Effect of lakeshore modification on structure and secondary production of macroinvertebrates in a large temperate lowland lake of Northeast Germany

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Summary

Many lake water bodies not attained the goal of the European Water Framework Directive (WFD) to achieve a good ecological state by 2015. This is, among other things, because the assessment and improvement of hydromorphological conditions of lakeshores has been neglected as an important component ensuring the ecological integrity of lake ecosystems. In recent years, macroinvertebrates were emphasized to be useful indicators for the assessment of lakeshore hydromorphology. Hence, in Europe macroinvertebrate-based assessment methods were developed to evaluate the hydromorphological conditions of lakeshores.

In this thesis, some of the uncertainties and missing aspects of existing macroinvertebrate-based assessment methods were addressed. The results were obtained by sampling macroinvertebrates and macrophytes at natural shores and at shores modified by marinas and beaches in three depth zones between April and November 2011 in a large lowland lake (Lake Scharmützelsee, Germany).

Firstly, I clarified that upper littoral macroinvertebrates should be used for assessing the hydromorphology of lakeshores. It was shown that the effect of lakeshore modification on macroinvertebrate diversity and community composition was most pronounced in the upper littoral and decreased to the profundal zone. Secondly, I demonstrated that a single seasonal sampling is sufficient to capture the compositional differences of macroinvertebrate communities associated with human lakeshore modification. Seasonal effects on upper littoral macroinvertebrate diversity and composition were less important than shore type in comparison with the middle littoral and profundal zone. Thirdly, upper littoral macrophyte communities were also affected by lakeshore modification and at the same time the most important variable structuring macroinvertebrate communities. Hence, the effects of different shore types on macrophytes were transferred to macroinvertebrates, but artificial substrates were also able to partly substitute macrophyte habitats as it was shown for the studied marinas. Since lakeshore modification affected macrophytes slightly differently than macroinvertebrates, macrophytes should be considered as an additional component in lakeshore assessment. Finally, secondary production as proxy to determine the effect of lakeshore modification on the functioning of macroinvertebrates was estimated. Estimation of secondary production requires the determination of biomass. Biomass was indirectly determined by using length-mass regressions established for macroinvertebrates from temperate lakes of the central European lowland. The result showed that total secondary production and secondary production of native taxa in the upper littoral was substantially lower at the studied beaches compared to natural sites. In contrast, upper littoral secondary production at marinas did not differ to natural sites, but secondary production of non-native taxa was significantly higher at marinas. No effects of lakeshore modification on secondary production were found with increasing depth. Different scenarios based on upscaling of site-specific production to whole lake ecosystem level gave evidence that the observed local impacts of lakeshore modification can translate into alterations of the functioning of macroinvertebrates at whole lake ecosystem level. In addition, it was emphasized that secondary production as a functional measure is more sensitive in detecting hydromorphological alterations than the structural measures diversity or biomass. Secondary production should therefore be included in existing lakeshore assessment methods. In order to obtain a comprehensive overview about the changes in the functioning of macroinvertebrates following lakeshore modification, it is recommended to consider not only total secondary production but also secondary production of functional groups. With these results, this thesis contributes to the mechanistic understanding of the effect of lakeshore modification on the functioning of macroinvertebrates and the consequences for the functioning of the whole lake ecosystem. The newly generated knowledge helps to optimize the development of successful lakeshore assessment tools and identification of management measures.

Zusammenfassung

Viele stehende Gewässer haben es nicht geschafft, das Ziel der Europäischen Wasserrahmenrichtline (WRRL) bis 2015 einen gut ökologischen Zustand zu erreichen. Dies liegt unter anderem an dem Versäumnis die Bewertung und Verbesserung des hydromorphologischen Zustands von Seeufern in bisherige Ansätze zu integrieren. Seeufer stellen eine wichtige Komponente von Seeökosystemen dar, um die Intaktheit dieser zu gewährleisten. In den vergangenen Jahren wurden Makroinvertebraten als brauchbare Indikatoren für die Bewertung der Seeuferhydromorphologie hervorgehoben. Daraufhin wurden in Europa einige Bewertungsmethoden basierend auf Makroinvertebraten entwickelt, um den hydromorphologischen Zustand von Seeufern beurteilen zu können.

In dieser Doktorarbeit werden einige Unsicherheiten und fehlende Aspekte existierender Makroinvertebraten-basierenden Bewertungsmethoden addressiert. Die Ergebnisse wurden erzielt, in dem Makroinvertebraten an natürlichen Seeufern und an Seeufern, modifiziert in Form von Häfen und Strände, in drei Tiefenzonen zwischen April und November 2011 an einem großen Tieflandsee (Scharmützelsee, Deutschland) beprobt wurden.

Als Erstes konnte ich aufzeigen, dass die Makroinvertebraten des oberen Litorals zur Bewertung der Hydromorphologie von Seeufern herangezogen werden sollten. Die Auswirkungen anthropogen modifizierter Seeufer auf die Diversität und Zusammensetzung der Makroinvertebraten waren am stärksten im oberen Litoral und nahmen zum Profundal hin ab. Zum Zweiten konnte ich nachweisen, dass eine Beprobung pro Jahr aussreicht, um die Unterschiede in der Makroinvertebraten-Gesellschaft als Folge von Seeufermodifikationen zu erfassen. Jahreszeitliche Einflüsse auf die Diversität und Zusammensetzung der Makroinvertebraten wurden im oberen Litoral von den Auswirkungen der modifizierten Seeufer überlagert, jedoch nicht mehr im mittleren Litoral und im Profundal. Drittens konnte ich zeigen, dass die Makrophyten-Gesellschaften des oberen Litorals ebenfalls von den Modifikationen des Seeufers beeinflusst waren. Gleichzeitig wurden Makrophyten als die bedeutenste Variable, die Makroinvertebraten-Gesellschaften strukturiert, identifiziert. Demnach übertrugen sich die Auswirkungen von Seeufermodifikationen auf Makrophyten weiter auf die Makroinvertebraten. Makropyhten-Habitate konnten jedoch teilweise durch künstliche Substrate ersetzt werden, wie an den Häfen aufgezeigt. Da sich

Seeufermodifikationen etwas anders auf Makrophyten auswirkten als auf Makroinvertebraten, sollten Makrophyten als zusätzliche Komponente zur Bewertung von Seeufern herangezogen werden. Abschließend wurde die Sekundärproduktion als Proxy zur Bestimmung der Auswirkungen von Seeufermodifikationen auf die Funktionalität von Makroinvertebraten abgeschätzt. Die Abschätzung der Sekundärproduktion erfordert die Bestimmung der Biomasse. Diese wurde indirekt mit Hilfe von Längen-Massen-Regressionen bestimmt. Die Längen-Massen-Regressionen wurden anhand von Makroinvertebraten aus Seen des zentraleuropäischen Tieflands erstellt. Im Ergebnis zeigte sich, dass die gesamte Sekundärproduktion und die Sekundärproduktion heimischer Taxa des oberen Litorals an den untersuchten Stränden, im Vergleich zu den natürlichen Stellen, beträchtlich verringert waren. Dagegen änderte sich die gesamte Sekundärproduktion an den untersuchten Häfen des oberen Litorals, im Vergleich zu den natürlichen Stellen, nicht. Der Anteil der Produktion von nichtheimischen Arten an den Häfen war jedoch höher gegenüber natürlichen Ufern. Keine Auswirkungen von Seeufermodifikationen auf die Sekundärproduktion konnte in den tieferen Wasserzonen gefunden werden. Unterschiedliche Szenarien, die auf Basis von Hochrechnung der standortspezifischen Sekundärproduktion auf Ebene des gesamten Sees erzeugt wurden, belegen dass lokale Auswirkungen von Seeufermodifikationen auch auf Ebene des gesamten Seeökosystems bemerkbar werden. Zusätzlich wurde bestätigt, dass die Sekundärproduktion als Maß für die Funktionalität eine höhere Sensitivität aufweist, Auswirkungen von Seeufermodifikationen zu erkennen, als die strukturellen Maße Diversität und Biomasse. Deshalb sollte die Sekundärproduktion in existierende Bewertungsmethoden für Seeufer aufgenommen werden. Um einen umfassenden Überblick über die Änderungen der Funktionalität von Makroinvertebraten als Folge von Seeufermodifikationen zu erhalten, wird nicht nur empfohlen die gesamte Sekundärproduktion, sondern auch die Sekundärproduktion funktioneller Gruppen zu berücksichtigen. Mit diesen Ergebnissen trägt die vorliegende Doktorarbeit zum mechanistischen Verständnis der Auswirkungen der Seeufermodifikation auf die Funktionalität der Makroinvertebraten und der Konsequenzen für das gesamte Seeökosystem bei. Das neu generierte Wissen hilft, die Entwicklung von erfolgsversprechenden Methoden für die Seeuferbewertung und Identifikation von Managementmaßnahmen zu optimieren.

Table of content

List of Figures

List of Tables

Abbreviation

AFDM	Ash Free Dry Mass
AIC	An Information Criterion
ANN	Artificial Neural Network
ANCOVA	ANalysis of COVariance
ANOVA	ANalysis Of VAriance
B	Biomass
Ca	Calcium
CAP	Constrained Analysis of Principle coordinates
Chl *a*	Chlorophyll a
CI	Confidence Interval
D	Germany
DISTLM	DIStance-based Linear Model
DK	Denmark
DM	Dry Mass
e.g.	for example
etc.	et cetera
Fin	Finland
FM	Fresh Mass
GB	Great Britain
HML	HydroMorphology of Lakes
IC	Central Italy
IN	Northern Italy
IndVal	Indicator species analysis
i.e.	id est
IR	IReland
LIMHA	Littoral Invertebrate Multimetric based on HAbitat samples
LIMCO	Littoral Invertebrate Multimetric based on COmposite samples
LLR	Log-Linear Regression
NLR	NonLinear Regression
nMDS	nonmetric MultiDimensional Scaling
P	(Secondary) Production
p	significance value
P/B	Production to biomass ratio
PC	Principal Component
PCA	Principal Component Analyses
perANOVA	permutation ANalysis Of VAriance
perMANOVA	permutation Multivariate ANalyses Of VAriance
PERMDISP	Test of homogeneity of dispersion
R^2	Coefficient of determination
S	Sweden
vs.	versus
WFD	Water Framework Directive

1 General introduction

1.1 The Water Framework Directive (WFD) and the present state of European lakes

The need to protect European waters has long been recognized. In December 2000, the European Water Framework Directive (WFD) 2000/60/EC (European Commission 2000) became mandatory as a result of a restructuring process of the European Water Policy. The overall goal was to provide non-legally binding and practical guidance documents in order to avoid further deterioration and achieve a good ecological status of rivers, lakes, transitional-, coastal-, as well as artificial- and heavily modified surface waters by 2015 (European Commission 2000).

In 2012, 44 % of more than 19,000 lake water bodies recorded in Europe did not achieve a good ecological status, according to the first River Basin Management Plans from 24 EU Member states, prepared on behalf of the WFD (ETC/ICM 2012 a). The bad status of the lakes was caused by two main pressures: diffuse sources from agriculture land causing nutrient enrichment and hydromorphological changes affecting, for example, habitat availability (ETC/ICM 2012 a). In the past decade, an enormous amount of effort has been put into an improvement of the water quality (Søndegaard & Jeppesen 2007). Despite these efforts, many lake water bodies will not achieve good ecological status in the coming years, because the assessment and improvement of hydromorphological conditions has been neglected as an important component ensuring the ecological integrity of lake ecosystems (Ostendorp et al. 2004).

Consequently, 29.1 % of the European lakes reported in the first River Basin Management Plans were affected by hydromorphological pressures. Even so, large differences exist between the Member States. Countries with more than half of their lakes affected by hydromorphological pressures often hold many reservoirs. In Germany, less than 10 % of the lakes were reported to be affected by hydromorphological alterations (ETC/ICM 2012 b).

1.2 Ecological necessity to assess and manage the hydromorphology of lakeshores

In general, hydromorphological alterations refer to changes in the hydrological regime and/or to modification of the morphological conditions. The hydrological regime, for example, can be changed by intervention into the dynamic of natural water level fluctuation, whereas morphological alteration can be caused by human-induced physical alterations of the lake morphology. In particular, the modification of lakeshores continuously increased in the past and is thought to further increase worldwide (Schnaiberg et al. 2002, Ostendorp 2004), because of ongoing growth in the global population (UNFPA 2014) associated with increases in housing development, recreational and commercial activities. Therefore, this thesis focuses on hydromorphological changes conducted along the shores of lakes (definition of lakeshores see excursion).

Excursion: Definition of lakeshores

The term 'lakeshore' commonly refers to the adjacent terrestrial part of lakes. In this thesis, the term 'lakeshore' comprises not only the terrestrial (riparian) zone but also the aquatic part (littoral) following Ostendorp et al. (2004) and Ostendorp (2014) (Figure 1-1). This definition emphasizes the characteristic of a transitional zone (ecotone) between land and water (Ostendorp 2014). In this thesis, the studied littoral zone is further subdivided following the terminology of Hutchinson (1967) who defined the area between the highest and lowest water level as eulittoral (Figure 1-1). The subsequent upper littoral is permanently covered by water and followed by the middle and lower littoral according to the distribution of macrophytes, which are an indicator for the availability of light, water level fluctuations and depth. Hence, the upper littoral is the zone of emergent rooted vegetation; the middle littoral is characterized by floating-leaved rooted vegetation whereas the lower littoral comprises submersed rooted macrophytes (Figure 1-1).

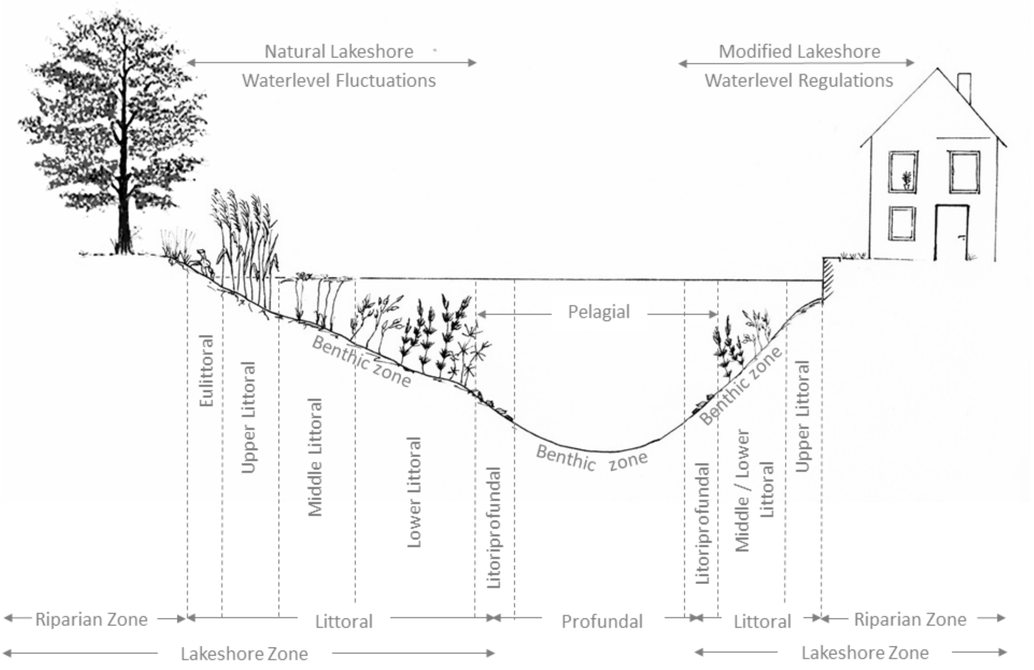


Figure 1-1: Land- and lakeside border of lakeshore zone following Ostendorp et al. (2004) and vertical lake zonation of the aquatic part according to Hutchinson (1967). Left hand side natural lakeshore. Right hand side human modified lakeshore.

One of the central features of lakes is the gradient of habitat-heterogeneity, which decreases from the eulittoral to the profundal through reduction of habitats and habitat complexity (e.g. Beauchamp et al. 1994). This phenomenon of high habitat-heterogeneity in the littoral can be attributed to the availability of physical structures and high wave disturbance. Physical structures such as macrophytes or coarse woody debris are absent in greater depth and wave disturbance that is responsible for alteration in the sediment particle size composition and organic matter content decreases with increasing depth (e.g. Rowan et al. 1992, Bloesch 1995, Cyr 1998). Consequently, lakeshores perform many ecological functions and have great ecological significance for the whole lake ecosystem (Vadeboncoeur et al. 2002). Some of the key functions of lakeshores include nutrient retention from the catchment, erosion control, contribution to self-purification of the entire water body, leaf litter decomposition and habitat provision (e.g. Ostendorp et al. 2004, Schmieder 2004, Strayer & Findlay 2010, Vadeboncoeur et al. 2011).

The ecological functioning of lakeshores can be drastically disturbed by lakeshore modification. In recent years, an increasing number of studies showed that lakeshore modification primarily affects habitat-heterogeneity by habitat loss and habitat alteration (e.g. Christensen et al. 1996, Francis et al. 2006, Brauns et al. 2011). Furthermore, lakeshore modification can cause changes in the hydrological regime through water level regulation (e.g. Furey et al. 2006, Cott et al. 2008, Wilcox & Nichols 2008), increase wave exposition and turbidity through a loss of macrophytes and increased boat traffic (Liddle & Scorgie 1980, Ostendorp 1995, Strayer and Findlay 2010) and prevent the aquatic-terrestrial coupling for example by barriers such as sheet pilings or a reduction of allochthonous organic matter input (e.g. Francis et al. 2007, Marburg et al. 2006, Roth et al. 2007).

All these effects were shown to generally reduce the diversity of littoral organisms and an alteration of their community composition. For example Radomski & Goeman (2001) observed a 66 % reduction of emergent and floating leaf vegetation along developed shorelines measured as number of homes per kilometer. Reduction in emergent plant abundance was also detected in further studies (Szajnowski 1983, Ostendorp et al. 1995, Jennings et al. 2003, Radomski 2006). Contrary, no effect was found on submerged plants in the majority of studies dealing with human lakeshore modification (Radomski & Goeman 2001, Elias & Meyer 2003, Jennings et al. 2003). Nevertheless, there are also studies existing that observed a reduction in richness and abundance of submerged plants due to human activities on lakeshores (e.g. Sukopp 1971, Liddle & Scorgie 1980, Bryan & Scarnecchia 1992, Stelzer 2003).

Linked to the reduction of macrophytes and other physical structures such as coarse woody debris or roots providing food and refuge in the littoral zone of lakes, an increasing number of studies reveal strong effects on fish and macroinvertebrates. Commonly, an increase in lakeshore development negatively affects diversity, abundance and changes in community composition of fish (e.g. Bryan & Scarnecchia 1992, Scheuerell & Schindler 2004, Gaeta et al. 2011, Lewin et al. 2014) and macroinvertebrates (e.g. Brauns et al. 2007 a, Rosenberger et al. 2008, Urbanič et al. 2012, McGoff & Sandin 2012). These effects are reinforced by ship induced waves, which have strong impacts on habitat complexity and thus on littoral organims (e.g. Gabel et al. 2011, Gabel et al. 2012, Schludermann et al. 2014). For macroinvertebrates it has also been demonstrated that lakeshore modification decreased the number of trophic links in the basis of the littoral food web as results of a decreased number of littoral habitats providing fewer food resources (Brauns et al. 2011).

Nevertheless, a generalization should not be made, because effects were shown to be species-specific and depend on the degree and type of modification as well as on natural characteristics of the lake ecosystem. For example, artificial structures such as ripraps, having high structural complexity, were found to be an acceptable alternative for fish and macroinvertebrate communities (Trial et al. 2001, Brauns et al. 2007 a). Similarly, the construction of rocky-crib piers resulted in an increase of fish richness and density in the littoral of the mountain Lake Tahoe. Lake Tahoe is naturally characterized by rocky habitats and almost no macrophytes in the littoral zone, consequently rocky-crib piers had no effect on macrophytes but increased habitat structure for fish (Beauchamp et al. 1994).

1.3 Assessing the hydromorphology of lakes and their shores according to the WFD

As a consequence of the unsatisfactory state of European lakes more than 10 year after the WFD, there is still the need for implementing efficient biological assessment methods and management measures to evaluate and improve the hydromorphology of lakes.

The implementation of the WFD includes an inventory survey, monitoring and assessment of the target water bodies, and when necessary an adoption of measures. Linked to these requirements is the development of standard assessment tools. For the classification of the ecological status, three quality components were proposed: 1) biological elements which are supported by 2) chemical and physico-chemical elements in order to achieve the good status and 3) hydromorphological elements to assign the high ecological status (European Commission 2000). This procedure has been suggested, because it is assumed that biological elements can only achieve moderate or lower status when the conditions of the other two elements are in line with the ecological status reached (WFD CIS Guidance Document No. 13 2005). The quality components are further subdivided depending on the water body. For lakes, the biological quality components are phytoplankton, aquatic flora, benthic invertebrates and fish, which are supported by the hydromorphological as well as chemical and physico-chemical elements.

The assessment of lakeshores is directly and indirectly required by the WFD. Lakeshores are considered directly by the biological quality elements, especially macrophytes and macroinvertebrates. The structure of lakeshores is directly mentioned as part of the hydromorphological quality component, necessary to classify lakes into the high ecological status (European Commission 2000). Lakeshores are mentioned indirectly in the first article of the WFD, which refers not only to the protection of aquatic ecosystems but also to '*[…]* wetlands directly depending on the aquatic ecosystems' (European Commission 2000). In accordance to the definition given for wetlands in the WFD, lakeshores are considered as wetlands and thus are relevant to achieve the objectives of the WFD to maintain ecosystem functions (WFD CIS Guidance Document No. 12 2003).

After the WFD (European Commission 2000) came into force, a vast number of more than 300 biological methods were developed to assess European surface waters. 27 % of these methods were established to detect hydromorphological changes, but mainly for rivers with a long tradition in using benthic macroinvertebrates for ecosystem assessment (Birk & Schmedtje 2005, Birk et al. 2012). Considerably less work has been done to detect hydromorphological changes of lakeshores, due to a lack of intense studies of the littoral zone (e.g. Vadeboncoeur 2002, Stoffels et al. 2005, Solimini et al. 2006). But fostered by the WFD (European Commission 2000), the scientific literature about the 'forgotten ecotone' lakeshore (Walz et al. 2002) increased. In this context, littoral macroinvertebrates were emphasized to be useful indicators for the assessment of hydromorphological conditions of lakeshores (e.g. Brauns et al. 2007 a, Solimini & Sandin 2012).

The suitability of macroinvertebrates as indicators for hydromorphology of lakeshores results from their highest diversity, typically found in the littoral zone of lakes (e.g. Heino 2000, Babler et al. 2008, Vadeboncoeur et al. 2011). For example, Vadeboncoeur et al. (2011) demonstrated that more than 93 % of invertebrate and fish species of the 14 world's largest lakes inhabit the nearshore littoral zone. The high diversity of littoral macroinvertebrates can be attributed to the high habitat-heterogeneity in this depth zone, which provides many ecological niches. This is reflected in various studies relating different environmental parameters to macroinvertebrate communities. It was found that habitat-heterogeneity is a major driving factor in structuring littoral macroinvertebrate communities and explains more of the variation in macroinvertebrate communities than, for example, nutrient enrichment and larger spatial scale (e.g. Heino 2000, Tolonen et al. 2001, Johnson & Goedkopp 2002, Stoffels et al. 2005, Brauns et al. 2007 b, McGoff & Sandin 2012, Verdonschot et al. 2012, McGoff et al. 2013 a).

The high diversity, especially of littoral macroinvertebrates, their ubiquitous occurrence, relatively short lifespans and low mobility in relation with a species-specific habitat binding supporting various behavioural and feeding traits shows their high potential to indicate changes in the hydromorphology of lakeshores. Such sensitive indicator organisms are important for the development of efficient lakeshore assessment methods.

1.4 Existing macroinvertebrate-based assessment methods and their uncertainties

In Europe, efficient macroinvertebrate-based assessment methods to evaluate the hydromorphological conditions of lakeshores have developed well in recent years (McGoff & Irvine 2009, Pilotto et al. 2011, Peterlin & Urbanič 2012, McGoff et al. 2013 b, Miler et al. 2013, Urbanič 2014, Miler et al. 2015). Most of these studies focused on the development of site-specific, multimetric indices based on (eu)littoral macroinvertebrates, regardless of lake type in one specific region of Europe. Only the two stressor-specific, multimetric indices LIMHA and LIMCO, developed within the WISER project (http://www.wiser.eu) for different geographic regions of Europe fulfill the requirements of the WFD (Miler et al. 2013). Extrapolation of the site-specific LIMCO index to whole lake level was successfully tested using a regression between this index and physical habitat assessment index scores calculated from the HML (*HydroMorphology of Lakes*) protocol (Ostendorp & Ostendorp 2015, Miler et al.

2015). Although the current approaches seem to be promising, the above-mentioned studies pointed out some uncertainties which should be clarified in order to conclude misleading decisions for management activities. In this thesis, the following uncertainties and missing aspects will be addressed:

Influence of water depth

There are promising assessment methods based on (eu)littoral macroinvertebrates (e.g. Miler et al. 2013, Urbanič 2014), but assessment based on sublittoral (middle/lower littoral) macroinvertebrates failed to clearly predict hydromorphological pressures (Pilotto et al. 2011). However, there is still no study available that investigated the effect of lakeshore modification along a gradient of water depth. But knowing the effect of lakeshore modification on macroinvertebrate communities of different depth zones is important for assessing human impacts in lakes. As a consequence of changing environmental conditions, macroinvertebrate communities are spatially distinct (e.g. Särkka 1983, Ali et al. 2002, Hämäläinen et al. 2003) and show generally highest diversity and production in the littoral zone, and a decrease in these community parameters with increasing depth (Babler et al. 2008, Butkas et al. 2010, Northington et al. 2010, Vadeboncoeur et al. 2011).

Influence of season

The development of assessment methods is usually based on samples taken during a single season (Miler et al. 2013, Urbanič 2014), although diversity and composition of littoral macroinvertebrate communities differ among seasons or even months (e.g. Reid et al. 1995, Tangen et al. 2003, Scheifhacken et al. 2007, Little 2008). In particular, the emergence of aquatic insects such as Chironomidae in summer can result in high intra-annual variation in macroinvertebrate abundance and composition (e.g. Trigal et al. 2006, Little 2008). Furthermore, abiotic parameters such as water level and wind exposure can change site characteristics such as substrate composition or periphyton growth resulting in monthly alteration of the macroinvertebrate community (Scheifhacken et al. 2007). However, it has also been shown that spatial heterogeneity reduces temporal variability in stream insect communities, because spatial heterogeneity positively influences community stability (Brown 2003). This may also apply to the upper littoral zone that is characterized by a high spatial heterogeneity.

Hence, it was suggested to clarify the effect of sampling season on the outcomes of the assessment methods (Miler et al. 2013).

Macrophytes

Macroinvertebrate-based assessment methods have to be stressor-specific, therefore existing methods relate environmental variables usually combined in one index to the macroinvertebrate communities (e.g. McGoff et al. 2013 b, Miler et al. 2013, Urbanič 2014). From the various environmental variables, macrophytes were shown to have a strong influence on the assessment results (e.g. McGoff & Irvine 2009). This is not surprising because macrophytes are known to strongly structure macroinvertebrate communities in lakes naturally covered with macrophytes (James et al. 1998, Cyr & Downing 1988, Thomaz & da Chuna 2010). To my knowledge, there is no study that simultaneously examines the effects of lakeshore modification on macrophyte and macroinvertebrate communities and tried to find the environmental variable(s) that explains most of the variance in macroinvertebrate communities between different types of lakeshore modification. Sufficient knowledge on the effects of lakeshore modification on macrophytes would not only help to improve lakeshore management, but could possibly be used to complement the macroinvertebrate-based assessment of lakeshore modification as proposed by Lyche-Solheim et al. (2013).

Structural measures versus functional measures

The available macroinvertebrate-based metrics to assess the effect of lakeshore modification are developed using structural measures such as diversity, abundance, biomass and composition. It can be assumed that the adverse effects of lakeshore modification on macroinvertebrate diversity would also result into lower secondary production, according to the diversity-production relationship (e.g. Loreau et al. 2001, Hooper et al. 2005). The diversity-production hypothesis states that the greater diversity, the larger the number of species with complementary traits of resource use, which in turn leads to higher resource exploitation and thus to higher secondary production or vice versa (e.g. Loreau et al. 2001, Hooper et al. 2005).

Secondary production refers to the formation of macroinvertebrate biomass through time and represents an organism's ability to fix and retain energy (Downing 1984, Benke 1993, Butkas et al. 2010, Dolbeth et al. 2012). Hence, secondary production can be used as proxy to determine the functioning of macroinvertebrates in lake ecosystems as it is a function of energy and material flow through food webs and linked to many ecosystem processes.

Knowing the effects of lakeshore modification on the functioning of macroinvertebrates can help to better understand the consequences of lakeshore modification on the entire lake ecosystem, because macroinvertebrates play a major role in the food web and nutrient cycling of lakes due to their intermediate trophic position (e.g. Covich et al. 1999, Schindler & Scheuerell 2002, Brauns et al. 2011). For example, shredders such as Crustacea accelerating decomposition of coarse organic matter into finer fraction (van Dokkum et al. 2002), which then can be further processed by gatherers such as Chironomidae or Oligochaeta. Another function of macroinvertebrates stems from controlling primary production through grazing on phytobenthos (e.g. Haglund & Hillebrand 2005, Peters & Traunspurger 2012) or consumption of phytoplankton through filter feeding (Kryger & Riisgård 1988, Musko & Bako 2005). Macroinvertebrates serve as food source for top-predators such as fish, birds or bats (e.g. Vander Zanden & Vadeboncoeur 2002, Fukui et al. 2006, Matuszak et al. 2014). Hence, macroinvertebrates link to the pelagic and terrestrial system owing to resource competition and trophic transfer through consumption (Polis et al. 1997, Vadeboncoeur et al. 2002). In addition, sediment-dwelling invertebrates such as Chironomidae contribute to the remobilization of nutrients through bioturbation (Schaller 2014). These behaviors, associated with consumption, egestion and excretion, lead to a strong influence of benthic macroinvertebrates on nutrient stoichiometry and nutrient cycling and thus directly on the food quality (Cross et al. 2005).

The advantage of using secondary production in assessment methods lies in the integration of static and dynamic components (Dolbeth et al. 2012). Such integrative approaches have been highly recommended as tools for assessing aquatic ecosystems (e.g. Benke & Huryn 2010, Dolbeth et al. 2012), because functional measures such as secondary production have been shown to be more sensitive in detecting changes in ecosystems while structural measures could not necessarily. For example, Whiles & Wallace (1995) could show that total macroinvertebrate abundance was similar before, during and after three years of seasonal insecticide treatment, whereas biomass and production decreased during the treatment and increased during the recovery phase. Likewise, Valentine-Rose et al. (2011) demonstrated that fish secondary production was most consistent in detecting the effect of fragmentation on tidal creek ecosystems compared to several structural measures. Lastly, Sandin &

Solimini (2009) compared eight studies in running waters and also showed that structural measures were not sufficient to detect all types of human impairment and recommended to use functional indicators.

The lower potential of diversity compared to secondary production in detecting ecosystem changes is a consequence of the two mechanisms' dominance and complementarity that determines trait diversity, which in turn controls ecosystem processes (Loreau et al. 2001). This will be illustrated by the following example derived from Loreau et al. (2001) that compares species richness and secondary production of two communities with equally high species richness. For the first community, it is assumed that species are rather equally abundant with complementary traits, whereas for the second community one species with some particular traits is dominant. Since the mechanism of complementarity tends to improve resource exploitations, the first community with equally abundant species appears to have high secondary production. In the second community, resource exploitation and consequently secondary production is lower, resulting from lower trait diversity caused by the dominance of one species. Hence, although species richness is similar, secondary production can differ between sites or ecosystem. Loreau et al. (2001) describes complementarity and dominance as two poles of a continuum. Intermediate scenarios could then show an effect of lakeshore modification on diversity but a stronger effect on secondary production.

So far, there is no study that addresses the effect of lakeshore modification on macroinvertebrate production, but comprehensive knowledge about the effect of lakeshore modification on the functioning of macroinvertebrates might help to develop sound assessment methods for lakeshore hydromorphology.

1.5 Scope of the thesis

The overall goals of the thesis were to examine the effects of lakeshore modification on macroinvertebrate communities in relation to water depth and season (Chapter 2), to observe the effects of different types of lakeshore modifications on macroinvertebrate communities in relation to macrophytes (Chapter 3), and to determine the effects of lakeshore modifications on the ecological functioning of macroinvertebrates at different spatial scales (habitat, depth zone, whole lake ecosystem) based on secondary production (Chapter 4). Finally, the estimation of secondary production is a challenging issue and based on the determination of macroinvertebrate biomass over time. Macroinvertebrate biomass can be indirectly determined by the application of length-mass regressions. Using Length-mass regressions is a widely-spread approach, but due to natural variations in species-specific length-mass relations it is recommended to establish own regressions for the system under study. Hence, a methodological scope of the thesis was to establish length-mass relationships for lake macroinvertebrates (Chapter 5).

The outcome of assessments of the ecological status of the littoral zone may differ with samples taken in different seasons. Knowing the influence of temporal variation on macroinvertebrate communities at modified shores is fundamental for the development of accurate assessment methods. Hence, macroinvertebrate communities of natural lakeshores were studied in comparison with modified lakeshores over a vegetation period at different depth zones to address the following hypothesis (Chapter 2):

1) **The effect of human modified lakeshores on macroinvertebrates is independent from season, because spatial heterogeneity has been shown to reduce temporal variability.**

The natural variability of macroinvertebrate communities is not only a result of temporal variations, but also determined by bathymetric variation due to substantial differences in environmental conditions. These differences in macroinvertebrate communities with depth are also important for assessing human impacts in lakes. Therefore, the macroinvertebrate communities were studied in the upper and middle littoral zone as well as in the profundal zone (Chapter 2) to address the second hypothesis:

2) **The effect of lakeshore modification on macroinvertebrates systematically differs among depth zones showing a decrease with increasing water depth.**

Furthermore, previous studies have shown that macrophytes can be also adversely affected by lakeshore modification. In order to quantify the effect of different types of lakeshore modification on macrophytes and macroinvertebrates, both communities were studied simultaneously to address the third hypothesis (Chapter 3):

3) **Macrophyte and macroinvertebrate communities vary between different types of lakeshore modification.**

Since macrophytes are an important habitat for macroinvertebrates, resulting generally in higher abundances and biomass of macroinvertebrates with increasing occurrence of macrophytes, the following hypothesis was set up based on the assumption that macrophytes are susceptible to lakeshore modification (Chapter 3):

4) **Macrophytes are the most important driving factor in structuring macroinvertebrate communities of different types of lakeshore modification.**

The knowledge about the effects of lakeshore modification on macroinvertebrate diversity and composition suggest that the production and thus the functioning of upper littoral macroinvertebrates at modified shore sites is lower than on natural sites, which leads to the following hypothesis (Chapter 4):

5) **Lakeshore modification decreases secondary production in the upper littoral zone as a consequence of reduced habitat-heterogeneity.**

Lakes are characterized by a decrease in production with increasing depth. Assuming that upper littoral macroinvertebrates of modified lakeshore are less productive, the following hypothesis was evaluated (Chapter 4):

6) **The depth-production relationship is altered at modified lakeshores, due to lower secondary production in the upper littoral.**

Since total secondary production does not necessarily reveal the entire consequences of lakeshore modification on the functioning of macroinvertebrates, hypotheses 5 and 6 were also examined with regard to secondary production for non-native species and functional groups (feeding types).

Proving that lakeshore modification results into a lower site-specific production of upper littoral macroinvertebrates does not reflect the consequences for the entire upper littoral nor for the whole-lake ecosystem. Assuming that the littoral zone contributes importantly to whole lake secondary production and lakeshore modification can strongly affect the littoral secondary production the last hypothesis was proposed (Chapter 4):

7) **Site-specific effects of lakeshore modification on littoral secondary production affect the production of the entire upper littoral and whole-lake ecosystem.**

Finally, in Chapter 6 an extended summary and synthesis based on the results obtained in this thesis is given. The outcomes important to understand how lakeshore modification affects the structure and functioning of macroinvertebrates are highlighted as a prerequisite for the development of effective assessments methods to evaluate the ecological state of lakeshore hydromorphology.

1.6 General methods and material

Lake Scharmützelsee

The study was conducted at Lake Scharmützelsee (52°15´ N, 14°03´ E), which is situated in the North-German lowland, approx. 45 km southeast from Berlin (Figure 1-2).

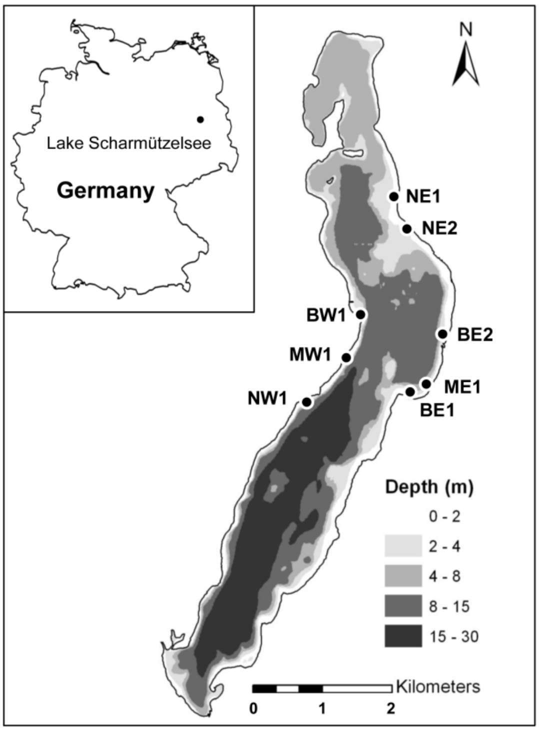


Figure 1-2: Lake Scharmützelsee and sampling sites (N = natural, M = marina, B = beach, E = east side, W = west side).

The lake was formed as a deep glacial channel lake during the last stage of the Pleistocene (Grüneberg et al. 2011) and is thus a typical glacial feature of the young moraine landscape. It is classified as a calcareous (40.3 mg L^{-1} Ca^{2+}; annual mean 2003 – 2009) stratified lowland lake with a comparatively long water residence time of 10 years and a small catchment (127.9 km^2) (Grüneberg et al. 2011). The catchment land use is dominated by forests (48 %), arable land (30 %) and urban area (8 %). Lake Scharmützelsee has a surface area of 12.1 km^2, a volume of $108.2 \cdot 10^6$ m^3 and is one of the largest lakes of the federal state of Brandenburg. The lake is subdivided into three basins: the polymictic north basin with a maximum depth of 7 m, a temporarily thermally stratified middle basin with a maximum depth of 11 m and the dimictic south basin with up to 29.5 m depth (Grüneberg et al. 2011). At the southern end, the lake is coupled to the Glubig and Storkower chain of lakes and thus connected to the navigable inland waters Dahme and Spree. This is an important characteristic with regard to the vulnerability to the immigration of Neobiota.

Ecological status

Lake Scharmützelsee was naturally mesotrophic with abundant submerged vegetation and summer Secchi depth of up to 3 m in the 1930s (Hilt et al. 2010). High nutrient loads between ~1950 and 1980 caused eutrophic conditions with phosphorous import between 0.17 t a^{-1} and 1.1 t a^{-1} in the 1980s (Grüneberg et al. 2011). In the 1990s, the external phosphorus load decreased, but the trophic state of the lake did not improve until 2003, when the lake changed back to almost mesotrophic conditions (Grüneberg et al. 2011) and thus to good chemical conditions according to the WFD (LUGV 2012). In 2011, annual mean concentrations in the epilimnion were 33.5 µg L^{-1} total phosphorus, 639 µg L^{-1} total nitrogen and 13.4 µg L^{-1} chlorophyll a. Mean Secchi depth was 2.7 m.

Although the lake is currently in good chemical condition, the overall assessment revealed only a moderate state according to the WFD (Grüneberg et al. 2011, LUGV 2012). This partly results from the low reaction time of organisms to environmental changes such as recovering from high nutrient load.

For the biological quality element phytoplankton the biomass decreased from about 27 µg L^{-1} Chl *a* before to about 11 µg L^{-1} Chl *a* after 2003 (mean of vegetation period April - October) combined with an alteration of the cyanobacterial species composition from a dominance of fine filamentous taxa to a dominance of Nostocales (Grüneberg et al. 2011). Despite these changes, phytoplankton of Lake Scharmützelsee is still classified as moderate (LUGV 2012).

Likewise, the coverage of macrophytes increased from less than 10 % in 1994 - 2003 to about 24 % in 2005/06 and the species number from five to 14 submerged macrophytes (Hilt et al. 2010, Grüneberg et al. 2011), but the ecological status of macrophytes failed to reach good conditions (LUGV 2012).

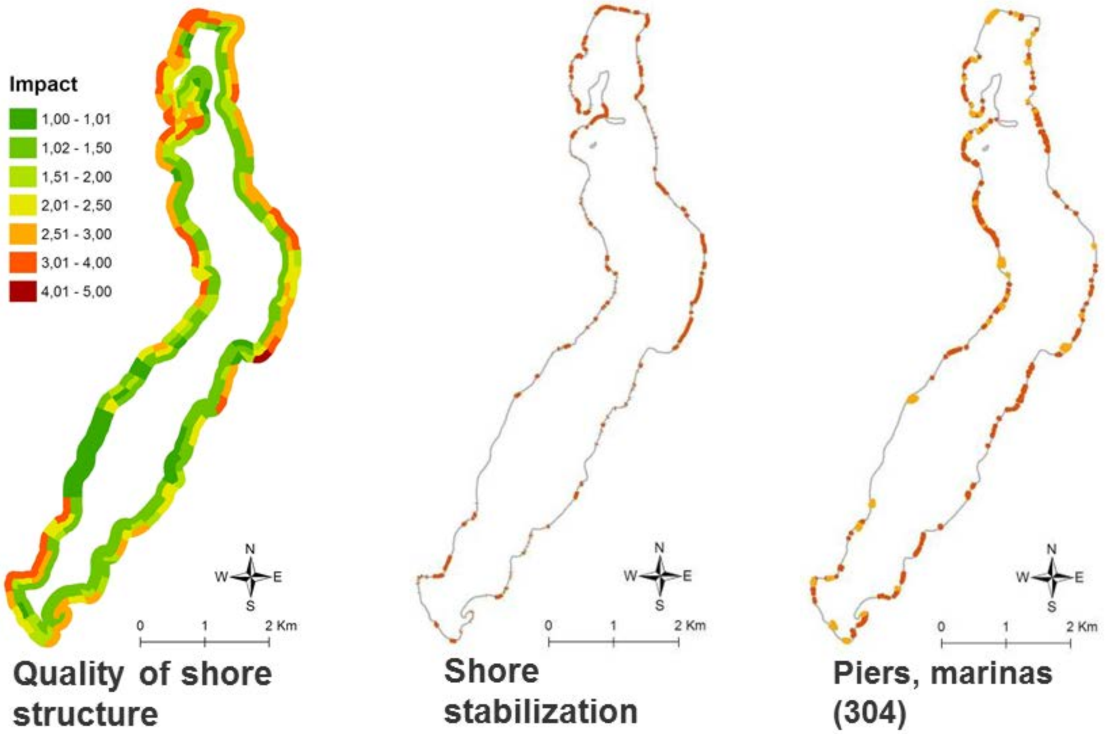
Similarly, macroinvertebrates were classified into moderate ecological status evaluated using the assessment method developed from Michels (2007). Additionally, the fresh biomass of macroinvertebrates was investigated in November 2010 along five east-west transects (Brämick et al. 2011). For comparison, the transects were selected at the same position as in 1935 (Wundsch 1940) and 2001 (Ordóñez Alfaro 2001). In general, a decrease of fresh weight (without Molluscs) was observed from 1935 (19.4 g m^{-2}) to 2001 (4.5 g m^{-2}) and 2010 (2.6 g m^{-2}), reflecting the effect of eutrophication on macroinvertebrates in the second half of the 20th century (Brämick et al. 2011).

Two fish surveys conducted in 2002 and 2010 also indicate the change in the trophic state of Lake Scharmützelsee. Roach and perch dominated in both years but with a shift from roach as the abundant fish in 2002 to perch in 2010. Simultaneously, zander decreased, a species having competitive disadvantage compare to the perch and pike in clear waters. Noteworthy is the discovery of the bitterling in 2010, because it was not recorded before but belongs to the reference fish fauna for this lake, which would lead to a higher ecological status according to the WFD (Brämick et al. 2011).

Despite an enhancement in the water quality an improvement of the biological quality elements may be unlikely, as long as the organisms are exposed to hydromorphological pressure (Ostendorp et al. 2004, Søndegaard & Jeppesen 2007).

Lakeshore characteristics

For Lake Scharmützelsee, a hydromorphological survey and assessment of the lakeshore was conducted in 2010 (Fernando 2011) applying the modified HML (*HydroMorphology of Lakes*) protocol of Ostendorp et al. (2008). The method assesses the riparian zone (epilittoral; 50 m landward from shoreline), the eulittoral (2.5 m on both sides of the shoreline) and the sublittoral (until max. depth of closed submerged macrophyte occurrence) (eu- & sublittoral ≙ upper littoral). All lakeshore sections are placed into impact classes from high (1) to bad status (5), according to the mapped objects such as areas of vegetation, piers and marinas, shoreline stabilization, beaches or sealed areas. Figure 1-3 shows that more than 90 % of the sublittoral zone exhibits good hydromorphological conditions reflected in the high proportion of green colour. For the eulittoral about 70 % were classified as 'good', but only less than 30 % achieved good conditions in the riparian zone. One of the major impacts are the over 300 piers and marinas and the shore reinforcements such as sheet pilings or wooden retaining walls that changed about 25 % of the ~29 km lakeshore (Figure 1-3). Another 18 % of the lakeshore is developed by beaches, grassland or parks. The remaining 57 % of the lakeshore comprises undeveloped, nearly natural shore sections characterized by reed belt and sedge swamps (Fernando 2011). Because of the varying lakeshore characteristics consisting of undeveloped and various kinds of developed sections, Lake Scharmützelsee is an excellent study object for morphological degradation.



Quality of shore structure

Shore stabilization

Piers, marinas (304)

Figure 1-3: Hydromorphological characterization of the lakeshore of Lake Scharmützelsee. On the left site, seven impact classes show the quality of the shore structure for the epi-, eu- and sublittoral from high (1) to bad status (5). The illustration in the middle presents the distribution of shore stabilizations. The right hand illustration demonstrates the distribution of small (red) and large (orange) piers and marinas (Fernando 2011).

Study sites

Eight study sites were selected, based on the digital data of the hydromorphological survey from the lakeshores of Lake Scharmützelsee (Fernando 2011) and on-site inspections. Sites with a very different degree of lakeshore modification and thus different habitat features were considered, e.g. sites with structural degradation and sites degraded by hydromechanical stress. Furthermore, to avoid edge effects from neighbouring shore features one study site should be at least 30 m wide (Brauns et al. 2010). Altogether, three undisturbed natural and five modified sites were selected, i.e. two marinas with sheet-pilings and three recreational beaches (two public and one private) (Figure 1-4). In order to consider the natural variability of wind at least one site per shore type at the exposed east shore and one at the wind-sheltered western shore were chosen.

