See	6.7	2.8	hypertrophic	121
Ra	Rangsdorfer See	2.4	1.5	hypertrophic	113
Ro	Röddelinsee	1.8	9.0	eutrophic	52
Ru1	Ruppiner See, northern basin	1.7	8.2	eutrophic	108
Ru2	Ruppiner See, southern basin	6.3	8.2	eutrophic	108
Sa	Sacrower See	1.1	19.3	eutrophic	122
Sc	Schwielochsee	11.5	2.0	hypertrophic	159
Sm1	Scharmützelsee, southern basin	10.7	9.9	eutrophic	64
Sm2	Scharmützelsee, northern basin	1.2	9.9	eutrophic	64
Sn	Schauener See	1.5	3.1	hypertrophic	222
So	Stolpsee	3.8	6.4	eutrophic	27
St	Stechlinsee	4.2	22.8	oligotrophic	13
Sw	Schwielowsee	7.9	2.8	hypertrophic	157
Un	Unteruckersee	10.4	9.2	mesotrophic	25
We	Werbellinsee	7.8	22.1	mesotrophic	26
Wi	Wittwesee	1.6	5.5	mesotrophic	14
Wo	Wolziger See	5.6	5.7	eutrophic	102
Wu	Wummsee	1.5	11.8	oligotrophic	18
Ze	Zechliner See	1.8	11.3	mesotrophic	26

Table 3. Environmental variables included in the lake-specific analysis and Pearson correlation coefficients with NMS axes (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

		NMS	
Number of axes		3	
Stress		0.13	
Cumulative variance (%)		86.0	
Variable (unit)	**Mean (min-max)**	**Axis 1**	**Axis 2**
Land use (%)			
Agriculture	17 (0-55)		
Forest	41 (0-93)	-0.46**	0.54***
Grassland	7 (0-24)	0.66***	-0.43**
Impervious surface	12 (0-60)		-0.54***
Water	8 (0-20)	-0.41**	
Habitat type (%)			
Coarse woody debris	39 (0-100)		0.56***
Pebbles	6 (0-83)	-0.44**	0.41*
Reed	60 (17-100)		
Roots	28 (0-100)	-0.51***	0.62***
Sand	50 (17-100)	-0.51**	
Stones	12 (0-67)	-0.53***	
Submerged macrophytes	18 (0-50)		0.48**
Lake water			
Conductivity (µS cm)	510 (216-1001)	0.45**	-0.61***
Dissolved oxygen (mg L^{-1})	10.7 (8.6-12.7)		
pH	8.5 (7.7-8.9)		
Temperature (°C)	13.0 (7.3-21.4)		
Total phosphorus (µg L^{-1})	89 (13-366)	0.76***	-0.70***
Hydrology			
Water residence time (year)	8.6 (0.0-57.8)	-0.35*	0.55***

Table 4. Pearson correlation coefficients of macroinvertebrate species with NMS axes of the lake-specific analysis. Only species with correlation coefficients $r > 0.55$ are shown (***$P < 0.001$).

Species	**Axis 1**	**Axis 2**
Alboglossiphonia heteroclita	0.60***	
Brachytron pratense		0.67***
Centroptilum luteolum		0.67***
Chironomidae	0.68***	
Cyrnus flavidus		0.60***
Dikerogammarus sp.		-0.60***
Dreissena polymorpha	-0.80***	
Gammarus pulex		0.78***
Halesus radiatus		0.58***
Haliplus fulvus		0.57***
Hydroglyphus hamulatus		0.60***
Kageronia fuscogrisea		0.59***
Leptophlebia marginata		0.65***
Lype phaeopa	-0.63***	
Nemoura cinerea		0.61***
Oulimnius sp.		0.79***
Oxyethira sp.		0.67***
Palpomyia sp.		0.80***
Pontogammarus robustoides		-0.65***
Potamopyrgus antipodarum	-0.77***	
Stagnicola sp.		0.62***

Table 5. Environmental variables included in the habitat-specific analysis and Pearson correlation coefficients with the NMS axes. Only significant relationships are shown (***$P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

		CWD	**Reed**		**Roots**	**Sand**		**Stones**	
Number of axes		2	3		2	2		2	
Stress		0.14	0.11		0.09	0.12		0.09	
Cumulative variance (%)		70.3	75.6		89.7	78.5		79.0	
	Mean (min-max)	**Axis 1**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Habitat attributes									
Sediment particle size (%)									
< 0.03 mm	0.7 (0.0-0.7)						-0.49*		
0.063-1.12 mm	88 (13.6-100)					0.47*			
> 2 mm	12 (0.1-85)					-0.45*			
Stem density (no. m^{-2})	129 (40-240)								
Wind exposure	0.8 (0.0-2.6)		0.63**					0.69***	
Lake water									
Conductivity (µS cm^{-1})	552 (371-791)	0.59*	-0.53*		-0.72**		-0.49*	-0.88***	
Dissolved oxygen (mg L^{-1})	11 (8.6-12.6)				0.67**				
pH	8.0 (6.3-8.6)	0.62*			-0.80***	0.44*		-0.73***	
Temperature (°C)	9.4 (6.4-11.6)						-0.66***		
Total phosphorus (µg L^{-1})	77 (25-168)	0.53*			-0.83***		0.52**		
Hydrology									
Water residence time (year)	12.3 (0.0-54.8)			-0.48*	0.73**			0.62**	-0.54*

Table 6. Area (km^2), trophic status, hydraulic residence time (RT, year)), shoreline length (L_{shore}, km), and the percentages of natural shorelines (Natural), retaining walls and ripraps (Erosion control), and beaches on total shoreline length at the seven studied lakes.

					Shoreline Type (%)		
Lakes	**Area**	**Trophic status**	**RT**	**L_{shore}**	**Natural**	**Erosion control**	**Beach**
Grienericksee	2.69	eutrophic	0.4	6.4	76	21	3
Langer See	2.51	hypertrophic	0.1	18.3	35	61	4
Müggelsee	7.70	eutrophic	0.2	11.1	63	29	8
Plauer See	6.70	hypertrophic	0.1	15.7	86	14	-
Ruppiner See	6.33	eutrophic	11.0	36.8	87	13	-
Unteruckersee	10.40	mesotrophic	2.0	16.7	91	8	1
Werbellinsee	1.80	mesotrophic	54.8	24.4	83	11	6

Table 7. Habitat types within the eulittoral and infralittoral zone sampled for macroinvertebrates. The number of replicates per habitat type is given in brackets.

