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Water level fluctuations and their effects on lake ecology

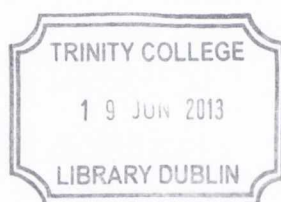
A dissertation submitted to the University of Dublin
for the Degree of Doctor of Philosophy

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University of Dublin, Trinity College, January 2013



Thesis 10126

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Summary

Escalating freshwater demand, triggered by population and economic growth, technological development, urbanization, land conversion and intensification of agriculture is one of the major challenges facing humankind. The problem is also likely to be exacerbated considerably by global climate change. Consequently, amplification of water level fluctuations is rapidly becoming one of the key disturbances of aquatic ecosystems globally, endangering ecosystem integrity and the provision of ecosystem goods and services.

Despite its growing prevalence, little is known about the ecological impacts of altered water level regimes on lake systems. Understanding the links among water level fluctuations (both natural and human-modified), the associated ecological responses and, ultimately, the effects on lake ecosystem integrity requires an approach that necessitates robust characterisation of the complex and multifaceted nature of water level regimes. Furthermore, this is the first study to characterise water level regimes of lakes using five key facets: magnitude, duration, frequency, timing and rate of change. I did this using an array of 915 metrics (including several novel metrics) to investigate water level regimes of 46 Irish lakes at a range of temporal scales. I then identified a parsimonious subset of metrics accounting for the majority of the variation in each of the five key facets, while concurrently minimising information redundancy. Characterising water level regimes in this way will aid the detection of explicit ecosystem responses attributable to the alteration of distinct facets of water level fluctuations. Further, I found strong evidence, that focusing on water level metrics that characterise only one temporal scale could yield incomplete and inaccurate conclusions.

The extent of water level amplitudes was associated with relative ecosystem size and were thus likely a function of lake residence time, while the frequency of extreme events was mediated by shoreline length and catchment slope. These findings reveal the potential to identify risks for lake hydrology based on lake catchment and landscape characteristics which may be crucial for preventing ecosystem degradation and for guiding efforts to restore or maintain ecosystem integrity and health.

Amplified water level fluctuations had a range of multifaceted and complex impacts on lake ecology. Extreme changes in the magnitude of water level fluctuations modified

directly the particle size distribution of littoral substrates, triggering geomorphological changes and reducing macrophyte cover. Therefore, as well as imposing direct physical stress upon benthic assemblages, amplified water level fluctuations also affected benthic organisms indirectly by causing habitat displacement and habitat loss. They also reduced the density and phylogenetic diversity of benthic assemblages.

Contrasting regimes of water level fluctuations generated a suite of community responses, altering significantly ecosystem structure and functioning. I found greater sensitivity of multivariate biological responses to amplified water level fluctuations compared with univariate biological metrics. My findings suggest that using multi-trait (biological and ecological) approach and incorporating sampling depth as a covariate might give a greater insight into revealing the impacts of environmental conditions and habitat changes on lake biota. Focusing on biological trait responses has the potential to expand biomonitoring approaches beyond traditional taxonomically-based assessments and to provide a causal diagnosis and mechanistic linkages of biotic responses to disturbances and environmental conditions, in general.

My research demonstrates that amplified water level fluctuations may have detrimental effects on the ecology of lake littoral zones with potentially significant knock-on effects on whole-lake and adjacent riparian ecosystems. The predicted increase of water demand and global mean temperature, coupled with higher frequency and intensity of extreme events, may intensify considerably the variability of water level fluctuations on a global scale, and thus exacerbate even further the detrimental impacts of extreme water level fluctuations on lake ecology and biodiversity, with significant impacts on the delivery of ecosystem goods and services.

НА СЕМЕЙСТВОТО И ЛЮБИМИТЕ МИ ХОРА,
БЛАГОДАРЯ ВИ ЗА ТЪРПЕНИЕТО, ПОДКРЕПАТА И ОБИЧТА ВИ!

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Water Level Fluctuations and their Effects on Lake Ecology

1. Introduction and Thesis Outline



Blessington Lake, photo by Vesela Evtimova

Displacement of the littoral zone in Blessington Lake, Co. Wicklow as a result of fluctuations in water levels

1.1. Introduction

Water, together with clean air, is one of the most important natural resources. It sustains life on Earth and is regarded as the “bloodstream of the biosphere” (Folke 2003, Ripl 2003, Rockstrom *et al.* 2007). Water covers 71% of the surface of Earth, yet only 2.5% is freshwater. The largest volume of freshwater is not directly accessible as it is stored in the icecaps and glaciers, which, together with groundwater account for 98.8% of global freshwater reserve (Shiklomanov & Rodda 2003). Water is a key resource for human health and prosperity (Moss 2010, UNESCO 2011) and the provision of good quality freshwater is the most precious ecosystem service on the planet, notwithstanding the remarkable difference between its intrinsic value and market price (Johnson *et al.* 2001, Gibbs 2006, Sukhdev 2009). Global water supplies are increasingly under pressure in the struggle to balance societal and environmental needs (Kennard *et al.* 2010a), highlighting the limited availability and fragility of renewable freshwater resources and related ecosystem services (Jackson *et al.* 2001, Sukhdev 2009). As lakes account for 87% of liquid surface freshwater (Shiklomanov 1993), increasing water consumption will pose enormous strains on lake ecosystems. In addition, freshwater ecosystems are defined largely by their hydrology (Saunders *et al.* 2002), thus requiring the assessment of the change in the ratio between water availability and enhanced water demand. Moreover, this necessitates considerably improved understanding of the impacts of dwindling water resources on water level regimes in standing water systems and the consequences of this for the integrity of the whole ecosystem.

1.2. Drivers of water level fluctuations and associated pressures

Water level fluctuations occur naturally in lakes, yet generally tend to be gradual and predictable in nature (Ward 1992, White *et al.* 2010). However, water level fluctuations may be modified significantly by anthropogenic factors and thus may, in turn, not only have hydrological and morphological impacts but may alter also lake quality and ecology and functioning of standing water and adjacent terrestrial ecosystems (Coops *et al.* 2003, Schmieder *et al.* 2004, Beklioglu 2007, Wantzen *et al.* 2008b, Zohary & Ostrovsky 2011). Socio-economic and technological development, human population growth, intensification of agriculture, urbanisation and associated

hydropower generation congruent with environmental degradation are leading drivers of water demand and the resulting alteration of water level regimes (Johnson *et al.* 2001, Shiklomanov & Rodda 2003, Palmer *et al.* 2004, Sophocleous 2004, Rockstrom *et al.* 2007, Palmer 2010, Vorosmarty *et al.* 2010, Rulli *et al.* 2013). Infrastructure development, for instance impoundment, dams and flood protection constructions are responsible for modification not only of habitat structure but also of the timing and amplitude of water level fluctuations in lakes (Baxter 1977, Yin & Yang 2012). Water regime management may either aim to stabilise water level fluctuations or may trigger increase in the amplitude of water level variations (Coops & Hosper 2002, Abrahams 2008, Zohary & Ostrovsky 2011).

Owing to the projected increase of frequency and magnitude of extreme climatic events, freshwater ecosystems, already damaged by the overuse of water, stand to be affected further by global changes (Shiklomanov & Rodda 2003, IPCC 2007). Predicted increases in average temperatures and frequencies of droughts and heat waves (Meehl & Tebaldi 2004, IPCC 2007) will intensify the usage of water and reduce its availability. Coupled with higher frequency of heavy precipitation events in some regions (Easterling *et al.* 2000), these will also have adverse effects on water quality and contamination of water supply. Additionally, elevated temperatures will affect the physical, chemical and biological properties of lakes and rivers, with predominantly unfavourable impacts on many sensitive freshwater species, on communities as a whole and on water quality (Gleick 1998, Jackson *et al.* 2001, IPCC 2007). Rising sea level will result in salinisation of groundwater supplies and will decrease further freshwater availability due to saltwater intrusion (IPCC 2007).

1.3. Impacts of altered water level fluctuations

1.3.1. Impacts on the physical and chemical characteristics of lakes

Among the direct effects of amplified water level fluctuations in lakes are the shift of littoral zones in both directions and the associated desiccation, possible fragmentation or loss of littoral habitats (Brauns *et al.* 2008, Tavast 2009, Zohary & Ostrovsky 2011). Altered water level fluctuations have the potential to fundamentally change the structure and biogeochemical characteristics of littoral sediment, as well as to lead to

erosion and reduction in the structural variability of benthic substrates and thus modify lake bed morphology and the physical structure of aquatic environments (Rorslett 1985, Hellsten *et al.* 1996, Prus *et al.* 1999, Lake *et al.* 2000, Coops & Houser 2002, Furey *et al.* 2004, Nowlin *et al.* 2004). Moreover, changes in water level may affect turbidity, oxygen, light and temperature regimes in lake water columns, and instigate release of nutrients and methane to water through the resuspension of bottom sediments (Juutinen 2001, Coops & Houser 2002, Acreman *et al.* 2005, Hofmann *et al.* 2008, Zohary & Ostrovsky 2011, Deegan *et al.* 2012). Significant water level fluctuations may also accrue changes in the input of allochthonous matter from the riparian zone (Wantzen *et al.* 2008a). They may decrease the availability of organic matter in lake sediments through reduction or elimination of aquatic and riparian vegetation, or increased erosion resulting from the lack of rooted macrophytes and decreased substrate stability (Valdovinos *et al.* 2007).

Many anthropogenic disturbances are, at least partially, confined to nearshore zones (Tolonen & Hämäläinen 2010). Effects of amplified water level fluctuations in lakes are likely to be greatest in littoral zones (Solimini *et al.* 2006, Wantzen *et al.* 2008b), where even small draw-downs could be translated into conversion of large areas of standing water to air-exposed habitats and vice versa (Palomäki 1994, Leira & Cantonati 2008). Thus, most studies of the impacts of water level fluctuations in lakes were focused on littoral zones (*e.g.* Fischer & Ohl 2005, Baumgärtner *et al.* 2008, Brauns *et al.* 2008, Wantzen *et al.* 2008b, McEwen & Butler 2009, White *et al.* 2010, Deegan *et al.* 2012).