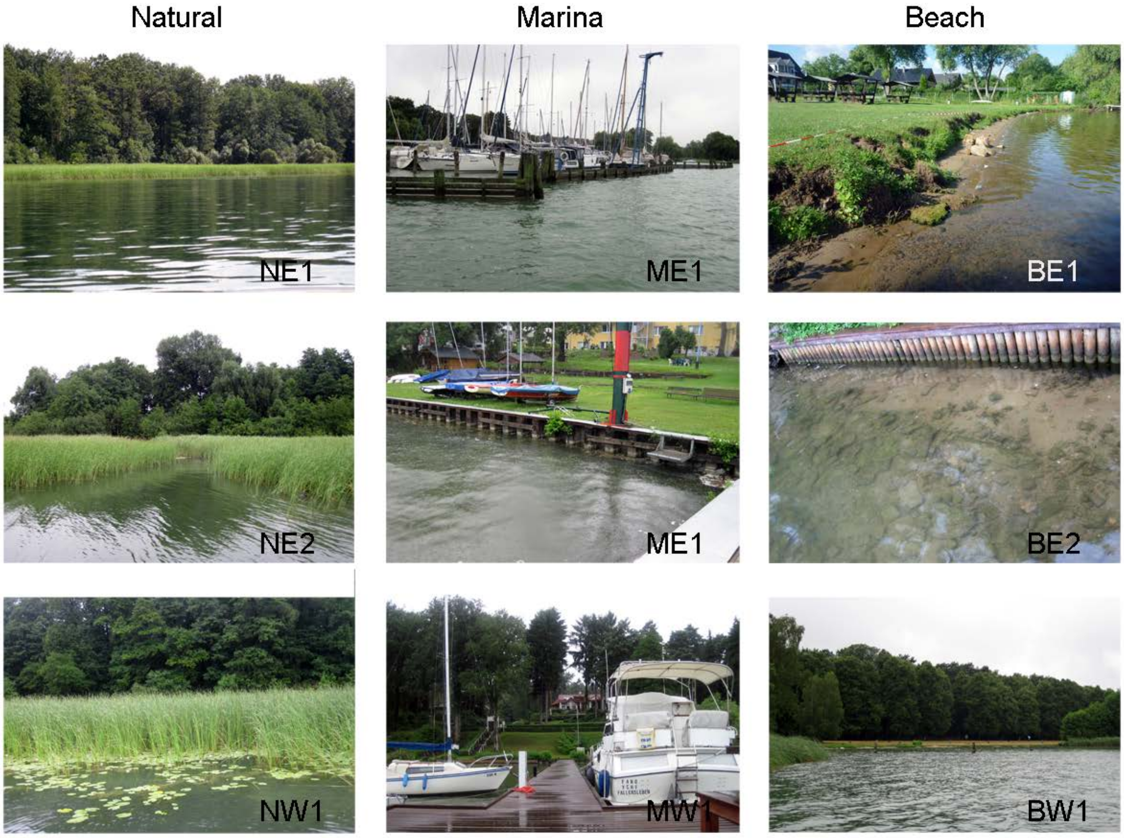


Figure 1-4: Sampling sites (N = natural, M = marina, B = beach, E = east side, W = west side).

All natural sites were characterized by dense reed belts, and their riparian vegetation was dominated by trees. In contrast, the riparian zone of all modified shores was clear-cut and characterized by adjacent lawns. The marinas were degraded by shore stabilization and piers, and were used for leisure boating with 45 (marina west) to about 70 (marina east) mooring places for small, private motor and sailing yachts. The marina at the east side of the lake was protected by wooden boards, because of the high exposition to waves. At the public beaches, no shore stabilization was present, but they were subjected by human trampling causing high turbation of the sediment. The shore of the private beach was stabilized by wooden boards, but it was not severely impacted by human trampling. Instead, the private beach was highly exposed to wind and waves.

Macroinvertebrate and macrophyte sampling and processing

A temporally-repeated observation of the macroinvertebrate and macrophyte community was conducted in order to determine the seasonal variability of the biological parameters species richness, abundance and biomass. Repeated observations are also obligatory when studying secondary production, because information about population dynamics is needed. Area-specific changes of the macroinvertebrate community should be observed for at least one year and in short intervals (Schwoerbel 1994). The choice of the sampling interval depends on the life cycle and growth rate of macroinvertebrates, but also on the amount of work and available resources. Studies on secondary production sampled mostly once a month (Benke & Huryn 2007). Accordingly, in this study macroinvertebrates were sampled monthly from April 2011 until November 2011 at four of the chosen study sites. The remaining four study sites were sampled only in April, July, September and November 2011, because of limited resources. An overview about the sampling frequency is given in Table 1-1.

Table 1-1: Overview of sampling frequency per sample site and depth zone in 2011. Grey: sampled, U: upper littoral, M: middle littoral, N = natural, M = marina, B = beach, E = east side, W = west side.

	Sampled monthly												**Sampled bi- or tri-monthly**											
	NE1			**NE2**			**ME1**			**BE2**			**BE1**			**NW1**			**MW1**			**BW1**		
	U	**M**	**P**	**U**	**M**	**P**	**U**	**M**	**P**	**U**	**M**	**P**	**U**	**M**	**P**	**U**	**M**	**P**	**U**	**M**	**P**	**U**	**M**	**P**
April	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
May	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨												
June	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨												
July	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
August	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨												
September	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
October	▨	▨	▨	▨	▨		▨			▨														
November	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

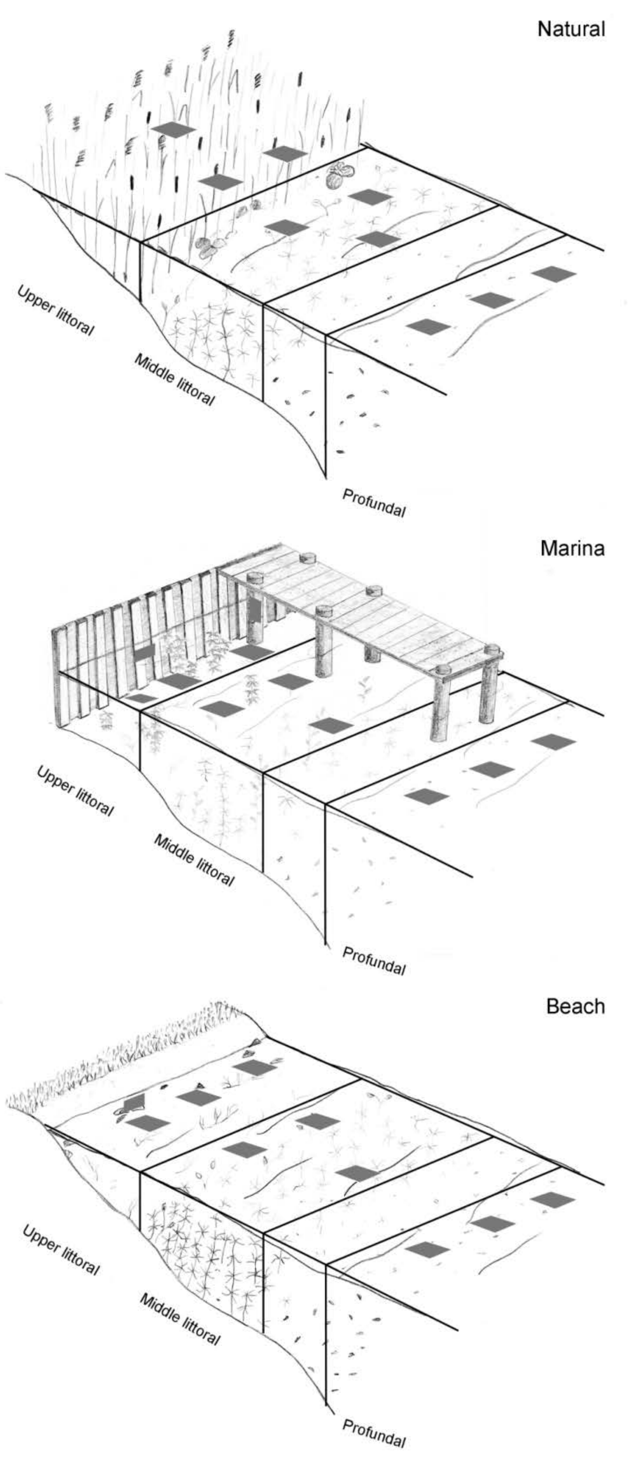


Figure 1-5: Example of belt transects for each shore type showing approximate locations of subsamples taken. Grey bocks = subsamples. Total area of subsamples per depth zone is 0.18 m². Upper littoral zone stretches between 0 m (marinas ~0.8 m) and ≤1.5 m, middle littoral between >1.5 m and 4 m and profundal >8 m depth.

Each study site was sampled in three water depth zones (terminology following Hutchinson 1967), i.e. the upper littoral (0 - ≤1.5 m water depth), middle littoral (>1.5 - 4 m) and in the upper profundal (>8 m) zone (Figure 1-5). The euphotic zone in Lake Scharmützelsee extends to about 7.5 m, so we defined the zone >8 m as belonging to the profundal zone. Thus, together with a minimum width of 30 m per studied site, belt transect were used as sampling design (Figure 1-5).

At each sample site, we sampled all habitat types separately in proportion to their total area from a total area per depth zone of 0.18 m² (Table 1-2, Figure 1-5). According to the standard sampling protocol for littoral macroinvertebrates from Germany (Brauns et al. 2010), the existing habitat types were sampled habitat-specific using the best adapted sampling technique.

Table 1-2: Percentages of habitats for each shore type and depth zone. The percentage of submerged macrophytes for each depth zone was calculated as the proportion of total macrophyte biomass at a given site to total macrophyte biomass across all sites. Therefore, the sum of habitat proportion per samples site and depth zone can exceed 100 %. N = natural, M = marina, B = beach, E = east side, W = west side.

	Shore type	**Natural**			**Marina**		**Beach**		
Depth zone	**Habitat**	NE1	NE2	NW1	ME1	MW1	BE2	BE1	BW1
Upper littoral	Reed	5	5	5					
	Sheet piling				5	5			
	Piles (Timber sheet)				5	5	5		
	Stones						5	5	
	Soft-bottom	95	95	95	90	90	90	95	100
	Submerged macrophytes	9	5	4	4	11	2	1	0
Middle littoral	Soft-bottom	100	100	100	100	100	100	100	100
	Submerged macrophytes	3	2	5	13	7	18	11	7
Profundal	Soft-bottom	100	100	100	100	100	100	100	100

In the upper littoral, a hand-net (500 µm mesh) was used for soft-bottom sediments and submerged macrophytes. For sheet pilings and timber sheet piles, I used a scrape net (500 µm mesh). Stones were collected randomly and macroinvertebrates were brushed off carefully. Reed was sampled by cutting 10 stems between the water bottom and the water surface and carefully handled as suggested by Moss et al. (2003). All stems in the reed bed were counted on an area between 0.2 to 1 m², depending on the density of emergent plants in the reed bed, in order to be able to quantify the biomass of reed per unit of area. In the middle littoral and profundal zone, a modified Van-Veen-grab (30 x 20 cm wide) was used for soft-bottom sediments and submerged macrophytes. Finally, all habitat samples at a sampling site and depth zone were pooled into a single composite sample and sieved through a 10 mm box sieve to separate submerged macrophytes from the remaining sample.

Submerged macrophytes were stored separately in bottles with lake water for later processing. In the laboratory, macroinvertebrates attached to emergent and submerged macrophytes were collected alive from the plants and added to the corresponding macroinvertebrate sample. Macrophytes were dried at 60°C for 24 h to determine the dry weight.

Following the AQEM consortium (2002), macroinvertebrate samples were processed by sub-sampling using a 6 x 5 or 4 x 3 gridded pan for large or small samples, respectively. At least 5 grids (1/6 of the sample) of large samples or 3 grids of small samples were sorted using a stereomicroscope. Prior to that, coarse material such as reed stems, leaf litter or filamentous algae, was separated from finer material with a 500 µm mesh sieve and also subsampled. In order to obtain the processed amount of coarse material the sorted and unsorted material was weighted and set in relation. The sorted individuals were identified to species level, if possible, except for Chironomidae (subfamily), other Diptera (family), Heteroptera (suborder), Lepidoptera (order), *Pisidium* spp. (genus), Turbellaria (class) and Oligochaeta (order).

Environmental variables

Environmental factors known to structure macroinvertebrate communities were measured for each study site, in order to find the most driving factors explaining differences in macroinvertebrate communities among shore types (Table 1-3). Wind exposure was calculated after Brodersen (1995), using data from a nearby weather station (Lindenberg 52° 13' N, 14° 07' E) from 2009-2011 (source: National Meteorological Service). The slope of the shore was calculated with ArcGis 10 (Esri) based on maps of water depth contours (MLUL 2002) for the upper and middle littoral separately.

Total macrophyte biomass was determined in September 2011, because it corresponds to the peak time of the vegetation period. Organic matter content of sediment was also sampled in this month by taking five sediment cores (6 cm inner diameter; Uwitec, Mondsee, Austria) at all sample sites in the upper and middle littoral. All samples were dried at 60°C for at least 12 hours. Ash free dry mass of the sediments was determined after combusting samples for 3 h at 500°C. For all profundal sites, unpublished data of the ‘Department of Freshwater Conservation’ were taken to calculate average organic matter content from three sampling points measured in April 2007.

Temperature was measured as a key factor for secondary production and logged from May until September/December 2011 every 20 min (VEMCO Minilog, VEMCO Division, AMIRIX Systems Inc., Bedford, Canada) in the upper littoral and middle littoral (2 m depth). The winter temperatures were completed by bimonthly recorded data within the lakes monitoring program using a Hydrolab DS5 multiparameter sonde (OTT Hydromet, Kempten, Germany). The data were used to calculate mean annual temperature for each sample site in 2011. Mean annual temperatures of the profundal were solely calculated from the database of the lakes monitoring program using all data recorded between eight and 15 m depth, because this refers to the sampling depth of macroinvertebrates. Subsequently, all data from the east- and all from the west side were averaged to obtain mean annual temperatures for the east- and west side of the profundal.

Habitat diversity was calculated as the Hill number index with Primer v6 (Clarke & Gorley 2006), based on mapping of the proportional distribution of all occurring habitats, which are reed, sheet piling, piles, stones, soft-bottom and submerged macrophytes (Table 1-2). Reed, sheet piling, piles, stones and soft-bottom were allocated to 100 %. The percentage of submerged macrophytes was calculated by determining the sampling site with the highest biomass of submerged macrophytes in September and set to 100 %. The percentage of submerged macrophyte biomass for the remaining sites was calculated in relation to the site with the highest biomass. The obtained results were added to 100 % obtained for the other habitats. A summary of all environmental data collected is given in Table 1-3.

Table 1-3: Environmental variables for each shore type and depth zone. Habitat diversity calculated as Hill number N1, Relative wind exposure: * fetch measured from the wave protection of marinas, Shore slope in degree, Organic matter content of sediment in % of dry sediment for September 2011 (Standard deviation for five replicates given) or as mean for the profundal taken from unpublished data of the department of freshwater conservation, Total macrophyte biomass (below water surface) in DW g m^{-2} for September 2011, Temperature in °C averaged for 2011. N = natural, M = marina, B = beach, E = east side, W = west side.

		Natural			**Marina**		**Beach**		
Depth zone	**Variable**	NE1	NE2	NW1	ME1	MW1	BE1	BE2	BW1
Upper littoral	Habitat number	3	3	3	4	4	3	4	1
	Habitat diversity	2.16	1.91	1.81	1.94	2.31	1.32	2.00	1.00
	Wind exposure	0.29	0.51	0.20	0.37*	0.40	0.52	1.05	0.59
	Shore slope	1.38	1.51	2.20	1.98	2.28	1.65	1.54	1.45
	Organic matter content of sediment	2.28 ± 0.45	0.98 ± 0.15	0.81 ± 0.24	1.90 ± 0.79	0.92 ± 0.35	0.64 ± 0.11	1.56 ± 0.28	1.13 ± 0.08
	Total macrophyte biomass	176.98	178.66	117.30	18.34	51.84	2.96	22.09	0.00
	Temperature	11.94	12.02	11.80	12.3	12.03	12.45	12.45	12.2
Middle littoral	Habitat number	2	2	2	2	2	2	2	2
	Habitat diversity	1.62	1.12	1.54	1.39	1.87	1.52	2.00	1.08
	Wind exposure	0.11	0.25	0.07	0.05*	0.07	0.04	0.16	0.05
	Shore slope	0.43	0.60	8.04	3.36	10.23	1.65	3.11	0.89
	Organic matter content of sediment	8.20 ± 0.66	1.67 ± 0.39	0.73 ± 0.11	5.36 ± 1.97	0.75 ± 0.04	3.19 ± 1.00	1.47 ± 0.18	3.70 ± 1.12
	Total macrophyte biomass	41.77	4.42	33.09	20.73	84.56	31.06	181.26	2.56
	Temperature	12.17	12.3	11.88	12.17	11.93	12.22	12.21	11.94
Profundal	Habitat number	1	1	1	1	1	1	1	1
	Habitat diversity	1	1	1	1	1	1	1	1
	Wind exposure	0.007	0.018	0.004	0.003	0.004	0.003	0.011	0.003
	Shore slope	3.10	0.81	17.19	0.71	5.84	1.00	4.17	2.44
	Organic matter content of sediment	20.69	20.69	20.69	20.69	20.69	20.69	20.69	20.69
	Total macrophyte biomass	0	0	0	0	0	0	0	0
	Temperature	8.71	8.71	9.69	8.71	9.69	8.71	8.71	9.69

1.7 List of publications and author contributions

This thesis is based on manuscripts that were published in scientific journals or prepared as manuscripts for submission, respectively. The manuscripts and relative contributions of the authors are listed in Table 1-4. Chapters 2-4 are partly shortened to avoid any repetition, especially with regard to the method sections.

Table 1-4: Publications & manuscripts used for the thesis and contribution of authors. Order of authors is descending with proportion of contribution. It has to be highlighted that the field and laboratory work was strong supported by technical and laboratory staff and many students (see acknowledgement). MB = Mario Brauns, AD = Andrew Dolman, BG = Björn Grüneberg, MM = Marlen Mährlein, MP = Marlene Pätzig, JR = Jacqueline Rücker, YV = Yvonne Vadeboncoeur.

<table>
<tr><th>Chapter</th><th>Study design</th><th>Field and laboratory work</th><th>Data preparation and analysing</th><th>writing</th></tr>
<tr><td>2</td><td colspan="4">Water depth but not season mediates the effects of human lakeshore modification on littoral macroinvertebrates in a large lowland lake
Pätzig, M., Grüneberg, B. & Brauns, M.
Fundamental and Applied Limnology, published 01 June 2015: DOI: 10.1127/fal/2015/0652</td></tr>
<tr><td></td><td>MB, BG & MP</td><td>MP, BG</td><td>MP with contribution of MB & AD</td><td>MP with contribution of MB & BG</td></tr>
<tr><td>3</td><td colspan="4">Marinas affect littoral macroinvertebrate and macrophyte communities differently than beaches compared to natural lakeshores
Pätzig, M.
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<tr><td></td><td>BG, JR, MB & MP</td><td>MP</td><td>MP with contribution of MB & AD</td><td>MP with contribution of MB, BG & JR</td></tr>
<tr><td>4</td><td colspan="4">Using benthic secondary production to determine functional disturbance following human lakeshore modification
Pätzig, M., Vadeboncoeur, Y. & Brauns, M.
Manuscript prepared for submission</td></tr>
<tr><td></td><td>MB, BG, JR & MP</td><td>MP</td><td>MP with contribution of MB & YV</td><td>MP with contribution of MB, YV and BG</td></tr>
<tr><td>5</td><td colspan="4">Length-mass relationships for lake macroinvertebrates corrected for back transformation and preservation effects
Mährlein*, M., Pätzig*, M., Brauns, M. & Dolman, A., *authors contributed equally to the manuscript
Hydrobiologia, accepted 30 September 2015</td></tr>
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2 Water depth but not season mediates the effects of human lakeshore modification on littoral macroinvertebrates in a large lowland lake

2.1 Introduction

The shores of lakes have a great ecological significance for ecosystem functioning (Vadeboncoeur et al. 2002), are hotspots of biodiversity (Vadeboncoeur et al. 2011) and also provide social- and economical values (Schmieder 2004, Strayer & Findlay 2010). The high functionality of lakeshores results from their complex and highly structured environment due to the fact that they are boundary regions between land and water. At the same time, the crucial importance of lakeshores for humans causes a continuous increase of shoreline development worldwide (Schnaiberg et al. 2002, Schmieder 2004). During the last decade, several studies have reported a reduction of littoral biodiversity and an alteration of littoral communities as the consequence of human shoreline development (e.g. Radomski & Goeman 2001, Scheuerell & Schindler 2004, Brauns et al. 2007 a). These observations and the requirements of the Water Framework Directive (WFD) (European Commission 2000) have fostered the limnological research to close gaps of knowledge and provide the ecological basis for the development of lakeshore assessment tools. Recent studies emphasized littoral macroinvertebrates to be useful indicators for the assessment of hydromorphological conditions of lakeshores and developed macroinvertebrate based multimetric indices (e.g. Gabriels et al. 2010, Solimini & Sandin 2012, Miler et al. 2013).

A major prerequisite for the development of macroinvertebrate based assessment methods is sufficient knowledge on the bathymetric and temporal variation, which may confound the response of macroinvertebrates to hydromorphological impairments. With regard to temporal variations, the development of assessment methods is usually based on samples taken during a single season (e.g. Gabriels et al. 2010, Miler et al. 2013, Urbanič 2014), although diversity and composition of littoral macroinvertebrate communities may differ among seasons (e.g. Reid et al. 1995, Scheifhacken et al. 2007, Little 2008). For example, Little (2008) found highest diversities of macroinvertebrates in Irish lakes in spring and again in autumn. Such patterns are usually the result of the emergence of aquatic insects, which are not present during summer. Consequently, the emergence of aquatic insects is leading to a seasonal or even monthly alteration of the macroinvertebrate community composition

(Scheifhacken et al. 2007). This implies that the outcome of assessments of the ecological status of the littoral zone may differ with samples taken in different seasons. However, a systematical evaluation as to whether the effect of shoreline development on littoral macroinvertebrates varies with season is missing.

Another component of variation affecting assessment methods stems from the vertical zonation of lakes, where water depth zones are colonized by spatially distinct macroinvertebrate communities due to substantial differences in environmental conditions (e.g. Särkka 1983, Ali et al. 2002, Hämäläinen et al. 2003). For example, the impact of waves has been shown to be a driving factor in the upper littoral with decreasing influence towards the profundal zone (Rowan et al. 1992). Such a vertical gradient of wave disturbance is accompanied by an alteration of the sediment particle size composition and organic matter content (Bloesch 1995, Cyr 1998). Sediment particle size together with other physical structures such as macrophytes or coarse woody debris is known to be responsible for high habitat heterogeneity of lake shores, and thus leading to diverse littoral macroinvertebrate communities in comparison with the profundal (e.g. James et al. 1998, Helmus & Sass 2008, Vadeboncoeur et al. 2011). These differences in macroinvertebrate communities with depth are also important for assessing human impacts in lakes. For example, Solimini & Sandin (2012) hypothesized that hydromorphological pressures may affect the upper littoral macroinvertebrate community stronger than those of the middle littoral or profundal zone (terminology following Hutchinson 1967). On the other hand, profundal macroinvertebrate communities have long been used as indicators for the trophic state of a lake (e.g. Thienemann 1931, Saether 1979). Recent studies highlight the role of profundal- but also lower and middle littoral macroinvertebrates to detect nutrient enrichment in lakes, whereas upper littoral macroinvertebrate communities are only marginally associated with the trophic state of a lake (Johnson 1998, O'Toole et al. 2008, Bazzanti et al. 2012). The low indicator value of littoral macroinvertebrate communities to assess eutrophication pressure is explained by the simultaneous occurrence of multiple pressures, such as acidification or hydromorphological degradation. For example, Pilotto et al. (2012) were able to demonstrate that lakeshore modification explained already more variation in the lower and middle littoral macroinvertebrate community than eutrophication, whereas the profundal community did not show any response to morphological pressures. Moreover, Brauns et al. (2007 b) could show that littoral macroinvertebrates are no meaningful indicator of the trophic state, since potential effects were superimposed by hydromorphological variables such as wind exposure and habitat complexity. Overall, these results suggest that effects of human shoreline modification on the diversity and composition of macroinvertebrates may differ among depth zones.

The purpose of this chapter was to evaluate the effects of different types of lakeshore modifications on the diversity and composition of the macroinvertebrate community of a large lowland lake in relation to water depth and season. We studied natural and modified shores in the upper littoral, middle littoral and upper profundal zone (1) to test whether the effect of human lakeshore modification on macroinvertebrates systematically differs among water depth zones. Furthermore, we (2) examined the hypothesis that the effect of human modified lakeshores on macroinvertebrates is independent from season.

2.2 Methods

Study sites and sampling

The study was conducted at Lake Scharmützelsee (Chapter 1.6) to investigate macroinvertebrate communities at three undisturbed natural and five modified sites, i.e. two marinas with sheet-pilings and three recreational beaches (two public and one private) (Chapter 1.6) along a depth gradient comprising the upper littoral, middle littoral and profundal (Chapter 1.6). In this chapter we only used the macroinvertebrate and macrophyte data from April, July, September and November 2011, because at these sampling times all eight study sites were included (Chapter 1.6). At each sample site we sampled all habitat types separately in proportion to their total area from a total area per depth zone of 0.18 m², as described in Chapter 1.6.

Statistical analysis

In order to identify the characteristic macroinvertebrate taxa associated to a particular depth zone and to a shore type per depth zone we used indicator species analysis (IndVal) using the R software (v3.0.1, R Development Core Team 2008) and the package ‘indicspecies’ (De Caceres & Legendre 2009, De Caceres 2013).

Macroinvertebrate diversity was quantified with the Hill number N1 and calculated with Primer v6 (Clarke & Gorley 2006). The Hill number N1 is the exponential of Shannon diversity and a conversion of a diversity index in true diversity with the unit ‘effective number of species’. Contrary to diversity indices, true diversity allows for directly comparing the values and facilitates the interpretation, because the Hill number is proportional to the number of species assuming all species are equally common. For example, a hypothetical and simplified macroinvertebrate community with eight equally-common species has a diversity of eight, and a community with sixteen equally-common species has a diversity of sixteen, whereas the Shannon diversity would be three and four for these two communities (Jost 2006).

To test for the effect of season and lakeshore modification on macroinvertebrate diversity, we carried out a global two-way permutation analysis of variance (perANOVA) for each depth zone separately using R with the R package 'lmPerm' (Wheeler 2010). Since permutation tests do not necessarily run all mathematically possible permutations, the corresponding p-values differed slightly each time a test was repeated. All tests were thus performed ten times and corresponding p-values are presented as the mean. For most comparisons, mean p-values were either clearly significant or not, so that variations obtained by permutations had no influence on the rejection or acceptation of the null-hypothesis. For the factor shore type and the interaction term shore type versus season in the profundal, the p-values shifted around the significance level of $p = 0.05$. Both factors exhibited significant mean p-values (0.040 & 0.047), but some of the calculated p-values were not significant (range: 0.025-0.050 & 0.032-0.065). With the aim of testing if shoreline modification alters the availability of the macrophytes as a habitat for macroinvertebrates, we compared macrophyte biomasses among shore types and season using a two-way perANOVA. We did not perform post-hoc test for all perANOVA's because we were primarily interested in the global effect of shore type.

Macroinvertebrate community composition was ordinated using Nonmetric multidimensional scaling (nMDS) based on Bray-Curtis similarities. Prior to statistical analysis, a fourth root transformation was applied to down-weight dominant taxa (Clarke & Gorley 2006). The global effect of season and shore type on community composition was then tested for each depth zone separately using two-way permutation multivariate analyses of variance (perMANOVA) with PERMANOVA+ for Primer v6 (Clarke & Gorley 2006, Anderson et al. 2008). We applied crossed designs, in order to solely detect the influence of season and lakeshore modification on the macroinvertebrate composition. Permutations of residuals were calculated under a reduced model with 9999 permutations and type III of sum of squares was chosen (Anderson et al. 2008).

2.3 Results

We recorded a total of 95 macroinvertebrate taxa from which the indicator species analysis (IndVal) revealed a total of 55 taxa as characteristic for the different water depth zones (Table 2-1). In the upper littoral, 46 macroinvertebrate taxa were identified as indicators (Table 2-1). For the middle littoral, the analysis revealed nine characteristic taxa and no characteristic taxa were found for the profundal zone (Table 2-1).

The IndVal analysis conducted for water depth nested in shore type revealed 26 macroinvertebrate taxa as indicators for natural sites in the upper littoral. At the upper littoral zone of marinas, 16 characteristic taxa were determined, which also included non-native taxa such as Pontogammaridae (Amphipoda) or *Potamopyrgus antipodarum* (Gastropoda) (Table 2-1). For the middle littoral, at natural sites, only *Caenis robusta* was detected as indicator species. Conversely, 11 indicator taxa were revealed in the middle littoral of the marinas (Table 2-1). Here, taxa associated with sandy sediments such as *Athripsodes cinereus*, *Molanna angustata* (Trichoptera) and *Unio tumidus tumidus* (Bivalvia) were recorded. No characteristic taxa were found for the beach neither in the upper- nor in the middle littoral. For the profundal no shore type specific taxa were achieved.

Table 2-1: Indicator species analysis of macroinvertebrates for each water depth zone and water depth zone nested in shore type. For each taxon, the indicator value and the level of significance is given (** 0.001, * 0.01).

			Depth zone		Natural		Marina	
		Taxon	**Upper littoral**	**Middle littoral**	**Upper littoral**	**Middle littoral**	**Upper littoral**	**Middle littoral**
1	**Amphipoda**	*Chelicorophium curvispinum*	0.70 **					0.72 **
2		*Dikerogammarus haemobaphes*	0.46 *					
3		*Dikerogammarus villosus*	0.73 **					
4		Pontogammaridae					0.50 *	
5		*Pontogammarus robustoides*	0.59 **					
6	**Bivalvia**	*Dreissena polymorpha*		0.92 **				
7		*Pisidium* spp.	0.70 **				0.89 **	
8		*Unio tumidus tumidus*					0.74 **	0.65 *
9	**Coleoptera**	*Donacia* spp.	0.55 **				0.75 *	0.50 *
10	**Diptera**		0.44 **		0.76 **			
11		Ceratopogonidae	0.65 **					0.85 **
12		Chironomini	0.89 **		0.80 **			
13		Corynoneurinae	0.61 **		0.88 **			
14		Orthocladiinae	0.96 **		0.90 **			
15		Tanypodinae			0.77 *			
16		Tanytarsini	0.94 **		0.72 *			0.77 *
17	**Ephemeroptera**	*Caenis horaria*	0.82 **				0.83 **	
18		*Caenis lactea*		0.56 *			0.68 *	

			Depth zone		Natural		Marina	
		Taxon	**Upper littoral**	**Middle littoral**	**Upper littoral**	**Middle littoral**	**Upper littoral**	**Middle littoral**
19		*Caenis luctuosa*	0.83 **				0.93 **	
20		*Caenis robusta*	0.76 **		0.98 **	0.64 *		
21		*Cloeon dipterum*	0.78 **					
22	**Gastropoda**	*Acroloxus lacustris*	0.56 **		0.91 **			
23		*Bithynia tentaculata*		0.89 **	0.73 **			
24		*Ferrissia clessiniana*	0.41 *					0.79 **
25		*Gyraulus albus*	0.59 **		0.76 *			0.69 **
26		*Gyraulus crista*		0.68 **	0.70 *			
27		*Gyraulus laevis*		0.76 **			0.86 **	
28		*Hippeutis complanatus*	0.61 **		1.00 **			
29		*Marstoniopsis scholtzi*	0.35 *		0.58 *			
30		*Menetus dilatatus*	0.43 **				0.55 *	
31		*Potamopyrgus antipodarum*		0.70 **			0.85 **	
32		*Radix auricularia/balthica*	0.58 **				0.79 **	
33		*Valvata piscinalis piscinalis*		0.92 **			0.91 **	
34	**Heteroptera**		0.60 **					
35	**Hirudinea**	*Alboglossiphonia heteroclita*	0.34 *		0.58 *			
36		*Alboglossiphonia hyalina*	0.37 *		0.65 *			
37		*Erpobdella octoculata/vilnensis*	0.53 **		0.87 **			
38		*Erpobdella testacea*	0.35 *		0.58 *			
39		*Helobdella stagnalis*	0.35 *		0.58 *			
40	**Isopoda**	*Asellus aquaticus*	0.50 **		0.82 **			
41	**Lepidoptera**		0.60 **					
	Odonata	*Ischnura elegans*	0.38 *					
		Platycnemis pennipes	0.58 **		0.68 **			
42	**Oligochaeta**		0.82 **				0.75 **	0.75 **
43	**Trichoptera**	*Agrypnia pagetana/picta*	0.43 **		0.62 *			
44		*Athripsodes aterrimus*	0.39 *					
45		*Athripsodes cinereus*					0.73 **	0.60 *
46		*Cyrnus crenaticornis*		0.35 *				
47		*Cyrnus flavidus*	0.41 *		0.60 *			
48		*Ecnomus tenellus*	0.71 **		0.79 **			
49		*Limnephilus stigma*	0.35 *					
50		*Molanna angustata*	0.36 *				0.56 *	0.50 *
51		*Mystacides longicornis/nigra*	0.60 **				0.89 **	
52		*Oecetis furva*	0.35 *					
53		*Oecetis ochracea*		0.44 *				
54		*Orthotrichia* spp.	0.67 **		0.79 *			
55		*Psychomyia pusilla*	0.43 **					0.50 *
56		*Triaenodes bicolor/unanimis*	0.35 *		0.58 *			
57	**Turbellaria**		0.53 **		0.80 **			

In the upper littoral zone the comparison of macroinvertebrate diversity revealed significant differences for the factor shore type but not for the factor season (Table 2-2). Similarly, significant differences among shore types were obtained for total macrophyte biomass in this depth zone (Table 2-2, Figure 2-1).

Table 2-2: Results of permutation analysis of variance of macroinvertebrate diversity and macrophyte biomass for every depth zone separately (df = degree of freedom, mean P = averaged probability value).

	Macroinvertebrates			**Macrophytes**		
Upper littoral	**Df**	**Mean P**	**Variance [%]**	**df**	**Mean P**	**Variance [%]**
Shore type	2	0.019	20.6	2	0.000	65.9
Season	3	0.083	15.7	1	0.851	0.1
Shore type x season	6	0.183	20.8	2	0.966	0.1
Residuals	20		42.9	26		33.9
Middle littoral	**Df**	**Mean P**	**Variance [%]**	**df**	**Mean P**	**Variance [%]**
Shore type	2	0.075	14.1	2	0.263	8.9
Season	3	0.026	27.5	1	0.747	0.4
Shore type x season	6	0.623	10.7	2	1.000	0.3
Residuals	20		47.8	26		90.4
Profundal	**Df**	**Mean P**	**Variance [%]**			
Shore type	2	0.040	13.1			
Season	3	0.017	22.1			
Shore type x season	6	0.047	28.9			
Residuals	20		35.9			

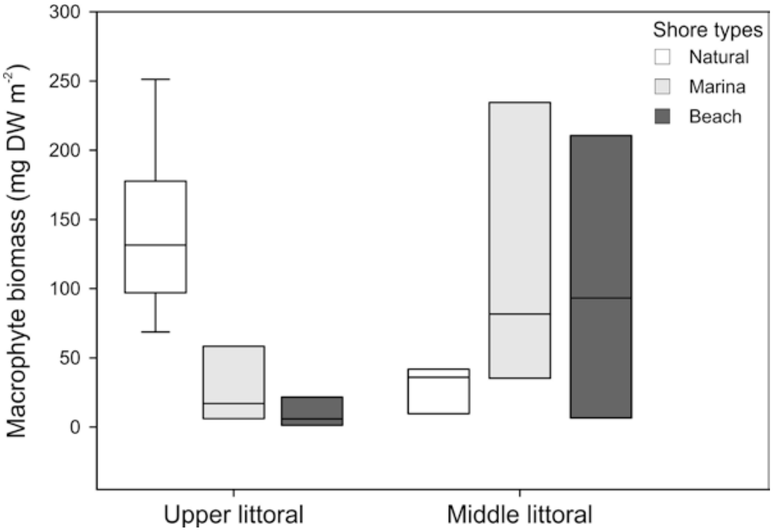

Figure 2-1: Total biomass of macrophytes averaged over sampling seasons at natural and modified shores. Boxes represent 25 % and 75 percentile, black line in box = median, end of vertical lines show 5 % and 95 % percentile.

With regard to the macroinvertebrate composition of the upper littoral, two-way perMANOVA revealed significant compositional differences between the shore types and between sampled seasons (Table 2-3). However, the square root of the estimated component of variation suggested that variation explained by the factor shore type was more than 4-times higher than for season (Table 2-3). The corresponding nMDS ordination (Figure 2-2) showed a clear separation between natural and modified sites in the upper littoral independently of season. Moreover, modified sites separated into marinas and beaches, displaying a gradient of lakeshore modification.

Table 2-3: Results of two-way crossed perMANOVA of macroinvertebrate community composition by season and shore type; Df = degree of freedom, Pseudo-F = Pseudo-F statistic, P(Perm) = probability value from permutation, EMS Sq. root = square root of the estimated component of variation, can be interpreted as percentage of variation.

Upper littoral	**Df**	**Pseudo-F**	**P**	**EMS Sq. root**
Shore type	2	14.2	0.034	28.5
Season	3	1.5	0.000	6.5
Shore type x season	6	0.9	0.660	0
Residuals	20			25.4
Middle littoral	**Df**	**Pseudo-F**	**P**	**EMS Sq. root**
Shore type	2	3.0	0.000	9.4
Season	3	3.5	0.000	12.1
Shore type x season	6	0.9	0.738	0
Residuals	20			21.4
Profundal	**Df**	**Pseudo-F**	**P**	**EMS Sq. root**
Shore type	2	1.5	0.200	3.8
Season	3	2.2	0.036	7.2
Shore type x season	6	1.1	0.321	4.3
Residuals	20			18.2

In contrast to the upper littoral, macroinvertebrate diversity in the middle littoral zone did not significantly differ among shore types, but significantly differed between seasons (Table 2-2). Conversely, total macrophyte biomass did neither significantly differ by shore type nor season (Table 2-2, Figure 2-1). Macroinvertebrate community composition of the middle littoral did not show a clear separation neither for shore type nor for season in the nMDS (Figure 2-2), but two-way perMANOVA indicated significantly different communities between shore types and between seasons (Table 2-3). The diverging results obtained by both analyses can be attributed to the reduction in dimensionality inherent in the nMDS, which is accompanied by a loss of information (Anderson et al. 2008). However, the explained variation of the factor season was 2-times higher in the middle- than in the upper littoral while the explained variation of the factor shore type was 3-times lower than in the upper littoral (Table 2-3).

In the profundal zone, macroinvertebrate diversity significantly differed with season and shore type. However, the significant interaction between both factors precluded us from relating differences in diversity to either shore type or season (Table 2-2). For community composition, no significant differences between shore types could be found. Instead, two-way perMANOVA revealed significant seasonal differences in community composition of this depth zone (Table 2-3) although the nMDS ordination showed no clear pattern again (Figure 2-2).

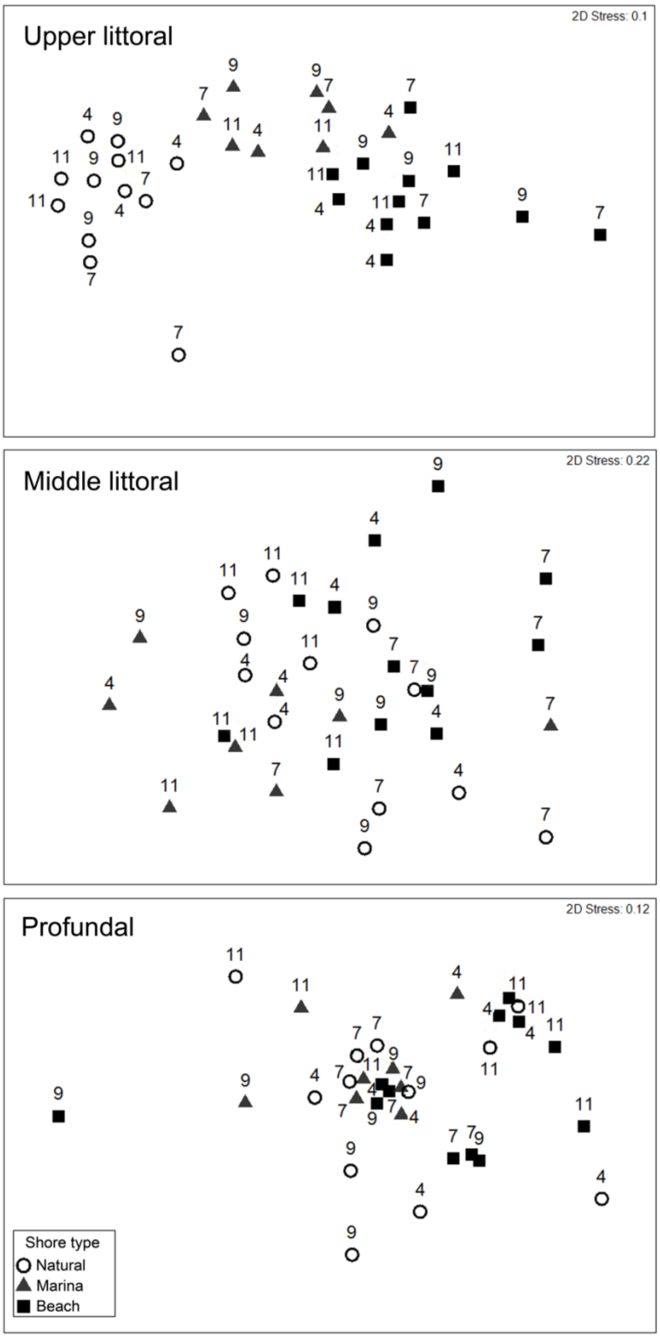

Figure 2-2: nMDS ordination of macroinvertebrate communities of natural and modified shore types separated into upper littoral, middle littoral and profundal zone. Numbers refer to sampling months, 4 = April, 7 = July, 9 = September, 11 = November.

2.4 Discussion

Recent studies emphasized littoral macroinvertebrates as useful indicators for the assessment of hydromorphological conditions of lakeshores (Brauns et al. 2007 a, Urbanič 2014) but the implementation of macroinvertebrates into assessment methods is hampered by the lack of knowledge on effects of season and water depth on the response of macroinvertebrates to lakeshore modification

Our depth-specific results demonstrated that water depth zones are characterized by distinct macroinvertebrate communities and that the effect of lakeshore modification on macroinvertebrate diversity and composition was most pronounced in the upper littoral, to a lower extent in the middle littoral and was not detectable in the profundal. Communities of the upper littoral zone significantly differed between shore types, and shore type explained a higher amount of variation within this depth zone than in the middle littoral or profundal zone. The strong impact of lakeshore modification in the upper littoral may primarily be attributed to the local effect of lakeshore modification on the high habitat heterogeneity and complexity in this depth zone (Brauns et al. 2007 a). Our studied natural sites supported a high number of characteristic species, due to complex three-dimensional structures provided by reed and submerged macrophytes. Thus, the macroinvertebrate community of natural sites significantly differed from modified sites. However, the effect of lakeshore modification varied between marinas and beaches. For example, compositional differences were larger between beaches and natural sites than between marinas and natural sites. This may be due to the absence of well-developed macrophyte stands at beaches caused by permanent stress via human trampling (Figure 2-1) (Sukopp 1971). Human trampling and the loss of macrophyte habitats directly alter the macroinvertebrate community of beaches (Liddle & Scorgie 1980). Moreover the loss of macrophytes may also reduce the shelter against wind- or ship-induced waves (Scheifhacken et al. 2007, Gabel et al. 2012). In contrast, local marinas are characterized by shore stabilization, piers and are not subject to human trampling. Therefore, submerged macrophytes were able to colonize the bottom of marinas and seem to appear partly as substitute for reed belts, which leads to a diverse and abundant macroinvertebrate community. These results are in line with the findings of Brauns et al. (2007 a), who showed that macroinvertebrates are able to found valuable substitute habitats such as ripraps at altered shores. Thus, at our studied lake, the response of the upper littoral macroinvertebrate community to lakeshore modification was primarily related to the alteration of macrophyte biomass that was significantly lower at modified lakeshores. This finding corroborates earlier studies showing that macrophytes are an important habitat for upper littoral macroinvertebrates (James et al. 1998) and were also shown to be important variables in the detection of hydromorphological alterations (e.g. McGoff & Irvine 2009, Jurca et al. 2012).

In the middle littoral, macrophyte biomass did not differ by lakeshore modification, and hence may have provided similar habitat conditions for macroinvertebrates irrespective of shore type. Consequently, the effect of lakeshore modification was 67 % lower on macroinvertebrate composition compared with the upper littoral. Furthermore, macroinvertebrate diversity of the middle littoral was not affected by lakeshore modification. However, perMANOVA revealed significant compositional differences, which may be attributed to the nature of the local marinas. Our studied marinas are large constructions extending down to the middle littoral and consequently alter the habitat configuration. Furthermore, the middle littoral is also situated in the area of wave protection by piers and therefore subject to increased sedimentation of fine material. Fine sediments were found to support macroinvertebrate abundance (James et al. 1998) which explains the detection of 11 indicator species from which *Molanna angustata*, Oligochaeta and *Unio tumidus tumidus* prefer soft-bottom sediments. Moreover, all identified indicator species were also selected for the upper littoral. A significant but low influence of habitat- or morphological variables on middle/lower littoral macroinvertebrates was also found in other studies. Simultaneously, these studies also showed a response of macroinvertebrates to environmental variables indicating eutrophication pressures (Free et al. 2009, Pilotto et al. 2012). Thus, the middle littoral seems to be a transitional zone, where macroinvertebrates respond to different human pressures, which limits a stressor-specific assessment of lake ecosystems.

In the profundal zone, macroinvertebrate composition did not significantly differ among shore types and differences in diversity could not unequivocally be related to differences in shore types due to significant statistical interactions with season. Since lakeshore modification at our studied lowland lake seems to act locally showing already a weak influence in the middle littoral, it appears to be unlikely that effects extended to the profundal. The decreasing effect of lakeshore modification from the middle littoral to the upper profundal has already been shown for subalpine lakes (Pilotto et al. 2012). This is not surprising, given that profundal taxa are used traditionally to indicate the trophic state of a lake (e.g. Thienemann 1931, Saether 1979). The lack of characteristic species in the profundal zone may be the result of the coarse taxonomic resolution of the recorded taxa. Hence, a better taxonomic resolution may result in the detection of indicator taxa.

The effects of season on the upper littoral macroinvertebrate diversity and composition were low compared to the effects of shore type according to the results of perMANOVA, which may be due to several reasons. First, spatial heterogeneity has been shown to reduce temporal variability in stream insect communities, because spatial heterogeneity positively influences community stability (Brown 2003). This may also apply to the studied upper littoral zone that is characterized by a high spatial heterogeneity. Stronger spatial than seasonal effects on littoral macroinvertebrate composition were also obtained by a study conducted at Lake Constance examining water level fluctuations and wind exposure (Scheifhacken et al. 2007). Second, it seems likely that the species turnover imposed by shore type was much stronger than the turnover imposed by the life cycle of aquatic insects including its emergence period. Consequently, in deeper depth zones the decreasing effect of shore type on the species turnover may have been fostered the significant appearance of seasonal effects on the macroinvertebrate communities. This is amplified by the natural distinction of macroinvertebrate communities between depth zones due to changing environmental conditions. The middle littoral has a naturally lower number of habitats, an accordingly lower spatial heterogeneity and hence, a temporal variability that was higher than in the upper littoral zone. There are several studies showing that temporal variation is even higher in profundal than in middle littoral macroinvertebrate communities. This has been attributed to a loss of profundal species during oxygen depletion periods but also due to competitive interactions between species for resources (e.g. Verneaux & Aleya 1998, Hämäläinen et al. 2003, Johnson 1998). In contrast to the literature, we found minor effects of season on the profundal communities in comparison with the middle littoral communities. One reason may be the short period of anoxic conditions in the sampled areas of the profundal zone, which persisted only between mid-July and end of September 2011 (unpublished data). Hence, communities from the profundal zone were only briefly subjected to oxygen depletion. Furthermore, a study on acidified Swedish lakes suggested that the rather simple profundal communities are more constant over years owing to more stable environmental conditions in comparison with the littoral zones (Stendera & Johnson 2008). Hence, the low effect of seasons in our study may be provoked by the low species diversity in the profundal.