	Reference	**Recreational use**	**Erosion control structure**	
	Natural shoreline	**Beach**	**Riprap**	**Retaining wall**
Eulittoral	Roots (5)	Sand (5)	Stones (5)	Concrete (5)
Infralittoral	Coarse woody debris (5)	-	-	-
	Reed (5)	-	Reed (2)	Reed (2)
	Sand (5)	Sand (5)	Sand (5)	Sand (5)
	Stones (5)	-	Stones (2)	Stones (5)

Table 8. Median relative abundance (range) of macroinvertebrate major groups at the four shoreline types, given separately for eulittoral and infralittoral zone. Significant differences (Mann-Whitney test) between natural and each type of developed shorelines are indicated by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

	Eulittoral zone				**Infralittoral zone**			
	Natural	**Beach**	**Retaining wall**	**Riprap**	**Natural**	**Beach**	**Retaining wall**	**Riprap**
Bivalvia	3.8 (0.0-9.1)	0.0 (0.0-0.2)	0.1 (0.0-1.8)	0.2 (0.0-27.1)	0.5 (0.0-5.3)	0.0* (0.0-0.1)	0.2 (0.0-5.6)	0.5 (0.0-20.3)
Chironomidae	74.4 (11.9-91.5)	91.7 (32.4-98.7)	87.1 (66.7-96.2)	85.7 (40.9-95.5)	87.6 (27.8-98.7)	96.0* (91.2-98.8)	82.3 (44.8-99.3)	86.0 (34.1-96.4)
Coleoptera	0.2 (0.0-2.2)	0.0* (0.0-0.0)	0.0 (0.0-0.1)	0.0 (0.0-0.2)	0.0 (0.0-2.1)	0.0 (0.0-0.0)	0.2 (0.0-0.2)	0.0 (0.0-0.1)
Crustacea	12.4 (0.4-69.7)	0.0* (0.0-6.1)	0.4 (0.1-7.0)	0.8 (0.1-30.7)	1.1 (0.0-38.4)	0.0* (0.0-0.4)	0.5 (0.0-46.3)	0.6 (0.0-28.9)
Ephemeroptera	1.3 (0.0-3.5)	0.0 (0.0-0.2)	0.0 (0.0-1.7)	1.3 (0.0-2.7)	0.2 (0.0-5.8)	0.0* (0.0-0.1)	0.1 (0.0-15.6)	0.4 (0.0-2.3)
Gastropoda	0.7 (0.2-6.7)	0.1* (0.0-0.4)	0.0** (0.0-0.0)	0.2 (0.1-0.5)	1.2 (0.0-12.5)	0.1 (0.0-0.5)	0.4 (0.0-1.3)	0.6 (0.1-6.5)
Hirudinea	0.0 (0.0-0.1)	0.0 (0.0-0.0)	0.0* (0.0-0.0)	0.0 (0.0-0.3)	0.0 (0.0-0.3)	0.0 (0.0-0.0)	0.0 (0.0-0.4)	0.0 (0.0-0.1)
Oligochaeta	1.2 (0.5-7.1)	6.6 (1.0-60.7)	10.9 (1.0-30.0)	1.6 (0.4-12.3)	2.6 (0.0-63.8)	3.1 (1.0-8.5)	9.8 (0.0-29.5)	4.0 (0.0-54.0)
Trichoptera	0.5 (0.4-0.8)	0.0** (0.0-0.1)	0.6 (0.1-2.7)	1.1 (0.1-5.4)	0.3 (0.0-1.2)	0.0*** (0.0-0.0)	0.6 (0.0-3.8)	0.1 (0.0-1.4)

Table 9. Median relative abundance (range) of the macroinvertebrate functional feeding groups at the four shoreline types, given separately for eulittoral and infralittoral zone. Significant differences (Mann-Whitney test) between natural and each type of developed shoreline are indicated by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

	Eulittoral zone				**Infralittoral zone**			
	Natural	**Beach**	**Retaining wall**	**Riprap**	**Natural**	**Beach**	**Retaining wall**	**Riprap**
Collector/Gatherer	10 (7-17)	13 (11-16)	9 (7-11)	9 (11-16)	17 (4-38)	13 (13-16)	14 (5-41)	16 (7-29)
Filterer	15 (12-37)	17 (16-17)	20 (15-35)	16 (16-17)	16 (7-37)	17 (16-17)	16 (11-67)	17 (16-75)
Parasite	21 (6-35)	28 (26-35)	30 (25-36)	21 (6-28)	14 (2-23)	27*** (22-28)	15 (3-23)	17 (2-23)
Piercer	33 (5-45)	28* (5-45)	26 (20-38)	33 (5-45)	21 (5-42)	30 (29-30)	28 (6-45)	25 (3-33)
Predator	4 (3-13)	4 (3-4)	3* (3-4)	3 (2-5)	5 (1-8)	4 (4-5)	5 (3-23)	4 (3-9)
Scraper	6 (4-8)	8* (6-8)	6 (5-14)	8 (2-12)	11 (4-17)	8 (8-10)	10 (6-19)	10 (3-14)
Shredder	2 (1-16)	0** (0-1)	0* (0-1)	1 (0-2)	2 (0-11)	0* (0-1)	1 (0-3)	1 (0-8)
Xylophagous	4 (0-18)	0* (0-0)	0* (0-0)	0 (0-1)	0 (0-67)	0 (0-0)	0 (0-0)	0 (0-0)

Table 10. Whole-lake littoral macroinvertebrate density and whole-lake littoral relative abundances of the macroinvertebrate major groups.

	Grienericksee	**Langer See**	**Müggelsee**	**Unteruckersee**	**Werbellinsee**
Whole-lake density	2250	8562	9148	3300	2184
Bivalvia	0.1	0.7	0.6	1.2	0.9
Chironomidae	86.5	96.4	84.6	72.5	76.9
Coleoptera	0.1	0.0	0.0	0.1	1.6
Crustacea	0.1	0.6	4.4	3.4	5.1
Ephemeroptera	1.7	0.1	0.7	0.2	3.5
Gastropoda	0.9	0.1	1.1	2.1	1.3
Hirudinea	0.1	0.0	0.0	0.0	0.0
Oligochaeta	9.0	0.6	6.8	18.5	8.0
Trichoptera	0.3	0.3	0.2	0.3	0.5

Table 11. Summary statistics of the littoral macroinvertebrate food webs at the three shoreline types (TL = trophic level).