1.3.2. Impacts of water level fluctuations on biota

The majority of research on water level fluctuations on biota originates from comparative studies on macrophytes (Rorslett 1984, Furey *et al.* 2004, Deegan *et al.* 2012). These studies have advanced our understanding of the ecological role of changes in water level regimes of lakes, yet they consistently comprise either single-lake studies or comparative studies of two water bodies with contrasting water level regimes. Since these studies are based largely on varying intra-annual amplitudes, they misrepresent the rather complex nature of water level regimes in lakes (White *et al.* 2010).

The central concept in the assessment of hydrological requirements of aquatic ecosystems is the natural-flow paradigm which emphasises the importance of natural hydrological variation in structuring freshwater assemblages (Poff *et al.* 1997, Richter *et al.* 1997, Baron *et al.* 2002). This concept was originally proposed for rivers, although it has also been applied to lakes (Saunders *et al.* 2002). Natural fluctuations in lake water levels could be essential for species survival and dispersion, and may facilitate the interaction between the open water, littoral zones and adjacent terrestrial ecosystems (Fig. 1.1). Unmodified water level fluctuations may, for example, promote macrophyte propagation through controlling sediment and nutrient composition and water depth (Gafny & Gasith 1999). Natural water level fluctuations are known to favour clear-water and macrophyte-dominated stable states in lakes (Coops & Houser 2002, Kalchev *et al.* 2007, Kalchev 2012). Moreover, together with natural river flows they play essential role for fish spawning and development (Halls & Welcomme 2004, Vassilev 2006, Carlson & Quinn 2007, Probst *et al.* 2009), and the reproduction of amphibians (Timmermans 2001). The ecological role of unmodified inter-annual variations in water levels and river flow regimes extends beyond the limits of water systems. High water levels may determine, for instance, the spatial pattern of tree regeneration in the adjacent riparian zone (Hall & Harcombe 1998) whereas natural decrease in water levels may be beneficial for migratory birds through providing food resources and increasing reproductive success (Desgranges *et al.* 2006, Anteau *et al.* 2012, Petkov 2012).

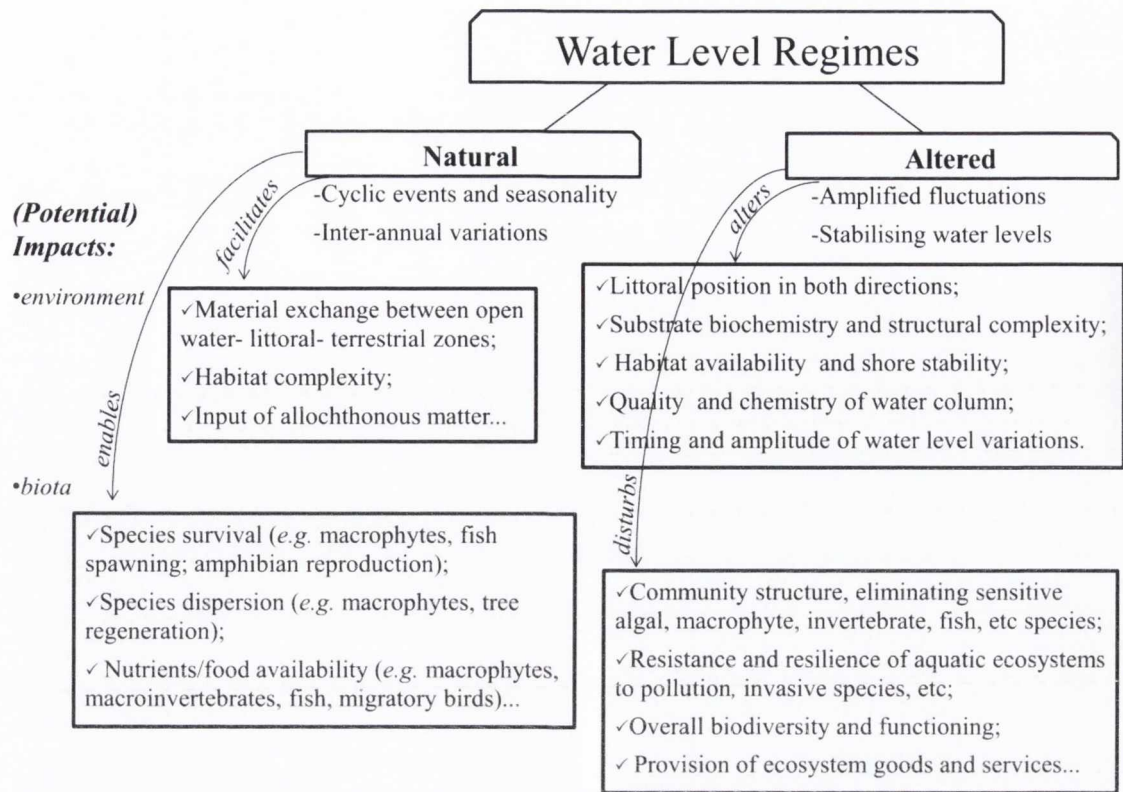


Fig. 1.1. Simplified scheme of the potential impacts of natural and modified water level regimes.

Freshwater communities are non-equilibrium systems whose dynamics largely follow hydrological disturbance regimes (Scarsbrook & Townsend 1993). Both artificially increasing water level fluctuations to extreme levels and decreasing the amplitude of natural water level variation and thus stabilising water level fluctuations (Fig. 1.1), as is the goal of head-pond (water impoundment used as an energy source) management for hydroelectricity, may lead to habitat and species loss (Hill *et al.* 1998). Over the last half-century, water abstraction has more than tripled (Connor *et al.* 2009), making human-induced amplification of water level fluctuations one of the major disturbances of aquatic ecosystems globally, endangering not only the integrity of ecosystems but also their capacity to provide ecosystem goods and services (Rockstrom *et al.* 2007, Palmer 2010). Modifying water level regimes in lakes through high and frequent draw-downs in water level, often characteristic of reservoirs used for hydropower generation, may reduce the availability of organic matter (Black *et al.* 2003, Valdovinos *et al.* 2007), lead to lower diversity or even

disappearance of macrophytes (Rorslett 1984, 1985, Valdovinos *et al.* 2007) and, therefore, loss of habitats and food resources for benthic assemblages. At present, more than 10,000 reservoirs have been constructed in Europe that make up almost one third of the continent's total 300,000 km² of standing waters (Bragg *et al.* 2003). As a result, there have been numerous studies focusing on benthic fauna in human-made water bodies, whose establishment may be considered as an extreme example of hydrological modification of an aquatic ecosystem. This extensive knowledge on reservoir biota could serve as a basis in the assessment of ecological impacts of altered water level fluctuations on littoral invertebrates.

Studies on the colonisation of reservoirs by benthic organisms date back to the late 1940s (Radford & Hartland-Rowe 1971). They could improve our understanding of the recovery mechanisms and response of assemblages subjected to dramatic changes in water level regimes. Baxter (1977) reviewed the earliest studies on the development of benthos in the first large artificial lakes (Grokiy and Kuybyshev reservoirs on the Volga River; Barrier Lake on the Kananaskis River; Goczalkowice Dam on the Vistula River; Lakes Volta and Kariba) and several small impoundments in Canada. He found that chironomid species were well adapted to be the first colonizers of flooded areas, being typical *r*-selected species with small body size, high fecundity and dispersal abilities (Baxter 1977). They were followed by bivalves with motile larvae and oligochaetes. Successively, Gizinski & Wolnomiejski (1982) and Krzyżanek (1991) reported a similar sequence of colonisation in the formation of benthic fauna in Polish reservoirs. Colonization of newly wetted areas is often driven by the availability of substrate and food resources. McLachlan (1970) found that the depth distribution pattern of chironomid was not affected by a drop in water level while a rise elicited a strong response from the larval communities modifying their annual succession. The species normally present were replaced entirely by the large larvae of *Chironomus transvaalensis*, causing a considerable increase in biomass and a change in the basic depth distribution pattern (McLachlan 1970).

Existing knowledge of the effects of water level regimes on benthic communities in lakes is based largely on a few case studies (Aroviita & Hämäläinen 2008). Enhanced water level fluctuations are thought to have been responsible for the decrease in littoral molluscs (Jurkiewicz-Karnkowska 1989). Faunal densities and diversity have

been found to be lower in reservoirs with greater ranges of water level changes and rates of erosion (Prus *et al.* 1999). In one of the very few multi-lake studies, Smith *et al.* (1987) found that littoral macrophyte and benthic assemblages were taxon rich when annual ranges of water fluctuation were low and very impoverished where either weekly range exceeded 0.5 m or maximum annual fluctuation exceeded 5 m. Hellsten *et al.* (1996) observed that larger invertebrates, such as those of Ephemeroptera and Amphipoda were likely more susceptible to increased intra-annual ranges, and were replaced by smaller organisms (Chironimidae and Oligochaeta) when lake water levels varied more. Valdovinos *et al.* (2007) compared the macroinvertebrate assemblages of a regulated and an unregulated lake in the Chilean Andes. They attributed the decrease in species richness, density and biomass in the regulated lake to desiccation, freezing of the biota, and removal of organic particles from the sediment, as well as to absence of aquatic macrophytes, factors all driven by variations in water level. These findings were in contrast with the results of Furey *et al.* (2006) who observed that macroinvertebrate density and biomass can be equal or greater in reservoirs under regular draw-down than these in natural lakes. Valdovinos *et al.* (2007) suggested that diversity of a variety of groups of littoral biota follow expectations of the intermediate disturbance hypothesis, with higher species diversity occurring at intermediate disturbance levels. Further, Furey *et al.* (2006) speculated that the effects of water abstraction extended beyond the draw-down exposure zone where the maximum densities and biomasses were recorded (especially for chironomids). The observed peaks below the exposure zone may reflect migration of fauna with receding water levels (Moon 1935).