In conclusion, we demonstrated that the effect of human lakeshore modification strongly affected the macroinvertebrate community of the upper littoral zone but decreased with water depth in our studied lowland lake. Hence, assessment methods should focus on macroinvertebrates from the upper littoral to assess hydromorphological pressures, because effects of lakeshore modifications are strongest and communities are most susceptible in this depth zone. Conversely, an assessment based on macroinvertebrate communities from deeper depth zones may only be meaningful in cases where lakeshore constructions extend into the middle littoral. Our results also suggest that a single seasonal sampling is sufficient to capture the compositional differences of macroinvertebrate communities associated with human lakeshore modification. These findings together with previous studies (e.g. Brauns et al. 2007 a, Urbanič et al. 2012, Miler et al. 2013) show that the effect of human lakeshore modification acts locally on the upper littoral macroinvertebrates and is independent from seasonal variation, suggesting that this may be a common phenomenon in lowland lakes of the temperate climate region.

3 Marinas affect littoral macroinvertebrate and macrophyte communities differently than beaches compared to natural lakeshores

3.1 Introduction

Worldwide, a continuous increase of lakeshore utilization is taking place (e.g. Schnaiberg et al. 2002, Ostendorp et al. 2004, Schmieder 2004). This leads to conflicts between environmental matters and social needs but also to multiple conflicts of interest between various actors in the human society (e.g. Ostendorp et al. 2003). Lake Scharmützelsee is one example affected by this intricate situation. The lake is located in the lowland of Northeast Germany (Brandenburg) and most of the lakeshore is naturally covered by a vital reed belt (Weiss 2012). Nowadays, over 300 piers and marinas interrupt the reed belt and about 25 % of the 29 km lakeshore is reinforced by sheet pilings, wooden retaining walls and other shore reinforcements. Beaches, grassland or parks cover another 18 % of the lakeshore (Fernando 2011).

In order to find a consensus-based solution between the different interest groups, since 2009 a lakeshore utilization strategy has been developed by a stakeholder commission consisting of representatives from the office of construction committee (Bauausschuss Amt Scharmützelsee), mayors of local communities, citizens' initiative of jetty lobby (Steglobby) and experts. This work revealed that there is a large need for science-based information about the effect of lakeshore modification on the flora and fauna of lakeshores. As a consequence, the department of freshwater conservation of the Brandenburg University of Technology, located at Lake Scharmützelsee, has intensified the research at the lakeshore of Lake Scharmützelsee. The scientific studies included mapping of the reed belt extension (Donath 2009), species composition and vitality of the reed (Möller 2011), GIS based analysis of the reed belt development within the last five decades (Weiss 2012) and a hydromorphological survey, as well as assessment of the lakeshore structure of Lake Scharmützelsee (Fernando 2011). Furthermore, the department supported the mapping of the avifauna (Haupt 2010) on behalf of the Amt Scharmützelsee.

This study extends the previous chapter that examined the global effect of lakeshore modification on macroinvertebrates. Here, the focus is on the assessment of the effect of different types of lakeshore modification on littoral macroinvertebrates. This is of great importance for a successful assessment and management of lakeshores, because previously published studies found that artificial structures used to stabilize lakeshores like ripraps can provide high structural complexity and therefore substitute complex natural habitats with regard to macroinvertebrate diversity and community composition (Engel & Pederson 1998, Brauns et al. 2007 a). Hence, human-induced lakeshore modification may not always have adverse effects on littoral macroinvertebrate communities.

Furthermore, this study aims to evaluate the global and pairwise effects of lakeshore modification on macrophyte diversity and composition, because macrophytes have important ecological functions in lake ecosystems, such as food and habitat provision or their positive influence on water quality (e.g. Thomaz & Chuna 2010, Sachse et al. 2014). Consequently, the loss of macrophytes associated with lakeshore modification can have large impacts on the entire lake ecosystem. For example, it has been shown that lakeshore modification strongly affects the vegetation cover and species richness of emergent vegetation and floating-leaf plants (Ostendorp 1995, Radomski & Goeman 2001, Elias & Meyer 2003, Jennings et al. 2003, Radomski 2006), but there is also evidence that abundance and species richness of submerged vegetation can strongly be affected by lakeshore modification (e.g. Sukopp 1971, Liddle & Scorgie 1980, Bryan & Scarnecchia 1992, Stelzer 2003). Clear cutting of macrophytes is by far the most important reason for the loss of lake vegetation. For example, owners of lakeshore properties remove lake vegetation to create beach conditions, but also every other type of intervention, such as the construction of marinas or lakeshore stabilization, causes the clearance of vegetation along the shoreline (Engel & Pederson 1998, Radomski & Goeman 2001, Elias & Meyer 2003, Jennings et al. 2003). These modification effects are further reinforced by, for example, boating or trampling through recreational activities (Sukopp 1971, Liddle & Scorgie 1980, Ostendorp 1995, Asplund & Cook 1997).

Detailed knowledge about the effect of lakeshore modification on macrophytes would not only help to improve lakeshore management, but could possibly be used to complement the macroinvertebrate-based assessment of lakeshore modification as proposed by Lyche-Solheim et al. (2013). Macrophytes reflect in addition to macroinvertebrates changes in the littoral zone. In a recently-published study, macrophytes were already successfully used to establish a water level drawdown index to reflect hydrological disturbance in regulated lakes of North Europe (Mjelde et al. 2013). A promising approach to assess structural degradation using submerged macrophytes has already been provided by Stelzer (2003) for Germany.

In addition, sufficient knowledge on the effects of lakeshore modification on macrophytes would help to better understand the effects on macroinvertebrates, because macroinvertebrates use macrophytes as habitats (e.g. James et al. 1998, Cyr & Downing 1988, Thomaz & da Chuna 2010).

In summary, the aim of this chapter was to examine the individual effects of three types of lakeshore modification on littoral macrophyte and macroinvertebrate communities at Lake Scharmützelsee and to identify the driving environmental factors structuring the macroinvertebrate communities of human-altered shore types. Macrophyte habitats were sampled together with macroinvertebrates at natural sites, marinas and beaches in the upper and middle littoral and in four different seasons to test the hypotheses that 1) macrophyte and macroinvertebrate communities vary between different types of lakeshore modification and 2) macrophytes are the most important driving factor in structuring macroinvertebrate communities at human-altered shore types.

3.2 Methods

Study sites and sampling

Macrophytes and macroinvertebrates were sampled in April, July, September and November 2011 from each of the eight study sites selected at Lake Scharmützelsee as described in Chapter 1.6. Since I could prove that lakeshore modification had no effect on the profundal macroinvertebrate community (Chapter 2); this part of the study only comprises the upper and middle littoral of Lake Scharmützelsee. For more details about the study sites and the sampling of macroinvertebrates and macrophytes, see Chapter 1.6.

Environmental factors

The five environmental variables wind exposure, slope, organic matter content of the sediment, macrophyte biomass and habitat diversity were measured for each study site per depth zone in order to find the most driving factors explaining differences in macroinvertebrate community composition among shore types. Determination of the environmental variables wind exposure, slope, organic matter content of the sediment were described and presented in Chapter 1.6: Table 1-3. Total macrophyte biomass and habitat diversity per site and depth zone were calculated for each of the four months included in this study (Appendix I).

Statistical analysis

Firstly, a descriptive statistical overview about taxa-specific macrophyte biomass and macroinvertebrate abundance data is given, in order to evaluate the dominance relation for the shore types of Lake Scharmützelsee.

Differences in macrophyte and macroinvertebrate communities between shore types were tested using uni- and multivariate statistical test (Figure 3-1). Global tests for macroinvertebrate diversity (Hill number N1, for explanation see Chapter 2.2) and total biomass of macrophytes were already carried out in Chapter 2, using two-way permutation analysis of variance (perANOVA). Pairwise tests were performed with Dunn’s non-parametric post-hoc test in R 3.2.0 (R Development Core Team 2008), using the function ‘kruskalmc’ from the R package ‘pgirmess’ (Giraudoux 2015). Since I was interested in the effect of lakeshore modification, and season has played a minor role in the global tests for macroinvertebrates (Chapter 2.3), but also for macrophytes (this chapter) the seasonal samples were treated as replicates for pairwise tests.

Macrophyte composition based on biomass was quantified using the Bray-Curtis similarity measure as described for macroinvertebrates in Chapter 2.2. Prior to statistical analysis, to all biomass values I added one, in order to consider samples without macrophytes. Furthermore, a fourth-root transformation was applied to down-weight dominant taxa (Clarke & Gorley 2006). A global effect of season and shore type on macrophyte community composition was then tested for each depth zone separately using two-way crossed permutation multivariate analyses of variance (perMANOVA) with PERMANOVA+ for Primer v6 (Clarke & Gorley 2006, Anderson et al. 2008). Permutations of residuals were calculated under a reduced model with 9999 permutations and type III of sum of squares was chosen (Anderson et al. 2008).

Significant results obtained by the global test of perMANOVA for macrophyte and macroinvertebrate communities can be attributed to distance between groups, but also to differences in dispersion. Therefore, I tested for homogeneity of dispersion using the PRIMER routine PERMDISP (Clarke & Gorley 2006, Anderson et al. 2008), when the global test of perMANVOA was significant for the factors shore type and season. This procedure is especially recommended when one factor depends on another factor and enables to verify the non-independency between different factors (Anderson et al. 2008). In my case, the factor shore type is nested in season, because one and the same site of a shore type sampled at different time points is influenced by different seasonal conditions. Applying PERMDISP particularly helps to interpret the results of the pairwise tests. Pairwise tests between shore types were performed for macroinvertebrate and macrophyte composition using the same settings for perMANOVA as for the global test.

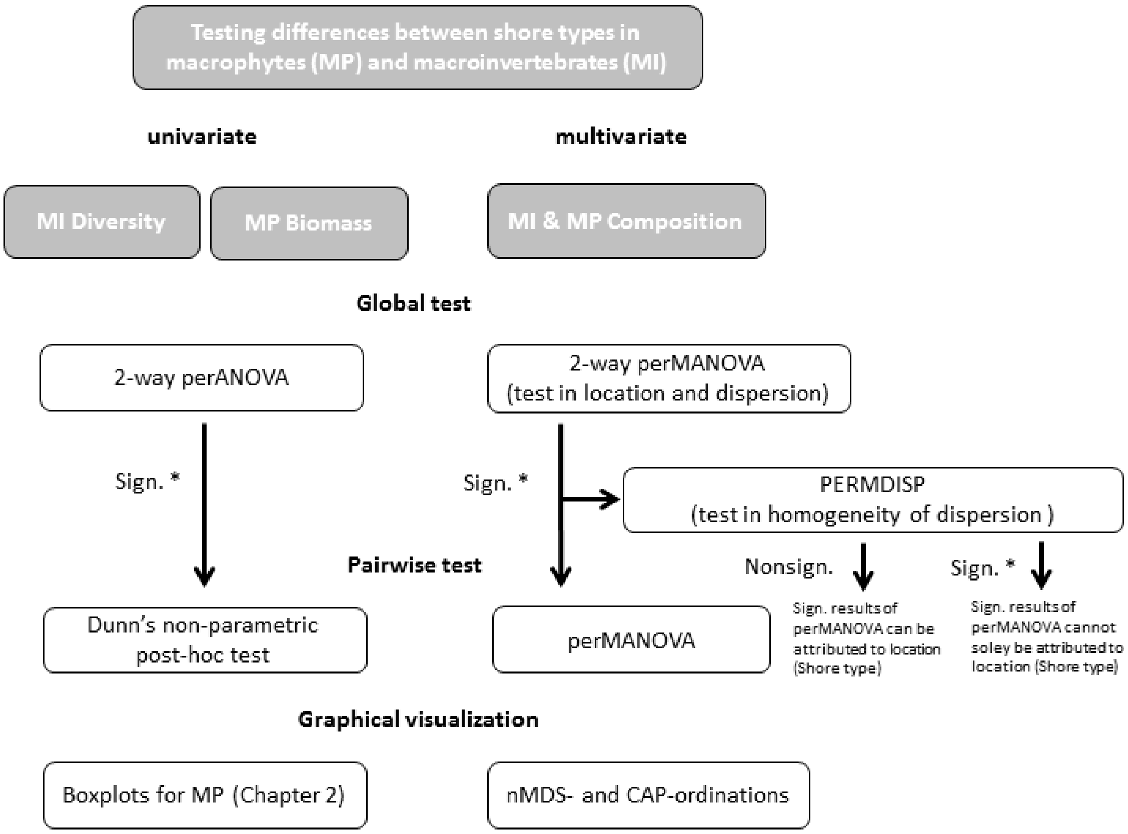

Figure 3-1: Overview about uni- and multivariate statistical tests to explain differences between shore types in macrophyte (MP) and macroinvertebrate (MI) communities.

Differences in macrophyte composition between shore types were visualized using nonmetric multidimensional scaling (nMDS). nMDS plots for macroinvertebrate composition were already shown in Chapter 2.3: Figure 2-2. Nevertheless, perMANOVA and nMDS revealed discrepancies between the results obtained for the macroinvertebrate composition in the middle littoral (Chapter 2.3: Table 2-3 and Figure 2-2). This can be attributed to the loss of information by graphical illustration of multidimensional data clouds in a two-dimensional space (Anderson et al. 2008). An indication of a poor performance can be obtained by the 2D stress value. For macroinvertebrate composition in the middle littoral, the 2D stress value exceeded 0.2 (Chapter 2.3: Figure 2-2), indicating a poor display of the multidimensional data cloud in a two-dimensional space (Clarke & Warwick 2001). A possibility to solve this problem is the performance of a constraint canonical analysis of principal coordinates (CAP). This PRIMER routine search for the axis which best separates the different groups and provides table of cross-validation to assess the validity and utility of the CAP model showing how well the principal coordinate axes discriminate between the groups (Anderson et al. 2008). I applied this method in this chapter to better graphically visualise the macroinvertebrate communities between shore types of the middle littoral to complement the result of the perMANOVA pairwise tests.

The driving environmental variables structuring different macroinvertebrate communities of the shore types in the two depth zones were identified using distance-based linear models (DISTLM) with Primer v6 (Clarke & Gorley 2006). The method analyses the relation between the multivariate macroinvertebrate data cloud, described by a Bray–Curtis resemblance matrix based on abundance data and the five following predictor variables: habitat diversity, total macrophyte biomass, slope, exposure and organic matter content of the sediment (Chapter 1.6: Table 1-3 & Appendix I). DISTLM provides a marginal test showing the relation between the response variable and a single variable and the best set of environmental variables that explain the macroinvertebrate composition variability. The DISTLM applied was based on step-wise selection procedure and the 'An Information Criterion' (AIC) (Akaike 1973). AIC was chosen, because unlike R^2, the values do not improve by adding more predictor variables (Anderson et al. 2008). Despite the flexibility of the method, the environmental variables should not be heavily skewed and transformed whenever necessary. The skewing of environmental data was tested using the Shapiro-Wilk Test and diagnostic plots in R 3.2.0 (R Development Core Team 2008), and transformed if necessary. In the upper littoral, all variables except for habitat diversity and in the middle littoral all environmental variables but macrophyte biomasses were log-transformed, due to positively skewed distribution. Inter-correlation was reviewed in PRIMER v6 with a correlation matrix. The usual cut-off of inter-correlated variables is 0.95 (Anderson et al. 2008). None of the variables exceeded this limit.

Additionally, environmental variables were overlaid as vectors over the nMDS or CAP-plots for macroinvertebrates communities, respectively, to examine the strength and direction between these environmental variables and the macroinvertebrate communities of the different sites.

3.3 Results

Effect of lakeshore modification on littoral macrophytes

Altogether, 13 macrophyte species occurred at the selected study sites of the upper littoral with *Typha angustifolia* and *Myriophyllum spicatum* being the most dominant species (Table 3-1). 65 % of total macrophyte biomass from the studied shore types of the upper littoral was found at natural sites, which predominantly consisted of *Typha angustifolia* and *Phragmites australis* (Table 3-1). Both species together composed ~70 % of the total macrophyte biomass at natural sites. The rootless submerged plants *Ceratophyllum demersum*, *C. submersum* and *Fontinalis antipyretica* contributed ~23 % to total biomass at natural sites (Table 3-1).

At the modified sites, emergent macrophytes were absent and total average biomass lower (Table 3-1). Emergent vegetation was partly replaced by the rooted submerged macrophytes *Elodea canadensis*, *Myriophyllum spicatum*, *Najas marina spp. intermedia*, *Potamogeton pectinatus/pusillus* and *Ranunculus circinatus* (Table 3-1). A distinction between macrophyte communities of marinas and beaches can be attributed to the generally larger total biomass at marinas (72.6 g DW m²) in comparison to beaches (11.8 g DW m²). At marinas, *Myriophyllum spicatum* dominated with 44.5 % of the total biomass, but this can be solely attributed to the occurrence of this plant species at the western marina. Contrary, *Ranunculus circinatus* was the species most dominant at the eastern marina. At beaches *Elodea canadensis* (37.5 % of the total biomass at beaches) and *Potamogeton pectinatus/pusillus* (37.7 %) were the most dominant species (Table 3-1). It has to be emphasized that the western beach did not harbour any macrophytes and *Elodea canadensis* was only found at the private beach.

The described differences between the shore types in this depth zone also became statistically significant in the global test for both community measures, i.e. total macrophyte biomass ($p = 0.000$, see also Chapter 2.3: Table 2-2 & Figure 2-1) and macrophyte community composition (Table 3-2).

Table 3-1: Average macrophyte biomass and proportion for each species per shore type for the upper littoral zone. Macrophyte biomass was averaged over season per site and then averaged per shore type. Plant growth form following Niedringhaus & Zander 1998, Zander et al. 1991, Wiegleb 1991. DM = dry mass, SD = standard deviation.

		Natural		**Marina**		**Beach**	
Plant growth form	**Species**	DM in g/m² ± SD	DM in %	DM in g/m² ± SD	DM in %	DM in g/m² ± SD	DM in %
Bryides	*Fontinalis antipyretica*	17.5 ± 5	11.1	14.3 ± 17.3	14.5		
Cerato-phyllides	*Ceratophyllum demersum*	16.0 ± 15.2	10.2	0.6 ± 0.8	0.8		
	Ceratophyllum submersum	3.1 ± 5.4	2.0				
	Utricularia vulgaris	0.6 ± 0.5	0.4	0.6 ± 0.9	0.9		
Eloeides	*Elodea canadensis*			0.5 ± 0	0.7	4.4 ± 7.7	37.5
	Najas marina spp. intermedia	0.1 ± 0.1	0.0	1.9 ± 2.6	2.6	0.8 ± 0.9	6.6
	Nitellopsis obtusa	9.4 ± 12.5	6	13.1 ± 6.2	18.0	1.9 ± 3.3	15.9
	Potamogeton pectinatus/pusillus	0.1 ± 0.2	0.1	4.3 ± 4.5	5.9	4.3 ± 4.6	36.7
	Potamogeton perfoliatus	0.1 ± 0.1	0.0				
Magno-graminoides	*Phragmites australis*	21.1 ± 13	13.4				
Magno-graminoides	*Typha angustifolia*	89.2 ± 68.1	56.8				
Myrio-phyllides	*Myriophyllum spicatum*			32.3 ± 45.7	44.5		
	Ranunculus circinatus			5.1 ± 5.8	7.0	0.4 ± 0.6	3.1
	Sum	**157.2**		**72.6**		**11.8**	

Table 3-2: Results of global two-way crossed perMANOVA of upper littoral macrophytes community composition by season and shore type; Df = degree of freedom, Pseudo-F = Pseudo-F statistic, P(perm) = probability value from permutation, EMS Sq. root = square root of the estimated component of variation, can be interpreted as percentage of variation.

Upper littoral	**Df**	**Pseudo-F**	**P(perm)**	**EMS Sq. root**
Shore type	2	32.4	0.000	9.4
Season	3	1.9	0.082	1.9
Shore type x season	6	0.7	0.792	0
Residuals	20			5.5

With regard to total macrophytes biomass, pairwise tests detected significant differences between natural sites and both modified shore types (Dunn's test: $p < 0.05$), but not between marinas and beaches (Dunn's test: ≥ 0.05), although marinas tended to have larger amounts of macrophyte biomass (Chapter 2.3: Figure 2-1). Pairwise tests for macrophyte community composition revealed significant distinctions between all three shore types in the upper littoral (Table 3-3, Figure 3-2). For macrophyte community composition I did not perform PERMDISP, because season was not significant in the upper littoral. Therefore, differences can be solely attributed to the effect of lakeshore modification.

Table 3-3: Results of pairwise two-way crossed perMANOVA of upper littoral macrophyte community composition by shore type; t = t-statistic is larger the greater the differences between two groups, P(perm) = probability value from permutation, Df = degree of freedom.

Macrophytes	**Upper littoral**		
Groups	**t**	**P(perm)**	**Df**
Beach vs. marina	2.5	0.007	12
Beach vs. natural	8.9	0.000	16
Marina vs. natural	5.0	0.000	12

In the middle littoral, only eight of the 13 species recorded in this study were recorded. *Nitellopsis obtus*a was with 71.5 % by far the most dominant species in this depth zone (Table 3-4). Nevertheless, when looking at the percentual proportion of *Nitellopsis obtus*a for each shore type, natural sites and beaches exhibited more than 90 % of this species, whereas marinas were composed of only 45.3 % *Nitellopsis obtusa.* Marinas harboured additionally a large amount of *Potamogeton pectinatus/pusillus* (48.8 %) (Table 3-4), attributable to the large biomass of this species observed at the marina from the east side of the lake.

However, in contrast to the upper littoral, the global test for the middle littoral found no significant differences for total macrophyte biomass and macrophyte composition between the studied shore types (Table 3-5, Figure 3-2 & Chapter 2.3: Table 2-2).

Table 3-4: Average macrophyte biomass and proportion for each species per shore type for the middle littoral zone. Macrophyte biomass was averaged over season per site and then averaged per shore type. Plant growth form following Niedringhaus & Zander 1998, Zander et al. 1991, Wiegleb 1991. DM = dry mass, SD = standard deviation.

		Natural		**Marina**		**Beach**	
Plant growth from	**Species**	DW in g/m² ± SD	DW in %	DW in g/m² ± SD	DW in %	DW in g/m² ± SD	DW in %
Bryides	*Fontinalis antipyretica*	0.3 ± 0.3	0.8	0.2 ± 0.2	0.1	0.1 ± 0.1	0.1
Cerato-phyllides	*Ceratophyllum demersum*			0.6 ± 0.9	0.4	3.5 ± 5.7	2.4
	Ceratophyllum submersum						
	Utricularia vulgaris	0.4 ± 0.4	1.3			0.2 ± 0.2	0.1
Eloeides	*Elodea canadensis*						
	Najas marina spp. intermedia			0.1 ± 0.1	0.1	0.3 ± 0.5	0.2
	Potamogeton pectinatus/pusillus			78.0 ± 106.9	48.8	3.7 ± 3.0	2.6
	Potamogeton perfoliatus			8.3 ± 11.1	5.2		
	Nitellopsis obtusa	31.6 ± 94.9	97.2	72.4 ± 1.9	45.3	137.8 ± 71.7	92.0
Myrio-phyllides	*Myriophyllum spicatum*	0.2 ± 0.4	0.7	0.4 ± 0.5	0.2		
	Ranunculus circinatus						
Magno-graminoides	*Phragmites australis*						
	Typha angustifolia						
	Sum	**32.6**		**160**		**145.6**	

Table 3-5: Results of global two-way crossed perMANOVA of middle littoral macrophyte community composition by season and shore type; Df = degree of freedom, Pseudo-F = Pseudo-F statistic, P(perm) = probability value from permutation, EMS Sq. root = square root of the estimated component of variation, can be interpreted as percentage of variation.

Middle littoral	**Df**	**Pseudo-F**	**P(perm)**	**EMS Sq. root**
Shore type	2	2.0	0.960	0.9
Season	3	24.3	0.000	4.9
Shore type x season	6	1.4	0.189	1.1
Residuals	20			2.8

Figure 3-2: nMDS ordination of macrophyte composition per shore type separated for the upper (2D Stress: 0.08) and middle littoral zone (2D Stress: 0.02).

Effect of lakeshore modification on littoral macroinvertebrates

From the 95 macroinvertebrate taxa recorded, 91 were found in the upper littoral. Oligochaeta, Chironomidae Gastropoda, *Pisidium* spp. and Ephemeroptera (descending order) were the most dominating groups over all sites in the upper littoral zone (Table 3-6). Table 3-6 showed that the macroinvertebrate groups in this depth zone differed in their proportional abundance between shore types even at higher taxonomic level.

At natural sites, Oligochaeta (~45 % from average abundance of natural sites) and Chironomidae (~39 %) were the most dominant groups followed by Ephemeroptera (~5 %) mainly represented by the mayfly *Caenis robusta* (Table 3-6, Appendix II). The diversity of predators such as Hirudinea, Odonata and Turbellaria etc. were high at natural site, but in relatively low abundances (Table 3-6). Other species such as *Asellus aquaticus* were restricted to this shore type (Table 3-6). In contrast, Unionidae and almost all *Pisidium* spp. were absent from natural sites (Table 3-6). In general, it is noticeable that the number of individuals observed at natural sites (10,773 m^2) was lower than for the studied marinas (18,672 m^2).

At marinas, Oligochaeta dominated (~43 % from average abundance of marinas) followed by *Pisidium* spp. (~15 %), Gastropoda (~18 %), Chironomidae (~12 %) and Ephemeroptera (~6 %) with the last one mainly represented by *Caenis luctuosa* (Table 3-6, Appendix II). The frequent occurrence of Gastropoda, also true for the beach sites, was caused by the massive presence of the snail *Potamopyrgus antipodarum* (Appendix II). In contrast, this snail was almost absent at natural sites.

Beaches only harboured an average of 7060 individuals/m^2 of macroinvertebrates at the studied sites of the upper littoral and were dominated by Gastropoda (~47 %), followed by Oligochaeta (~21 %), Chironomidae (~15 %) and *Pisidium* spp. (~10 %) (Table 3-6).

Table 3-6: Average number of individuals and proportion for each group of upper littoral macroinvertebrates. Individual numbers were averaged over season per site and then averaged per shore type. Ind. No = individual number, SD = standard deviation.

Upper littoral	**Natural**		**Marina**		**Beach**	
Group	Ø Ind. No. ± SD	Ind. No. %	Ø Ind. No. ± SD	Ind. No. %	Ø Ind. No. ± SD	Ind. No. %
Asellus aquaticus	88 ± 67	0.8				
Ceratopogonidae	121 ± 56	1.1	118 ± 29	0.6	17 ± 20	0.2
Chironomidae	4249 ± 718	39.4	2283 ± 1809	12.2	1071 ± 212	14.7
Coleoptera	8 ± 13	0.1	125 ± 123	0.7	13 ± 16	0.2
Dreissena polymorpha	224 ± 151	2.1	297 ± 82	1.6	157 ± 155	2.1
Ephemeroptera	549 ± 78	5.1	1191 ± 970	6.4	221 ± 100	3.0
Gastropoda	140 ± 55	1.3	3440 ± 3121	18.4	3398 ± 2430	46.6
Heteroptera	15 ± 13	0.1	34 ± 18	0.2	55 ± 48	0.8
Hirudinea	41 ± 7	0.4			14 ± 12	0.2
Lepidoptera	42 ± 22	0.4	28 ± 6	0.1	2 ± 3	0.0
Odonata	61 ± 19	0.6	26 ± 37	0.1		
Oligochaeta	4868 ± 1490	45.2	7942 ± 4862	42.5	1510 ± 1064	20.7
other Diptera	43 ± 26	0.4				
Pisidium spp.	81 ± 93	0.8	2868 ± 1261	15.4	703 ± 441	9.7
Pontogammaridae	82 ± 25	0.8	162 ± 78	0.9	86 ± 97	1.2
Trichoptera	82 ±6	0.8	88 ± 21	0.5	31 ± 30	0.4
Turbellaria	78 ± 41	0.7	47 ± 34	0.3		
Unionidae			23 ± 8	0.1	6 ± 7	0.1
Sum	**10,773**		**18,672**		**7285**	

In the upper littoral zone, lakeshore modification had a significant global effect on macroinvertebrate diversity ($p = 0.019$, Table 3-10, see also Chapter 2.3: Table 2-2) and community composition ($p = 0.034$, Table 3-10, see also Chapter 2.3: Table 2-3). For macroinvertebrate diversity, a pairwise test revealed significant differences between natural sites and beaches (Dunn’s test: $p < 0.05$), but no significant differences were found neither between natural sites and marinas nor between marinas and beaches (Dunn’s test: $p \geq 0.05$). Contrary to diversity, macroinvertebrate community composition differed significantly between all shore types (Figure 3-3, Table 3-7). Since PERMDISP revealed no differences in homogeneity of dispersion of the macroinvertebrate data between shore types ($p = 0.48$), the significant results obtained by pairwise test can solely be attributed to differences between shore types independent of season (explanation see Figure 3-1).

Table 3-7: Results of pairwise two-way crossed perMANOVA of upper littoral macroinvertebrate community composition by shore type; t = t-statistic value is higher the larger the differences between two groups, P(perm) = probability value from permutation, Df = degree of freedom.

Macroinvertebrates	**Upper littoral**		
Groups	**t**	**P(perm)**	**Df**
Beach vs. marina	2.6	0.001	12
Beach vs. natural	4.8	0.000	16
Marina vs. natural	3.4	0.000	12

In the middle littoral, 65 of the 95 taxa recorded were found. Macroinvertebrates from marinas differed in comparison to natural sites and beaches. This can mainly be attributed to densities of Oligochaeta with in average 3393 individuals/m², whereas natural sites and beaches exhibited only 1138 or 1438 individuals/m² of Oligochaeta, respectively (Table 3-8). Densities of Chironomidae and *Dreissena polymorpha* also contributed to the larger total number of individuals at marinas (Table 3-8). Compared to the upper littoral, the abundances of macroinvertebrate groups had greater similarity between shore types in the middle littoral (Table 3-8).

Significant differences were detected in the global test for macroinvertebrate community composition of different shore types in the middle littoral ($p = 0.000$, Table 3-10, see also Chapter 2.3, Table 2-3). Therefore, I performed pairwise tests, which identified significant dissimilarities between marinas and beaches and between marinas and natural sites (Table 3-9). Since PERMDISP again revealed no significant differences in homogeneity of dispersion between the shore types ($p = 0.99$), the detected differences in macroinvertebrate composition only resulted from differences between shore types. This result was also reflected in the constrained ordination of the CAP-analysis (Figure 3-3). In contrast, no significant differences were found for macroinvertebrate diversity between shore types in the middle littoral ($p = 0.075$, Table 3-10, see also Chapter 2.3: Table 2-2).

Table 3-8: Average number of individuals and proportion for each group of middle littoral macroinvertebrates. Individual numbers were averaged over season per site and then averaged per shore type. Ind. No = individual number, SD = standard deviation.

Middle littoral	**Natural**		**Marina**		**Beach**	
Group	Ø Ind. No. ± SD	Ind. No. %	Ø Ind. No. ± SD	Ind. No. %	Ø Ind. No. ± SD	Ind. No. %
Asselus aquaticus						
Ceratopogonidae	53 ± 78	1.0	102 ± 10	1.3	12 ± 11	0.2
Chironomidae	521 ± 72	9.6	797 ± 211	10.2	348 ± 94	6.9
Coleoptera			20 ± 5	0.3	29 ± 9	0.6
Dreissena polymorpha	923 ± 529	17.0	1330 ± 35	17.0	984 ± 1068	19.6
Ephemeroptera	215 ± 57	3.9	314 ± 97	4.0	214 ± 37	4.3
Gastropoda	1537 ± 1126	28.3	1148 ± 897	14.7	1460 ± 755	29.1
Heteroptera	7 ± 13	0.1	42 ± 27	0.5	32 ± 55	0.6
Hirudinea	16 ± 13	0.3	3 ± 4	0.0	21 ± 5	0.4
Lepidoptera			4 ± 6	0.1	2 ± 3	0.0
Odonata	55 ± 60	1.0	9 ± 13	0.1	10 ± 12	0.2
Oligochaeta	1138 ± 361	20.9	3393 ± 1365	43.4	1438 ± 195	28.6
other Diptera			19 ± 20	0.2		
Pisidium spp.	783 ± 610	14.4	489 ± 227	6.3	323 ± 500	6.4
Pontogammaridae	71 ± 86	1.3	84 ± 58	1.1	83 ± 34	1.6
Trichoptera	67 ± 38	1.2	55 ± 16	0.7	60 ± 68	1.2
Turbellaria	49 ± 62	0.9				
Unionidae	5 ± 5	0.1	15 ± 3	0.2	6 ± 2	0.1
Sum	**5441**		**7825**		**5020**	

Table 3-9: Results of pairwise two-way crossed perMANOVA of middle littoral macroinvertebrate community composition by shore type; t = t-statistic value is higher the larger the differences between two groups, P(perm) = probability value from permutation, Df = degree of freedom.

Macroinvertebrates	**Middle littoral**		
Groups	**t**	**P(perm)**	**Df**
Beach vs. marina	2.1	0.001	12
Beach vs. natural	1.3	0.071	16
Marina vs. natural	1.8	0.007	12

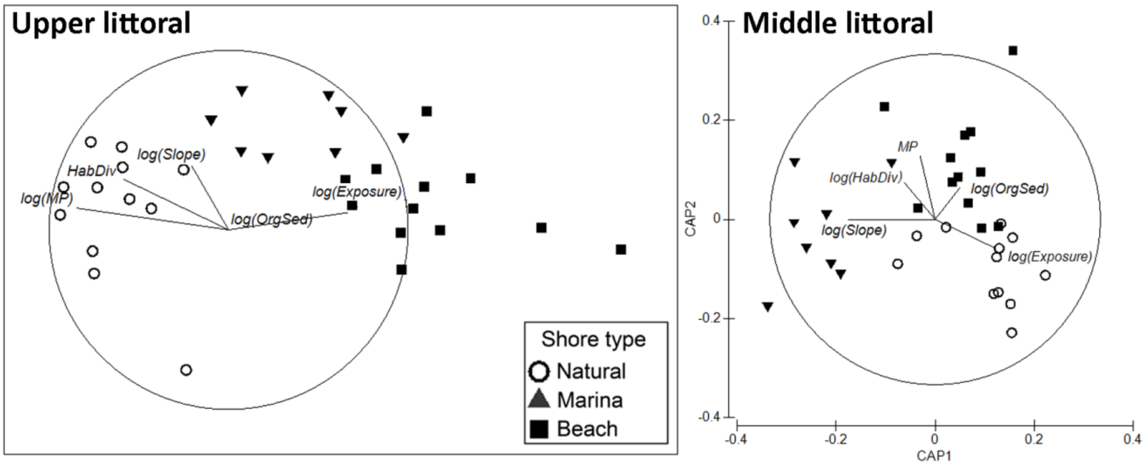

Figure 3-3: Ordination of macroinvertebrate composition per shore type separated for the upper and middle littoral zone. Upper littoral based on nMDS ordination (2D Stress: 0.1). Middle littoral based on CAP ordination. MP = macrophyte biomass, OrgSed = organic matter content of sediment, Exposure = wind exposure, HabDiv = habitat diversity.

In summary, I first could show that lakeshore modification primarily has local effects on macrophyte and macroinvertebrate communities of the upper littoral zone (Table 3-10). Secondly, in the upper littoral macroinvertebrate communities from beaches differed significantly from natural sites with regard to diversity and composition. Marinas only differed significantly from natural sites with regard to macroinvertebrate composition (Table 3-10). Hence, different types of lakeshore modification affect macroinvertebrate communities differently. Composition of upper littoral macrophytes also differed between all shore types, but biomass was significantly lower at beaches and marinas compared to natural sites. Consequently, macrophytes reacted differently to different types of lakeshore modification than macroinvertebrates. Thirdly, in the upper littoral, the explained variation was larger for macroinvertebrate community composition than for diversity between shore types, resulting only in significant difference between natural and beach sites for diversity (Table 3-10). Fourthly, in the middle littoral only macroinvertebrates showed significant differences between shore types, due to a different composed community at marinas (Table 3-10).

Table 3-10: Summary of global and pairwise tests for macroinvertebrate diversity, macrophyte biomass and community composition of both organism groups. Global test for diversity were carried out applying two-way permutation analyses of variance (perANOVA), followed by Dunn's nonparametric post-hoc test for shore types. Global and pairwise test for community composition was performed with permutation multivariate analyses of variance (perMANOVA). D = diversity N1, C = community composition, B = biomass. Empty = not significant (p ≥ 0.05).

	Macroinvertebrates				**Macrophytes**			
	Upper littoral		Middle littoral		Upper littoral		Middle littoral	
Global test	D	C	D	C	B	C	B	C
Shore type	0.019	0.034		0.000	0.000	0.000		
Season		0.000	0.026	0.000				0.000
Pairwise test for shore types								
Natural vs. marinas		0.000		0.007	< 0.05	0.000		
Natural vs. beaches	< 0.05	0.000			< 0.05	0.000		
Marinas vs. beaches		0.001		0.001		0.007		

Environmental factors structuring macroinvertebrate communities

In the upper littoral, marginal test of the DISTLM analysis showed that all variables apart from organic matter content of the sediment had a significant relation to the macroinvertebrate community data (Table 3-11). Macrophyte biomass alone explained ~35 % of the variability followed by wind exposure (~21 %). The DISTLM step-wise procedure selected the three variables macrophyte biomass, slope and wind exposure for the model best, explaining the variability in the macroinvertebrate communities (AIC = 214.14, R^2 = 0.47). The environmental variables laid over the nMDS-plot (Figure 3-3) showed a positive relation of macroinvertebrates at natural sites to macrophyte biomass followed by habitat diversity, whereas the modified shore types, particularly the beach sites were positively related to wind exposure. Slope rather explained variation within the shore types, but explained variability as low (Table 3-11, Figure 3-3).

Table 3-11: Marginal tests of DISTLM step-wise procedure for the upper littoral showing the significant realtion of environmental variables to macroinvertebrate community composition. OrgSed = organic matter content of sediment, MP = total macrophyte biomass, Pseudo-F = Pseudo-F statistic, P = probability value, Prob. % = probability in percent/explained variability.

Marginal tests	**Pseudo-F**	**P**	**Prob. %**
Log(Exposure)	8.13	0.000	21.32
Log(Slope)	2.36	0.049	0.07
Log(OrgSed)	0.66	0.663	0.02
Log(MP)	15.94	0.000	34.69
Habitat diversity	6.74	0.000	0.18

In the middle littoral, marginal test of the DISTLM analysis showed that three of five variables were significant in relation to the macroinvertebrate data (Table 3-12). Macrophyte biomass again was the major driving factor of macroinvertebrate community composition in this depth zone, but explained only 10.6 % of the variability in the macroinvertebrate data. The DISTLM step-wise procedure selected the three variables macrophytes biomass, slope and habitat diversity for the model best explaining the variability in the macroinvertebrate community (AIC = 202.91, $R^2 = 0.26$). The environmental variables laid over the CAP-plot (Figure 3-3) showed a positive relation of slope with most samples taken at the marinas. Macrophyte biomass was rather related to the second axis and thus positively related to most of the beach sites but negatively to the natural sites (Figure 3-3).

Table 3-12: Marginal tests of DISTLM step-wise procedure for the middle littoral showing the significant relation of environmental variables to macroinvertebrate community composition. OrgSed = organic matter content of sediment, MP = total macrophyte biomass, Pseudo-F = Pseudo-F statistic, P = probability value, Prob. % = probability in percent/explained variability.

Marginal tests	Pseudo-F	P	Prob. %
Log(Exposure)	1.31	0.202	0.04
Log(Slope)	2.73	0.003	0.08
Log(OrgSed)	1.93	0.036	0.06
Log(MP)	3.55	0.000	10.59
Habitat diversity	1.74	0.065	0.05

3.4 Discussion

In general, the results showed that the effect of lakeshore modification on macrophytes and macroinvertebrates were strongest at the upper littoral, but to a different degree depending on the shore type. In the middle littoral, modifications only appeared to have an effect when they were directly carried out in this depth zone, as it was the case for the studied marinas. Consequently, lakeshore modifications primarily has local effects on organism (see Chapter 2.4 & e.g. Brauns et al. 2007 a).

Lakeshore modification affects biomass and species composition of macrophytes

In the upper littoral, total macrophyte biomass was significantly lower at the studied beaches and marinas compared to the natural sites. The two modified shore types did not differ significantly from each other in their total macrophyte biomass, although marinas tended to have higher values. Contrary macrophyte community composition differed between all shore types.

The high biomass and different community composition of natural sites can be attributed to the high macrophyte biomass from emergent macrophytes and rootless submerged plants. In contrast, the examined modified shore types harboured no emergent macrophytes and far less rootless submerged plants. The absence of emergent macrophytes at modified sites is a result of clear cutting to make the lakeshore of Lake Scharmützelsee useable for recreational activities. The strong decrease of emergent macrophytes caused by clear cutting is a phenomenon observed in many studies and has been attributed to the higher sensitivity of emergent plants to lakeshore modification in comparison to submerged macrophytes (e.g. Radomski & Goeman 2001, James et al. 1998, Jennings et al. 2003). Contrary rooted submerged macrophytes were able to establish at the studied marinas and beaches where the environmental conditions were suitable. Many of the macrophytes species observed at the modified shore types are indicators of physical disturbance or have a wide ecological amplitude (Stelzer 2003). For example *Myriophyllum spicatum* dominated at marinas, a species known to have a wide ecological amplitude with regard to structural degradation. At beaches *Elodea canadensis* dominated, a species recognized as disturbance indicator for structural degradation (Stelzer 2003).

The compositional differences between marinas and beaches can be attributed to the differing exposition to wave energy. At beaches, harsh conditions that arise from high wave exposition and human trampling only allow the establishment of repent, submerged macrophytes with low plant height. In contrast, at marinas more fragile plants with larger plant height can grow, because of lower wave exposition facilitated by wave breaker or through locations naturally sheltered from wind and the absence of human trampling. The observed differences between the modified shore types indicate that lakeshore modification not only affects emergent macrophyte stands of natural sites but also submerged macrophytes of modified shore types in dependency of the type of impairment.

In the middle littoral (1.5 - 4 m depth), the macrophyte community did not significantly differ from each other and was dominated by *Nitellopsis obtus*a independently of the shore type. This is in accordance to the macrophyte mapping conducted at Lake Scharmützelsee in 2006 (Hilt et al. 2010) and 2011 (van de Weyer et al. 2012) and gives evidence that submerged macrophytes of this depth zone are not influenced by lakeshore modification. The decreasing influence of lake shore modification on macrophytes with depth was also found by Bryan & Scarnecchia (1992).

Lakeshore modification affects diversity and composition of macroinvertebrates

In the upper littoral, macroinvertebrate diversity was significantly lower at the studied beaches compared to natural sites but not at marinas, whereas community composition differed between all shore types. A graphical representation of the habitat characteristics and macroinvertebrate communities of the three studied shore types natural, marina and beach for the upper littoral zone is given in Figure 3-4.

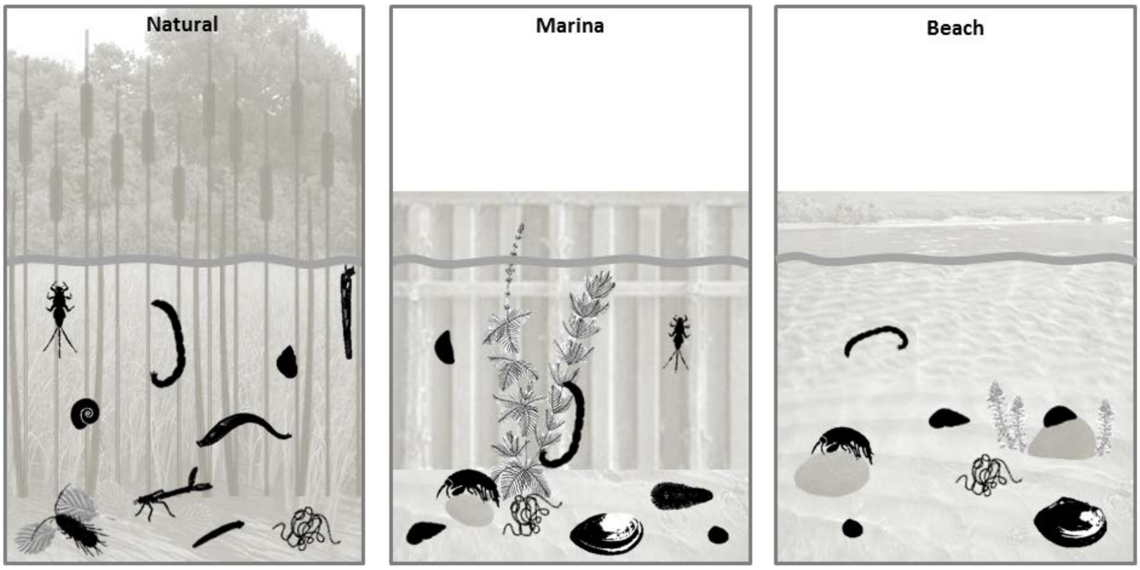

Figure 3-4: Graphical representation of habitat characteristics and macroinvertebrate communities of the three studied shore types natural, marina and beach for the upper littoral zone of Lake Scharmützelsee. Descriptions see text.

At natural sites, the three-dimensional structures of the reed belt provided complex habitats and supported a high diversity of macroinvertebrates, including a large number of indicator species (Chapter 2.3: Table 2-1). For example, the two habitat specialists *Bithynia tentaculata* and *Ischnura elegans* were identified as indicator species. Both species were also selected among four indicators of undeveloped sites in the study of Brauns et al. (2007 a). Another species only found at the studied natural sites and thus sensitive to morphological pressures was *Asellus aquaticus*. This species was also identified as an indicator species for natural sites of the Mediterranean Lake Piediluco (Mastrantuono et al. 2015). *Asellus aquaticus* is a species exploiting coarse organic matter such as allochthonous leaf litter from reed or riparian trees (Murphy & Learner 1982). Furthermore, the presence of various predator species like Odonata, Hirudinea or Turbellaria was also typical for the natural sites of Lake Scharmützelsee and reflects the abundance of prey on natural sites.

However, despite the high macroinvertebrate diversity at natural sites, Oligochaeta and Chironomidae were exceptionally dominant in the macroinvertebrate community of natural sites. This can be explained by the preference of reed as habitat for biofilm-associated Oligochaeta and Chironomidae taxa living as miners (Dvorak & Best 1982, Löhlein 1996). The third dominant group at natural sites was Ephemeroptera mainly represented by the mayfly *Caenis robusta. C. robusta* favours high organic matter content of the sediment and can adapt to relatively low oxygen content (Malzacher 1986), which can be low in reed belts (personal observation).

In contrast, the modified shore types marina and beach revealed a relatively high occurrence of *Pisidium* spp. and Gastropoda in the upper littoral zone, with the latter one mainly consisting of the invasive species *Potamopyrgus antipodarum*. This snail is a habitat generalist and known to colonize disturbed habitats (Ponder 1988). Since the studied marinas and beach sites are characterized by a larger proportion of bare sediment in comparison to natural sites, sediment-dwelling organisms such as *Potamopyrgus antipodarum* and *Pisidium* spp. but also Unionidae find more valuable habitats (Mouthon & Magny 2004). Another characteristic of the modified sites, especially of beaches, was the lower diversity and abundance of predator species. This can be explained by their rapid disappearance with habitat loss in case they are specialized on preys which decrease in abundance with increasing habitat loss (Ryall & Fahrig 2006).

Although the studied modified sites were clearly distinct in their community composition from natural sites, differences were also observed between marina and beach sites. Beaches but not marinas differed in their diversity from natural sites. At marinas, the abundance of macroinvertebrates tended to be higher compared to natural sites as a consequence of large individual numbers mainly observed for Oligochaeta. Since many Oligochaeta are detritus feeders, the high occurrence might be attributable to increased sedimentation of fine particular organic material within the protected areas of the local marinas. Another reason could be the high biomass of *Myriophyllum spicatum* and *Ranunculus circinatus* observed at marinas. In particular, *Myriophyllum spicatum* is a plant species recognized to support high abundances of

Oligochaete but also Chironomidae (Dvorak & Best 1982). Both plant-species might generally provide respectable refuge and food for macroinvertebrates owing to the high surface area formed by dissected leafs (Cheruvelil et al. 2002, Tessier et al. 2004). Hence, the large habitat-heterogeneity partly provided by macrophytes and partly by artificial hard substrates such as piles or sheet pilings (included in variable habitat diversity) as well as the lower sediment disturbance at marinas, led to further abundant and shore type-specific taxa. For example, these include *Pisidium* spp., Ephemeroptera, *Dreissena polymorpha, Molanna angustata etc.* (see Table 3-6 & Chapter 2.3: Table 2-1). Consequently, marinas also provide valuable habitats for a diverse macroinvertebrate community, but harbouring more non-native taxa compared to natural sites.