		Grienericksee			Langer See			Unteruckersee		
		Natural	**Retaining wall**	**Beach**	**Natural**	**Retaining wall**	**Beach**	**Natural**	**Retaining wall**	**Beach**
No. of habitats		5	2	1	4	3	1	5	3	1
No. of food resources (TL 1)		7	3	2	6	4	2	5	4	3
TL 2	No. of species	16	2	3	9	7	2	15	14	6
	Biomass (g C m^{-2})	3.87	1.26	1.01	15.94	5.54	1.21	11.78	4.04	3.50
TL 3	No. of species	2				2			1	
	Biomass (g C m^{-2})	0.09				0.15			0.03	
No. of trophic links		44	6	9	36	22	5	40	37	17
TL 1 - TL 2		40	6	9	36	18	5	40	35	17
TL 2 - TL 3		4				4			2	

Table 12. Percentage of macroinvertebrate biomass derived from the food resources at natural shorelines, retaining walls and beaches at the three studied lakes (TL = trophic level). Values in parentheses refer to the contribution of the food resources to macroinvertebrate biomass including the biomass of *Dreissena polymorpha* (Bivalvia). See chapter 4 for further explanation.

	Grienericksee				**Langer See**				**Unteruckersee**			
	Natural		**Retaining wall**	**Beach**	**Natural**	**Retaining wall**		**Beach**	**Natural**	**Retaining wall**		**Beach**
	TL 2	**TL 3**	**TL 2**	**TL 2**	**TL 2**	**TL 2**	**TL 3**	**TL 2**	**TL 2**	**TL 2**	**TL 3**	**TL 2**
Allochthonous POM	**11**	**29**		**12**	**5 (3)**	**1 (0)**						
Alder leaves	4	29		12	1 (1)	1 (0)						
Riparian vegetation	7				4 (2)							
Detritus	**9**		**19**		**0 (0)**			**5**	**52 (33)**	**57 (51)**		**82**
Reed					0 (0)							
Sand	9		19					5	52 (33)	57 (51)		56
Submerged macrophytes												26
Periphyton	**54**	**65**	**36**		**36 (18)**	**56 (29)**	**67 (67)**		**14 (9)**	**13 (12)**	**68 (68)**	
CWD	28	65			34 (17)				12 (8)			
Concrete						2 (1)				5 (5)		
Reed	22				2 (1)				0 (0)			
Stone	4		36			54 (28)	67 (67)		2 (1)	8 (7)		
Seston	**26**	**6**	**45**	**88**	**59 (79)**	**43 (71)**	**33 (33)**	**95**	**34 (58)**	**30 (37)**	**32 (32)**	**18**

Table 13. Elemental composition (median, range) of consumers and their food resources among the three studied shoreline types. Elemental imbalance was calculated as the difference (median, range) between a food resource and its consumer. All ratios are molar. Significant differences (Kruskal-Wallis test, Dunn's multiple comparisons) between natural and developed shorelines are indicated by asterisks (**$P < 0.01$, * $P < 0.05$).

	Consumer			**Food resource**			**Elemental imbalance**		
	Natural	**Retaining wall**	**Beach**	**Natural**	**Retaining wall**	**Beach**	**Natural**	**Retaining wall**	**Beach**
Scraper									
C:P	131 (105-375)	143 (102-248)		257 (142-526)	152** (92-260)		106 (-204-416)	-6** (-106-129)	
C:N	6 (5-7)	6 (5-7)		15 (9-22)	10** (9-15)		8 (4-17)	5** (3-9)	
N:P	24 (19-58)	25 (18-36)		16 (14-25)	14** (9-18)		-6 (-42-2)	-11* (-27- -4)	
Collector									
C:P	123 (64-155)	118 (90-139)	91 (87-143)	249 (135-776)	167* (155-261)	176* (117-445)	142 (8-712)	55* (28-127)	58* (6-307)
C:N	5 (5-7)	5 (5-7)	5 (5-6)	18 (11-30)	18 (10-20)	19 (12-21)	12 (6-24)	11 (8-15)	14 (7-16)
N:P	23 (14-30)	21 (17-28)	18 (17-24)	15 (6-33)	10* (9-14)	12 (6-23)	-4 (-17-20)	-10 (-16- -6)	-10 (-17- -1)

Table 14. Geographical location, area (km^2), trophic status, and hydraulic residence time (RT, year) of the studied lakes.

	Geographical location				
	Latitude	**Longitude**	**Area**	**Trophic state**	**RT**
Grienericksee	53°06’22”	12°53’12”	2.69	eutrophic	0.40
Langer See	52°24’32”	13°36’50”	2.51	hypertrophic	0.10
Müggelsee	52°26’16”	13°38’55”	7.70	eutrophic	0.16
Plauer See	52°23’33”	12°26’33”	6.70	hypertrophic	0.01
Unteruckersee	53°16’41”	13°51’51”	10.40	mesotrophic	2.00
Werbellinsee	52°55’16”	13°42’43”	1.80	mesotrophic	54.79

Table 15. Median (range) relative abundances of the major invertebrate taxonomic groups at the five studied habitat types present in the eulittoral and infralittoral zone. Significantly lower abundances (Mann-Whitney test, Bonferroni adjusted *P*) between root and infralittoral habitats are indicated by asterisks (***P* < 0.01, * *P* < 0.05).