It is important to note that freshwater communities are exposed to a range of natural and anthropogenic disturbances varying in strength, frequency, predictability, duration, and spatial scale and it is quite rare for a single perturbation to disrupt a freshwater ecosystem (Lake *et al.* 2000). Therefore, the multifactor interactions and complexity of freshwater lakes and reservoirs necessitate taking into consideration various abiotic and biotic factors when studying impacts of water fluctuations. Reservoirs are often created by damming a river bed and exhibit a large catchment area. Hence, they are highly sensitive to anthropogenic impacts originating in the catchment such as nutrient loading, heavy metals or organic toxic pollutants from agriculture, industry or settlements (Lake *et al.* 2000, Solimini *et al.* 2006).

1.4. Bioindicators of hydrological pressures

Sustainable management of global water resources requires identifying suitable bioindicators for investigating in detail the effects of alteration in water level regimes. Townsend *et al.* (1997b) suggest that an appropriate measure of disturbance would vary according to the organisms of interest. Littoral invertebrates are capable of reflecting different anthropogenic perturbations through changes in the structure or functioning of their assemblages (*e.g.* Hering *et al.* 2004, O'Toole *et al.* 2008). Their ubiquitous presence (Lenat & Smock 1980), relative longevity (Usseglio-Polatera *et al.* 2000), the large number of species involved (Rosenberg *et al.* 1997), and their intermediate position in energy flow through food webs (Ward 1992, Wallace 1996), make benthic macroinvertebrates excellent candidates for ecologically relevant bioindicators of ecosystem disturbances. Some taxa respond sensitively to nutrient enrichment (Carpenter *et al.* 1985, O'Toole *et al.* 2008, Donohue *et al.* 2009a, Donohue *et al.* 2009b), acid stress (Groom & Hildrew 1989, Økland 1992, Johnson *et al.* 1993, Tixier & Guerold 2005) or a number of other climatological, morphological, navigational and recreational human impacts (Solimini *et al.* 2006, Brauns *et al.* 2007b, Brauns *et al.* 2008). Moreover, benthic invertebrates, having generally limited mobility and being highly dependent on their habitat (Tolonen *et al.* 2001, Schindler & Scheuerell 2002, Tolonen 2004, Tolonen *et al.* 2005, Brauns *et al.* 2007a), are likely to be very sensitive to habitat loss (Hering *et al.* 2004). They may be particularly sensitive to water level fluctuations and the associated alteration in sediment exposure, temperature regime, wave-induced sediment redistribution and primary productivity (McEwen & Butler 2009), anthropogenic shoreline development and hydrological impacts in general (Ward 1992, Brauns *et al.* 2007b).

Substantial knowledge on quantifying flow regimes and the ecological effects of modified flow regimes using benthic biota already exists for rivers and streams (*e.g.* Scarsbrook & Townsend 1993, Grimm *et al.* 1997, Townsend *et al.* 1997b, a, Miller *et al.* 2007, Dunbar *et al.* 2010), although this knowledge is not readily transferable to littoral macroinvertebrates in lakes. Miller *et al.* (2007) found that even though the magnitude and duration of discharge reductions can potentially determine river macroinvertebrate responses to water withdrawals, hydrological disturbance alone did not have direct impacts. Rather, the synergistic effects of multiple environmental

stressors altered the structure and functioning of macroinvertebrate assemblages (Miller *et al.* 2007). The increase of the magnitude and duration of low flow events increased the likelihood of observing adverse indirect effects on taxon richness of macroinvertebrates from 54 stream sites in New Zealand (Townsend *et al.* 1997a). There was a negative relationship between richness and proportion of substratum made up of small particles and a positive relationship between refugia and taxon richness, but the factor best accounting for variation in taxonomic richness was bed disturbance (Townsend *et al.* 1997a). Dunbar *et al.* (2010) observed a positive relationship between antecedent low and high flow events and the lotic-invertebrate index for flow evaluation with the registered effects being much stronger in Autumn samples in comparison with Summer samples. The lotic-invertebrate index was introduced by Extence *et al.* (1999) and links qualitative and semi-quantitative changes in riverine benthic macroinvertebrate species and families to prevailing flow regimes. The lotic-invertebrate index is calculated as the sum of all individual taxon flow scores divided by the number of taxa involved in the calculations (Extence *et al.* 1999).

A few studies focused explicitly on exploring the capacity of benthic invertebrates to reflect human-induced alteration of water level regimes of lakes. They aimed at illustrating to water regulators the differences between various regulation practices, through studying the response of littoral macrozoobenthos biomass to water level regulation (Palomäki 1994, Hellsten *et al.* 1996). Palomäki (1994) proposed a measure of the relationship between annual water level fluctuations, lake size and littoral invertebrates inhabiting clear and oligotrophic reservoirs and lakes. It incorporated the logarithm of the biomass index, computed as the ratio between annual range of water level fluctuations in the preceding year and Secchi disk depth in open water season. The benthos biomass at all depths in the littoral decreased with increased water level fluctuations, provided that the transparency of the water was uniform. In addition, Palomäki (1994) found that greater amplitudes of water level disturbed benthos zonation.

Further, Hellsten *et al.* (1996) developed an ecologically-based regulation practice (ERP) to several hydroelectric Finnish lakes. The proposed ERP sought to provide a tool for hydropower companies to compare the relative differences between various

water level fluctuations and may be utilised as an estimation of the impact of water level regulation on the recreational use of shore areas, flooding and fishery. Hellsten *et al.* (1996) found that the harmful impacts on benthic fauna (including biomass reduction and compositional shift) depended both on annual range and water quality, with clear water lakes being more resistant to water level regulation than humic lakes. Since the lake littorals were subjected to freezing during the winter months, the ERP proposed a higher winter water level target, thus avoiding decrease in the biomass and species richness of benthic macroinvertebrates and a reduction of the spawning areas of fish. A well-defined target for the spring flood water level was proposed, together with stable summer water levels and that during the open water period, high water levels should be avoided in the regulated lake (Hellsten *et al.* 1996).

1.5. Implications of amplified water level fluctuations

1.5.1. Ecosystem-level implications

Amplified water level fluctuations cause not only fragmentation of the physical environment, shore instability and deteriorate habitats and food resources for invertebrates through elimination of macrophytes, but they can also lead to increased turbidity, degradation of water quality and ecosystem integrity, reducing the reliability of ecosystem goods and services (Gleick 2003, Ostendorp *et al.* 2004, Schmieder 2004, Sophocleous 2004, Acreman *et al.* 2005, Rockstrom *et al.* 2007). Hydrological perturbations may disrupt within- and among-system linkages (Lake *et al.* 2000) and reduce the resistance and resilience of littoral zones to other disturbances (Folke 2003). For instance, species loss might free-up ecological niches and thus facilitate the invasion of alien species and their establishment in ecosystems (Hunt & Jones 1972, Rapport *et al.* 1998, Naeem 2009). In addition, littoral zones provide disproportionately important feeding and breeding habitat for whole-lake food webs (Vander Zanden & Vadeboncoeur 2002, Sabo *et al.* 2009, Hampton *et al.* 2011) and, even though the effects of altered water level regimes are likely to be particularly strong in littoral zones (Solimini *et al.* 2006, Leira & Cantonati 2008), they affect the functioning and stability of the whole lake ecosystem. Moreover, benthic invertebrate consumers form key links in not only whole-lake food webs but also in adjacent terrestrial ones through affecting how much and by what pathways energy and

essential nutrients flow at ecosystem level (Vander Zanden & Vadeboncoeur 2002, Hebert *et al.* 2008, Sabo *et al.* 2009, Wesner 2010, 2011). Therefore, the effects of alterations to natural patterns of water level fluctuations may not be limited to aquatic ecosystems but may have significant effects on associated terrestrial ecosystems.

1.5.2. Societal implications

Water demand is exceeding the capacity of available freshwater resources to supply sustainable life-support functions for humankind worldwide (Vorosmarty *et al.* 2000, Folke 2003, Sophocleous 2004, Sternberg 2006). Global freshwater availability and quality are demonstrating an alarming decline and could be translated further into serious social effects at local and global scales (Palmer 2010). Water scarcity and depletion of water resources are rapidly becoming key drivers of water, food and energy insecurity globally (Rockstrom *et al.* 2007, Brown *et al.* 2010, International Bank for Reconstruction and Development 2010, Porter *et al.* 2011), thus threatening to become the most urgent issue facing humankind (Sophocleous 2004, Vorosmarty *et al.* 2010). The per capita availability of freshwater is declining worldwide, and contaminated water remains the greatest single environmental cause of human sickness and death (Arthurton *et al.* 2007). Water use will likely comprise the most important driver of human conflicts in the next century, and will probably be the key determinant of human migration patterns, particularly in regions that are already experiencing water stress and with limited access to food resources and safe drinking water (Zhang *et al.* 2007). There have been 1,831 water-based interactions (both conflictual and cooperative) over the last fifty years and 40% of the world's population depend on the water resources of more than 270 transboundary river basins around the world (Connor *et al.* 2009, UNESCO 2011). Conflicts can arise regarding quality, allocation, infrastructure, joint management, irrigation and other activities that are water-dependent (Shiklomanov & Rodda 2003, World Water Assessment Programme 2009, UNESCO 2011). This trend of aquatic ecosystem degradation and depletion of freshwater resources can be reversed when governments, industry and research combine their efforts. Therefore, improved assessment, management and forecasting of water resources will aid more efficient allocation of water globally and among competing needs (Jackson *et al.* 2001) and reduce the pressure on water resources.

