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Effects of shoreline modification on lake littoral macroinvertebrate assemblages

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Thesis submitted in fulfilment for the degree of Doctor of Philosophy to the University of Dublin, Trinity College

2012

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Summary

The general aim of this study was to explore the effects of shoreline modifications on the structure of littoral macroinvertebrate assemblages in lakes, across the gradients of nutrients and alkalinity concentrations. Following this general aim, several aspects of the topic were investigated. The first aim was to establish whether shoreline habitat characteristics influence the composition of littoral macroinvertebrate assemblages. For this purpose, characteristics of shoreline habitats were recorded using the Lake Habitat Survey and associated with the assemblages at each site across six studied lakes. The relevance of specific shoreline features in structuring the macroinvertebrate composition was estimated. The aim was, therefore, to establish the relative influence of shoreline features on the composition of macroinvertebrate assemblages, with special attention to diversity-related characteristics of the shorelines. Results indicated that the community composition of the littoral macroinvertebrates was affected by morphological features of the shoreline zone when the effects of nutrients and alkalinity were taken into account. However, shoreline features were less important in structuring the macroinvertebrate assemblages than the chemical and physical properties of the water column. In addition, pressures related to anthropogenic activities and hydrological pressures were demonstrated to have influence on the composition of the littoral assemblages. Among the habitat features, the macrophyte- and substrate-related diversity features were most important for structuring the macroinvertebrate assemblages across Hab-plots. Aside from the direct effect of the littoral zone features, macorinvertebrate assemblages were influenced by riparian zone land-cover.

The second aim was to assess the impact of riparian and littoral morphological modification on littoral macroinvertebrate assemblages using diversity and abundance measures in generalised and simple linear mixed-effects models. Within this goal, the effect of morphological modification was estimated, while accounting for the effect of other environmental variables including the concentrations of nutrients. According to the results of the mixed-effects models, diversity measures of macroinvertebrate assemblages were affected by shoreline modifications, when unmodified and modified littoral shorelines were compared and after the effects of other environmental factors were accounted for. In contrast, abundances of assemblages from modified riparian zone were increased compared with assemblages from unmodified and modified littoral shorelines. TP concentrations were demonstrated to negatively affect the taxon richness and

Margalef diversity index of littoral macroinvertebrate assemblages, while the abundances were not affected. According to the results of the taxon richness model, the response of the assemblages to anthropogenic pressures (nutrient enrichment and shoreline modifications) varied depending on the type of mesohabitat. Moreover, nutrient enrichment was demonstrated to reduce the differences among the assemblages from distinctive mesohabitats. Surprisingly, there was no interaction between the effects of TP concentrations and shore modifications on either diversity measures or abundances of littoral macroinvertebrates.

The third aspect of this study was to elucidate the effects of shoreline modifications using the ecological traits of littoral macroinvertebrate assemblages. This compared the efficiency of two different approaches in assessment of shoreline modifications using littoral macroinvertebrates. The first approach was based on the resemblance matrix of the composition of macroinvertebrate assemblages and the second approach was based on the specific preferences of individual taxa toward mesohabitat types. Since the second approach reflects the response from the autecological information of the species, it was, therefore, expected to provide more insight into the mechanisms of shoreline modification pressure. Correspondingly, Indicator Value analysis and consequently applied mixed-effects model revealed taxa with specific mesohabitat preferences to be affected by the complexity of the littoral zones in oligotrophic and mesotrophic lakes. Based on these results, stenotopic species (habitat specialists) are proposed as the key to understanding the mechanisms of the impact of morphological alterations along littoral zones of lakes without high nutrient enrichment. Finally, it could be suggested that metrics based on autecological information of macroinvertebrate taxa have potentially higher sensitivity for identifying the impact of altered shoreline morphology than community structure and individual indicator taxa.

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1. Introduction

1.1 General research aims

The general aim of this study was to explore the effects of shoreline modifications on the structure of littoral macroinvertebrate assemblages in lakes, across the gradients of nutrients and alkalinity concentrations. Following this general aim, several aspects of the topic were investigated. The first aim was to establish whether shoreline habitat characteristics influence the composition of littoral macroinvertebrate assemblages. For this purpose, characteristics of shoreline habitats were recorded using the Lake Habitat Survey and associated with the assemblages at each site across six studied lakes. The relevance of specific shoreline features in structuring the macroinvertebrate composition was estimated. The aim was, therefore, to establish the relative influence of shoreline features on the composition of macroinvertebrate assemblages, with special attention to diversity-related characteristics of the shorelines. Since diversity features provide the basis for conservation of a lake ecosystem, the connection between these features and actual communities is of high importance for conservation management.

The second aim was to assess the impact of riparian and littoral morphological modification on littoral macroinvertebrate assemblages using diversity and abundance measures. Within this goal, the effect of morphological modification was estimated, while accounting for the effect of other environmental variables including the concentrations of nutrients. Eutrophication is one of the major pressures in lake ecosystems. It was, therefore, important to distinguish between the effects of the two pressures: shoreline modification and nutrient enrichment.

The third aspect of this study was to elucidate the effects of shoreline modifications using the ecological traits of littoral macroinvertebrate assemblages. This compared the efficiency of two different approaches in assessment of shoreline modifications using littoral macroinvertebrates. The first approach was based on the resemblance matrix of the composition of macroinvertebrate assemblages and the second approach was based on the specific preferences of individual taxa toward mesohabitat types. Since the second approach reflects the response from the autecological information of the species, it was, therefore, expected to provide more insight into the mechanisms of shoreline modification pressure.

1.2 Thesis structure

The thesis is laid out as follows:

- **Chapter 1** explains the main aims of the study and introduces the background information on littoral shoreline habitats, the Water Framework Directive, lake habitats surveying, littoral benthic macroinvertebrates and shoreline modifications.
- **Chapter 2** describes the studied lakes, general field and laboratory methods, and the main steps within the statistical analysis.
- **Chapter 3** assesses the importance of shoreline habitat variability in structuring the littoral macroinvertebrate assemblages in lakes.
- **Chapter 4** explores the effects of shoreline modification and nutrient enrichment on the diversity and abundance of lake littoral macroinvertebrates.
- **Chapter 5** investigates whether the approach based on autecological information is better at capturing the effect of shoreline modifications than the approach based on taxonomic composition of littoral macrobenthic assemblages in lakes.
- **Chapter 6** discusses the general findings of the thesis and highlights the main conclusions of the research.

1.3 Lake shoreline habitats

Freshwater species and habitats are assumed to be amongst the most threatened in the world (Millennium Ecosystem Assessment, 2005). The main threats to the health of freshwater ecosystems are catchment land-use disturbances, alterations of hydrological regimes and introductions of non-native species; therefore appropriate management of activities related to these threats should have positive effects for conservation of freshwater bodies (Saunders *et al.*, 2002). The importance of the preservation of the littoral zone of shorelines is underlined by the fact that littoral communities provide a range of functions in lake ecosystems (Schmieder, 2004). The operational definition of a lakeshore zone (here lake shoreline), given by Rowan *et al.* (2004), includes littoral, exposed shore and riparian zone, and it is specific for each lake because of the differences induced by bedrock geology, mode of formation, age, depth, shape, surface area, and water level fluctuations. Physical aspects of shoreline habitats play an important role in shaping the structure and functions of aquatic ecosystems (Kalff, 2001). Littoral zones of lakes usually contain a number of habitat patches (Tokeshi, 1994) and can be described as a mosaic of mesohabitats (White & Irvine, 2003). Mesohabitats arise through the interactions of hydrological and geomorphological forces, originally defined as medium-scale habitat patches in streams by Armitage *et al.* (1995). Complexity of lake ecotones between water and land (Schiemer *et al.*, 1995) poses a challenge for robust classification of physical habitats in the littoral, riparian and exposed shore zones.

There have been many scientific studies devoted to the exploration of the complex relationships between habitat characteristics and residential biota (e.g., Liddle & Scorgie, 1980; Tolonen *et al.*, 2001; O'Toole *et al.*, 2008; Rosenberger *et al.*, 2008). In recent years, many restoration programmes in developed countries have led to improved water quality. At the same time, the impact of pressures other than the organic pollution became apparent (Sondergaard & Jeppesen, 2007). For example, morphological alterations of the shoreline zone are considered to be as widespread as eutrophication according to research conducted in U.S. northeastern lakes by Whittier *et al.* (2002).

1.3.1 The Water Framework Directive

Hydromorphology may be defined as the form, structure and hydrological regime of surface waters (Rowan *et al.*, 2004). This definition incorporates the physical and chemical properties of water which, meanwhile, support the functioning of an aquatic ecosystem. In this view, hydromorphology comprises both forms and processes which shape the physical structure of habitats in the water body, and is focused on exploration of the complex interactions between water and sediments.

The EU Water Framework Directive (European Commission, 2000), an integral legal act in the field of EU water policy, has introduced a qualitatively distinct approach to water quality assessments by establishing three aspects of quality elements (biological, hydromorphological and physicochemical). Hydromorphology, as defined by the Directive, comprises hydrological regimes and morphological conditions of lakes, among other inland water bodies. Hydrological regime is defined by the following elements: quantity and dynamics of water flow, residence time and connection to the groundwater body. Lake depth variation, quantity, structure and substrate of the lake bed, and structure of the lake shore present morphological conditions of a water body. These elements are jointly defined as the hydromorphological elements supporting the existing biological features. The uniqueness of the Directive lies in the fact that it emphasises the importance of the aquatic biota in the assessments of the quality of aquatic ecosystems and the need for an integral ecosystem approach (Logan & Furse, 2002). The purpose of the Directive is to establish a framework for protection of lakes and other water bodies. Moreover, the primary goal of the Directive is to maintain or achieve good ecological status of all natural water bodies by the year 2015. In order to achieve this, biological, hydromorphological and physicochemical quality elements should correspond to the proposed quality standards. For the hydromorphological quality elements, only requirements for high status are defined in Annex V in the Directive. Following the definition, high status is reflected through the totally to nearly undisturbed conditions regarding the hydrological regime – the quantity and dynamics of flow, level, residence time, and the resultant connection to ground waters. Morphological conditions, defined as the lake depth variation, quantity and structure of the substrate, and both the structure and condition of a lake shore zone correspond totally or nearly totally to the undisturbed conditions. Moreover, hydromorphological quality related to good or moderate status is defined as conditions consistent with the respective status specified for the biological quality elements.

The process of ecological assessment of a lake should begin with the identification and classification of the lake type according to non-biological attributes (Bragg *et al.*, 2003). In addition, natural hydromorphological and physicochemical conditions, together with corresponding biological reference conditions are to be established. The hydromorphological features of lakes have been assessed by many authors (e.g., Bragg *et* *al.*, 2003), and recently a number of projects funded by policy agencies such as SNIFFER (Scotland and Northern Ireland Environmental Forum for Environmental Research) have focused on assessing the hydromorphological status of inland water bodies (Rowan *et al.*, 2004).

1.3.2 Lake habitat surveying

Although the assessment of hydromorphology is not one of the mandatory tasks set by the Water Framework Directive, the development of methods for the assessment of hydromorphological conditions will contribute to the identification of pressures coming from hydromorphological alterations. In the course of the implementation needs of the WFD, the European Committee for Standardization (CEN) has recently developed standards for assessing the hydromorphological features of rivers (CEN, 2003). Furthermore, trials of the Lake Habitat Survey technique have showed that this technique could contribute to the future design of European standards for assessment of lake hydromorphology (Rowan *et al.*, 2006). Techniques for assessing lake hydromorphology range from large-scale (e.g., remote sensing and database information) to small-scale (e.g., field survey). For overall assessment, it would be the most appropriate to use a combination of techniques.

The development of assessment techniques for hydromorphological features in European lakes has been given an impetus because of the objectives of the Water Framework Directive. Previously, the US Environmental Protection Agency developed procedures for monitoring physical characteristics of lakes, as part of the Environmental Monitoring and Assessment Program (EMAP) group for Surface Waters (Baker *et al.*, 1997). This is considered to be the most significant standard tool for lake habitat assessment (Rowan *et al.*, 2006). The general purpose of the method is to record physical characteristics of lake habitats and shoreline disturbances, in order to rate the physical habitat integrity. According to EMAP – FOML (Field Operation Manual for Lakes) principles, physical habitat information is collected through field surveys which cover the riparian and littoral habitats, measurements of temperature and dissolved oxygen at the index site, and desktop-based surveys from which data such as lake surface area and catchment land use can be derived. On these premises, the results of surveys provide a view into the relationship between indirect (catchment-scale) influences and direct (local) forces that affect aquatic biota (Baker *et al.*, 1997). The procedure also identifies the major or simply observable activities and stressors and provides subjective judgement of their impact on lakes.

A technique for recording of lakeshore features by Rowan *et al.* (2004), called Lake Habitat Survey (LHS) was introduced with intentions to contribute to the objectives of the Water Framework Directive. LHS provides a standard method for characterising the physical habitats of standing waters: lakes, reservoirs and ponds. LHS comprises quantitative and semi-quantitative observations of the structure of the bank, vegetation and anthropogenic disturbances of the shoreline zone. Measurements and observations in the littoral zone deal with water depth, bottom substrate, and near-shore fish and macrophyte cover. The survey is designed to assess the whole-lake hydromorphological features, with data derived from detailed recording of the shoreline features at chosen sites of a lake, together with a meso-scale survey including riparian land-use, records of the pressures and modifications to the hydrological regime, temperature and oxygen gradient at the deepest point of the lake (Index-site), and basic background information about lake depth, surface and catchment area, altitude and conservation status (Rowan *et al.*, 2006). The output data from LHS survey comprise two indices: Lake Habitat Quality Assessment (LHQA), a quantitative measure of habitat quality evaluated through observable diversity, naturalness of physical structures and the presence of ecologically valuable habitat features, and Lake Habitat Modification Score (LHMS) which accounts for the morphological disturbances and introduced species present along the lakeshore, represented as a single value for the whole lake. During construction of the LHS methodology, expert opinions were used to decide about significance of distinct pressures and identify thresholds leading to likely degradation of the ecological state (Rowan *et al.*, 2006).

A modified LHQA has been tested against species richness and abundance of littoral macroinvertebrate communities within 10 sampling sites (Hab-Plots) in a single lake (McGoff & Irvine, 2009). The results showed that there is positive correlation between the measurements of habitat quality and macroinvertebrate taxa richness of both adults and larvae found in the littoral zone. Moreover, the results showed that macrophytes and complexity of riparian vegetation were most likely drivers for a modified LHQA score, which may be misleading in cases where habitats of naturally low diversity are present, for example in wave-washed rocky shores of pristine lakes.

1.4 Littoral benthic macroinvertebrates

1.4.1. Macroinvertebrates as indicators of ecological quality

Macroinvertebrates may be defined as organisms that inhabit bottom substrata (e.g. sediments, logs, macrophytes, filamentous algae) or the surface of freshwater for, at least, one part of their life cycles (Kalff, 2001). The structure of macro-invertebrate communities is known to vary in lakes of different types or lakes that possess different pressures. Numerous biotic and abiotic factors affect the distribution of macro-invertebrates. Eutrophication is regarded as the main pressure to lake ecology (Schindler, 2006).

Benthic macroinvertebrates have often been used as biological indicators of aquatic ecosystem stress (Atrill, 2002). Although chemical and physical measurements have traditionally been used to evaluate the ecological quality of water bodies, biotic elements in an aquatic system would appear to represent ecological conditions more faithfully than water chemistry, providing an indication of past as well as current conditions. The use of macro-invertebrates in the assessment and monitoring of water bodies has several advantages, including their ubiquitous distribution and abundance, sedentary nature, the relatively large number of species, high respiration rates, and long life-histories, and well developed qualitative sampling methods and taxonomy (Rosenberg & Resh, 1993). While a few methods of ecological status assessments are based on monitoring species presence or absence (Hellawell, 1986), a community-based analysis is more prevalent (Attrill, 2002). The main advantage of the community-level approach is highlighted by viewing a community as an integrative multispecies indicator of stressors in aquatic ecosystems (Attrill, 2002).

Many biotic scores exist to aid the assessment of river ecological status using macro-invertebrates, but the majority of these are not appropriate for use in lakes (Donohue *et al.*, 2009a). Research regarding the potential of lake littoral macro-invertebrates for classification purposes is increasing, however, owing to the requirements of the WFD (European Commission, 2000), and this may examine the structure of macro-invertebrate communities present or indicator species. Finally, knowledge about the habitat requirements of littoral macroinvertebrates is still limited (Webb & Lott, 2006).

1.4.2 Littoral macroinvertebrates in the assessment of lake pressures

The effect of habitats on benthic communities has been speculated to be pronounced in the littoral zone of lakes, owing to the often more diverse and complex habitats present in this part of a lake ecosystem (Strayer & Findlay, 2010). Tackling the issue of multi-pressure situations is important because of possible implications for environmental resource management (Whittier *et al.*, 2002). Furthermore, recognising the scale of the pressure is required for effective restoration programmes. Distinguishing between, for example, the effects of water quality and the effects of habitat structure on biological conditions is important for adequate stream management (Davies *et al.*, 2000). Since many ecosystems experience impact of more than one pressure at the same time, the question arises of ranking those pressures on a scale of their relative importance. At the community level, careful selection of indicators might be crucial, since a recent survey of the effects of trophic states in German (Brauns *et al.*, 2007b) and Finish (Tolonen *et al.*, 2001) lowland lakes, showed that littoral macroinvertebrate communities were more dissimilar among different habitat types then among different trophic states. Contrasting results were shown by White & Irvine (2003) who found that physical, chemical and other environmental variables have a greater overall effect on littoral macroinvertebrates than the type of substrate. These contrasting findings clearly emphasise the necessity for further studies on the relevance of littoral macroinvertebrates as indicators of trophic state, as well as their potential for indicating pressures related to shoreline morphology alteration. Moreover, the importance of the scale of observation must not be neglected in impact assessments, especially because of the "noise" induced by the multitude of influencing environmental factors. White & Irvine (2003) suggested this obstacle could be avoided by using the mesohabitat scale and by sampling the well-defined types of visually distinctive habitats in ecological classification assessments.

1.5 Shoreline modifications

The shoreline zone of lakes is commonly affected by anthropogenic activities (Brauns *et al.*, 2007a; De Sousa *et al.*, 2008; Rosenberger *et al.*, 2008). The observable effect of these modifications is most likely related to changes in the structure of macrophyte communities. Macrophytes were identified as an important driver in the assessment of habitat quality scores (LHQA), together with complexity of riparian vegetation (McGoff & Irvine, 2009). It was previously found that habitats which contain macrophytes provide greater taxa richness and abundance when compared with non-vegetated mesohabitats

(Kornijow, 1989; White & Irvine, 2003). This can be explained by high complexity of littoral habitats (Johnson & Goedkoop, 2002) which provide shelter from fish predators (Diehl, 1992) and physical disturbances (Gabel *et al.,* 2008). Among the other biotic components of lakes, impact of shoreline modifications was studied firstly on littoral fish communities (Jennings *et al.*, 1999) most likely because of their commercial importance.

An example of the effect of shoreline modifications on littoral macroinvertebrate assemblages is given by Brauns *et al.* (2007b). They investigated the effect of three types of man-made shoreline modifications on littoral macroinvertebrates by comparing communities from morphologically altered sites with those from non-altered littoral zones in lowland lakes of different trophic states and relative proportions of altered shores. They used indicators of community structure such as taxa richness and abundance (of taxa and functional feeding groups) to show the difference between the natural and altered habitats. Among tested habitats, beaches had the most significant impact on taxa richness and abundance. Interestingly, communities from artificial rip-rap structures were not significantly different from those from natural sites, which was most probably owing to their resemblance to the natural habitats. The authors concluded that species known as habitat specialists were most severely affected by shoreline modifications, if these resulted in decreased number of habitat types. Moreover, the impact of the shoreline modifications on littoral macroinvertebrates depended on the extent to which the habitat heterogeneity was reduced. Finally, the study by Brauns *et al.* (2007b) promoted the usefulness of habitat specialists as indicators of stress in the assessment of morphological modification.

2. Materials and methods

2.1 Study lakes

The effects of morphological modification along lake shorelines were explored across nine Irish lakes (Figure 2.1) during 2009. From a list of 60 candidates, the lakes were chosen to represent a nutrient gradient (Total Phosphorus (TP) concentrations between 9 and 81 μg l^{-1}, based on averaged measurements from the previous 2-7 years, depending on the lake in question), while alkalinity values varied in the moderate to high category (45 – 119 mg $CaCO_3$ l^{-1}) (Table 2.1). Morphological modifications in littoral and riparian zones were identified *prior to* sampling using Ordnance Survey topological maps. According to their geographic position and morphological characteristics, selected lakes were categorised as shallow lowland lakes having a mean depth of up to 5.4 m, and reaching maximal altitude of 90 m (Table 2.2).

Table 2.1. Water chemistry values from each of the studied lakes, measured in April/May 2009.

Lake	pH	Alkalinity (mg $CaCO_3$ L^{-1})	Colour (PtCo)	Conductivity (μS cm^{-1})	TP* (μg L^{-1})	TOC (mg L^{-1})	TN (mg L^{-1})
Muckno	7.33	61.04	40	235	43.3(45.4)	8.1	1.6
Oughter	7.63	78.52	55	235	46.5(62.7)	10.3	0.8
Brackley	7.44	45.16	86	146	42.4(37.8)	9.9	0.8
Garadice	7.63	66.72	91	183.9	32.8(26.8)	9.9	0.8
Scur	7.44	57.36	138	157.7	96.4(80.7)	10.5	0.7
Rinn	7.78	116.04	143	279	83.9(77.9)	14.3	1.2
Rea	8.26	245.96	19	299	12.3(8.8)	4.2	0.7
Carra	7.97	91.56	29	493	15.2(11.5)	5.9	0.8
Cullin	8.39	119.08	65	268	17.2(29.1)	10.7	0.9

* - historical TP values given in parentheses (averaged values for previous 2-7 years)

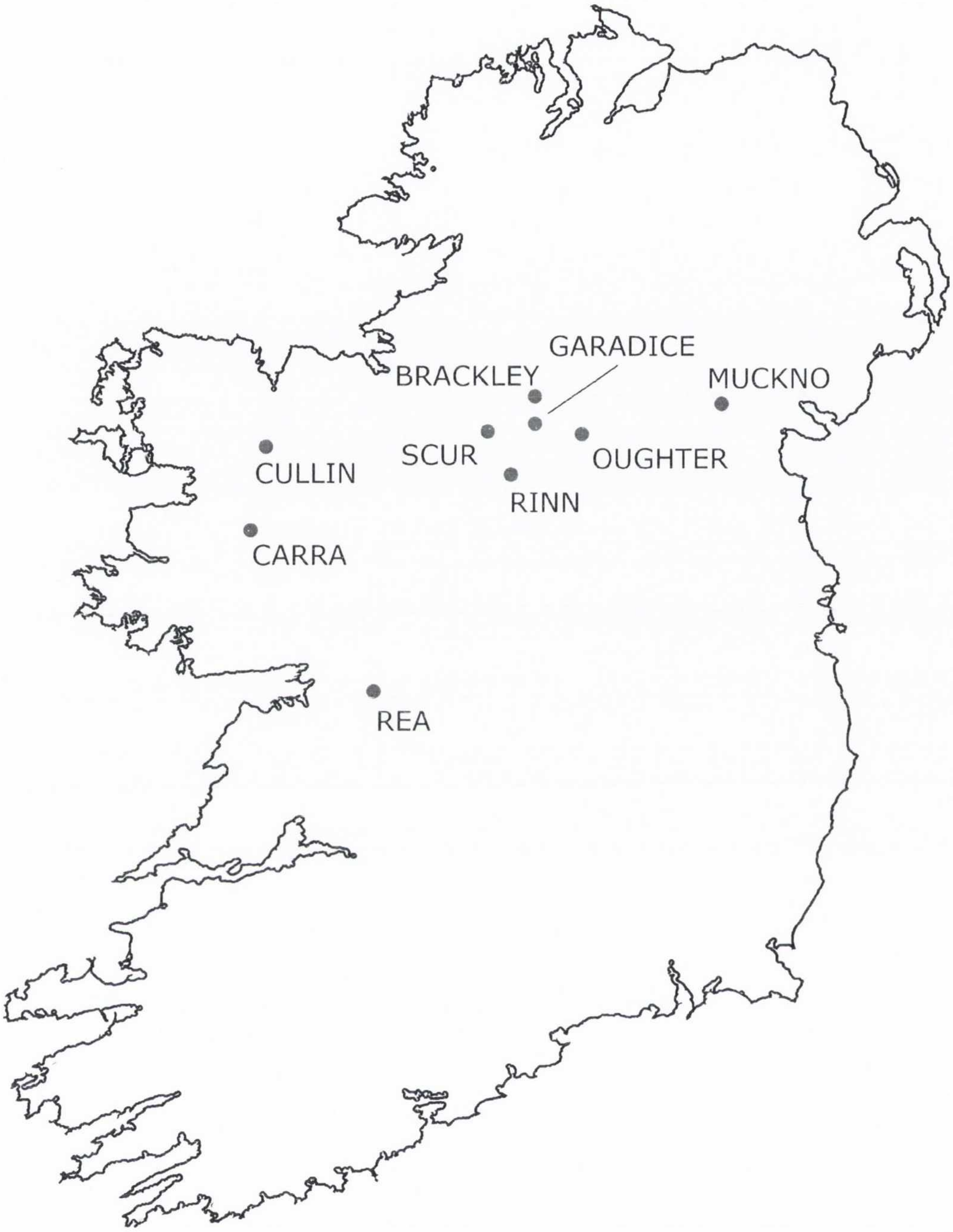


Figure 2.1. Locations of the studied lakes across the island of Ireland

Table 2.2. Morphometric features and geographic position of the studied lakes

Lake	Lake area (km^2)	Mean depth (m)	Eastings	Northings	Lake_altitude (m)
Muckno	3.5434	5.4	285627	318883	90
Oughter	6.5821	2.6	235720	306792	47.7
Brackley	1.6646	2.34	219258	320580	58.3
Garadice	3.8758	2	218496	311341	49.9
Scur	1.1323	2	203070	308602	63.6
Rinn	1.6452	2	210133	292700	37.6
Rea	2.9988	3.99	161513	215479	84.6
Carra	15.5787	1.75	118999	272739	15
Cullin	10.9	5	122877	302771	7.9

2.2 Sampling protocol and laboratory processing

In order to assess the effect of shoreline morphology and modifications on littoral macroinvertebrates, shorelines of nine lakes were sampled extensively in April/May and August/September 2009. Physical characteristics of the shorelines were recorded at each site for the nine lakes, using the Lake Habitat Survey (LHS) protocol (Rowan *et al.*, 2004; 2006). Sites were photographed from the lake, and GPS coordinates were recorded. Two different sampling protocols were used to collect macroinvertebrate samples: mesohabitat- or composite- scale sampling. Different sampling protocols allowed the response of littoral macroinvertebrate assemblages to the pressures to be captured using either habitat-specific signals (based on mesohabitat sampling) or whole-site signals (based on composite sampling) of the investigated littoral macroinvertebrate assemblages.

2.2.1 Mesohabitat-scale (habitat-specific) sampling

This sampling protocol was aimed at capturing the habitat-specific signal within a site. The method entailed sampling three mesohabitats at designated sampling site as defined in White & Irvine (2003). The mesohabitat was considered as any habitat (macrophytes, sand, stone, concrete or grass) that occupied at least 10% of the total site area.Each mesohabitat was sampled for 20 sec across an area of $1m^2$. According to this approach, different types of mesohabitats such as macrophytes, sand, stone, concrete or grass were identified within each site *prior to* sampling. At each site, three samples were taken from different mesohabitats in order to resemble the diversity of the mesohabitats within the site. If the site comprised only one type of mesohabitat, three 1m^2 areas were randomly chosen for sampling in order to have a balanced design.

2.2.2. Composite-scale (whole-site) sampling

The second sampling protocol was aimed at capturing the whole-site signal. The method consisted of collecting macroinvertebrates from different mesohabitats proportionally and across the whole site for one minute, allowing for the multihabitats approach, described in the AQEM Manual (2002). The purpose of the multihabitats approach was to collect macroinvertebrates from as many dominant mesohabitats present within a site. The dominant mesohabitats were considered to be any mesohabitats occupying at least 10% of the area of within the whole site. Macroinvertebrates were collected from the dominant mesohabitats proportionally, meaning the sampling effort was divided proportionally among the dominant mesohabitats at the site.

2.2.3 Field sampling, sorting and identification

For both methods, macroinvertebrate samples were collected with a standard FBA handnet with a mesh size of 0.5 mm, using kick sample technique. The technique comprises collecting the substrate from the bottom, by sweaping the net across the bottom disturbed by vigorous kicks and shuffles of the feet, during the specific amount of time and across the specific area of the habitat type. Although the kick sample technique is of qualitative type, it is commonly used in freshwater research, especially for diversity-related explorations. Samples were preserved on site, with 70% Industrialised Methylated Spirit, and stored in dark plastic bottles for later processing in the laboratory.

In the laboratory, each sample was sieved to remove the alcohol and the sample was spread over a white sorting tray with the addition of water. Macroinvertebrates were removed from the sample and sorted into broad morphological types. Afterwards, they were placed in small glass bottles labelled and stored for later identifying. Macroinvertebrates were preserved in 95% Industrialised Methylated Spirit. Identification was carried out using an Olympus binocular microscope SZ X12, with a fibre optic light source Olympus KL 1500 LCD. Individuals were identified to the highest taxonomical resolution possible, using the following keys: Elliott (1977), Macan (1977), Elliott & Mann (1979), Richoux (1982), Fitter & Manuel (1986), Elliott *et al.* (1988), Friday (1988), Savage (1989; 1999), Gledhill *et al.* (1993), Edington & Hildrew (1995), Miller (1996), Nilsson (1997), Reynoldson & Young (2000), and Wallace *et al.* (2003). In most cases, species or genus level was recorded. Hydracarina, Hydrozoa and Porifera were excluded from the taxonomic analysis. The insect family Chironomidae, some Coleoptera larvae and subclass Oligochaeta were not identified to a higher taxonomic resolution.

2.3 Water chemistry measurements

Water samples were collected from every lake at three random sites in April/May 2009. After collection, water samples were stored in a dark, cold place and analysed within 5 days for alkalinity, conductivity, pH, colour, total phosphorus (TP), total nitrogen (TN), and non-dissolved total organic carbon (TOC). All chemistry analyses were performed in the laboratory.

Alkalinity was measured by titration with 0.01M H_2SO_4 to an end point of pH 4.5 within two minutes. This is recommended by Mackereth *et al.* (1989) for samples with an alkalinity higher than 20 mg l^{-1} $CaCO_3$. The volume of H_2SO_4 at the end point was recorded. The calculation used was Equation 1:

$$\text{Alkalinity (mg l}^{-1}\text{ CaCO}_3) = \text{ml titrant} * 20 \qquad \text{(Equation 1)}$$

Conductivity and pH were measured for the samples using a standard pH meter (Jenway 4330 Conductivity and pH meter). The colour of each sample was measured using a Hach DR5000 spectrometer.