	Eulittoral	**Infralittoral**			
	Roots	**CWD**	**Reed**	**Sand**	**Stones**
Bivalvia	0.0	0.0	0.0	48.1	0.0
	0.0-0.2	0.0-0.0	0.0-2.2	8.4-67.3	0.0-0.3
Coleoptera	9.6	4.5	1.4**	0.2**	0.4*
	1.4-37.0	0.0-56.1	0.0-5.0	0.0-3.1	0.0-21.3
Crustacea	0.0	0.0	0.0	0.0	0.0
	0.0-3.8	0.0-0.6	0.0-10.6	0.0-0.1	0.0-0.2
Ephemeroptera	16.3	0.7*	2.6	26.3	5.1
	7.7-48.5	0.0-27.8	0.0-35.6	0.2-57.3	0.2-54.0
Gastropoda	23.1	6.1	51.7	20.9	11.2
	3.8-73.3	1.5-71.7	23.6-92.7	0.0-76.9	0.1-65.9
Heteroptera	0.3	0.0	0.6	2.4	0.3
	0.0-3.8	0.0-0.9	0.0-20.7	0.5-6.9	0.0-1.0
Hirudinea	0.7	0.4	0.9	0.2	0.3
	0.0-4.8	0.0-3.3	0.0-2.8	0.0-2.1	0.0-1.5
Odonata	4.0	0.0	0.4	0.0	0.0**
	0.0-9.4	0.0-0.5	0.0-1.4	0.0-0.1	0.0-0.2
Trichoptera	27.4	75.7	23.1	3.7**	60.7
	11.3-42.3	19.8-98.1	4.3-67.3	1.5-19.0	18.0-97.3
Turbellaria	0.3	0.0	0.0	0.0	0.3
	0.0-35.8	0.0-11.8	0.0-1.8	0.0-0.1	0.0-13.3

Table 16. Indicator species analysis of the five studied habitat types present in the eulittoral and infralittoral zone. For each indicator species, its indicator value and level of significance (***$P < 0.001$, ** $P < 0.01$, * $P < 0.05$) is given.

	Eulittoral	**Infralittoral**			
	Roots	**CWD**	**Sand**	**Stones**	**Reed**
Gastropoda					
Gyraulus crista			46*		
Valvata piscinalis			48*		
Bivalvia					
Pisidium casertanum			88***		
P. henslowanum			75***		
P. moitessierianum			38*		
P. nitidum			100***		
P. subtruncatum			50**		
P. supinum			50**		
Unio tumidus			63***		
Ephemeroptera					
Caenis horaria			61*		
Odonata					
Ischnura elegans	69***				
Heteroptera					
Micronecta sp.			79***		
Coleoptera					
Cercyon sp.	32*				
Dryops sp. larvae	33*				
Haliplus flavicollis	46*				
Orectochilus villosus larvae		43*			
Trichoptera					
Goera pilosa				46*	
Lype phaeopa		67**			
Molanna angustata			43**		
Tinodes waeneri				64**	

Table 17. Median (range) relative abundances of the invertebrate functional feeding groups at the five studied habitat types present in the eulittoral and infralittoral zones. Significantly lower abundances (Mann-Whitney test, Bonferroni adjusted *P*) between root and the infralittoral habitat types are indicated by asterisks (****P* < 0.001, ** *P* < 0.01).

	Eulittoral	**Infralittoral**			
	Root	**CWD**	**Reed**	**Sand**	**Stone**
	33.9	17.6	30.1	45.3	22.9
Collector/Gatherer	16.9-44.6	2.1-37.9	9.6-50.2	14.7-64.5	5.3-62.5
	1.7	5.6	4.1	48.3	5.1
Filterer	0.0-6.8	1.4-9.3	1.3-7.2	9.6-69.2	1.8-8.7
	6.4	6.3	7.3	0.7**	5.1
Piercer	1.1-15.4	2.7-25.1	1.1-22.9	0.0-3.6	0.8-32.9
	18.9	15.9	8.0	1.5**	14.8
Predator	2.9-47.7	2.8-74.0	1.0-10.9	0.2-6.4	4.4-48.2
	24.2	37.0	43.8	12.0	28.6
Scraper	9.2-37.3	5.6-61.9	27.3-55.0	0.1-31.0	11.6-58.6
	7.0	2.3**	8.2	3.0**	1.8***
Shredder	5.0-20.4	0.1-6.3	2.0-14.1	0.3-5.8	0.0-4.9
	0.7	1.5	0.0	0.0**	0.0
Xylophagous	0.0-4.2	0.0-44.4	0.0-7.1	0.0-0.0	0.0-3.0

Table 18. Flow conditions in the wave tank. For each shear stress level applied (combination of bucket weights [kg] and water depths [cm]), the mean (± SE) respective wave height (cm) and velocity (cm s^{-1}), as well as the calculated shear stress value (N m^{-2}) with its coefficient of variation (CV, *n* = 10) is given. The level of significance (*P*) refers to the test of differences between two consecutive shear stress levels (ANOVA, Scheffé's post hoc, *n* = 10).

Weight	Water depth	Wave height	Wave velocity	Shear stress	*P*	CV
8	15	1.50 ± 0.02	11.18 ± 0.06	0.432 ± 0.002	<0.001	2.17
10	15	2.50 ± 0.03	19.29 ± 0.11	0.751 ± 0.003	<0.001	1.55
12	15	3.64 ± 0.03	28.16 ± 0.01	1.111 ± 0.004		1.13
14	15	4.85 ± 0.03	33.74 ± 0.09	1.254 ± 0.004	<0.001	1.50
16	15	6.45 ± 0.04	39.32 ± 0.11	1.369 ± 0.004	<0.001	1.00
18	15	6.92 ± 0.04	42.37 ± 0.10	1.483 ± 0.003	<0.001	0.81
20	15	7.42 ± 0.04	45.22 ± 0.10	1.579 ± 0.002		0.39
22	15	7.96 ± 0.04	47.45 ± 0.10	1.636 ± 0.003	<0.01	0.54
10	10	5.00 ± 0.04	46.29 ± 0.09	1.985 ± 0.005	<0.05	0.74
12	10	5.44 ± 0.03	50.85 ± 0.13	2.189 ± 0.005	<0.001	0.36

Table 19. Sigmoid regression analysis (ln $y = b_0 + b_1/t$) between number of detached individuals and shear stress. For each test, the R^2 value (adjusted for degrees of freedom), the corresponding significance levels (***$P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. not significant) and the curve coefficients (b_0 / b_1) are given (CWD = coarse woody debris).

	CWD	**Reeds**	**Roots**	**Sand**	**Stones**
Bithynia tentaculata	0.81*** (7.9 / -94.0)	0.48* (2.4 / -56.3)	0.52* (3.3 / -75.3)	0.96*** (8.0 / -80.1)	0.02 n.s. (1.8 / -26.0)
Calopteryx splendens	0.66* (1.8 / -9.7)	0.64* (9.2 / -157.8)	0.05 n.s. (-9.1 / -14.3)	0.94*** (3.8 / -12.5)	0.79*** (2.5 / -8.5)
Dikerogammarus villosus	0.84*** (6.1 / -71.3)	0.92*** (2.8 / -15.3)	0.06 n.s. (-9.2 / -14.4)	0.81*** (3.8 / -24.0)	0.56** (3.7 / -80.2)
Gammarus roeseli	0.92*** (3.1 / -14.8)	0.94*** (6.6 / -70.0)	0	0.77** (3.7 / -21.0)	0.88*** (3.5 / -21.3)
Laccophilus hyalinus	0.92*** (8.0 / -78.6)	0.91*** (4.0 / -21.5)	0.12 n.s. (-0.5 / -5.0)	0.98*** (4.0 / -16.7)	0.88*** (4.2 / -25.0)

Table 20. Mean number (± SE) of detached individuals ($n = 3$) for the cross combinations of species and habitats studied (CWD = coarse woody debris).