At beach sites, low macroinvertebrate abundances and no indicator species were found compared to natural sites and marinas. This is in accordance with Brauns et al. (2007 a) and results from the low species diversity consisting of habitat generalist common at all shore types. Habitat generalists are adapted to a wide range of environmental conditions and do not need a variety of complex habitats. The beaches generally showed low habitat diversity and mainly consisted of bare sediment and additionally of some stones and repent submerged macrophytes such as *Elodea canadensis*.

The different response observed for upper littoral macroinvertebrates to hydromorphological lakeshore modification with different degree of degradation is in line with previous findings and reflects their susceptibility along a gradient of decreasing habitat-heterogeneity (Bänziger 1995, Brauns et al. 2007 a, McGoff & Irvine 2009, Mastrantuono et al. 2015).

In the middle littoral, macroinvertebrate communities were distinct with regard to composition between marinas and natural sites as well as marinas and beaches. The studied marinas are large constructions extending down to the middle littoral and are characterized by the previously-mentioned wave breakers or through locations naturally sheltered from wind (see also Chapter 2.4). This characteristic may resulted in a distinct macroinvertebrate community, characterized by a high abundance of Oligochaeta but also Chironomidae as well as 11 indicator taxa (see also Chapter 2.4 & 2.3: Table 2-1). Similarly to the upper littoral, high abundances of Oligochaeta might be attributable to increased sedimentation of fine particular organic material. Soft-sediment is also preferred habitat for other taxa identified as indicator species at the marinas, for example *Unio tumidus tumidus* and *Molanna angustata* (see also Chapter 2.4 & 2.3: Table 2-1). Contrary, the large occurrence of the invasive mussel *Dreissena polymorpha* might be facilitated by pieces of wooden boards I observed, probably dropped off from boats, and providing hard colonization substrate for this mussel (Lancioni & Gaino 2006). Overall, a significant but low influence of habitat- or morphological variables on middle/lower littoral macroinvertebrates was also found in other studies (Chapter 2, Free et al. 2009, Pilotto et al. 2012).

Macrophytes influence macroinvertebrates

The concurrent results about lakeshore effects on macrophytes and macroinvertebrates already showed that macrophytes must have a large influence on the formation of macroinvertebrate communities. The results of DISTLM gave evidence that macrophyte biomass was the most influencing environmental factor structuring macroinvertebrate communities of different shore types in the upper littoral zone. Macrophyte biomass also played the major role for the composition of macroinvertebrates in the middle littoral. Hence, according to the second hypothesis macrophytes are the most important driving factor in structuring macroinvertebrate communities of different shore types.

When macroinvertebrates highly depend on macrophytes, they also must be influenced by the same environmental factors that control macrophyte communities. In accordance to previous studies (e.g. Brauns et al. 2007 a, Scheifhacken et al. 2007), I could show that slope and wind exposure explained some of the variability in macroinvertebrate communities of the studied shore types in both of the studied littoral zones. Slope and wind exposure are two important variables that directly and indirectly influence macrophytes communities. Steeper slopes lead to higher wave dissipation energy that increases shear stress on macrophytes until the detachment of plants (e.g. Duarte & Kalff 1986, Azza et al. 2007).

Slope and wind exposure are further known to influence substrate stability and sediment composition in the littoral, two factors which also affect macrophyte and macroinvertebrate communities (e.g. Rasmussen & Rowan 1997, Cyr 1998, Tolonen et al. 2001). In my study, organic matter content of sediment did not explain differences in the macroinvertebrate communities of different shore types in the upper littoral sites. In general, a decrease in organic matter content of sediment is expected at modified sites due to relocation in deeper depth zone caused by a loss of physical retentions such as reed belts or coarse woody debris (Francis et al. 2007). According to this, the organic matter content at natural sites should be regarded as much higher. But natural sites were only sampled at the lakeward side of the reed belt, which was characterized by a low stem density. This obviously facilitated the translocation of sediment organic matter into deeper depth zones at these locations. As a result, the quantified organic matter content of the sediment at natural sites was similar to that of modified sites. From personal observation, I can derive that the average organic matter content of sediment at natural sites of Lake Scharmützelsee might be much higher, but shows a decrease from the shoreward side to the lakeward side within the reed belt.

Overall, the results clearly illustrate the well-known relation between macrophytes and macroinvertebrates (Cyr & Downing 1988, James et al. 1998, Tessier et al. 2004) and highlight the need to include macrophytes when assessing lakeshore modification.

Implication for lakeshore assessment and management

For the development of lakeshore utilization strategies for temperate lowland lakes, the following recommendation can be derived from the results presented in this chapter.

Firstly, for both organism groups, the effects of lakeshore modification became only apparent in the upper littoral and thus were locally restricted. Hence, assessment methods should focus on macroinvertebrates and macrophytes from the upper littoral to assess hydromorphological pressures.

Secondly, since macrophytes also strongly reacted to lakeshore modification but differed in their response compared to macroinvertebrates they should be considered as a further component for the assessment of lakeshore modifications to complement the benthic invertebrates multimetric indices, as proposed by Lyche-Solheim et al. (2013). A good approach to assess structural degradation using submerged macrophytes was already provided by Stelzer (2003) for Germany. Contrary, an assessment only based on helophytes was not promising, because the naturally variability of these plants was too high (Bryan & Scarnecchia 1992, Stelzer 2003), resulting in contrasting response to chemical and structural pressures (Stelzer 2003). Despite the potential of macrophytes to indicate hydromorphological alteration of lakeshores, macroinvertebrates are more sensitive to this type of human pressure, due to their high diversity, various behavioural and feeding traits and ubiquitous occurrence also at macrophyte-free lakes.

Thirdly, macroinvertebrates were affected at both modified shore types mainly caused by the effects of lakeshore modification on macrophytes. Consequently, the reed belt should be protected whenever possible, because it provides complex three-dimensional habitats supporting a diverse and abundant macroinvertebrate community. In addition, a recent study showed that a critical reed belt width of 27 - 32 m is required to efficiently protect littoral macroinvertebrates against anthropogenic wave disturbances generated by ship traffic (Lorenz et al. 2015).

Modified sites should be examined for their potential of ecological renaturation with the aim to increase habitat-heterogeneity, for example, by supporting abundant and diverse macrophyte communities or by the insertion of natural or artificial substrates such as coarse woody debris or ripraps (Brauns et al. 2007 a, Lorenz et al. 2015). In case of Lake Scharmützelsee, it would be advisable to preserve the extensive nature of the marinas, which provide a habitat for submerged macrophytes and thus provide suitable conditions for macroinvertebrates. The installation of wave breakers at other public and private properties lakewards from the potential edge of the reed belt would also help to decrease wind exposure and thus would facilitate macrophyte growth (Ostendorp 2009). In addition, ecological restructuring of the marinas and a thoughtful planning of new multiuser marinas, preferably at naturally sparsely vegetated areas should be taken into account (e.g. Jansen 1993, Ostendorp 2009).

Nevertheless, it must be clear that the resulting macroinvertebrate communities at modified sites will always differ from the communities in the reed belt with having the potential of a high diversity, but they may also comprise more non-native species. Permanent monitoring would help to detect extreme shifts in the dominance relation of the macroinvertebrate community caused by non-native species, in order to intervene at the right time.

Fourthly, the results show that macroinvertebrate community composition is a more sensitive measure for detecting ecological changes than diversity, which supports the development of multimetric indices for lakeshore assessment.

Finally, I could show that marinas differed to natural sites and beaches in regards to community composition in the middle littoral as a consequence of the large constructions extending down to this depth zone. Hence, although the assessment of hydromorphological condition of lakeshores should be based on upper littoral macroinvertebrates, management activities should also comprise the middle littoral.

Taking these results into consideration, a profound development of a lakeshore utilization strategy would help to solve conflicts between different interest groups and even has the potential to increase diversity at the lakeshore of temperate lowland lakes characterized by reed belts.

4 Using benthic secondary production to determine functional disturbance following human lakeshore modification

4.1 Introduction

Lakeshores perform many ecological functions resulting from their complex and highly structured environment due to the fact that they are boundary regions between land and water. Lakeshores regulate the exchange of matter fluxes between land and water (e.g. Ostendorp et al. 2004, Schmieder 2004, Strayer & Findlay 2010). From the terrestrial site they filter diffuse nutrient inputs from adjacent agricultural land, whereas from the lake ward site macrophyte stands, stones or roots dissipate wave energy and thus protect against erosion (Schmieder 2004, Strayer & Findlay 2010). Moreover, lakeshores substantially contribute to the self-purification of lake ecosystems, for example by stabilizing the clear water conditions through macrophytes (e.g. Sachse et al. 2014), which for example act as sediment traps and take up nutrients (Scheffer et al. 1993). Another example is the processing of organic matter such as the breakdown of leaf litter from macrophytes or riparian vegetation by invertebrate shredders, bacteria and fungi (e.g. Hieber & Gessner 2002, Brady & Turner 2010, Ágoston-Szabó et al. 2014). Furthermore, lakeshores provide many habitats and thus are hotspots for biodiversity of the whole lakes ecosystem (e.g. Heino 2000, Babler et al. 2008, Vaceboncoeur et al. 2011). The high diversity leads to complex littoral benthic food webs (Brauns et al. 2011), which are linked to pelagic food webs (Vadeboncoeur et al. 2002). Littoral benthic macroinvertebrates are an essential component in the energy and material flow through whole lake food webs (Covich et al. 1999, Vadeboncoeur et al. 2002), because they connect benthic and pelagic pathways by providing a substanital amount to the fish diet (Vander Zanden & Vadeboncoeur 2002, Vander Zanden et al. 2006).

In lake ecosystems, recent studies demonstrated that macroinvertebrate secondary production was generally highest in the littoral zone and decreased with increasing depth (Babler et al. 2008, Butkas et al. 2010, Northington et al. 2010). For example, for the oligotrophic Crampton Lake average secondary production in the littoral zone was 4.8–6.5 but decrease to 3.2–4.5 g DM m^{-2} y^{-1} in the profundal zone. Potential determinants which were shown to influence the depth-production relationship were predation by fish, allochthonous inputs, lake size, depth, trophic state, water circulation, sedimentation, oxygen content and dominance relation of macroinvertebrates (Babler et al 2008, Northington et al. 2010), all of these changing along a vertical gradient of increasing depth (e.g. Särkka 1983, Ali et al. 2002, Hämäläinen et al. 2003). Besides these potential determinants the influence of changing habitat-heterogeneity along a vertical depth-gradient should have an important effect on the relation between water depth and secondary production. For example the littoral zone is characterized by more complex habitats compared to deeper depth zones and in accordance to the habitat-heterogeneity hypothesis supports a diverse macroinvertebrate community (e.g. Heino 2000, Vadeboncoeur et al. 2011, Jurca et al. 2012). The greater the diversity, the larger the number of species with complementary traits of resource use which leads to higher resource exploitation and thus to higher secondary production (e.g. Loreau et al. 2001, Hooper et al. 2005).

However, the depth-production relationship may be susceptible to alterations of habitat-heterogeneity of the littoral zone. Such changes are usually associated with human lakeshore modification (Brauns et al. 2011). For example, habitat-heterogeneity decreases when coarse woody debris is removed from lakeshores to make them accessible (Christensen et al. 1996, Francis et al. 2006). Likewise, lakeshores covered with riparian vegetation, reed belts or submerged macrophyte stands lose habitats as a consequence of clear cutting while simultaneously exposition to wave energy increases (e.g. Jennings et al. 2003, Radomski 2006). A loss in habitats at modified lakeshores and an increase in shear stress of waves were shown to decrease littoral macroinvertebrate diversity and alter macroinvertebrate community composition (e.g. Brauns et al. 2007 a, Gabel et al. 2008, Brauns et al. 2011, McGoff et al. 2013 a). Since lakeshore modifications were shown to affect structural measures of macroinvertebrates just locally (Brauns et al. 2007 a, Chapter 2 & 3), it can likewise be expected that secondary production may also show only a locally restricted response. So far there is no study which examined the effects of lakeshore modification on secondary production neither locally in the upper littoral zone, not to mention in comparison to deeper depth zone. This would be a prequesite to estimate the extent to which local changes in secondary production may affect the functioning of macroinvertebrates for the entire lake ecosystem and thus whole lake ecosystem functioning.

Although secondary production is an integrative measure (e.g. Dolbeth et al. 2012), it does not necessarily reveal the entire consequences of lakeshore modification on the functioning of macroinvertebrates when only looking at total secondary production. That is because total production may not change with anthropogenic disturbance (De

Lange et al. 2004) or can even increase (Hall et al. 2006, Sousa et al. 2008), but changes in the functionality may result from a shift in production between functional groups (Dolbeth et al. 2012). Composition of feeding types was shown to change as a consequence of lakeshore modification. For example, abundance of piercer or xylophagous species can be reduced or displaced resulting from a loss of macrophytes and coarse woody debris. Furthermore it has been shown, that lakeshore modification can cause a shift in abundance proportion from grazer to more detrivorous species (Bänziger 1995, Brauns et al. 2007 a, Rosenberg et al. 2008). The increase in opportunistic species accompanied by a reduction in faunal complexity redirects the energy flow through the food web (Dolbeth et al. 2012, Sousa et al. 2011). This also often happens when non-native invasive species enter a system using the provided food sources more effectively (Strayer et al. 1999, Hall et al. 2006, Sousa et al. 2008, Ozersky et al. 2012). The potential influence of non-native species on ecosystem functioning is well known, showing that invasive species can have large effects on most ecosystem functions (Charles & Dukes 2007, Strayer 2012 and references therein). Hence, the examination of production from non-native species and functional groups should be included when examining ecosystem functioning (Hall et al 2006, Heino 2008, Sousa et al. 2011). A profound understanding of the effects of lakeshore development on the production of non-native species and functional groups is fundamental to understand the impacts on the functioning of macroinvertebrates.

Here, we aimed to compare macroinvertebrate secondary production between natural shores and shorelines modified by marinas and beaches in three water depth zones. We first hypothesized that lakeshore modification decreases secondary production in the upper littoral zone as a consequence of reduced habitat-heterogeneity. Assuming that upper littoral macroinvertebrates of modified lakeshore are less productive, we also hypothesized that the depth-production relationship is altered at modified lakeshores. The two hypotheses were examined with regard to total production, but also production of feeding types to account for the varying roles of functional groups in controlling the basal production and providing food for higher trophic level. Moreover, we also compared biomass and production of native versus non-native species, which is linked to possible changes in feeding types at disturbed sites. Thirdly, we hypothesized that site-specific effects of lakeshore modification on littoral secondary production affect the production of the entire upper littoral and whole-lake ecosystem, respectively, because the littoral zone contributes importantly to whole lake secondary production and lakeshore modification can strongly affect the littoral secondary production.

4.2 Methods

Study sites and sampling

The study was conducted at Lake Scharmützelsee (Chapter 1.6) at three undisturbed natural and five modified sites, i.e. two marinas with sheet-pilings and three recreational beaches (two public and one private) (Chapter 1.6). Each study site was sampled in the upper littoral, middle littoral and upper profundal zone (hereinafter called profundal), following a habitat-specific sampling design (Chapter 1.6). As described in Chapter 1.6, four of the eight sites were examined monthly from April 2011 until November 2011 (two natural sites, the private beach and the marina at the East shore of the lake), whereas the remaining four study sites were sampled only in April, July, September and November 2011 (the two public beaches and the natural site as well as the marina at the West shore of the lake) (Chapter 1.6: Table 1-1). Samples were not taken during winter month due to limited personnel capacity for sampling and laboratory work. However, we expected growth rates of macroinvertebrates to be low due to low water temperatures but this assumption may lead to slight overestimates in production (Dolbeth et al. 2012).

Macroinvertebrate samples were processed by sub-sampling following the AQEM consortium (2002) and sorted using a stereomicroscope. Individuals were identified to species level if possible, except for Chironomidae (subfamily), other Diptera (family), Heteroptera (suborder), Lepidoptera (order), *Pisidium* spp. (genus), Turbellaria (class) and Oligochaeta (class).

Environmental variables

Environmental variables known to potentially drive macroinvertebrate production were measured for each study site as described and presented in Chapter 1.6: Table 1-3, i.e. habitat diversity, wind exposure, littoral slope, water temperature and organic matter content of the sediment as well as macrophyte biomass in the upper, middle littoral and profundal in order to find the most driving factors explaining differences among shore types.

Food resource availability, quantified as organic matter content and chlorophyll a from different substrates, was determined for the five study sites at the East shore of the lake in the upper and middle littoral (2 m depth) (Kluge 2012). Chlorophyll a of the sediment as well as organic matter content and chlorophyll a of loosely attached biofilm from reed, stones and artificial substrates (sheet piles, wooden piles) were collected taking three to six replicates in the beginning of April, end of June and beginning of September. Sampling seasons were selected in accordance to major changes in the seasonal succession of phytoplankton communities in Lake Scharmützelsee (Figure 4-1). Sediment samples for chlorophyll a were taken from sediment cores in the field with a small syringe retaining the top 2 ml volume for further processing in the laboratory. Organic matter from artificial substrates and stones was removed from a surface area of 30 cm². The biofilm from about 10 - 14 cm long reeds stems was brushed off in the laboratory and the area of reed stems was determined using a measuring tape. Organic matter content of biofilm was determined in the same way as described for organic matter content of sediment in Chapter 1.6. Samples were dried at 60°C for at least 12 h and ash free dry mass was determined after combusting at 500°C for 3 h. Chlorophyll a from the different substrates was analysed using a modified method according to Nusch (1980).

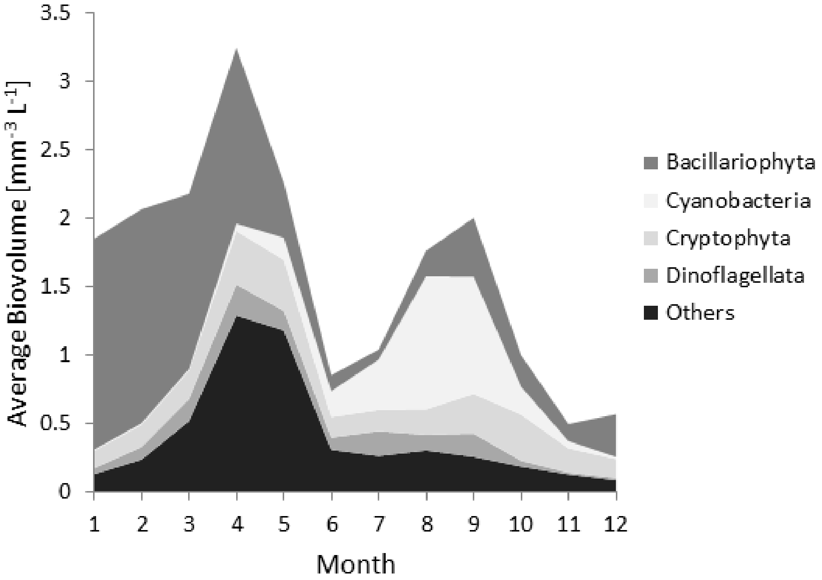

Figure 4-1: Phytoplankton development in Lake Scharmützelsee in the years 2004-2011 measured at the station in the deep southern basin by the Department of Freshwater Conservation (BTU Cottbus-Senftenberg. Biovolume averaged per month (Rücker unpublished).

Macroinvertebrate biomass and secondary production

We used 90 of the 95 macroinvertebrate taxa recorded in Lake Scharmützelsee to estimate biomass and secondary production. Taxa with abundances less than 1 % of total abundance were not included, i.e. Coleoptera, Lepidoptera, Turbellaria, Heteroptera and other Dipteran, except for Unionidae due to their high individual biomass. For the considered taxa, an appropriate body dimension according to Chapter 5.3: Table 5-1 was measured for each available individual to the nearest 0.01 mm using a stereomicroscope. Dry mass of Oligochaeta was weighed directly to the nearest 0.01 mg, due to high number of damaged individuals. Macroinvertebrate biomass was estimated by applying allometric length-mass relationships. Since length-mass relationships can differ between ecosystem type and geographic region it is recommended to establish length-mass relationships for the target ecosystem to avoid serious under- or overestimations of the true body mass (Baumgärtner & Rothhaupt 2003, Méthot et al. 2012). We established own length-mass relationships for the majority of observed taxa (Chapter 5.3: Table 5-1). Since the error structure was multiplicative and thus best described by log-linear regression, we also corrected for bias introduced by log transformation followed by back transformation. Moreover, since length-mass regressions were established on preserved animals we also calculated conversion factors to adjust for preservation effects (Chapter 5.3: Table 5-2). For the remaining taxa we applied length-mass regressions provided in the literature. An overview of the applied regressions, correction and conversion factors is given in Appendix III.

Using regressions on large individuals outside of the length range can lead to serious errors, because an increase in mass is higher for older larger individuals than for younger shorter ones (Johnston & Cunjak 1999). Hence, we assigned length measures of large individuals outside the specific length range of a taxon's regression to the maximum value of the taxon's specific regression range, which was the case for 0.2 % of the measurements.

Determination of secondary production is usually done using classical methods such as the increment summation or size-frequency method. But classical cohort or non-cohort methods often cannot be used for all taxa when looking at the whole community production, because the complete growth period is rarely fully covered and it is difficult to cover the entire size or age structure of all taxa (Butkas et al. 2010, Dolbeth et al. 2012). Therefore, the usage of empirical methods can be a promising short cut approach, especially when looking at whole community production, or when aiming to determine spatial comparisons of community production from different habitats (Dolbeth et al. 2012). According to Dolbeth et al. (2012) at least 35 empirical models have been published, seven of them solely for freshwater ecosystems. Empirical 1- and 2-parameter models use independent biotic parameters to predict secondary production, whereas more complex ≥3-paramter models also include environmental parameters. We chose the multi-parameter artificial neural network (ANN) model of Brey et al. (1996) and Brey (2012), which was shown to outperform other empirial models tested in recent studies (Dolbeth et al. 2005, Cusson & Bourget 2005). The ANN model relies on 20 biotic and abiotic input variables (Table 4-1) and predicts the production to biomass ratio P/B from which production can be calculated (Brey 2012). We used the ANN model to calculate P/B for each taxon per shore type and depth zone and then calculated taxon-specific production by multiplying it with mean annual biomass. Total production per sample site was derived by summing all taxon-specific production-values.

Table 4-1: Overview of the 20 input parameters used to estimate secondary production with the ANN model Brey et al. (1996) and Brey (2012).

Biotic input parameters	**Unit**	**Source of data**
Body mass	in Joule	Measured as average individual body mass converted to Joule (conversion factors see Appendix III)
Taxonomic group	Mollusca, Annelida, Crustacea, Echinodermata or Insecta	Taken from ASTERICS Version 4.0.4 (Astercis 2014)
Mobility	Infauna, sessile, crawler or facultative swimmer	
Feeding type	Herbivore, omnivore or carnivore	

Abiotic input parameters	**Unit**	**Source of data**
Mean annual temperature	Degree Celsius	Measured at eight sites in three depth zones with temperature logger and completed by bimonthly recorded data using a multiparameter sonde
Depth	Meter	Taken from depth of temperature measurements
Ecosystem type	Lake, river, marine, subtidal or exploited	

From the 20 input variables the average individual body mass for each taxon is the most important one. The averaging of the individual weight per taxa and site was done by using the geometric mean, because the growth of macroinvertebrates is naturally exponential and not linear (Benke & Huryn 2007). This procedure also helps to adjust for the different temporal sampling frequency between the eight transects.

The effect of different sampling frequency on production estimates was tested with the four transects sampled in eight month. From these 12 sampling sites (four shore types x three depth zones) production values calculated based on eight months were compared with production values calculated based only on the four months April, July, September and November. These are the four months from which we have data for the other four transects. Confidence intervals showing the variability in production estimates of the ANN model were used to test if model accuracy was lower or higher than deviation of total production estimates per sample site caused by varying sampling frequency. This procedure allowed us to draw conclusion whether we can use the low frequently sampled transect for interpreting the effect of lakeshore modification on secondary production. As shown in Figure 4-2, confidence intervals of model accuracy between these two scenarios (eight and four months) highly overlapped and the bias due to different sampling frequency was negligible.

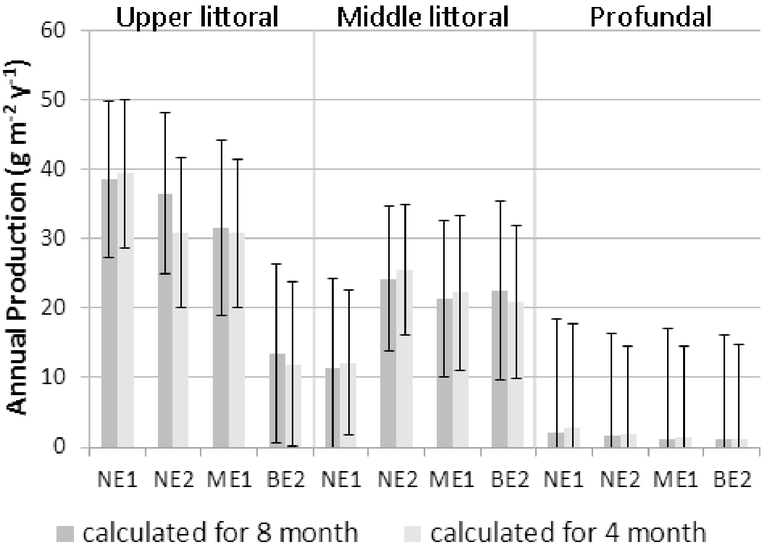

Figure 4-2: Results of effects of different sampling frequency on production estimates calculated with the ANN model (Brey et al. 1996, Brey 2012). Confidence intervals present the accuracy of the ANN model. A high overlap of confidence intervals between eight and four sampled season indicates a low effect on production estimates due to varying sampling frequency. N = natural, M = marina, B = beach, E = east side, W = west side.

Hence, it can be concluded that variability due to different sampling frequency was much lower compared to the variability in production estimates of the ANN model. Therefore, the production values presented in this study are based on all available data independently of sample frequency.

Statistical analysis

We used response ratio to quantify the effect of lakeshore modification on the three community parameters diversity, biomass and secondary production. The effect size between natural and modified sites is expressed as the natural logarithm of the response ratio R (Hedges et al. 1999):

$$\mathrm{R} = X_E/X_C, \quad \ln(\mathrm{R}) = \mathrm{L} = \ln(\mathrm{X}_E) - \ln(\mathrm{X}_C)$$

In our case X_E the experimental group was described by the values of the modified sites marina and beach, whereas X_C (control group) referred to the natural sites. Response ratio L was calculated for each pair of natural versus modified sites (3 beaches x 3 natural sites: n = 9; 2 marinas x 3 natural sites: n = 6) per depth zone. Subsequently the response ratios L were averaged and 95 % CI calculated per shore type and depth zone. The response ratio L was also calculated for production and biomass of native versus non-native taxa and feeding types to gain a better understanding of the functioning of macroinvertebrates in lake food webs. Information about affiliation to non-native taxa and feeding types were obtained from the software ASTERICS Version 4.0.4 (Astercis 2014). To test for significant differences in the effect of lakeshore modification on macroinvertebrate community parameters one-sample t-tests were performed for all response ratios using SPSS Version 22.0 (IBM Corp., Armonk, NY). A significant deviation of the response ratios from zero reflects a significant effect of lakeshore modification on macroinvertebrate community measures compared to natural sites.

Differences in macroinvertebrate diversity, biomass and production between depth zones were tested using Kruskal-Wallis test using R 3.2.0 (R Development Core Team 2013) and the function ‘kruskal.test’. In case of rejection of the null hypothesis we applied Dunn’s non-parametric post-hoc test using the function ‘kruskalmc’ from the R package ‘pgirmess’ (Giraudoux 2015).

Whole lake secondary production

To calculate the production for the whole upper littoral, site-specific production values were averaged for each shore type. The shore-type specific production values were then weighted by the percentage share of the shore types to the total upper littoral area to obtain a single area-weighted production estimate for the entire upper littoral. The percentage share of the shore types to the total upper littoral area was determined by a hydromorphological survey and reed mappings of the lakeshore at Lake Scharmützelsee visualized in GIS (Fernando 2011, Weiss 2012). The area of the natural shore type was determined by the area covered with reed. The beaches comprised 0.8 % of the total upper littoral area according to the hydromorphological survey. Hence, the production value of the marina was allocated to the remaining area of the upper littoral with various kinds of lakeshore modifications.

For the middle littoral and profundal zones only a mean of the site-specific production values was computed to obtain a single production value per depth zone. The depth-specific production values were multiplied with the specific area of each depth zone and summed up to estimate real whole lake secondary production of our studied lowland lake.

Based on the estimated production values, we calculated 231 scenarios with different shore type-area combinations to determine how local alterations of secondary production translate into whole-lake effects. The scenarios were achieved by changing the proportional amount for each of the three shore types on the total area of the upper littoral zone in steps of 5 % including the scenario that the entire lakeshore is natural and covered by reed but also that the entire lakeshore is completely modified either by characteristics of beaches or marinas, respectively.

Finally, to quantify the potential effect of varying lakeshore modification on the simulated production values the response ratio L was calculated between the estimated production values assuming the entire lakeshore would be covered by reed (control group X_C) and all other 230 scenarios (experimental group X_E). Response ratios were plotted against percentage proportion of beach and percentage proportion of marina in a 3-dimensional scatterplot using the R package 'scatterplot3d' function 'scatterplot3d' (Ligges & Maechler 2003). This procedure was carried out twice, once for the upper littoral and secondly for the whole-lake ecosystem.

Examining environmental variables in relation to total production

In order to find the main environmental variables responsible for differences in secondary production, first principal components analyses (PCA) were carried out using habitat diversity, slope, exposure, mean annual temperature, organic matter content of sediment and macrophyte biomass. Prior to the analysis environmental variables were tested for normality using Shapiro-Wilk Test and diagnostic plots in R 3.2.0 (R Development Core Team 2013) and transformed if necessary. After transformation, the environmental variables were normalised. Then, PCAs were performed for each shore type over all depth zones to find the main driving factors explaining their environmental characteristics. Subsequently, for each PCA the scores of all principal components with an eigenvalue about one or higher were used as explanatory variables and correlated with total production values applying linear regressions in R 3.2.0 with the function 'lm'.

Since the variables describing food source availability (organic matter content of biofilm and chlorophyll a content of biofilm and sediment) were measured with insufficient replication per shore type (natural n = 2, marina n = 1, beach n = 2) scatter plots were used to relate the values to total production to give at least a rough description of the underlying relationship.

4.3 Results

Effect of lakeshore modification on secondary production in the upper littoral zone

In the upper littoral, site-specific secondary production was in average highest at natural sites and marinas (37 ± 1.3 & 39.4 ± 11.2 g m^{-2} y^{-1}) and much lower at beaches (11.9 ± 4.1 g m^{-2} y^{-1}) (all secondary production estimates of this chapter and additional information on area are summarized in Appendix IV). Hence, the response ratio for production at marinas did not differ significantly from zero (natural sites) (one-sample t-test $p = 0.657$), whereas the response ratio for production at beaches was significantly lower (one-sample t-test $p = 0.000$) (Figure 4-3). In addition, response ratios for diversity and biomass of beaches were also significantly lower (one-sample t-test diversity: $p = 0.008$, biomass: $p = 0.019$) (Figure 4-3). In contrast, response ratio for diversity at marinas did not differ significantly (one-sample t-test: $p = 0.538$), while for biomass it was significantly higher than zero (one-sample t-test $p = 0.000$) (Figure 4-3).

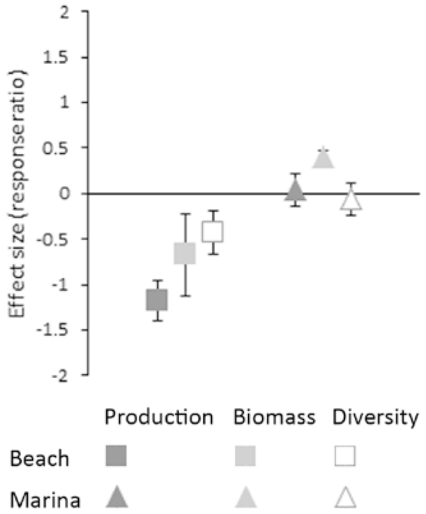

Figure 4-3: Effect sizes of total production, biomass and diversity of macroinvertebrates for the shore types beach and marina of the upper littoral. Effect sizes were calculated as natural logarithm of the response ratio and presented with 95 % confidence intervals. A positive response ratio indicates an increase in secondary production compared to natural sites (zero line) and a negative response ratio a decrease. Differences are statistically significant when confidence intervals do not cross the zero line.

Although response ratios for total production and diversity were not significant at marinas, differences were found in the proportional amount of non-native taxa to total production. In general, the production of native taxa only dominated at natural sites in the upper littoral zone (~85 %) (Figure 4-4). At modified sites, especially at beaches, native and non-native taxa contributed almost equally to total secondary production (Figure 4-4).

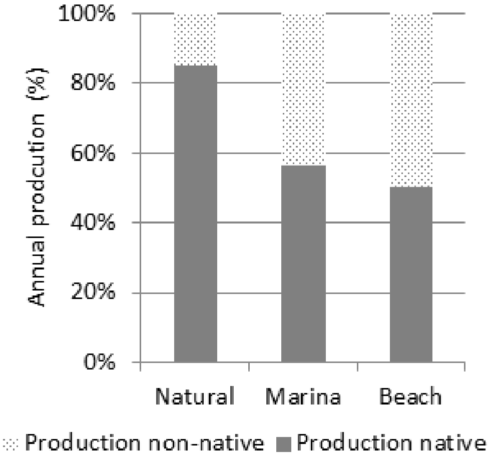

Figure 4-4: Proportional amount of non-native macroinvertebrate production to total production in the upper littoral.

Accordingly, at beaches the production of native taxa was very low and significantly different from zero (one-sample t-test: p = 0.000), but there was no effect with regard to non-native taxa (one-sample t-test: p = 0.843) (Figure 4-5). Similarly, the response ratio for biomass of native taxa was significantly lower at beaches (one-sample t-test: p = 0.022), but no differences were found for non-native taxa (one-sample t-test: p = 0.196) (Figure 4-5). The situation was slightly different at marinas which showed no significant differences in the response ratio for production of native taxa (one-sample t-test: p = 0.11), whereas for non-native taxa the response ratio was significantly higher (one-sample t-test: p = 0.000). Likewise, the response ratio for biomass of native taxa did not significantly differ at marinas (one-sample t-test: p = 0.21), while for non-native taxa it was significantly positive (one-sample t-test: p = 0.000), but the response ratio was much lower (Figure 4-5).

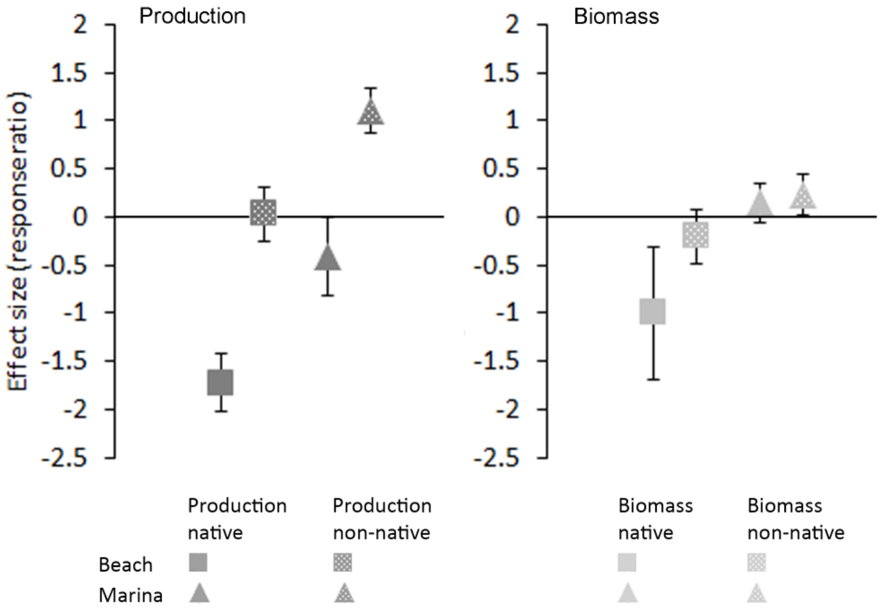

Figure 4-5: Effect sizes of native and non-native production and biomass of macroinvertebrates for the shore types beach and marina of the upper littoral. Analyses are as in Figure 4-3.

Moreover, in the upper littoral the modified shore types also differed from natural shores with regard to the proportional amount of production and biomass from feeding types (Figure 4-6). Response ratios for production of feeding types were generally higher for marinas than for beaches, but showed a similar pattern in change of effect direction (Figure 4-6). For example, response ratios of parasites, predator but also miners were significantly lower for marinas and beaches (all one-sample t-test

$p < 0.5$). At beaches, response ratios for production of grazer and shredder was very low compared to natural sites (one-sample t-tests: $p = 0.000$), whereas filter feeders did not significantly differed from zero (one-sample t-test: $p = 0.051$) (Figure 4-6). At marinas, filter feeders were even much more productive compared to natural sites and exhibited the highest response ratio significantly different from zero (one-sample t-test: $p = 0.001$). Significantly higher response ratios were also observed for shredder and gatherer at marinas (one-sample t-test: $p = 0.002$ & 0.016) (Figure 4-6). The response ratios for biomass from the different feeding types in the upper littoral zone showed a similar pattern in comparison with production, but were generally higher which sometimes resulted in different effects. For example, no effect on biomass of gatherer at beaches was apparent, although response ratio of production was low (Figure 4-6).

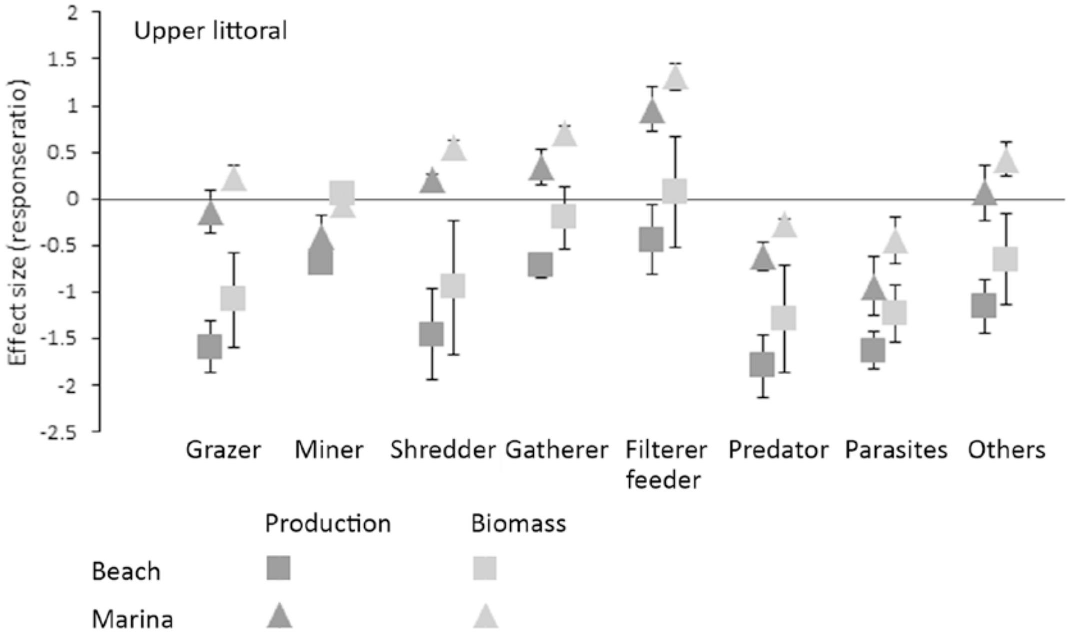

Figure 4-6: Effect sizes of production and biomass of macroinvertebrate feeding types for the shore types beach and marina of the upper littoral. Analyses are as in Figure 4-3.

Effect of lakeshore modification on depth-production relationship

Macroinvertebrate diversity, biomass and production were highest in the upper and middle littoral zone and did not significantly differ between these two depth zones (Dunn's test: $p \geq 0.05$), but were significantly lower in the profundal (Dunn's test: $p < 0.05$, Figure 4-7). However, the upper littoral zone revealed higher average production values (28.21 ± 14.35g m^{-2} y^{-1}) compared to the middle littoral (18.98 ± 4.3 g m^{-2} y^{-1}), but simultaneously exhibited high variability with the lowest production estimates in upper littoral being lower than the lowest in the middle littoral (Figure 4-7). The three lowest production estimates with an average of 11.9 ± 4.2 g m^{-2} y^{-1} were observed at the three beach sites in the upper littoral. Hence apart from beaches the upper littoral zone showed higher production values than the middle littoral zone.

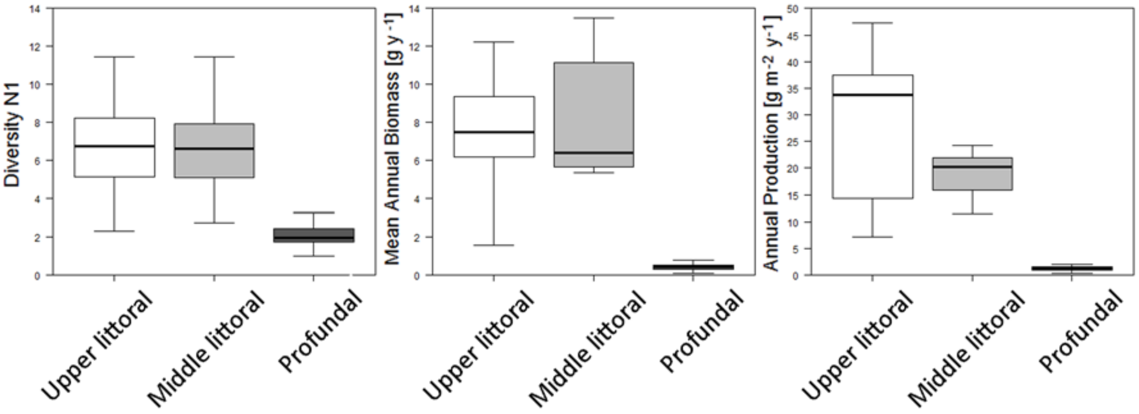

Figure 4-7: Boxplots for macroinvertebrate diversity, biomass and production between the three depth zones upper, middle littoral and profundal. Boxes represent 25 % and 75 % percentile, black line in box = median, end of vertical lines show 5 % and 95 % percentile.

The observed effects of lakeshore modification on upper littoral macroinvertebrates were neither detectable in the middle littoral nor in the profundal zone (one-sample t-test: $p \geq 0.05$) (Figure 4-8). One exception was the significant lower response ratio for diversity at beaches in the profundal (one-sample t-test: $p = 0.035$), but response ratio differed only marginally (Figure 4-8).

Three other exceptions were detected for the response ratios of feeding types. Predator showed significantly higher response ratios for production at marinas and beaches in the middle littoral (one-sample t-test: p = 0.02 & 0.019). Contrary, parasites showed significantly lower response ratios for biomass at marinas in this depth zone (one-sample t-test: $p = 0.032$). Another exception was the significant lower response ratio of production and biomass for predators at beaches in the profundal (one-sample t-test: p = 0.041 & 0.011) (Figure 4-9).

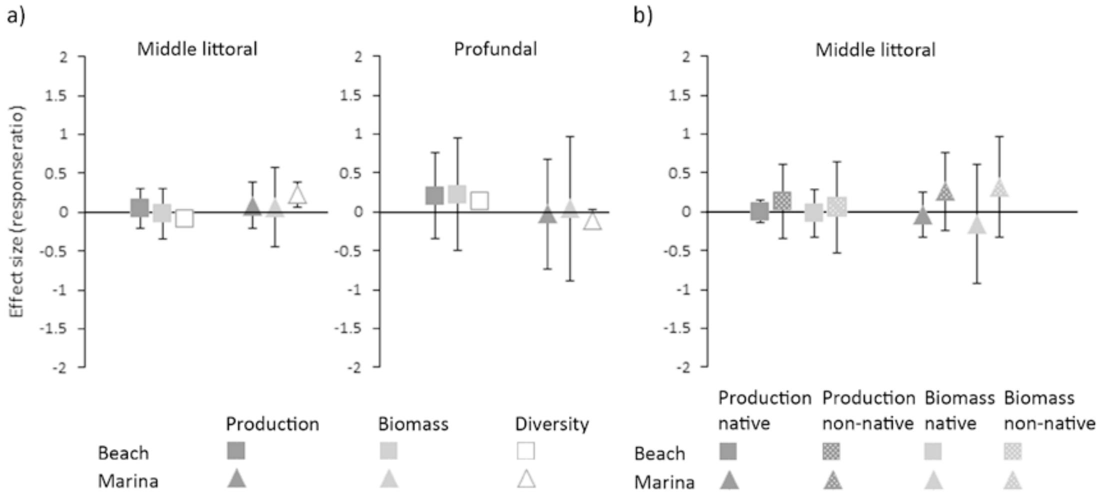

Figure 4-8: Effect sizes of (a) total macroinvertebrate production, biomass and diversity, and (b) native and non-native macroinvertebrate production and biomass. Analyses are as in Figure 4-3.

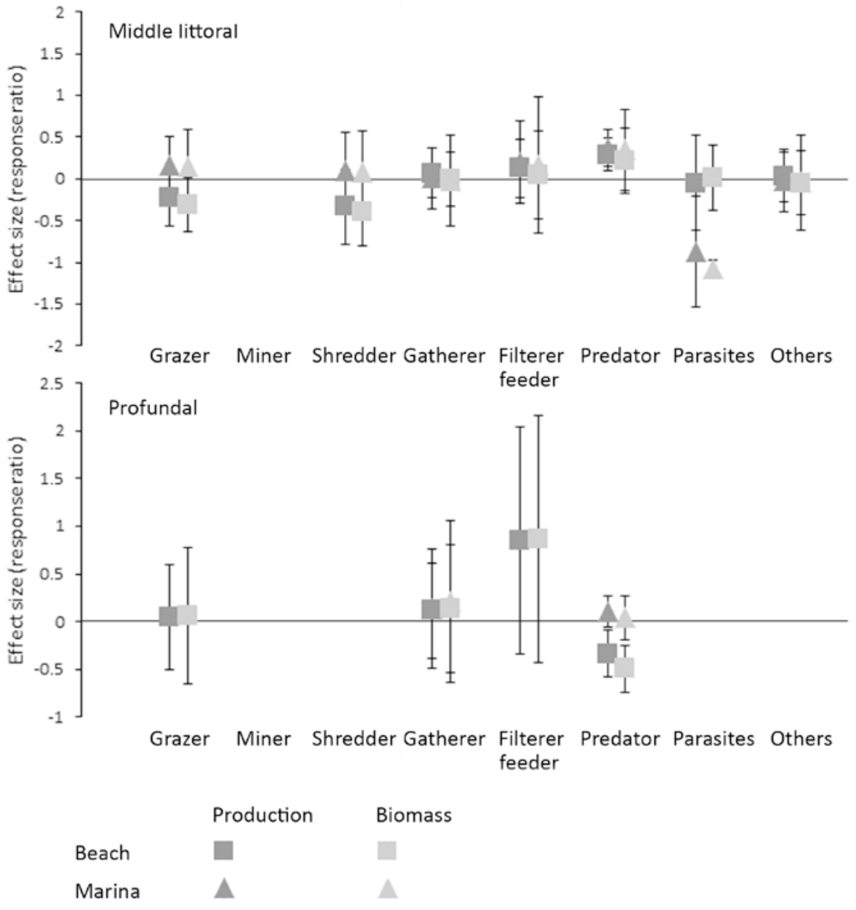

Figure 4-9: Effect sizes of production and biomass of macroinvertebrate feeding types for the shore types beach and marina of the middle littoral and profundal. Analyses are as in Figure 4-3.

Driving environmental factors of macroinvertebrate secondary production

The first two axes of the PCA performed to determine the environmental characteristics of the three shore types explained more than 90 % of the variation (Table 4-2).