Analysis of total phosphorus was performed according to the method described by Eisenreich *et al.* (1975). The method comprised of making up a digestion reagent by dissolving 6 g of $K_2S_2O_8$ in c. 80 ml of double distilled water (D.D.W.), containing 10 ml of 3.6 N H_2SO_4. These were dissolved using a sonicator and the reagent was made up to 100 ml using D.D.W. A mixed reagent was made up by adding 113.5 ml 3.6 N H_2SO_4, 25 ml of antimony stock, 25 ml molybdate stock and 0.2 g ascorbic acid in order, and mixing well after each addition. The reagent was then made up to 100 ml using D.D.W. Standards of 0 mg l^{-1}, 0.01 mg l^{-1}, 0.025 mg l^{-1}, 0.05 mg l^{-1}, 0.1 mg l^{-1} and 0.2 mg l^{-1} of total phosphorus were made up. 25 ml of standards and samples were pipetted into autoclaveable bottles and 5 ml of digestion reagent added. These were loosely capped before autoclaving for 30 minutes at 15 psi. Once cooled to room temperature 5 ml of the digested sample was pipetted into a test tube, with 1 ml of mixed reagent. The absorbance was measured at 882 nm on a spectrophotometer (Hach DR5000) after the colour had developed for ten minutes. The concentration could then be calculated from the standard curve according to(eq. 2.):

$$\text{Concentration } \mu gl^{-1} = (\text{absorption} - \text{c intercept}) / \text{slope} * 1000 \qquad \text{(Equation 2)}$$

For TN and TOC analysis water samples were acidified by adding 1-2ml of HCL on site. The samples were analysed using the method of high temperature digestion on Elementar Analyzer (vario TOC cube).

2.4 Statistical analysis

2.4.1 Exploratory data analysis

All statistical analyses regarding the data exploration were performed using the computer language R, version 2.13.0 (R Development Core Team, 2011). Boxplots and Cleveland dotplots were used to identify unusual patterns in the dataset and to check for possible outliers in both response and explanatory variables (Zuur *et al.*, 2010). Since the explanatory variables had different scales of magnitude, they were standardised by subtracting each value from the mean value and then divided by the standard deviation of the variable in question, with the exception of geomorphological values "eastings" (longitude – distance from east coast of Ireland) and "lake area", which were ranked instead. In the case of TP concentrations, historical values were used in the analysis instead of the ones obtained by the measurements. This was done in order to account for the seasonal fluctuations in nutrients concentrations owing to primary production etc.

Explanatory variables were initially grouped into three categories – nutrients (TOC, TN and TP), physico-chemical (alkalinity, colour, and conductivity), and geomorphologically related variables (eastings and lake area). Environmental variables within the first two groups were inspected for correlations with a Pearson product-moment correlation matrix, since strong correlations among explanatory variables may impact estimations of the coefficients in multiple regression (Montgomery *et al.*, 2006). It was expected that variables from the same category would be correlated among one another. For example, alkalinity and pH in the lake water are clearly related (Irvine *et al.*, 2002). Consequently, variables which were least correlated among one another were selected for further analyses. The chosen combination of environmental variables was tested for multicollinearity using Variance Inflation Factors (VIF) according to Montgomery *et al.* (2006). Explanatory variables with highest VIF values were removed from the set until the VIF values of each variable was ≤ 3 (Zuur *et al.*, 2010). Finally, the following set of environmental variables had appropriately low VIF scores (Table 2.3): alkalinity, TP, eastings and lake area.

Table 2.3. Variance inflation factors of continuous explanatory variables in mixed-effects models

Explanatory variable	VIF score
Lake area	1.765952
Alkalinity	1.748206
Eastings	1.902479
TP concentrations	1.927943

The selected set of variables was used to generate the full models. In order to decrease the number of unnecessary variables within the initial full model, potential interactions between each of these covariates and shore type were examined using coplots and conditional boxplots.

2.4.2 Model selection and validation

R package "lme4" was used to fit simple linear and generalised mixed-effects models (Bates & Maechler, 2010). Mixed-effects models, in general, are useful in cases where it is needed to accommodate the spatial autocorrelation structure in the dataset (McCulloch & Searle, 2001). Generalised mixed-effects models have been proposed for analysing data with non-normal types of distribution and random effects (Bolker *et al.*, 2009).

Model selection, invariably for simple or generalised linear mixed-effects models, was performed using the information-theoretic approach (Burnham & Anderson, 2002). The model selection in the case of simple linear mixed-effects models was conducted following the protocol suggested in Zuur *et al.* (2009). In the case of generalised linear mixed-effects models, the selection procedure was conducted as outlined by Bolker *et al.* (2009). Generalised mixed-effects models were run with a probabilistic Poisson distribution, which is recommended for count data (O'Hara & Kotze, 2009; Zuur *et al.*, 2009). The full model was based on *a priori* hypotheses that included previously selected environmental covariates and their interactions, as well as the random terms accounting for the spatial hierarchy of the samples. Models were compared using backward and forward step-wise selection procedures (Whittingam *et al.,* 2006). The model selection procedure was based on the corrected Akaike's Information Criterion (AICc). Corrected AIC is an adjusted estimation of the AIC in cases where the total number of samples is less than three times the total number of estimated variables in the model (Burnham &

Anderson, 2004). Lower AICc values indicated more parsimonious models. If models differed by ≤ 2 positive AIC values (more complex – less complex model), then there was sufficient evidence to retain them, while higher differences indicated unreliable selections (Burnham & Anderson, 2004). In cases of nested models and when selecting the random part of a model, alternative likelihood-ratio tests were also used (Zuur *et al.,* 2009). The optimal structure of the random part of each model was decided depending on the results of likelihood ratio tests performed on nested models estimated using restricted maximum likelihood estimation (REML). The best structure of the fixed part was evaluated using likelihood ratio tests together with AICc values estimated using maximum likelihood estimation (ML). Values of coefficients from the most parsimonious model were estimated using REML. An α significance level of 0.05 was used for testing the statistical significance of the null-hypotheses in all analyses.

The final (most parsimonious) models were checked (validated) to verify the underlying statistical assumptions using the graphical methods. Homogeneity of variance and independence among samples were assessed by plotting the residuals (Appendix: Figures A.1- A.6), or plotting the residuals against the fitted values and against the explanatory variables, respectively. Normality was evaluated using Quantile-Quantile plots of residuals. Finally, all generalised models were checked for overdispersion, as suggested in Bolker *et al.* (2009).

3. Importance of habitat variability in structuring the macroinvertebrate assemblages across lake shorelines

3.1 Introduction

Complexity of lake ecotones between water and land (Schiemer *et al.*, 1995) poses a challenge for robust classification of physical habitats in the littoral, riparian and exposed shore zones. The Lake Habitat Survey (LHS) provides a method for characterising the physical habitats of standing waters: lakes, reservoirs and ponds (Rowan *et al.,* 2006). The method comprises qualitative and pseudo-quantitative observations of the structure of the bank, vegetation and anthropogenic disturbances of the shoreline. It provides a scoring of morphological features and quality of the littoral and riparian zones, including an estimate of the anthropogenic disturbance. The survey is designed to assess whole-lake hydromorphological features, with data derived from the detailed recording of shoreline features at chosen sites around the lake, together with the meso-scale survey including riparian land-use, records of pressures and modifications to the hydrological regime, and the temperature and oxygen gradient at the deepest point of a lake. In addition, basic background information on the lake depth, surface area, catchment area, altitude and conservation status is derived from maps and desk study (Rowan *et al.,* 2004; 2006). The output data from the LHS survey include two indices. The first is the Lake Habitat Quality Assessment (LHQA), a measure of habitat quality evaluated through observable diversity, naturalness of physical structure and the presence of ecologically valuable habitat features. The second index is the Lake Habitat Modification Score (LHMS) which accounts for existing hydromorphological modifications including shore zone modifications, intensive use, in-lake pressures, hydrological structures, pressure from erosion and introduced plant and animal species. During the development of the LHS methodology (Rowan *et al.*, 2004), expert opinions were used to: 1) agree about the likely significance of the individual pressures and 2) identify the thresholds leading to the likely degradation of ecological status.

Knowledge about the habitat requirements of littoral macroinvertebrates is still limited (Webb & Lott, 2006). Although land-water ecotones are valuable components of lake ecosystems because they provide a variety of habitats, their role in structuring the aquatic assemblages is rarely investigated when compared with the terrestrial or aquatic studies of diversity and habitat associations (Pieczyńska, 1990). Habitat structure in a variable environment affects stream macroinvertebrate assemblages in a complex way (Tokeshi &

Taniguchi, 2004). Lake shoreline complexity is also important in structuring littoral benthic communities (Johnson & Goedkoop, 2002).

The aim of this Chapter is to asses the relevance of the LHS for the littoral macroinvertebrate community composition by relating the habitat features recorded by the LHS to community multivariate metrics across randomly chosen sites in six lakes of contrasting nutrient concentrations. Specifically, goals were to:

1) Examine the structure of shoreline habitats across study lakes using LHS mesohabitat variables. The LHS provides the amalgamation of habitat characteristics which describe the essential morphological (physical) features of lake habitats. In terms of the shoreline zone, LHS metrics describe the characteristics of riparian, exposed shore and littoral habitats. Moreover, they provide information on existing human-induced disturbances, which are termed "human pressures" in the LHS field form.

2) Assess the importance of shoreline habitat features in structuring littoral macroinvertebrate assemblages. By associating the community composition with the environmental variables using canonical correspondence analysis it was possible to identify the LHS metrics that are likely to be important drivers of the community composition of the littoral macroinvertebrates in six of the studied lakes. This provides a test for the first hypothesis that the community composition of littoral macroinvertebrates is influenced by the morphological features of the shoreline zone, in addition to responding to the variation in TP concentrations and alkalinity.

3) Compare the relative importance of factors explaining the variation of the macroinvertebrate community composition. Earlier research on the Irish lakes (White & Irvine, 2003) suggested a greater effect of lake-specific physical, chemical and other environmental variables on the macroinvertebrate assemblages than that corresponding to the within-lake substrate type. Based on these findings, a second hypothesis was that the TP concentrations and alkalinity play more important roles in structuring the macroinvertebrate communities than habitat features.

4) Analyse the LHQA-associated metrics to identify which diversity features were important for structuring the macroinvertebrate assemblages across Hab-Plots.

3.2 Materials and methods

3.2.1 Shoreline habitat surveying

Shoreline habitat surveying was conducted in late August and early September 2009. Nine lakes were surveyed at ten evenly-spaced sites around each lake, following Rowan *et al.* (2006). Information about the physical characteristics of the shoreline, called Hab-Plot in the LHS filed form, was recorded at each site. A Hab-Plot comprises 15m of shoreline including the riparian zone extending 15m from the bank top, and the littoral zone as the area from the waterline to 10m offshore. The exposed shore, if present, is located between the riparian and littoral zone and may include beach and/or bank face (Rowan *et al.*, 2004). Detailed information about the features recorded on the LHS field form (Rowan *et al.*, 2004) comprises either numerical estimations, recordings of presence/absence of a certain feature, and categories or estimates of percentage classes of the areal coverage. In addition, all Hab-Plots were photographed both from the shore and from the lake. GPS coordinates were recorded at each site. The Hab-Plot survey was complemented by a lake-perimeter survey, which is intended to capture the most important shoreline characteristics and pressures up to 50m into the riparian zone, in-lake pressures and obvious modifications of the hydrological regime over the entire lake area.

The data collated in the LHS survey were used to calculate the Lake Habitat Quality Assessment (LHQA) and Lake Habitat Modification Score (LHMS). LHQA- and LHMS-associated metrics are presented in the Tables 3.1 and 3.2. The scores can range between 0 (lowest quality) and 108 (highest quality) for LHQA, and between 0 (least impacted) and 42 (most impacted) for LHMS. While previous LHS metrics were applicable at the whole-lake level, quantification of the habitat diversity and heterogeneity at the level of the individual Hab-Plots was performed using the Habplot Quality Assessment (HabQA) scoring following McGoff & Irvine (2009). This scoring system, originally developed from the Lake Habitat Quality Assessment (LHQA) of the LHS, was used to assess the habitat quality based on 13 site-specific elements. The maximum HabQA score achievable per site is 13, indicating the highest habitat quality, while the minimum is 0.

Table 3.1. LHQA-associated metrics and LHQA scoring (*sensu* Rowan *et al.*, 2004)

Lake Zone	Characteristic measured	Measurable feature
Riparian	Vegetation structural complexity	Proportion of Hab-Plots with complex or simple riparian vegetation structure
	Vegetation longevity/stability	Proportion of Hab-Plots with >10% cover of trees with DBH>0.3m
	Extent of natural land-cover types	Proportion of Hab-Plots with either natural/semi-natural woodland, wetland, moorland heath or rock, scree and dunes
	Diversity of natural land-cover types	Number of natural cover types recorded
	Diversity of bank top features	Number of bank top features recorded
Shore	Shore structural habitat diversity	Proportion of Hab-Plots with an earth or sand bank > 1m
	Bank naturalness	Proportion of Hab-Plots with trash-line
	Diversity of natural bank habitat	Number of natural bank materials recorded
	Beach naturalness	Proportion of Hab-Plots with natural beach material
	Extent of natural littoral zones	Proportion of Hab-Plots with natural littoral substrate
	Diversity of natural littoral zone types	Number of natural littoral substrate types recorded
	Extent of macrophyte cover	Average of total macrophyte cover over all Hab-Plots
		Number of Hab-Plots where macrophyte cover extends lakewards
	Diversity of macrophyte structural types	Number of macrophyte cover types recorded (not including filamentous algae)

Table 3.1 continued: LHQA-associated metrics (*sensu* Rowan *et al.*, 2004)

Lake Zone	Characteristic measured	Measurable feature
Whole Lake	Extent of littoral habitat features	Average of total cover for fish over all plots
	Diversity of littoral habitat features	Number of littoral habitat feature types recorded
	Diversity of special habitat features	Number of special habitat features (excl. diseased alders)
		Number of islands
		Number of deltaic depositional features recorded (excl. unvegetated sand and silt deposits)

Table 3.2. LHMS-associated metrics (Rowan *et al.*, 2006)

PRESSURE	ZONE	Measurable feature- no. of plots or features
Shore zone modification	Shore	Bank face modifications
	Beach	Beach modifications
	Whole lake	Hard bank engineering (closed)
		Hard bank engineering (open)
		% section hard engineering
		% shoreline hard engineering
Shore zone intensive use	Riparian	Dominant land cover
	Whole lake	Commercial activities
		Residential areas
		Roads, rails, paths
		Parks and gardens
		Camping and caravans
		Recreational beaches
		Educational recreation
		Litter, dump, landfill
		Quarrying or mining
		Coniferous plantation
		Evidence recent logging
		Improved grassland = Pasture
		Soil poaching (trampling) = Observed grazing
		Tilled land
		Orchard
		% section non-natural
		% shoreline non-natural
In-lake use	Whole lake	Bridges
		Causeways
		Fish cages (aquaculture)
		Commercial fishing (nets/traps)
		Sediment extraction/dredging
		Dumping
		Macrophyte manipulation
		Motorboat activities
		Non-motor boat activities
		Angling from boat
		Angling from shore
		Non-boat recreation/swimming
		Wildfowling and hunting
		Introduced species
		Fish stocking
		Navigation channels
		Power lines
		Chemical applications
		Surface films
Hydrology	Whole lake	Bank erosion
		Aggrading vegetated deltaic deposit
		Stable vegetated islands (deltaic)
		Deltaic unvegetated gravel deposit
		Deltaic unvegetated sand/silt/clay deposit
Introduced species	Whole lake	

3.2.2 Biological sampling and laboratory processing

Biological sampling was conducted simultaneously with the LHS surveying at six of the nine lakes. Lough Cullin, Lough Oughter and Lough Garadice were omitted because of the recorded presence of the non-indigenous benthic macroinvertebrate species *Dreissena polymorpha.* Six sites were chosen randomly from among ten Hab-Plots at each lake. Owing to the logistical constraints including in particular the time required for processing the samples in the laboratory, the number of sampling sites was decreased from ten as specified in the original LHS design, to six. A rationale for this decision was based on the results of the initial LHS trials (Rowan *et al.,* 2006) which showed that the overall habitat structure of the shorelines can be captured with six to eight Hab-Plot observations, especially in smaller lakes. A sampling site at each Hab-Plot was defined as a 15m long stretch of the littoral zone, with variable width depending on the wadeable depth (up to approximately 1m). Macroinvertebrates from different mesohabitats were sampled proportionally and across the whole site for one minute in total, using composite-scale sampling protocol, described in Chapter 2, Section 2.2.2. Samples were collected from 36 sites across six lakes. Samples were sieved and preserved on site with 70% Industrialised Methylated Spirit. In the laboratory, individual organisms were identified to the highest taxonomical resolution possible using the following keys: Elliott (1977), Macan (1977), Elliott & Mann (1979), Richoux (1982), Fitter & Manuel (1986), Elliott *et al.* (1988), Friday (1988), Savage (1989, 1999), Gledhill *et al.* (1993), Edington & Hildrew (1995), Miller (1996), Nilsson (1997), Reynoldson & Young (2000), and Wallace *et al.* (2003). Hydracarina, Hydrozoa and Porifera were excluded from the taxonomic analysis. The insect family Chironomidae, some Coleoptera larvae and subclass Oligochaeta were not identified to a higher taxonomic resolution.

3.2.3 Water chemistry measurements

Water samples were collected at ca. 30cm below the surface from every lake at the deepest point. Water samples were stored in a dark, cold place and analysed within five days of sampling for alkalinity, conductivity, pH, colour, chlorophyll *a*, total phosphorus, total nitrogen and dissolved and non-dissolved total organic carbon (DTOC and TOC, respectively). The laboratory analyses are outlined in further detail in Chapter 2.

3.2.4 Statistical analysis

The detailed information of riparian, exposed shore and littoral zone features was recorded with 96 variables in the LHS form. Of these, 86 were non-redundant (recorded as presence or, in the case of numerical estimates, a value other than 0 in at least one Hab-Plot). All redundant variables belonged to the category of human pressures. These were: residential structures, roads and railways, unsealed tracks and pathways, improved grassland, recreational pressures, and the presence of hard bank engineering as a nominal variable. In addition, a new score for pressures (number of shoreline pressures) was derived by summing all pressures present in the immediate vicinity of the sampled shoreline site (within 50m of the Hab-Plot). For the purpose of elucidating a clearer signal of the physical habitat, only features which were recorded across at least 5% of all Hab-Plots were retained as individual variables in the subsequent analyses, except in the case of anthropogenic pressures.

Principal Component Analysis (Jolliffe, 2002) was used to graphically illustrate the relationship between different habitat variables derived from the LHS form (Zuur *et al.*, 2007). The LHS metrics were initially divided into four groups: riparian and exposed shore, littoral substrates, littoral vegetation and the category of human pressures. Since semi-aquatic and aquatic plants of the littoral zone are an important component of habitats for macroinvertebrates, the structure of littoral vegetation was described separately from the rest of the littoral attributes. Additionally, littoral habitat features comprising overhanging vegetation, woody debris and underwater tree roots were included in the littoral group together with the texture of the littoral substrate. Correlation biplots were created for each group separately using both pseudo-quantitative and nominal (presence/absence) variables.

Macroinvertebrate community composition across the six lakes was investigated using non-metric Multi-Dimensional Scaling (MDS) and clustering with the software PRIMER Version 6.1.11 (Clarke & Warwick, 2001). Detrended Canonical Analysis (DCA) was performed on both untransformed and squared-root transformed datasets with downweighting of the rare taxa, in order to decide on the type of constrained analysis (unimodal or linear gradient). The gradients obtained as lengths of the 1st axis were 3.23 and 2.73 SD units, respectively. ter Braak (1986) suggested that if gradients are longer than 2, unimodal methods should be used. Therefore, relationships between the community composition and the environmental variables were examined with Canonical Correspondence Analysis (CCA). CCA is an ordination method, based on the theory of existing optima of species niche tolerances (Legendre & Legendre, 1998). It is a direct gradient analysis, combining multiple regression and ordination methods of multivariate response and explanatory environmental variables. The species matrix was squared-root transformed and downweighted for the rare taxa (Legendre & Birks, 2010). The environmental variables were first standardised by mean and standard deviation, since they comprised different scales. Since the multicolinearity among explanatory variables poses a serious problem for the estimation of regression coefficients in multiple linear regression (Montgomery *et al.*, 2006), four data sets (riparian and exposed shore, littoral, aquatic vegetation and pressures metrics) were first analysed using CCA with forward selection. This allowed selection of a subset of habitat metrics with low cross-correlation, as suggested by Lepš & Šmilauer (2003). The second pooled CCA with forward selection was performed on the combined variables which came out as significant from the previous, separate, CCA analyses. The variables which contributed significantly to the explanation of the variance in the pooled CCA were further tested using CCA without forward selection. The significance of these environmental variables was assessed by employing the Monte Carlo permutation tests with maximal number of permutations (9999), followed by Bonferroni correction of the *P*-values (Cabin & Mitchell, 2000). Partial CCA (pCCA) with 199 permutation tests was used to establish the statistically significant portion of any individual variable. The Monte Carlo permutation test was also used to assess the significance of relationships between environmental variables and community composition, by assessing the significance of all eigenvalues with 199 permutations. The threshold value for significant portion of explained variation was $\alpha=0.05$. All ordination-associated analyses were performed with the CANOCO software package (Version 4.5, ter Braak & Šmilauer, 2002).

3.3 Results

3.3.1 General habitat description based on LHS variables

Riparian zone and exposed shore

The diversity of habitats occupying the exposed shore and adjacent riparian area (up to 15m from the bank top) was determined primarily by the presence of the vegetation layers: trees, shrubs, saplings, tall herbs and grasses. The riparian zones of the studied lakes were characterised either by the presence of the higher vegetation layers (trees, shrubs) or plain short herbs and grasses (Figure 3.1). According to the PCA plot, the presence of beaches and bank top features such as bedrock or boulders was associated with the exposed shore (higher maximum fetch), bare ground and artificial structures.

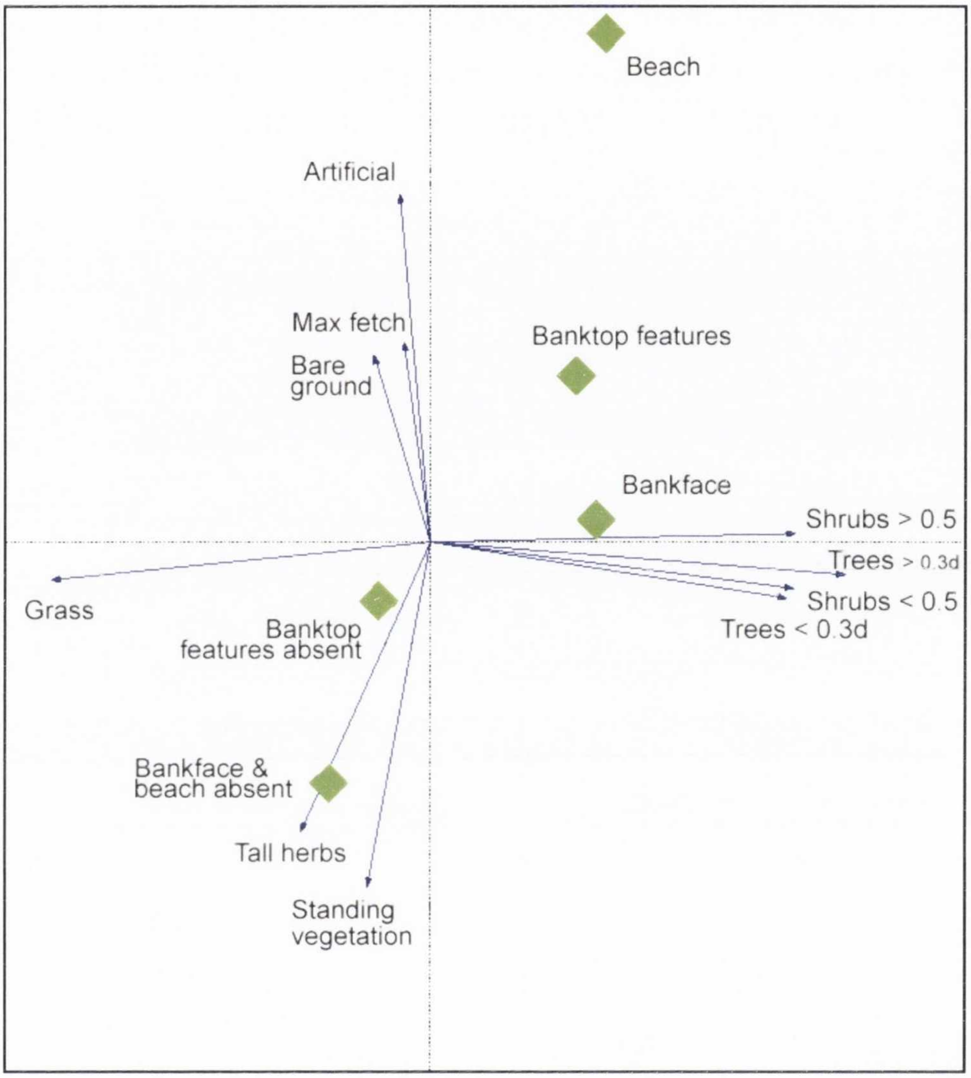


Figure 3.1. PCA correlation biplot of riparian and exposed shore features. Nominal variables (presence/absence of beach and bankface, presence of bank top) were added to the plot as supplementary variables.

Littoral zone

The structure of the littoral substrate was captured by the measure of the lake depth at 10 m from the waterline and the estimated cover of the categories of littoral substrate texture. The correlations among the substrate textures (Figure 3.2) implied that the presence and estimated amount of cobbles was frequently associated with the presence of pebbles. Moreover, the amount of both cobbles and pebbles was inversely related to the estimated quantity of the silt and clay. Meanwhile, bedrock and boulders were often found together and prevailed in combination with the larger-sized substrate. From the PCA plot (Figure 3.2) the strong relationship between the presence of overhanging vegetation, underwater tree-roots and woody debris can be noted.

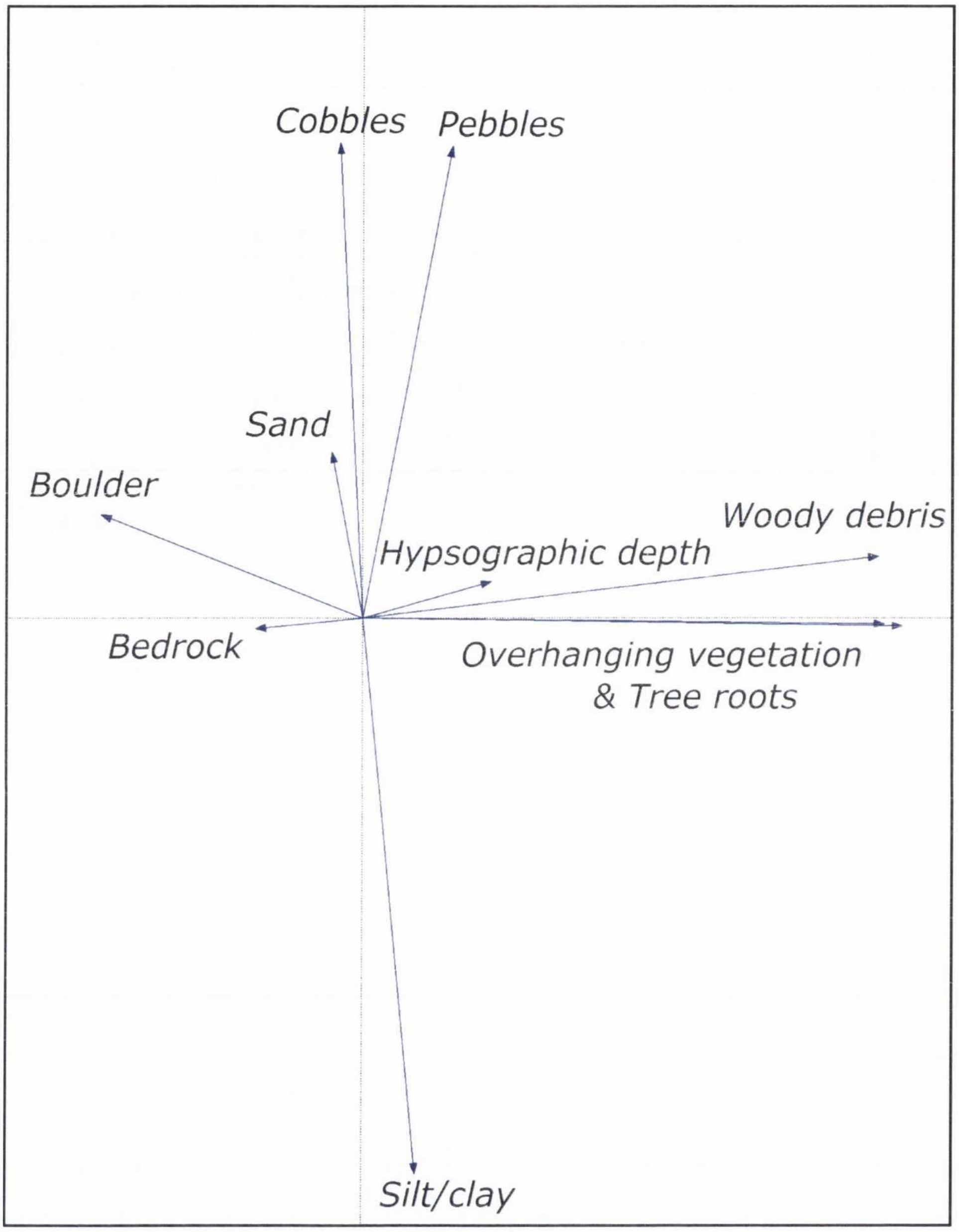


Figure 3.2. PCA correlation biplot of littoral zone features: texture of littoral substrate and special littoral features

Littoral vegetation

Distinctive forms of macorphytes were found to be correlated (Figure 3.3). For example, the presence of emergent broad-leaved macrophytes was associated with the presence of reeds, sedges and rushes. These were further found to be associated with the submerged broad-leaved and floating macrophytes with roots. Submerged stiff-leaved macrophytes were found in associations with submerged fine-dissected leaved and linear-leaved macrophytes, where present. In addition, the presence of phytobenthos was found to be inversely related to the presence of emergent macrophyte types.