1.6. Thesis outline and research objectives

1.6.1. Thesis outline

This PhD research comprises three interlinked sets of studies (Fig. 1.2). The study design includes analyses of long-term time series of daily water levels from 46 lakes, a multi-lake observational study and a manipulative experiment to address the following two principal objectives: to (1) propose metrics quantifying water level fluctuations in lakes and identify which landscape factors contribute most strongly to the regulation of spatial patterns of water level fluctuations and (2) elucidate the ecological effects of amplified water level fluctuations and the mechanisms underpinning those effects.

Chapter 1 introduces the general background and need of the study, together with the main research aims.

In Chapter 2, a detailed multi-lake study, I quantify and describe the nature and extent of water level fluctuations in Irish lakes at various temporal scales, as well as the factors regulating them. These findings served as guidance for the identification of suitable amplitude for the investigation of amplified water level fluctuations (Chapter 3).

Chapter 3 investigates the direct effects of amplified water level fluctuations on benthic biota and the mechanisms underpinning these through the experimental manipulation of water level.

Chapter 4 examines the differences in natural benthic assemblages between lakes that experience high and low water level fluctuations. The monthly and annual range data from the lakes studied in Chapter 2 were used to identify the two groups of potential lakes for the field surveys, as well as for the timing of the sampling.

Chapter 5 synthesises the key findings from Chapters 2, 3 and 4 and incorporates recommendation for future work, implications for environmental monitoring and mitigation together with some implications of fluctuating water levels on ecosystem services.

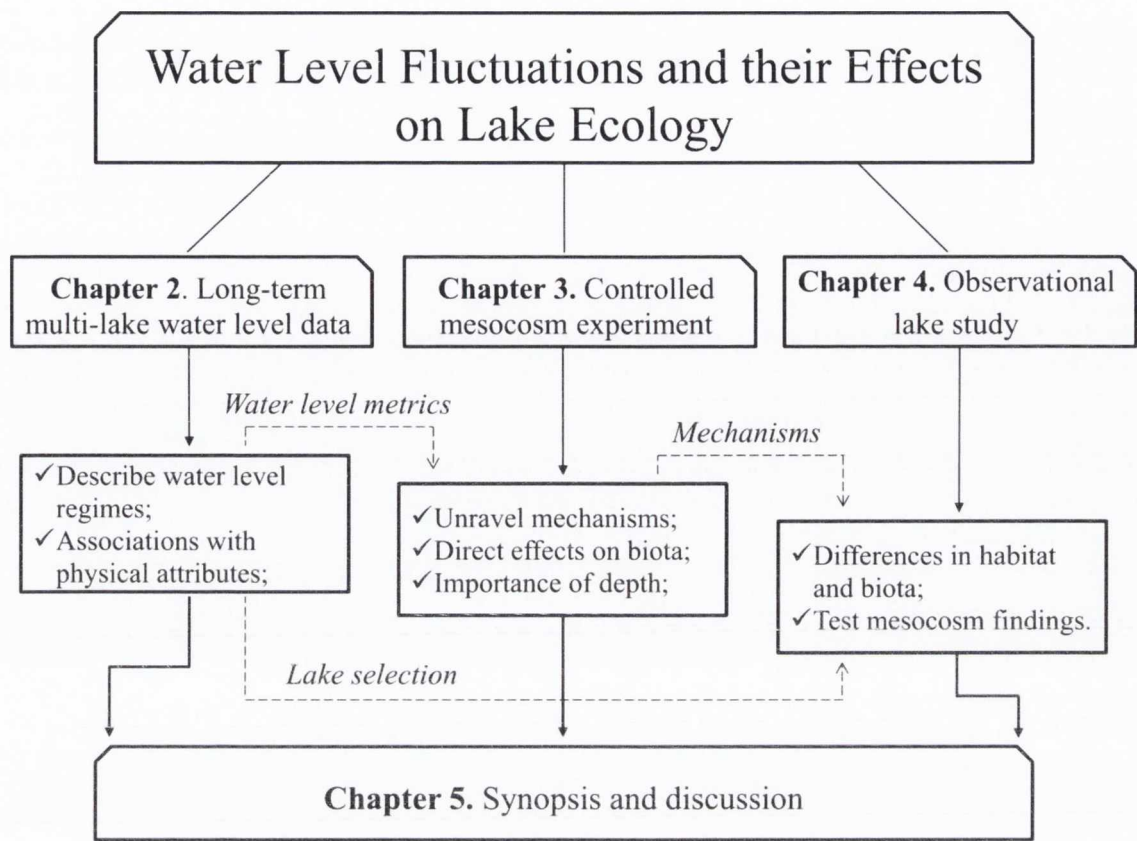


Fig. 1.2. Structure and outline of the thesis.

1.6.2. Research hypotheses

This thesis explores the following four key hypotheses:

Hypothesis 1:

There are significant associations between water level fluctuations and the physical characteristics of lakes and their catchment attributes.

Landscape context is critical for interpreting ecosystem responses to pressures. The hydromorphological disturbances exerted on littoral biota, and in particular water level fluctuations, may vary in accordance with relative ecosystem size or ecosystem connectivity. The aim of Chapter 2 is to quantify and characterise multi-decadal temporal and spatial variability in water level regimes of Irish lakes. Upon the identification of a parsimonious subset of water level metrics that account for most of

the variability in water level regimes, I explore their association with catchment characteristics. Freshwater ecosystems are long known to be affected by catchment and landscape characteristics in general (Leopold 1941). The catchment is the basic organisational unit for understanding and managing freshwater ecosystem processes (Brown *et al.* 2010) and conservation efforts need to be aimed at whole-catchment management (Saunders *et al.* 2002). Furthermore, freshwater systems are defined largely by their hydrology, and hydrological regimes could be thought as of result of the complex natural processes which operate on a catchment scale (Smakhtin 2001). Therefore, to further enhance our ability to describe and predict water level regimes, to assess their impacts, we need to encompass characteristics of the lake catchment and its surrounding landscape.

Hypothesis 2:

Amplified water level fluctuations alter the structure and functioning of littoral assemblages.

In Chapter 3, I describe an experiment done in outdoor mesocosms that mimic the littoral zone of natural lakes. It examines the effects of amplified water level fluctuations on the structure or functioning of lake biotic assemblages. In Chapter 4, I then describe a comparative study of eight Irish lakes with contrasting regimes of water level fluctuations and representing a broad range of physical and chemical characteristics, which was done to test the findings of the mesocosm experiment in natural ecosystems. To enhance the mechanisms and detection of specific impacts of WLF under multiple stressor scenarios I employed a multi-trait approach for both the experimental and the observational studies.

Hypothesis 3:

Greater amplitude of fluctuations affects habitat structure of littoral zones.

Receding and increasing water may have multilevel impacts on lake littoral zones. Fluctuations in water levels are not only shaping the communities directly but comprise a key driver of their physical habitat through modifying habitat structure

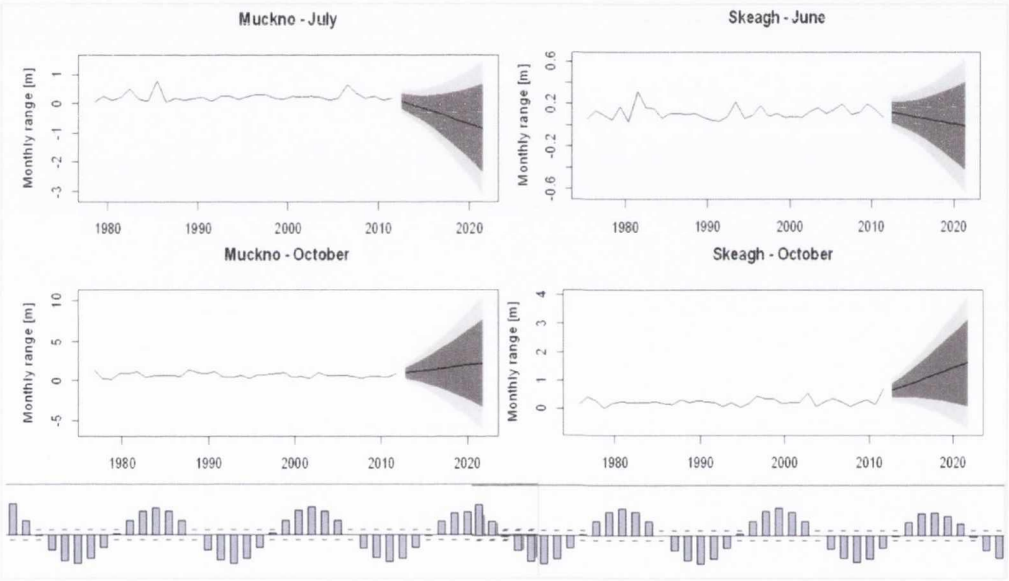
and substrate heterogeneity. I test this hypothesis in Chapter 4 by comparing habitat structure in lakes with high and low amplitudes of water level fluctuations.

Hypothesis 4:

The effects of water level fluctuations depend upon their interaction with sampling depth.

I examine whether the effects of water level fluctuations interact with the position of benthic assemblages along the shore (*i.e.* whether effects vary along the depth gradient) for a broad range of univariate and multivariate community responses, through both controlled experimental conditions (Chapter 3) and observational studies (Chapter 4).

2. Characterising Water Level Fluctuations in Lakes:
Metrics, Seasonality and Relationships with Catchment
Attributes



Time series plots with probable future scenarios of the minimal and maximal mean monthly ranges of water levels in Loughs Muckno (Co. Monaghan) and Skeagh (Co. Cavan).