The ordination plots displayed a gradient of water depth along principal component (PC) 1 for all three shore types (Figure 4-10). In all three cases, the sites of the profundal were clearly separated from the littoral sites. Differences between sites of the upper littoral and middle littoral were more pronounced in the ordination plot of the natural shore type, but diminished at both modified shore types. PC 1 of natural sites and marinas generated a combination of all variables except for slope, with macrophyte biomass being the strongest predictor for natural sites and habitat diversity for marinas. At natural sites and marinas depth and organic matter content of sediment were negatively, whereas macrophyte biomass, habitat diversity and temperature were positively related to PC1. Hence, the variables macrophyte biomass and habitat diversity describe an increase of habitat-heterogeneity with decreasing depth. PC 2 mainly reflected differences in the slope between the sites of the two shore types natural and marinas (Figure 4-10, Table 4-2). In contrast, PC1 for beaches was more strongly associated with depth, exposure, temperature and organic matter content of sediment than with habitat diversity and macrophyte biomass. Instead habitat diversity and macrophyte biomass were related to PC2 (Figure 4-10, Table 4-2).

Table 4-2: Results of PCA for PC 1 and PC 2 per shore type over all water depth zones. OM = organic matter content.

	Natural		**Marina**		**Beach**	
	PC1	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
Eigenvalue	5.73	1.7	6.45	1.15	4.85	1.14
% Variation	70.6	21.0	80.5	14.3	74.8	17.5
Eigenvectors						
Habitat diversity	**0.37**	0.12	**0.45**	-0.16	**0.30**	**-0.58**
Exposure	**0.36**	-0.13	**0.42**	-0.19	**0.50**	0.22
Slope	-0.21	**0.94**	0.12	**0.90**	-0.03	-0.25
Macrophyte biomass	**0.45**	0.12	**0.36**	0.16	0.28	**-0.64**
Temperature	**0.40**	0.03	**0.39**	0.13	**0.44**	0.043
OM of sediment	**-0.38**	-0.25	**-0.41**	-0.11	**-0.44**	-0.17
Depth	**-0.42**	-0.09	**-0.40**	0.29	**-0.44**	-0.33

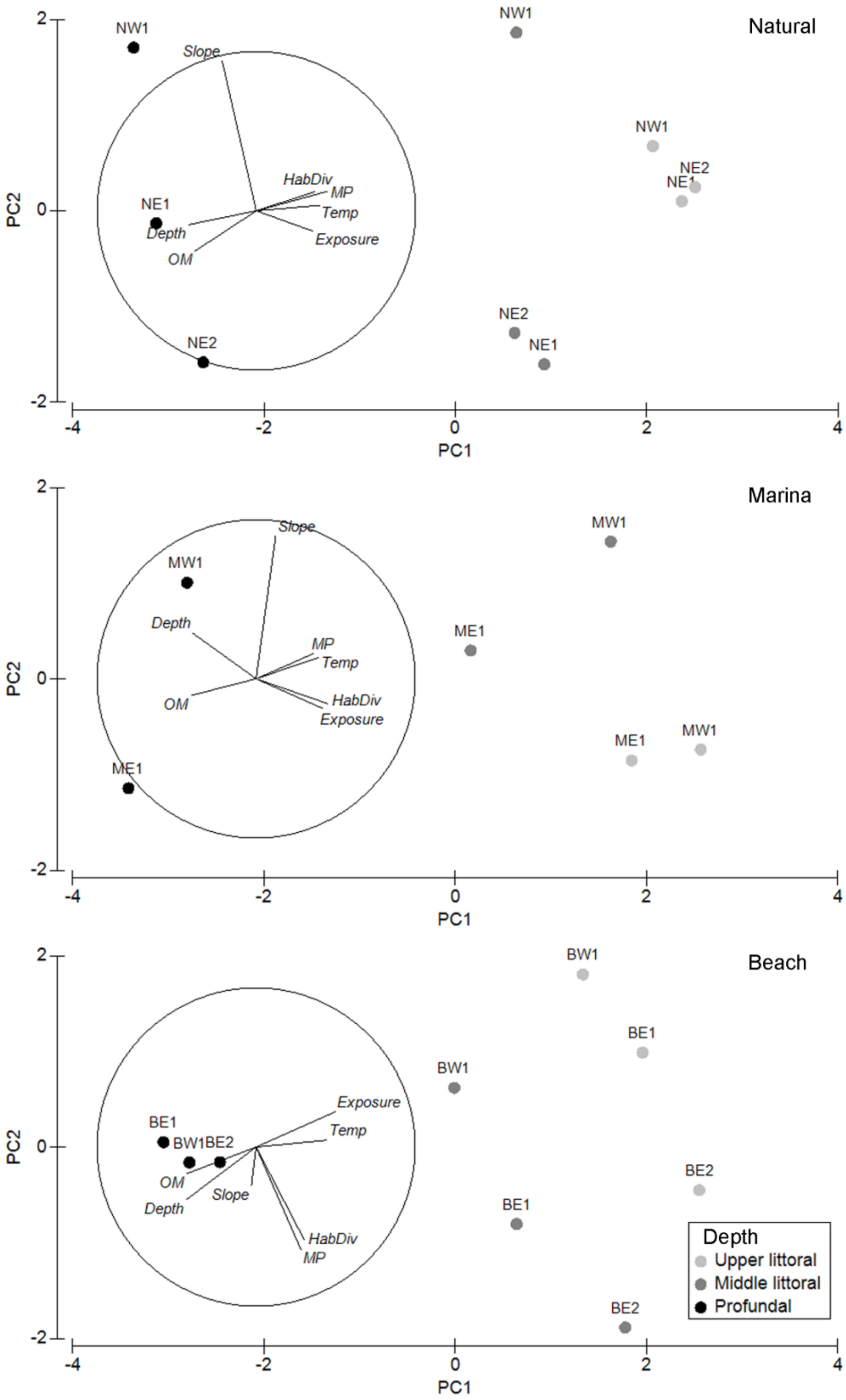

Figure 4-10: PCA-ordination plot of environmental variables for the upper, middle littoral and profundal. MP = macrophyte biomass, OM = organic matter content of sediment, Exposure = wind exposure, HabDiv = habitat diversity, Temp = mean annual temperature. N = natural, M = marina, B = beach, E = east side, W = west side.

Linear regressions showed that total secondary production was significantly positively related to PC 1 for all three shore types, but did not show a significant relation to PC 2 (Table 4-3). Hence, high values of secondary production were related to high habitat-heterogeneity described as macrophyte biomass and habitat diversity, high temperatures and exposure, but negatively to depth and organic matter content of sediment.

Table 4-3: Results of linear regressions between production values and PCA scores of PC1 and PC2.

	Natural			Marina			Beach		
	p value	t value	adj R^2	p value	t value	adj R^2	p value	t value	adj R^2
PC 1	0.000	7.1	0.86	0.013	4.25	0.77	0.012	3.34	0.56
PC 2	0.735			0.508			0.315		

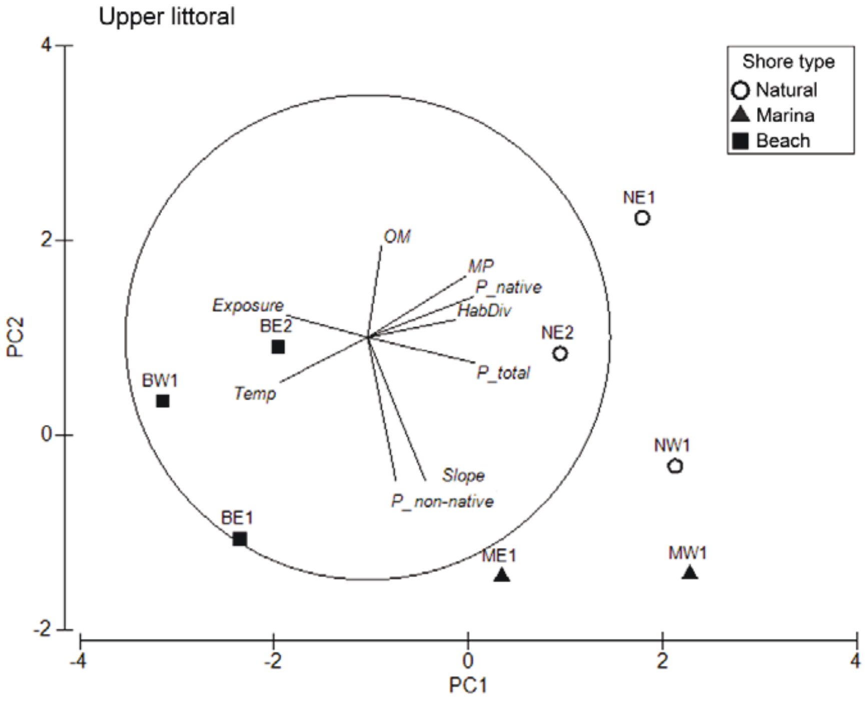

Figure 4-11: PCA-ordination plot of environmental variables and secondary production for the upper littoral zone. P_total = total production in g m^{-2} y^{-1}, P_native = production of native taxa in g m^{-2} y^{-1}, P_non-native = production of non-native taxa in g m^{-2} y^{-1}, MP = macrophyte biomass, OM = organic matter content of sediment, Exposure = wind exposure, HabDiv = habitat diversity, Temp = mean annual temperature. N = natural, M = marina, B = beach, E = east side, W = west side.

The first two axes of the PCA performed for the upper littoral explained 71.9 % of the variation between all studied sites. Natural sites and marinas were positively related to PC 1 (Figure 4-11). Contrary, beaches were strongly negatively correlated to PC 1. Furthermore, PC 1 showed a gradient from high to low total and native production as well as macrophyte biomass and habitat diversity. Hence, PC 1 separated sites with high production and high habitat- heterogeneity (natural sites and marinas) from sites with low production and low habitat-heterogeneity (beaches). In addition beaches were positively related to wind exposure and temperature. PC 2 mainly reflected differences in production of non-native taxa and slope mainly associated with the marinas and the public beach at the east shore (BE1) (Figure 4-11).

Additional information about the relation of food source availability and secondary production showed a moderate negative dependency of production on AFDM and chlorophyll a data of biofilm from reed, stones and artificial substrates with higher amount at beaches and lower on natural sites (Figure 4-12). Furthermore, scatterplots for production and chlorophyll a data of the sediment revealed no relationship (Figure 4-12).

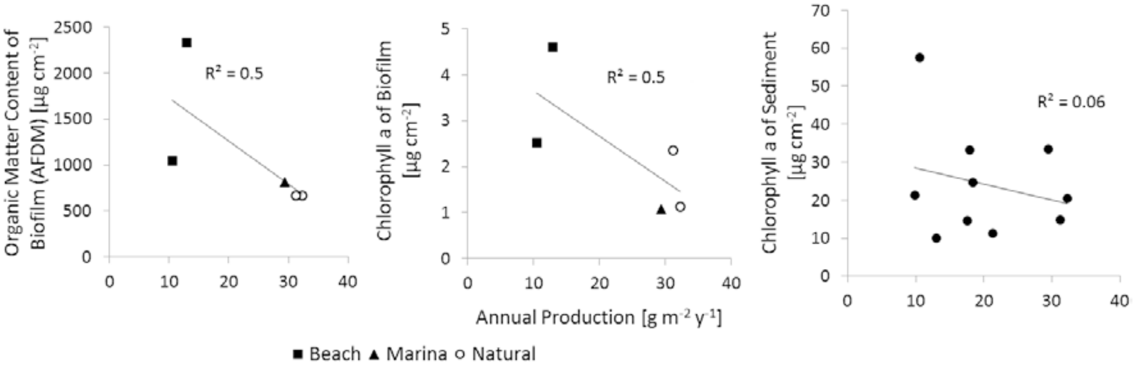

Figure 4-12: Annual production correlated with organic matter content of biofilm (left) and chlorophyll a of biofilm (middle) for the five sites sampled at the east side of the upper littoral. Right: Annual production correlated with organic matter content of sediment for the five sites sampled at the east side of the upper and middle littoral.

Whole lake secondary production

Estimates of site-specific secondary production were scaled up to the production of the entire depth zone and to whole lake production. Altogether 98.8 tons dry mass of macroinvertebrates and in average 8.19 g m^{-2} y^{-1} were estimated for Lake Scharmützelsee in the year 2011. In the upper littoral zone secondary production was in total 31.94 t y^{-1}. This value considers the proportional amount of shore types to total surface area in this depth zone. Hence, natural sites contributed with 19.06 t y^{-1} the largest amount to total production of the upper littoral, whereas marinas supplemented 12.78 t y^{-1}. Since beaches made up a very small proportion of the total upper littoral area, they only added 0.08 t y^{-1} to total secondary production. In the middle littoral 56.18 t y^{-1} and in the profundal 10.69 t y^{-1} of secondary production were estimated. In these two depth zones the proportional area of shore types were not taken into account for the averaging of secondary production values, because secondary production did not differ between shore types (Appendix IV). In general, 32.3 % of the whole lake secondary production took place in the upper littoral, although the surface area of this depth zone comprised only 7 % of total lake area. The middle/lower littoral contributed more than the half to the whole lake secondary production, whereas the profundal added only 10.8 %, even though it covered almost 70 % of the lake area.

The estimated total secondary production for the upper littoral zone and for the entire lake showed a positive response ratio and thus slightly higher secondary production values in comparison to the modelled natural conditions of the lakeshore (represented by the square in Figure 4-13). In line with that the simulation revealed an increase in secondary production up to 2 % at whole lake level (response ratio = 0.02) or up to 6.5 % in the upper littoral (response ratio = 0.06) assuming the entire lakeshore would consist of the examined marinas (Figure 4-13). Contrary, in case the entire lakeshore would show the characteristics of the examined beaches, the simulation indicated a decrease in secondary production by 21.6 % at the whole lake level (response ratio = -0.24) and by 67.8 % in the upper littoral zone (response ratio = -1.13) (Figure 4-13).

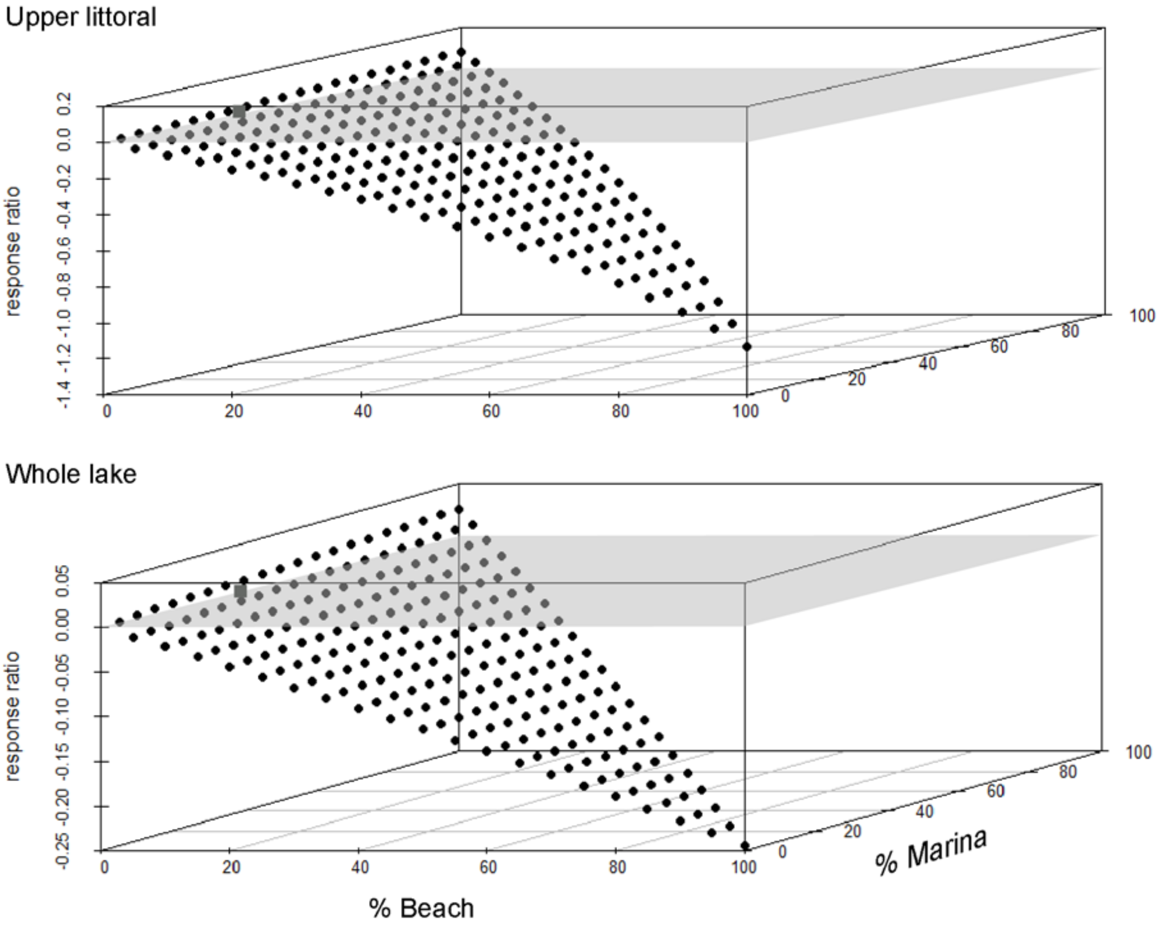

Figure 4-13: 3D-scatterplots for the 230 simulated response ratios showing changes in secondary production at beaches and marinas compared to natural sites (response ratio of zero = grey area) for the upper littoral and the whole lake. X- and z-axis give the percentual amount for each of the two modified shore types on total area of the upper littoral zone. Missing part to 100 % corresponds to the proportional amount of natural area. The squares represent the estimated total secondary production for Lake Scharmützelsee in 2011.

4.4 Discussion

Uncertainties in secondary production estimation

The estimation of secondary production is a challenging issue especially when aiming to estimate total community production in the field. In order to show the constraints of our production estimates we identify and discuss possible bias and uncertainties of the presented data. This is important when comparing the production estimates with other research studies on secondary production but also when using them for calculation of energy and material flow through the lake food web.

First of all it is well known that the sampling effort can have large influences on production estimations (e.g. Cusson et al. 2006, Dolbeth et al. 2012). The omitting of winter samples (December – March) in our study might have overestimated total annual production, because lower biomass values caused by higher mortality during winter month would probably decrease the estimation of annual production (Dolbeth et al. 2012). However, no different effects of lakeshore modification compared to autumn or spring were expected due to little biological activities caused by low temperatures in this season.

Furthermore we used mesh sizes of 500 µm which is known for inadequate sampling of small taxa especially juvenile stages resulting in lower production estimates (Cusson & Bourget 2005). In addition, our results are biased towards lower secondary production because we did not include other meiofauna such as Ostracodes, Acari, etc. which can comprise together with the juvenile stages up to 50 % of total benthic production (Strayer and Likens 1986, Stead et al. 2005). Furthermore, we excluded groups of macroinvertberbrate with abundances lower 1 % including Coleoptera, Turbellaria, Heteroptera, Lepidopetra and other Diptera, but contained Unionidae due to their high biomasses.

Another error sources stems from using the empirical ANN model. Although the model predicts the log(P/B) on geometric mean quite reasonably ($R^2 = 0.801$), back-transformation to natural scale in arithmetic units always leads to an underestimation of P/B and P (Smith 1993). Underestimation caused by back-transformation was shown to be around 10 % for the ANN model (Brey 2012).

Moreover, it is known that biomass or secondary production can change with depth. For the entire profundal zone only the production estimates obtained from the upper profundal (>8 - 15 m) were used for upscaling. We think this procedure was representative for our lake, because in Lake Scharmützelsee no clear pattern of biomass along a depth gradient in the profundal was observed which can be attributed to the heterogeneous bathymetry of the lake (Brämick et al. 2011).

Finally, the estimated community production may be little lower, because we summed up the production estimates of all considered taxa regardless whether they are prey, predators or parasites, although secondary production is not additive (Waters 1977).

According to the identified error sources it can be expected that real secondary production would have been generally higher. Since natural sites and in our case also marinas are characterized by high diversity there is a greater probability to miss juvenile stages and other meiofauna during sampling. Hence, for natural sites and marinas real production would probably even differ stronger to production of beaches. Thus our results only showed the lower limit of lakeshore modification effects for site-specific production at beaches.

Lastly, our estimates for larger spatial scale relied on the assumption that the marinas are representative for all modified shore section except for the very low amount of beaches occurring at Lake Scharmützelsee. But many of the modified shore section considered as marinas at Lake Scharmützelsee do not show the same characteristics, particular in relation to macrophyte stands, therefore real production may be rather lower than estimated. Hence, our production estimates for the entire Lake Scharmützelsee are conservative. The inclusion of other shore types especially those shaped by property owners would most likely give lower estimates. Consequently, also the simulated production estimates would change depending on the shore types included.

Effect of lakeshore modification on upper littoral secondary production

Our results demonstrated that lakeshore modification can cause a reduction of secondary production in the upper littoral zone. But we also showed that the effects of lakeshore modification on secondary production differed between marinas and beaches. Beaches had substantially lower site-specific production of macro-invertebrates than marinas and natural sites. In accordance to our first hypothesis this was mainly the result of reduced habitat-heterogeneity described by macrophyte biomass and habitat diversity. The higher temperatures observed at beaches, probably resulting from low shading effects through the loss of macrophytes (e.g. Johnson & Jones 2000), could not compensate for the lower biomass and production of macroinvertebrates at beaches. Lower secondary production at sites with low macrophyte occurrence was also shown for intertidal macroinvertebrate communities (Dolbeth et al. 2003). In contrast, secondary production of marinas was even slightly higher than at natural shorelines. This can partly be explained by the higher habitat diversity observed at marinas including the influence of submerged macrophyte biomass. Furthermore, there may be other factors increasing the production of marinas which were not covered in this study. For example, a higher surface heterogeneity of the sediment was observed due to small pieces of wooden boards, probably dropped off from boats, which were not quantitatively measured. However, an absent effect of anthropogenic disturbance on total secondary production or even an increase in secondary production has been found in other studies and was explained by a shift in taxa contributing to secondary production (e.g. Johannsson et al. 2000, De Lange et al. 2004, Hall et al. 2006).

We also found effects of lakeshore modification on the contribution of non-native taxa to secondary production. A higher percentage of secondary production of non-native taxa was observed at marinas and beaches compared to natural sites. In addition, at marinas even a positive effect on secondary production of non-natie taxa was found in relation to natural sites. The potential influence of non-native species on ecosystem functioning is well known, showing that invasive species can have large effects on most ecosystem functions (Charles & Dukes 2007, Strayer 2012 and references therein). Changes in the energy transfer through the food web by non-native species will be illustrated with *Potamopyrgus antipodarum*, because this invasive mud-snail was shown to be a key species at modified sites in Lake Scharmützelsee (Chapter 2 & 3). *P. antipodarum* uses the provided food sources more effectively and by doing so it does not only change the structure of algae and native macroinvertebrate communities, but can also dominate the nitrogen and carbon cycling (Hall et al. 2003, Krist & Charles 2012, Moore et al. 2012). Moreover, *P. antipodarum* is known to be of limited value as source of energy for fish and often passes the digestive system alive (Vinson & Baker 2008). Since fish rely up to 65 % on whole-lake benthic secondary production (Vander Zanden & Vadeboncoeur 2002), a shift in secondary production towards non-digestible food sources and a decrease in total secondary production at modified lakeshores should strongly affect fish production. A displacement of native species by non-native species with different traits followed by a change in the energy flow through the food web was also shown in further studies (e.g. Strayer et al. 1999, Hall et al. 2006, Sousa et al. 2008, Ozersky et al. 2012).

Nevertheless, a shift in the contribution of production from feeding types was not only a consequence of competitive advantages of invaders but also happened due to direct effects of lakeshore modification on composition of native macroinvertebrates (see also Chapters 2 and 3). For example, predator and parasites were the only feeding types clearly negatively affected in production by lakeshore modification at beaches and marinas. Predator or parasites are one of the first taxa disappearing with habitat loss in case they are specialized on preys which decrease in abundance with increasing habitat loss (Ryall & Fahrig 2006). The third feeding type negatively affected at both modified shore types was miners which obviously did not find enough plant substrate such as reed. In addition, the less dense macrophytes stands, especially at beaches, favoured the colonization of filter feeder such as *Pisidium* spp. or Unionidae. Therefore secondary production of filter feeder at beaches was almost not affected compared to natural sites, and at marinas the production of filter feeder was even much higher. The increased uptake of food sources from the pelagic compartment through filter-feeders can redirect the energy and material flow between the benthic and pelagic compartment. The importance of cross-habitat trophic linkages connected by benthic invertebrates for the functioning of whole lake food webs was recently emphasized by Sierszen et al. (2014).

Food source availability quantified as organic matter content of sediment did not contribute to explain the difference of secondary production between shore types. This might be attributable to the different accumulation and transposition rate, which can be assumed to be higher in areas with low wave exposition, such as the reed belt or within the area of the marinas. But the variable reflected a gradient from low to high organic matter content with increasing depth and thus rather revealed a decrease in sediment heterogeneity.

Organic matter content and chlorophyll a of biofilm from the upper littoral zone were related to secondary production and showed a slight tendency towards higher amount at beaches, whereas chlorophyll a of sediment exhibited no relation to production. In summary, the variables used to describe food source availability did not explain the differences between secondary production of different shore types, but it has to be stressed that the amount of food source availability per shore type was only compared based on data collected on areas with the same size. However, the results suggest that food source availability is not the driving factor that explains differences in secondary production. This is in accordance with a recently published study demonstrating that habitat characteristics such as oxygen availability and temperature limited secondary production, but not benthic primary production (Craig et al. 2015).

Similar to secondary production, the diversity of macroinvertebrates was lower at beaches but did not differ at marinas compared to natural sites. This gives evidence that a reduction in diversity is accompanied by a decrease in the functioning of macroinvertebrates. However, the effects on diversity were weakened compared to the effects on secondary production; therefore diversity did not adequately detect the effects of lakeshore modification on the functioning of macroinvertebrates. Biomass even showed partly different response to lakeshore modification than secondary production or diversity. This variation in effect size between the different metrics can mainly be attributed to the different community composition between the shore types (Chapters 2 & 3) harbouring taxa with different life cycles as an adaption to the appearing environmental conditions. For example the marina in the upper littoral had no effect on production and diversity but positive effects on biomass. High biomass but low turnover of biomass and thus lower production results from species with long life-cycles such as Unionidae, from which *Unio tumidus tumidus* was even selected as indicator species at marinas (Chapter 2). Hence, in line with previous finding, secondary production is a more sensitive metric than structural measures for detection of ecosystem disturbances (Lugthart & Wallace 1992, Whiles & Wallace 1995, Valentine-Rose et al. 2011).

Effect of lakeshore modification on depth-production relationship

Our results demonstrated that site-specific diversity, biomass and the production of macroinvertebrates were highest in the littoral compared to the profundal. The high secondary production in the upper littoral zone was predominantly explained by the variables habitat diversity and macrophytes biomass describing high habitat-heterogeneity. Higher habitat-heterogeneity of the littoral zones promoted higher diversity due to more niche availability and in line with the diversity-production relationship led to higher secondary production (e.g. Loreau et al. 2001, Hooper et al. 2005). Furthermore, the secondary production of the upper littoral zones was positively influenced by higher temperatures (Chapter 1.6: Table 1-3) favouring biological activities such as reproduction or feeding (Plante & Downing 1989). In the middle littoral, lower production values were a result of decreased habitat diversity and reduction of habitat complexity provided by macrophyte, which were characterized by monotone plant beds consisting of *Nitellopsis obtus*a in this depth zone (see Chapter 3.3). The profundal was characterized by low temperatures, the absence of complex habitats such as macrophytes and high organic matter content referring to more homogenous conditions of the sediment in this depth zone. Consequently, these unfavourable conditions caused a crucial reduction in secondary production in the profundal, which could obviously not be stimulated by other environmental factors or competitive advantages. The observed depth-specific pattern in Lake Scharmützelsee is in line with previous findings from other lakes (e.g. Kajak

1978, Dermott 1988, Lindegaard 1992, Butkas et al. 2010) and highlights the role of the littoral zone for secondary production.

Furthermore we could show that lakeshore modification affected diversity, biomass and secondary production only in the upper littoral zone. The effects of lakeshore modification were not detectable in any deeper depth zone. As a consequence variability of secondary production was highest in the upper littoral caused by low production estimates for beaches which were lower in this depth zone than in the middle littoral zone. Hence, in agreement with our second hypothesis, the depth-production relationship was altered at beaches, where secondary production increased and not decreased from the upper to the middle littoral. This can be attributed to the severe loss of habitats especially provided by macrophytes in the upper littoral and to the frequent disruption of the sediment due to higher wave exposition and human trampling. At marinas the depth-production relationship was not altered, because similar to natural sites habitat diversity was still one of the major factors positively influencing secondary production.

Whole lake secondary production

Our results of depth-specific upscaling demonstrated that about one third of whole lake secondary production was provided by the upper littoral zone, although the surface area of this depth zone comprised only 7 % of total lake area. In contrast, the profundal only added 10.8 %, even though it covered almost 70 % of the lake area. Hence, despite of the low littoral area including the effect of lakeshore modification on secondary production the littoral zone played a central role in contributing to whole lake secondary production of Lake Scharmützelsee. This is in line with recent findings and highlights the littoral role in contributing to whole lake secondary production also for rather large and deep lakes (Babler et al. 2008, Northington et al. 2010, Butkas et al. 2010).

In general, average whole lake secondary production for Lake Scharmützelsee was estimated with 8.19 g DM m^{-2} y^{-1} and thus in the range of previously published studies showing that whole-lake secondary production varies between 0.3 - 97.8 (3050.9) g DM m^{-2} $y^{-}1$ (Northington et al. 2010). Since we applied a method for estimating secondary production not commonly used for lake macroinvertebrates a detailed comparison with the existing estimates of secondary production will not be performed to exclude misleading conclusions.

The estimated total amount of secondary production for Lake Scharmützelsee was slightly higher compared to the amount of a simulated lake with entirely natural lakeshores. This is attributable to the large amount of lake section assigned to marinas which revealed slightly higher secondary production estimates then natural sites. Consequently, negative effects on the total secondary production caused by lakeshore modification became only apparent in scenarios with increasing proportional amount of the shore type beach in the upper littoral zone. Hence it can be suggested that a reduced energy and material transfer through lake food webs only occurs at lakes with lakeshores showing beach characteristics. Anyway, as we described above the functioning of macroinvertebrates can also change dramatically assuming all modified sections exhibit the characteristics of marinas due to the difference in non-native production and compositional changes in feeding types. Thus, according to our third hypothesis local impacts of lakeshore modification can translate into alterations of the functioning of macroinvertebrate at whole lake ecosystem level; because the upper littoral zone contributes importantly to whole lake secondary production and lakeshore modification can strongly affect upper littoral secondary production. It can further be concluded that if the functioning of macroinvertebrates at whole lake ecosystem level changes, the functioning of the entire lake ecosystem changes due to alteration in the energy and material flow through the food web. Since secondary production is merely a proxy for the energy and material transfer through the food web future studies should complement the results obtained in this thesis by examining fish production and matter fluxes between trophic compartments as already suggested by Brauns et al. (2011). This will truly allow to quantify the effects of lakeshore modification on whole lake ecosystem functioning.

Conclusion

We could show for the first time that lakeshore modification affected not only diversity and biomass, but also the production of macroinvertebrates in the upper littoral zone. Thereby effects on secondary production were stronger than adverse effects found on structural measures of macroinvertebrate communities. Furthermore, the upper littoral zone exhibited the highest average site-specific estimates of secondary production and contributed 32.3 % to whole lake secondary production. This was not the case if we estimated secondary production for the three studied shore types separately. Here we could demonstrate that the depth-production relationship was altered at beaches with lower production estimated in the upper littoral than in the middle littoral. Although we could not observe this alteration of the depth-production relationship for marinas, our results highlight the role of compositional changes in non-native species and functional groups to understand effects of lakeshore modification on the functioning of macroinvertebrates.

The local effect of lakeshore modification on secondary production was mainly attributed to the loss of habitat-heterogeneity naturally highest in the upper littoral zone. Therefore we conclude that human induced habitat loss alters the functioning of macroinvertebrates at modified lakeshores. Upscaling of site-specific production estimates to the entire upper littoral zone and to whole lake level showed that local effects of lakeshore modification can translate into alterations of the functioning of macroinvertebrates at whole lake ecosystem level. These results suggest that the ecological functioning of lakes can be drastically disturbed following lakeshore modification, which should force decision makers to face up to the ecological, social and economic consequences of lakeshore development.

For a successful assessment and management of lakeshores a profound understanding about the effects of anthropogenic disturbances on ecosystem functioning is fundamental (Sousa et al. 2011, Strayer 2012). Our results suggest that secondary production as an integrative measure rather than structural measures of macroinvertebrates should preferably be used to evaluate the potential consequences of lakeshore modification on ecosystem functioning, because secondary production was more sensitive. For the assessment of lakeshores we further conclude from our results that a successful assessment of lakeshores should incorporate the proportional amount of production from non-native species and functional groups. This allows finding effects on the functioning of macroinvertebrates at modified sites where no distinctions in total secondary production are detectable compared to reference sites. Finally, improving habitat-heterogeneity at modified lakeshores should counteract human induced lakeshore modification and preserves the functioning of littoral macroinvertebrates important for the functioning of the entire lake ecosystem.

5 Length-mass relationships for lake macroinvertebrates corrected for back transformation and preservation effects

5.1 Introduction

The estimation of biomass of freshwater macroinvertebrates is a necessary step when studying life-histories, community relationships, transfer of energy, and turnover of biomass in food webs (Rigler & Downing 1984). As an alternative to the direct determination of body mass, indirect methods based on functions describing length-mass relationships are widely used to obtain rapid estimates of individual mass from measurements of macroinvertebrate body dimensions (Burgherr & Meyer 1997). In addition to their efficiency, indirect methods have the advantage that the measured individuals are not destroyed and are available for further analysis (Meyer 1989).

Since it is not always possible to establish length-mass relationships using organisms from the ecosystem under study, it is common practice to use published relationships (e.g. Smock 1980, Benke et al. 1999). It is important that these were determined using organisms from the same ecosystem type and geographic region because length-mass relationships can differ between habitats, leading to serious under- or overestimations of the true body mass when relationships from a different habitat are used (Baumgärtner & Rothhaupt 2003, Méthot et al. 2012). Many compilations of length-mass relationships published for freshwater macroinvertebrates are now available (e.g. for North America: Smock 1980, Benke et al. 1999, Johnston & Cunjak 1999, Méthot et al. 2012, New Zealand: Towers et al. 1994, Europe: Mason 1977, Poepperl 1998, Baumgärtner & Rothhaupt 2003), but most were established for macroinvertebrates from streams or rivers. For European lakes only two compilations are available, one for shallow lakes in the United Kingdom (Mason 1977) and one for the prealpine Lake Constance (Baumgärtner & Rothhaupt 2003).

Aside from the lack of relationships for lakes, there is some dispute in the literature about the best way to estimate length-mass relationships, particularly when the aim is to use them to predict mass from length. Macroinvertebrate length-mass relationships are usually nonlinear and can be described by a power function:

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

M = mass, L = length of body dimension and a and b are parameters estimated by fitting the function to data (Wenzel et al. 1990, Johnston & Cunjak 1999, Baumgärtner

& Rothhaupt 2003). As well as being nonlinear, the variance, or “scatter”, around length-mass relationship is usually greater for large than for small individuals; in statistical terms, the variance of the relationship is proportional to the mean and the error structure is multiplicative (Xiao et al. 2011). It is common practice to logarithmically transform the length and mass measurements so that the power function becomes the linear function (Bottrell 1976):

$$\ln \mathrm{M} = \ln a + \ln \mathrm{L} \cdot b \qquad (2)$$

On the transformed logarithmic scale, the error structure becomes additive, the variance in mass is equal for all lengths, and the linear function (2) can be easily fitted to data using simple linear regression (Xiao et al. 2011). The resulting equation predicts log mass from log length, but these can be back transformed to get predictions on the original unlogged scale (Xiao et al. 2011).

However, this procedure has been criticised on the grounds that a) log transformation makes it more difficult to identify outliers in the data, b) the log transformation makes the assumption that errors (variation) are multiplicative rather than additive, and c) the resulting equation predicts geometric mean mass for a given length and not the arithmetic mean (Packard 2009, Packard et al. 2010). Packard (2009) and Packard et al. (2010) recommend instead that nonlinear regression should be used on untransformed data. In response, Kerkhoff & Enquist (2009) argue that a) on the original arithmetic scale it is only outliers at the “long” end of the scale that will be easily seen, and b) the assumption of multiplicative errors is a feature, and not a bug, of the log transformation because in nature variation is usually multiplicative (Kerkhoff & Enquist 2009, Glazier 2013). Xiao et al. (2011) used simulation to demonstrate that the correct method depends on the error structure of the data and that assuming an incorrect error distribution will lead to biased estimates of the parameters and predictions that are poor over some range of the data, e.g. by consistently over- or underpredicting the mass of small individuals. Xiao et al. (2011) recommend comparing the likelihood of models with additive and multiplicative error structures to determine the best regression method.

If likelihood analysis indicates that log-linear regression should be used, the problem remains that back transformed mass predictions will be biased. This is because the log-linear regression models the mean of the log transformed mass, i.e. the geometric mean, and the geometric mean is always less than the arithmetic mean (Smith 1993, Hayes & Shonkwiler 2006). For example, the geometric mean for the values 10, 100 and 1000 is 100, whereas the arithmetic mean of the same numbers is 370 (Hayes &

Shonkwiler 2006). However, rather than avoiding log transformation, correction factors can be estimated to correct this bias (Hayes & Shonkwiler 2006), and here we use and test the smearing factor (Duan 1983) a simple and robust nonparametric correction factor, which makes no assumptions about the error distribution (Smith 1993).

While most published length-mass relationships have been estimated using unpreserved or frozen animals (e.g. Smock 1980, Benke et al. 1999, Baumgärtner & Rothhaupt 2003), most studies use these relationships on preserved animals (Leuven et al. 1985, Edwards et al. 2009). Preservation is especially needed for studies investigating biomass or secondary production of the entire macroinvertebrate community, where it is impossible to process the samples immediately after sampling (Edwards et al. 2009). In older studies preservation with hazardous substances such as formalin or Kahle’s solution was conducted, as it has less influence on the preserved objectives. Meanwhile the most common preservative is ethanol. However, ethanol preservation causes a release of organic components such as enzymes or lipids resulting in mass changes, with more than 50 % loss observed in some cases (Howmiller 1972). The mass loss has to be accounted for and many conversion factors are available (e.g. Howmiller 1972, Dermott & Paterson 1974, Wiederholm & Eriksson 1977, Landahl & Nagell 1978, Leuven et al. 1985, von Schiller & Solimini 2005). But using conversion factor to correct for changes in mass of preserved animals also leads to incorrect biomass estimates when body mass is predicted from regressions established on unpreserved animals. This is also a consequence of preservation in ethanol causing changes in macroinvertebrate length due to dehydration of the internal tissues and contraction of muscles (Britt 1953, Lasenby et al. 1994, Leuven et al. 1985, von Schiller & Solimini 2005). This has fostered other authors to establish conversion factors for length changes (Britt 1953, Lasenby et al. 1994, Edwards et al. 2009). Another possibility is to use length-mass relationships based on preserved animals and subsequently apply a factor to convert from preserved to unpreserved mass (Leuven et al. 1985). The application of conversion factors for mass changes instead of conversion factors for length changes has the advantage that they also could be used to correct for mass changes of preserved animals weighed directly, where length is not measured.

The main objective of this study was to provide length-mass relationships for macroinvertebrates from temperate lakes of the central European lowland. In order to fulfil the demanding requirements of sound length-mass relationships our associated research objectives were fourfold: 1) We aimed to clarify the appropriate statistical approach by comparing log-linear and nonlinear methods of estimating these relationships, and 2) by testing the smearing correction factor for removing the bias in mass estimates that is introduced by log- and back-transformation when using log-linear models. 3) We present conversion factors to correct for mass changes caused by preservation in ethanol. Lastly, 4) we aimed to assess the transferability of these length-mass relationships by comparing within- and between-lake mass predictions using our data, and by comparing our length-mass data with comparable published relationships from other regions.

5.2 Methods

Sampling & sample processing

Macroinvertebrates were sampled in 2008 in Lake Schulzensee (53° 14′ 46.09″ N, 13° 16′ 26.00″ E) and Lake Rathsburgsee (53° 11′ 59.11″ N, 13° 56′ 24.68″ E), and in 2011 in the littoral zone (0 - 4m depth) of Lake Scharmützelsee (52° 15′ 0″ N, 14° 3′ 0″ E). All three lakes are located in Northeast Germany in the federal state of Brandenburg. Lake Schulzensee and Lake Rathsburgsee have surface areas of around 0.03 km² and maximum depths of 4 - 5 m, while Lake Scharmützelsee has a surface area of 12 km² and a maximum depth of 29.5 m (Grüneberg et al. 2011). The sampled area of all three lakes is characterized by sandy substrate mostly covered with macrophytes, flat or shallowly sloping shores, exposed- and unexposed shores as well as low water level fluctuations. Macroinvertebrate sampling was carried out with a modified Ekman-Birge-grab and a hand net (500 µm mesh size) in different habitats, depths of the littoral and seasons to cover the natural variability in length and mass. Immediately after sampling, macroinvertebrates were preserved in 96 % ethanol. In the laboratory the individuals were identified to the lowest taxonomic level possible and then stored in glass vials with 70 % ethanol for at least 50 days until the mass loss due to preservation was stable (Leuven et al. 1985).

After mass stabilization, length and mass measurements were conducted on undamaged individuals having all appendages. For each taxon an appropriate body dimension was measured to the nearest 0.01 mm (Figure 5-1, Table 5-1). For the head width of insects, we did not measure the broadest section of the head as usually recommended in the literature, because we observed that the position of the broadest section of the head capsule varies between different larval stages of the same species;

e.g. it is sometimes found in front of the eyes in younger stages but behind the eyes in older stages. Instead, we choose easy to find fixed points for taxa with similar characteristics (Figure 5-1).

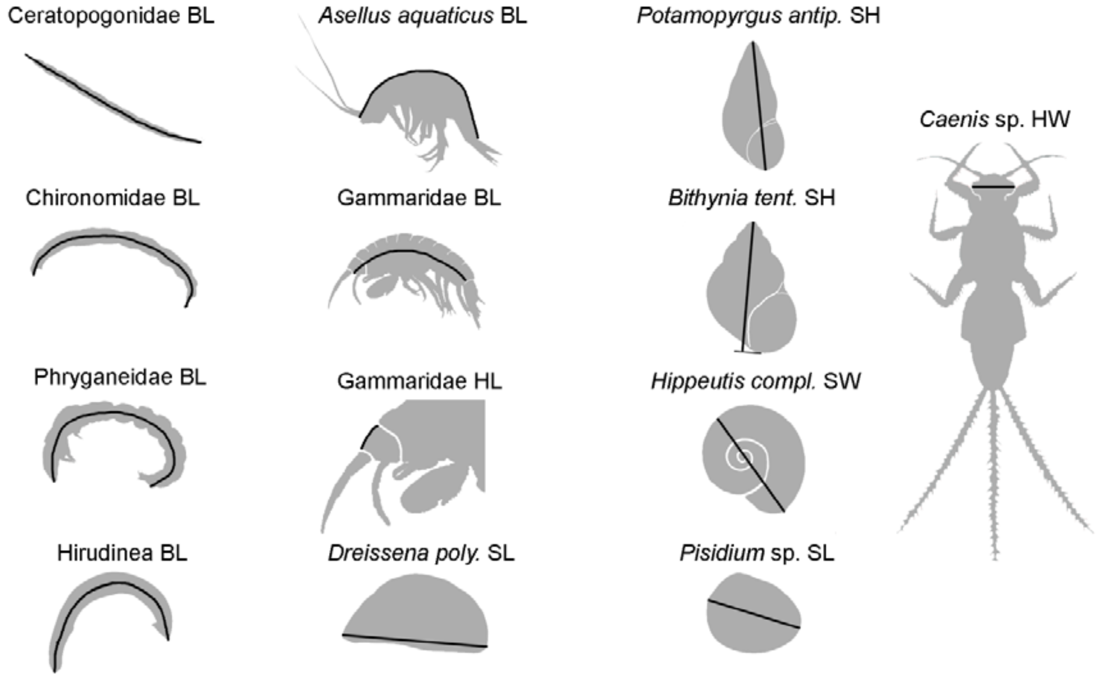

Figure 5-1: Black lines illustrate the measured body parts for the studied taxa. Some of the taxa presented stand for multiple taxa measured in the same way, these are: Phryganeidae BL for *Athripsodes* sp. BL, Hydroptilidae BL, *Molanna angustata* BL, *Mystacides longicornis/nigra* BL and *Oecetis* sp. BL; Gammaridae BL and HL for *Chelicorophium curvispinum* BL and HL; *Hippeutis complanatus* SW for *Gyraulus* sp. SW and *Valvata cristata* SW; *Pisidium* sp. SL *for Valvata piscinalis* SL; *Caenis* sp. HW for Ephemeroptera HW, Trichoptera HW and Odonata HW. (BL = body length, HL = head length, HW = head width, SH = shell height, SL = shell length, SW = shell width).

The measured individuals were then dried for 24 hours at 60°C in pre-weighed aluminium dishes, and the dry mass (DM) was weighed to the nearest 0.01 mg (Mettler AT261). For the zebra mussel *Dreissena polymorpha*, we removed the shell using hot water to determine DM without shell (Zwarts 1991). The removal of shells from Gastropoda and small Sphaeriidae was impossible, therefore we determined the ash free dry mass (AFDM) by combusting individuals for five hours at 450°C. In general, only large animals were weighed individually, otherwise we weighed several individuals of a similar length together and calculated a mean individual mass to reduce measurement error.

To establish preservation conversion factors, a separate set of macroinvertebrate samples was taken from Lake Scharmützelsee in January 2013. Individuals were identified and processed on the same or the following day. For each conservation factor established for aggregated major taxonomic groups, eight to 22 replicates with 1 - 8 individuals from one taxon covering different sizes were used. Different numbers of identified taxa were only used for Hirudinea (4 taxa) and Trichoptera (6 taxa). Half of the individuals for each major taxonomic group were weighed directly and the other half stored in 10 ml glass vials filled with 70 % ethanol in the dark to exclude potential effects on mass due to light (Leuven et al. 1985). The unpreserved animals were first carefully dried on filter paper and then weighed to the nearest 0.01 mg to determine the fresh mass (FM). Subsequently, unpreserved DM was determined by drying individuals for 24 h at 60°C. Small molluscs were combusted at 450°C for 5h to measure the unpreserved AFDM. The DM and AFDM of the preserved individuals for each major taxonomic group was measured in the same way as the unpreserved individuals after 50 days (Leuven et al. 1985).

Statistical analysis

Macroinvertebrate length-mass relationships were established at species level if possible. In cases where species level identification was not possible, or there were not enough individuals, species were grouped into the subsequent higher taxonomic level. Based on this data, the following steps were carried out to create bias-corrected length-mass regression for preserved macroinvertebrates.

Data were first tested for gross outliers by plotting log-transformed mass against length estimates for each taxon and mass measurement. For many taxa there was a problem with the mass estimates of very short individuals, particularly when mass was given as AFDM. There were two related problems. 1) The absolute portion of measurement error was constant and was therefore proportionally larger for small individuals than for large individuals. After log-transformation this measurement error showed up as increased variance at the small end of the length scale. 2) When the true mass of individuals was low enough to be close to the lower limit of the mass balance, some mass estimates become zero, or even negative during the estimation of AFDM. During log-transformation these zero or negative estimates have to be excluded and this introduces a bias at very short lengths because those individuals whose mass was overestimated are retained but those for whom mass was underestimated are lost from the sample. This problem was solved by determining, for each taxon, a lower length threshold below which estimates of mass become unreliable. All individuals below this length were removed from the data set which eliminated the bias caused by exclusion and removed the very variable mass measurements of extremely short individuals.