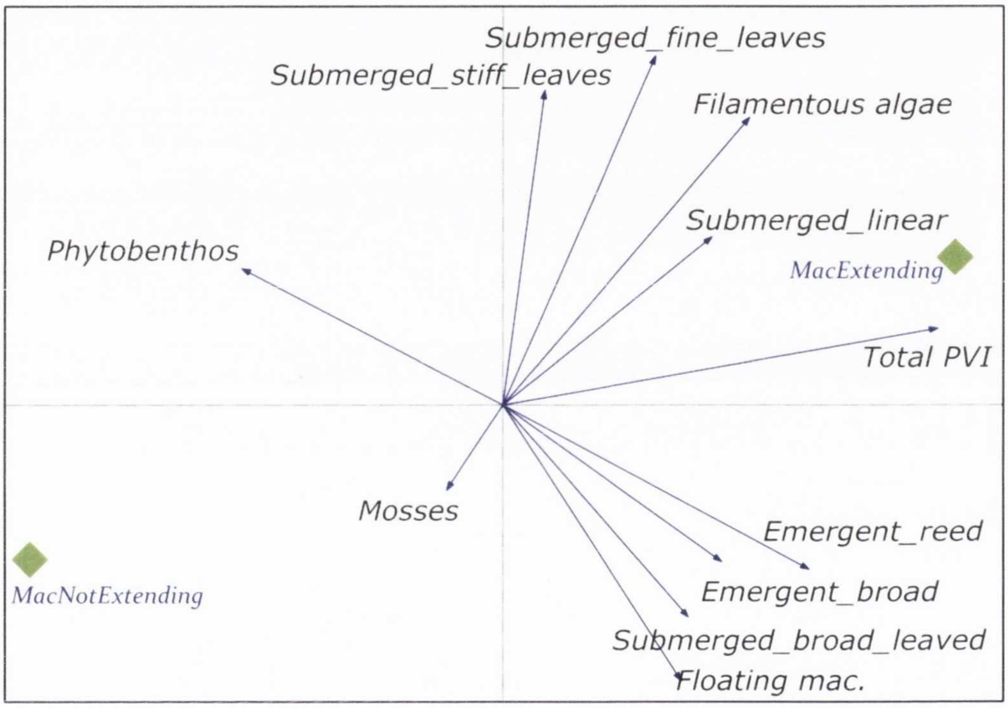


Figure 3.3. PCA correlation biplot of littoral vegetation types. Extending of macrophytes beyond the boundaries of the Hab-Plot (more than 10m from the waterline) is presented as a nominal variable and added afterwards to the original PCA plot.

Shoreline pressures

Recordings of the human-induced shoreline pressures based on the 10 Hab-Plots in each of the nine studied lakes revealed five abundantly present pressure types: proximity of roads and railways, proximity of improved grassland, recreational pressures, proximity of unsealed tracks and footpaths, and presence of hard bank engineering (Figure 3.4). According to the PCA correlation biplot (Figure 3.4), the number of pressures

(TotalPressures) was positively correlated to the rest of the pressures, and therefore chosen to represent the effect of shoreline pressures in the subsequent analysis.

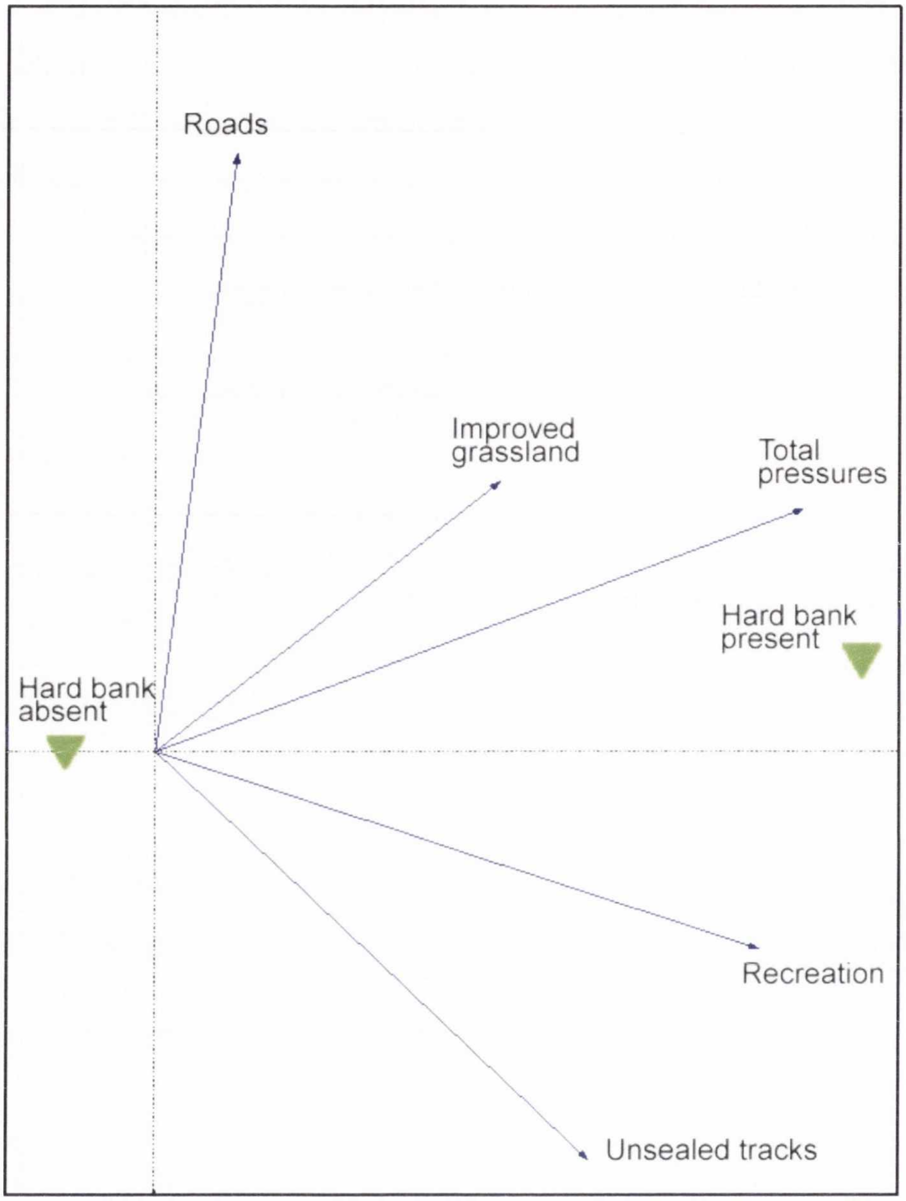


Figure 3.4. PCA correlation biplot of selected pressures. Presence of hard bank engineering is presented as a nominal variable and added subsequently to the original PCA plot.

Lake Habitat Scoring

The LHMS and LHQA calculated for the lakes ranged between 4 and 12, and between 41 and 56, respectively (Figure 3.5 and 3.6). The scores were not correlated (r=-0.2, p>0.5 for n=6). Values of HabQA scoring varied between 2.00 and 8.25.

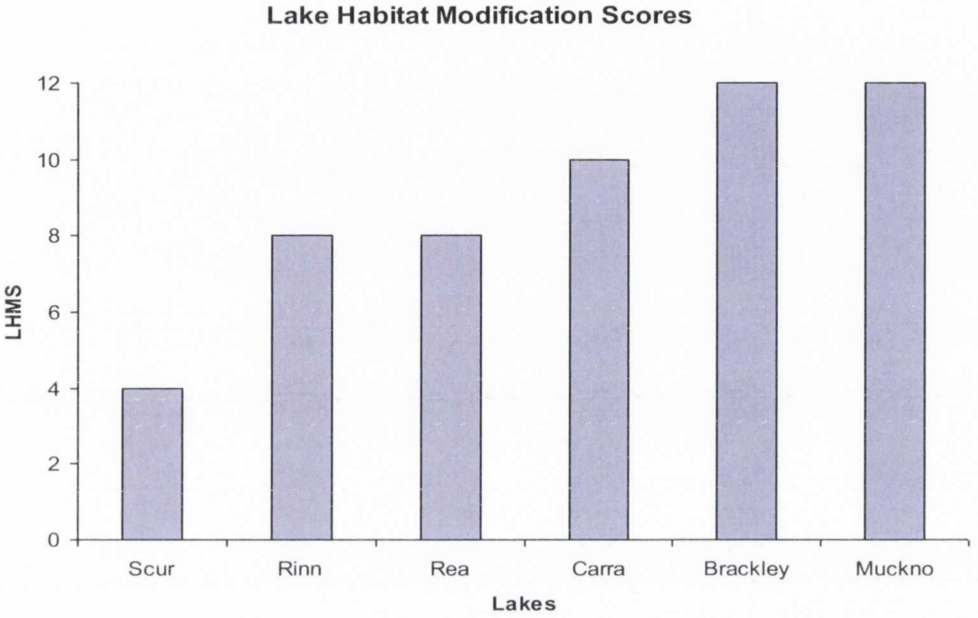


Figure 3.5. Bar-chart representing values of Lake Habitat Modification Scores across six lakes

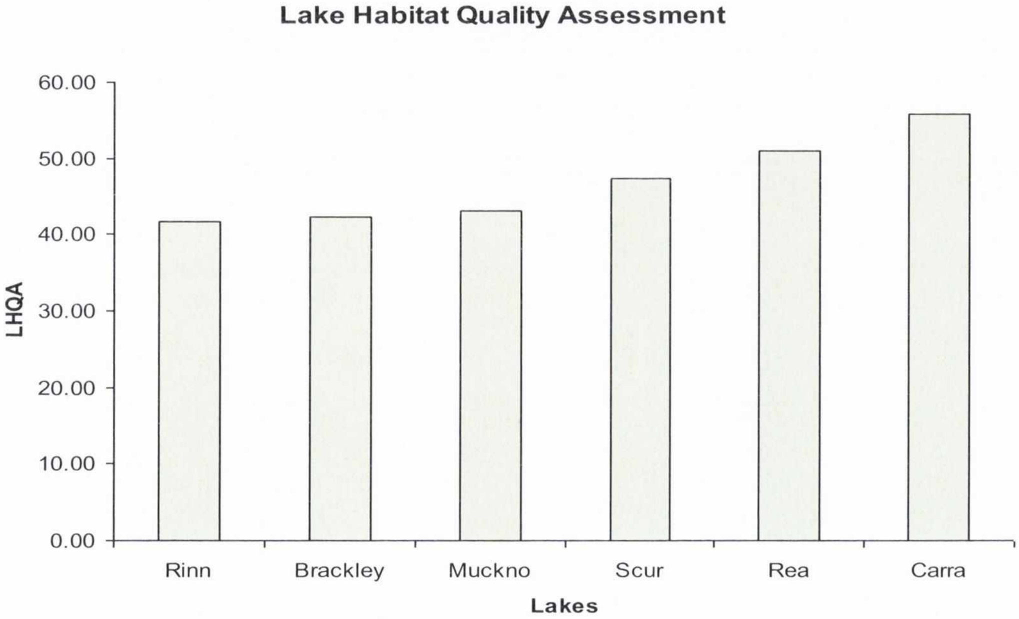


Figure 3.6. Bar-chart representing values of Lake Habitat Quality Scores across six lakes

3.3.2 Patterns in the composition of macroinvertebrate assemblages

Similarities among the relative abundances from different lakes are presented in a non-metric MDS plot (Figure 3.7). Results of clustering indicated that community composition from different sites of the same lake had a similarity level of 37% for three of the investigated lakes (Rea, Carra and Rinn), when results of multidimensional scaling were overlaid with the results of the cluster analysis. The communities from three other lakes (Brackley, Muckno and Scur) were clustered together (Figure 3.7). However, the results of pairwise ANOSIM comparisons revealed that communities from all lakes were significantly different (global R=0.695, P< 0.001) with the exception of Lough Brackley and Scur (pairwise test, R=0.124, P=0.113).

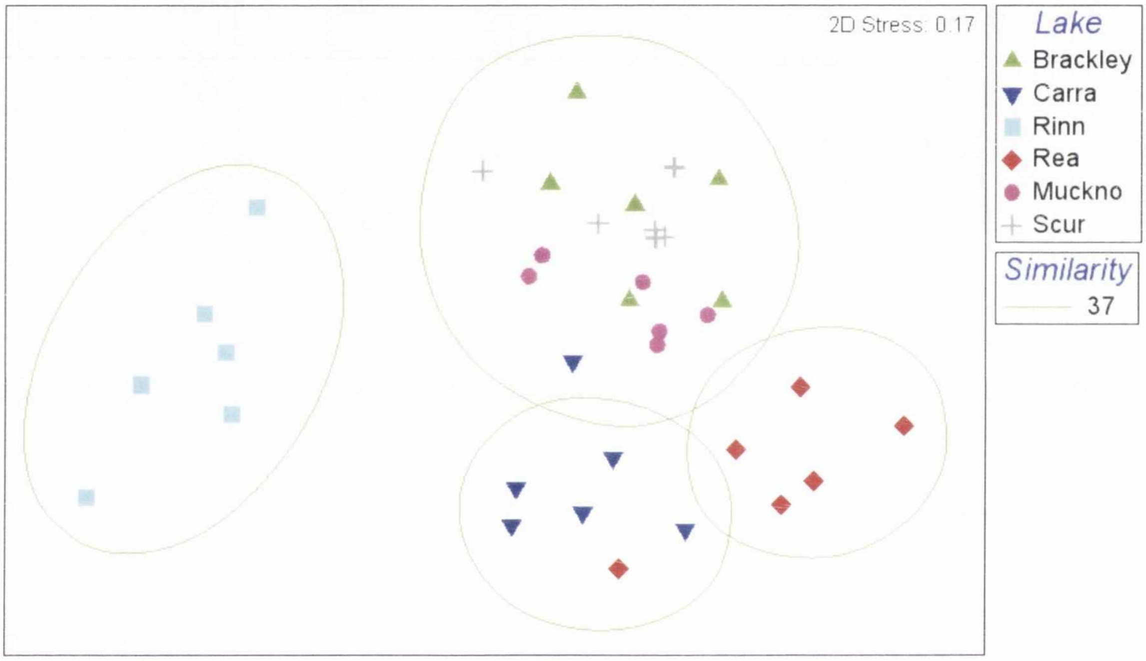


Figure 3.7. MDS of Bray-Curtis similarities from square-root transformed littoral macroinvertebrate abundance data with cluster analysis overlaid at 37% similarity (stress=0.17). Each lake is illustrated with a unique symbol (see legend).

3.3.3 Linking the environmental variables and the macroinvertebrate assemblages

The results of canonical correspondence analysis were based on a species matrix containing 190 taxa. The total inertia of the analysed species matrix was 2.59. The variables which contributed significantly to the explained variance in the littoral macroinvertebrate dataset (9999 permutations, $P<0.05$ after Bonferroni correction) were: alkalinity, total phosphorus, submerged stiff-leaved macrophytes, number of pressures within the Hab-Plot and extending of macrophytes lakewards (Table 3.3). The matrix of environmental data explained 38% of the total variance in the species matrix. The first axis explained 14.5% of the total variance in the matrix of the community composition (38.3% of the explained part of the variance). The second and third axes accounted for 9.3% and 5.1% of the total variance, respectively. The significance of the obtained CCA model was confirmed by the results of the Monte Carlo permutation test for all eigenvalues together and the first axis separately (both tests with 199 permutations, $P=0.005$).

Table 3.3. Conditional effects of significant environmental variables according to the CCA with forward selection.

Variable	$\lambda 1$	P	% Variance
Alkalinity	0.3	<0.001	11.58
TP	0.25	<0.001	9.65
Inundated Vegetation	0.13	0.001	5.02
Number of Pressures	0.11	0.001	4.25
Extending of Macrophytes	0.1	0.004	3.86
Submerged Macrophytes	0.09	0.007	3.47

Partial CCA was performed on groups of variables to assess the relative importance of the water chemistry (TP and alkalinity), the morphological habitat features (submerged macrophytes and extending of macrophytes lakewards), as well as shoreline and hydrological pressures (indicated by the number of individual pressures at each Hab-Plot and the inundated vegetation). The results (Figure 3.8) indicated that chemistry accounted for almost half (47%) of the total explained variance. Shoreline and hydrological pressures accounted for 24% of explained variance and habitat variables were a little less important (19% of total explained variance). Joint variance was present between water chemistry and the other two groups of variables, accounting for 5% of the total explained variance in each case.

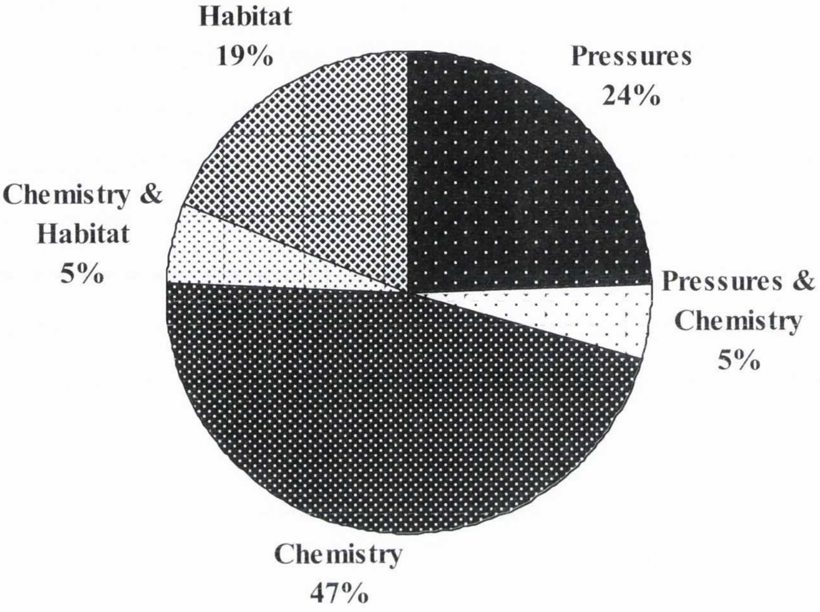


Figure 3.8. Variance partitioning of taxa matrix constrained by habitat (Habitat), shoreline and hydrological pressures (Pressures) and water chemistry (Chemistry) variables, as well as a combination of chemistry and habitat or chemistry and pressures (Chemistry & Habitat, Pressures & Chemistry, respectively). Percentages of the explained variance accounted for by each group of variables are given next to the labels.

3.3.4 Habitat diversity driving the macroinvertebrate assemblages

Diversity of physical habitats across shorelines was evaluated using HabQA scoring, with scores ranging between 2 and 8.25 across shorelines. HabQA scoring was found to explain an insignificant and minor portion of the total variance in the macroinvertebrate community composition (2.8% of total variance explained, P= 0.58), when TP and alkalinity were accounted for (Figure 3.9).

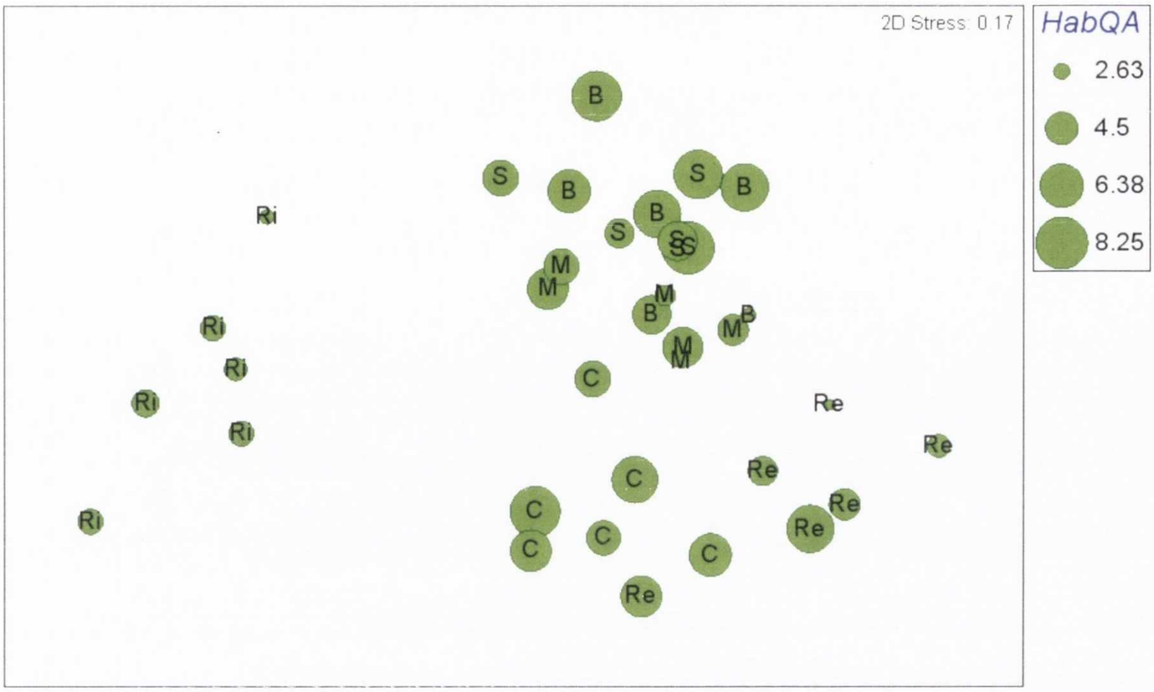


Figure 3.9. MDS of Bray-Curtis similarities from square-root transformed littoral macroinvertebrate abundance data with superimposed circles of increasing size with increasing values of the HabQA scores. Names of the lakes are given by letters (B – Brackley, C – Carra, M – Muckno, Re – Rea, Ri – Rinn, S – Scur)

Complexity and diversity of habitat features were explored using partial CCA with the metrics which comprised the LHQA score (Table 3.1). TP and alkalinity were accounted for as covariables, while pressures-related variables were not used in the analysis since it was shown previously that they did not have any joint effect with the habitat variables (Figure 3.8). Moreover, shoreline and hydrological pressures were inversely correlated with the habitat diversity and complexity *per se*, which is why they were discarded from the diversity-based partial CCA. According to the results of the partial CCA, four LHQA-associated metrics were important in structuring the littoral macroinvertebrate composition, by explaining 15% of the total variance after accounting for TP and alkalinity. The first axis accounted for 37.8% of total explained variance and was best explained by extending of macrophytes lakewards (MacExtending/MacNotExtending) and by the presence/absence of native woodland in the riparian zone (Wood/Open Canopy) (Figure 3.10 and Table 3.4). The second axis accounted for around 29.1% of total explained variance and was best explained by the diversity of the littoral substrate texture (LittSubstrateDiv). The third axis explained 19.1%, while the fourth accounted for 14% of the total explained variance and was best related to the diversity of littoral aquatic vegetation (AqVegDiv).

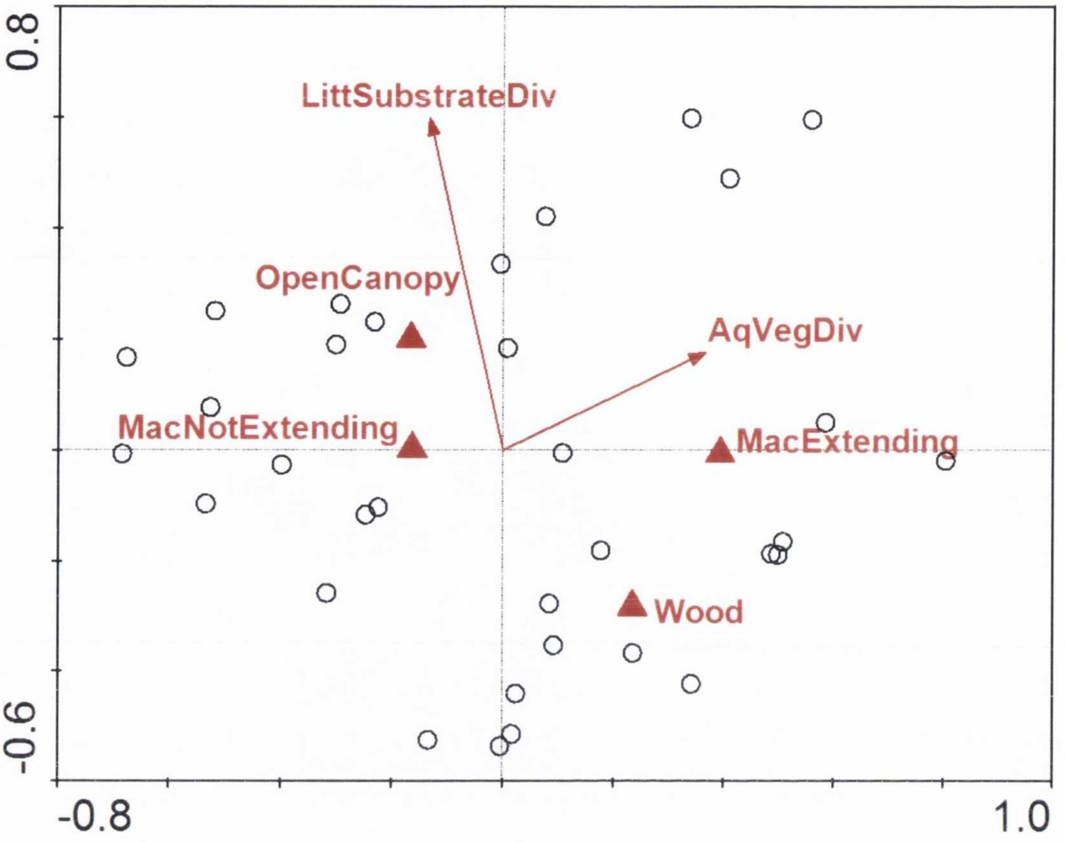


Figure 3.10. CCA-ordination of all sites with significant LHQA-associated metrics gradients indicated by arrows and projected 'MacExtending/MacNotExtending' and 'Wood/Open Canopy' centroids. The horizontal line represents the 1st CCA axis and the vertical line represents the 2nd CCA axis.

Table 3.4. Inter-set correlation coefficients of significant LHQA-associated variables. Values in bold are the highest for a particular variable

	Axes			
Variable	Ax_1	Ax_2	Ax_3	Ax_4
Littoral Substrate Texture	-0.55	**0.56**	-0.21	0.35
Diversity of Aquatic Vegetation	0.41	0.30	-0.04	**-0.74**
Riparian Woodland	**0.57**	-0.42	-0.49	0.12
Extent of Macrophytes	**0.70**	0.12	-0.05	0.58

3.4 Discussion

It is well established that the community composition of lake littoral macroinvertebrates is affected by nutrient concentrations (Brodersen *et al.,* 1998; Donohue *et al.* 2009a) and alkalinity is important in distinguishing lakes and their communities (Heino, 2000; O'Toole *et al.*, 2008). However, characteristics of local (meso)habitats are also important in structuring the community composition. It is difficult to establish whether the signals of water chemistry or the physical habitat features are more important in structuring of the littoral communities. This may be owing to the existence of direct and indirect links between the physical-chemical properties of the water body and their morphological attributes. Therefore, many authors have attempted to disentangle the effects of these two major factors in structuring the lake littoral communities (Heino, 2000; Tolonen *et al.* 2001; White & Irvine 2003; Brauns *et al.*, 2007a; Tolonen & Hamalainen, 2010). Tolonen *et al.* (2001) found that habitat structure was more important than water chemistry for structuring the composition of littoral macroinvertebrate communities in three basins of a Finnish lake. Similar results were reported on a bigger set of lakes by Heino (2000) and again by Tolonen & Hamalainen (2010). The results of White & Irvine (2003) and Trigal *et al.* (2006) confirmed this, by detecting discriminate assemblages at distinct mesohabitats when the community of a single lake was investigated. However, habitat signal was weaker than the lake signal when assemblages from 21 lakes and two distinct types of mesohabitats were compared in Irish lakes (Irvine & White, 2003). This is in concordance with the results of this study, which showed that water-column variables were more important than both habitat features and shoreline pressures. Although Brauns *et al.* (2007a) also found that assemblages from distinct substrates were more dissimilar among habitats than among nutrient states, it could be speculated that some of the German lakes from this study were exposed to the stronger hydromporphological pressures in general (Brauns *et al.*, 2007b), which consequently may have induced a stronger distinction between types of habitats and associated shoreline communities.

Furthermore, the results revealed that the most important variables in structuring the littoral assemblages, along with the alkalinity and TP, were shoreline pressures, inundated riparian vegetation and macrophytes as the structural component of the littoral habitats. The importance of habitat features for littoral macroinvertebrates was investigated in more detail by disentangling the effects of separate LHQA-associated metrics. The LHQA metrics (Rowan *et al.,* 2004) represent an attempt to, first, summarize the variety of habitat attributes and, second, provide ecologically meaningful characteristics of the habitats which would serve as a proxy of habitat value for conservation. This study provided further development on the topic, by examining the association between the composition of the macroinvertebrate assemblages and shoreline features across six lakes.

Macrophytes have previously been found to be relevant for structuring the macroinvertebrate communities (Kornijow, 1989; Tolonen *et al.*, 2001; 2005). The results of this study concurred with this, as it indicated the importance of the extent of macrophytes and the diversity of the littoral aquatic vegetation in structuring of the littoral macroinvertebrate assemblages. McGoff & Irvine (2009) found, similarly, that the extent of macrophytes and total PVI was positively correlated with the abundance of littoral macroinvertebrates in upper basins of Lough Carra. However, the abundance and composition of macrophytes were found to be affected by the impacts of eutrophication (Downing *et al.*, 2004), suggesting the connection between nutrients and macrophyte community composition. For example, Moss (1983) highlighted the association between the nutrient state and succession of aquatic plants in the Norfolk Broads wetland system. According to this author, three phases in succession were described: 1) a low-growing phase with Charophyta and *Najas marina*, 2) a tall-growing phase characterised by species of *Myriophyllum, Ceratophylum and Potamogeton* spp. associated with filamentous algae, floating, floating-leaved or emergent plants which would eventually overtake, and 3) a phytoplankton-dominated phase without macrophytes. The first phase was related to low concentrations of phosphorus, the third phase to high concentrations of phosphorus, and the second phase was induced by intermediate concentrations of TP. Consequently, the structure of the macroinvertebrate communities is expected to change with different types of aquatic vegetation (Hargeby, 1990; van den Berg *et al.*, 1997). It was speculated that the influence of macrophytes on macroinvertebrate communities could be caused by an indirect link (Pinel-Alloul *et al.,* 1996; van den Berg *et al.*, 1997) since macrophytes provide food resources, as well as shelter from fish predators (Diehl, 1992) and physical disturbances (Gabel *et al.,* 2008).

In addition, the results of this study showed that the diversity of littoral habitat texture also had important role in structuring the community composition. This is in concordance with the results of a study by Doeg *et al.* (1989), who found distinctive drift assemblages associated with substrata of differing particle size in lotic environments. Similarly, White & Irvine (2003) found distinctive littoral macroinvertebrate communities to be associated with particular substrate particle sizes among mesohabitats.

McGoff (2009) found that the structure of the riparian zone was associated with the littoral macroinvertebrate communities in a marl lake. The results of this study confirm McGoff's finding by elucidating the effect of the presence of natural riparian land-cover (woodland and wetland in the cases of the study lakes) on studied macroinvertebrate assemblages, which is consistent with the findings of other researchers (Brauns *et al.*, 2007b; De Sousa *et al.* 2008; Rosenberger *et al.,* 2008) who reported that residential development in the riparian zone of the lakes was associated with the composition of the littoral macroinvertebrate communities. Contradictory to these results, Helmus & Sass (2008) did not find any short-term effects of the reduction of coarse woody debris on littoral macroinvertebrates, leading to the hypothesis that the temporal scale in the study of shoreline alterations is important.