	CWD	**Reeds**	**Roots**	**Sand**	**Stones**
Bithynia tentaculata	8 ± 0.2	1.23 ± 0.0	1.47 ± 0.1	10.54 ± 0.4	2.23 ± .0.1
Calopteryx splendens	2.97 ± 0.1	0.8 ± 2.1	0.03± 0.0	13.27 ± 0.3	6.5 ± 0.3
Dikerogammarus villosus	2.9 ± 0.1	4.73 ± 0.1	0.03 ± 0.0	8.96 ± 0.2	0.9 ± 0.1
Gammarus roeseli	7.47 ± 0.1	5.07 ± 0.5	0.0 ± 0.0	8.5 ± 0.3	7.9 ± 0.2
Laccophilus hyalinus	10.54 ± 0.2	10.58 ± 0.3	1.47 ± 0.1	11.94 ± 0.3	9.62 ± 0.3

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Appendix I

Table 1. Median elemental composition (range) of food resources and macroinvertebrates included in the food webs at the three studied shoreline types. All ratios are molar.

	Natural shoreline			**Retaining wall**			**Beach**		
	C:N	**C:P**	**N:P**	**C:N**	**C:P**	**N:P**	**C:N**	**C:P**	**N:P**
Food resources									
Allochthonous POM									
Alder leaves	24 (22-27)	1858 (908-2808)	73 (42-104)	45	1682	38	33	951	29
Riparian vegetation	22 (15-29)	559 (440-678)	26 (23-28)						
Detritus									
Reed	18	202	12						
Sand	20 (18-22)	175 (111-239)	9 (5-13)	28 (25-31)	226 (189-263)	8 (6-10)	23 (21-25)	216 (117-374)	9 (5-17)
Submerged macrophytes							17	245	14
Periphyton									
Coarse woody debris	17 (16-19)	268 (230-331)	15 (15-18)						
Concrete				15 (10-19)	265 (142-388)	17 (14-20)			
Reed	15 (11-16)	249 (197-299)	17 (16-20)						
Stone	16 (15-18)	250 (222-279)	15 (15-16)	12 (10-15)	163 (92-247)	14 (9-16)			
Seston	8 (8-12)	127 (107-257)	16 (14-21)	8 (8-12)	127 (107-257)	16 (14-21)	8 (8-12)	127 (107-257)	16 (14-21)

Table 1. continued

	Natural shoreline			**Retaining wall**			**Beach**		
	C:N	**C:P**	**N:P**	**C:N**	**C:P**	**N:P**	**C:N**	**C:P**	**N:P**
Macroinvertebrates									
Acroloxus lacustris	5 (5-6)	112 (109-130)	22 (22-22)						
Anodonta cygnea	5 (5-5)	56 (25-87)	11 (5-17)	5	41	9	5	55	12
Asellus aquaticus	5	64	14						
Bithynia leachi	5 (5-6)	132 (124-141)	24 (23-25)						
Bithynia tentaculata	5 (5-6)	134 (123-155)	25 (23-30)	6 (5-6)	141 (138-156)	26 (23-28)			
Caenis sp.	5	120	24						
Chelicorophium curvispinum	6 (6-6)	87 (86-88)	14 (14-15)	6 (6-6)	93 (92-93)	15 (15-15)			
Chironominae	6 (5-7)	142 (116-169)	23 (20-25)	7 (5-7)	142 (116-169)	23 (20-25)	5 (5-5)	110 (81-164)	23 (17-30)
Cloeon dipterum	5	110	23						
Dikerogammarus haemobaphes	6	101	18						
Dikerogammarus villosus	5 (5-6)	105 (101-107)	19 (19-20)	6	102	18			
Dreissena polymorpha	5 (5-5)	118 (103-122)	22 (21-24)	5 (5-5)	120 (120-122)	24 (24-24)			
Ecnomus tenellus				7	165	25			
Erpobdella octoculata	5	139	29	5 (5-5)	163 (154-172)	34 (33-36)			
Gyraulus albus	5	145	28						
Haliplus sp.	6	375	58						
Lype phaeopa	6	187	33						
Molanna angustata	6	86	15	7	132	20			

Table 1. continued

	Natural shoreline			Retaining wall			Beach		
	C:N	**C:P**	**N:P**	**C:N**	**C:P**	**N:P**	**C:N**	**C:P**	**N:P**
Mystacides niger/longicornis	6 (6-7)	180 (157-268)	30 (23-42)						
Oligochaeta	6 (5-6)	112 (88-136)	20 (17-23)	5	95	18	5	91	18
Oulimnius sp.	7	155	23						
Physa fontinalis	5	109	21						
Pisidium sp.	5	95	20	5	98	21	5 (5-5)	102 (99-106)	21 (21-22)
Platambus maculatus	5	244	39						
Pontogammarus robustoides	5 (5-5)	89 (86-100)	18 (17-19)	5	93	18	5 (5-5)	90 (89-90)	19 (19-19)
Potamopyrgus antipodarum	6 (5-6)	132 (127-136)	25 (23-26)	6 (5-6)	138 (138-139)	24 (23-25)	6 (5-6)	143 (127-136)	24 (23-26)
Radix balthica	5 (5-5)	116 (99-122)	24 (22-26)	5	121	25			
Sphaerium corneum	5	132	27				5	122	24
Tinodes waeneri	6 (6-6)	183 (134-199)	31 (24-32)	6 (5-7)	163 (131-248)	28 (22-36)			
Unio tumidus				6	65	11	6	65	12
Valvata piscinalis				5	118	22			

Table 2. δ13C and δ15N values (‰) of food resources and macroinvertebrates at the Grienericksee. The mean (± SD) is given if a macroinvertebrate species was recorded on more than one habitat at the shoreline types.