A log-linear regression (LLR) and a nonlinear regression (NLR) were fitted to the screened DM and AFDM data for each taxon. The LLR was fitted using R's standard function for fitting linear models, "lm" (R Development Core Team 2013). This model assumes an additive, normally distributed error distribution after log transformation, and therefore a multiplicative, lognormal error distribution on the untransformed scale.

$$\ln M = \ln a + b \cdot \ln \mathrm{L} + \varepsilon \qquad \varepsilon \sim \mathrm{N}(0,\sigma) \qquad (3)$$

The parameters ln a and b are the intercept and slope of the linear regression function, M = mass, L = length of body dimension, ε = a normally distributed error term with mean = 0 and standard deviation = σ. We write ln a here to indicate that once back-transformed, i.e. e^a, it is equivalent to parameter a in the nonlinear model. The nonlinear regression model (NLR) was fitted to the untransformed length and mass values using R's function, "nls", for nonlinear regression. This model assumes an additive normally distributed error distribution on the untransformed scale.

$$\mathrm{M} = a \cdot \mathrm{L}^{b} + \varepsilon \qquad \varepsilon \sim \mathrm{N}(0,\sigma) \qquad (4)$$

For each taxon, the likelihood of the data given each of the two fitted models was compared and used to determine the most appropriate regression model. Because the two models were fitted to different versions of the mass data, original and log transformed, the likelihoods reported by the software could not be compared. However, comparable likelihoods were calculated by using the fitted parameters and variance components from the models with the appropriate probability density functions, as described by Xiao et al. (2011). For each log-linear regression, likelihoods for each observed mass were calculated using the lognormal probability density function (because the LLR assumes lognormal errors on the original scale) parameterized using the predicted mass for each observation as the mean (i.e. a different mean parameter for each observation), and the standard deviation of the residuals as the standard deviation. The product of these likelihoods gave the likelihood of the data given in the model. The same procedure was used for each nonlinear regression but with the normal probability density function instead of the lognormal one (because the NLR assumes normal errors on the original scale).

For each log-linear model (LLR) a smearing factor (SF) (Duan 1983, Hayes & Shonkwiler 2006) was calculated to adjust to the fact that the geometric mean mass is being predicted and not the arithmetic mean. The smearing factor is calculated by taking the mean of the back-transformed residuals from the fitted model, in this case a $\log_e$ (ln) transformation was used so the formula is:

$$SF = \frac{1}{n} \cdot \sum_{i=1}^{n} e^{\varepsilon_i} \qquad (5)$$

where ε_i are the residuals from the fitted log-linear model.

The corrected mass estimate for an individual of a given length L is then calculated as follows

$$\mathrm{M}_{SE} = e^{\ln a + b \cdot \ln \mathrm{L}} \cdot SF \qquad (6)$$

To evaluate the fit of the models, the total predicted mass of each taxon was compared to the measured total mass of each taxon. Linear regressions were fitted between percentage errors in individual mass estimates and individual lengths, and the slopes of these relationships were used to test for systematic biases such as a tendency to over- or under predict the mass of long or short individuals.

To estimate factors to convert between dry mass of preserved and unpreserved individuals, a regression model was fitted predicting log DM from log FM (Figure 5-2), with the same slope for preserved and unpreserved individuals but with different intercepts. The difference between these intercepts (Figure 5-2) gives the estimated conversion factor. Initial testing indicated that the slope of the relationship did not differ between taxa (ANOVA, F = 1.178, p = 0.278, df = 24), and so a common slope (but different intercepts) was used for all taxa (equivalent to an ANCOVA). Doing so reduced the variance in the estimated relationships. Conversion factors were tested whether they differed significantly between taxa or whether it would be appropriate to use common correction factors for broad taxonomic groups. In addition, conversion factors for calculating AFDM from DM were also established, in order to use them for energy budget or material flow studies.

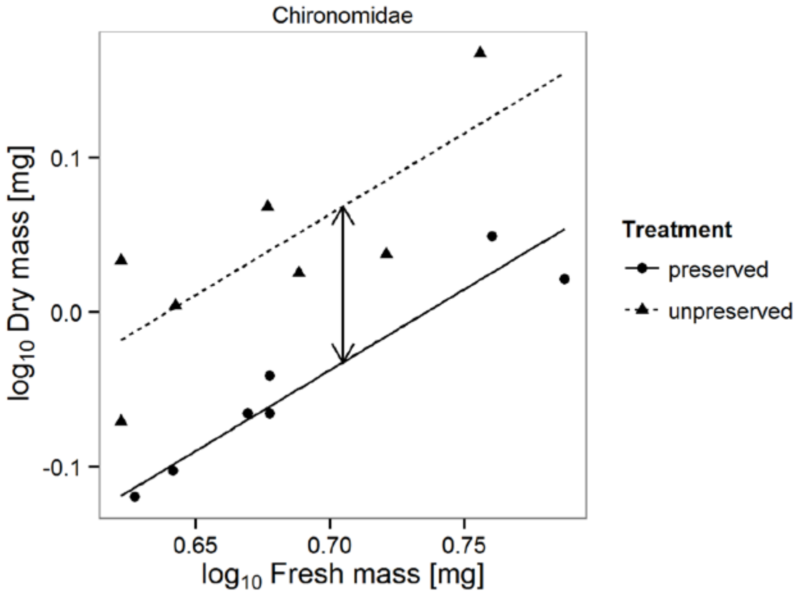

Figure 5-2: Example of the relationship between fresh and dry mass for preserved and unpreserved individuals for Chironomidae. The arrow indicates the correction factor for converting preserved into unpreserved mass.

To assess the transferability of the fitted length mass relationships between different lakes, lake specific log-linear models and smearing factors were estimated for taxa that had minimum sample sizes of 20 in more than one lake. These lake-specific models were then used to predict mass for the same and different lake(s) and the accuracies of these predictions were compared. Finally, length-mass data collected here were compared with length mass relationships published in Méthot et al. (2012), which used very similar methods to those here and included five taxa identified to a similar taxonomic level.

Example R code for fitting log-linear regression models and estimating the smearing correction factor is provided in Appendix V. The length-mass and alcohol preservation data used in this study are provided online: http://dx.doi.org/10.5281/zenodo.21002.

5.3 Results

For the vast majority of taxon and body dimension combinations, the likelihood of the data was higher given a log-linear versus a nonlinear regression model: 41 of 42 for length-dry mass and 10 of 10 for length-ash free dry mass relationships. The one exception was for DM of *Caenis horaria* (Ephemeroptera) Stephens, 1835, where only

7 data points were available. A table of likelihoods, and likelihood ratios between the log-linear and nonlinear models, is provided in Appendix VI.

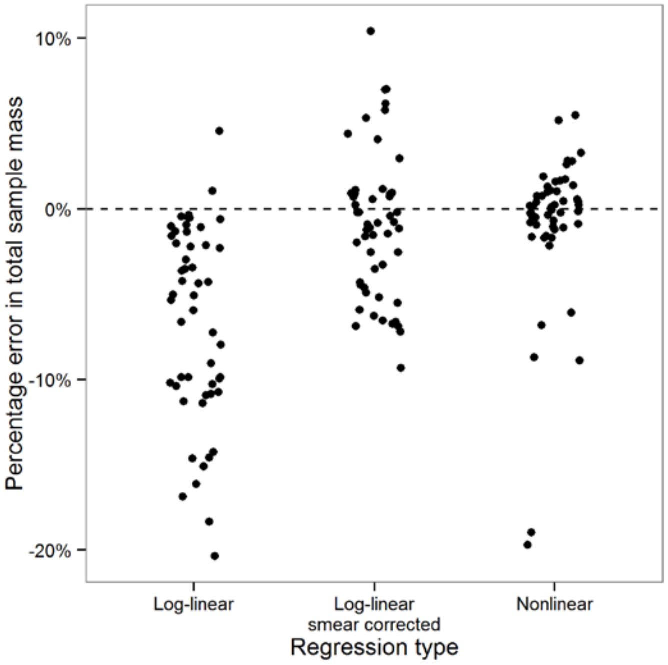

Figure 5-3: Error in total predicted mass. Each dot represents the estimated total sample mass for one taxon predicted from a log-linear, nonlinear, and smearing-corrected log-linear regression model. Estimates are biased to be too low when an uncorrected log-linear model is used. After smearing correction the estimates are unbiased.

Using nonlinear regression, mass estimates for complete samples were unbiased (Figure 5-3), however this was only because biased estimates for short and long individuals cancelled each other out. For most taxon-body combinations, nonlinear additive error models resulted in biased parameters and a poor fit over some range of the data. For example, for individuals of *Caenis robusta* (Ephemeroptera) Eaton, 1884 with head widths of less than 0.7 mm, almost all data points were above the estimated nonlinear regression line (Figure 5-4). We found statistically significant relationships between individual prediction errors (residuals) from nonlinear models and measured length for 29 of 52 taxon and body dimension combinations ($p < 0.05$ for 29 out of 52). Residual plots for Anisoptera and *C. robusta* are given as examples (Figure 5-5).

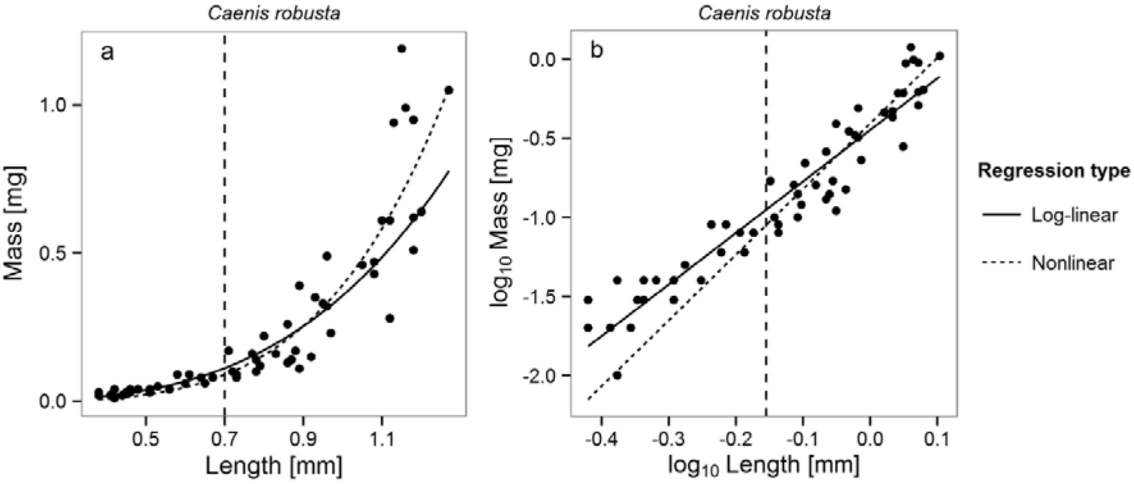

Figure 5-4: The relationship between length and mass for *Caenis robusta*, estimated by log-linear and nonlinear regression, shown on untransformed axes (a) and $\log_{10}$ transformed axes (b). Nonlinear regression results in a function that underestimates mass for short individuals, but this is only clear when viewed on log transformed axes. The vertical dashed line indicates a length of 0.7 mm which is referred to in the main text.

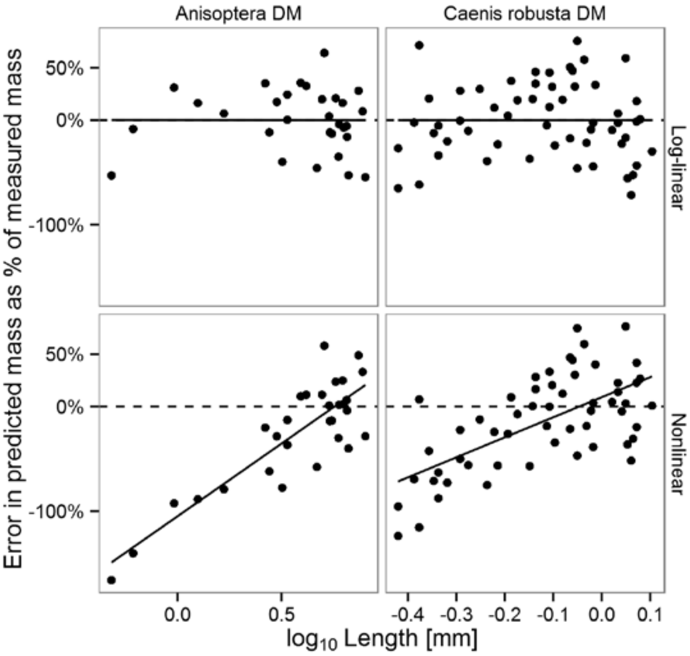

Figure 5-5: The relationship between length and percentage error in predicted mass of individuals for two example taxa, Anisoptera and *Caenis robusta*. Solid lines show the fitted regression models, dashed lines indicate the ideal situation with no relationship between length and % error. For the log-linear model the dotted line is obscured by the regression line. The nonlinear model results in very large proportional errors for small individuals.

In contrast, log-linear regression models gave a good fit to mass for both long and short individuals (e.g. Figure 5-4), with no significant ($p \geq 0.05$) relationships between prediction errors and length measurements (Figure 5-5). However, due to the log transformation, relationships gave biased estimates of total mass on the original untransformed scale (Figure 5-3). Estimated total mass was on average 7 % lower than the observed total mass (Figure 5-3) and for some taxa as much as 20 % too low. Applying the smearing factor almost completely removed this bias. After correction, estimated total sample mass was on average only 1 % lower than real total sample mass (Figure 5-3). We provide summary information for these fitted length-mass relationships and smearing factors in Table 5-1, corresponding plots are provided in Appendix VII.

Table 5-1: Parameters of the length-mass relationship $\mathbf{M}_{SE} = e^{\ln a + b \cdot \ln \mathbf{L}} \cdot SF$ for preserved benthic macroinvertebrates of combined lake, where M = mass [mg] and L = body dimension [mm]. The conversion indicates the used body dimension BL = Body length, HL = Head length, HW = head width, SBL = soft body length, SH = Shell height, SL = Shell length, SW = Shell width. AFDM = ash free dry mass, DM = dry mass, n = number of caps, length range = min. and max. length of body dimension, r^2 = coefficient of determination, SF = Duan´s smearing factor, SE = standard error, cut off = value under the screened outliers were deleted.

Taxon	Conversion	n	a	ln a ± SE	b ± SE	SF	r²	Length range	Cut off
Amphipoda									
Chelicorophium curv.	BL –› DM	34	0.0167	-4.09 ± 0.26	2.10 ± 0.23	1.07	0.76	1.43 - 5.08	
	HL –› DM	28	0.9067	-0.10 ± 0.36	2.16 ± 0.41	1.15	0.52	0.23 - 0.66	
Pontogammaridae	BL –› DM	93	0.0037	-5.59 ± 0.15	3.02 ± 0.07	1.05	0.96	2.22 - 17.34	2.00
	HL –› DM	86	0.8741	-0.13 ± 0.07	3.95 ± 0.15	1.13	0.89	0.46 - 2.14	
Bivalvia									
Dreissena poly.	SL –› DM	37	0.0201	-3.91 ± 0.13	2.16 ± 0.07	1.06	0.97	1.07 - 20.87	
Pisidium sp.	SL –› AFDM	58	0.0043	-5.45 ± 0.13	5.02 ± 0.14	1.08	0.96	1.13 - 4.31	1.10
	SL –› DM	52	0.1037	-2.27 ± 0.06	3.70 ± 0.06	1.01	0.99	1.13 - 4.31	
Diptera									
Ceratopogoninae	BL –› DM	6	0.0004	-7.92 ± 0.25	2.72 ± 0.10	1.00	0.99	7.32 - 16.95	
Chironomidae	BL –› DM	352	0.0009	-7.00 ± 0.11	2.59 ± 0.05	1.11	0.90	3.12 - 26.58	3.00
Chironomini	BL –› DM	119	0.0010	-6.93 ± 0.15	2.50 ± 0.06	1.10	0.93	3.13 - 26.58	3.00
Orthocladiinae	BL –› DM	25	0.0006	-7.40 ± 0.27	2.74 ± 0.15	1.03	0.94	3.26 - 9.53	3.00
Tanypodinae	BL –› DM	19	0.0097	-4.63 ± 0.18	1.44 ± 0.10	1.02	0.92	2.24 - 10.35	2.00
Tanytarsini	BL –› DM	46	0.0068	-5.00 ± 0.14	1.39 ± 0.10	1.04	0.83	2.06 - 9.52	2.00
Ephemeroptera									
Caenis sp.	HW –› DM	75	0.3706	-0.99 ± 0.05	3.28 ± 0.12	1.06	0.92	0.38 - 1.27	0.38
Caenis horaria	HW –› DM	7	0.4471	-0.80 ± 0.03	4.82 ± 0.22	1.00	0.99	0.79 - 1.23	0.75
Caenis robusta	HW –› DM	63	0.3565	-1.03 ± 0.06	3.26 ± 0.14	1.07	0.91	0.38 - 1.27	0.38
Cloeon dipterum	HW –› DM	25	0.5957	-0.52 ± 0.18	2.98 ± 0.27	1.15	0.84	0.24 - 1.12	
Gastropoda									
Anisus vortex	SW –› AFDM	8	0.0107	-4.54 ± 0.16	2.28 ± 0.13	1.01	0.98	1.51 - 7.62	
Bithynia tentaculata	SH –› AFDM	83	0.0596	-2.82 ± 0.09	3.16 ± 0.06	1.06	0.97	0.77 - 10.66	
Gyraulus sp.	SW –› AFDM	187	0.0129	-4.35 ± 0.06	2.67 ± 0.08	1.04	0.90	1.01 - 4.91	1.00
Gyraulus albus	SW –› AFDM	64	0.0199	-3.92 ± 0.06	2.33 ± 0.07	1.02	0.95	1.01 - 4.91	1.00
Gyraulus crista	SW –› AFDM	93	0.0105	-4.56 ± 0.08	2.76 ± 0.14	1.03	0.87	1.03 - 2.8	1.00
Hippeutis compla.	SW –› AFDM	58	0.0109	-4.52 ± 0.12	2.62 ± 0.14	1.05	0.88	1.26 - 4.13	1.25
Potamopyrgus anti.	SH –› AFDM	73	0.0251	-3.69 ± 0.08	2.07 ± 0.06	1.03	0.94	1.06 - 5.56	1.00
Valvata cristata	SW –› AFDM	22	0.0192	-3.95 ± 0.15	2.71 ± 0.21	1.05	0.89	1.03 - 3.06	1.00
Valvata piscinalis	SL –› AFDM	35	0.0130	-4.34 ± 0.13	3.38 ± 0.12	1.05	0.96	1.036 - 4.65	
Hirudinea									
Erpobdella sp.	BL –› DM	12	0.0090	-4.71 ± 0.14	2.37 ± 0.05	1.01	1.00	3.81 - 33.81	3.00

Taxon	Conversion	n	a	ln a ± SE	b ± SE	SF	r²	Length range	Cut off
Isopoda									
Asellus aquaticus	BL → DM	37	0.0049	-5.32 ± 0.22	2.83 ± 0.12	1.11	0.94	1.39 - 15.24	
Odonata									
Anisoptera	HW → DM	30	0.1708	-1.77 ± 0.12	3.11 ± 0.08	1.05	0.98	0.48 - 8.01	
Zygoptera	HW → DM	42	0.1146	-2.17 ± 0.08	3.13 ± 0.08	1.02	0.98	0.88 - 4.19	0.75
Ischnura elegans	HW → DM	12	0.1316	-2.03 ± 0.06	3.03 ± 0.07	1.00	1.00	1.02 - 3.81	
Trichoptera									
Athripsodes sp.	BL → DM	52	0.0045	-5.40 ± 0.21	2.44 ± 0.15	1.09	0.84	2.07 - 11.33	2.00
	HW → DM	19	5.4061	1.69 ± 0.15	3.60 ± 0.19	1.04	0.95	0.27 - 0.75	
Cyrnus sp.	HW → DM	48	0.6545	-0.42 ± 0.06	2.84 ± 0.17	1.07	0.86	0.44 - 1.5	
Cyrnus crenatico.	HW → DM	29	0.6486	-0.43 ± 0.06	2.92 ± 0.17	1.04	0.91	0.44 - 1.28	
Cyrnus flavidus	HW → DM	11	0.4276	-0.85 ± 0.24	4.44 ± 0.85	1.09	0.75	0.91 - 1.5	
Cyrnus trimacul.	HW → DM	8	0.7180	-0.33 ± 0.21	2.43 ± 0.49	1.12	0.80	0.45 - 1.37	
Ecnomus tenellus	HW → DM	32	0.8883	-0.12 ± 0.16	3.14 ± 0.22	1.05	0.92	0.34 - 0.89	0.25
Hydroptilidae	BL → DM	23	0.0019	-6.28 ± 0.59	2.52 ± 0.50	1.12	0.55	2.05 - 4.54	2.00
Orthotrichia sp.	BL → DM	9	0.0005	-7.62 ± 0.67	4.18 ± 0.66	1.02	0.85	2.34 - 3.38	2.30
Oxyethira sp.	BL → DM	16	0.0020	-6.23 ± 0.76	3.05 ± 0.68	1.05	0.59	2.47 - 4.01	2.40
Limnephilidae	HW → DM	78	1.6033	0.47 ± 0.06	4.01 ± 0.14	1.08	0.91	0.60 - 2.14	0.50
Anabolia furcata	HW → DM	24	1.7453	0.56 ± 0.09	4.12 ± 0.26	1.06	0.92	0.72 - 1.61	
Limnephilus sp.	HW → DM	73	1.5160	0.42 ± 0.06	3.90 ± 0.10	1.11	0.96	0.25 - 2.14	
Molanna angustata	BL → DM	12	0.0025	-5.99 ± 0.44	2.49 ± 0.23	1.06	0.92	2.79 - 12.87	
Mystacides long./ni.	BL → DM	14	0.0020	-6.23 ± 0.49	2.52 ± 0.29	1.10	0.86	2.50 - 10.47	0.30
	HW → DM	5	4.8419	1.58 ± 0.78	4.34 ± 0.98	1.06	0.87	0.39 - 0.6	0.30
Oecetis sp.	BL → DM	13	0.0078	-4.86 ± 0.35	1.75 ± 0.39	1.11	0.65	1.38 - 4.89	
	HW → DM	22	0.7949	-0.23 ± 0.13	2.61 ± 0.14	1.03	0.96	0.23 - 0.98	
Phryganeidae	BL → DM	17	0.0020	-6.21 ± 0.31	2.57 ± 0.13	1.04	0.96	5.01 - 23.28	4.00
	HW → DM	20	1.0435	0.04 ± 0.10	4.62 ± 0.21	1.09	0.97	0.54 - 2.38	0.50
Psychomyiidae	HW → DM	13	1.2502	0.22 ± 0.43	3.47 ± 0.60	1.14	0.75	0.35 - 0.84	0.30

Macroinvertebrate taxa lost between 16 % (Hirudinea, see Table 5-2) and 30 % (*Caenis* sp.) DM, or 14 % to 37 % AFDM during the 50-day preservation period. A likelihood ratio test indicated that there was no statistically significant difference between the ten taxa in the proportion of mass lost during preservation (F = 0.53, df = 9, P = 0.85) and therefore we also calculated overall conversion factors for lake macroinvertebrates based on all ten taxa (DM 22 %; AFDM 20 %).

Table 5-2: Conversion factors for masses ash free dry mass (AFDM) and dry mass (DM), allowing for calculation from preserved (pres.) mass to unpreserved (unpres.) mass. Lwr and upr give the lower and upper 95 % confidence interval for this conversion factor and rem% indicates the remaining mass after preservation, or after ignition.

	Pres. DM to unpres. DM					**Pres. AFDM to unpres. AFDM**					**Pres. DM to pres. AFDM**				
Taxa	n	Factor	lwr	upr	rem %	n	Factor	lwr	upr	rem %	n	Factor	lwr	upr	rem %
overall macroinvertebrates	68	1.29	1.10	1.50	77.6	66	1.25	1.07	1.46	79.9					
Amphipoda															
Corophiidae	4	1.39	1.13	1.71	72.0	4	1.46	1.16	1.84	68.4	8	0.74	0.70	0.78	73.8
Gammaroidea	7	1.25	1.07	1.46	79.9	7	1.37	1.16	1.63	72.9	14	0.70	0.67	0.73	70.1
Bivalvia															
Dreissena polymorpha	9	1.32	1.15	1.51	75.9	9	1.28	1.10	1.48	78.4	19	0.91	0.88	0.94	91.0
Diptera															
Ceratopogoninae	4	1.28	1.04	1.57	78.4	4	1.33	1.05	1.67	75.4	8	0.86	0.81	0.91	85.6
Chironomidae	7	1.26	1.07	1.47	79.6	7	1.25	1.05	1.49	80.0	14	0.80	0.76	0.83	79.8

	Pres. DM to unpres. DM					Pres. AFDM to unpres. AFDM					Pres. DM to pres. AFDM				
Taxa	n	Factor	lwr	upr	rem %	n	Factor	lwr	upr	rem %	n	Factor	lwr	upr	rem %
Ephemeroptera															
Caenis sp.	6	1.43	1.20	1.69	70.0	4	1.58	1.21	2.05	63.4	12	0.76	0.72	0.81	76.1
Hirudinea (*Erpobdella* sp., *Helobdella stagnalis*, *Piscicola* sp., *Theromyzon tessulatum*)	8	1.19	1.03	1.38	83.8	8	1.17	1.00	1.36	85.8	17	0.94	0.91	0.98	94.0
Isopoda															
Asellidae	6	1.24	1.05	1.47	80.5	6	1.27	1.05	1.53	78.7	12	0.69	0.66	0.72	69.1
Oligochaeta	5	1.42	1.18	1.71	70.6	5	1.42	1.16	1.74	70.3	10	0.66	0.62	0.69	65.5
Trichoptera (Hydroptilidae, Limnephilidae, *Molanna angustata*, *Mystacides* sp., Psychomiidae)	11	1.25	1.10	1.42	79.9	11	1.21	1.06	1.39	82.4	22	0.87	0.84	0.90	87.0

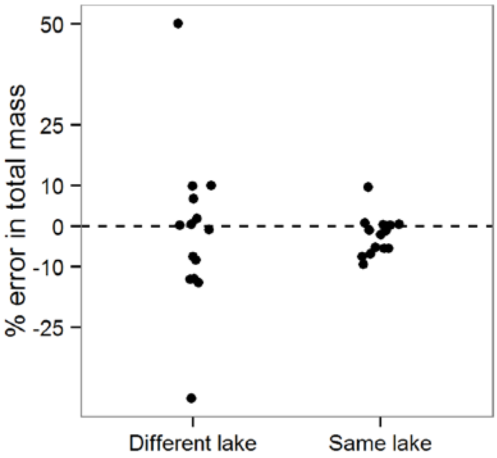

Figure 5-6: Percentage errors in estimates of total sample mass when length mass relationships estimated using individuals from a single lake were used to predict the mass of individuals from the same lake, and from a different lake. Comparisons were made for 7 taxa with at least 20 individuals sampled in each of two lakes.

There were five taxa that had sample sizes of 20 or more in multiple lakes. With the exception of two large outliers for the Chironomidae, whole sample mass predictions using lake-specific log-linear models and smearing correction factors had a similar range of error when they were applied to the same or to a different lake (Figure 5-6). Of the five taxa in common between this study and Méthot et al (2012), four of their length-mass relationships corresponded well with our data (Figure 5-7). Méthot's equation for Caenidae was a poor fit to our data, however, their relationship had an R^2 of 0.12.

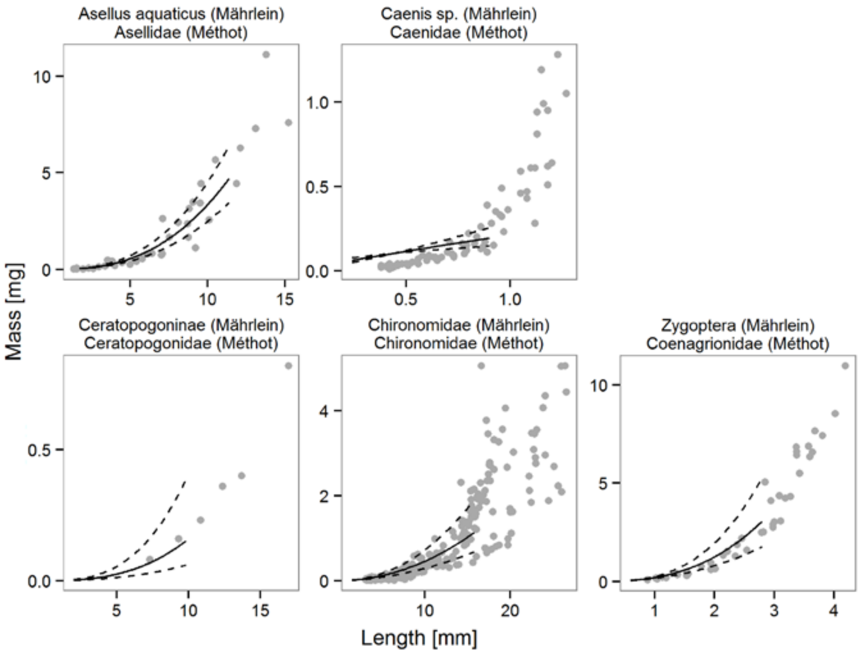

Figure 5-7: Length mass relationships estimated by Méthot et al. (2012) plotted over individuals sampled for this study. The solid lines show regression equations, including smearing factors, from Table 2 of Méthot et al. (2012). Dashed lines show ± 1 SE for the parameters of the equation. Grey points are length-mass data from this study.

5.4 Discussion

Our results clearly demonstrate that the establishment of length-mass relationships for lake macroinvertebrates relies on the appropriate processing of samples and sound statistical treatment of the data. We found that log-linear regression was much better than nonlinear regression for fitting power law relationships to macroinvertebrate length-mass data, because the underlying error structure is multiplicative. Although Xiao et al. (2011) found that some (17 %) of the 471 allometric relationships they tested were better characterized by additive error, their data included many "morphological and physiological allometries between organismal traits" that were unlike those between body dimensions and mass. We expect multiplicative error to be the general case for length-mass relationships of macroinvertebrates. Xiao et al. (2011) demonstrated that models that assume the wrong error structure produce biased estimates of the parameters a, and b, of the power law function (Eq. 1) and result in curves that are a poor fit over some range of the data. In our case, using nonlinear regression would result in a poor fit to the small individuals in a sample and very large proportional errors in their mass estimates (Figure 5-4 and Figure 5-5).

Although log-linear regression provided a good fit to the length-mass relationships along the entire range of body lengths, the mass predictions themselves are slightly biased because it is the geometric mean, rather than the arithmetic mean, that is being predicted. We found mass to be underestimated by an average of 7 %, but the smearing factor (Duan 1983) was very effective at removing this bias. We estimated smearing factors of between 1.00 (BL-DM Ceratopogonidae) and 1.15 (HW-DM *Cloeon dipterum*, Ephemeroptera (Linnaeus 1761)), underestimation was more pronounced, and hence smearing factors larger, for relationships with more scatter (lower R^2). Thus the use of a correction factor will be more important for taxa with more variable body forms. For example, in comparison to Arthropoda, shelled Mollusca are not so variable in their body form due to their stable inflexible shell and thus received low smearing factors (<1.08 in all our cases). The study of Méthot et al. (2012) is the only other study we know to have used the smearing factor for benthic freshwater macroinvertebrate length-mass relationships, and they too found that smearing factors for Mollusca (<1.12) were relatively low compared to those for other taxa in their study.

The smearing factors in Table 5-1 should be applied when using our estimated length-mass relationships to predict mass from the lengths of newly measured organisms. However, since the value of a smearing factor depends on the distribution of residuals in a specific regression, it is specific to that estimated length-mass relationship. In other words, our smearing factors are only valid for their corresponding relationship published in this study, and they cannot be used to correct predictions from other, previously published, length-mass relationships. Likewise the smearing factors in Méthot el al. (2012) only apply to the relationships in that study.

The length-mass regressions in this study were established with specimens preserved in 70 % ethanol for at least 50 days. This duration is recommended by Leuven et al. (1985) if processing of the samples within two days after collection is not possible. It allows stabilization of length and mass changes (e.g. Leuven et al. 1985, Lasenby et al. 1994, Edwards et al. 2009) and enables comparable length-mass regressions to be established on specimens preserved for 50 days or longer. If estimates of unpreserved mass are desired then a preservation correction factor should be applied to convert estimated preserved DM to unpreserved DM, or preserved AFDM to unpreserved AFDM respectively. We provide conversion factors for 10 macroinvertebrate taxa that correspond to a remaining mass of between 70 % and 84 % after preservation. These are consistent with the majority of published values. For example, Leuven et al. (1985) observed a remaining DM of 80 % for *Erpobdella octoculata* (Hirudinea) (Linnaeus, 1758), 80 % for *Glyptotendipes* sp. (Chironomidae) and 84 % for *Asellus aquaticus* (Crustacea) (Linnaeus, 1758) after three months preservation with ethanol. Although existing studies report preservation effects for single taxa, we did not find large differences in the size of the preservation effect between our 10 studied taxa. Therefore we provide an overall preservation conversion factor (DM = 1.288, AFDM = 1.252), estimated using all 10 taxa, for use on similar taxa that have been weighed without shells.

Comparing the two potential sources of error that we have quantified, the bias due to log transformation was relatively small, a 7 % underestimate on average, compared with a bias of 20 - 30 % if the effects of preservation were not accounted for. Other errors may be introduced if the length measurement is not performed on precisely the same body part as done here (Figure 5-1), or if the regressions are applied to individuals whose lengths lie outside range of those used to fit the models (Table 5-1). Furthermore it is recommended to use the lowest taxonomic level possible, because generalization may lead to inaccurate estimates (Benke et al. 1999, Méthot et al. 2012). However, for groups such as Chironomidae, identification is often only feasible to subfamily (e.g. Orthocladiinae and Tanypodinae) or tribe (e.g. Tanytarsini and Chironomini), and therefore regression equations from groups can also be valuable. We therefore provide both species level regressions and some for higher taxonomic groupings.

Our ability to characterise between-lake variation in length-mass relationships was limited, because for most taxa our data came from just two lakes. For those comparisons we could make, prediction errors were only slightly larger between lakes than within a lake. The one exception was for the Chironomidae, but in this case the large difference was likely due to a difference in the species composition, and so the error had more to do with using relationships for higher taxa, than it did with using a relationship from a different location. The similarity of the length-mass relationships between the three lakes allowed us to establish combined lake regressions. Since all three lakes are located in Central Europe it is likely that they can be used for most lakes with similar characteristics in this region.

A comparison of our length-mass relationships with regressions provided in the literature was only possible for those in Méthot et al. (2012), which were estimated using species from the large lowland Lake Saint-Pierre in the cool temperate zone of

Québec, Canada. While the relationship for Caenidae provided by Méthot et al. (2012) deviated substantially from our *Caenis* sp. data, we cannot be sure that the species involved were the same, and the uncertainty of measuring the broadest section of the head capsule in Méthot et al. (2012) may have contributed to the very low R^2 (0.12) they obtained. In contrast, when the taxon was precisely identified, our data compare well with the equations of Méthot et al. (2012). This suggests that our relationships can be quite confidently transferred to lakes in other geographic regions with similar environmental conditions, such as the Central European lowlands (covering parts of Germany, Poland, Denmark, Netherlands and Belgium) or the temperate lowland zone of North-America.

However, care should be taken when transferring length-mass relationships between locations with different physical characteristics. Baumgärtner & Rothhaupt (2003) found intra-specific differences in length-mass relationships between individuals living in stream versus littoral habitats of Lake Constance. They concluded that differences were explained by differences in the type of flow velocity between the sites. We would advocate that our regressions should not be applied to ecosystem with fundamentally different physical characteristics such as climate or flow velocity that influence the growth of macroinvertebrates. Further research to estimate the variability of length-mass relationships for the same taxa between lakes, and between habitats with different characteristics, would be valuable and lead to a better understanding of intraspecific variation in allometric relationships.

In summary, our study provides 52 length-mass relationships for littoral macroinvertebrates sampled from three Central European lakes, together with correction factors for the bias induced by log transformation and the effects of preservation in ethanol. These relationships can be used to obtain rapid estimates of body mass when studying ecosystems functioning of lakes (Rigler & Downing 1984). Furthermore, we show that log-linear regression, with smearing correction factors, is superior to nonlinear regression for those who need to establish length-mass relationships for new taxa and or regions.

6 Extended summary and synthesis

6.1 Extended summary

Rationale and research aims

The WFD came into force in 2000 to provide non-legally binding and practical guidance documents to protect the waters of Europae and to achieve a good ecological state by 2015 (European Commission 2000). Many lake water bodies will not achieve this goal in the coming years. This is, among other things, because the assessment and improvement of hydromorphological conditions of lakeshores has been neglected as an important component ensuring the ecological integrity of lake ecosystems (Ostendorp et al. 2004). Lakeshores are of ecological significance for the functioning of the whole lake ecosystem (Schmieder 2004, Vadeboncoeur et al. 2002).

Although the knowledge about the effects of lakeshore modification on macroinvertebrates has expanded in recent years, a thorough understanding is missing about the functioning of macroinvertebrates. Furthermore, there is no study that has examined the impact of lakeshore modification on macroinvertebrates in relation to macrophytes, although macrophytes are known to be important habitats for macroinvertebrates. Finally, no systematical evaluation of water depth and seasonal influence on the effect of lakeshore modification on macroinvertebrate community structure has been carried out. Filling these knowledge gaps enlarges the mechanistic understanding of lakeshore modification effects on the structure and functioning of macroinvertebrate communities and contributes to the development of successful lakeshore assessment tools and management activities.

In this thesis, I examined the effects of lakeshore modification on macroinvertebrate communities in relation to water depth and season (Chapter 2), observed the effects of different types of lakeshore modifications on macrophytes in relation to macroinvertebrate communities (Chapter 3), and determined the effects of lakeshore modifications on the ecological functioning of macroinvertebrates at different spatial scales (habitat, depth zone, whole lake ecosystem) by estimating secondary production (Chapter 4). Seven hypotheses (see Chapter 1.5) were tested with macroinvertebrate data from a field survey along eight transects at the lowland Lake Scharmützelsee. The eight transects presented three shore types (natural, marina and beach) and were sampled between April and November 2011 in three depth zones (upper littoral, middle littoral and upper profundal). Figure 6-1 summarizes the main results gained from testing the seven hypotheses in Chapter 2, 3 & 4.

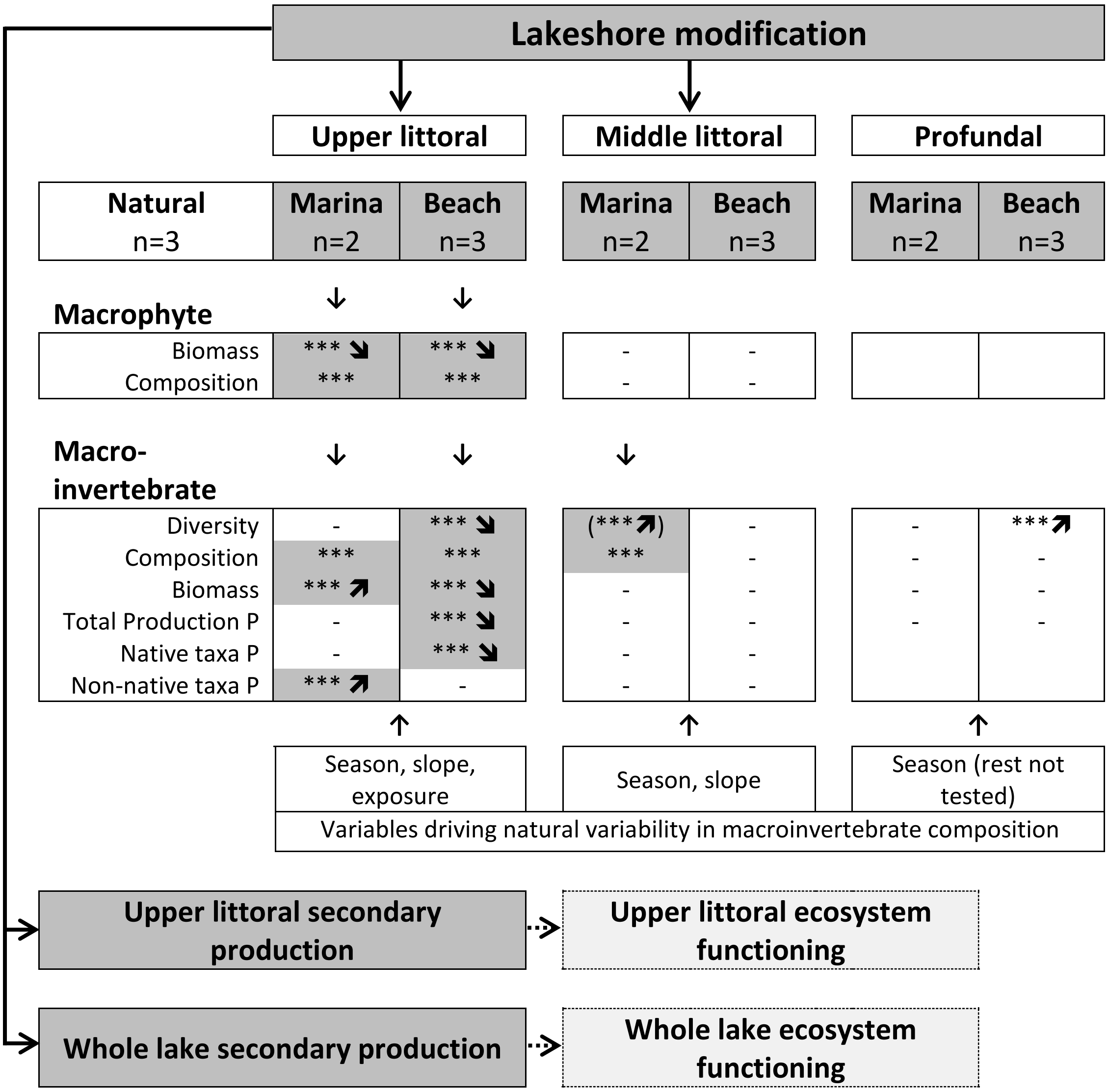

Figure 6-1: Overview of the main results obtained in this thesis. Legend: → observed effect (dotted = derived effect), grey = effect attributable to lakeshore modification, *** significantly different from natural, - not significant different from natural, empty = not tested, () differing results obtained for permutation ANOVA in chapter 3 and effect size in chapter 4.

Influence of water depth and seasonal variation on the effect of lakeshore modification on macroinvertebrate community structure

There is an increasing number of studies showing that lakeshore modification results in a loss of habitat-heterogeneity, followed by adverse effects on diversity and community composition of littoral macroinvertebrates accompanied by a homogenization process across Europe (e.g. Brauns et al. 2007 a, Brauns et al. 2011, McGoff et al. 2013 a). Additionally, recent studies have emphasized littoral macroinvertebrates to be useful indicators for the assessment of hydromorphological conditions of lakeshores and developed macroinvertebrate-based multimetric indices (e.g. Solimini & Sandin 2012, Miler et al. 2013, Urbanič 2014). But a systematic evaluation as to whether the effect of human lakeshore modification on littoral macroinvertebrates varies with season and between depth zones is missing, although these natural factors may confound the response of macroinvertebrates to hydromorphological impairments.

Macroinvertebrates from natural and modified shores (marinas and beaches) were sampled in three depth zones over four months between April and November 2011. The examination confirmed **hypothesis 1** that the effect of human lakeshore modification on macroinvertebrates systematically differs among water depth zones. The effect of lakeshore modification on macroinvertebrate diversity and community composition was most pronounced in the upper littoral but decreased with water depth in the studied lowland lake (Figure 6-1). This result supports the findings by Brauns et al. (2007 a), who showed that lakeshore modification acts locally due to the effects on habitat-heterogenity. In this study, habitat-heterogeneity of the upper littoral was presumably reduced as a consequence of alteration in macrophyte biomass that was significantly lower at modified lakeshores (Figure 6-1).

In the middle littoral, the effect of lakeshore modification was less important and no longer present in the profundal zone. The result is not surprising, because macroinvertebrates of the profundal zone have long been used as indicators for the trophic state of a lake (e.g. Thienemann 1931, Saether 1979). Hence, from the results of this study together with the results from Free et al. (2009) and Pilotto et al. (2012), it can be concluded that the middle littoral seems to be a transitional zone, where macroinvertebrates respond to different human pressures, which limits a stressor-specific assessment of lake ecosystems.

In accordance to **hypothesis 2**, the effects of human lakeshore modification on upper littoral macroinvertebrate diversity and composition were shown to be independent from season, because seasonal effects were less important than effects of the shore type (Figure 6-1). Hence, the seasonal influence did not weaken the strong effects of lakeshore modification on macroinvertebrates of the upper littoral zone. Conversely, in the middle littoral and even stronger in the profundal zone, seasonal variability was more important in structuring macroinvertebrates communities than different shore types (Figure 6-1). The varying influence of season on macroinvertebrates among depth can be explained by a decrease in habitat-heterogeneity with increasing depth, because spatial heterogeneity positively influences community stability, which was shown to reduce temporal variability (Brown 2003).

Effect of lakeshore modification on littoral macrophytes and macroinvertebrates

Human lakeshore modification was shown to adversely affect littoral macrophytes and macroinvertebrates in previous studies (e.g. Bryan & Scarnecchia 1992, Radomski 2006, Brauns et al. 2007 a, McGoff et al. 2013). Macrophytes are well known to be an important habitat for macroinvertebrates (e.g. Cyr & Downing 1988, James et al. 1998, Thomaz & da Chuna 2010) and were proposed to be potential indicators for structural degradation of lakeshores (Stelzer 2003, Lyche-Solheim et al. 2013). This suggests that the effect of lakeshore modification on macroinvertebrates may primarily depend on adverse effects of lakeshore modification on macrophytes. So far there is no study that has explicitly addressed the consequences of different types of lakeshore modification on macrophytes and macroinvertebrates. Thus, littoral macrophytes were sampled together with littoral macroinvertebrates to observe the relation between both organism groups and to test if macrophytes are an important driving factor in structuring macroinvertebrate communities at modified lakeshores.

The study demonstrated that the biomass of macrophytes and the diversity of macroinvertebrates were highest in the upper littoral, but simultaneously the effects of lakeshore modification were locally restricted and therefore most pronounced in this depth zone. Upper littoral macrophytes were reduced in biomass and altered in community composition at marinas and beaches compared to natural sites (Figure 6-1). These results are in accordance with previously published studies on macrophytes showing detrimental effects particularly on emergent but also on submerged macrophytes (e.g. Bryan & Scarnecchia 1992, Radomski & Goeman 2001, Elias & Meyer 2003, Jennings et al. 2003). Slightly different results were obtained for upper littoral macroinvertebrates, which showed significant lower diversity at beaches but not at marinas compared to natural sites. Contrary, community composition differed significantly between all three shore types, but macroinvertebrate composition at marinas was less distinct from natural sites than beaches (Figure 6-1).

The results highlight the importance of the upper littoral zone as a habitat for many aquatic organisms and show the high susceptibility of this depth zone against varying effects of lakeshore modification. However, the study also confirmed that lakeshore modification not necessarily causes a detrimental structural degradation, but can also lead to new habitats (here at marinas) supporting a diverse but compositional different macroinvertebrate community in comparison to natural sites. This finding complements previous studies that showed that artificial structures such as ripraps used to stabilize lakeshores can substitute complex natural habitats (Engel & Pederson 1998, Brauns et al. 2007 a, McGoff et al. 2009).

In the middle littoral, effects of lakeshore modification became only statistically important with regard to community composition of macroinvertebrates at marinas (Figure 6-1). This can be attributed to the large constructions of the marinas extending down to the middle littoral.

Hence, the examination confirmed **hypothesis 3** predominantly for the upper littoral that macrophyte and macroinvertebrate communities vary between different types of lakeshore modification.

As a consequence, differences in community composition of macroinvertebrates were mainly explained by macrophyte biomass. Hence, according to **hypothesis 4** for both depth zones, macrophytes were shown to be the most important environmental factor structuring macroinvertebrate communities. The environmental variables wind exposure and slope also contributed to explain the variability of macroinvertebrate communities, but did not contribute to describe differences among shore types (Figure 6-1). Wind exposure and slope are known to influence substrate stability and sediment composition and thus macrophyte and macroinvertebrate communities (e.g. Rasmussen & Rowan 1997, Cyr 1998, Tolonen et al. 2001, Duarte & Kalff 1986, Azza et al. 2007).