Although the number of lakes involved in this study was too small to consider comparing the efficiency of the LHQA and LHMS as proxies of the community composition, it is important to assess their usefulness in the assessment of habitat diversity and presence of hydromorphological alterations. The scores were not correlated, suggesting that habitat quality was not related to the estimated hydromorphological pressures across investigated shorelines. Presence and intensity of human pressures recorded in the immediate vicinity of a Hab-Plot and represented as a number of pressures, was the only variable related to the morphological pressures with a weak but significant association with the macroinvertebrate community composition (Table 3.3). The pressures accounted for in the LHS field form were generally related to the human settlements and recreational activities along the investigated shorelines. Low encounter of shore zone pressures and anthropogenic disturbances was supported by the generally low LHMS scores. With the LHMS values ranging between 4 and 12 (out of 32), the studied lakes had low morphological impact according to Rowan *et al.* (2006). The authors investigated 84 lakes in England and found that the lakes which were considered to have low human impact had scores between 0 and 12. It is therefore important to recognise the limitations of this study in terms of examining the importance of the hydromorphological alterations on a whole-lake level.

Among the variables found to significantly influence the composition of littoral macroinvertebrate assemblages was the presence of the inundated vegetation. As this variable is effectively an estimate of the water level rise, it reflected the effect of altered hydrology in terms of flooded conditions. As the summer of 2009 was generally very wet (MET Annual Report, 2009), the water levels were higher on average although the sampling period was chosen with the aim to record the LHS metrics while the water levels were low. The presence of standing water and the inundated vegetation were especially notable in Lough Rinn, and were reflected through the distinct pattern of the assemblages from this lake (Figure 3.7). It was suggested before that macroinvertebrate communities can be affected by water level fluctuations (Palomaki, 1994; Scheifhacken *et al.*, 2007; Zohary & Ostrovsky, 2011).

The effect of habitats on benthic communities has been speculated to be more pronounced in the littoral zone of the lakes, owing to the often more diverse and complex habitats present in this part of a lake ecosystem (Strayer & Findlay, 2010). This implies that quantification of the variability of the shoreline features is of primary importance for ecological applications such as conservation and restoration programmes. Habitat attributes captured by the LHS metrics in this study were generally interlinked. This was reflected through a number of correlated features, as shown in the PCA correlation biplots (Figure 3.1, 3.2 and 3.3). Therefore, many of the features recorded by the LHS are perhaps redundant when assessing the effects on the structure of the investigated assemblages, and the application of the full sweep of LHS metrics in ecological assessments should be revised. However, only 38% of the variance was explained by the set of environmental variables from this study. While the question of the usefulness of the direct gradient analysis can always be posed, the inherent variability of the natural communities must also be considered. The variability is commonly described as the "noise" in the community pattern. Part of this noise is probably caused by the biotic interactions, which are hypothesised to be more important in lakes than in streams (Harrison & Hildrew, 1998). Furthermore, factors on greater spatial scales should be considered when exploring lake communities (Johnson & Goedkoop, 2002; Feld & Hering, 2007).

3.5 Conclusions

The results presented in this chapter show that:

- The Lake Habitat Survey technique provides a comprehensive and detailed description of the physical habitats, by capturing the array of morphological and hydrological attributes across lake shorelines. The shoreline features of the studied lakes were variable and interlinked among themselves.
- The community composition of the littoral macroinvertebrates was affected by the morphological features of the shoreline zone when the effects of nutrients and alkalinity were taken into account.
- The habitat features were less important in structuring the macroinvertebrate assemblages than the chemical and physical properties of the water column. In addition, shoreline and hydrological pressures were demonstrated to have influence on the composition of the littoral assemblages.
- Among habitat features, the macrophyte- and substrate-related diversity features were most important for structuring the macroinvertebrate assemblages across Hab-Plots. Aside from the direct effect of the littoral zone features, macorinvertebrate assemblages were influenced by the riparian zone land-cover.

4. Effects of shoreline modification and nutrient enrichment on the diversity and abundance of macroinvertebrate assemblages in lakes

4.1 Introduction

Habitats are important in shaping the structure and function of aquatic ecosystems. In lakes, a shore zone includes littoral, shoreline and riparian habitats (Ostendorp, 2004). Lakeshore configurations depend on the bedrock geology, mode of formation, age, depth, shape and surface area of the lake, as well as on short-term natural processes that impact the lake (Kalff, 2001). Anthropogenic activities may substantially affect the lakeshore zone (Liddle & Scorgie, 1980; Rosenberger et *al*., 2008). In theory, diversity of habitats controls biological diversity. High complexity of habitats intuitively suggests more available "niche-space", and is hypothesised to provide refuge from predation in freshwaters (Tolonen *et al*., 2001). Reducing the complexity of littoral zones may, therefore, negatively impact benthic macroinvertebrate communities (Gabel *et al*., 2008).

Artificial man-made structures are a rare but increasing example of hydromorphological pressures found in Irish lakes. Although thoroughly studied in streams (Feld, 2004; Lorenz *et al*., 2004), the effects of morphological pressures in lakes have been poorly examined (Brauns *et al*., 2007b). While eutrophication is regarded as the main pressure to lake ecology (Schindler, 2006), defining and estimating the importance of hydromorphological pressures is noted as a major concern in the Article 5 of the EU Water Framework Directive (European Commission, 2000). The Directive emphasises the importance of the aquatic biota, including benthic macroinvertebrates, and the necessity to establish an integral approach in the quality assessments of aquatic ecosystems. Although benthic invertebrates have been commonly used in the assessments of freshwater quality in general (Rosenberg & Resh, 1993), the littoral component of macrobenthic assemblages has seldom been reported as an indicator of trophic status in lakes (Brodersen *et al*., 1998; Brauns et al. 2007a; Donohue *et al*.; 2009a). It has been demonstrated that habitat characteristics play an important role in structuring littoral invertebrate communities (Tolonen *et al.* 2001; White & Irvine, 2003). Therefore, it is necessary to incorporate a physical habitat evaluation when assessing anthropogenic disturbances using littoral benthos (Tolonen & Hamalainen, 2010).

Since freshwater ecosystems may encounter multiple pressures such as nutrient enrichment, acidification, hydrological or morphological alterations at once, it becomes important to rank the impact of each pressure as well as the consequences of their dynamic interactions. More importantly, tackling the issues arising from multiple pressures will provide the basis for implementing environmental resource management strategies (Whittier et al., 2002).

In Chapter 3 it was demonstrated that the community composition of littoral macroinvertebrates was affected by the morphological features of the shoreline after the effects of nutrients and alkalinity were taken into account. Among the morphological features, the substrate and macrophytes in the littoral zone were most important for structuring the macroinvertebrate assemblages. Aside from the effect of littoral zone features, macorinvertebrate assemblages were influenced by land-cover in the riparian zone.

The aims of this part of the study were to:

1) assess the impact of altered riparian and littoral morphological structure on univariate response - diversity measures of macroinvertebrate assemblages (taxon richness, abundance and Margalef diversity), and

2) distinguish between the impact of nutrient enrichment and morphological alteration, while accounting for the other hydro-chemical properties of the water column, lake morphometric features and differences in mesohabitat types. In addition, Donohue *et al.* (2009b) demonstrated that benthic assemblages homogenise owing to nutrient enrichment. Therefore, it was tested here whether nutrient enrichment homogenised littoral macroinvertebrate assemblages by reducing the differences in the diversity of the assemblages from distinctive mesohabitats. Finally, it was assumed that both nutrient enrichment and shoreline modifications decreased the diversity of macroinvertebrates in the littoral zone; therefore, an interaction in the form of amplification of the effects of the two pressures would be expected.

The following hypotheses are proposed:

Hypothesis 1: Taxon richness, abundance and diversity of macrobenthic communities at morphologically altered littoral (modified littoral) and riparian (modified riparian) shore types are decreased in comparison with the communities from semi-natural woodland (unmodified) shore type.

Hypothesis 2: Nutrient enrichment decreases the differences in the diversity of littoral macroinvertebrate assemblages from distinctive mesohabitats.

Hypothesis 3: There is an interaction between the effect of shoreline modifications and nutrient enrichment on littoral macrobenthic assemblages.

4.2 Materials and methods

4.2.1 Study Lakes

The effects of morphological modifications along riparian and littoral shoreline were explored across nine lakes. The lakes were chosen to represent a nutrient gradient (Total Phosphorus - TP concentratrions - between 9 and 81 μg l^{-1}), while alkalinity values varied from moderate to high category (from 45 – 119 mg $CaCO_3$ l^{-1}). Morphological modifications in littoral and riparian zones were identified *prior to* sampling using Ordnance Survey topological maps. According to the geographic position and morphological characteristics, selected lakes were categorised as shallow lowland lakes having a mean depth of up to 5.4 m, and reaching maximal altitude of 90 m (Lough Muckno).

4.2.2 Sampling design

In spring 2009, the physical characteristics of the shoreline were recorded at each site for the nine lakes, using the Lake Habitat Survey (LHS) protocol (Rowan *et al.*, 2004, 2006). Sites were photographed from the lake, and GPS coordinates were recorded. For each lake, three shore types were chosen to represent:

a) "unmodified"(UM) – sites without obvious morphological modification, a riparian zone usually dominated by (semi)natural wood or scrub

b) "modified riparian" (MR) – sites with a modified riparian zone, usually a pasture or improved (fertilized) grassland, where woody vegetation was usually absent or minimal

c) "modified littoral" (ML) – sites with a modified littoral and riparian zone having artificial morphological structures such as a paved slipway, a concrete embankment, an artificial beach or jetty.

Nine sites were sampled from each of the nine studied lakes to obtain triplicates for each shore type. A sampling site was defined as a 25m long stretch of littoral zone, with a variable width that depended on the wadeable depth (generally up to 0.75m). Two different methods were used to collect samples at each site. The first method entailed sampling three mesohabitats, as defined in White & Irvine (2003), for 20 seconds each across an area of $1m^2$. The second method consisted of collecting macroinvertebrates from different mesohabitats proportionally and across the whole site for one minute, allowing for the multihabitats approach, described in the AQEM Manual (2002). According to this approach, dominant types of mesohabitats were identified within each site *prior to* sampling. The dominant type (macrophytes, sand or stone) was considered any mesohabitat that occupied at least 10% of the total site area and was, therefore, proportionally included in the composite sampling. Each site had three types of mesohabitats at the most, and if fewer were present, 1m^2 areas were randomly chosen for sampling in order to have a balanced design. Composite samples were collected proportionally from all mesohabitats occupying at least 5% of the site area. Mesohabitat and composite types of sampling allowed the response of the littoral macroinvertebrate assemblages to the pressures captured by either the habitat-specific signal (based on mesohabitat sampling) or the whole-site signal (based on composite sampling) to be analysed.

Macroinvertebrate samples were collected with a standard FBA handnet with a mesh size of 0.5 mm. Samples were preserved on site, with 70% Industrialised Methyllated Spirit, and stored in dark plastic bottles for later processing in the laboratory. Individuals were identified to the highest taxonomical resolution possible, using the following keys: Elliott (1977), Macan (1977), Elliott & Mann (1979), Richoux (1982), Fitter and Manuel (1986), Elliott *et al.* (1988), Friday (1988), Savage (1989; 1999), Gledhill *et al.* (1993), Edington and Hildrew (1995), Miller (1996), Nilsson (1997), Reynoldson & Young (2000), and Wallace *et al.* (2003). Hydracarina, Hydrozoa and Porifera were excluded from the taxonomic analysis. The insect family Chironomidae, some Coleoptera larvae and subclass Oligochaeta were not identified to a higher taxonomic resolution.

4.2.3 Water chemistry measurements

Water samples were collected from every lake at three random sites, using a weighted plastic 5 l bottle attached to a 10m long rope. Water samples were stored in a dark, cold place and analysed within 5 days for alkalinity, conductivity, pH, colour, chlorophyll *a*, total phosphorus, total nitrogen and dissolved and non-dissolved total organic carbon (DTOC and TOC, respectively).

4.2.4 Statistical analysis

All statistical analyses including data exploration were performed using the statistical programming language R version 2.13.0 (R Development Team, 2010). R package "lme4" was used to generate generalized and simple linear mixed-effects models (Bates & Maechler, 2010). Mixed-effects models are useful when it is necessary to allow for the spatial dependency structure in the dataset (McCulloch & Searle, 2001). Simple linear mixed-effects models(LMMs) are used for data with normal distribution, while generalised mixed-effects models(GLMMs) have been proposed for analysing data with non-normal types of distribution and random effects (Bolker *et al.*, 2009).

To test the proposed hypotheses, an assortment of LMMs and GLMMs was used. Three types of response variables were used to explore the effect of shoreline modifications, nutrient enrichment and their interactions, from both composite- and mesohabitat-samples datasets. Taxon richness and the Margalef diversity index were used as measures of diversity, while log-transformed abundance was used as an abundance measure. The Margalef diversity index represents another measure of taxon richness, albeit standardised for the number of individuals (Magurran, 2004), in order to account for the potential differences in sampling effort at different shore types.

Based on composite samples, the full model of taxon richness comprised two-way interactions between the shoreline modifications and each of the explanatory variables, as well as lake and site factors in the random part. In the mesohabitat-samples dataset, the full model of taxon richness comprised the three-way interactions of the shoreline modifications, mesohabitat types and each of the explanatory variables, with lake and site factors in the random part. In both models, the taxon richness was considered to have a Poisson distribution. The shoreline modification types and mesohabitat types were investigated in combination with various environmental variables, such as TP, alkalinity, lake area and eastings as fixed explanatory variables with interactions. Furthermore, the random part of the model implied the hierarchical structure of the sampling design. The combination of fixed and random variables that resulted in the most parsimonious models to describe the taxon richness were chosen according to the model selection criterion described in Chapter 2 under the Section 2.4.2.

The LMMs were applied to the Margalef diversity and log-transformed abundance in order to investigate the impacts of shoreline modifications and nutrient enrichment on the diversity and abundance of littoral macroinvertebrate assemblages. Based on the composite samples, the full models of the two response variables comprised two-way interactions between the shoreline modifications and each of the explanatory variables, as well as lake and site factors in the random part. Additionally, the full mesohabitat-based models incorporated a hierarchical structure with mesohabitat types in three-way interactions with shoreline types and the rest of the explanatory variables.

Since it was speculated that the relationship between the changes in the macroinvertebrate communities and nutrient concentrations might be non-linear, each optimal model was compared with a model incorporating the additional quadratic TP values. None of the models retained the quadratic structure in the selection process. Similarly, the interaction between the effect of the alkalinity and TP was evaluated in the model selection, since these two factors can strongly influence macrobenthic communities (O'Toole *et al.*, 2008). However, the interaction term was discarded from all final models. Finally, validation of the best models was performed using graphical techniques by checking the homogeneity, normality and independence of residuals against explanatory variables. Plots of model residuals for each of the final models are shown in the Appendix (Figures A.1 to A.6).

4.3 Results

4.3.1 Diversity features of littoral macroinvertebrate assemblages in studied lakes

Littoral macroinvertebrate assemblages from the nine lakes were highly diverse. In total, 294 taxa (189 species) were recorded, of which only 18 taxa (seven species) were found in all lakes, and 53 (around 28%) taxa were confined to a single lake. Despite the high overall diversity, there was also high variability in the diversity of macroinvertebrate assemblages among the lakes (Figure 4.1). The lake with the lowest taxon richness of littoral macrobenthic assemblages was Muckno (74 taxa in total), while highest taxon richness was found in Brackley and Lough Carra (177 and 130 taxa, respectively).

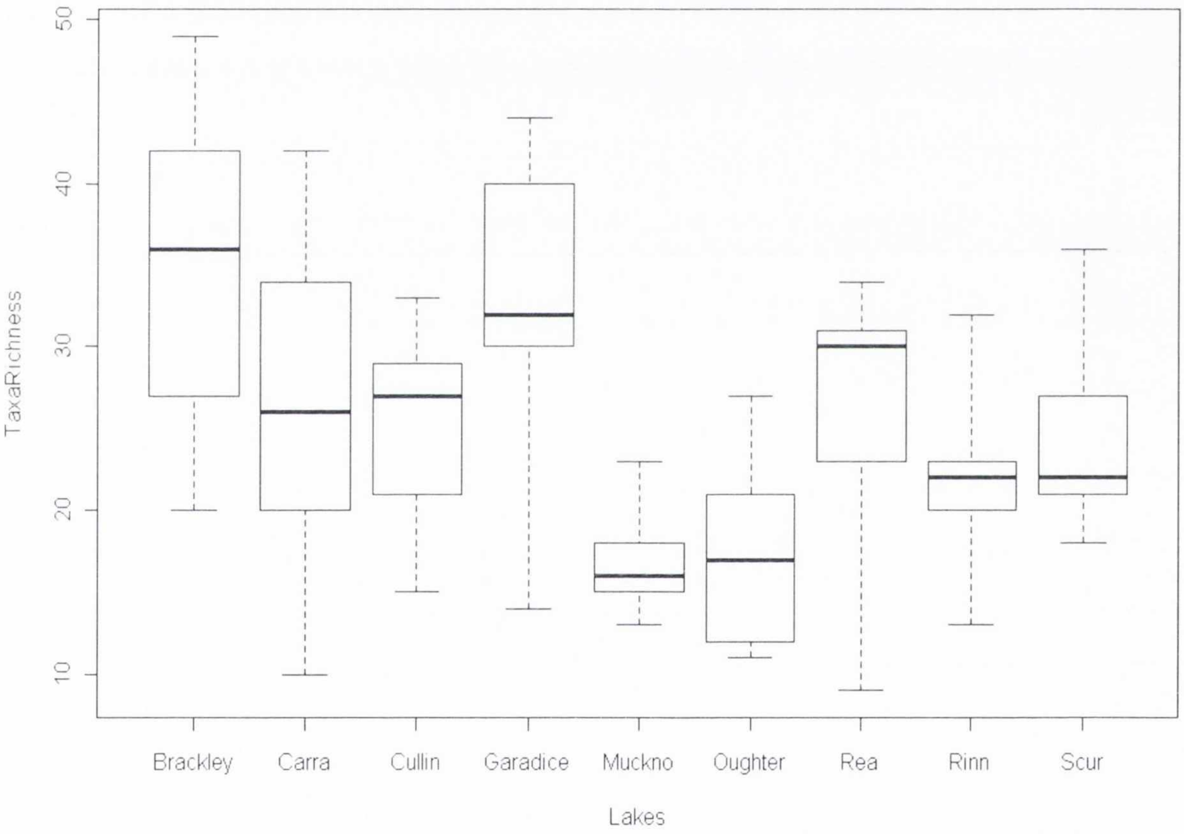


Figure 4.1. Boxplot representing taxon richness variation among different lakes from composite samples (median, 1^{st}, 3^{rd} quantile represented by the box, whiskers indicate range, n = 9 per lake).

A cumulative dominance plot was used to graphically present the relative abundances against the ranked species from mesohabitat samples pooled from the three types of shoreline (Figure 4.2). Species were ranked according to their importance in terms of relative abundance. Taxa with the highest relative abundance (7 most abundant taxa) from modified littoral zones showed higher dominance and lower evenness compared with assemblages from unmodified sites (judged by the elevated shape of the curve). In comparison with the unmodified and modified littoral shore, the curve representing the assemblages from sites with riparian modifications was intermediate in shape. In all three cases of shore types, the 10 most abundant taxa comprised around 80% of the whole assemblage. Assemblages from sites with littoral modifications had the fewest taxa, while the assemblages from sites with modified riparian zone had the most.

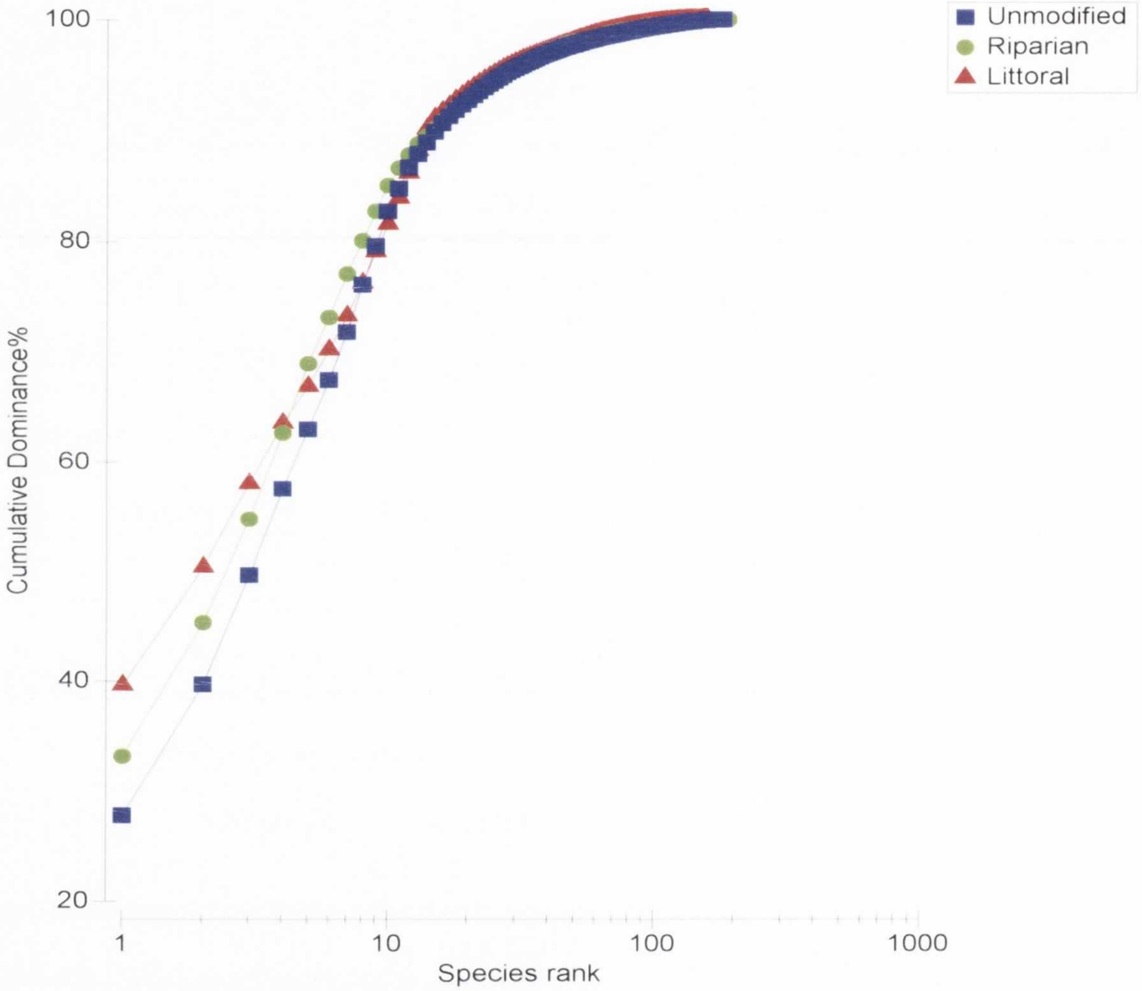


Figure 4.2. Cumulative dominance (based on relative abundance of species) in relation to ranked species (logarithmic scale) for pooled mesohabitat samples from the three types of shoreline (UM - unmodified, MR - modified riparian, ML – modified littoral shoreline) averaged across nine lakes.

4.3.2 Effects of TP gradient and morphological modification on taxon richness

The effects of shoreline modifications on the benthic assemblages were examined by analysing and comparing taxon richness from the unmodified shorelines with taxaon richness from the shore types with modified riparian and modified littoral zones. Two models were derived, the first one based on mesohabitat and the second on composite samples.

Mesohabitat samples

The most parsimonious model for taxon richness values from mesohabitat samples incorporated alkalinity, eastings (distance from east coast of Ireland) and mesohabitat types interacting with shore type and TP concentrations, as fixed explanatory variables. In the random part of the model, lake and site factors accounted for the variation in taxon richness among lakes and among sites. According to the results of this model, taxon richness from mesohabitats was generally negatively affected by the increase of TP concentrations, distance from east coast of Ireland, alkalinity and lake area (Table 4.1). Moreover, the taxon richness from distinctive mesohabitats differed in their response to the effect of shore modification and TP concentrations, respectively. For instance, the model results suggest that the decrease in taxon richness values was most prominent at sites with a sandy substrate in modified littoral shorelines (Figure 4.3).

Table 4.1. Results of generalized mixed-effects model for taxon richness from mesohabitat samples. (UM- unmodified, MR- modified riparian, ML – modified littoral shoreline; categories in parentheses set as reference levels, "X" indicates interaction). *AICc*=150.6

	Estimated Coeff.	SE	z-value	*P*
Lake Area	-0.090	0.021	-4.199	<0.001
TP concentrations	-0.313	0.080	-3.929	<0.001
Shore type:ML(UM,sand)	-0.473	0.145	-3.253	0.001
Shore type:MR(UM,sand)	-0.030	0.127	-0.238	0.812
mesohabitat:sand(macrophytes)	-0.058	0.131	-0.439	0.661
mesohabitat:stone(macrophytes)	-0.094	0.103	-0.905	0.366
Eastings	-0.097	0.022	-4.481	<0.001
Alkalinity	-0.207	0.054	-3.802	<0.001
TP conc. X sand(macrophytes)	0.189	0.089	2.114	0.035
TP conc. X stone(macrophytes)	0.018	0.074	0.248	0.805
TP conc. X stone(sand)	-0.171	0.089	1.916	0.055
Shore type:ML(UM) X sand(macrophytes)	-0.491	0.228	-2.158	0.031
Shore type:ML(UM) X macrophytes(stone)	0.031	0.192	0.163	0.870
Shore type:ML(UM) X sand(stone)	-0.460	0.201	-2.291	0.022
Shore type: MR(UM) X stone(sand)	-0.104	0.152	-0.682	0.495
Shore type:MR(UM) X sand(macrophytes)	-0.131	0.178	-0.737	0.461
Shore type: MR(UM) X stone(macrophytes)	0.107	0.147	0.726	0.468

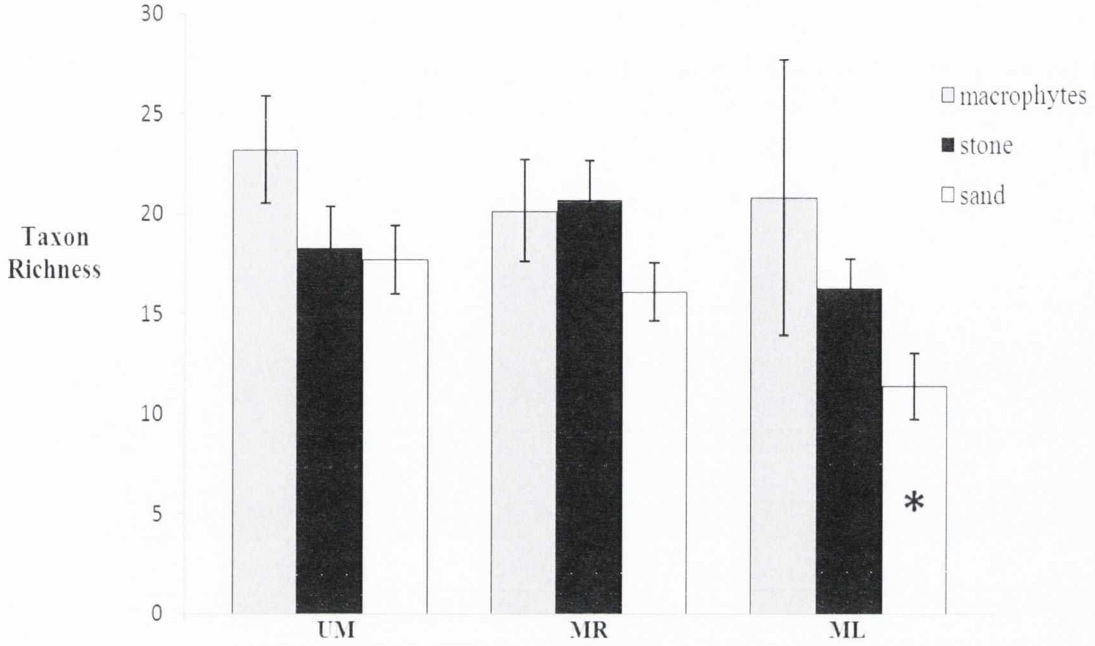
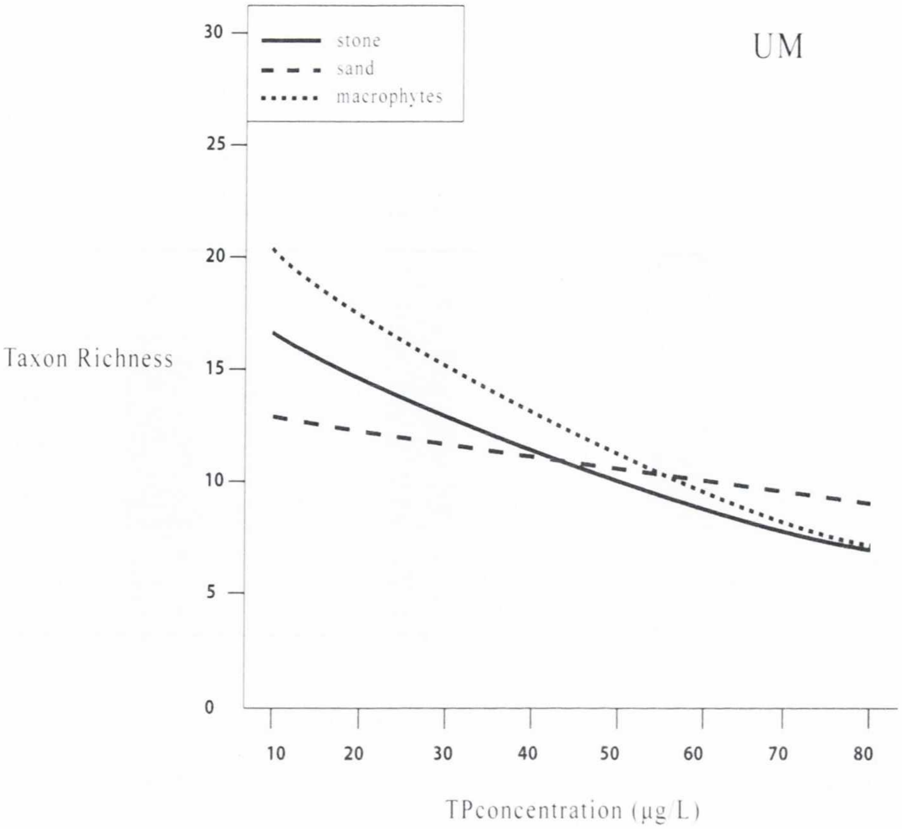


Figure 4.3. Mean (±2SE) predicted taxon richness from mesohabitat samples across different shore types (UM - unmodified, MR - modified riparian, ML – modified littoral shoreline) and mesohabitat types, for mean values of other factors and median lake. Asterisk indicates significantly different mesohabitat from the particular type of shore.