	Natural shoreline		**Retaining wall**		**Beach**	
	$\delta^{13}C$	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Food resources						
Allochthonous POM						
Alder leaves	-29.9	1.5			-29.7	-0.3
Riparian vegetation	-30.6	1.8				
Detritus						
Sand	-26.7	5.5	-21.0	3.5		
Periphyton						
Coarse woody debris	-28.3	4.6				
Reed	-27.7	4.8				
Stone	-21.3	3.5	-16.9	2.2		
Seston	-24.1	4.0	-24.1	4.0	-24.1	4.0
Macroinvertebrates						
Acroloxus lacustris	-27.7	5.3				
Asellus aquaticus	-29.1	3.6				
Bithynia leachi	-29.6 ± 0.1	3.6 ± 0.0				
Bithynia tentaculata	-30.2	3.4				
Caenis sp.	-29.5	3.0				
Chironominae	-26.4 ± 2.0	4.2 ± 0.3	-21.9 ± 0.8	4.0 ± 0.2	-26.9 ± 0.4	5.3 ± 0.5
Cloeon dipterum	-28.8					
Dikerogammarus haemobaphes	-30.3	4.5				
Erpobdella octoculata	-28.3	6.7				
Lype phaeopa	-27.9	4.8				

Table 2. continued

	Natural shoreline		**Retaining wall**		**Beach**	
	$\delta^{13}C$	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Mystacides niger/longicornis	-29.9 ± 0.6	4.9 ± 0.3				
Oligochaeta	-27.9	6.7				
Oulimnius sp.	-23.4	2.1				
Platambus maculatus	-30.1	6.6				
Potamopyrgus antipodarum	-28.6	3.5			-24.7 ± 0.6	4.1 ± 0.4
Radix balthica	-27.6	3.9				
Sphaerium corneum	-30.4	4.4			-27.1	5.3
Tinodes waeneri	-21.8	2.0	-18.3	2.1		

Table 3. δ13C and δ15N values (‰) of food resources and macroinvertebrates at the Langer See. The mean (± SD) is given if a macroinvertebrate species was recorded on more than one habitat at the shoreline types.

	Natural shoreline		**Retaining wall**		**Beach**	
	$\delta^{13}C$	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Food resources						
Allochthonous POM						
Alder leaves	-29.8	0.9	-30.1	3.1		
Riparian vegetation	-34.4	5.5				
Detritus						
Reed	-28.3	7.1				
Sand					-27.4	5.5
Periphyton						
Coarse woody debris	-29.8	6.7				
Concrete			-28.7	9.6		
Reed	-29.0	10.5				
Stone			-29.9	10.6		
Seston	-33.5	9.5	-33.5	9.5	-33.5	9.5
Macroinvertebrates						
Acroloxus lacustris	-29.5	10.1				
Anodonta cygnea	-34.2	8.2				
Bithynia tentaculata	-33.2 ± 0.6	7.6 ± 1.1	-33.1 ± 1.0	7.9 ± 0.0		
Chironominae	-32.1 ± 1.5	8.2 ± 0.2	-31.1 ± 1.1	8.3 ± 0.9	-31.6 ± 0.6	9.2 ± 0.2
Dikerogammarus villosus	-32.4 ± 0.5	9.2 ± 0.1	-30.8	9.1		
Dreissena polymorpha	-33.5 ± 0.1	8.8 ± 0.2	-33.0 ± 0.3	7.9 ± 0.9		
Ecnomus tenellus			-32.6	10.7		
Erpobdella octoculata			-30.8	9.6		

Table 3. continued

	Natural shoreline		**Retaining wall**		**Beach**	
	$\delta^{13}C$	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Gyraulus albus	-30.8	8.7				
Potamopyrgus antipodarum			-31.3	9.9		
Radix balthica	-31.9	10.5 ± 0.5				
Sphaerium corneum						
Tinodes waeneri	-30.5	8.8	-29.6 ± 0.0	9.3 ± 1.1		
Unio tumidus			-32.9	8.9	-32.9	9.8

Table 4. δ13C and δ15N values (‰) of food resources and macroinvertebrates at the Unteruckersee. The mean (± SD) is given if a macroinvertebrate species was recorded on more than one habitat at the shoreline types.

	Natural shoreline		**Retaining wall**		**Beach**	
	$\delta^{13}C$	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Food resources						
Detritus						
Sand	-20.3	8.4	-15.3	7.9	-14.3	9.2
Submerged macrophytes					-14.2	8.4
Periphyton						
Coarse woody debris	-24.6	9.6				
Concrete			-9.6	6.6		
Reed	-22.1	8.4				
Stone	-16.8	9.9	-15.5	8.9		
Seston	-26.7	9.0	-26.7	9.0	-26.7	9.0
Macroinvertebrates						
Acroloxus lacustris	-24.1	9.6				
Anodonta cygnea	-24.9	11.8	-25.2	10.1	-25.0	9.2
Bithynia tentaculata	-23.6 ± 1.0	10.0 ± 0.7	-20.8 ± 0.5	7.6 ± 0.3		
Caenis sp.						
Chelicorophium curvispinum	-27.3 ± 0.5	10.8 ± 0.0	-25.5 ± 0.2	10.0 ± 0.1		
Chironominae	-23.8	10.5	-21.4	9.6	-21.5 ± 1.0	10.2 ± 0.2
Dreissena polymorpha	-27.0 ± 0.4	9.3 ± 0.3	-25.5	9.4		
Erpobdella octoculata			-19.0	11.0		
Haliplus sp.	-22.1	8.3				
Molanna angustata	-23.8	11.1	-21.3	10.2		

Table 4. continued

	Natural shoreline		**Retaining wall**		**Beach**	
	$\delta^{13}C$	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Mystacides niger/longicornis	-22.7	9.6				
Oligochaeta	-24.6	9.8	-23.2	11.0	-21.0	9.7
Physa fontinalis			-21.4	8.7		
Pisidium sp.	-24.2	9.3	-22.8	9.7	-22.1 ± 0.2	8.6 ± 0.2
Pontogammarus robustoides	-21.8 ± 0.3	9.1 ± 0.3	-19.6	7.9	-19.7 ± 0.0	9.6 ± 0.1
Potamopyrgus antipodarum	-22.6 ± 0.9	9.8 ± 0.1	-20.9	8.2	-19.2	8.8
Radix balthica	-21.3	8.5	-19.6	7.4		
Tinodes waeneri	-20.7	6.5	-16.1 ± 0.2	5.8 ± 0.7		
Valvata piscinalis			-19.6	7.8		