Effect of lakeshore modification on secondary production of macroinvertebrates

Lakeshores perform many ecological functions resulting from their complex and highly structured environment due to the fact that they are boundary regions between land

and water (e.g. Ostendorp et al. 2004, Schmieder 2004, Strayer & Findlay 2010). In accordance to the habitat-heterogeneity hypothesis, the littoral zone supports a diverse and productive macroinvertebrate community (e.g. Heino 2000, Babler et al. 2008, Vadeboncoeur et al. 2011). Since secondary production is a function of energy and material flow through the food web, it can be used as a proxy to determine the functioning of macroinvertebrates in ecosystems (Downing 1984, Benke 1993, Butkas et al. 2010, Dolbeth et al. 2012). So far, there is no study that has examined the effect of lakeshore modification on littoral secondary production and the consequences for the depth-production relationship and whole lake secondary production.

Macroinvertebrates were sampled at the same sites as described above. All eight study sites were sampled in April, July, September and November 2011 and four of the eight sites were additionally examined in May, June, August and October 2011.

This study demonstrated for the first time that lakeshore modification significantly reduced total secondary production at beaches (Figure 6-1). Hence, **hypothesis 5** can be accepted for beaches, where secondary production was lower as a consequence of lower habitat-heterogeneity. Habitat-heterogeneity was described as macrophyte biomass and habitat diversity, and frequent disturbance of the sediment caused by wind exposition with the last one enhanced by human trampling at this shore type. Lower secondary production at sites with low macrophyte occurrence was also shown for intertidal macroinvertebrate communities (Dolbeth et al. 2003). At upper littoral marinas, artificial substrates such as sheet pilings and piles may partly substitute the loss of macrophytes habitats with the result that marinas did not differ from natural sites in the upper littoral zone (Figure 6-1). Thus, in accordance with other studies, habitat-heterogeneity was the most driving factor structuring littoral macroinvertebrate communities (e.g. Heino 2000, Tolonen et al. 2001, Johnson & Goedkopp 2002, Brauns et al. 2007 b, McGoff & Sandin 2012).

However, an effect of anthropogenic disturbance was also found at marinas when examining the contribution of non-native taxa and feeding types to secondary production. At both modified sites, native and non-native taxa contributed almost equally to total secondary production while native taxa only dominated at natural sites (~85 %) in this depth zone (Figure 6-1). The displacement of native taxa by non-native taxa with different traits changes the energy flow through the food web, has also been found in other studies (e.g. Strayer et al. 1999, Hall et al. 2006, Sousa et al. 2008, Ozersky et al. 2012). In addition, the results highlight that secondary production is a more sensitive metric than structural measures (diversity and biomass) for detection of ecosystem disturbances, which is in accordance with other studies (Whiles & Wallace 1995, Lugthart & Wallace 1992, Valentine-Rose et al. 2011).

Furthermore, the results for beaches confirmed **hypothesis 6** that the depth-production relationship can be altered as a consequence of lakeshore modification. At beaches, secondary production was lower in the upper littoral zone than in the middle littoral zone. The depth-production relationship did not change at marinas and was similar to that of the natural sites (Figure 6-1).

Finally, different scenarios based on the upscaling of site-specific production estimates to depth zones and the whole lake level proofed that site-specific effects of lakeshore modification on littoral secondary production affect secondary production of the entire upper littoral and whole-lake ecosystem (**hypothesis 7**) (Figure 6-1). Since total secondary production did not differ between natural sites and marinas, the effect in the scenarios only became apparent with an increasing proportional amount of the shore type beach on the area of the upper littoral zone. Assuming the entire lakeshore shows the characteristics of the examined beaches, the secondary production would be 68 % lower in the upper littoral and 22 % lower for the whole lake. However, changes in the energy and material flow across habitat boundaries originating from macroinvertebrates can lead to an altered functioning of the whole lake ecosystem, whether production decreases in general or caused by compositional changes in macroinvertebrate communities, for example, by increased production of non-native taxa (Figure 6-1).

In conclusion, Chapter 4 demonstrated that adverse effects of lakeshore modification on secondary production were locally restricted and therefore most pronounced in the upper littoral. Hence, lakeshore modification mainly characterized by a loss in habitat-heterogeneity alters the functioning of macroinvertebrates at local scale but also at a whole lake level. These results emphasize the importance of macroinvertebrates in connecting trophic pathways across habitats (Covich et al. 1999, Vadeboncoeur et al. 2002), essential for the functioning of whole lake food webs, for example, by providing a substantial amount to the fish diet (Vander Zanden & Vadeboncoeur 2002, Vander Zanden et al. 2006, Sierszen et al. 2014). A broad picture about changes in the functioning of macroinvertebrate can thereby only be detected when considering not only total secondary production but also the role of compositional changes in non-natives species and functional groups.

However, since secondary production is merely a proxy for energy and material transfer through the food web, future studies should complement the results obtained in this thesis by examining fish production and matter fluxes between trophic compartments as already suggested by Brauns et al. (2011). This will truly allow to quantify the effect of lakeshore modification on whole lake ecosystem functioning.

6.2 Synthesis

In the last two decades, the intrinsic importance of lakeshores and their central meaning for the whole lake ecosystem has been recognized (e.g. Engel & Pederson 1998, Schmieder 2004, Vadeboncoeur et al. 2002). In Europe particularly, the WFD (European Commission 2000) stimulated research activities in the littoral zone to broaden the knowledge for the development of successful assessment methods for lakeshores (e.g. WISER project, http://www.wiser.eu). This thesis highlights the importance of lakeshores, especially of the upper littoral zone, for biodiversity and sheds light on the following topics not included in previous studies that aimed to develop sound assessment methods based on macroinvertebrates:

- Influence of water depth on the outcome of lakeshore assessment methods
- Influence of season on the outcome of lakeshore assessment methods
- Macrophytes as an additional component for lakeshore assessment
- Structural- versus functional measures

Finally, the transferability to other shore types and lake ecosystems is discussed.

Water depth determines the effect of lakeshore modification on macroinvertebrates

Most of the present lakeshore assessment methods focus on the development of multimetric indices based on (eu)littoral macroinvertebrates (e.g. Miler et al. 2013, Urbanič 2014). This thesis confirms this approach of using upper/(eu)littoral macroinvertebrates for the assessment of lakeshore hydromorphology. I could demonstrate for the first time that the effects of lakeshore modification on diversity, composition and secondary production were most pronounced in the upper littoral and decreased with increasing depth (Chapter 2 and 4). In addition, this thesis could show that lakeshore modification adversely affected upper littoral macrophyte biomass and community composition (Chapter 2, 3 & 4). Hence, in the upper littoral zone, human-driven modification had the strongest impacts.

Hydromorphological changes along with a reduction of habitat-heterogeneity expressed as macrophyte biomass and habitat diversity had a particularly strong local impact on the upper littoral macroinvertebrate community. One consequence is an altered depth-production relationship demonstrated for the modified shore type beach. At beaches, lower secondary production was found in the upper littoral zone than in the middle littoral, although macroinvertbrate productivity is generaly highest in the upper littoral. Since the upper littoral zone was shown to contribute significantly to whole lake secondary prodcution, lower secondary production as a result of lakeshore modification in this depth zone would affect the functioning of the entire lake ecosystem.

Season does not determine the effect of lakeshore modification on macroinvertebrates

The effect of sampling season was emphasized as an uncertainty of available methods assessing lakeshore modification based on structural measures of macroinvertebrates (e.g. Miler et al. 2013), because of inter-annual variation in macroinvertebrate communities. Seasonal variations mainly occur as a result of population dynamics from aquatic insects and the influence of abiotic parameters that change over time (e.g. Scheifhacken et al. 2007, Little 2008). Autumn and spring were the preferred sampling seasons in most studies, because highest diversities and abundances of macroinvertebrate are usually found in these two seasons in the temperate zone, due to univoltine life cycles of aquatic insect taxa with the emergence period in summertime (Little 2008). This procedure can be maintained, because this thesis demonstrated that lakeshore modification stronger affected upper littoral macroinvertebrates than season (Chapter 2). Thus, a single seasonal sampling independently of sampling time is sufficient to capture the compositional differences of littoral macroinvertebrate communities associated with human lakeshore modification.

Secondary production as an additional measure to assess lakeshore hydromorphology (Chapter 4) relies on the sampling season(s) (Beukema & Dekker 2013). Future research should make the effort to find the optimal season(s) for lakeshore assessment, based on secondary production, to reduce sampling and laboratory work. This would be practicable when using empirical models such as the ANN model, developed to predict secondary production from one sampling date (Brey et al. 1996, Brey 2012, Beukema & Dekker 2013).

Macrophytes as an additional component for lakeshore assessment

I showed that community composition of macrophytes and macroinvertebrates differed between all three studied shore types. Contrary, the univariate measures macrophyte biomass and macroinvertebrate diversity were differently affected by lakeshore modification. Macrophyte biomass significantly varied between natural and modified sites, but not between modified sites. Macroinvertebrate diversity significantly differed between modified sites and between beaches and natural sites, but not between natural sites and marinas. Hence, macrophytes should be considered as an additional component for the assessment of lakeshore modifications to complement multimetric indices based on (eu)littoral macroinvertebrates. This was proposed by Lyche-Solheim et al. (2013), because macrophytes indicate degradations in the littoral zone. A promising approach to assess structural degradation using submerged macrophytes was already provided by Stelzer (2003) for Germany. Contrary, an assessment only based on helophytes was not promising, because the natural variability of these plants was too high (Bryan & Scarnecchia 1992, Stelzer 2003) resulting in contrasting response to chemical and structural pressures (Stelzer 2003). Hence, future research could refine the approach developed for submerged macrophytes by Stelzer (2003), and distinguish indication of structural deficits from trophic state indication. However, a drawback of using macrophytes to assess lakeshore modification is that they cannot be applied for lakes without macrophytes.

Structural versus functional measures

I demonstrated that lakeshore modification resulted in lower secondary production where diversity was also low (beaches). Contrary, secondary production was not affected by lakeshore modification at sites with similar high diversity as on natural sites (marinas). This is in accordance to the diversity-production hypothesis generally stating that with increasing diversity, productivity is growing (e.g. Loreau et al. 2001, Hooper et al. 2005).

In addition, effect size of total secondary production was higher than for the structural measures of diversity and biomass. This confirms that secondary production is a more sensitive measure of hydromorphological changes of lakeshore (Chapter 4) compared to the structural measures diversity and biomass. A higher sensitivity of secondary production compared to structural measures in detecting ecosystem changes was also found in previous studies (e.g. Whiles & Wallace 1995, Valentine-Rose et al. 2011).

It has to be stressed that the structural measure macroinvertebrate composition better reflected the effect of the two studied modified shore types on macroinvertebrate communities (Chapter 3) than total secondary production (Chapter 4). Nevertheless, secondary production is a major path of energy and material flow through the ecosystem and thus reflects many ecosystem processes. It integrates more information on human disturbances than structural measures. Hence, secondary production should be included as an additional measure in available macroinvertebrate-based assessment methods to assess the functioning of ecosystems. The use of functional measures to complement structural-based methods to assess the ecological integrity of ecosystems was suggested previously. Incorporating both measures give a more complete picture of ecosystem integrity (e.g. Sandin & Solimini 2009, Benke & Huryn 2010, Dolbeth et al. 2012).

In addition to total secondary production, approaches that account for the proportional amount of functional groups to total production should be included in lakeshore assessment methods. Human disturbances do not necessarily cause a change in total diversity or total secondary production but in the proportional amount of non-native taxa and feeding types to total production. This was shown for the studied marinas (Chapter 4). Buffgani & Comin (2000) could demonstrate that the estimation of secondary production for dominant or indicator groups was effective in assessing the ecological integrity of mountain streams. Approaches that include the concept of functional groups would allow getting a more comprehensive overview into the changes of ecosystem functions caused by human impairments. Functional groups help to detect these changes due to their specific functional traits that respond differently to ecosystem changes (e.g. Loreau et al. 2001, Hooper et al. 2005, Heino 2005 & 2008).

The implementation of secondary production as an integrative measure in assessment methods was not feasible in the past due to its high resource requirements. However, new methodological advances and improved understanding of lakeshore modification on littoral macroinvertebrate communities, allows a reconsideration of this principle. For example, the empirical ANN model (Brey 2012) applied in this thesis permits a relatively fast determination of secondary production. Only biomass and average individual body mass is needed (apart from annual temperature) to estimate secondary production using the ANN model in addition to community composition and abundances required for the WFD (European Commission 2000) in any case. Total biomass per taxon can simply be weighted and divided by the number of the taxa to achieve average individual body mass. Of course this is an extra step, but in respect to the foregone laborious sorting and identifying of taxa, not a huge expenditure of time (Tolonen & Hämäläinen 2010). The underestimation of production estimates from the ANN model or other models based on least squares fitting should be solved by implementing a correction factor for back-transformation from geometric to arithmetic mean (Hayes & Shonkwiler 2006). Solving these issues clears the way for using secondary production in lakeshore assessment methods.

In this thesis, the effects of lakeshore modification on macroinvertebrates were evaluated comparing the two shore types marina and beach with natural sites. Especially for beaches the results are similar to those obtained in other studies (Brauns et al. 2007 a, Mastrantuono et al. 2015) and reflect the low ecological value of these sites due to the loss of habitat and physical instability of the substrate. The studied marinas feature characteristics often described as hard-altered sites, which circumscribe structures such as concrete walls or sheet pilings. In accordance to the studied ripraps of Brauns et al. (2007 a) and the hard-altered sites of Mastrantuono et al. (2015), the habitat value of this shore types was less affected, resulting in weaker effects of lakeshore modification on the macroinvertebrate community. However, it is not simply possible to transfer the findings of the studied marinas to other sites assigned to marinas or hard-altered, because the specific characteristics found at the two marinas studied in Lake Scharmützelsee. For example, the existence of wave breakers and the presence of submerged macrophytes might not be found at other sites within the lake or in other lakes. However, by using habitat-heterogeneity as a major driving factor, the results of this thesis can be applied to others apart from the studied shore types. Independently of the shore type, high habitat-heterogeneity should stimulate diverse and productive macroinvertebrate communities, whereas low habitat-heterogeneity should lead to lower macroinvertebrate diversity and secondary production.

The findings of this thesis were only observed from Lake Scharmützelsee located in the Central European region. The study of Miler et al. (2013) showed that the composition of macroinvertebrate communities is distinct between the four geographical regions Western (IR/GB), Northern (S/FIN), Southern (IC/IN) and Central Europe (D/DK). However, the effects of lakeshore modification on macroinvertebrates were similar; the metrics needed only be adjusted to the geographical regions. In general, previous studies in Europe were conducted at many lakes with different trophic level, latitudes and altitudes (e.g. Brauns et al. 2007 a, Urbanič et al. 2012, Miler et al. 2013, Mastrantuono et al. 2015). All these studies showed similar effects of lakeshore modification on macroinvertebrates and identified appropriate indicator species. In addition, it was demonstrated for 46 lakes across Europe that habitat-alteration and near-shore land-use pressure homogenizes littoral macroinvertebrate communities (McGoff et al. 2013 a). Hence, the results of this thesis seem to be transferable to a wide range of lakes although outside from the Central European region.

Different findings might be expected for natural lakeshores without macrophytes. The habitat-heterogeneity at the shores of Lake Scharmützelsee was mainly provided by macrophytes. Hence, adverse effects of lakeshore modification on macrophytes were transferred to macroinvertebrates. In natural lakes with fewer or no macrophytes, habitat-heterogeneity may be provided by other structures such as stones or coarse woody debris. In such lakes, the reduction of habitat-heterogeneity can but must not influence macroinvertebrate diversity and community composition (De Sousa et al. 2008, Helmus & Sass 2008).

In a nut-shell, this thesis gives a mechanistic understanding about the effects of lakeshore modification on structure and secondary production of macroinvertebrates in lake ecosystems. For the first time, it could be demonstrated that local effects of lakeshore modification on secondary production can translate into alterations of the functioning of macroinvertebrates at whole lake ecosystem level. Furthermore, this thesis clarifies that upper littoral macroinvertebrates should be used for assessing the hydromorphology of lakeshores. In addition, it was shown that a single seasonal sampling is sufficient to capture the compositional differences of macroinvertebrate communities associated with human lakeshore modification. Finally, it was emphasized that secondary production as a functional measure is more sensitive in detecting hydromorphological alterations than the structural measures diversity or biomass. Secondary production should therefore be included in existing lakeshore assessment methods. In addition, it is recommended to consider not only total secondary production but also secondary production of functional groups.

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9 Appendix

Appendix I

Total macrophyte biomass and habitat diversity per month. B = beach, M = marina, N = natural, E = east side, W = west side, 4 = April, 7 = July, 9 = September, 11 = November, MP = Macophyte, DW = dry weight, HabDiv = Habitat diversity.

sampling site	Month	Upper littoral MP DW g m²	HabDiv	Middle littoral MP DW g m²	HabDiv
BE1	4	1.00	1.22	19.56	1.54
	7	10.03	1.60	221.44	1.86
	9	3.96	1.38	32.06	1.73
	11	2.41	1.31	2.66	1.09
BE2	4	2.11	1.57	1.00	1.00
	7	22.47	2.21	251.51	1.82
	9	23.09	2.22	182.26	1.92
	11	1.00	1.48	1.00	1.00
BW1	4	1.00	1.00	1.00	1.00
	7	1.00	1.00	156.30	1.95
	9	1.00	1.00	3.56	1.12
	11	1.00	1.00	1.00	1.00
ME1	4	4.74	1.71	1.00	1.00
	7	61.55	2.48	285.49	1.77
	9	19.34	2.15	21.73	1.58
	11	2.21	1.58	1.00	1.00
MW1	4	16.91	2.10	1.00	1.00
	7	181.28	2.21	79.81	1.99
	9	52.84	2.46	85.56	1.99
	11	14.01	2.03	1.00	1.00
NE1	4	129.19	1.93	1.00	1.00
	7	136.02	2.18	39.63	1.81
	9	177.98	2.22	42.77	1.83
	11	124.94	2.03	1.00	1.00
NE2	4	178.99	1.98	1.00	1.00
	7	283.40	2.10	36.98	1.78
	9	179.66	2.11	5.42	1.19
	11	169.65	1.38	1.00	1.00
NW1	4	90.58	1.76	1.00	1.00
	7	60.77	1.60	65.32	1.95
	9	118.30	2.03	34.09	1.75
	11	91.30	1.98	10.64	1.35

Appendix II

Average individual number per square meter and standard deviation for macroinvertebrate taxa of the three studied shore types per depth zone. Number of macroinvertebrates was averaged over season per site and then averaged per shore type.

	Upper littoral			Middle littoral			Profundal		
Taxon	**Natural**	**Marina**	**Beach**	**Natural**	**Marina**	**Beach**	**Natural**	**Marina**	**Beach**
Amphipoda									
Chelicorophium curvispinum	82 ± 41	172 ± 192	95 ± 79		42 ± 8	21 ± 3			
Dikerogammarus haemobaphes	83 ± 40	172 ± 60	38 ± 5	239 ± 0	35 ± 43	53 ± 35			
Dikerogammarus villosus	127 ± 44	184 ± 105	225 ± 88	53 ± 4	159 ± 129	110 ± 67			
Obesogammarus crassus	13 ± 0	26 ± 0							
Ponto-gammaridae		117 ± 0		23 ± 0	49 ± 32				
Pontogammarus robustoides	80 ± 45	109 ± 48	57 ± 20	66 ± 0	37 ± 20	62 ± 33			
Bivalvia									
Anodonta anatina				6 ± 0	6 0				
Anodonta cygnea		8 ± 0		6 ± 0	6 0				
Dreissena polymorpha	237 ± 136	319 ± 56	141 ± 112	868 ± 468	1322 ± 24	1288 ± 945			
Pisidium spp.	99 ± 59	3202 ± 853	720 ± 313	746 ± 554	543 ± 157	248 ± 387	67 ± 0		15 ± 3
Unio pictorum pictorum		20 ± 6	6 ± 0	11 ± 0	6 ± 0	6 ± 0			
Unio tumidus tumidus		29 ± 2	8 ± 4	6 ± 0	25 ± 6	7 ± 2			
Coleoptera									
Coleoptera			15 ± 0						
Donacia spp.		110 ± 115	35 ± 18		17 ± 0				
Haliplus spp.	23 ± 0	38 ± 10	15 ± 0			34 ± 8			
Orectochilus villosus Lv.			15 ± 0						
Peltodytes spp.					23 ± 0				
Platambus maculatus Lv.			6 ± 0			23 ± 0			

		Upper littoral			Middle littoral			Profundal	
Taxon	Natural	Marina	Beach	Natural	Marina	Beach	Natural	Marina	Beach
Diptera									
Ceratopogonidae	112 ± 46	125 ± 20	14 ± 15	56 ± 60	104 ± 7	18 ± 4			
Chironomini	9931 ± 3112	3555 ± 2727	928 ± 391	1192 ± 130	1267 ± 146	894 ± 149	219 ± 111	187 ± 56	300 ± 33
Corynoneurinae	169 ± 90	43 ± 0							
Orthocladinae	3134 ± 546	384 ± 101	377 ± 215	31 ± 9	65 ± 30	32 ± 7	10 ± 0		
other Diptera	45 ± 23				24 ± 14				
Tanypodinae	577 ± 101	226 ± 200	6 ± 0	188 ± 35	220 ± 12	105 ± 38	54 ± 28	44 ± 0	114 ± 53
Tanytarsini	6580 ± 1011	3286 ± 2930	1983 ± 339	426 ± 348	1207 ± 142	277 ± 162	13 ± 8		8 ± 3
Ephemerotpera									
Caenis horaria	451 ± 225	959 ± 785	36 ± 13	178 ± 105	213 ± 17	147 ± 33			
Caenis lactea	20 ± 2	265 ± 66	31 ± 12	201 ± 199	333 ± 209	35 ± 36			
Caenis luctuosa	71 ± 9	2653 ± 2384	478 ± 314	365 ± 120	605 ± 19	359 ± 76			
Caenis robusta	1555 ± 440	58 ± 16	14 ± 4	48 ± 22	22 ± 0	6 ± 0			
Cloeon dipterum	145 ± 52	92 ± 19	18 ± 7	24 ± 0	53 ± 26				
Gastropoda									
Acroloxus lacu.	133 ± 81								
Anisus spp.	95 ± 0								
Bithynia leachii leachii	24 ± 0								
Bithynia tentaculata	36 ± 29	47 ± 0	±	73 ± 30	205 ± 125	397 ± 267			
Ferrissia clessiniana	56 ± 24	113 ± 9	262 ± 0		45 ± 3				
Gyraulus albus	131 ± 50	180 ± 0		19 ± 3	118 ± 0				
Gyraulus crista	171 ± 68	59 ± 36		137 ± 126	33 ± 0	222 ± 163			
Gyraulus laevis	35 ± 19	114 ± 67	16 ± 9	74 ± 80	316 ± 121	128 ± 40			
Hippeutis complanatus	377 ± 210								
Marstoniopsis scholtzi	68 ± 22								
Menetus dilatatus	71 ± 0	38 ± 0			11 ± 0				
Potamopyrgus antipodarum	138 ± 64	19144 ± 7144	5131 ± 2755	5408 ± 4088	5349 ± 1675	6913 ± 3228			
Radix auricularia/ balthica	18 ± 6	58 ± 23	13 ± 7	42 ± 0					
Valvata cristata	80 ± 0								
Valvata piscinalis piscinalis	24 ± 0	48 ± 37	8 ± 3	183 ± 103	45 ± 4	257 ± 161			

Taxon	Upper littoral Natural	 Marina	 Beach	Middle littoral Natural	 Marina	 Beach	Profundal Natural	 Marina	 Beach
Heterotpera									
Heteroptera	20 ± 4	39 ± 12	83 ± 1	22 ± 0	36 ± 18	95 ± 0			
Hirudinea									
Alboglossiphonia heteroclita	39 ± 24					23 ± 0			
Alboglossiphonia hyalina	49 ± 1			23 ± 0	±	11 ± 0			
Erpobdella nigricollis	18 ± 0								
Erpobdella octoculata/ vilnensis	40 ± 15								
Erpobdella spp.	62 ± 10				6 ± 0				
Erpobdella testacea	52 ± 29								
Helobdella stagnalis	39 ± 13								
Piscicolidae	25 ± 7		19 ± 3	23 ± 0	6 ± 0	17 ± 6			
Theromyzon tessulatum	13 ± 0								
Isopoda									
Asellus aquaticus	71 ± 46								
Lepidoptera									
Lepidoptera	47 ± 18	26 ± 4	6 ± 0		8 ± 0	6 ± 0			
Odonata									
Aeshnidae	11 ± 0								
Cercion lindenii		42 ± 0		119 ± 0					
Coenagrion puella/ pulchellum	46 ± 0				17 ± 0				
Coenagrionidae					19 ± 0				
Erythromma najas	47 ± 0	71 ± 0							
Ischnura elegans	61 ± 17	42 ± 0		47 ± 0	19 ± 0	14 ± 9			
Platycnemis pennipes	77 ± 21	52 ± 0			17 ± 0				
Oligochatea									
Oligochaeta	4825 ± 1366	6653 ± 3291	1738 ± 838	1049 ± 254	3715 ± 942	1396 ± 160	356 ± 120	199 ± 64	259 ± 59

		Upper littoral			Middle littoral			Profundal	
Taxon	Natural	Marina	Beach	Natural	Marina	Beach	Natural	Marina	Beach
Trichoptera									
Agraylea multipunctata	102 ± 66								
Agraylea sexmaculata			6 ± 0		6 ± 0				
Agrypnia obsoleta/ varia	25 ± 3				11 ± 0				
Agrypnia pagetana/ picta	43 ± 22	14 ± 0							
Athripsodes aterrimus	28 ± 16	392 ± 0	31 ± 0	119 ± 0					
Athripsodes cinereus	11 ± 0	94 ± 5	48 ± 19	32 ± 28	48 ± 1	24 ± 0			
Cyrnus crenaticornis					6 ± 0	20 ± 4			
Cyrnus flavidus	53 ± 13	24 ± 0		33 ± 0					
Cyrnus trimaculatus	47 ± 0								
Ecnomus tenellus	93 ± 36	37 ± 12	24 ± 9		22 ± 0	6 ± 0			
Halesus radiatus		78 ± 0							
Holocentropus picicornis	41 ± 21				24 ± 0				
Hydroptila spp.	69 ± 21								
Leptocerus tineiformis	32 ± 0			51 ± 47	11 ± 0	11 ± 0			
Limnephilus stigma	40 ± 34	24 ± 0							
Molanna angustata		38 ± 0	23 ± 12		18 ± 9				
Mystacides azurea			11 ± 0						
Mystacides longicornis/ nigra	35 ± 15	42 ± 7	10 ± 1	24 ± 0	20 ± 0	24 ± 0			
Oecetis furva	44 ± 6		6 ± 0						
Oecetis ochracea	38 ± 24	25 ± 0	35 ± 19	21 ± 2	31 ± 4	18 ± 8			
Oecetis testacea			23 ± 0						
Orthotrichia spp.	261 ± 68	102 ± 121	14 ± 5	66 ± 31	122 ± 18	184 ± 154			
Oxyethira spp.	83 ± 54	136 ± 0	11 ± 0	66 ± 70	52 ± 28	19 ± 8			

	Upper littoral			Middle littoral			Profundal		
Taxon	**Natural**	**Marina**	**Beach**	**Natural**	**Marina**	**Beach**	**Natural**	**Marina**	**Beach**
Phryganea bipunctata/ grandis	10 ± 5								
Psychomyia pusilla	10 ± 5	38 ± 0	23 ± 12		18 ± 9				
Tinodes waeneri waeneri	26 ± 9	93 ± 24	104 ± 53		11 ± 0				
Triaenodes bicolor/ unanimis	53 ± 8								
Turbellaria									
Tricladida	70 ± 32	56 ± 23		56 ± 44					

Appendix III

Overview about the applied length-mass-regressions, conversion factors for preservation and conversion factors from mass to Joule per taxa. l-m = length-mass, BL = Body length, HL = Head length, HW = head width, SBL = soft body length, SH = Shell height, SL = Shell length, SW = Shell width. n = number of replicates, a and b are the intercept and slope of the linear regression, r² = coefficient of determination, smear = Duan´s smearing factor, length range = min/max = minimum and maximum length of body dimension, AFDM = ash free dry mass, DM = dry mass, *with shell, 34.4 % AFDW relative to total DW

	Length-mass regression												**Conversion preserved to unpreserved**				**Conversion mass to Joule (Brey 2010)**		
Taxon	**l-m-regression origin**			**Conversion**	**n**	**a**	**b**	**smear**	**r²**	**min**	**max**	**Taken from**	**Shell**	**Mass type**	**factor**	**Taken from**	**origin**	**factor**	**Unit**
Amphipoda																			
Chelicorophium curvispinum	*Chelicorophium curvsipinum*	BL	–›	DW	34	0.0167	2.10	1.07	0.76	1.43	5.08	Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Corophium	13.794	J / mgDW
Dikerogammarus spp. *Dikerogammarus villosus* *Dikerogammarus haemobaphes* *Obesogammarus crassus* Pontogammaridae *Pontogammarus robustoides*	Pontogammaridae	BL	–›	DW	93	0.0037	3.02	1.05	0.96	2.22	17.34	Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Gammarus	15.944	J / mgDW
Bivalvia																			
Anodonta anatina *Anodonta cygnea* *Anodonta* spp. *Unio pictorum pictorum* *Unio* spp. *Unio tumidus tumidus*	*Anodonta grandis simpsoniana*	SL	–›	DW (soft tissue)	170	0.0004	3.42	/	/	18.00	80.00	Hanson et al. 1988, aus Benke 1999	yes	AFDW	/	/	Anodonta *Unio pictorum* *Unio* *Unio tumidus*	18.701 19.837 18.766 17.696	J / mgDW J / mgDW J / mgDW J / mgDW
Pisidium spp.	*Pisidium* sp.	SL	–›	AFDM	58	0.0043	5.02	1.08	0.96	1.13	4.31	Maehrlein et al. (subm.)	yes	AFDW	/	/	Pisidium	20.981	J / mgAFDW
Dreissena polymorpha	*Dreissena polymorpha*	SL	–›	DW	37	0.0201	2.16	1.06	0.97	1.07	20.87		no	DW	1.288	Maehrlein et al. (subm.)	Bivalvia	17.834	J / mgDW
Ceratopogonidae																			
Ceratopogonidae	Ceratopogoninae	BL	–›	DW	6	0.0004	2.72	1.00	0.99	7.32	16.95	Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Ceratopogoninae	20.108	J / mgDW
Chironomidae																			
Chironomidae	Chironomidae	BL	–›	DW	352	0.0009	2.59	1.11	0.90	3.12	26.58	Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Chironomidae	20.684	J / mgDW
Chironomini	Chironomini	BL	–›	DW	119	0.0010	2.50	1.10	0.93	3.13	26.58								
Corynoneurinae	Tanytarsini	BL	–›	DW	46	0.0068	1.39	1.04	0.83	2.06	9.52								
Orthocladinae	Orthocladiinae	BL	–›	DW	25	0.0006	2.74	1.03	0.94	3.26	9.53								
Tanypodinae	Tanypodinae	BL	–›	DW	19	0.0097	1.44	1.02	0.92	2.24	10.35								
Tanytarsini	Tanytarsini	BL	–›	DW	46	0.0068	1.39	1.04	0.83	2.06	9.52								
Ephemeroptera																			
Caenis horaria *Caenis lactea* *Caenis luctuosa* *Caenis* spp.	*Caenis* spp.	HW	–›	DW	75	0.3706	3.28	1.06	0.92	0.38	1.27	Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Caenis	28.118	J / mgDW
Caenis robusta	*Caenis robusta*	HW	–›	DW	63	0.3565	3.26	1.07	0.91	0.38	1.27								
Cloeon dipterum	*Cloeon dipterum*	HW	–›	DW	25	0.5957	2.98	1.15	0.84	0.24	1.12		no	DW	1.288	Maehrlein et al. (subm.)	Baetidae	19.298	J / mgDW
Gastropoda																			
Acroloxus lacustris	Ancylidae	AW	–›	DW*	134	0.0288	2.70	1.04	0.97	0.80	5.90	Méthot et al. 2012	no	DW	/	/	Gastropoda	17.966	J / mgDW
Anisus spp. *Anisus vortex*	*Anisus vortex*	SW	–›	AFDW	8	0.0107	2.28	1.01	0.98	1.51	7.62	Maehrlein et al. (subm.)	yes	AFDW	/	/	Gastropoda	22.47	J / mgAFDW
Bithynia leachii leachii *Bithynia tentaculata*	*Bithynia tentaculata*	SH	–›	AFDW	83	0.0596	3.16	1.06	0.97	0.77	10.66								
Ferrissia clessiniana	Ancylidae	AW	–›	DW*	134	0.0288	2.70	1.04	0.97	0.80	5.90	Méthot et al. 2012	no	DW	/	/	Gastropoda	17.966	J / mgDW
Gyraulus albus *Gyraulus laevis*	*Gyraulus albus*	SW	–›	AFDW	64	0.0199	2.33	1.02	0.95	1.01	4.91	Maehrlein et al. (subm.)	yes	AFDW	/	/	Gastropoda	22.47	J / mgAFDW
Gyraulus crista	*Gyraulus crista*	SW	–›	AFDW	93	0.0105	2.76	1.03	0.87	1.03	2.8								
Hippeutis complanatus	*Hippeutis complanatus*	SW	–›	AFDW	58	0.0109	2.62	1.05	0.88	1.26	4.13								
Marstoniopsis scholtzi	*Bithynia tentaculata*	SH	–›	AFDW	83	0.0596	3.16	1.06	0.97	0.77	10.66								
Menetus dilatatus	*Gyraulus albus*	SW	–›	AFDW	64	0.0199	2.33	1.02	0.95	1.01	4.91								
Potamopyrgus antipodarum *Radix auricularia/ balthica*	*Potamopyrgus antipodarum*	SH	–›	AFDW	73	0.0251	2.07	1.03	0.94	1.06	5.56								
Valvata cristata	*Valvata cristata*	SW	–›	AFDW	22	0.0192	2.71	1.05	0.89	1.03	3.06								
Valvata piscinalis piscinalis	*Valvata piscinalis piscinalis*	SL	–›	AFDW	35	0.0130	3.38	1.05	0.96	1.036	4.65								
Hirudinea																			
Alboglossiphonia heteroclita *Alboglossiphonia hyalina* *Alboglossiphonia* spp.	*Glossiphonia complanata*	BL	–›	DW	97	0.1200	2.00	/	0.64	/	/	Edwards et al.	no	DW	1.288	Maehrlein et al. (subm.)	Glossiphonia	20.833	J / mgDW

	Length-mass regression											Conversion preserved to unpreserved				Conversion mass to Joule (Brey 2010)		
Taxon	**l-m-regression origin**	**Conversion**	**n**	**a**	**b**	**smear**	**r²**	**min**	**max**		**Taken from**	**Shell**	**Mass type**	**factor**	**Taken from**	**origin**	**factor**	**Unit**
Erpobdella nigricollis *Erpobdella octoculata* *Erpobdella octoculata/ vilnensis* *Erpobdella* spp. *Erpobdella testacea* *Erpobdella testacea/ nigricollis*	*Erpobdella* spp.	BL –› DW	12	0.0090	2.37	1.01	1.00	3.81	33.81		Maehrlein et al. (subm.)					Erpobdella	17.074	J / mgDW
Helobdella stagnalis	*Helobdella stagnalis*	BL –› DW	19	0.0645	2.12	/	0.62	/	/		Edwards et al.							
Hemiclepsis marginata *Piscicola geometra* Piscicolidae	*Erpobdella* spp.	BL –› DW	12	0.0090	2.37	1.01	1.00	3.81	33.81		Maehrlein et al. (subm.)							
Theromyzon tessulatum	*Glossiphonia complanata*	BL –› DW	97	0.1200	2.00	/	0.64	/	/		Edwards et al.					Glossiphonia	20.833	J / mgDW
Isopoda																		
Asellus aquaticus	*Asellus aquaticus*	BL –› DW	37	0.0049	2.83	1.11	0.94	1.39	15.24		Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Isopoda	14.772	J / mgDW
Odonata																		
Anisoptera	Anisoptera	HW –› DW	30	0.1708	3.11	1.05	0.98	0.48	8.01		Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Odonata	20.297	J / mgDW
Cercion lindenii *Coenagrion puella* *Coenagrion pulchellum* Coenagrionidae *Erythromma najas* *Erythromma* spp. *Ischnura elegans* *Platycnemis pennipes* Zygoptera	Zygoptera	HW –› DW	42	0.1146	3.13	1.02	0.98	0.88	4.19		Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Odonata	20.297	J / mgDW
Oligochaeta																		
Oligochaeta	biomass directly measured											no	DW	1.288	Maehrlein et al. (subm.)	Oligochaeta	18.453	J / mgDW
Trichotpera																		
Agrypnia obsoleta/ varia *Agrypnia pagetana/ picta* *Agrypnia* spp. *Agrypnia varia* *Anabolia furcata*	Phryganeidae	BL –› DW	17	0.0020	2.57	1.04	0.96	5.01	23.28		Maehrlein et al. (subm.)	no	DW	1.288	Maehrlein et al. (subm.)	Agrypnia	10.175	J / mgDW
Athripsodes albifrons/ bilineatus/ commutatus *Athripsodes aterrimus* *Athripsodes cinereus* *Athripsodes* spp.	*Athripsodes* sp.	BL –› DW	52	0.0045	2.44	1.09	0.84	2.07	11.33							Trichotpera	19.917	J / mgDW
Cyrnus crenaticornis	*Cyrnus crenaticornis*	HW –› DW	29	0.6486	2.92	1.04	0.91	0.44	1.28							Polycentropo-didae	23.867	J / mgDW
Cyrnus flavidus *Cyrnus* spp.	*Cyrnus* sp.	HW –› DW	48	0.6545	2.84	1.07	0.86	0.44	1.5									
Ecnomus tenellus	*Ecnomus tenellus*	HW –› DW	32	0.8883	3.14	1.05	0.92	0.34	0.89							Trichotpera	19.917	J / mgDW
Halesus radiatus	Phryganeidae	BL –› DW	17	0.0020	2.57	1.04	0.96	5.01	23.28							Limnephilidae	16.269	J / mgDW
Hydroptila spp. Hydroptilidae	Hydroptilidae	BL –› DW	23	0.0019	2.52	1.12	0.55	2.05	4.54							Trichotpera	19.917	J / mgDW
Leptoceridae	*Athriposdes* sp.	HW –› DW	19	5.4061	3.6	1.04	0.95	0.27	0.75									
Leptocerus tineiformis	*Mystacides longicornis/nigra*	BL –› DW	14	0.0020	2.52	1.10	0.86	2.5	10.47									
Limnephilinae	Phryganeidae	BL –› DW	17	0.0020	2.57	1.04	0.96	5.01	23.28							Limnephilidae	16.269	J / mgDW
Molanna angustata	*Molanna angustata*	BL –› DW	12	0.0025	2.49	1.06	0.92	2.79	12.87							Trichotpera	19.917	J / mgDW
Mystacides azurea *Mystacides longicornis/ nigra* *Mystacides* spp.	*Mystacides longicornis/nigra*	BL –› DW	14	0.0020	2.52	1.10	0.86	2.5	10.47									
Oecetis furva *Oecetis ochracea* *Oecetis* spp. *Oecetis testacea*	*Oecetis* sp.	BL –› DW	13	0.0078	1.75	1.11	0.65	1.38	4.89									
Orthotrichia spp.	*Orthotrichia* sp.	BL –› DW	9	0.0005	4.18	1.02	0.85	2.34	3.38									
Oxyethira spp.	*Oxyethira* sp.	BL –› DW	16	0.0020	3.05	1.05	0.59	2.47	4.01									
Psychomyia pusilla	Psychomyiidae	HW –› DW	13	1.2502	3.47	1.14	0.75	0.35	0.84									
Psychomyiidae	Phryganeidae	BL –› DW	17	0.0020	2.57	1.04	0.96	5.01	23.28									
Tinodes waeneri waeneri	Psychomyiidae	HW –› DW	13	1.2502	3.47	1.14	0.75	0.35	0.84									
Triaenodes bicolor	*Mystacides longicornis/nigra*	BL –› DW	14	0.0020	2.52	1.10	0.86	2.5	10.47									

Appendix IV

Overview about the estimated site-specific as well as area-weighted production values and area per depth zone for Lake Scharmützelsee. P = secondary production, SD = standard deviation, *all: for the upper littoral shore type area-weighted, for middle littoral and profundal all shore types averaged

Depth zone	Shore type	site-specific P g m^{-2} y^{-1} ± SD	Area in m²	area-weighted P g m^{-2} y^{-1}	Total P t y^{-1}	P in %	Area in %
Upper littoral	Natural	**37.01** ± 1.33	515,004	37.01	19.06	19.3	4.3
	Marina	**39.43** ± 11.16	324,298	39.43	12.79	12.9	2.7
	Beach	**11.94** ± 4.2	6,618	11.94	0.08	0.1	0.06
	Average	28.21 ± 14.35	845,920	**37.74**	31.93	32.3	7.0
Middle littoral	Natural	18.62 ± 6.52					
	Marina	19.52 ± 2.7					
	Beach	18.97 ±4.3					
	Average	**18.98** ± 4.3	2,960,168	**18.98**	56.18	56.9	24.5
Profundal	Natural	1.39 ± 0.91					
	Marina	1.07 ± 0.27					
	Beach	1.34 ± 0.18					
	Average	**1.29** ± 0.52	8,263,911	**1.29**	10.69	10.8	68.5
Whole lake	*		12,069,999	**8.19**	**98.80**	100	100

Appendix V

Example R code for estimating length-mass relationships by fitting log-linear models.

Simulating data

In this first code block we simulate some fake length-mass data to illustrate some of the issues when estimating length-mass relationships with log-linear regression models.

```
# load require packages
library(ggplot2)
library(knitr)
library(gridExtra)
library(dplyr)
# set seed of random number generator
# so that the simulated data set is always the same
set.seed(1)
# assign values to parameters of the length-mass relationship
a <- 0.5
b <- 3
# sample size
n <- 50
# standard deviation of simulated biological variation
sd <- 0.2
# standard deviation of simulated measurement error
sd_measure <- 1
# randomly draw lengths uniformly between 0.1, and 4 mm
dat <- data.frame(
length = runif(n, 0.1, 4)
)
# simulate observed mass given multiplicative biological variation
# and additive measurement error
dat$mass <- 10^((log10(a) + log10(dat$length) * b) + rnorm(n, mean = 0, sd = sd)) +
rnorm(n, 0, sd_measure)
# sort data set shortest to longest
dat <- arrange(dat, length)
# print first 10 rows of data set
kable(head(dat, 10), caption = "First 10 rows of the simulated
length-mass data, ordered by increasing length")
```

Table 1: First 10 rows of the simulated length-mass data, ordered by increasing length

length	mass
0.1522223	0.0434463
0.1909917	1.3455509
0.3409665	0.6044584
0.5209801	1.5294185
0.5896649	-1.1272670
0.7885713	1.2675724
0.8262486	0.7508307
0.8865595	-0.1671617
0.9033008	0.6373670
0.9273558	-0.8049359

Problems with negative mass estimates

Measured mass esimates can sometimes be zero or negative for the smallest individuals when their mass approaches the limits of the equipment.

Exclude mass <= 0 mg

In code chunk 2 we exclude all data points that are <= 0 and then fit a log-linear regression model.

```
dat_sub_neg <- subset(dat, mass > 0)
# fit log-linear regression model
lm1 <- lm(log10(mass) ~ log10(length), data = dat_sub_neg)
# get estimated parameter values
a_est <- 10^coef(lm1)[1]
b_est <- coef(lm1)[2]
# get predicted "fitted" masses
dat_sub_neg$fttd <- fitted(lm1)
# plot the data + fitted regression on original and log10 transformed scales
p1 <- dat %>%
ggplot(aes(x = length, y = mass)) %>%
+ geom_point() %>%
+ scale_x_continuous(expression(Length~"[mm]")) %>%
+ scale_y_continuous(expression(Mass~"[mg]")) %>%
+ theme_bw() %>%
+ theme(aspect.ratio = 1) %>%
+ geom_line(data = dat_sub_neg, aes(x = length, y = 10^fttd))
p2 <- p1 %>%
+ scale_x_continuous(expression(Length~"[mm]"), trans = "log10", breaks = c(0.25, 1, 4)) %>%
+ scale_y_continuous(expression(Mass~"[mg]"), trans = "log10") %>%
+ expand_limits(x = 0.25, y = c(0.1, 100))
p12 <- arrangeGrob(p1, p2, nrow = 1)
p12
```

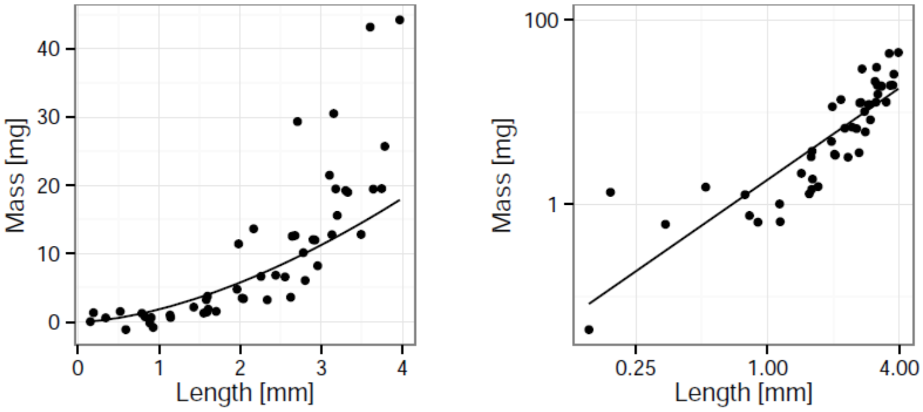


Figure 1: Simulated length-mass data on original scales (left) and log10 transformed scales (right). The regression line shows a log-linear model fit to the data with zero or negative mass estimates removed.

If zero and negative values are simply removed the resulting data set is distorted for short individuals. This is because only those whose mass was by chance overestimated are retained.

The estimated values of the parameters a and b are very different from the values assigned in code block 1.
a_est = 1.8409244
b_est = 1.6487659

Exclude length < 1 mm

In this code chunk we instead exclude all individuals whose lengths are below 1 mm. Then we refit the log-linear model.

```
dat_sub_short <- subset(dat, length >= 1)
lm2 <- lm(log10(mass) ~ log10(length), data = dat_sub_short)
a_est <- 10^coef(lm2)[1]
b_est <- coef(lm2)[2]
dat_sub_short$fttd <- fitted(lm2)
p3 <- dat_sub_short %>%
ggplot(aes(x = length, y = mass)) %>%
+ geom_point() %>%
+ scale_x_continuous(expression(Length~"[mm]")) %>%
+ scale_y_continuous(expression(Mass~"[mg]")) %>%
+ theme_bw() %>%
+ theme(aspect.ratio = 1) %>%
+ geom_line(data = dat_sub_short, aes(x = length, y = 10^fttd))
p4 <- p3 %>%
+ scale_x_continuous(expression(Length~"[mm]"), trans = "log10", breaks = c(1, 2, 4)) %>%
+ scale_y_continuous(expression(Mass~"[mg]"), trans = "log10") %>%
+ expand_limits(x = 1, y = 100)
p34 <- arrangeGrob(p3, p4, nrow = 1)
p34
```

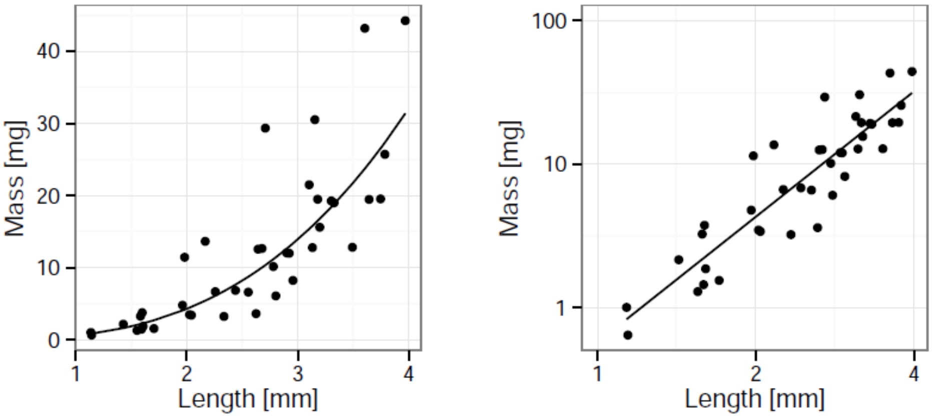


Figure 2: Simulated length-mass data with indivduals <1 mm long removed.