Increasing phosphorus concentrations reduced the differences in taxon richness values in all mesohabitat types (Figure 4.4). Furthermore, the model results indicated that the phosphorus concentrations had less of an effect on unmodified sites with sandy substrates when compared with assemblages from stone or macrophyte-dominated substrates. The results of the model indicated that there was no interaction between the effect of shoreline modification and nutrient enrichment (TP concentrations), as the interaction term was discarded during the model selection.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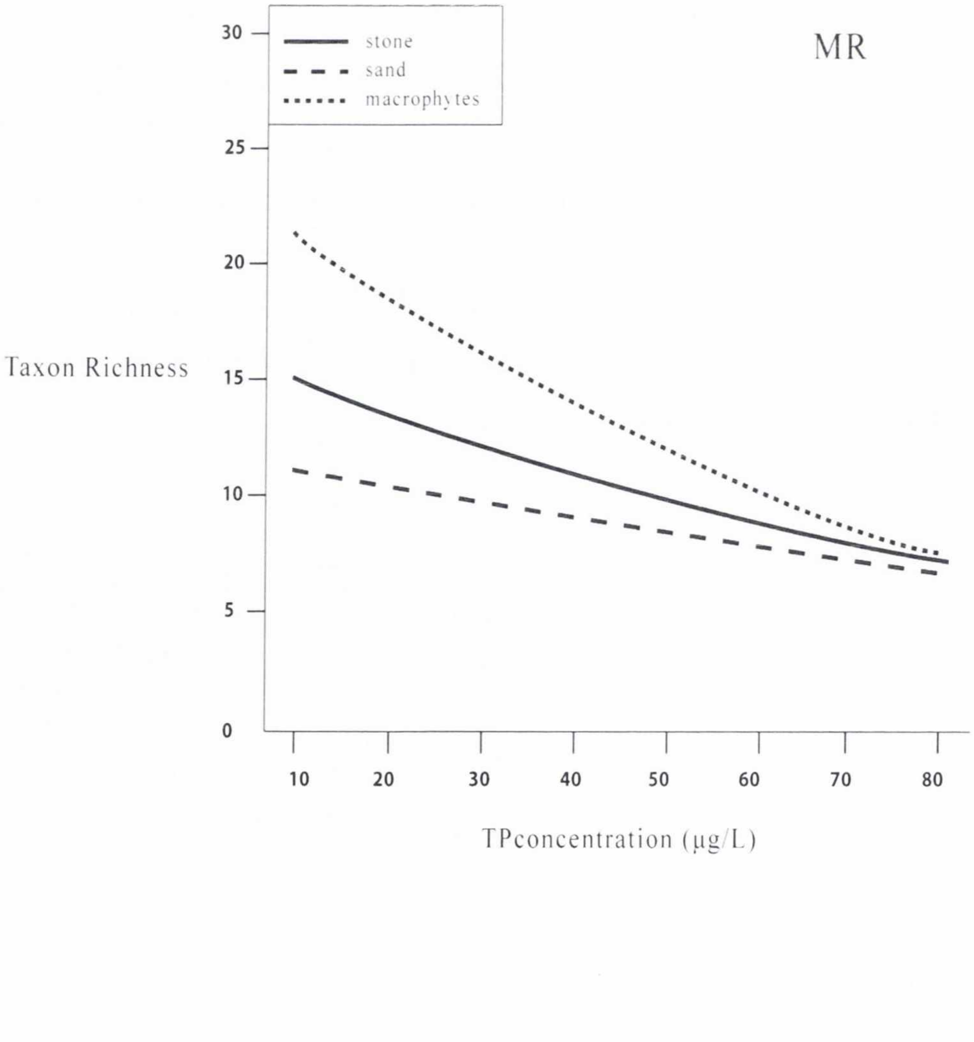
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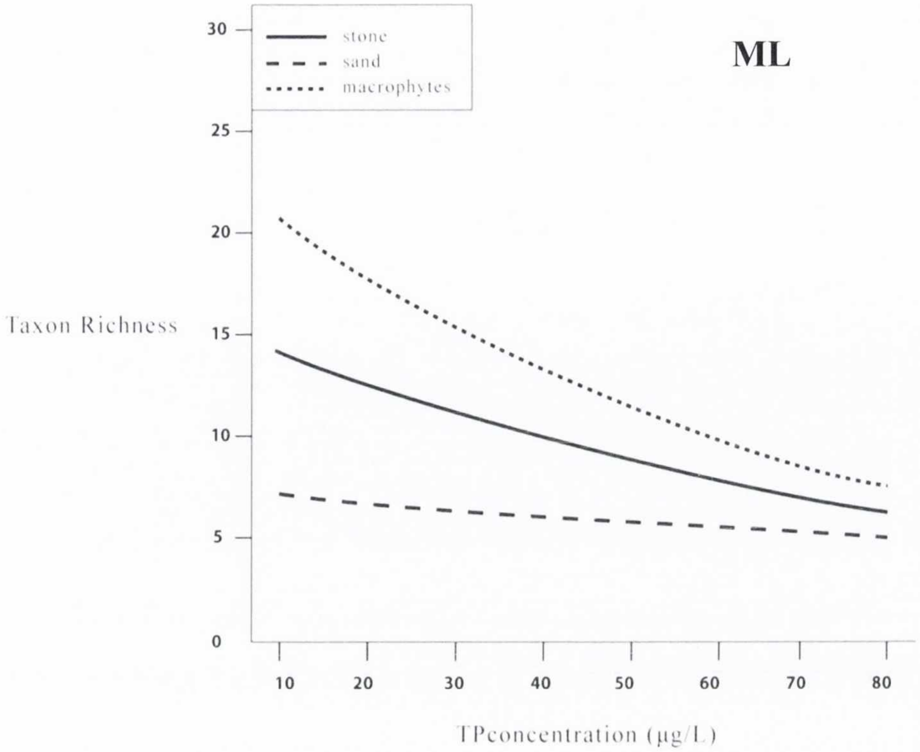

Figure 4.4. Visualisation of the model illustrating the change in taxon richness in relation to the TP gradient at different habitat patches (macrophytes-, sand- and stone-dominated) from UM - unmodified, MR - modified riparian and ML - modified littoral shoreline, based on mesohabitat samples. The other covariates (alkalinity, lake area and distance from east coast of Ireland) were set to mean values.

Composite samples

The final (most parsimonious) model included shore modification, distance from east coast of Ireland and alkalinity as fixed main variables, while all interaction terms between shore modifications and environmental variables were discarded. In the random part of the model, lake factor accounted for the variation in taxon richness among lakes. Both the eastings and alkalinity variables had negative estimated slope coefficients suggesting a negative effect on taxon richness (Table 4.2, Figure 4.5). TP was dropped from the final model, meaning that the relationship between taxon richness and phosphorus concentrations was not captured by the composite samples. After model simplification, the taxon richness from the modified riparian shore was not found to be significantly different from the unmodified shore, while the taxon richness at sites with littoral modifications was significantly decreased (Figure 4.6).

Table 4.2. Results of generalised mixed-effects model for taxon richness from composite samples. (UM - unmodified, MR - modified riparian, ML – modified littoral shoreline; categories in parentheses set as reference levels). *AICc*= 47.0

	Estimated Coeff.	SE	z-value	*P*
Shore type:ML(UM)	-0.196	0.069	-2.840	0.005
Shore type:MR(UM)	-0.066	0.067	-0.997	0.319
Alkalinity	-0.254	0.101	-2.512	0.012
Eastings	-0.106	0.037	-2.831	0.005

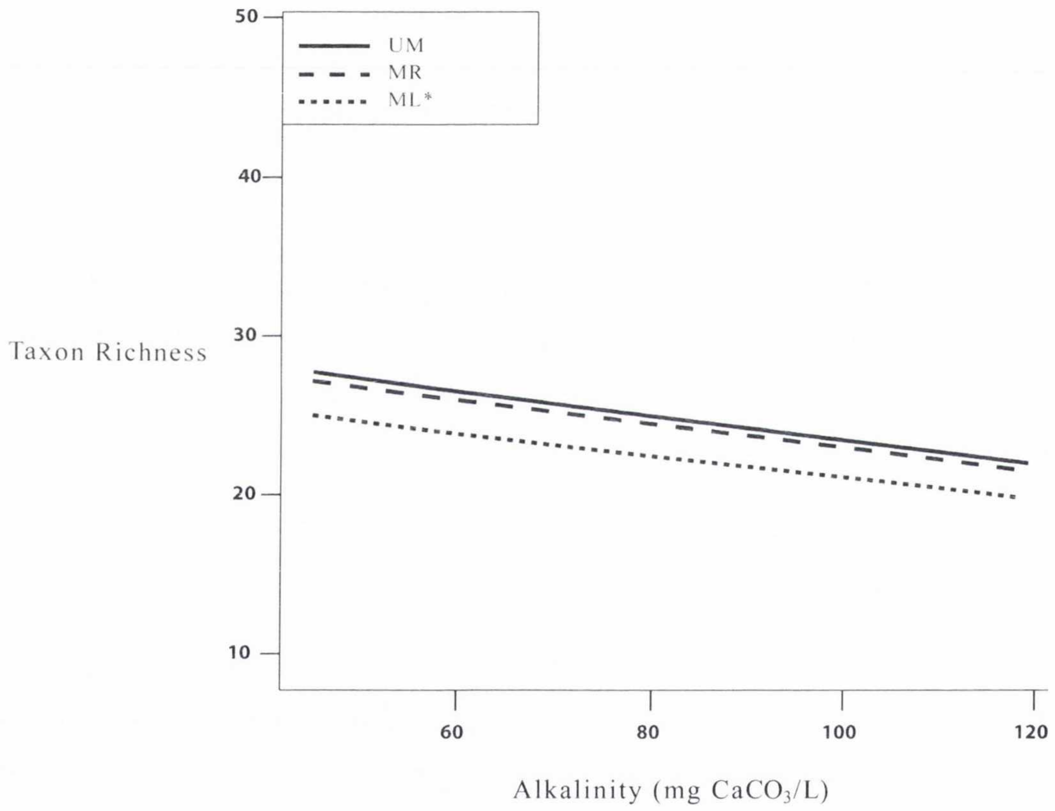

Figure 4.5. Visualisation of the model illustrating the difference in response of taxon richness to alkalinity gradient at different shore types (UM- unmodified, MR - modified riparian and ML - modified littoral shoreline), based on composite samples. Asterisk indicates shoreline type significantly different from the unmodified shoreline.

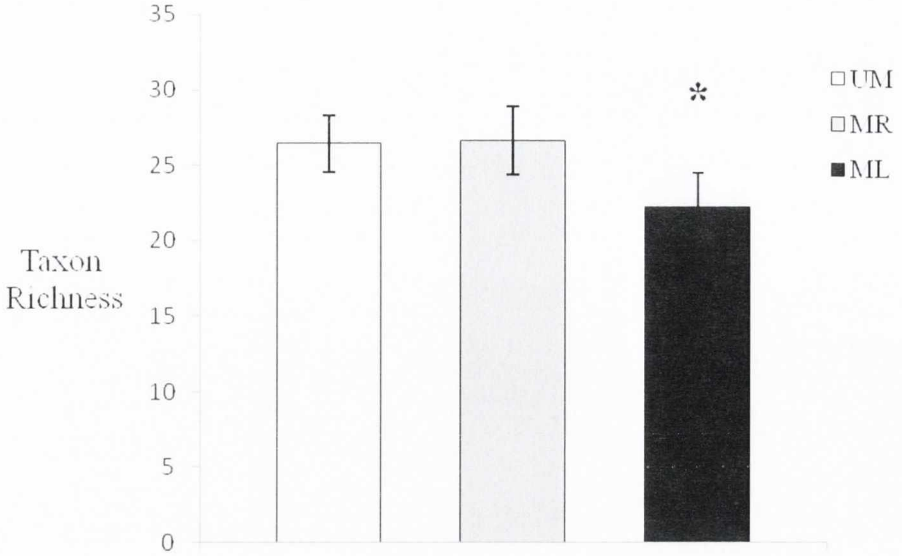

Figure 4.6. Mean of the predicted taxon richness values (±SE) from composite samples across different shore types (UM - unmodified, MR - modified riparian and ML - modified littoral shoreline; n= 27 for each shore type). Asterisk indicates shoreline type significantly different from the unmodified shoreline.

4.3.3 Effects of TP gradient and morphological modification on total abundance of littoral macroinvertebrate assemblages

Mesohabitat samples

Parameters retained in the log-transformed abundances model from the mesohabitat dataset were categories of shoreline modification, mesohabitat types, alkalinity, and the distance from the east coast of Ireland. Random part of the model accounted for the variation among lakes and sites within shoreline types. Both the alkalinity and the distance from the east coast of Ireland were estimated to reduce abundances across sites. Total abundances from modified riparian shores were significantly increased in comparison with the abundances from the unmodified shore types. In addition, the log-transformed abundances were highly significantly decreased at sandy habitat patches in comparison with stony and macrophyte substrates (Table 4.3). The nutrient-related (TP) variable was discarded in the early stages of the model selection, indicating its effect on total abundance was not significant.

Table 4.3. Results of linear mixed-effects model for log-transformed abundance from mesohabitat samples. (UM - unmodified, MR - modified riparian, ML – modified littoral shoreline; categories in parentheses set as reference levels). *AICc*= 643.0

	Estimated Coeff.	SE	t-value	*P*
Shore type:ML(UM)	-0.324	0.233	-1.391	0.169
Shore type:MR(UM)	0.724	0.237	3.049	0.003
Mesohabitat:sand(macrophytes)	-0.488	0.168	-2.904	0.004
Mesohabitat:stone(macrophytes)	0.057	0.134	0.426	0.670
Mesohabitat:sand(stone)	-0.545	0.164	-3.331	0.001
Eastings	-0.125	0.050	-2.522	0.045
Alkalinity	-0.387	0.131	-2.949	0.026

Composite samples

The most parsimonious model of log-transformed abundances from the composite samples was fitted with the shore modification types and the alkalinity as fixed terms and lake as a random term. Similar to the mesohabitat model, the abundances from the riparian modifications were significantly increased in comparison with the abundances from the unmodified shore, while the abundances of the modified littoral and unmodified shore type could not be distinguished (Figure 4.7; Table 4.4). Moreover, the alkalinity was shown to have an overall negative effect on the log-transformed abundances. The nutrient-related (TP) variable was discarded in the earlier stages of the model selection, as in the mesohabitat model.

Table 4.4. Results of linear mixed-effects model for log-transformed abundances from composite samples. (UM - unmodified, MR - modified riparian, ML – modified littoral shoreline; categories in parentheses set as reference levels). *AICc*= 206.37

	Estimated Coeff.	SE	t-value	*P*
Shore type:ML(UM)	-0.162	0.263	-0.617	0.539
Shore type:MR(UM)	0.382	0.161	2.370	0.021
Alkalinity	-0.282	0.090	-3.127	0.017

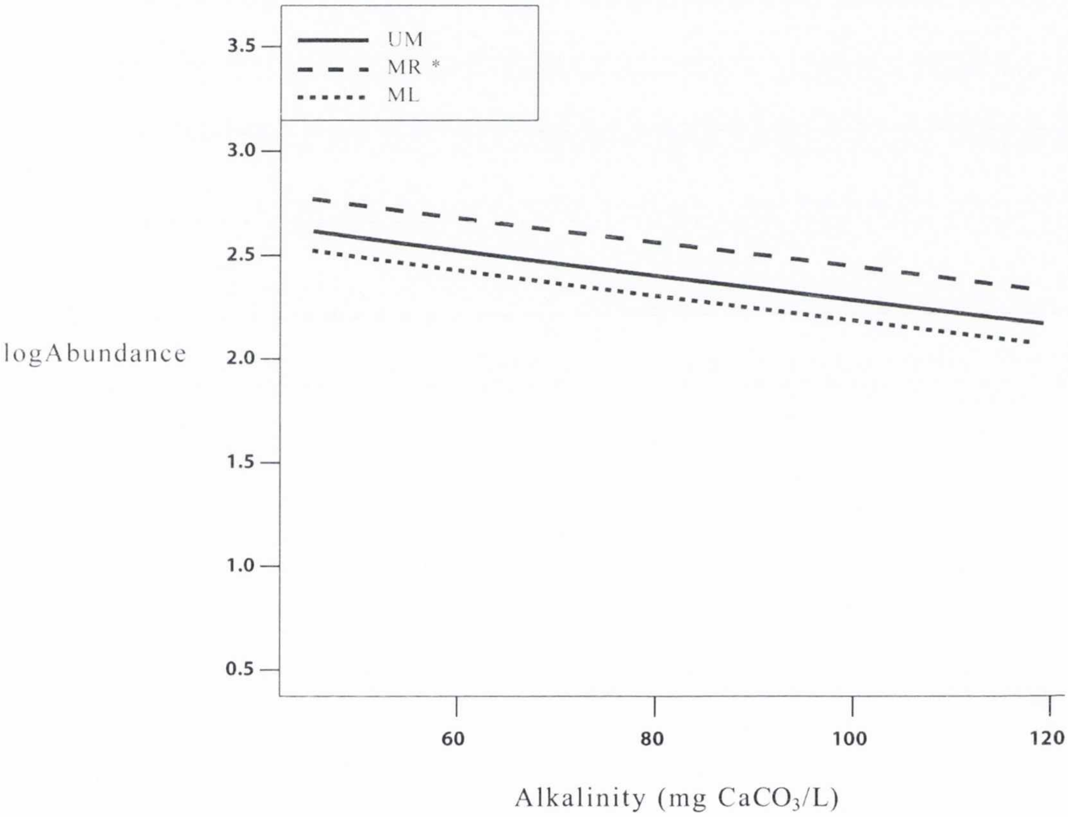

Figure 4.7. Visualisation of the model illustrating the difference in response of log-transformed abundances to an alkalinity gradient at different shore types (UM - unmodified, MR - modified riparian, ML – modified littoral shoreline), based on composite samples.

4.3.4 Effects of TP gradient and morphological modification on the Margalef diversity index

Mesohabitat samples

The most parsimonious model for the Margalef diversity index comprised the mesohabitat type, the area of the lake, the distance from the east coast of Ireland, alkalinity, and a nutrient related parameter (TP concentrations). Lake and site factors were retained in the random part of the model. The model results revealed a significant decrease in the assemblage diversity from the sandy habitat patches when compared with the macrophyte-dominated habitats (Table 4.5). Furthermore, Margalef diversity was negatively affected by the area of the lake, the distance from the east coast of Ireland, and TP concentrations (Table 4.5). All the interaction terms were removed from the final model.

Table 4.5. Results of linear mixed-effects model for Margalef diversity index from mesohabitat samples (UM - unmodified, MR - modified riparian, ML – modified littoral shoreline; categories in parentheses set as reference levels). *AICc*= 576.9

	Estimated Coeff.	SE	t-value	*P*
TP concentrations	-0.562	0.103	-5.438	0.006
Mesohabitat:sand(macrophytes)	-0.471	0.159	-2.960	0.004
Mesohabitat:stone(macrophytes)	-0.159	0.131	-1.218	0.225
Mesohabitat: sand(stone)	-0.311	0.152	-2.040	0.043
Eastings	-0.091	0.040	-2.288	0.084
Alkalinity	-0.205	0.104	-1.973	0.120
Lake Area	-0.200	0.039	-5.200	0.007

Composite samples

The most parsimonious model based on the Margalef diversity index for assemblages from composite samples included categories of different shoreline modifications, TP variable and lake area as fixed terms and lake as a random term. The estimated coefficients revealed a significant decrease of diversity at sites with littoral and riparian modifications when compared with morphologically unmodified sites (Table 4.6, Figure 4.8). Increased TP concentrations, distances from east coast of Ireland and lake area were shown to decrease diversity of macroinvertebrate assemblages from the studied lakes. The interaction between TP concentrations and shoreline types was not significant.

Table 4.6. Results of linear mixed-effects model for Margalef diversity index from composite samples (UM - unmodified, MR - modified riparian, ML – modified littoral shoreline; categories in parentheses set as reference levels). *AICc*= 238.12

	Estimated Coeff.	SE	t-value	*P*
Shore type:ML(UM)	-0.374	0.179	-2.086	0.041
Shore type:MR(UM)	-0.519	0.179	-2.899	0.005
TP concentrations	-0.677	0.223	-3.034	0.023
Lake Area	-1.565	0.620	-2.524	0.045

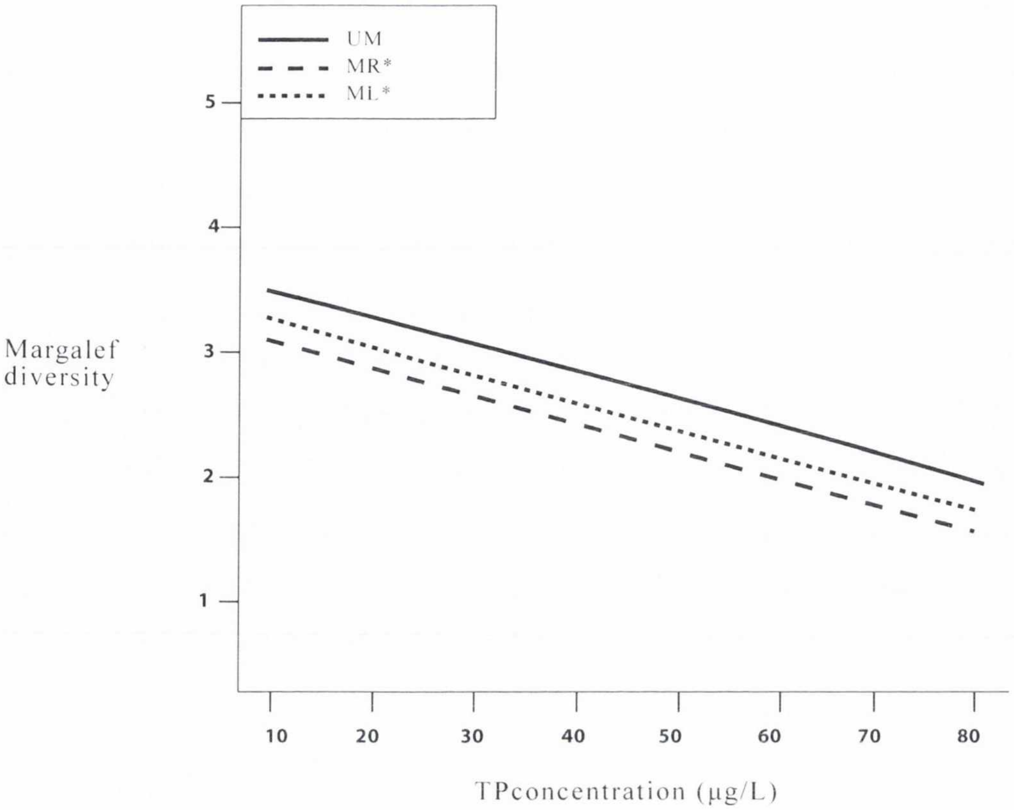

Figure 4.8. Visualisation of the model illustrating the difference in response of Margalef diversity index to a TP gradient at different shore types (UM - unmodified, MR - modified riparian and ML - modified littoral shoreline), based on composite samples. The other relevant covariates (alkalinity, distance from east coast of Ireland and lake area) were set to mean values.

4.4 Discussion

4.4.1 Effect of shore modification on diversity and abundance of littoral macroinvertebrates

The results of the mixed models investigating the richness and abundance of littoral macroinvertebrate assemblages from nine lakes revealed that taxon richness, abundance and Margalef diversity index were affected by the morphological modifications of shore zone over and above the effect of nutrient enrichment. These results are consistent with the findings of Brauns *et al.* (2007b) who investigated the effect of three types of man-made shoreline modifications on littoral macroinvertebrate assemblages by comparing communities from altered sites with those of non-altered littoral sites. This was done in lowland lakes of different trophic status and varying proportions of altered shoreline. The authors found a significant decrease of species richness in eulittoral macrobenthic communities at beaches and retaining walls, and a positive correlation between the number of habitat types (habitat heterogeneity) and species richness. This is in concordance with the results of this study, where a significant decrease of taxon richness was found at modified littoral sites in both composite and mesohabitat samples, with sandy substrate having the lowest taxon richness values. However, the results of both models based on composite and mesohabitat samples showed a significant increase in abundance of littoral assemblages from modified riparian sites. Although the scope of this study was not focused on capturing the among-sites effects of nutrient enrichment, it may be speculated that the increase in littoral macroinvertebrate abundances was caused by the local effects of grasslands (sites with riparian modification). Namely, the potential application of fertilisers and the spread of cattle manure could have increased the levels of nutrients in the surface waters through the runoff (Carpenter *et al.,* 1995), and therefore potentially increased the productivity of periphyton in the littoral zone of the sites with altered riparian zone (Rosenberger *et al.*, 2008). Moreover, the open-canopy conditions at grasslands may increase the temperature of water owing to the loss of shade (Johnson & Johnes, 2000). Finally, the results of k-dominance curves showed that modified riparian habitats supported highest taxon richness of macroinvertebrates, on average. However, according to both the mesohabitat and composite model, taxon richness from modified riparian shoreline was not significantly different from the unmodified shorelines when the effects of the other environmental variables were taken into account. Therefore, a combination of increased food resources (periphyton) and water column temperature could lead to the increase in abundance, but not richness of the littoral macroinvertebrate taxa from modified riparian (grassland) shores compared with the assemblages from unmodified (woodland-dominated) shorelines.

Morphological modifications are strongly related to changes in the structure of macrophyte communities and in the complexity of riparian vegetation (McGoff & Irvine, 2009), which is, meanwhile, positively related with the number and abundances of macroinvertebrate taxa (Thomaz *et al.*, 2008). Brauns *et al.* (2007b) also found that macroinvertebrate densities decrease at altered shorelines among sites, while they increased among lakes owing to the increasing abundances of Chironomidae. The results of the abundance and Margalef diversity models revealed a significant decrease in response values at sandy mesohabitats in comparison with macrophytes and stony habitats. This can be explained by the fact that sandy habitat patches provide fewer ecological niches owing to their lack of structural complexity. In addition, it was confirmed that the habitats with increased structural complexity provide shelter from the wave-induced stress for the littoral macroinvertebrates (Gabel *et al.*, 2008). Moreover, shorelines which contain macrophytes provide both greater taxon richness and abundance of littoral macrobenthic communities compared with non-vegetated habitats (White & Irvine, 2003).

4.4.2 Effect of TP: Nutrient enrichment diminishes distinctiveness of mesohabitat assemblages

While eutrophication is regarded as the main pressure to lake ecology (Schindler, 2006), the littoral component of macrobenthic assemblages has only occasionally been reported as an indicator of trophic status in lakes (Brodersen *et al.*, 1998; Brauns *et al.,* 2007a; Donohue *et al.* 2009a). A number of authors (Tolonen *et al.* 2001; Johnson & Goedkoop, 2002; White & Irvine, 2003) have attempted to disentangle the influence of habitat characteristics and nutrient enrichment with various outcomes. For instance, White & Irvine (2003) suggested that the mesohabitat approach should be preferably used in ecological assessments of littoral zones of lakes. In agreement with this, Tolonen & Haimalainen (2010) demonstrated that the effect of nutrient enrichment can be captured only by sampling macroinvertebrates from distinctive mesohabitats. Results of the models partially supported these findings, by demonstrating the negative effect of TP concentrations on taxon richness and Margalef diversity of assemblages from mesohabitat samples. On the other hand, the Margalef diversity model captured the negative effect of TP on littoral macroinvertebrate assemblages based on composite samples also. In addition, the significant interaction between the effect of TP and different mesohabitat types suggest that the response of the assemblages to nutrient enrichment differs depending on the type of mesohabitat. More specifically, the results indicated decreased differences among the richness values of assemblages from distinctive mesohabitats. The reason for this could be found in the actual mechanisms of the pressures and, related to them, the characteristics of the habitats. For instance, habitat homogenisation or reduction of habitat heterogeneity has been hypothesised to cause a decrease in the β-diversity of macrobenthic assemblages (Donohue *et al.*, 2009b). It could be, therefore, speculated that homogenising effect manifested through decreased differences in taxon richness values was caused by the differences in buffering capacity of mesohabitats with regard to nutrient enrichment. In contrast, abundances of the studied assemblages were found to be unaffected by the TP concentrations based on neither mesohabitat nor composite samples.

Determining the influence of multiple pressures and their interactions is an important step in the management and conservation of freshwaters (Richter *et al.*, 1997; Ormerod *et al.*, 2010). According to the results of the models, there was no interaction between the effects of TP concentrations and shore modifications on either diversity metrics or abundances of littoral macroinvertebrates. This was surprising, since both the effect of nutrient enrichment and shoreline modifications were established as significant according to the majority of the studied models. Furthermore, since it was hypothesised that both types of pressures have similar mechanisms of impact on macroinvertebrate assemblages, the amplified effect was expected. However, according to the results of the models shoreline modifications do not have a more deteriorating effect on macroinvertebrate assemblages in nutrient-enriched lakes compared with nutrient-poor lakes.

4.4.3 Effect of alkalinity, distance from east coast of Ireland and lake area on diversity and abundance of littoral macroinvertebrates

The influences of water chemistry, lake morphometric and geo-morphological features on the structure of benthic macroinvertebrate communities have been widely studied. Within water chemistry, alkalinity has an important role in determining the littoral macroinvertebrate community composition (Little *et al.*, 2006; O'Toole *et al.*, 2008). A study on benthic algae from Ireland (Leira *et al.,* 2009) revealed taxonomically distinctive benthic algal communities in lakes of low (<20 mg $CaCO_3$ l^{-1}), medium (20-100 mg $CaCO_3$ l^{-1}) and high (>100 mg $CaCO_3$ l^{-1}) alkalinity categories. According to Leira *et al.* (2009), more taxonomically distinctive assemblages were found in lakes of moderate alkalinity compared with lakes of both low and high alkalinity. This is consistent with the results of this study, where lakes belonged to medium and high alkalinity water bodies, with alkalinity values ranging between 45 and 119 mg $CaCO_3$ l^{-1}. Across this range of the study lakes, alkalinity was found to decrease taxon richness, total abundance and Margalef diversity values.

The geographic position of a lake generally affects its characteristics and communities (Kratz *et al.*, 1998). In a Swedish study, the variance of benthic communities in stony habitats was explained by the differences in habitat-scale variables. However, smaller variation was accounted for by the geographic position and the other regional-scale variables of the lakes (Johnson *et al.*, 2004). In concordance, the results from the nine lakes studied here show that the distance from east coast of Ireland plays significant role in defining macroinvertebrate diversity, by inversely affecting the taxon richness, abundance and Margalef diversity index. This pattern may be supported by the paths of post-glacial colonisation of Ireland (Preece *et al.* 1986), which assumed the existence of a land-bridge connection at the eastern coast of the island. However, more recent studies indicated that the process of deglaciation of the island of Ireland was more complex, including the rise of the Irish sea level, which definitively negates the theory about the existence of a land-bridge connection between Ireland and Britain (Edwards & Brooks, 2008).