2.1. Introduction

As societies become more urban and more technology- and electricity-dependent they become more water-dependent, thus eliciting concerns for conservation and restoration of healthy lake ecosystems (Liermann *et al.* 2012) and raising appreciation of the value of clean water (Vorosmarty *et al.* 2010). Lakes constitute only 0.26% of Earth's freshwater which accounts for 0.013% of the hydrosphere (Hutchinson 1975, Wetzel 2001, Shiklomanov & Rodda 2003). Currently the provision of clean freshwater is the most valuable ecosystem service in the world, regardless of the striking difference between its value and market price (Johnson *et al.* 2001, Sukhdev 2009). Maintaining ecosystem integrity and recognising the intrinsic value of good quality water should accrue sustainable management of global water resources, effectiveness and optimization in water use and mitigation of impacts of climate change in order to prevent further deterioration of the condition of water bodies (Vorosmarty *et al.* 2000, Gleick 2003, Sophocleous 2004, IPCC 2007).

The hydrological cycle, in particular hydrological fluxes, plays a central role in understanding water availability. Humankind would use all available water rapidly were it not replenished by atmospheric input of precipitation (Dodds 2002). Alterations of hydrological regimes through various human activities, such as impoundment through the construction of dams and flood protection structures, despite being aimed at increasing water security, typically lead to habitat and biodiversity loss and degradation of water quality (Baxter 1977, Hill *et al.* 1998, Schmieder *et al.* 2004). Solar energy and evaporation are key drivers of water fluxes (Dodds 2002). Thus, it is not surprising that there is strong evidence indicating a notable amplification of the global water cycle over the last half century (IPCC 2007). The intensification of the global water cycle that is expected to occur, were global temperatures to increase by as little as 2° to 3°C, is as much as between 16 and 24% (Durack *et al.* 2012). Thus, additional pressure could potentially be exerted on the hydrology and water quality of lakes, as they comprise an integral feature of the global hydrological system (O'Sullivan & Reynolds 2004).

In order to protect and manage water resources in Europe in a sustainable manner, the European Parliament has adopted the Water Framework Directive (WFD; 2000/60/EC). It requires the achievement of good ecological and chemical status for all surface waters by 2015. As stated in Annex V of the WFD, the elements of hydromorphology supporting the biological elements comprise the hydrological regime and morphological conditions. Robust assessment of ecological impacts of hydromorphological disturbances is therefore essential for the achievement of the environmental objectives set by the WFD. As a result, there has been increased interest within the scientific community on the environmental effects of water level fluctuations in recent years (*e.g.* Gafny & Gasith 1999, Tanner *et al.* 1999, Håkanson *et al.* 2000, Burton *et al.* 2002, Coops & Hosper 2002, Coops *et al.* 2004, Dinka *et al.* 2004, Schmieder *et al.* 2004, Chow-Fraser 2005, Van Geest *et al.* 2005, Van De Meutter *et al.* 2006, Beklioglu 2007, Hofmann *et al.* 2008, Leira & Cantonati 2008, Mastrantuono *et al.* 2008, SNIFFER 2008, Wantzen *et al.* 2008a, Sasikala *et al.* 2009).

Understanding the links among hydrological processes (natural and human-impacted), the associated aquatic ecological responses and, ultimately, the effects on ecosystem integrity requires an approach that incorporates the identification of robust measures quantifying the multifaceted nature of lacustrine hydrological regimes across time. Previous research on hydrological regimes focused mainly on river flows, resulting in the development of a considerable diversity of metrics. Numerous studies acknowledged that the dynamic character of river flows could be characterised successfully by five key facets: magnitude, frequency, duration, timing and rate of change of hydrological conditions (*e.g.* Richards 1990, Poff *et al.* 1997, Richter *et al.* 1997, Olden & Poff 2003, Fig. 2.1). The majority of extant metrics quantify one of these facets.

While river flow regimes have been reasonably well-studied and described (*e.g.* Richards 1990, Poff *et al.* 1997, Richter *et al.* 1997, Puckridge *et al.* 1998, Richter *et al.* 1998, Olden & Poff 2003, Huh *et al.* 2005, Poff *et al.* 2006, Kennard *et al.* 2010a, Kennard *et al.* 2010b), the quantification of water level regimes in lakes have received less immediate attention. There are many challenges in describing hydrological regimes in lakes and elucidating the associations between water levels

and lake ecology or management. Some of these include a scarcity of long-term water level records and high resolution data on reference lakes exhibiting natural WLF (Coops *et al.* 2003, Acreman *et al.* 2005). Description and quantification of lake water level fluctuations could be facilitated through the use of similar methodologies to those applied to rivers (Schmieder 2004, Wantzen *et al.* 2008a, Fig. 2.1). Characterising water level regimes in this way could aid identification of explicit ecosystem responses attributable to the alteration of distinct facets of water level fluctuations (Richter *et al.* 1998).

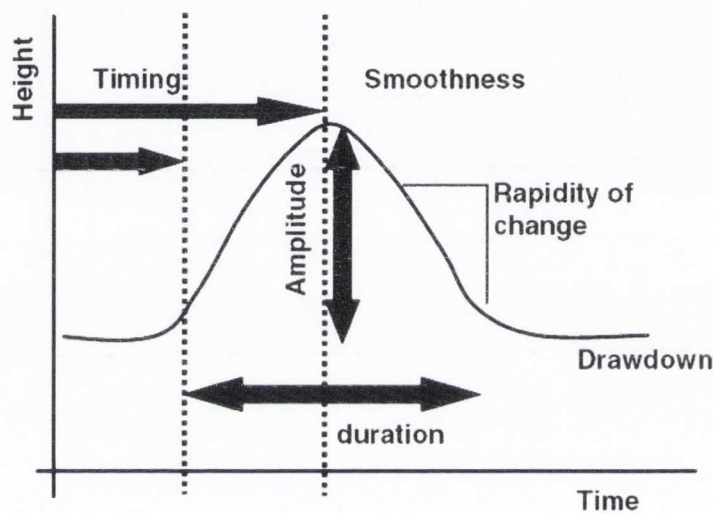


Fig. 2.1. Characteristics of a floodpulse (adapted from Wantzen *et al.* 2008a).

The physical structure of aquatic environments is defined principally by landscape geomorphology and hydrology. In particular, the habitat structure of lake littoral zones is determined largely by physical processes (Dodds 2002, O'Sullivan & Reynolds 2004). Direct effects of changes in hydrology and associated fluctuations in water level include the shift of lakeshore and the modification of lake bed morphology (Hofmann *et al.* 2008, Zohary & Ostrovsky 2011). Such impacts on the physical environment may trigger changes in habitat complexity and availability, causing shoreline instability and reducing the resistance and resilience of littoral zones to other disturbances. Lake littoral ecotones link pelagic with terrestrial habitats and are known to be key contributors to not only the overall biodiversity and functioning of lake systems but also the landscapes in which they are embedded (Wetzel 2001, Ostendorp *et al.* 2004, Hampton *et al.* 2011). Moreover, the magnitude

and timing of water level fluctuations are vital components of water level regimes and identifying the timing of extreme water levels and maximal amplitudes could be crucial not only for evaluating ecological degradation but also for risk assessment, water resources management and provision of ecosystem services (Fitzpatrick & Bree 2001, Wantzen *et al.* 2008a, Brown *et al.* 2010, Yin & Yang 2012).

The intensity and frequency of disturbances are known to be important drivers of the responses of ecosystems to perturbations (Townsend *et al.* 1997a, García Molinos & Donohue 2010, Pincebourde *et al.* 2012). Therefore, reliable prediction of the impact of disturbances should incorporate their frequency and temporal oscillations and consider effects at different temporal scales. The patterns of water level fluctuations are likely to be regulated strongly by the physical characteristics of drainage networks and lake catchments (Coops *et al.* 2003). Frequent short-term changes in water level impose direct hydrodynamic stress on littoral biota and on substrate in the shore zone thus affecting shore erosion, resuspension of particles, nutrients and methane, together with abrasion of biofilms, productivity and species competition (Hellsten 1988, Hofmann *et al.* 2008). In contrast, large amplitudes, which are more characteristic of long-term WLF, may lead to substrate modification and slow displacement of littoral zones with abiding changes in oxygen supply and renewal of deep water, or in habitat availability for biota adapted to aquatic or terrestrial conditions (Hofmann *et al.* 2008). In addition, long-term changes alter abundance, structure and diversity of riparian and aquatic communities (Sinclair 1965, Smith *et al.* 1987, Schmieder *et al.* 2004). On the other hand, the interplay between short-term and long-term WLF can comprise additional distinct forms of perturbation to those resulting from the individual processes (Hofmann *et al.* 2008, García Molinos & Donohue 2011).

Detailed multi-lake studies on patterns of lake water levels at a range of temporal scales are lacking. Moreover, little is known about the key physical characteristics of catchments that moderate these patterns. The goals for the work presented in this chapter are to: (1) describe the amplitude and variability of water level fluctuations in Irish lakes at four temporal scales: weekly, monthly, seasonal and annual; (2) investigate seasonality and identify extreme events and periods of maximal fluctuations in water level; (3) identify a parsimonious subset of hydrological indices

that characterise the five facets of water level regimes in lakes and (4) explore relationships between lake water level fluctuations and the physical characteristics of lakes, their catchments and the surrounding landscape (Fig. 2.2).