The estimated parameter values are now much closer to the values assigned in code block 1
a_est = 0.5744776
b_est = 2.90222

Correcting bias in mass estimates from log-linear models

The fitted length-mass relationship is now a good fit all the range of lengths but nevertheless, if an estimate is made of the total mass of the sample it will be a biased underestimate.

```
sample_mass <- sum(dat_sub_short$mass)
est_sample_mass <- sum(10^dat_sub_short$fttd)
```

Mass of complete sample = 487 mg
Estimated mass of complete sample = 442 mg
In the following two code chunks we calculate the smearing correction factor and apply it to the predicted masses from the log-linear model

```
Calculate the smearing correction factor
smear_factor <- mean(10^(residuals(lm2)))
# Multiply the predicted masses by the smearing factor
dat_sub_short$fttd_smear <- 10^dat_sub_short$fttd * smear_factor
```

Smearing correction factor = 1.12

```
sample_mass <- sum(dat_sub_short$mass)
est_sample_mass <- sum(10^dat_sub_short$fttd)
bias_corrected_est_sample_mass <- sum(dat_sub_short$fttd_smear)
```

Mass of complete sample = 487 mg
Estimated mass of complete sample = 442 mg
Bias corrected mass of complete sample = 494 mg
Finally we plot the uncorrected and bias corrected length-mass relationships on the original untransformed scale.

```
p5 <- p3 %>%
+ geom_line(data = dat_sub_short, aes(x = length, y = fttd_smear), colour = "Red")
p5
```

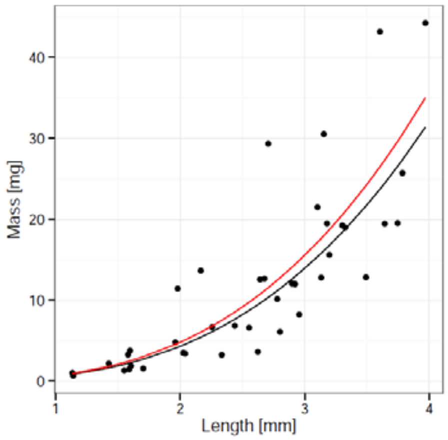


Figure 3: Simulated length-mass data with fitted log-linear regression model (black) and bias-corrected log-linear model (red).

Appendix VI

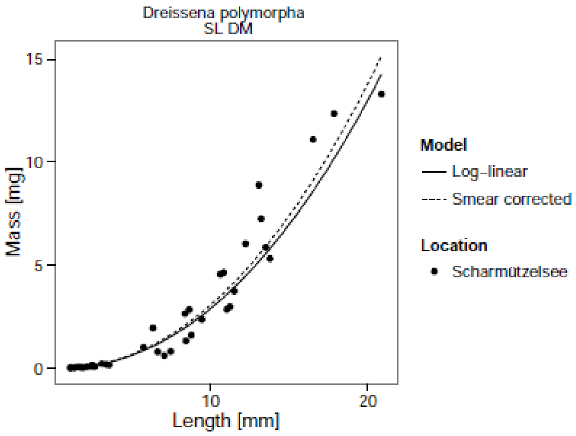
A table of log-likelihoods and likelihood ratios for log-linear and nonlinear models predicting body mass from body length measurements for aquatic benthic invertebrates.

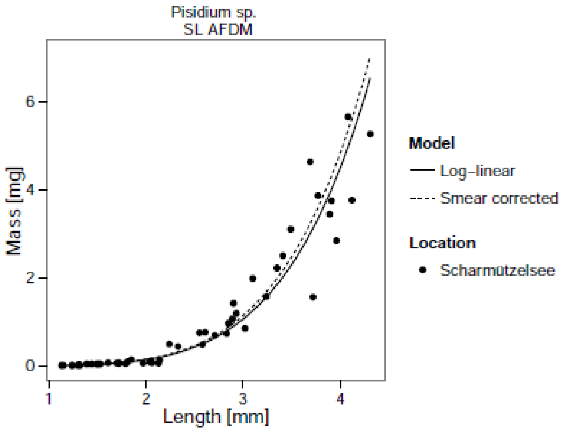
Taxon	Conversion	n	Log-linear	Nonlinear	Likelihood ratio	Best model
Anabolia furcata	HW –› DM	24	-41.83	-59.58	35.51	Log-linear
Anisoptera	HW –› DM	30	-76.48	-125.61	98.27	Log-linear
Anisus vortex	SW –› AFDM	8	18.24	14.26	7.97	Log-linear
Asellus aquaticus	BL –› DM	37	-9.2	-49.61	80.82	Log-linear
Athripsodes sp.	BL –› DM	52	83.69	49.92	67.54	Log-linear
Athripsodes sp.	HW –› DM	19	14.37	-5.61	39.96	Log-linear
Bithynia tentaculata	SH –› AFDM	83	-177.24	-249.81	145.14	Log-linear
Caenis horaria	HW –› DM	7	14.72	15.37	-1.29	Nonlinear
Caenis robusta	HW –› DM	57	89.67	39.39	100.55	Log-linear
Caenis spp.	HW –› DM	69	108.08	49.05	118.05	Log-linear
Ceratopogonidae	BL –› DM	6	16.82	14.36	4.91	Log-linear
Chelicorophium curvsipinum	BL –› DM	28	38.94	34.29	9.29	Log-linear
Chelicorophium curvsipinum	HL –› DM	28	29.5	20.67	17.66	Log-linear
Chironomidae	BL –› DM	334	223.52	-234.99	917.02	Log-linear
Chironomini	BL –› DM	119	66.01	-113.61	359.23	Log-linear
Cloeon dipterum	HW –› DM	25	30.96	13.45	35.01	Log-linear
Cyrnus crenaticornis	HW –› DM	29	15.79	-0.81	33.19	Log-linear
Cyrnus flavidus	HW –› DM	11	-8.12	-8.41	0.58	Log-linear
Cyrnus sp.	HW –› DM	48	-0.37	-23.59	46.44	Log-linear
Cyrnus trimaculatus	HW –› DM	8	-1.69	-5.97	8.55	Log-linear
Dreissena polymorpha	SL –› DM	37	-7.46	-49.8	84.67	Log-linear
Ecnomus tenellus	HW –› DM	20	37.76	16.36	42.78	Log-linear
Erpobdella spp.	BL –› DM	12	-8.9	-24.48	31.17	Log-linear
Gyraulus albus	SW –› AFDM	58	141.16	120.03	42.26	Log-linear
Gyraulus crista	SW –› AFDM	63	196.55	190.62	11.87	Log-linear
Gyraulus sp.	SW –› AFDM	121	302.61	266.19	72.83	Log-linear
Hippeutis complanatus	SW –› AFDM	52	116.05	106.98	18.14	Log-linear
Hydroptilidae	BL –› DM	23	60.96	60	1.92	Log-linear
Ischnura elegans	HW –› DM	12	8.83	0.11	17.44	Log-linear
Limnephilidae	HW –› DM	78	-176.05	-240.21	128.31	Log-linear
Limnephilus sp.	HW –› DM	73	-92.9	-219.48	253.15	Log-linear
Molanna angustata	BL –› DM	12	11.37	7.5	7.73	Log-linear
Mystacides longicornis/nigra	BL –› DM	14	21.42	8.31	26.23	Log-linear
Mystacides longicornis/nigra	HW –› DM	5	7.12	5.68	2.89	Log-linear
Oecetis sp.	BL –› DM	13	35.53	34.98	1.1	Log-linear
Oecetis sp.	HW –› DM	16	35.11	33.2	3.82	Log-linear
Orthocladiinae	BL –› DM	25	65.83	52.22	27.22	Log-linear
Orthotrichia sp.	BL –› DM	9	32.54	28.11	8.86	Log-linear
Oxyethira sp.	BL –› DM	16	40.29	38.5	3.58	Log-linear
Phryganeinae	BL –› DM	17	3.24	-27.61	61.69	Log-linear
Phryganeinae	HW –› DM	20	-20.95	-56.41	70.9	Log-linear
Pisidium sp.	SL –› AFDM	52	42.11	-32.76	149.75	Log-linear
Pisidium sp.	SL –› DM	52	-23.29	-76.59	106.6	Log-linear
Pontogammaridae	BL –› DM	87	-95.21	-168.55	146.68	Log-linear
Pontogammaridae	HL –› DM	86	-135.42	-171.57	72.29	Log-linear
Potamopyrgus antipodarum	SH –› AFDM	73	99.07	80.91	36.31	Log-linear
Psychomyiinae	HW –› DM	13	15.67	11.2	8.93	Log-linear
Tanypodinae	BL –› DM	19	44.96	34.7	20.51	Log-linear
Tanytarsini	BL –› DM	40	120.28	104.95	30.67	Log-linear
Valvata cristata	SW –› AFDM	22	43.61	43.6	0.01	Log-linear
Valvata piscinalis piscinalis	SL –› AFDM	35	34.63	-4.39	78.05	Log-linear
Zygoptera	HW –› DM	42	-15.88	-38.08	44.4	Log-linear

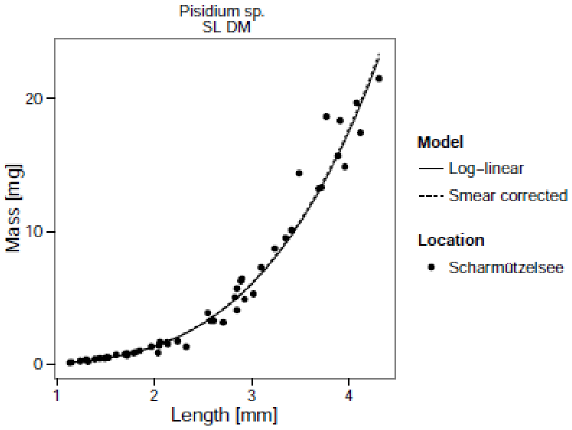
Appendix VII

Scatter plots between measured length and mass for each taxon together with the fitted log-linear and smearing corrected log-linear regression models.

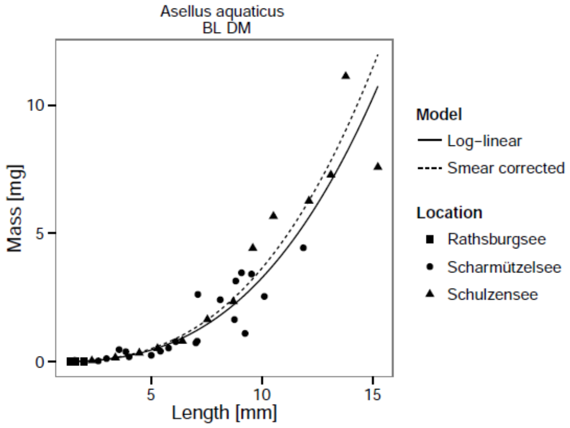
Bivalvia

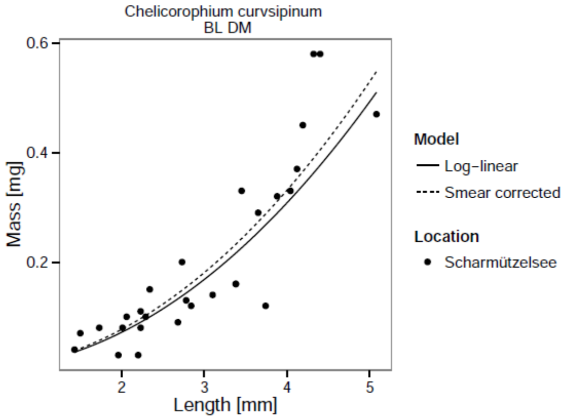


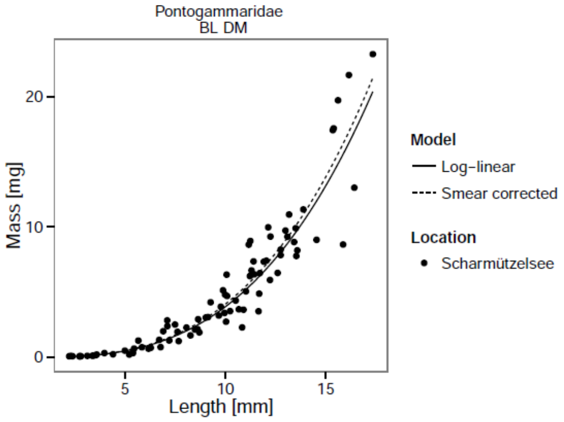


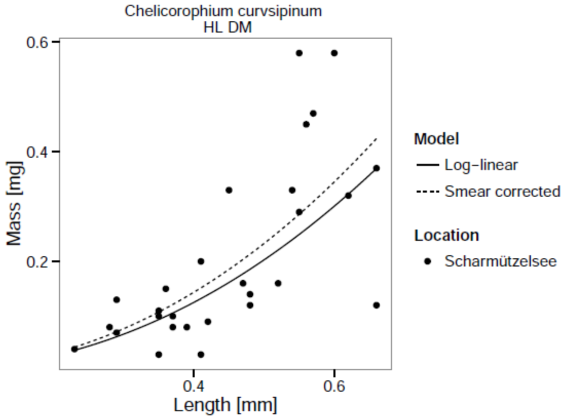


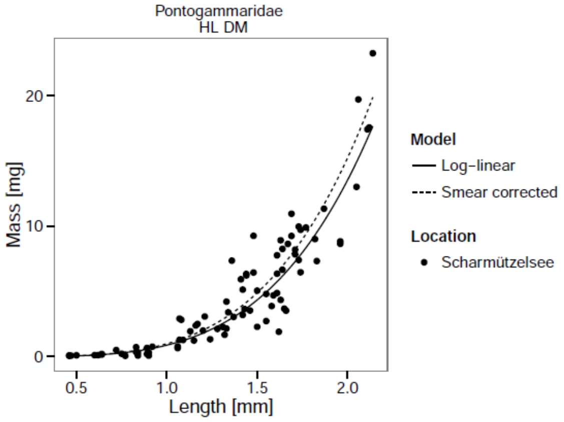
Crustacea



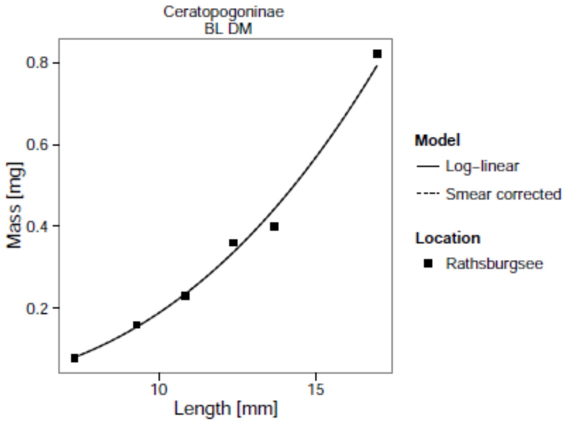

Chelicorophium curvsipinum
BL DM
Mass [mg]
0.6
0.4
0.2
2
3
4
5
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee

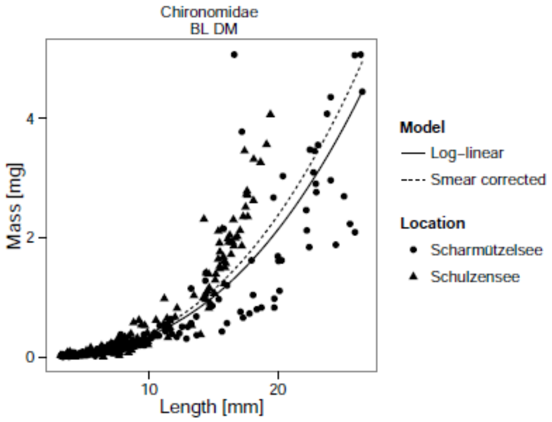

Pontogammaridae
BL DM
Mass [mg]
20
10
0
5
10
15
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee

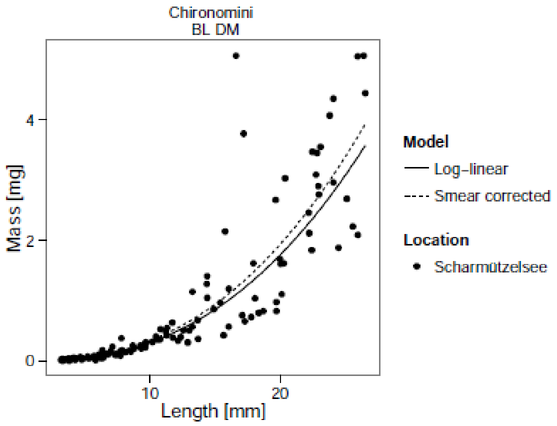

Chelicorophium curvsipinum
HL DM
Mass [mg]
0.6
0.4
0.2
0.4
0.6
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee

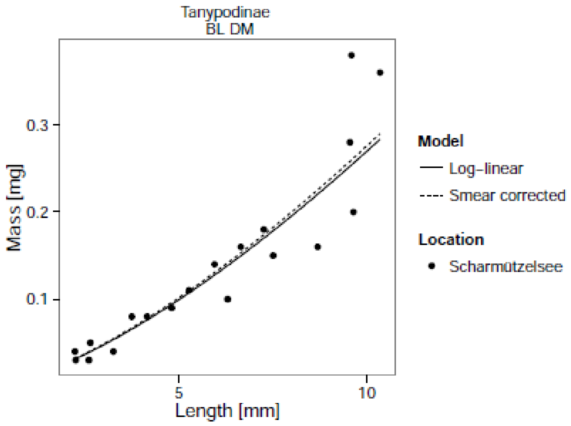

Pontogammaridae
HL DM
Mass [mg]
20
10
0
0.5
1.0
1.5
2.0
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee

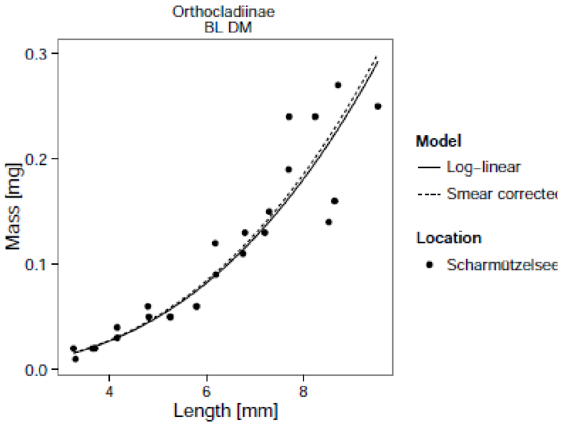
Diptera

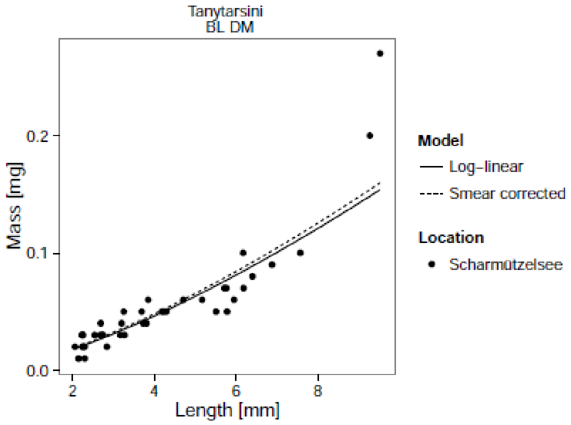

Ceratopogoninae
BL DM
Mass [mg]
0.8
0.6
0.4
0.2
10
15
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
■ Rathsburgsee


Chironomidae
BL DM
Mass [mg]
4
2
0
10
20
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee
▲ Schulzensee

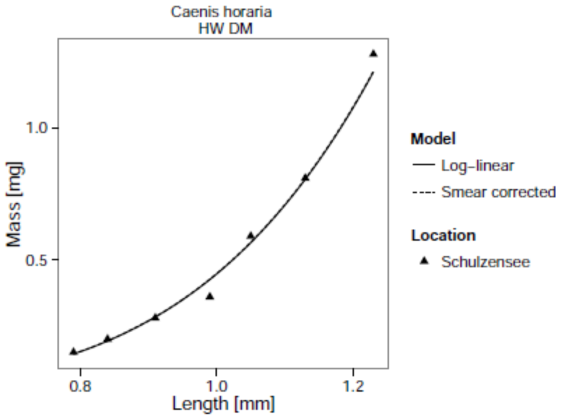


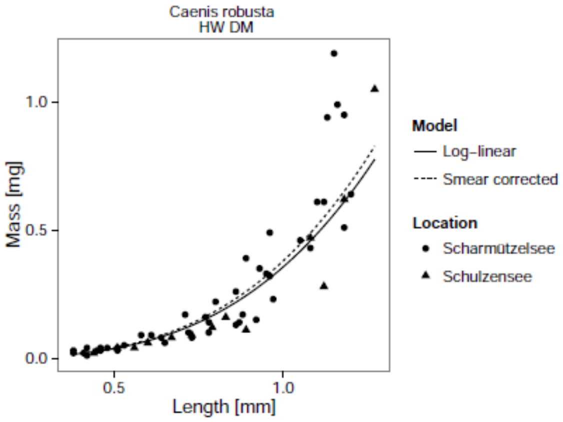


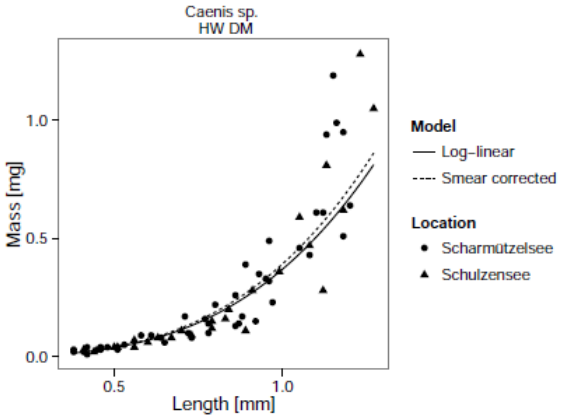


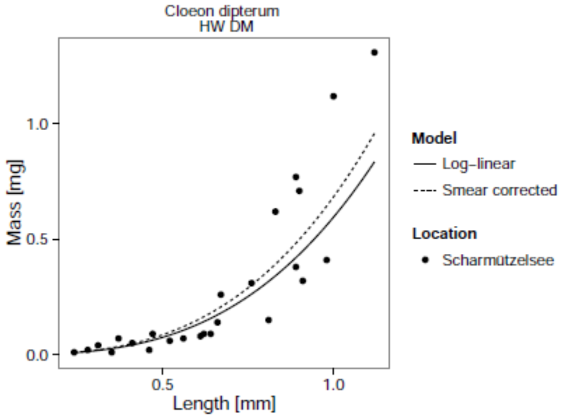


Ephemeroptera

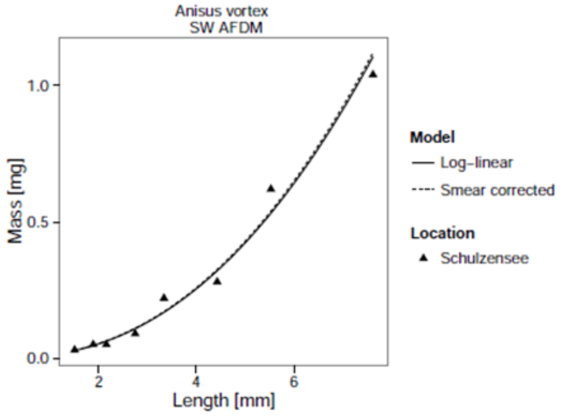


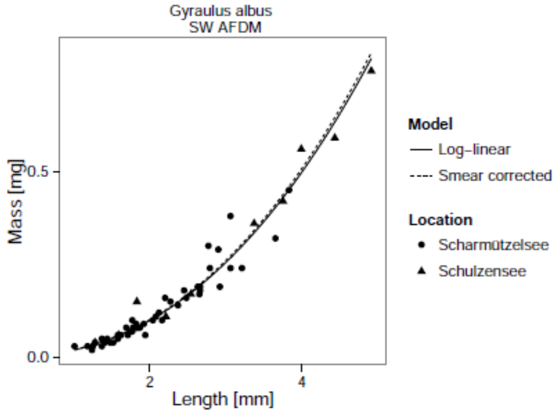


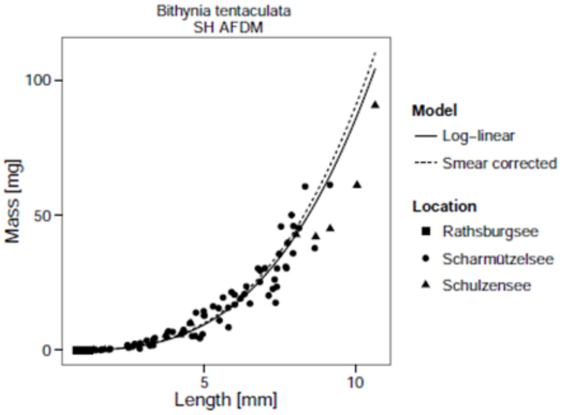

Caenis sp.
HW DM
Mass [mg]
0.0
0.5
1.0
0.5
1.0
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee
▲ Schulzensee

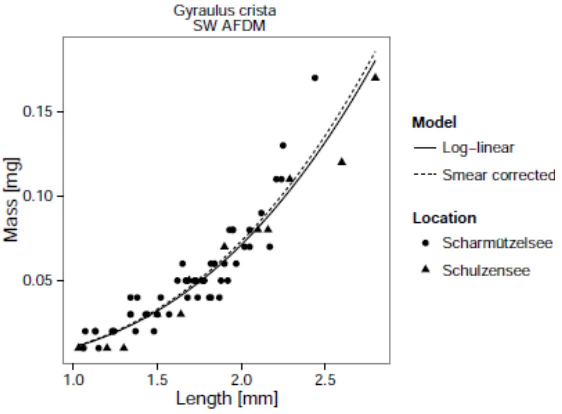

Cloeon dipterum
HW DM
Mass [mg]
0.0
0.5
1.0
0.5
1.0
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee

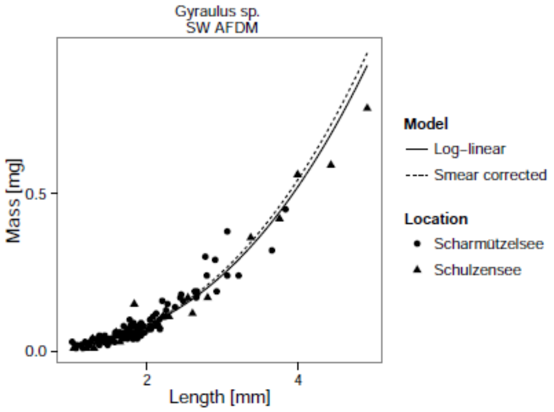
Gastropoda

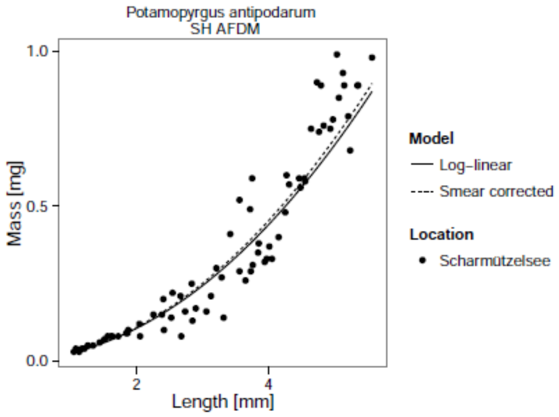

Anisus vortex
SW AFDM
Mass [mg]
0.0
0.5
1.0
2
4
6
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
▲ Schulzensee

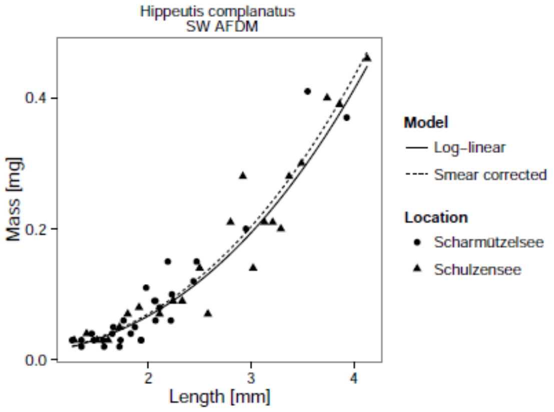

Gyraulus albus
SW AFDM
Mass [mg]
0.0
0.5
2
4
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee
▲ Schulzensee

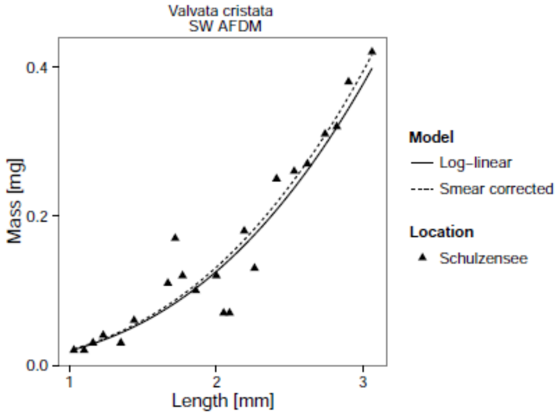

Bithynia tentaculata
SH AFDM
Mass [mg]
0
50
100
5
10
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
■ Rathsburgsee
● Scharmützelsee
▲ Schulzensee

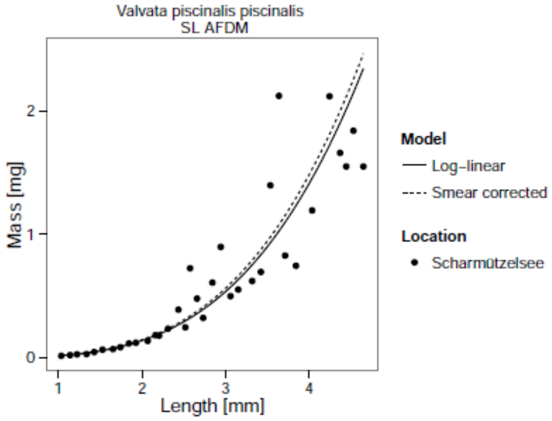

Gyraulus crista
SW AFDM
Mass [mg]
0.05
0.10
0.15
1.0
1.5
2.0
2.5
Length [mm]
Model
— Log–linear
---- Smear corrected
Location
● Scharmützelsee
▲ Schulzensee


Gyraulus sp.
SW AFDM
Mass [mg]
0.0
0.5
Length [mm]
2
4
Model
Log–linear
Smear corrected
Location
● Scharmützelsee
▲ Schulzensee

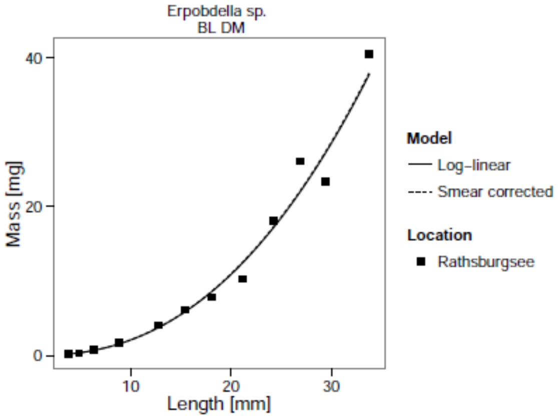

Potamopyrgus antipodarum
SH AFDM
Mass [mg]
0.0
0.5
1.0
Length [mm]
2
4
Model
Log–linear
Smear corrected
Location
● Scharmützelsee


Hippeutis complanatus
SW AFDM
Mass [mg]
0.0
0.2
0.4
Length [mm]
2
3
4
Model
Log–linear
Smear corrected
Location
● Scharmützelsee
▲ Schulzensee

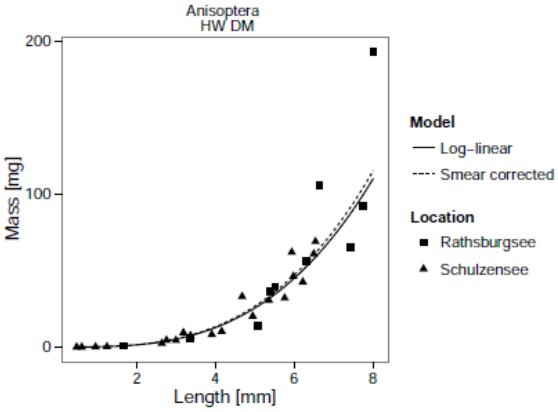

Valvata cristata
SW AFDM
Mass [mg]
0.0
0.2
0.4
Length [mm]
1
2
3
Model
Log–linear
Smear corrected
Location
▲ Schulzensee

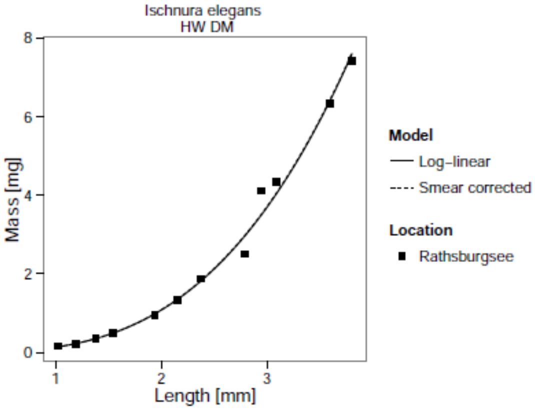

Valvata piscinalis piscinalis
SL AFDM
Mass [mg]
0
1
2
Length [mm]
1
2
3
4
Model
Log–linear
Smear corrected
Location
● Scharmützelsee

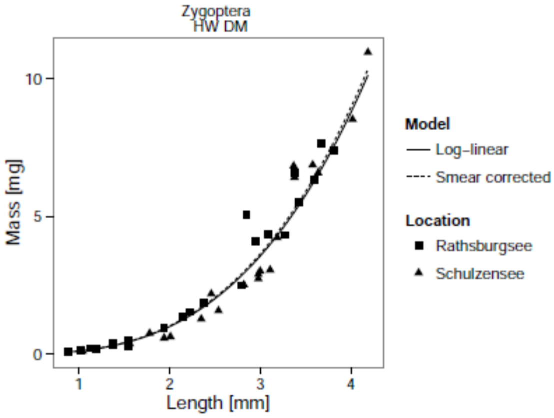
Hirudinae



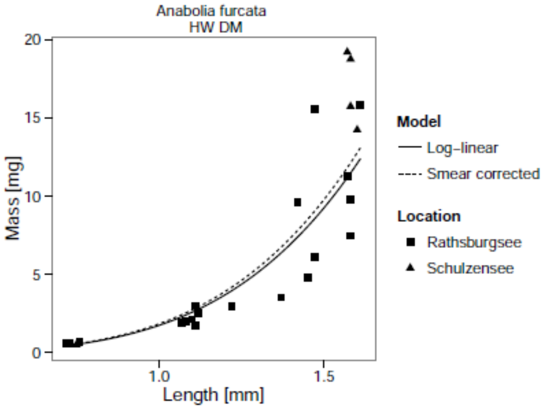
Odonata

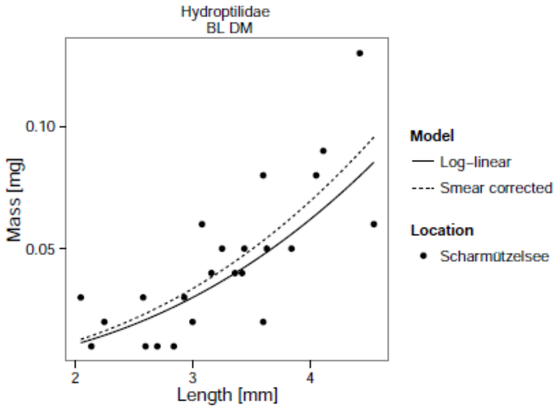


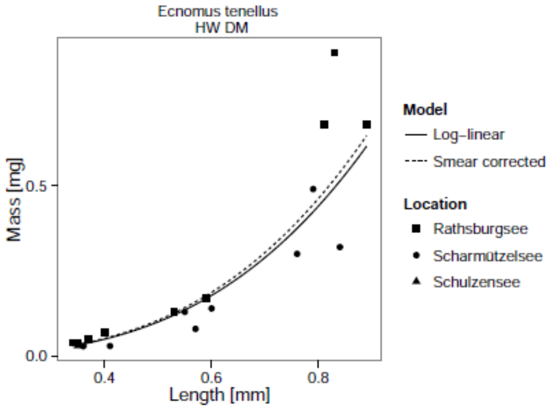


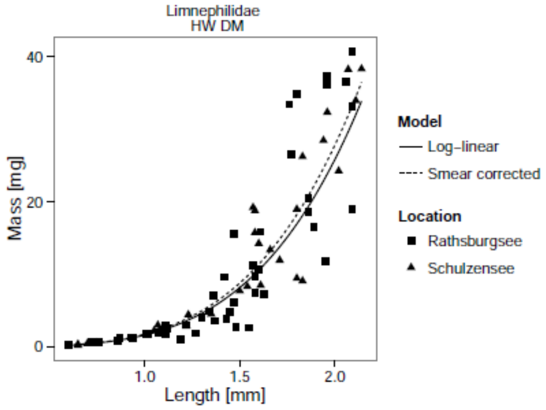


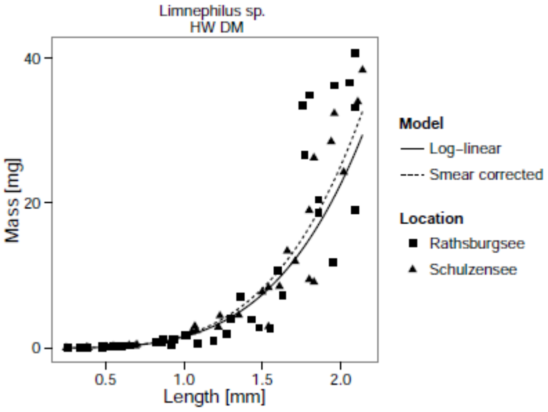
Trichoptera

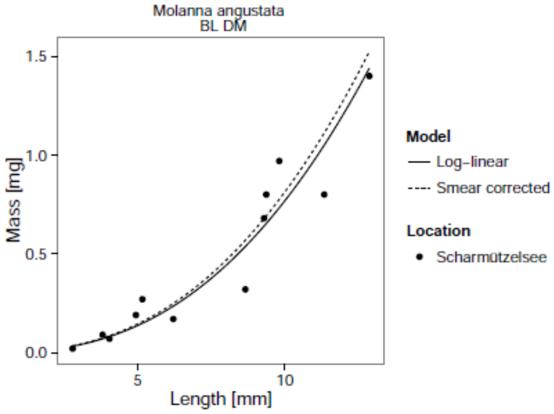


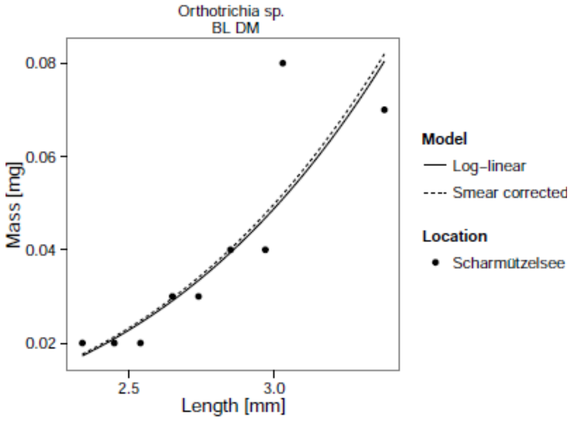


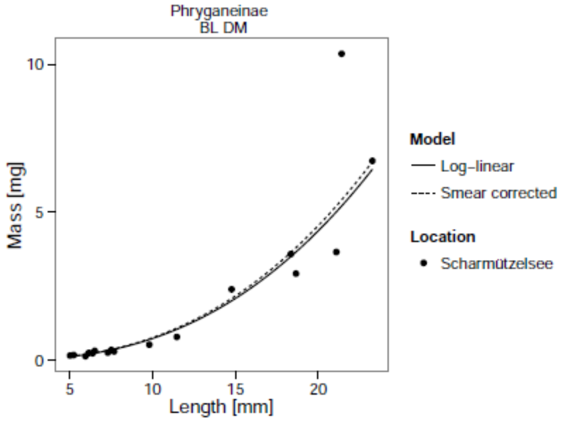


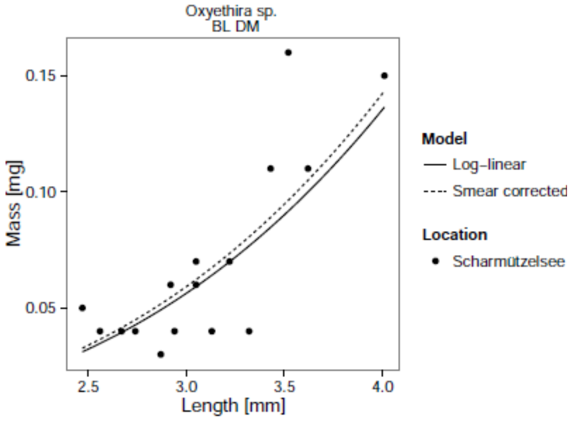


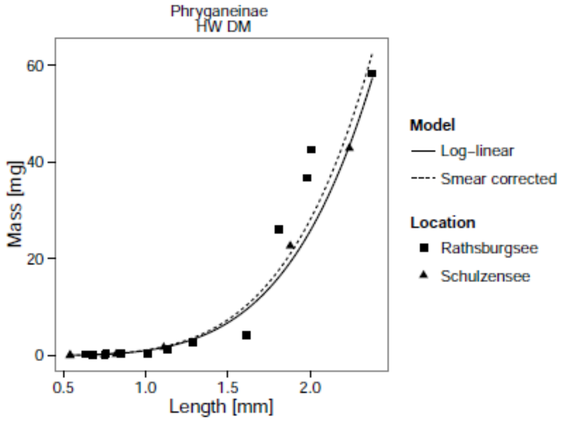


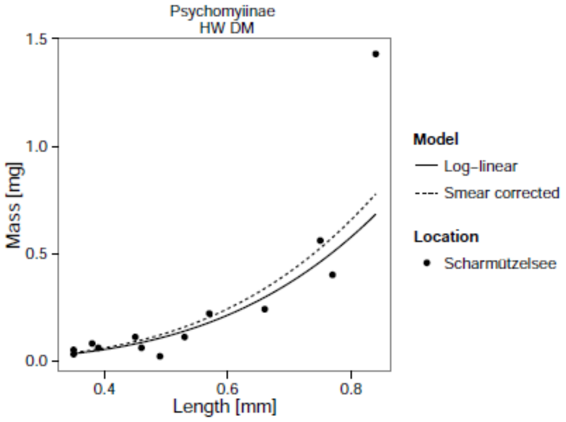



Orthotrichia sp.
BL DM
Mass [mg]
0.02
0.04
0.06
0.08
2.5
3.0
Length [mm]
Model
Log–linear
Smear corrected
Location
Scharmützelsee

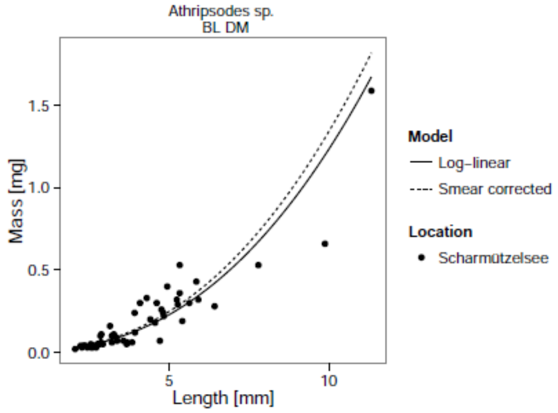

Phryganeinae
BL DM
Mass [mg]
0
5
10
5
10
15
20
Length [mm]
Model
Log–linear
Smear corrected
Location
Scharmützelsee

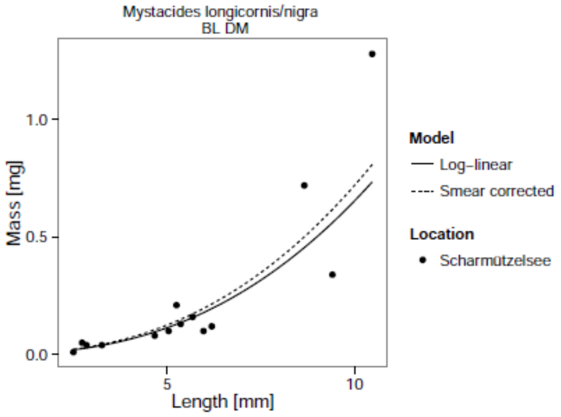

Oxyethira sp.
BL DM
Mass [mg]
0.05
0.10
0.15
2.5
3.0
3.5
4.0
Length [mm]
Model
Log–linear
Smear corrected
Location
Scharmützelsee

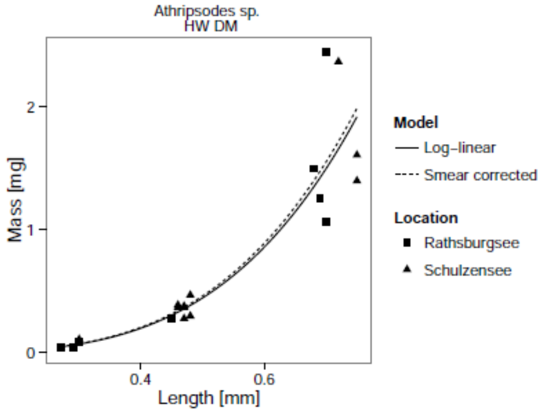

Phryganeinae
HW DM
Mass [mg]
0
20
40
60
0.5
1.0
1.5
2.0
Length [mm]
Model
Log–linear
Smear corrected
Location
Rathsburgsee
Schulzensee

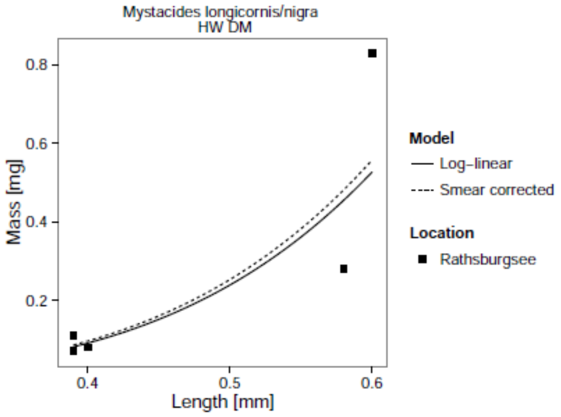

Psychomyiinae
HW DM
Mass [mg]
0.0
0.5
1.0
1.5
0.4
0.6
0.8
Length [mm]
Model
Log–linear
Smear corrected
Location
Scharmützelsee

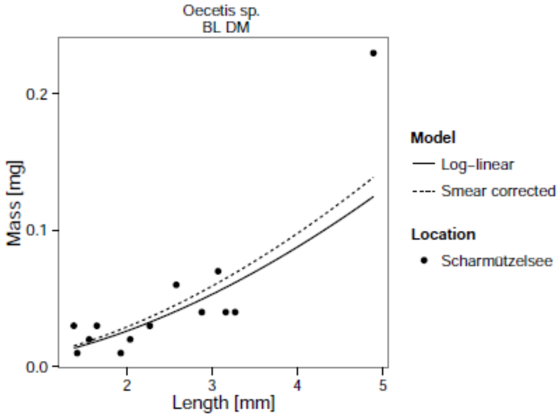
Leptoceridae

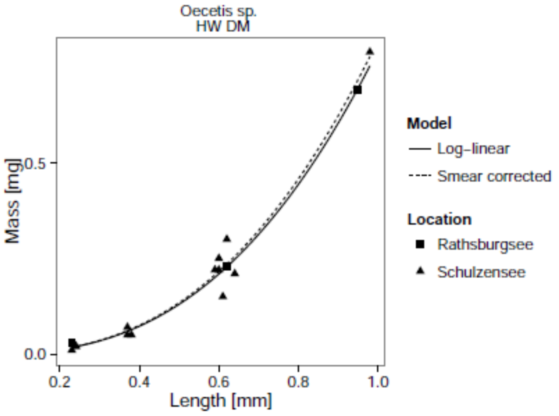












Polycentropodidae