In this study, the results of mesohabitat models based on taxon richness and Margalef diversity index indicated that lake size inversely influences the diversity of the littoral macroinvertebrates. Many studies have explored the relationship between lake size and taxon richness. Although the results of this study seem contrary to common knowledge and ecological theory, various authors have failed to demonstrate the expected positive relationship between the area of the lake and the diversity within invertebrate communities. Dodson (1992) found strong positive correlation between lake area and number of cladoceran zooplankton species, suggesting lake size promotes higher heterogeneity of habitats. The positive relationship was also confirmed by Heino (2000) and in the special cases for the fauna of snails (Hrabik *et al.* 2005). In contrast, Nilsson *et al.* (1994) found a negative relationship between the diversity of the dytiscid beetles and water body area, based on smaller lakes and ponds. This was speculated to be induced by the higher immigration rates of vagile animals (Hrabik *at al.* 2005). Some other authors declined the existence of any relationship between the diversity and lake area (Zenker & Baier, 2009). Meanwhile, Moss *et al.* (2003) stated that shallow lakes with areas between 50 ha and 10,000 ha did not differ significantly in terms of ecological characteristics.

4.4.4 Variability of assemblages within the lake littoral zone

This study showed that littoral communities vary widely both across lakes and within lakes. Even within a lake, variation between sites remained significant. This pattern could be owing to the high variability of littoral zones *per se* as trophic state and variation of biotic components can have dramatic impact on benthic communities (Tate & Hershey, 2003). the fact that factor site was retained in all models, indicates the importance of within-lake variance, which is consistent with the findings of White & Irvine (2003), who described a higher similarity among the communities within a lake than among the lakes.

4.4.5 Application of mixed-effects models in studies of lakes

Mixed-effects models are very flexible in allowing for hierarchical structure of the data, complex design and unbalanced dataset (Crawley, 2007). They definitely have very high potential in limnological, and general ecology-based studies. A special case of mixed-effects model, generalized mixed-effects model may provide better insight and reveal patterns of the data that have non-normal distributions (Bolker *et al.*, 2009). In general, non-linear types of regressions are applicable and, in many cases, even more appropriate for exploration and explanation of complex processes in nature. In this study, the flexible use of random elements in the mixed-effects models permitted findings to be generalised from all the investigated lakes and, therefore, the study was not limited to drawing separate conclusions for each lake. The fact that linear mixed-effects models are based on multiple linear regressions allow the simultaneous analysis of multiple factors (pressures) which is desirable in the observational type of studies. In addition, mixed-effects models also allow ANCOVA designs (Crawley, 2007), through application of both continuous and categorical types of variables simultaneously. Regarding the procedure of choosing the best model, mixed-effects models are designed to allow an information-theoretic approach, which is preferred and more reliable compared with stepwise modelling (Burnham & Anderson, 2001; Whittingham *et al.*, 2006). Finally, mixed-effects models allow clear identification of interactions among covariates.

4.5 Conclusions

The results presented in this chapter showed that:

- There is a relationship between the diversity measures of macroinvertebrate assemblages and the effect of shoreline modifications, even after the effects of other environmental factors are accounted for.
- Taxon richness and Margalef diversity of littoral macroinvertebrate assemblages were diminished at shorelines with littoral modifications compared with shorelines without modifications, while the taxon richness from shorelines with only riparian modifications was not affected compared with unmodified shorelines. In contrast, abundances of assemblages from modified riparian zone were increased compared with assemblages from unmodified and modified littoral shorelines.
- TP concentrations were demonstrated to negatively affect the taxon richness and Margalef diversity index of littoral macroinvertebrate assemblages, while the abundances were not affected.
- According to the results of the taxon richness model, the response of the assemblages to the anthropogenic pressures (nutrient enrichment and shoreline modifications) varies depending on the type of mesohabitat. Moreover, nutrient enrichment was demonstrated to reduce the differences among the assemblages from distinctive mesohabitats.
- There was no interaction between the effects of TP concentrations and shore modifications on either diversity measures or abundances of littoral macroinvertebrates.

5. What better captures the impact of shoreline modifications: mesohabitat-specific taxa or composition of littoral macroinvertebrate assemblages?

5.1 Introduction

Benthic macroinvertebrates are commonly used as indicators in assessments of water quality because of their sedentary nature, longevity of life cycles, ubiquitous occurrence/distribution, variety and general sensitivity to changes of environmental factors (Rosenberg & Resh, 1993). Monitoring of benthic invertebrate fauna is proposed by EU legislation as part of the integrated approach to managing aquatic habitats (Logan & Furse, 2002). Annex V of the EU Water Framework Directive (European Commission, 2000) defines the taxonomic composition, abundance, ratio of sensitive to insensitive taxa and the level of diversity of benthic invertebrate fauna as important elements in ecological status assessment of waterbodies.

While a few methods of ecological status assessments are based on monitoring species presence or absence (Hellawell, 1986), a community-based analysis is more prevalent (Attrill, 2002). The main advantage of the community-level approach is highlighted by viewing a community as an integrative multispecies indicator of stressors in aquatic ecosystems (Attrill, 2002). The task of explaining the species abundance distributions within communities has been tackled by a number of theories and resulted in the formulation of several mathematical models (for example Fisher, 1943; Pielou, 1969). At the same time, the variation in species occurrences is reflected through their uneven distributions (Magurran & Henderson, 2003), adding to the variability of community structure (Hellawell, 1986). However, community-level assessment has low potential for indentifying the underlying causes of changes (Adams, 2003). Biological (e.g. maximal body size, feeding habits, locomotion) or ecological traits (e.g. tolerance to organic pollution, substrate preferences, biogeographical distribution) of benthic freshwater macroinvertebrates (Usseglio-Polatera *et al.,* 2000) offer an alternative approach for establishing the link between biological communities and habitat pressures (Townsend & Hildrew, 1994). The trait approach provides a promising method for detecting mechanisms underlying the response of littoral macroinvertebrates to pressures by relying not only on community composition but also on autecological characteristics of species within communities (Menezes *et al.,* 2010).

The effect of eutrophication on littoral macroinvertebrate assemblages is frequently investigated (Brodersen *et al.*, 1998; Tolonen *et al.* 2001; Brauns *et al.,* 2007a). In contrast, few attempts have been made to identify the effects of lake shoreline modifications in terms of shoreline degradation (Brauns *et al*, 2007b,; Rosenberger *et al.,* 2008). The identification of the response of stream macroinvertebrates (Lorenz *et al.,* 2004) to hydromorphological alterations (Raven *et al.*, 2002) is more advanced, yet little is known about the effects of altered morphology on benthic macroinvertebrates in either lenthic or lotic freshwaters.

The results of Chapter 3 showed the importance of habitat features in structuring macroinvertebrate assemblages. In Chapter 4, the relationship between the taxa richness and diversity of macroinvertebrate assemblages and the effect of shoreline modifications was established. Taxon richness was diminished at shorelines with littoral modifications compared with shorelines without modifications, while the taxon richness from shorelines with only riparian modifications was not affected compared with unmodified shorelines. TP concentrations were demonstrated not to interact with the effect of shoreline modifications. Furthermore, the decrease of richness and diversity was speculated to be induced by the homogenization of the habitats owing to the morphological modifications and nutrient enrichment. This speculation was based on the findings of Donohue *et al.* (2009b) who demonstrated that macroinvertebrate assemblages in lakes have reduced heterogeneity with increasing nutrient enrichment.

The primary goal of this study was to identify whether the morphological modifications of shorelines across nine studied lakes had an effect on littoral macroinvertebrate assemblages. This was tested using two approaches: 1) a community composition-based approach where community composition provides the basis for a resemblance matrix using multivariate analysis and 2) an indicator-based approach with Indicator Value Analysis. The first approach is lead by the assumption that the response of assemblages to the modification of physical habitat yields common change in the pattern of the community composition. The indicator approach is based on the premise that species tolerant or sensitive to modifications of shoreline zones can serve as indicators of the altered shoreline morphology. Benthic freshwater macroinvertebrates have specific habitat requirements. For example, insect fauna prefer specific habitats regarding the oviposition, pupation and habitats for terrestrial-dwelling adult stages (Rosenberg & Resh, 1993). It is proposed here that the loss of diversity/richness could be caused indirectly by the loss of available niches caused by the pressure.

The second goal of this study was to provide an explanation for the mechanisms inducing the changes in macroinvertebrate assemblages at altered shorelines. More physically complex habitats support greater species richness (Bell *et al.*, 1991), and this relationship has also been demonstrated for littoral macroinvertebrate assemblages (Brauns *et al.*, 2007b), although the response can be species-specific (Tokeshi & Taniguchi, 2004). Donohue *et al.* (2009b) suggested that homogenization of assemblages was most likely caused by the decrease in number of habitat specialists. It is assumed that habitat specialists are lost owing to anthropogenic disturbances, as demonstrated in coral reef fish communities (Munday, 2004). Presuming that the disturbance can be quantified by the changes in habitat structure, it is hypothesised that species with specific habitat requirements (stenotopic species) would diminish in structurally simplified sites. To test this, a measure of littoral habitat complexity was devised and used as one of the explanatory variables in a generalized linear mixed-effects model with a number of taxa with specific mesohabitat preferences (mesohabitat-specific taxa) as the response variable.

The following hypotheses were proposed:

Hypothesis 1: Species' individual sensitivities/tolerances toward shoreline modifications provide more insight into the effects of altered shoreline morphology than the composition of littoral macroinvertebrate assemblages.

Hypothesis 2: Diminished complexity of littoral habitats reduces the number of mesohabitat-specific taxa.

5.2 Materials and methods

5.2.1 Sampling of macroinvertebrates

The data for this study were based on the dataset from all nine lakes (see p.10 for lake descriptions) of varying nutrient concentrations (TP ranging between 9 and 81 $\mu g\ l^{-1}$) and alkalinity values in the moderate to high category (from 45 – 119 mg $CaCO_3\ l^{-1}$). Samples were collected in April and May 2009. Sampling sites were chosen according to the presence/absence of shoreline modifications along riparian or littoral and riparian zones. For each lake, three shoreline types were identified to represent:

a) "unmodified"(UM) – sites without obvious morphological modification, a riparian zone usually dominated by (semi-) natural wood or scrub

b) "modified riparian" (MR) – sites with a modified riparian zone, usually pasture or improved (fertilized) grassland, where woody vegetation is usually absent or minimal

c) "modified littoral" (ML) – sites with modified littoral and riparian zones reflected through artificial morphological structures such as paved slipway, concrete embankment, and artificial beach or jetty.

Nine sampling sites were chosen to represent shoreline types in triplicates. Sampling for macroinvertebrate fauna was conducted according to the protocol for mesohabitat and composite sampling design explained in Chapter 2. Macroinvertebrate samples were collected with a standard FBA handnet with a mesh size of 0.5 mm. Samples were preserved on site with 70% Industrialised Methylated Spirit and stored in dark plastic bottles for later processing in the laboratory. Individuals were identified to the highest taxonomic resolution possible, usually species, using standard keys.

5.2.2 Water chemistry analyses

Water samples were collected from every lake at three random sites along the shorelines using a weighted plastic 5 l bottle attached to a 10 m long rope. Water samples were analysed in the laboratory for alkalinity, conductivity, pH, colour, chlorophyll *a*, total phosphorus, total nitrogen and dissolved and non-dissolved total organic carbon (DTOC and TOC, respectively). The procedures for the laboratory analyses were explained in more detail in Chapter 2.

5.2.3 Multivariate analysis of macroinvertebrate community composition

Both mesohabitat and composite samples datasets were analysed in order to test the hypotheses of this study. Within each dataset, taxa comprising species (and genera where further identification was not possible) were included in the analyses. The initial data matrix comprised 203 taxa in total.

Community composition was analysed using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McArdle & Anderson, 2001) in the PRIMER Version 6.1 (PRIMER-E Ltd., Plymouth, UK). PERMANOVA tests for the simultaneous response of resemblance-based variables to one or more factors in an ANOVA design, using permutation methods (Anderson *et al.*, 2008). A pseudo F statistic represents analog to the F statistic in ANOVA, but it does not have a known distribution under the true null hypothesis. The *P*-value is calculated by a permutation (or randomization) technique. In this case, the relative abundances of macroinvertebrate assemblages were first square-root transformed to downweight the importance of abundant species. Afterwards, Bray Curtis similarity matrix was generated. *A posteriori* pairwise comparisons were carried out on factors found to be significant within the PERMANOVA model. This was calculated by taking the pairs to be compared and calculating the pseudo t as the square root of pseudo-F, similar to a t-test in univariate analysis. If the number of permutations was fewer than 100, Monte-Carlo sampling was used to obtain Monte-Carlo *P*-values, as recommended by Anderson *et al.* (2008). An α significance level of 0.05 was used for all analyses. Non-metric Multi Dimensional Scaling (MDS), based on the square-root transformed Bray-Curtis resemblance matrix, was used to visualise community composition. TP concentrations and alkalinity were included in the analysis as continuous covariables, while shoreline modification type was used as a fixed factor. Lakes (composite samples dataset) and lakes, sites and types of mesohabitats (mesohabitat dataset) were included as random terms in order to control for the variability at different spatial scales, and to avoid pseudo-replication (*sensu* Hulbert, 1984). In the PERMANOVA design, sites were nested within lakes, and mesohabitats within sites. Continuous explanatory variables were standardised prior to the analyses. The procedure of model selection was similar to the procedure for mixed-effects models, explained in Chapter 2 under the section Model selection.

5.2.4 Indicator Value Analysis

Indicator Value Analysis (IndVal Analysis) is based on an asymmetrical approach for finding indicator species, by combining the relative abundances and relative frequencies of occurrence of species (Dufrene & Legendre, 1997). Indicator species are usually species with narrower niche breadth. The Indicator Value is based only on species-specific abundance and occurrence comparisons. Therefore, the abundances of other species have no influence on the Indicator Value of a specific species.

$$\mathrm{IndVal}_{ij} = A_{ij} * B_{ij}$$

where A_{ij} stands for specificity (relative abundance) and B_{ij} for fidelity (relative frequency of occurrence) of species $_i$ at the shoreline type $_j$.

IndVal Analysis was used for assessing:

a) the species with specific shoreline type preferences ("shoreline indicators"), by calculating the Indicator Values based on the abundance of taxa.

b) the species with specific mesohabitat preferences (mesohabitat-specific taxa), by calculating the Indicator Values based on the presence/absence of taxa. According to Dufrene & Legendre (1997), using presence/absence instead of abundances provides an efficient way for identifying more robust indicator taxa.

All IndVal Analyses were performed in computer language R version 2.13.0 (R Development Team, 2011). Manipulation of the taxa dataset was done in the R package "vegan" (Oksanen *et al.*, 2010) and IndVal Analysis was performed using the "labdsv" package (Roberts, 2010) and 4200 permutations to obtain *P*-values for each Indicator Value.

5.2.5 Measure of habitat complexity within the littoral zone

In order to account for the structural complexity of habitats within the littoral zone of each site, a measure of habitat complexity was calculated. Firstly, up to three dominant types of mesohabitats (at least 10% of the total site area) were identified *a priori* at each site. Each type of mesohabitat was assigned a weight based on their structural complexity (Table 5.1). It was, therefore, assumed that concrete or sand represent structurally less complex mesohabitat types than stones, while stony mesohabitats comprise less complex environment than macrophyte- or grass- dominated mesohabitats. At the same time, the naturalness of mesohabitats was not included as a quality parameter of the measure of complexity. Consequently, artificial substrates such as concrete were assigned the same weight as sand, which is considered a natural mesohabitat in the littoral zone of some lakes.

The measure of complexity was calculated by summing together the individual weights of three independent mesohabitat samples. For example, if three types of mesohabitats occurred in the littoral zone of the sampling site, and these were stone, sand and concrete, the value of habitat complexity for the site was 2+1+1=4. Furthermore, calculation of the measure of complexity was always based on three mesohabitat samples, regardless of the number of available mesohabitat types. This way, the importance of the complexity of the present mesohabitat(s) was underlined while the number of different mesohabitats (habitat heterogeneity within each site) was not taken into account. Consequently, the lowest value of the metric was 3 (in the case of a site with a prevalence of structurally simple mesohabitat type such as sand: 1+1+1=3) and the highest 9 (in the case of a site with a prevalence of highly complex mesohabitat type such as macrophytes: 3+3+3=9).

Table 5.1. Individual weights of mesohabitat types

Mesohabitat type	Weight
Concrete	1
Sand	1
Stone	2
Grass	3
Macrophytes	3

5.2.6 Habitat complexity-based mixed-effects model

A generalised linear mixed-effects model was used to analyse the effect of habitat complexity on the number of species with specific mesohabitat preferences, called mesohabitat-specific taxa, across lakes of a) varying trophic states (from oligotrophic to eutrophic); and b) alkalinity categories (moderate and high). The R package "lme4" was used to generate generalized and simple linear mixed effects models (Bates & Maechler, 2010). The relationship was modelled using a Poisson distribution.

$Y_{ij} \sim \text{Poisson}(\mu_{ij})$

$\log(\mu_{ij}) = \alpha + \beta_1 X_{ij} + \beta_2 Y_{ij} + \beta_3 X_{ij} Y_{ij} + a_{ij} + \varepsilon_{ij}$

with error distribution $\varepsilon_{ij} \sim N(0, \sigma^2)$

where Y is the response (number of mesohabitat-specific taxa), α is the intercept, β_n are the estimated coefficients of the slopes of X and Y or the explanatory variables (habitat complexity and trophic levels) and their two-way interaction in the fixed part of the model, a_{ij} is the random part of the model, ε_{ij} is the error term for each level of lake i and site j. Initially, the full model included the alkalinity factor also, among fixed terms. The trophic factor comprised three levels – oligotrophic, mesotrophic and eutrophic. These were decided based on TP concentrations determined in the water column, where oligotrophic lakes were considered those with TP concentrations less than 20 $\mu g\ l^{-1}$ and eutrophic lakes were considered those with TP concentrations higher than 45 $\mu g\ l^{-1}$. Consequently, TP concentrations in mesotrophic lakes ranged between 20 and 45 $\mu g\ l^{-1}$. Lakes were divided into two categories of alkalinity – moderate (between 20 – 100 mg $CaCO_3\ l^{-1}$) and high alkalinity (above 100 mg $CaCO_3\ l^{-1}$). Lake factor was included as a random term. After the model selection procedure, explained in Chapter 2, both alkalinity and its interactions were discarded from the final, most parsimonious model.

5.3 Results

5.3.1 Effects of shoreline modifications on community composition

Composite samples

The structure of littoral macroinvertebrate assemblages was significantly affected by the TP gradient (Table 5.2), while the effect of the alkalinity and its interactions with TP and different shoreline types were not significant. After the effect of TP gradient was accounted for, a significant interaction was found between the shoreline types (fixed term) and lakes (random term) (Table 5.2). However, when tested separately using pair-wise tests, the effects of different shoreline types were not found to significantly affect the composition of littoral macroinvertebrate assemblages in any of the studied lakes. However, there was significant variability in the structure of the assemblages among lakes. The list of species recorded in each lake is given in Appendix, Table A.1.

Table 5.2. Results of the final PERMANOVA model showing the effect of shoreline type and TP on littoral macroinvertebrate composition based on composite samples.

Source	df	Sum of squares	Mean square	Pseudo-F	*P*
TP	1	24492	24492	2.56	**0.0094**
Sh (Shoreline type)	2	4831.4	2415.7	1.15	0.3
TP x Sh	2	5517	2758.5	1.31	0.1
La (Lake)	5	47787	9557.3	5.98	**0.0001**
Sh x La	12	25140	2095	1.31	**0.0105**
Residual	54	86164	1595.6		
Total	80	2174000			

Mesohabitat samples

PERMANOVA revealed a significant interaction between the effect of TP gradient and shoreline type on the composition of littoral macroinvertebrate assemblages from mesohabitat samples (Table 5.3). Similar to the results of the analysis performed on the composite samples, the interactions between alkalinity and TP or different shoreline types did not significantly affect the composition of macroinvertebrate assemblages. In addition, the estimated variability in the composition of the studied littoral macroinvertebrate assemblages among lakes, sites and mesohabitat types was significant.

Table 5.3. Results of the final PERMANOVA model showing the effect of shoreline type and TP on littoral macroinvertebrate composition based on mesohabitat samples.

Source	df	Sum of squares	Mean square	Pseudo-F	*P*
TP	1	65310	65310	2.4	**0.007**
Sh (Shoreline type)	2	11317	5658.3	1.4	0.09
TPxSh	2	15422	7711.1	1.89	**0.005**
Lake	7	183470	26210	6.51	**0.0001**
Site(Lake)	68	272690	4010.1	2.05	**0.0001**
Mesohabitat(Si(La))	44	5610	1275	1.28	**0.025**
Residual	116	114900	990.56		
Total	240	7192100			

In order to examine the possible interaction between the effect of TP concentration and the type of shoreline in more detail, lakes were grouped into three trophic categories (oligotrophic – below 20 μg l^{-1}; mesotrophic – between 20-45 μg l^{-1}; and eutrophic – above 45 μg l^{-1} TP). PERMANOVA was then performed with the trophic categories, shoreline types and their interactions as main fixed terms. Lake, site factor and types of mesohabitats were specified as random terms. The results confirmed the significant effects of trophic state on the community composition (Figure 5.1) while the shoreline types and their interactions with the trophic categories were not significant (Table 5.4). Among the random effects, lakes and sites contributed significantly to the variability in the structure of the littoral macroinvertebrate assemblages.

Table 5.4. Results of the final PERMANOVA model showing the effect of shoreline type and TP on littoral macroinvertebrate composition from mesohabitat samples.

Source	df	Sum of squares	Mean square	Pseudo-F	*P*
Tr(Trophic category)	2	89539	44770	1.69	**0.045**
Sh(Shoreline type)	2	11491	5745.5	1.4	0.088
ShxTr	4	21514	5378.5	1.31	0.086
Lake	6	1.5821E5	26369	6.45	**0.001**
Site(Lake)	66	2.6942E5	4082.2	3.73	**0.001**
Residual	161	1.76E5	1093.2		
Total	241	7.2619E5			

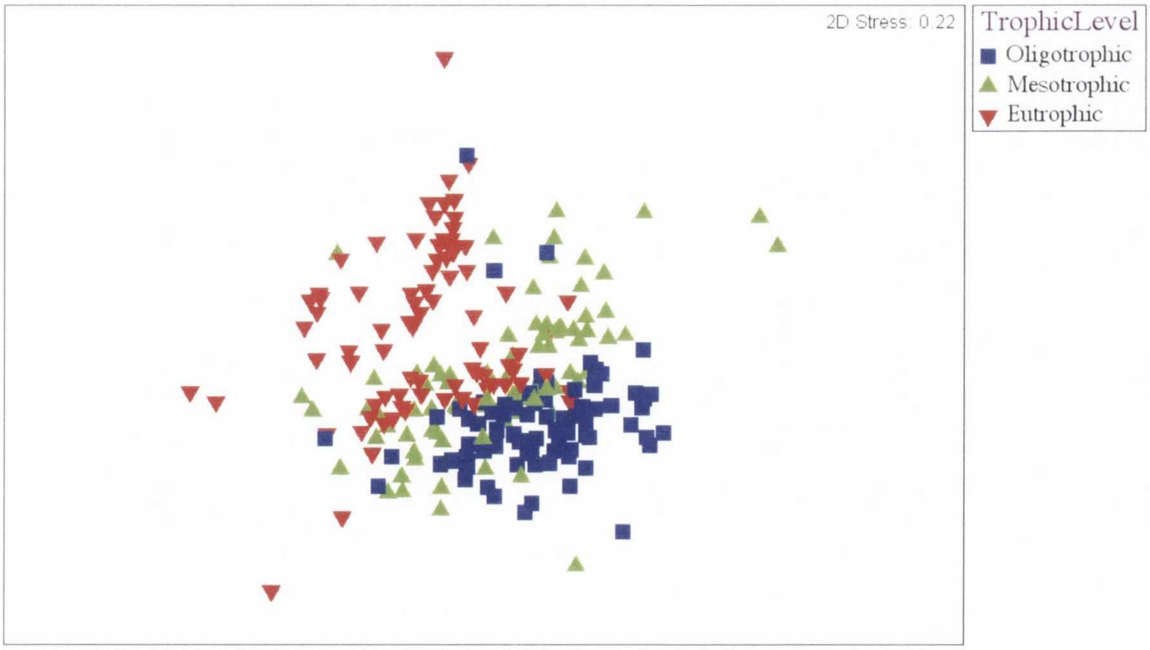

Figure 5.1. MDS of littoral macroinvertebrate composition based on mesohabitat samples, square-root transformed with Bray-Curtis similarity.(n = 243)

5.3.2 Effects of shoreline modifications on individual taxa – "shoreline indicators"

Indicator Value Analysis revealed three species as indicators of unmodified and modified riparian zones among the composite samples (Table 5.5). The analysis performed on mesohabitat samples revealed 14 "shoreline indicator" taxa (including the three species from composite samples). An equal number of taxa was associated with the unmodified and modified riparian shoreline (six), while only two species, *Elmis aenea* and *Valvata cristata* were indicators of modified littoral zone. However, except for the hemipteran species *Callicorixa praeusta* from composite samples, Indicator Values of the rest of the species did not exceed 0.25 (25%). In addition, five of the "shoreline indicator" taxa (Table 5.5) were considered potentially sensitive to the TP concentrations by Donohue *et al.* (2009a).

Table 5.5. Species associated with specific shoreline types (IndVal Analysis) and their TP sensitivity (*sensu* Donohue *et al.*, 2009a). Information based on absolute abundances of taxa from M- mesohabitat or C-composite samples

Species/Genera	Shoreline type	Ind. Value(M/C)	TP sensitivity	Sample type
Elmis aenea (larva)	ML	0.07*	+	M
Valvata cristata	ML	0.06*	-	M
Gammarus pulex	MR	0.13**	+	M
Callicorixa praeusta	MR	0.12**/0.27*	-	M+C
Psychomyia fragilis	MR	0.1**	+	M
Limnephilus vittatus	MR	0.07**	-	M
Tinodes pallidulus	MR	0.07**	-	M
Triaenodes bicolor	MR	0.07*	+	M
Polycelis nigra/tenuis	UM	0.24*	-	M
Kageroniafuscogrisea	UM	0.12**/ 0.25*	+	M+C
Planaria torva	UM	0.07*	-	M
Haliplus confinis (adult)	UM	0.07*	-	M
Planorbis carinatus	UM	0.07*	-	M
Halesus radiates	UM	0.06*/0.14*	-	M+C

Significance codes: '***'$P<0.001$ '**' $P<0.01$ '*' $P<0.05$;

Sample type codes: M - mesohabitat samples, C – composite samples

Shoreline type abbreviations: UM – unmodified, ML – modified littoral, MR – modified riparian

5.3.3 Effects of littoral habitat complexity on taxa with specific mesohabitat preferences

The measure of littoral habitat complexity was tested against shoreline types across all lakes. The results revealed significantly lower littoral habitat complexity at shorelines with littoral modification in comparison with the unmodified sites (Welch's two sample t-test=3.02, df=50.6, *P*=0.003), while shorelines with riparian modification did not have significantly different habitat complexity (Welch's two sample t-test=0.78, df=47.5, *P*=0.4) compared with the unmodified shorelines (Figure 5.2). Moreover, when the measure of littoral habitat complexity was tested against the trophic state, no significant differences were found in habitat complexity from distinctive trophic categories ($F_{2,78}$=0.71, *P*=0.5).

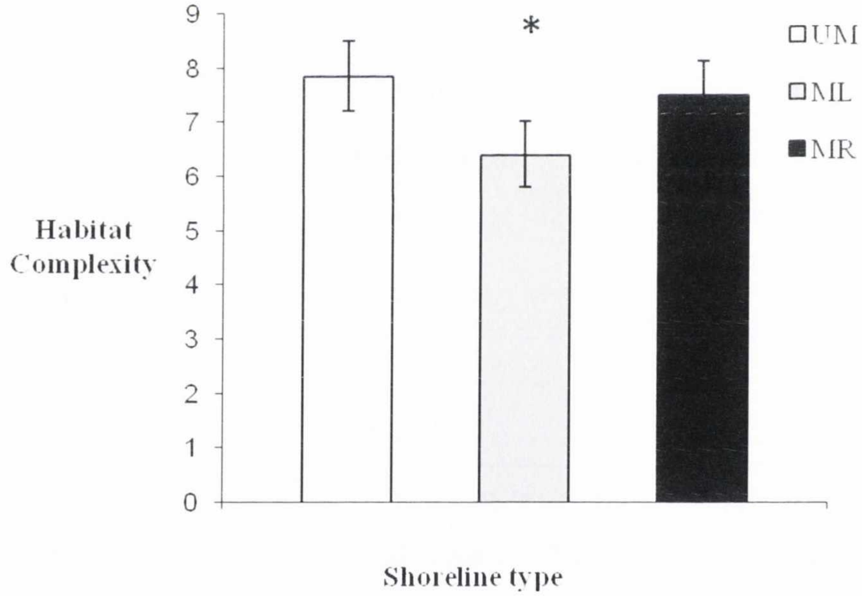

Figure 5.2. Histogram of mean values of measure of habitat complexity across different shoreline types (mean±SE for n= 27 for each shoreline type, UM – unmodified, ML – modified littoral, MR – modified riparian). The shoreline significantly different from the UM is marked with the star.

In order to determine which taxa had specific mesohabitat requirements, IndVal Analysis was performed on mesohabitat samples across all shoreline types. The analysis indicated 30 taxa with specific mesohabitat preferences (mesohabitat-specific taxa) (Table 5.6). Of these, one species *Sigara falleni* was confined to artificial substrate (concrete) and four taxa were associated with the flooded grass habitats. Nineteen taxa (61%) were characteristic for macrophyte mesohabitats, four species were associated with stony mesohabitats and three species with sandy patches. When results based on mesohabitat preferences were compared with the results of the previous (shoreline) indicator analysis, 5 out of 14 shoreline indicator taxa had specific mesohabitat preferences: *Polycelis nigra/tenuis, Callicorixa praeusta, Planorbis carinatus, Haliplus confinis* and *Triaenodes bicolor* (Table 5.6). All “shoreline indicator” species with specific mesohabitat preferences were associated with macrophytes.

Table 5.6. Mesohabitat-specifix taxa according to IndVal Analysis. Taxa sensitive to TP gradient noted with "+" (*sensu* Donohue *et al.*, 2009a). "Shoreline indicator" taxa are marked with (*).