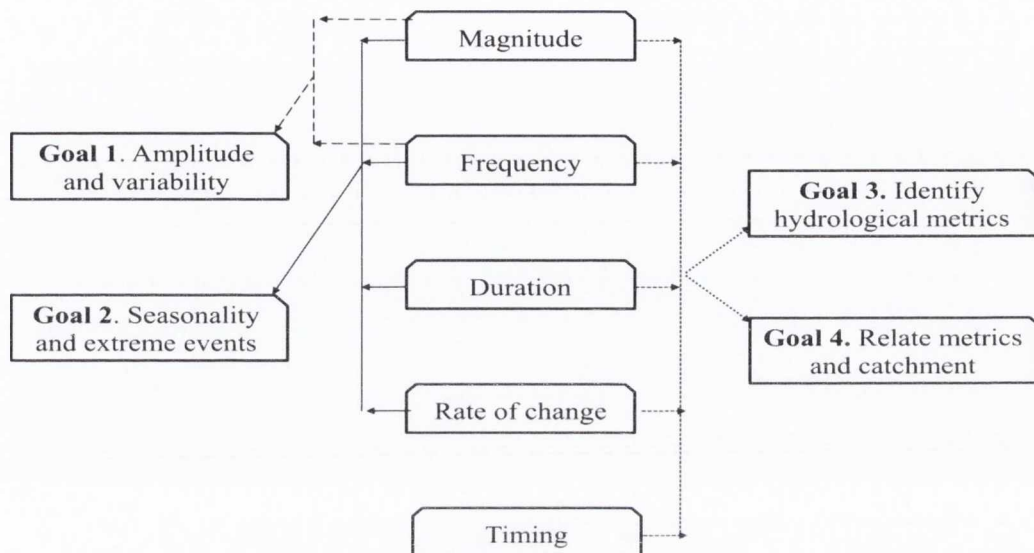


Fig. 2.2. Diagram, relating each goal of Chapter 2 to the proposed specific facets of water level regimes.

2.2. Methods

2.2.1. Data sources

I collated long-term data of mean daily water level (MDWL) readings for 63 Irish lakes (Appendix 2.1, Fig. 2.3), with some of the measurements commencing in 1952 (mean record length 26 ± 12 years). The majority of the raw data were obtained from the Irish Environmental Protection Agency (EPA) HydroNet web site (accessed in February 2009, April 2011 and May 2012, <http://hydronet.epa.ie/> 2012). Information on additional lakes was provided by the EPA, the Office of Public Works and the Electricity Supply Board. Historical water level records were collected at a network of water level stations operated by local authorities throughout the Republic of Ireland, using autographic recorders or data loggers. The zero level of the staff gauges in each lake was surveyed relative to a local datum, Poolbeg or Malin Head Ordnance Datum levels (<http://hydronet.epa.ie/> 2012). Thus, water levels in individual lakes are not directly comparable among lakes. All recorded historical changes in the baseline

(zero) level for the staff gauge of each lake for the complete record period were accounted and corrected for. Data quality varied over time and among lakes. Thus, after collating the data, I performed an additional quality check and the water level readings of questionable quality were replaced with missing values to create a time series of mean daily water level readings spaced evenly in time.

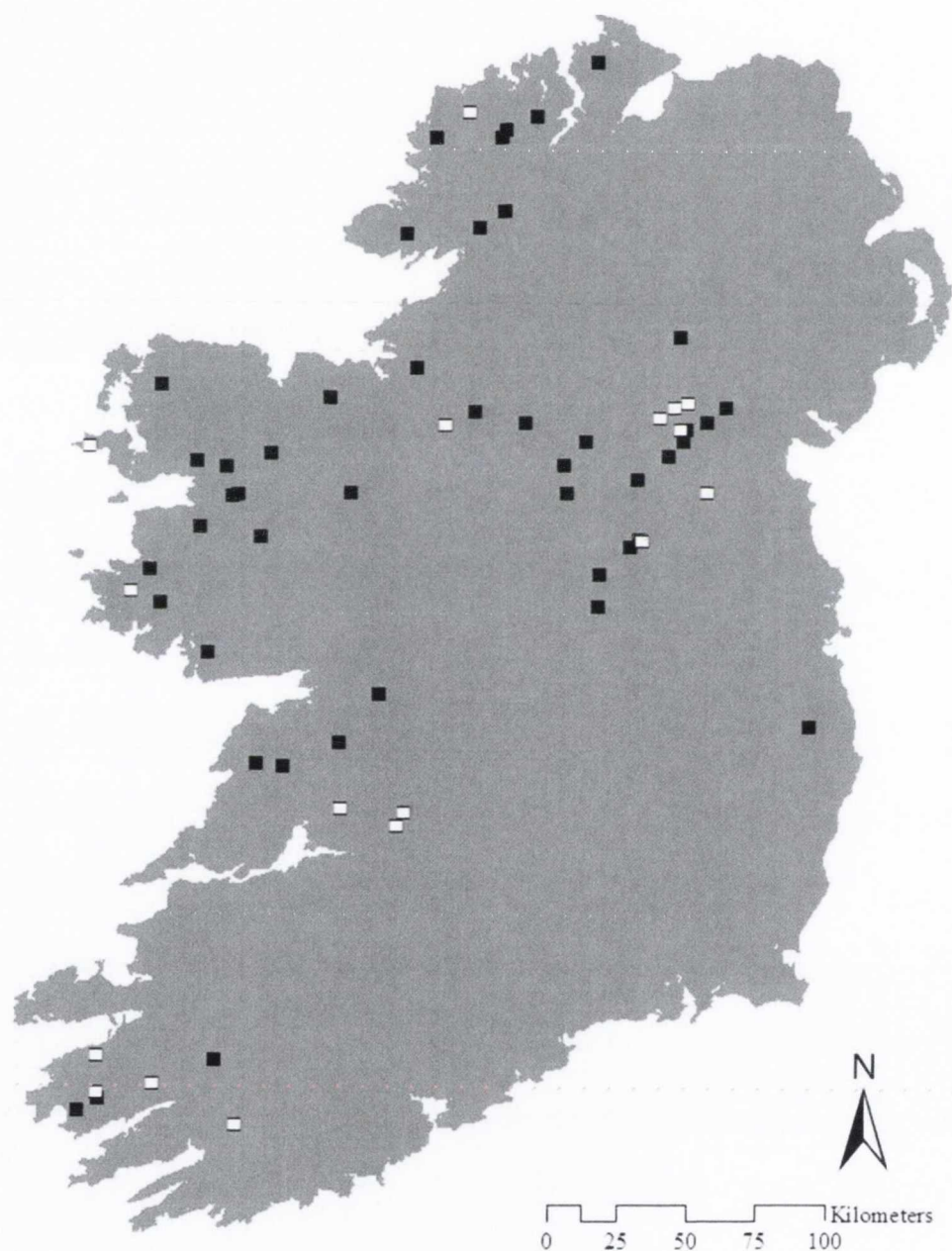


Fig. 2.3. Locations of the 63 lakes for which water level data was collated. Lakes denoted by open squares had unsatisfactory water level data quality and only lakes denoted by closed squares were included in the further analyses.

2.2.2. Data analyses

Since Richards (1990) and Kennard *et al.* (2010a) suggested that ten years or more are needed to ensure stability of the derived flow duration statistics and handle the individual annual variability effects of the time series, I used water level data from a subset of 46 Irish lakes to study and describe the overall magnitudes and patterns of water level regimes. The selected lakes represent a range of water level regimes with good data quality and time series in excess of ten years in every case. The minimum dataset length was 3978 daily readings. For analyses done at seasonal time scales, I defined Spring as occurring between March and May, Summer between June and August, Autumn between September and November and Winter between December and February.

Water level metrics

I calculated 915 water level metrics using daily, weekly, monthly, seasonal and annual water level data (Appendix 2.2). Most of the metrics I used were adapted flow metrics typically used in the assessment of hydrological flow regimes in rivers and streams (Jowett & Duncan 1990, Richards 1990, Poff *et al.* 1997, Puckridge *et al.* 1998, Richter *et al.* 1998, Olden & Poff 2003, Kennard *et al.* 2010a). In addition, I derived Low (LWI) and High (HWI) Water Level measures as the ratio of the lowest or highest mean daily water level for a certain time interval (week, month, season or year) to the mean daily water level averaged across the specified time period. I also defined the temporal rate of change of selected water level metrics through time. This was calculated for water level ranges (SI_R), LWI (SI_{LWI}) and HWI (SI_{HWI}) and measured as the slope of change across weekly, monthly, seasonal and annual temporal scales. These metrics therefore incorporate not only the amplitude of water level but the nature of changes across temporal scales for each lake. Seasonality (*sensu* Cryer & Chan 2008) was characterised further through performing monthly and seasonal analyses. Both overall monthly and seasonal mean water level metrics, as well as individual monthly (from January through December) and seasonal (for Spring, Summer, Autumn and Winter) metrics were used. In order to study the relative contribution of each month or season within the year to the mean monthly or seasonal water level, I derived the mean index of the mean monthly and seasonal

water levels. In the same way the mean monthly or seasonal water level index and the monthly or seasonal ranges index were calculated for each month and season.

The derived water level metrics (WLM) were then grouped to represent the five underlying facets of hydrological regimes (adapted from Poff *et al.* 1997, Richter *et al.* 1998), which are:

- Magnitude;
- Frequency;
- Duration and length of rise and drop events in water level;
- Timing and predictability of extreme events;
- Reversals and temporal rate of change (Fig. 2.1; Appendix 2.2).

Numeric measures of central tendency (*e.g.* mean, median), and spread (*e.g.* coefficient of variation or standard deviation, skewness and kurtosis) were calculated for individual metrics when feasible. Moreover, interquartile range and median absolute deviation were included in the analyses as measures of spread resistant to outliers (Verzani 2002). I included the spread S_{50} , as it is less subjective to record length than other measures of dispersion (Richards 1990, Puckridge *et al.* 1998). Various within-lake measures were associated with extreme events as defined by IPCC (2007). Such measures include the frequency of occurrence and the timing (predictability) of extremely high (exceeding the 90th percentile of the full record) and extremely low (below the 10th percentile) water level events, or the variation of maximal and minimal water level or amplitude of fluctuations. The very unlikely events when water level was above the 99th percentile or below the 1st percentile of mean daily water level were also included in analyses to provide an insight into the occurrence of extreme flooding or draw-down of water level (Appendix 2.2). Data describing the physical characteristics of lakes, their catchments and the surrounding landscape were also compiled for each of the selected lakes (Table 2.1).