Appendix II

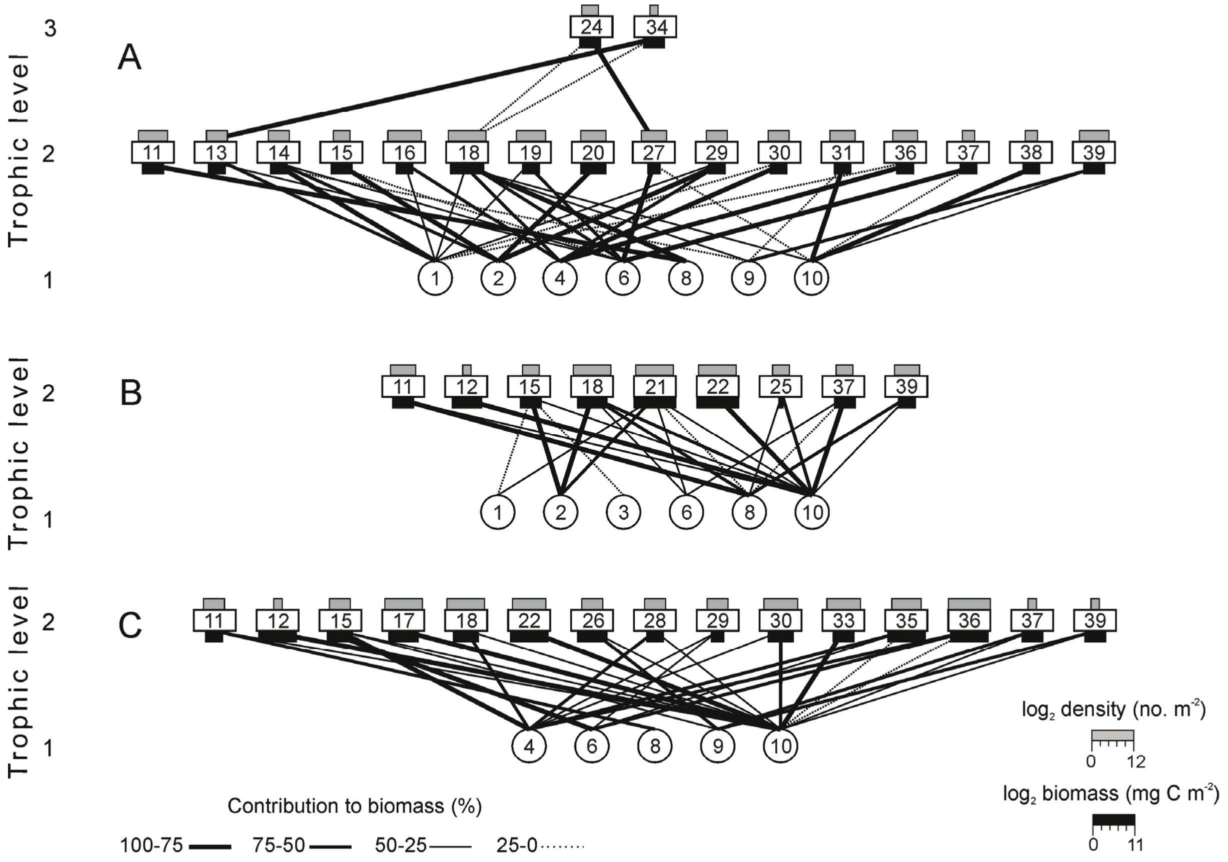

Fig. 1. Macroinvertebrate food webs of natural shorelines at the (A) Grienericksee, (B) Langer See and (C) Unteruckersee. The width of the grey and black bars indicates the species-specific log$_2$ density and the log$_2$ biomass, respectively. Line thickness corresponds to the percentage contribution of the lower trophic level to the biomass of the next higher trophic level. If a species was recorded on more than one habitat, means for density, biomass and percentage contribution to biomass are given. The vertical position of food resources and macroinvertebrates represents their trophic level. Food resources were assigned to trophic level one, the trophic level of macroinvertebrate consumers was calculated after Vander Zanden and Rasmussen (1999) but rounded to integers to improve readability. Food resources (circles) are: Allochthonous POM in the form of (1) alder leaves and (2) riparian vegetation; Detritus (3) in reed stands, (4) on sand, and (5) from submerged macrophytes; Periphyton on (6) coarse woody debris, (7) concrete, (8) reed, and (9) stones; and (10) seston. Species (squares) are: (11) *Acroloxus lacustris*, (12) *Anodonta cygnea*, (13) *Asellus aquaticus*, (14) Bithynia *leachi*, (15) *Bithynia tentaculata*, (16) *Caenis* sp., (17) *Chelicorophium curvispinum*, (18) Chironominae, (19) *Cloeon dipterum*, (20) *Dikerogammarus haemobaphes*, (21) *Dikerogammarus villosus*, (22) *Dreissena polymorpha*, (23) Ecnomus *tenellus*, (24) *Erpobdella octoculata*, (25) Gyraulus *albus*, (26) *Haliplus* sp., (27) *Lype phaeopa*, (28) *Molanna angustata*, (29) *Mystacides niger/longicornis*, (30) Oligochaeta, (31) *Oulimnius* sp., (32) *Physa fontinalis*, (33) *Pisidium* sp., (34) *Platambus maculatus*, (35) *Pontogammarus robustoides*, (36) *Potamopyrgus antipodarum*, (37) *Radix balthica*, (38) *Sphaerium corneum*, (39) *Tinodes waeneri*, (40) *Unio tumidus*, and (41) *Valvata piscinalis*.