Species/Genera	Distinctive mesohabitats					TP sensitivity
	concrete	grass	macrophytes	sand	stone	
Sigara falleni	+					-
Dryops sp.(larva)		+				+
Gammarus lacustris		+				+
Carychium sp.		+				-
Galba truncatula		+				-
Limnephilus lunatus			+			+
Caenis luctuosa			+			-
*Polycelis nigra/tenuis**			+			-
Asellus aquaticus			+			-
Crangonyx pseudogracilis			+			+
*Triaenodes bicolor**			+			+
Radix labiata			+			+
Callicorixa praeusta *			+			-
Cymatia bonsdorffii			+			-
Bithynia tentaculata			+			-
*Planorbis carinatus**			+			-
Dendrocoelum lacteum			+			-
Mystacides azurea			+			+
*Haliplus confinis (adult)**			+			-
Leptophlebia vespertina			+			+
Haliplus obliquus (adult)			+			-
Holocentropus dubius			+			+
Coenagrion lunulatum			+			-
Gammarus duebeni				+		-
Ephemera danica				+		-
Potamopyrgus antipodarum				+		-
Oulimnius tuberculatus					+	+
Centroptilum luteolum					+	+
Tinodes waeneri					+	-
Polycentropus flavomaculatus					+	+

A generalized linear mixed-effects model of the measure of habitat complexity, based on composite samples, revealed a significant positive relationship between the number of species with specific mesohabitat preferences and the littoral habitat complexity in oligotrophic and mesotrophic lakes (Table 5.7). This relationship was not apparent in eutrophic lakes (Figure 5.3).

Table 5.7. Results of a generalized linear mixed-effects model for number of mesohabitat-specific taxa from composite samples (n=81, Lake groups=9)

Variable	Estimate	S.E.	z	*P*
Habitat Complexity (HC)	0.10197	0.04832	2.11	**0.03***
Trophic category: meso	0.43349	0.46487	0.933	0.3
Trophic category: eutrophic	0.46091	0.47702	0.966	0.3
HC vs. mesotrophic cat.	-0.06565	0.06569	-0.999	0.3
HC vs. eutrophic cat.	-0.12985	0.06612	-1.964	**0.05** *

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

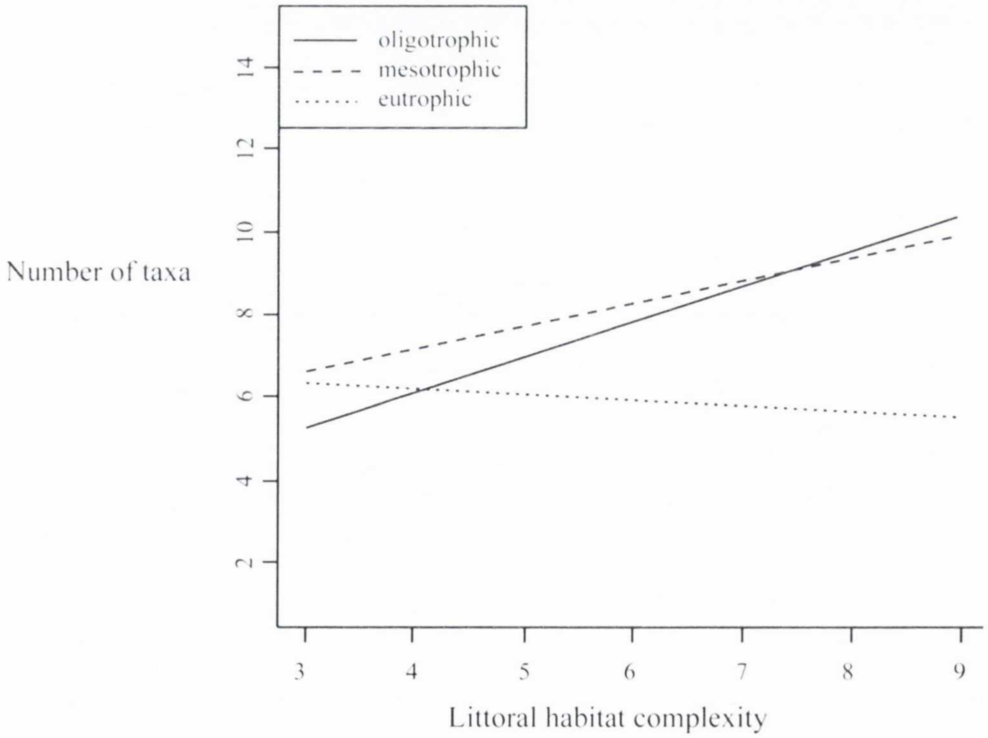

Figure 5.3. Interaction plot of change in number of mesohabitat-specific taxa among different trophic categories.

5.4 Discussion

The results of this study indicated no effect of shoreline modifications on the composition of littoral macroinvertebrate assemblages across lakes of differing trophic states. The effect of shoreline modifications was not apparent even when shorelines were compared within each of the studied lakes. In contrast with these results, several lake surveys found macroinvertebrate community composition to be significantly affected by shoreline development (De Sousa *et al.*, 2008; Rosenberger *et al.*, 2008).

While the effect of shoreline modifications was not apparent, the effect of TP concentrations on littoral macroinvertebrates was significant based on both composite and mesohabitat samples. This result is in agreement with previous studies exploring the impact of nutrient enrichment on littoral macroinvertebrates (Brodersen *et al.*, 1998; Tolonen *et al.*, 2001; Brauns *et al.*, 2007). Furthermore, the effect of alkalinity was not significant in any of the PERMANOVA models, which was in contrast with the findings from Irish (Little *et al.*, 2006) and European lakes (O'Toole *et al.*, 2008). However, Donohue *et al.* (2009b) demonstrated that nutrient enrichment homogenised lake macroinvertebrate assemblages over and above the effect of alkalinity, at both among- and within-lake scales. Similarly, the results of this study imply that the effect of TP may have masked the effect of alkalinity on composition of the littoral macroinvertebrate assemblages. This speculation is supported by the fact that Little *et al.* (2006) found the effect of alkalinity on littoral macroinvertebrate assemblages from lakes with low concentrations of nutrients.

While PERMANOVA models failed to show the difference in the structure of macroinvertebate assemblages, Indicator Value Analysis revealed a group of taxa characteristic of particular shoreline types. Similar to the results of Brauns *et al.* (2007b), who found distinctive taxa to be primarily associated with less morphologically altered shorelines, the results of this study revealed a higher number of "shoreline indicators" as being characteristic of unmodified and modified riparian shorelines (seven for each type). In contrast, only two taxa were confined to the modified littoral zone. However, rather low values of the IndVal metric (less than 25% in all but one case) suggested either a) low specificity or b) low fidelity of species (Dufrene & Legendre, 1997). Upon the examination of the distribution of the "shoreline indicator" taxa, it was revealed that coleopteran larva *Elmis aenea*, trichopteran larvae *Psychomyia fragilis* and *Tinodes palidulus* occurred at only two lakes, while *Limnephilus lunatus* was recorded in only three of the studied lakes. Therefore, these species could be considered as rare for this dataset. Moreover, some of the taxa may be sensitive to the nutrient gradient and their usefulness as indicators of shoreline modifications could be impaired by the trophic conditions of lakes. This was the case with indicators of littoral modification: *Elmis aenea,* which is considered "TP sensitive" according to Donohue *et al.* (2009a) and *Valvata cristata,* which occurs in well-oxygenated still waters according to Kerney (1999). In addition, examination of the ecology of "shoreline indicator" species revealed that some of the species have a preference for highly alkaline waters. For example, *Kageronia fuscogrisea* and *Planorbis carinatus* occur more frequently in limestone lakes (Greenhalgh & Ovenden, 2007; Kerney, 1999).

There were more "shoreline indicators" according to the mesohabitat than according to the composite samples, which implies that mesohabitat preferences may play an important role in determining the species prevalence toward a specific type of shoreline. The results of the analysis on mesohabitat preferences revealed five "shoreline indicators" with specific habitat preference; all species were characteristic of macrophyte-dominated mesohabitats. This was also confirmed in the following examples from the literature. Haemipteran *Callicorixa praeusta*, a common and abundant species in the British Isles, was associated with highly productive stagnant waters with reeds. In addition, owing to its migration capability, it is considered to be a pioneer species in new or temporary habitats (Savage, 1989). The Trichopteran larva *Triaenodes bicolor* is widespread and abundant in lakes and ponds in the British Isles. It is characterised by its swimming ability and occurs in stagnant and slow flowing waters among vegetation (Hickin, 1967). The freshwater snail *Planorbis carinatus* is found in weedy habitats of relatively small size and minimal flow (Boycott, 1936; Kerney, 1999). The water-beetle *Haliplus confinis* frequently occurs in pools of cut-over bogs and fens and less frequently in mesotrophic lakes. This species could also be associated with charophytes on which the larvae feed (Holmen, 1987). However, some species recorded in this study were not found to be confined to a particular type of mesohabitat, although the literature suggested a habitat preferences. For example, the mayfly *Kageronia fuscogrisea* is considered the only member of the Heptagenidae family that selects well-vegetated areas. It is scarce or local in Great Britain and other parts of Europe, but has widespread distribution in Ireland (Kelly-Quinn & Bracken, 2000). On the other hand, the freshwater shrimp *Gammarus pulex*, an invasive species in Ireland (McLoughlin & Reynolds, 2001), can occur in a wide variety of standing and running-waters (Gledhill *et al.*, 1993).

In general, species which show broad environmental tolerances can be considered habitat generalists, while species with very specific and narrow environmental tolerances are considered habitat specialists. As a consequence, habitat specialists use smaller habitat units (Kolasa & Pickett, 1989) and they appear to be more influenced by habitat loss than habitat generalists (Tilman *et al.*, 1994; Munday, 2004). Since the dataset used in this study was too small to be used in determining whether a species is a habitat specialist or a generalist, the information on preferences toward certain mesohabitats was used only as a guide for determining potential habitat specialists. Comparing the results obtained by Indicator Value Analysis with the literature sources, however, supported the interpretation of habitat preferences for the majority of species. For example, the hemipteran *Sigara falleni* was the only species characteristic of concrete, a type of mesohabitat present only at shorelines with littoral modifications. It is one of the most common water bugs on the British Isles, albeit a poor colonizer (). It prefers slow-flowing and stagnant alkaline waters. Two snail taxa were associated with flooded grass mesohabitats: *Carychium* sp., which is not considered a truly aquatic taxon, owing to its distribution at the edge of the waterbodies and in damp places (Macan, 1977); and *Galba truncatula*, which is considered an amphibious species, often found at the margins of a variety of wetlands (Boycott, 1936). Macrophyte-dominated mesohabitats were associated with the hemipteran *Cymatia bonsdorffii* (Savage, 1989), the damselfly *Coenagrion lunulatum* (Nelson *et al.*, 2011), the trichopteran larvae *Limnephilus lunatus, Holocentropus dubius,* and *Mystacides azurea* (Hickin, 1967), the mayfly larva *Kageronia fuscogrisea* (Kelly-Quinn & Bracken, 2000) and *Bythinia tentaculata* (Boycott, 1936). *Tinodes waeneri* builds mud tunnels on large stones or rocks (Hickin, 1967) and *Ephemera danica,* widespread species with a preference towards silty and muddy substrates, probably owing to its burrowing preferences (Kelly-Quinn & Bracken, 2000).

The information in the literature on a few species was inconsistent with the results of IndVal Analysis. For instance, *Caenis luctuosa* is common in Ireland and found typically in lakes with silty substrate in high densities (Kelly-Quinn & Bracken, 2000), although in this study it was characteristic of macrophyte mesohabitats. *Centroptilum luteolum* has a widespread distribution in Europe, occurring in both lentic and lotic habitats and associated with vegetated areas and slow currents (Kelly-Quinn & Bracken, 2000), while in this study it was associated with stony mesohabitats.

The drawback of the asymmetric indicators analysis (Dufrene & Legendre, 1997) is that it does not take into account more than one pressure or factor important for the distribution of taxa. Similarly, the community structure is the result of influences of more than one factor in a multifaceted reality. One of the assumptions of this study was that species can be indicators of more than one pressure; hence the application of the mixed-effects model with multiple explanatory covariates.

The results of the most parsimonious habitat complexity-based model showed: 1) the positive relationship between the complexity of the littoral habitats and the number of species with specific mesohabitat preferences in oligotrophic and, less distinctly, in mesotrophic lakes; 2) higher number of mesohabitat-specific species at unmodified sites in comparison with shorelines with littoral modification; and 3) that the number of mesohabitat-specific species from unmodified shores and shorelines with riparian modifications were not significantly different. In addition, shorelines with littoral modification were demonstrated to have less complex littoral zones than shorelines with only riparian or shorelines without any type of morphological alterations. Similar results were obtained in the study of Brauns *et al.* (2007b) who found that shorelines with low structural complexity did not have characteristic species in the eulitoral zone. Furthermore, the same authors found no significant difference between the communities of natural shorelines and ripraps (boundary walls comprising large boulders), which they suggested was owing to the similarity in structural complexity. Therefore, the shorelines with riparian modification did not have significantly lower number of mesohabitat-specific taxa when compared with the unmodified shorelines, most likely because of their similar structural complexity.

Among the available types of mesohabitats, macrophyte-associated habitat patches were assumed to be structurally most complex. The majority (18 out of 30) of the littoral invertebrate taxa with specific mesohabitat preferences were associated with them. The interactions between macroinvertebrates and macrophytes are complex (Parsons & Matthews, 1995), since macrophytes indirectly provide food resources through higher amounts of organic matter and substrate for epiphytic algae and biofilm. In terms of the food resources, research conducted in the lower littoral zone (2 m depth) of two arctic lakes discovered that potential resources of organic matter were significantly higher in both rock and macrophyte patches in comparison with the open-mud habitats (Beaty *et al.,* 2006). Consequently, the results of the species richness assessment revealed that open-mud assemblages had significantly lower richness in comparison with the rock- or macrophyte–associated assemblages (Beaty *et al.,* 2006). Moreover, aquatic plants provide a direct food source for some invertebrates (e.g. larva of the water beetle *Haliplus* *confinis* which feeds on Charophytes). Macrophyte beds add heterogeneity of habitats *per se*; therefore, differences in the morphological structure of macrophytes influence the abundance of phytophilous macroinvertebrates (Parsons & Matthews, 1995). In addition, macrophytes play an important role in regulating predator-prey interactions in littoral habitats (Tolonen *et al.*, 2003), and provide shelter from hydrological disturbances such as waves (Gabel *et al.*, 2008).

A considerable number of taxa with specific mesohabitat preferences were also deemed as "TP sensitive" species according to Donohue *et al.* (2009a). Nevertheless, they were still included in the total number of mesohabitat-specific taxa, with the premise that inclusion of a nutrient-related factor in models could control for the potential masking effect of nutrients. Indeed, the final model of the mesohabitat-specific taxa response revealed significant interaction between the trophic categories and a measure of habitat complexity. More specifically, while the higher habitat complexity increased the number of mesohabitat-specific taxa in nutrient-poor lakes, the effect of increased nutrient concentrations reduced that effect. This result is supported by Donohue *et al.* (2009b) who proposed the reduction of the habitat heterogeneity as one of the mechanisms causing the homogenisation of macroinvertebrate assemblages.

Understanding the mechanisms of changes in littoral macroinvertebrate assemblages is necessary for the development of the pressure-specific tools for the assessment of shoreline modifications. On the other hand, the knowledge on the background mechanisms underpins the use of the functional aspect of macroinvertebrate taxa or assemblages. Examples of the functional aspect are ecological traits – characteristics that reflect a species adaptation to its environment (Statzner *et al.*, 2001). The advantage of this essentially functional approach is reflected through overcoming the initial issues that emerge in the community composition-based assessments, such as effects of biogeography, influence of geology and climate characteristics (Doledec *et al.*, 2011). This study highlights the advantages of applying habitat preferences as the functional approach rather than the approach based on community composition, termed as taxonomy-based approach (Menezes *et al.,* 2010), to the pressure-effect assessments. The functional trait approach is based not only on taxonomy but also on ecological characteristics of the recorded species – for example their habitat requirements. It has the potential, therefore, to detect the cause of a disturbance and provide hypotheses for the mechanisms which dictate the observed response of the littoral macroinvertebrates. At the same time, the application of the functional approach necessitates the broadening of knowledge on autecological aspects of lake littoral macroinvertebrates. Their potential for indicating ecotone integrity, like in case of *Ephemera danica* (Free *et al.*, 2009), should lead to further fundamental and applied investigations in freshwater ecology.

5.5 Conclusions

The results of this Chapter demonstrated that:

- The composition of littoral macroinvertebrate assemblages was not significantly related to the shoreline modifications, based on both composite and mesohabitat sampling.
- Of 203 recorded taxa, 14 were found to be characteristic of particular shoreline types. A number of species occurred more frequently at unmodified (6) and modified riparian shorelines (6) while only two species were associated with the shorelines with littoral modifications.
- Although the IndVal Analysis was more successful in assessing the differences in shoreline types, a few issues regarding this method (potential rarity and nutrient-sensitivity of species) may arise.
- Taxa with specific mesohabitat preferences were affected by the complexity of the littoral zones in oligotrophic and mesotrophic lakes.
- Based on these results, stenotopic species (habitat specialists) are proposed as the key to understanding the mechanisms of the impact of morphological alterations along littoral zone of lakes without high nutrient enrichment.
- Metrics based on autecological information of macroinvertebrate taxa have potentially higher sensitivity for identifying the impact of altered shoreline morphology than community structure and individual indicator taxa.

6. Discussion and conclusions

6.1 Complexity of littoral habitats

6.1.1 Relation between the littoral complexity and nutrient enrichment

While eutrophication is regarded as the main pressure to lake ecology (Schindler, 2006), the littoral component of macrobenthic assemblages has only occasionally been reported as an indicator of trophic status in lakes (Brodersen *et al.*, 1998; Brauns et al. 2007a; Donohue *et al.*; 2009a). Donohue *et al.* (2009b) hypothesised that the nutrient enrichment in lakes was reflected through the blanketing of the lakebed with organic sediments and reduction of structural heterogeneity from macrophytes. As a consequence, assemblages of benthic macroinvertebrates became less heterogeneous. Based on this finding, it was hypothesised in Chapter 4 that the nutrient enrichment would induce the decrease in the differences among taxon richness values of macroinvertebrates from distinctive mesohabitats. Results revealed that the nutrient enrichment in lakes negatively affected the richness of littoral macrobenthic assemblages and that the strength of the effect was different for assemblages from different mesohabitats. However, in Chapter 5 it was shown that the structural complexity of lake shorelines was not significantly different in lakes of differing trophic states. Moreover, it was shown that there was an interaction between the effects of nutrient enrichment and complexity of shoreline habitats on the number of taxa with specific mesohabitat preferences. In nutrient-enriched lakes, there was no relationship between the habitat complexity and a number of mesohabitat-specific taxa. This could be caused by the negative effect of nutrient enrichment on the available habitats. Therefore, results from Chapter 5 suggest that nutrient enrichment would be manifested not through the complexity but some other characteristic of the habitats – for example their buffering capacity for nutrients.

On the other hand, habitat complexity played an important role in predicting the number of mesohabitat-specific taxa in oligotophic and mesorophic lakes. Brauns *et al.* (2007a) found, similarly, taxon richness to increase with the higher complexity of the littoral habitats and habitat specialists to be associated with a certain type of shoreline habitats in several German lakes. In general, species with very specific and narrow environmental tolerances are considered habitat specialists. As a consequence, habitat specialists use smaller habitat units (Kolasa & Pickett, 1989) and they appear to be more influenced by habitat loss than habitat generalists (Tilman *et al.*, 1994; Munday, 2004). Accordingly, it can be proposed that the impact of shoreline modifications was manifested through the loss of available habitats for taxa. Similar explanation could be used to explain why modified riparian zone was not affecting the diversity of the littoral macroinvertebrate assemblages, as suggested in Chapter 4. Shorelines with the riparian modification did not have significantly different structural complexity in the littoral zone compared with the unmodified shores according to the results from Chapter 5.

6.1.2 Macrophytes provide complexity and heterogeneity to the littoral shores

In this study, macrophytes were considered primarily as the part of the physical habitat in relation to the littoral macroinvertebrates. Nevertheless, aquatic littoral vegetation represents the biotic and almost inevitable component of the freshwater ecosystems and as such its role must be evaluated in concordance with this. The response of macrophyte communities to application of nutrient enrichment pressures could lead to changes from clear-water to turbid-water state in a shallow lake (Scheffer *et al.,* 1993), which, in turn, can have an effect on the benthic community structure.

Results from Chapter 3 and Chapter 5 indicate an important role of macrophytes for the structure of the littoral macroinvertebrate assemblages. In Chapter 3, macrophyte-related diversity measures were demonstrated to influence the composition of the littoral macroinvertebrate assemblages. Furthermore, in Chapter 5, the results of the analysis on mesohabitat preferences revealed the majority of the taxa to be associated with macrophyte stands. Since the highest weight of the complexity categories was established for macrophyte-dominated mesohabitats, and these mesohabitats had the highest number of the associated species, it could be speculated that macrophytes played a major role in determining diversity in the studied lakes.

Macrophytes have previously been found to be relevant for structuring the macroinvertebrate communities (Kornijow, 1989; Tolonen *et al*., 2001; 2005). The results of this study concurred with this, indicating the importance of the extent of macrophytes and the diversity of the littoral aquatic vegetation in structuring of the littoral macroinvertebrate assemblages. McGoff & Irvine (2009) found, similarly, that the extent of macrophytes and total PVI was positively correlated with the abundance of littoral macroinvertebrates in upper basins of Lough Carra. However, the abundance and composition of macrophytes were found to be affected by the impacts of eutrophication (Downing *et al.*, 2004), suggesting the connection between nutrients and macrophyte community composition. Consequently, the structure of the macroinvertebrate communities is expected to change with different types of aquatic vegetation (Hargeby, 1990; van den Berg *et al.*, 1997). It was speculated that the influence of macrophytes on macroinvertebrate communities could be caused by an indirect link (Pinel-Alloul *et al.,* 1996; van den Berg *et al.*, 1997) since macrophytes provide food resources, as well as shelter from fish predators (Diehl, 1992) and physical disturbances (Gabel *et al.,* 2008).

6.2 Shoreline modification as a type of lake pressures

6.2.1 Scale issues

The results of this study revealed that the univariate diversity measures and abundances of littoral macroinvertebrate assemblages can be affected by a number of environmental factors. Having established the existence of the relationship, the question of which scale – mesohabitat (mesohabitat samples) or whole-site (composite samples) – is better at capturing the response signal arises. Johnson & Goedkoop (2002) demonstrated the higher importance of the local (small-scale) habitat features in comparison with the factors that affect littoral macroinvertebrates at larger scales (ecosystem or lake, riparian, catchment and ecoregion). Having found that the biggest percentage of variance in community composition was explained by the variables at the habitat scale, they explain this by emphasizing the direct relationship between the organisms and their habitat (template). According to Chapter 4, an assessment of the effects of shoreline modifications can be performed using univariate diversity measures and abundances of littoral macroinvertebrate assemblages, both on the mesohabitat and whole-site scale. On the other hand, the effect of TP concentrations was not found to significantly affect the taxon richness of littoral macroinvertebrates at the whole-site scale, while abundances were not responding to the nutrient enrichment at any scale. With regards to the distribution of the taxa, higher number of "shoreline indicators" was found according to the mesohabitat compared with the composite samples, which implies that mesohabitat preferences play an important role in determining the species prevalence toward a specific type of shoreline. This result also suggests that mesohabitats as recorded by a researcher could be considered as a small enough habitat unit to indicate if a species is a habitat specialist. Finally, the choice of mesohabitat can significantly alter or bias the assessment of both shoreline modifications and nutrient enrichment. This was shown in Chapter 4 by the indication of the interaction between the mesohabitat types on one side, and shoreline modifications and nutrient enrichment, on the other.

6.2.2 Coping with the multiple pressures

Many lakes are subject to multiple pressures. In this study, it was attempted to incorporate the investigation of the effects of multiple pressures in the assessment model. The WFD (European Commission, 2000) necessitates inclusion of multiple pressures-based metrics in the status assessments models. Hence, the mixed-effects models, used for the assessment of the effects of shoreline modifications and nutrient enrichment, also incorporated other environmental variables (alkalinity, eastings and lake area). Interestingly, alkalinity gradient was demonstrated to be important in explaining variation in the composition of the littoral macroinvertebrates according to the results of Chapter 3. However, the results of PERMANOVA models from Chapter 5 revealed that this factor was discarded, while the effect of TP gradient on similarity of littoral macroinvertebrate assemblages from different shoreline types was significant. Lakes in this study belonged to medium and high alkalinity water bodies, with alkalinity values ranging between 45 and 119 mg $CaCO_3$ l^{-1}. Across this range of the study lakes, alkalinity was found to decrease the taxon richness, total abundance and Margalef diversity values. Donohue *et al.* (2009b) demonstrated that nutrient enrichment homogenised lake macroinvertebrate assemblages over and above the effect of alkalinity, at both among- and within-lake scales. Similarly, the results of this study imply that the effect of TP may have masked the effect of alkalinity on composition of the littoral macroinvertebrate assemblages. This speculation is supported by the fact that Little *et al.* (2006) found the effect of alkalinity on littoral macroinvertebrate assemblages from lakes with low concentrations of nutrients.

6.3 Advantages of using the mixed-effects models

In comparison with the CCA (ter Braak & Šmilauer, 2002) and in general multivariate methods, the advantage of using mixed effects models is in their flexibility regarding the study design. In practice, this means allowing for almost any kind of the experimental design, which in case of multivariate methods can be more difficult to achieve. For example, CANOCO allows split-plot design but with only two levels (ter Braak & Šmilauer, 2002). Alternatively, CCA or RDA can be used for partitioning the variations across different levels (spatial scale), however the methods are restricted to the amount of variation and cannot define the type of the relationships among the response and hierarchically presented factors. Similarly, PERMANOVA (Anderson *et al.*, 2008), which is similar to the mixed-effects models in terms of model selection procedure, allows only for the factorial design and categorical explanatory variables, since it is based on the rules of ANOVA with permutational tests.

Non-normal distribution of data and non-linear relationships in nature should lead towards the increased usage of the LMMs and GLMMs (Zuur *et al.*, 2009). The mixed-effects models are very flexible in allowing for hierarchical structure of the data, complex design and unbalanced dataset (Crawley, 2007). They definitely have high potential in limnological, and general ecology-based studies. In this study, the flexible use of random elements in the mixed-effects models permitted generalisation of findings from all the investigated lakes and, therefore, the study was not limited to drawing separate conclusions for each lake. The fact that linear mixed-effects models are based on multiple linear regressions allows the simultaneous analysis of multiple factors (pressures) which is desirable in observational type of studies. In addition, mixed-effects models also allow ANCOVA designs (Crawley, 2007), reflected through the application of both continuous and categorical types of variables simultaneously. Regarding the procedure of choosing the best model, mixed-effects models are designed to allow the information-theoretic approach, which is preferred and more reliable compared with the stepwise modelling (Burnham & Anderson, 2001; Whittingham *et al.*, 2006). Finally, mixed-effects models allow the clear identification of interactions among covariates, which is desirable in this world of multifaceted ecological reality.

6.4 Study limitations

This study was based on nine or six lakes, all of which occur in a single Ecoregion. The study of nine lakes, chosen to represent a gradient in nutrient concentrations and either moderate or high alkalinity concentrations, recorded few morphological alterations across the shorelines. With the LHMS values ranging between 4 and 12 (out of 32), the studied lakes had low morphological impact according to Rowan *et al.* (2006). The authors investigated 84 lakes in England and found that the lakes which were considered to have low human impact had scores between 0 and 12. It is therefore important to recognise the limitations of this study in terms of examining the importance of the hydromorphological alterations on the whole-lake level.

Furthermore, the study did not address effects of seasonal fluctuations on the effect of altered habitats. Solimini *et al.* (2006) speculated that the seasonal changes in macroinvertebrate communities could be induced not only by complex life cycles of aquatic insects, but also owing to the seasonal changes in habitats. It is also possible that the influence of seasonal water level fluctuations, which may significantly affect the littoral macroinvertebrate communities (Scheifhacken *et al.*, 2007), can affect the structure of the littoral macroinvertebrate assemblages. However, since this study was based on the elucidation of the effects of the pressures primarily on a spatial scale, the effect of shoreline modifications was assessed only in one season (spring 2009). Furthermore, it is necessary to underpin the importance of biotic interactions and their effect on littoral communities since Harrison & Hildrew (1998) hypothesised that the biotic interactions may be stronger in lakes than in streams.

6.5 General suggestions for future work

The results of this study imply on the need of the pressure-specific tools for detection of changes in freshwater (lake) ecosystems using littoral macroinvertebrates. With the long tradition of using the community structure through the multivariate metrics, or, alternatively, indicator species with niche optima or preferences toward a certain level of the organic pollution (Hellawell, 1986), it is necessary to revise the existing and adopt more flexible ways of assessing the ecological state of water bodies, and not only the effects of nutrient enrichment (organic pollution).

Understanding the mechanisms of changes in littoral macroinvertebrate assemblages is necessary for the development of the pressure-specific tools for the assessment of shoreline modifications. On the other hand, the knowledge on the background mechanisms underpins the use of the functional aspect of macroinvertebrate taxa or assemblages. Examples of the functional aspect are ecological traits – characteristics that reflect a species adaptation to its environment (Statzner *et al.*, 2001). The advantage of this essentially functional approach is reflected through overcoming the initial issues that emerge in the community composition-based assessments, such as effects of biogeography, influence of geology and climate characteristics (Doledec *et al.*, 2011). This study highlights the advantages of applying habitat preferences as the functional approach rather than the approach based on community composition, termed as taxonomy-based approach (Menezes *et al.,* 2010), to the pressure-effect assessments. The functional trait approach is based not only on taxonomy but also on ecological characteristics of the recorded species – for example their habitat requirements. It has the potential, therefore, to detect the cause of a disturbance and provide hypotheses for the mechanisms which dictate the observed response of the littoral macroinvertebrates. At the same time, the application of the functional approach necessitates the broadening of knowledge on autecological aspects of lake littoral macroinvertebrates. Their potential for indicating ecotone integrity, like in case of *Ephemera danica* (Free *et al.*, 2009), should lead to further fundamental and applied investigations in freshwater ecology.

Finally, from the results of this study, it could be proposed for the assessment of conservation value of lakes to be based on habitat diversity, complexity and heterogeneity of shorelines. LACON (Palmer, 2008) is one of the few comprehensive conservation assessment frameworks proposed for lakes. It is based on the assessment of four attributes of conservation value: naturalness, representativeness, rarity and diversity. The Lake Habitat Survey technique, as outlined in Chapter 3, provided a comprehensive and detailed description of the physical habitats, by capturing the array of morphological and hydrological attributes across lake shorelines. The shoreline attributes captured by the LHS metrics were generally interlinked. This was reflected through a number of correlated LHS variables. Therefore, many of the features recorded by the LHS are perhaps redundant when assessing the effects on the structure of the investigated assemblages, and the application of the full sweep of LHS metrics in ecological assessments should be considered further.

6.6 Conclusions

Overall conclusions from this study are:

The community composition of the littoral macroinvertebrates was affected by the morphological features of the shoreline zone when the effects of nutrients and alkalinity were taken into account. However, shoreline features were less important in structuring the macroinvertebrate assemblages than the nutrients (TP) and alkalinity in the water column. In addition, pressures related to the anthropogenic activities and hydrological pressures were demonstrated to have influence on the composition of the littoral assemblages. Among habitat features, the macrophyte- and substrate-related diversity features were most important for structuring the macroinvertebrate assemblages across Hab-plots. Aside from the direct effect of the littoral zone features, macorinvertebrate assemblages were influenced by the riparian zone land-cover.