Table 2.1. Catchment and landscape characteristics of the 46 lakes used to characterise water level regimes. CA denotes catchment area; SA – lake surface area; SD – standard deviation.

Lake number	Lake	Catchment area (ha)	Lake surface area (ha)	Ratio of lake surface area: catchment area	Mean catchment slope	Shoreline length (km)	Length upstream tributaries (km)
1	Adeery	789.5	17.5	0.02	8.5	2.1	20065
2	Akkibon	785.2	44.5	0.06	6.8	3.6	na
3	Allen	42888.3	3331.9	0.08	6.2	53.2	563351
4	Anure	3717.5	132.6	0.04	7.8	15.0	47500
5	Bane	350.3	75.1	0.21	4.9	5.0	74
6	Bawn	6575.6	30.4	0.01	4.9	3.9	0
7	Beltra	9776.8	401.7	0.04	8.3	16.7	170778
8	Carra	10899.0	1557.9	0.14	1.4	75.3	53844
9	Carrowmore	8790.1	911.2	0.10	4.4	24.8	110749
10	Cloonaugh	1014.2	125.7	0.12	15.5	9.4	9731
11	Cullin	39707.6	1019.3	0.03	2.9	25.6	na
12	Currane	11066.1	1028.1	0.09	183.7	32.4	148418
13	Cutra	12384.0	382.0	0.03	3.3	16.9	145676
14	Dan	6321.7	102.4	0.02	9.6	6.3	70758
15	Derryclare	11182.6	222.5	0.02	10.4	20.6	257644

Chapter 2. Characterising Water Level Fluctuations in Lakes: Metrics, Seasonality and Relationships with Catchment Attributes

Lake number	Lake	Catchment area (ha)	Lake surface area (ha)	Ratio of lake surface area: catchment area	Mean catchment slope	Shoreline length (km)	Length upstream tributaries (km)
16	Dromore	52.3	4.8	0.09	4.9	1.0	0
17	Easky	1060.3	118.7	0.11	6.9	6.1	18131
18	Egish	928.8	111.4	0.12	4.4	10.0	0
19	Emy	382.1	52.4	0.14	3.8	3.6	-
20	Ennell	12998.4	1151.5	0.09	1.1	27.4	69970
21	Eske	8010.9	385.2	0.05	9.9	15.5	172568
22	Fad	316.3	40.2	0.13	5.2	3.9	1810
23	Fee	1566.1	172.8	0.11	9.4	10.5	42932
24	Feeagh	8404.8	393.1	0.05	10.7	13.7	143225
25	Fern	20671.4	180.3	0.01	6.4	7.2	354853
26	Gartan	7737.1	202.8	0.03	7.6	12.7	128760
27	Garty	2080.8	82.2	0.04	4.4	4.8	0
28	Gill	39066.6	1375.3	0.04	6.0	36.0	501230
29	Gleincmurrin	6723.9	162.3	0.02	3.8	18.8	98561
30	Gowna	12294.7	1146.7	0.09	2.8	80.4	0
31	Guitane	1902.2	245.4	0.13	13.6	7.4	18638
32	Inchiquin	14357.8	107.3	0.01	3.5	5.9	45928
33	Islandeady	5871.6	138.5	0.02	3.1	11.8	89836

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Lake number	Lake	Catchment area (ha)	Lake surface area (ha)	Ratio of lake surface area: catchment area	Mean catchment slope	Shoreline length (km)	Length upstream tributaries (km)
34	Lannagh	6574.3	59.1	0.01	3.1	8.1	94173
35	Lene	1312.8	414.5	0.32	2.6	14.4	1488
36	Lickeen	908.8	83.9	0.09	3.4	6.3	10746
37	Moher	644.6	36.3	0.06	3.8	3.4	4740
38	Mourne	848.7	66.3	0.08	5.2	5.2	0
39	Muckno	16359.2	354.3	0.02	4.1	24.4	0
40	Nadreegeel	872.1	84.3	0.10	4.3	10.0	9495
41	Oughter	56691.5	658.2	0.01	3.4	69.8	0
42	Owel	4812.1	1017.6	0.21	1.3	18.2	24601
43	Rea	1197.2	299.9	0.25	2.2	8.4	2740
44	Sillan	5291.6	161.5	0.03	5.1	10.9	0
45	Skeagh	534.2	61.0	0.11	4.5	5.3	1603
46	Urlaur	1807.2	114.5	0.06	1.4	9.6	3041

I used Minitab (version 15, Minitab Inc., PA, USA); EViews (version 5, Quantitative Micro Software, CA USA); Excel (version 2007, Windows OS, Microsoft®) and a combination of computer VBA and Excel macros for data management and descriptive summary statistics. Statistical analyses were conducted in R Version 2.15.0 (R Development Core Team 2012) using the TinnR interface (Faria *et al.* 2011).

Characterisation of water level regimes and relationships with catchment characteristics

A combination of three complementary methods was used to identify a parsimonious subset of water level metrics accounting for the majority of variation in water level regimes, while concurrently minimising information redundancy. These included analyses of correlation matrices and variance inflation factors (VIF) followed by principal component analysis (PCA). While Pearson correlation matrices were used to assess the multicollinearity among metrics, VIF measured the change of variance owing to collinearity among variables (Montgomery & Peck 1992). Highly correlated metrics with $r > 0.9$ and VIF in excess of 50 (Zuur *et al.* 2007) were excluded from further analysis. All selected metrics were then centered and standardised to remove differences in scales of measurement. In the subsequent PCA, principal components that accounted for at least 10% of variability in the data were retained for further analysis. Loadings of the water level metrics on each significant principal component were used to identify the metrics explaining the dominant patterns of variation provided by the pool of water level metrics. Five or more water level metrics loading strongly on the retained principal components, representing each of the key facets of water level regimes, were selected for further analyses. The PCA was conducted in CANOCO (version 4.5, Wageningen University, The Netherlands).

A backward VIF selection procedure was used to assess multicollinearity among catchment characteristics. Variables with VIF values ≥ 5 were excluded from further analyses (Montgomery & Peck 1992, Zuur *et al.* 2007). Upon the identification of the reduced subset of metrics characterising water level regimes and catchment attributes, I used quantile regression (Koenker 2012) to identify catchment and landscape features that associated most strongly with lake water level regimes. Quantile

regression can be applied to highly skewed data and is robust even to extreme outliers (Jalali 2011). Potential quantile models were identified for each of the selected principal components, as well as for selected water level metrics. Model selection was based on the second-order Akaike Information Criterion (AICc). The use of AICc is preferred for small (with respect to the estimated parameters) sample size (Burnham & Anderson 2002). In addition, to further interpret the relative likelihood of a model given the data, I compared the ratio of Akaike weights ω_i (*i.e.* evidence ratio) of all models with AICc $\Delta_i \leq 2$, where $\Delta_i = \text{AICc}_i - \text{AICc}_{\min}$ (Burnham & Anderson 2002). When models had $\Delta_i \leq 2$, I applied the principle of parsimony and selected the model with the fewest parameters (Zuur *et al.* 2007). The AICc values of candidate models were compared to the AICc of the null model (*i.e.* with the overall mean value as the only parameter). I used bootstrapping (R=1000) to derive parameter estimates and their error terms. The algorithm used to compute the fit was a modified version algorithm for l1-regression of Barrodale and Roberts (Koenker & D'Orey 1987, Koenker & d'Orey 1994).

2.3. Results

2.3.1. Amplitude and general patterns of water level fluctuations

Lake water level regimes were characterized by considerable variability over time and across all temporal scales examined (Fig. 2.4). Range peakedness of the probability distribution relative to a normal distribution (quantified by the kurtosis) also differed among lakes and temporal scales (Appendix 2.3). The kurtosis of the ranges of some lakes (*e.g.* Anure, Guitane, Lannagh and Dan) was consistently low across temporal scales, while for others it varied greatly. For instance, peakedness was high for the weekly range and low for the seasonal and annual ranges in Loughs Cara, Ennell, Gowna and Oughter, while in Loughs Muckno and Sillan it was low for monthly and seasonal ranges and higher for weekly and annual ranges (Fig. 2.4, Appendix 2.3).

(a)