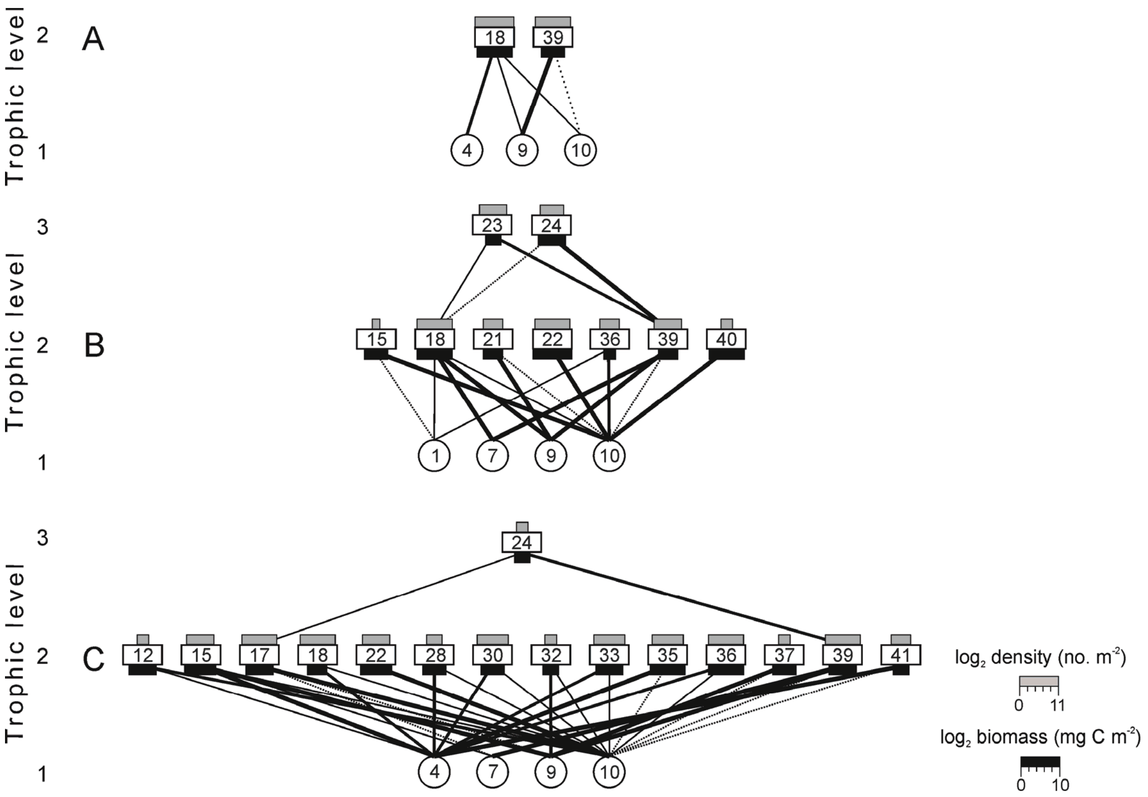

Fig. 2. Macroinvertebrate food webs of retaining walls at the (A) Grienericksee, (B) Langer See and (C) Unteruckersee. See Figure 1 for codes to food resources and species.

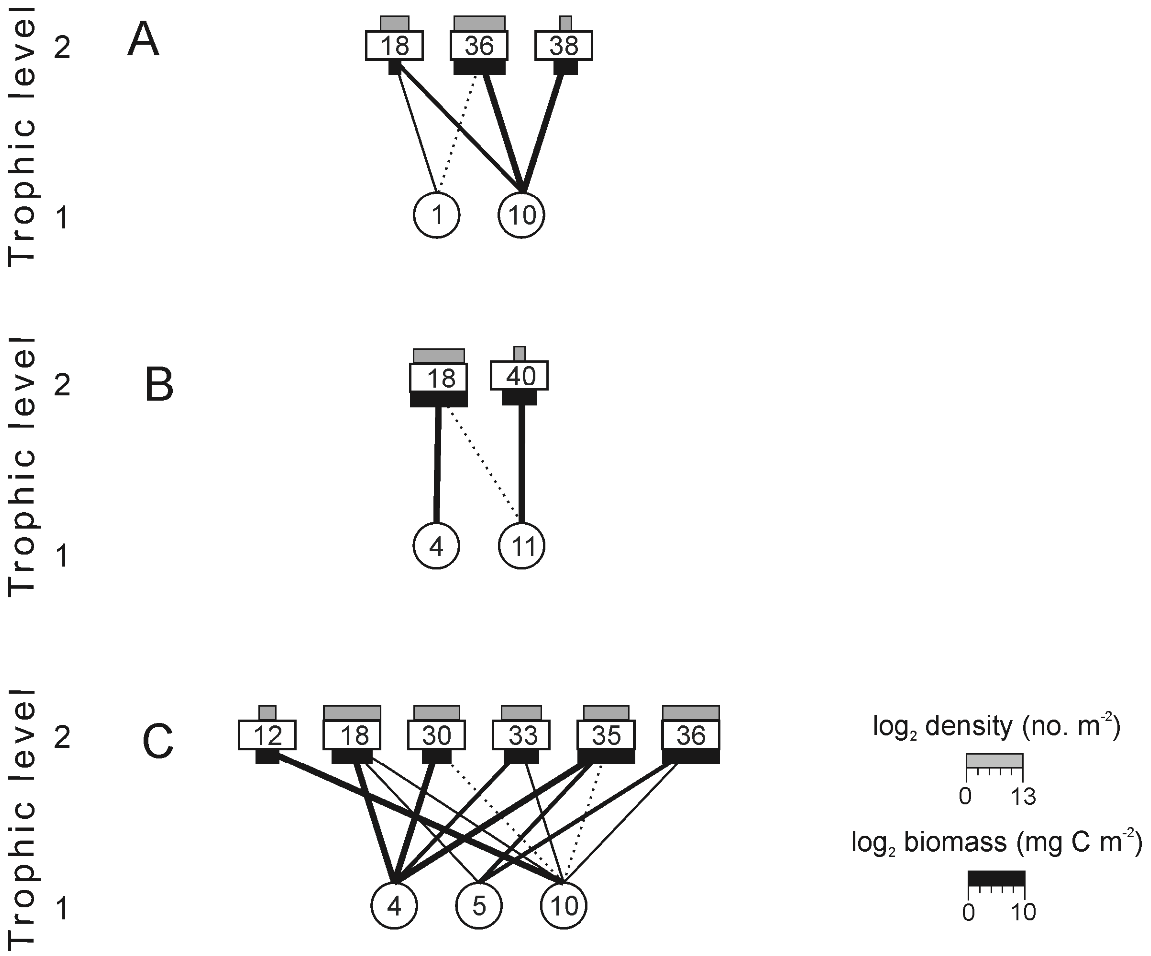

Fig. 3. Macroinvertebrate food webs of recreational beaches at the (A) Grienericksee, (B) Langer See and (C) Unteruckersee. See Figure 1 for codes to food resources and species.