The diversity measures of macroinvertebrate assemblages were affected by the shoreline modifications, when unmodified and modified littoral shorelines were compared and after the effects of the other environmental factors were accounted for. More specifically, taxon richness and Margalef diversity of littoral macroinvertebrate assemblages were diminished at shorelines with littoral modifications compared with shorelines without modifications, while the taxon richness from shorelines with only riparian modifications was not affected compared with unmodified shorelines. In contrast, abundances of assemblages from modified riparian zone were increased compared with assemblages from unmodified and modified littoral shorelines. TP concentrations were demonstrated to negatively affect the taxon richness and Margalef diversity index of littoral macroinvertebrate assemblages, while the abundances were not affected. According to the results of the taxon richness model, the response of the assemblages to the anthropogenic pressures (nutrient enrichment and shoreline modifications) varied depending on the type of mesohabitat. Moreover, nutrient enrichment was demonstrated to reduce the differences among the assemblages from distinctive mesohabitats. Surprisingly, there was no interaction between the effects of TP concentrations and shore modifications on either diversity measures or abundances of littoral macroinvertebrates.

Indicator Value analysis revealed 14 species to be characteristic of the specific shoreline type, among 203 recorded taxa. A number of species occurred more frequently at unmodified (6) and modified riparian shorelines (6) while only two species were associated with the shorelines with littoral modifications. Although the IndVal Analysis was more successful in assessing the differences in shoreline types compared with the multivariate analysis of the community composition, a few issues regarding this method (potential rarity and nutrient-sensitivity of species) may arise. On the other hand, taxa with specific mesohabitat preferences were affected by the complexity of the littoral zones in oligotrophic and mesotrophic lakes. Based on these results, stenotopic species (habitat specialists) are proposed as the key to understanding the mechanisms of the impact of morphological alterations along littoral zone of lakes without high nutrient enrichment. Finally, metrics based on autecological information of macroinvertebrate taxa have potentially higher sensitivity for identifying the impact of altered shoreline morphology than community structure and individual indicator taxa in low and moderately enriched lakes.

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APPENDIX

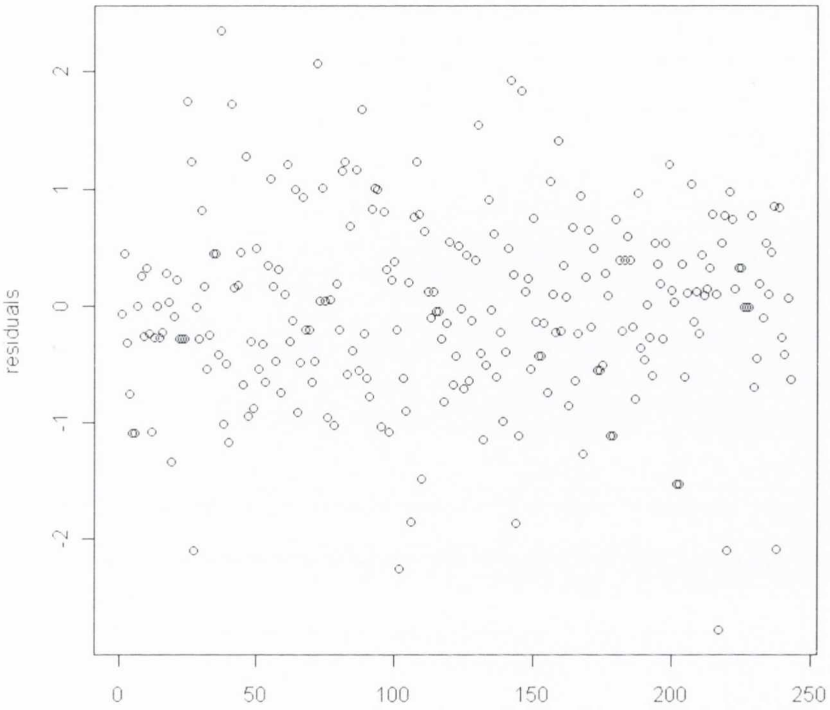

Figure A.1. Residuals plots for taxon richness model based on mesohabitat samples

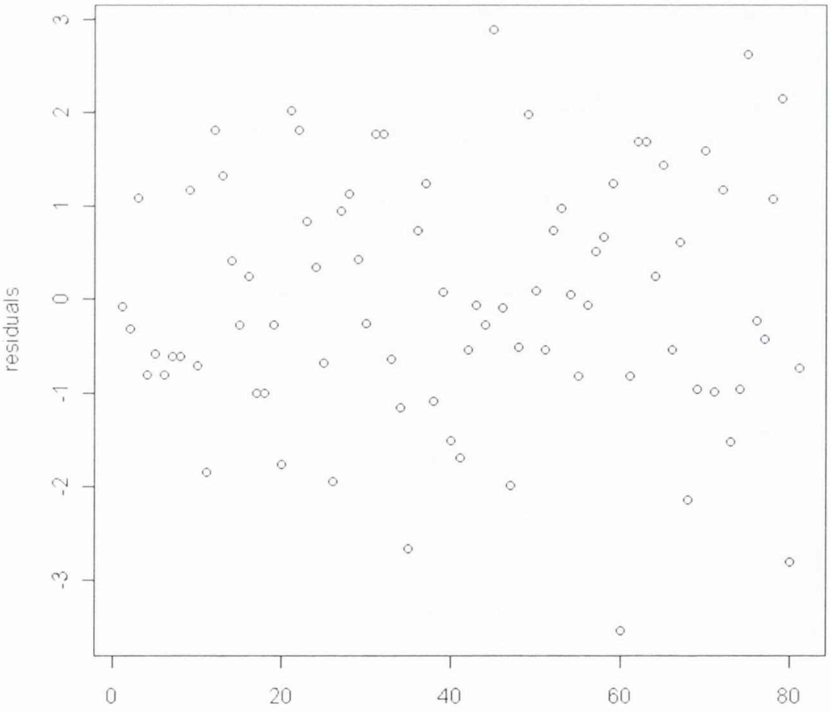

Figure A.2. Residuals plots for taxon richness model based on composite samples

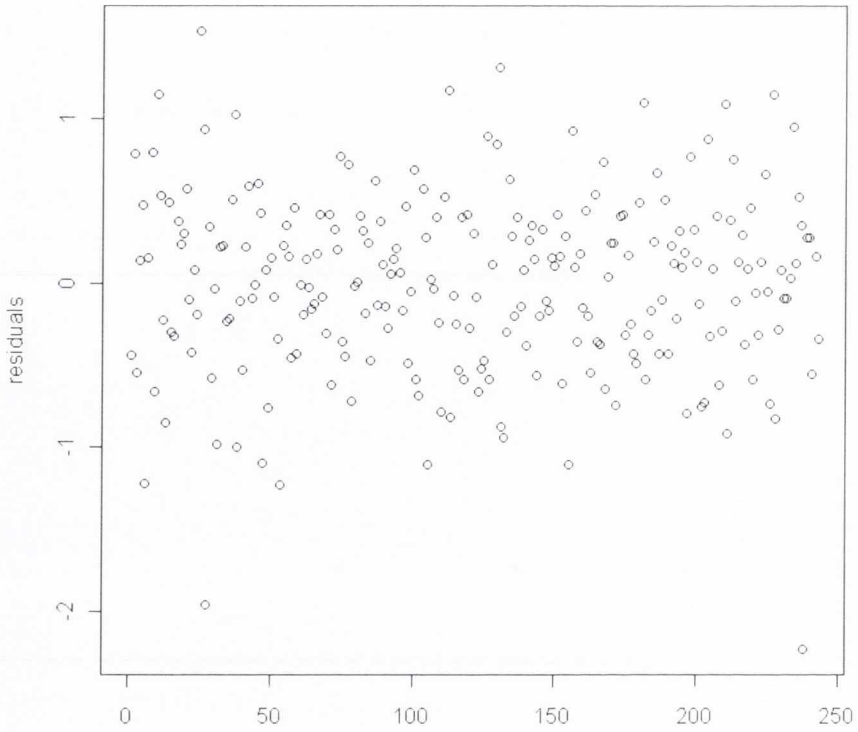

Figure A.3. Residuals plots for log-abundances model based on mesohabitat samples

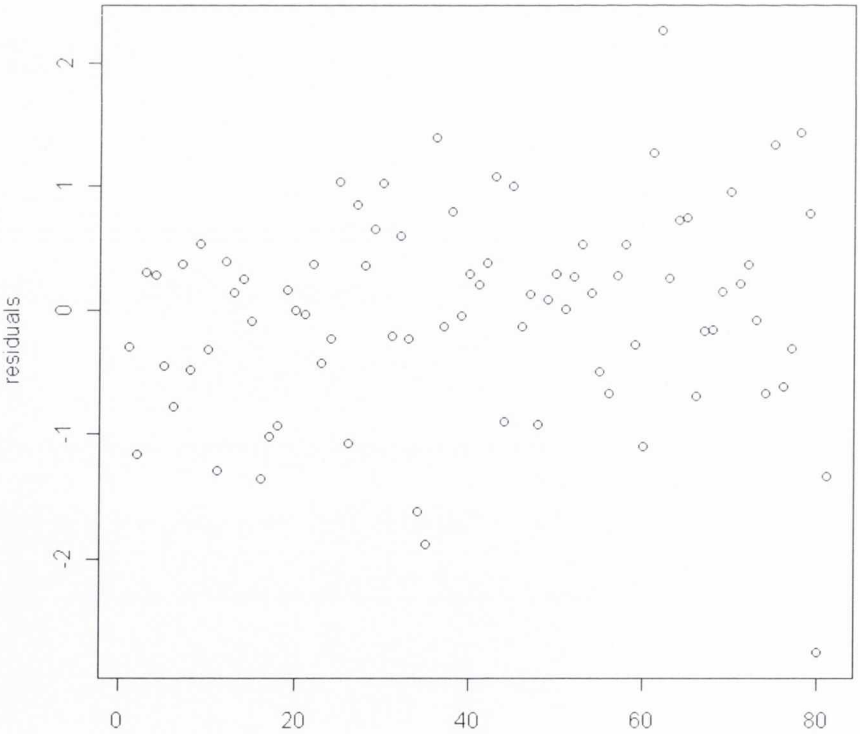

Figure A.4. Residuals plots for log-abundances model based on composite samples

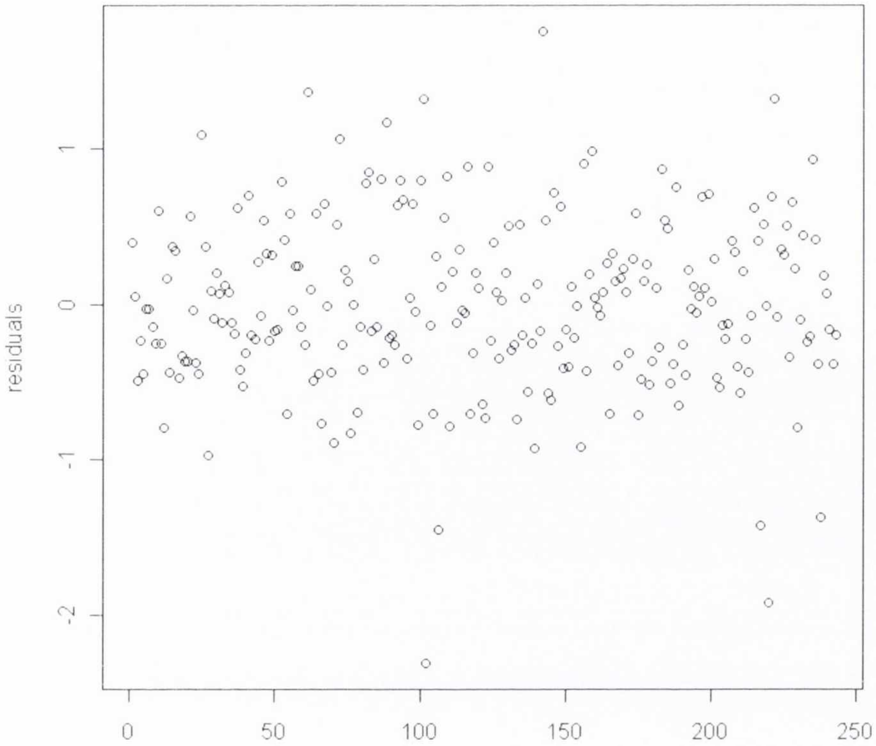

Figure A.5. Residuals plots for Margalef diversity model based on mesohabitat samples

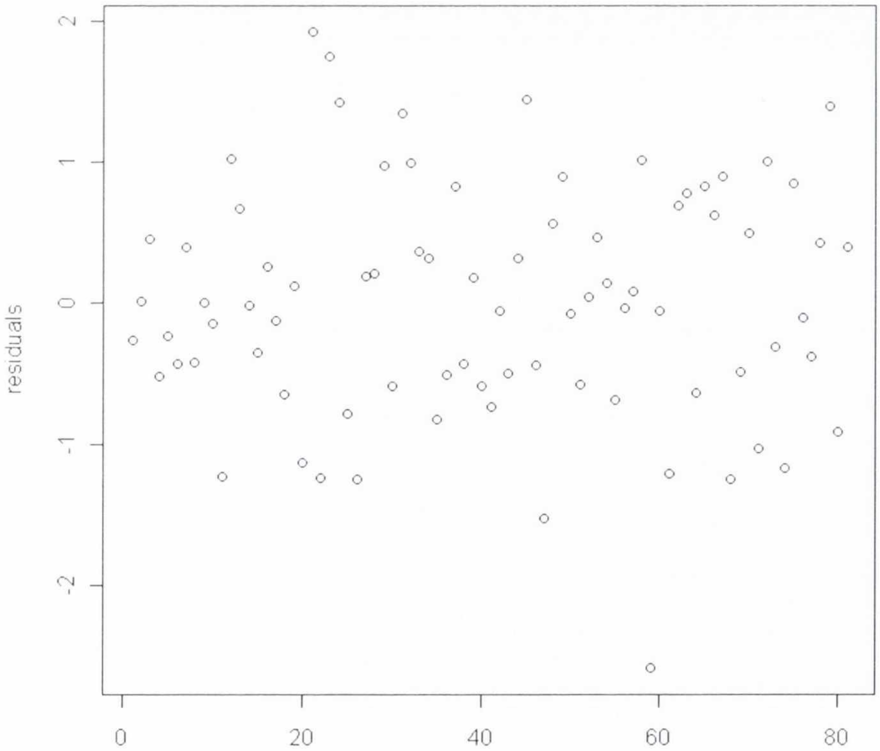

Figure A.6. Residuals plots for Margalef diversity model based on composite samples

Table A.1. List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Porifera					+				
Porifera indet.					+				
Cnidaria									
Hydridae indet.	+		+	+	+	+		+	
Platyhelminthes									
Polycelis nigra/tenuis	+	+	+	+	+	+	+	+	+
Polycelis felina (Dalyell, 1814)	+			+			+	+	
Dendrocoelum lacteum (O. F. Müller, 1774)	+		+	+	+		+	+	
Dugesia lugubris/polychroa	+	+	+	+	+	+	+	+	+
Planaria torva (O. F. Müller, 1774)	+	+					+	+	+
Nematoda									
Nematoda indet.	+	+	+	+	+	+	+	+	+
Mollusca									
Gastropoda									
Ancylus fluviatilis (O. F. Müller, 1774)			+	+					
Acroloxus lacustris (Linnaeus, 1758)			+	+	+	+			
Bithynia leachi (Sheppard, 1823)			+	+			+		+
Bithynia tentaculata (Linnaeus, 1758)		+	+	+	+	+	+		+
Carychium sp.						+			
Potamopyrgus antipodarum (J.E. Gray, 1843)	+		+	+	+	+		+	+
Marstoniopsis insubrica (Kuster, 1853)	+		+					+	
Omphiscola glabra (O. F. Müller, 1774)			+	+		+			
Stagnicola palustris (O. F. Müller, 1774)		+	+	+		+			
Radix labiata (Rossmassler, 1835)	+		+	+		+	+	+	+
Lymnaea stagnalis (Linnaeus, 1758)		+					+		
Galba truncatula (O. F. Müller, 1774)						+			
Myxas glutinosa (O. F. Müller, 1774)							+		
Theodoxus fluviatilis (Linnaeus, 1758)	+				+		+	+	
Physa fontinalis (Linnaeus, 1758)			+				+		+
Physa heterostropha (Say, 1821)			+						
Gyraulus albus (O. F. Müller, 1774)	+	+	+	+	+	+	+	+	+
Planorbis carinatus (O. F. Müller, 1774)			+	+			+		+

Table A.1. continued List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Gastropoda									
Bathyomphalus contortus (Linnaeus, 1758)		+	+			+	+		
Gyraulus crista (Linnaeus, 1758)			+		+				
Gyraulus laevis (Alder, 1838)	+		+	+	+	+		+	
Anisus vortex (Linnaeus, 1758)				+					
Anisus vorticulus (Troschel, 1834)						+			
Anisus septemgyratus (Rossmassler, 1835)						+			
Planorbis planorbis (Linnaeus, 1758)			+						
Hippeutis complanatus (Linnaeus, 1758)			+			+	+		
Segmentina nitida (O. F. Müller, 1774)				+					+
Succineidae indet.		+	+	+		+			
Valvata cristata (O. F. Müller, 1774)	+	+	+				+	+	+
Valvata macrostoma Morch, 1864			+	+					+
Valvata piscinalis (O. F. Müller, 1774)	+		+				+	+	
Vertiginidae indet.						+			
Viviparidae indet.				+					
Zonitidae indet.				+		+			
Bivalvia									
Dreissena polymorpha (Pallas, 1771)		+		+		+			
Sphaeriidae indet.	+	+	+	+	+	+	+	+	+
Annelida									
Hirudinea									
Erpobdella octoculata (Linnaeus, 1758)	+		+		+		+	+	+
Alboglossiphonia heteroclita (Linnaeus, 1761)			+						+
Glossiphonia complanata (Linnaeus, 1758)			+				+		+
Glossiphonia paludosa (Carena, 1824)			+	+					+
Helobdella stagnalis (Linnaeus, 1758)	+		+	+	+		+	+	
Hemiclepsis marginata (O. F. Müller, 1774)		+							
Theromyzon tessulatum (O. F. Müller, 1774)	+		+		+	+	+	+	+
Placobdella costata (Fr. Müller, 1846)			+						
Piscicola geometra (Linnaeus, 1758)							+		

Table A.1. continued List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Oligochata									
Oligochaeta indet.	+	+	+	+	+	+	+	+	+
Arthropoda									
Malacostraca									
Amphipoda									
Crangonyx pseudogracilis Bousfield, 1958	+	+	+	+	+	+	+	+	+
Gammarus duebeni Liljeborg, 1852		+	+	+	+	+	+		+
Gammarus lacustris Sars, 1863	+		+	+		+		+	+
Gammarus pulex (Linnaeus, 1758)	+			+		+	+	+	
Gammarus tigrinus Sexton, 1939				+					
Niphargus sp.		+							+
Isopoda									
Asellus aquaticus (Linnaeus, 1758)	+	+	+	+	+	+	+	+	+
Proasellus meridianus (Racovitza, 1919)									+
Maxillopoda									
Arguloida									
Argulus sp.							+		+
Ostracoda									
Ostracoda indet.	+		+	+	+		+	+	+
Arachnida									
Araneae									
Argyroneta aquatica (Clerck, 1757)		+			+	+	+		+
Acari (infraclass)									
Acari indet.	+	+	+	+	+	+	+	+	+
Entognatha									
Collembola									
Collembola indet.	+	+	+	+	+	+	+	+	+
Insecta									
Coleoptera									
Alticinae indet.					+	+			
Galerucinae indet.		+	+						
Macroplea sp.		+							

Table A.1. continued List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Coleoptera									
Chrysomelidae juv. indet.						+			
Dryops sp. juv.	+	+	+			+		+	+
Agabus sp. juv.		+	+						
Graptodytes pictus (Fabricius, 1787)						+			
Hydroporus obscurus Sturm, 1835									+
Hydroporus sp. juv.			+						+
Hygrotus inaequalis (Fabricius, 1787)			+			+			
Hygrotus quinquelineatus (Zetterstedt, 1828)			+			+			
Laccophilus biguttatus Kirby, 1837									+
Laccophilus sp. juv.		+					+		
Nebrioporus depressus (Fabricius, 1775)			+	+		+			
Nebrioporus elegans (Panzer, 1794)	+	+		+		+		+	
Nebrioporus assimilis (Paykull, 1798)									+
Porhydrus lineatus (Fabricius, 1775)		+				+			
Rhantus sp. juv.					+				
Hydroporinae juv. indet.				+			+		+
Elmis aenea (P.W.J. Müller, 1806)			+				+		
Esolus parallelepipedus (P.W.J. Müller, 1806)			+		+		+		+
Limnius volckmari (Panzer, 1793)		+	+	+		+	+		+
Oulimnius tuberculatus (P.W.J. Müller, 1806)	+		+	+	+	+	+	+	+
Gyrinus sp. juv.			+	+	+	+	+		
Gyrinus caspius Menetries, 1832				+					
Gyrinus aeratus Stephens, 1835		+	+	+					
Orectochilus villosus (O. F. Müller, 1776)			+	+					+
Brychius sp. juv.							+		
Haliplus confinis Stephens, 1828		+	+	+		+			
Haliplus flavicollis Sturm, 1834			+			+			
Haliplus fluviatilis Aube, 1836			+	+		+			+
Haliplus immaculatus Gerhardt, 1877			+			+			
Haliplus lineolatus Mannerheim, 1844			+	+					
Haliplus obliquus (Fabricius, 1787)									+

Table A.1. continued List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Coleoptera									
Haliplus sp. juv.		+	+	+		+	+		+
Helophorus brevipalpis Bedel, 1881		+	+	+	+	+			
Helophorus sp. juv.		+		+		+			
Hydraena gracilis Germar, 1824			+						
Hydraena palustris Erichson, 1837			+		+				
Ochthebius nanus Stephens, 1829		+							+
Enochrus testaceus (Fabricius, 1801)					+				
Hydrophilidae juv. indet.				+		+			
Laccobius sp. juv.	+							+	
Laccobius colon (Stephens, 1829)			+			+	+		+
Noterus clavicornis (De Geer, 1774)			+						
Donacia sp.			+			+			
Plateumaris sp.			+						
Noteridae juv. indet.			+			+			
Diptera									
Ceratopogonidae indet.	+	+	+	+	+	+	+	+	+
Chironomidae indet.	+	+	+	+	+	+	+	+	+
Culicidae indet.				+					
Dixidae indet.		+	+						
Dolichopodidae indet.		+				+			
Empididae indet.			+	+		+			+
Ephydridae indet.		+				+			
Limoniidae indet.					+				
Psychodidae indet.	+	+	+	+	+	+		+	+
Rhagionidae indet.						+			
Sciomyzidae indet.						+			
Tabanidae indet.			+			+			+
Tipulidae indet.		+	+			+			
Ephemeroptera									
Baetis rhodani (Pictet, 1843)			+	+					
Centroptilum luteolum (O.F. Müller, 1776)	+		+	+	+	+	+	+	

Table A.1. continued List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Ephemeroptera									
Cloeon simile Eaton, 1870							+		+
Cloeon dipterum (Linnaeus, 1761)			+			+			+
Caenis horaria (Linnaeus, 1758)	+	+	+	+	+	+	+	+	+
Caenis luctuosa (Burmeister, 1839)	+	+	+	+	+	+	+	+	+
Caenis rivulorum Eaton, 1884			+	+					
Caenis macrura Stephens, 1835			+	+					
Ephemera danica (O.F. Müller, 1764)			+	+	+	+	+		+
Serratella ignita (Poda, 1761)			+						
Heptagenia sulphurea (O.F. Müller, 1776)							+		
Kageronia fuscogrisea (Retzius, 1783)		+	+	+	+	+	+		
Leptophlebia marginata (Linnaeus, 1767)			+						
Leptophlebia vespertina (Linnaeus, 1758)			+						+
Paraleptophlebia werneri Ulmer, 1920			+						
Siphlonurus lacustris (Eaton, 1870)						+			
Heteroptera									
Arctocorisa germari (Fieber, 1848)	+							+	
Callicorixa praeusta (Fieber, 1848)	+	+	+	+	+	+	+	+	+
Callicorixa wollastoni (Douglas & Scott, 1865)	+	+	+					+	
Corixa dentipes Thomson, 1869		+							
Corixa iberica Jansson, 1981				+					+
Corixa panzeri Fieber, 1848									+
Cymatia bonsdorffii (C.R. Sahlberg, 1819)		+	+		+				+
Sigara distincta (Fieber, 1848)	+		+	+	+	+	+	+	+
Sigara dorsalis (Leach, 1817)		+	+	+	+	+	+		+
Sigara falleni (Fieber, 1848)	+	+	+	+	+	+		+	
Sigara fallenoidea (Hungerford, 1926)				+		+	+		
Sigara fossarum (Leach, 1817)			+		+	+			+
Sigara limitata (Fieber, 1848)					+				
Sigara scotti (Douglas & Scott, 1868)						+			+
Sigara stagnalis (Leach, 1817)									
Micronectinae indet.		+	+	+	+	+	+		+

Table A.1. continued List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Heteroptera									
Notonecta glauca (Linnaeus, 1758)		+	+		+				+
Notonecta oblique Thunberg, 1787			+						
Veliidae indet.	+	+						+	
Mesovelia furcata Mulsant & Rey, 1852		+							
Lepidoptera									
Parapoynx stratiotata (Linnaeus, 1758)									+
Cataclysta lemnata (Linnaeus, 1758)		+							
Lepidoptera indet.			+	+		+			
Megaloptera									
Sialis lutaria (Linnaeus, 1758)	+	+	+			+		+	+
Odonata									
Coenagrion mercuriale (Charpentier, 1840)				+		+			
Coenagrion lunulatum (Charpentier, 1840)			+						+
Coenagrion puella/pulchellum			+			+			
Enallagma cyathigerum (Charpentier, 1840)		+	+		+		+		+
Erythromma najas (Hansemann, 1823)			+	+	+	+			
Ischnura elegans (Vander Linden, 1820)			+		+	+			+
Libellula quadrimaculata (Linnaeus, 1758)			+			+			
Orthetrum cancellatum (Linnaeus, 1758)									+
Orthethrum coerulescens (Fabricius, 1798)									
Sympetrum danae (Sulzer, 1776)									+
Sympetrum fonscolombei (Selys, 1840)									
Plecoptera									
Nemoura cinerea (Retzius, 1783)		+							
Plecoptera indet.		+							
Trichoptera									
Ecnomus tenellus (Rambur, 1842)	+		+					+	+
Goera pilosa (Fabricius, 1775)			+	+					
Agraylea sp.			+						
Hydroptila sp.			+				+		
Orthotrichia sp.				+					

Table A.1. continued List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Trichoptera									
Lepidostoma hirtum (Fabricius, 1775)			+	+			+		+
Adicella reducta (McLachlan, 1865)			+	+			+		
Athripsodes aterrimus (Stephens, 1836)			+		+		+		+
Athripsodes cinereus (Curtis, 1834)	+		+	+	+		+	+	+
Athripsodes bilineatus (Linnaeus, 1758)			+						+
Ceraclea annulicornis (Stephens, 1836)				+					
Ceraclea fulva (Rambur, 1842)							+		
Mystacides longicornis (Linnaeus, 1758)	+		+	+	+		+	+	+
Mystacides azureus (Linnaeus, 1761)	+		+	+	+		+	+	+
Oecetis furva (Rambur, 1842)			+	+					
Oecetis lacustris (Pictet, 1834)			+		+				
Oecetis ochracea (Curtis, 1825)			+				+		
Setodes argentipunctellus (McLachlan, 1877)									+
Triaenodes bicolor (Curtis, 1834)	+		+		+	+		+	
Ylodes reuteri (McLachlan, 1880)			+						
Anabolia nervosa (Curtis, 1834)	+	+	+	+	+			+	+
Anabolia brevipennis (Curtis, 1834)	+		+					+	
Glyphotaelius pellucidus (Retzius, 1783)	+							+	
Halesus radiatus (Curtis, 1834)	+	+	+		+			+	
Limnephilus auricula Curtis, 1834				+					
Limnephilus binotatus Curtis, 1834			+						
Limnephilus centralis Curtis, 1834			+						
Limnephilus coenosus Curtis, 1834					+				
Limnephilus flavicornis (Fabricius, 1787)			+						+
Limnephilus lunatus Curtis, 1834	+		+	+	+	+	+	+	+
Limnephilus marmoratus Curtis, 1834			+		+				+
Limnephilis nigriceps (Zetterstedt, 1840)			+						
Limnephilus rhombicus (Linnaeus, 1758)				+					
Limnephilus sparsus Curtis, 1834						+			
Limnephilus vittatus (Fabricius, 1798)			+	+		+			
Stenophylax permistus McLachlan, 1895									+

Table A.1. continued List of littoral invertebrate taxa recorded from nine Irish lakes in April/May 2009

Taxon name	Lakes								
	Muckno	Oughter	Brackley	Garadice	Scur	Rinn	Rea	Cullin	Carra
Trichoptera									
Nemotaulius punctatolineatus (Retzius, 1783)									+
Grammotaulius nigropunctatus (Retzius, 1783)			+						
Molanna albicans (Zetterstedt, 1840)									
Wormaldia sp.	+							+	
Agrypnia obsolete (Hagen, 1864)							+		+
Agrypnia varia (Fabricius, 1793)							+		
Phryganea bipunctata (Retzius, 1783)					+				
Trichostegia minor (Curtis, 1834)									+
Cyrnus trimaculatus (Curtis, 1834)			+	+	+				
Holocentropus dubius (Rambur, 1842)	+		+	+	+		+	+	
Holocentropus picicornis (Stephens 1836)			+						+
Plectrocnemia conspersa (Curtis, 1834)	+		+	+	+		+	+	
Plectrocnemia geniculata McLachlan, 1871			+						+
Polycentropus kingi McLachlan, 1881	+		+	+	+		+	+	+
Polycentropus flavomaculatus (Pictet, 1834)	+		+	+	+		+	+	
Polycentropus irroratus Curtis, 1835	+							+	+
Lype phaeopa (Stephens 1836)					+				+
Lype reducta (Hagen, 1868)			+						+
Psychomyia fragilis (Pictet, 1834)							+		+
Psychomia pusilla (Fabricius, 1781)							+		
Tinodes dives (Pictet, 1834)			+	+			+		+
Tinodes maculicornis (Pictet, 1834)			+				+		
Tinodes pallidulus McLachlan, 1878							+		+
Tinodes unicolor (Pictet, 1834)							+		+
Tinodes waeneri (Linnaeus, 1758)	+		+	+	+		+	+	+
Sericostoma personatum (Kirby & Spence, 1826)			+				+		+