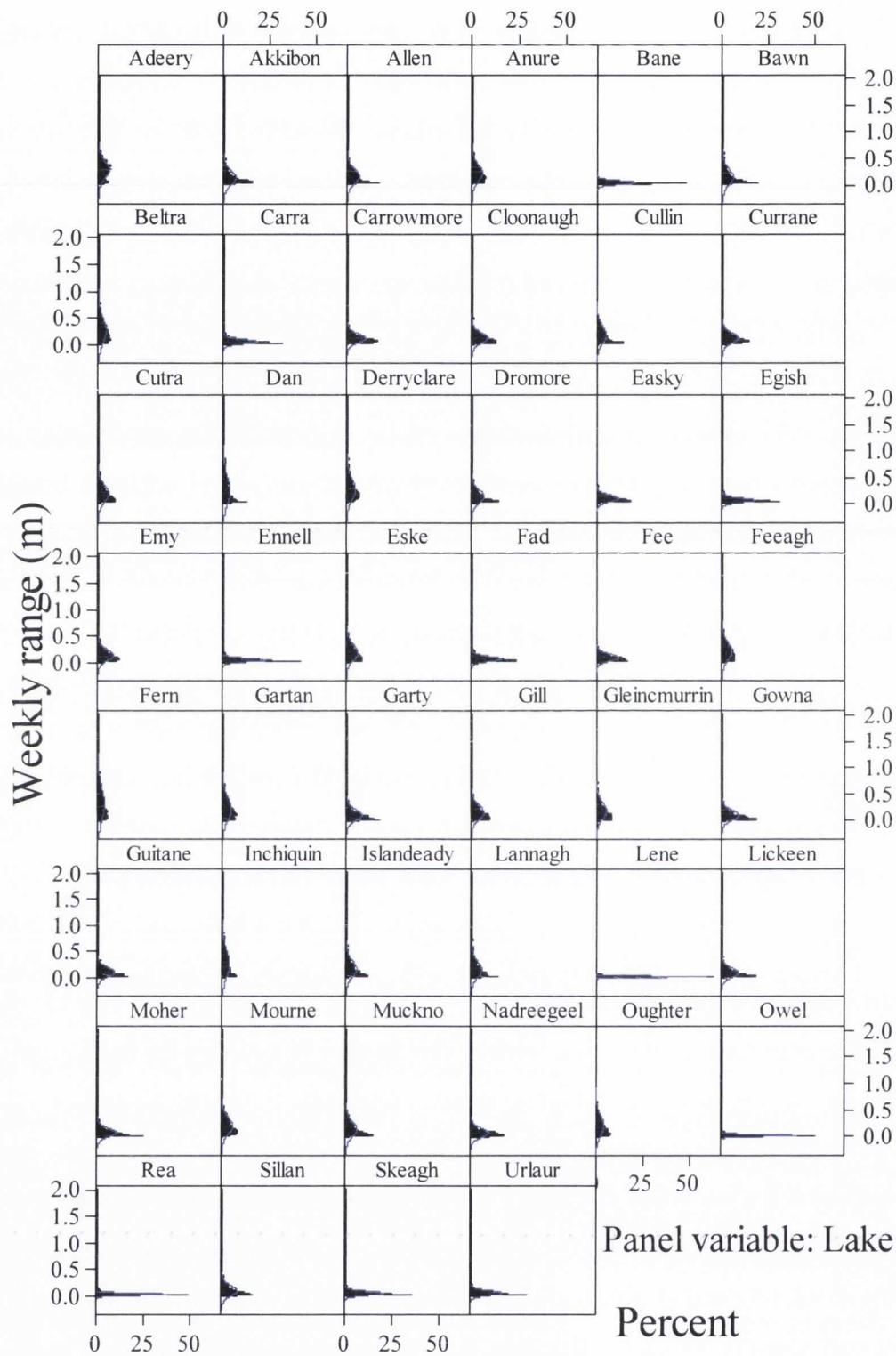


Fig.2.4. Continued.

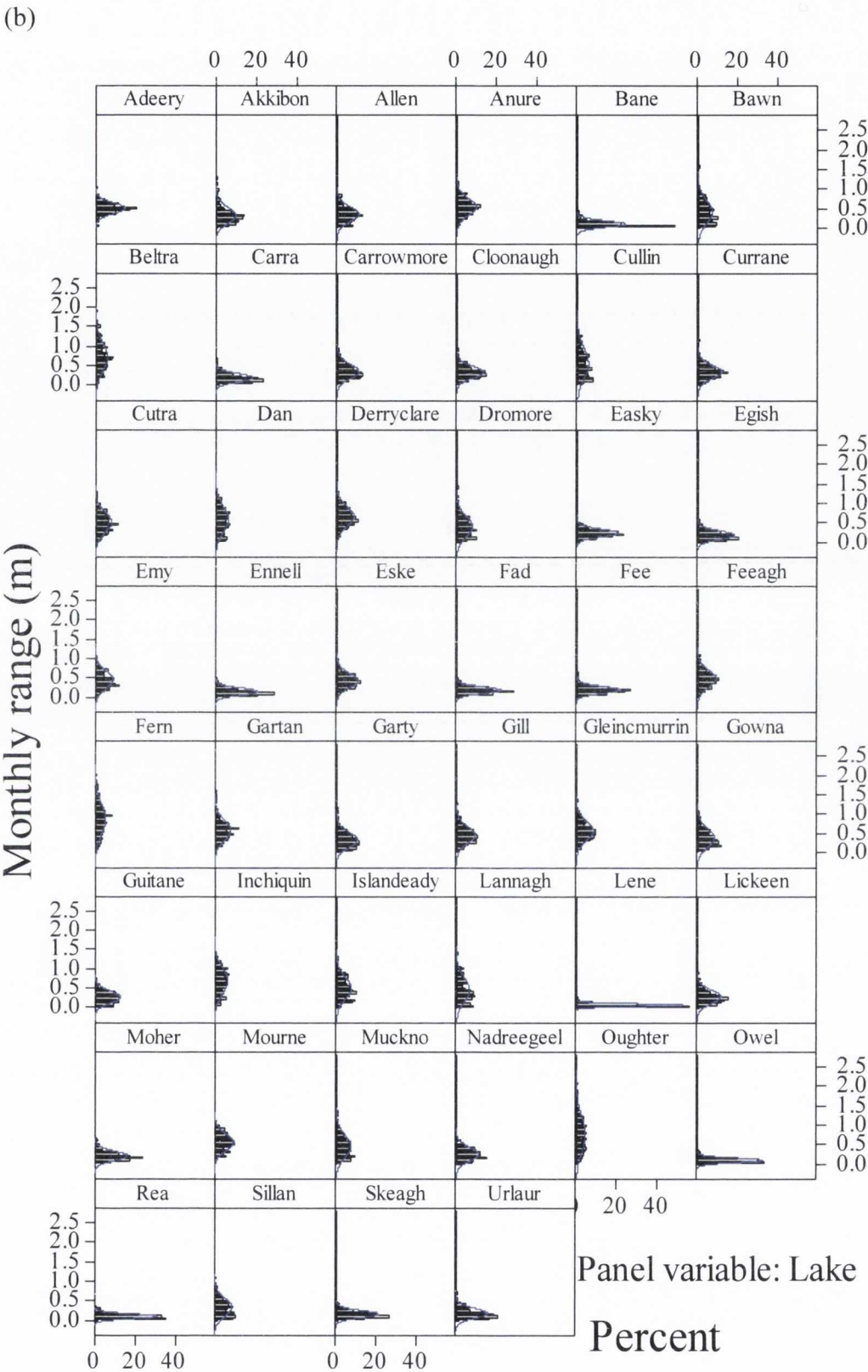


Fig.2.4. Continued.

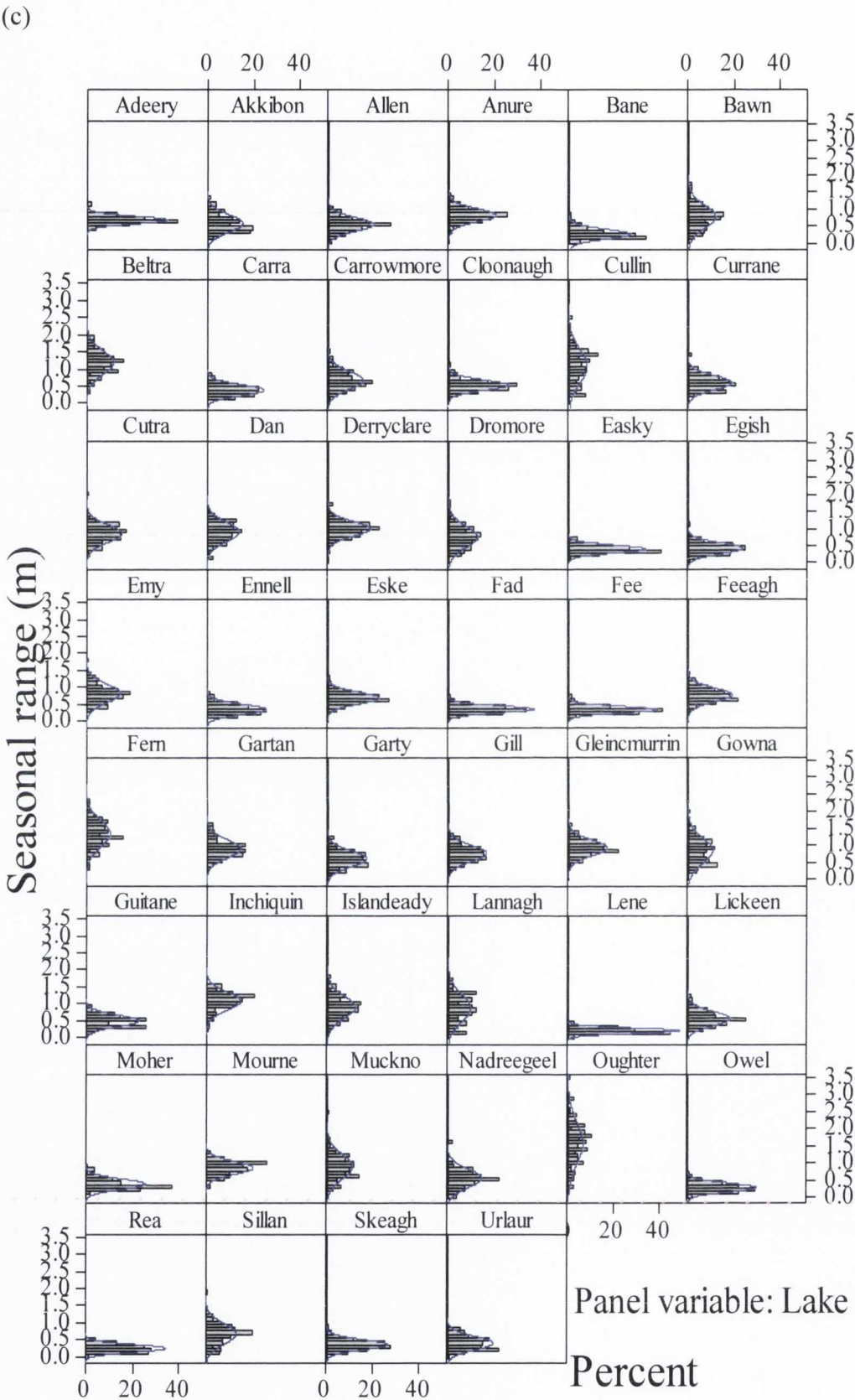


Fig.2.4. Continued.

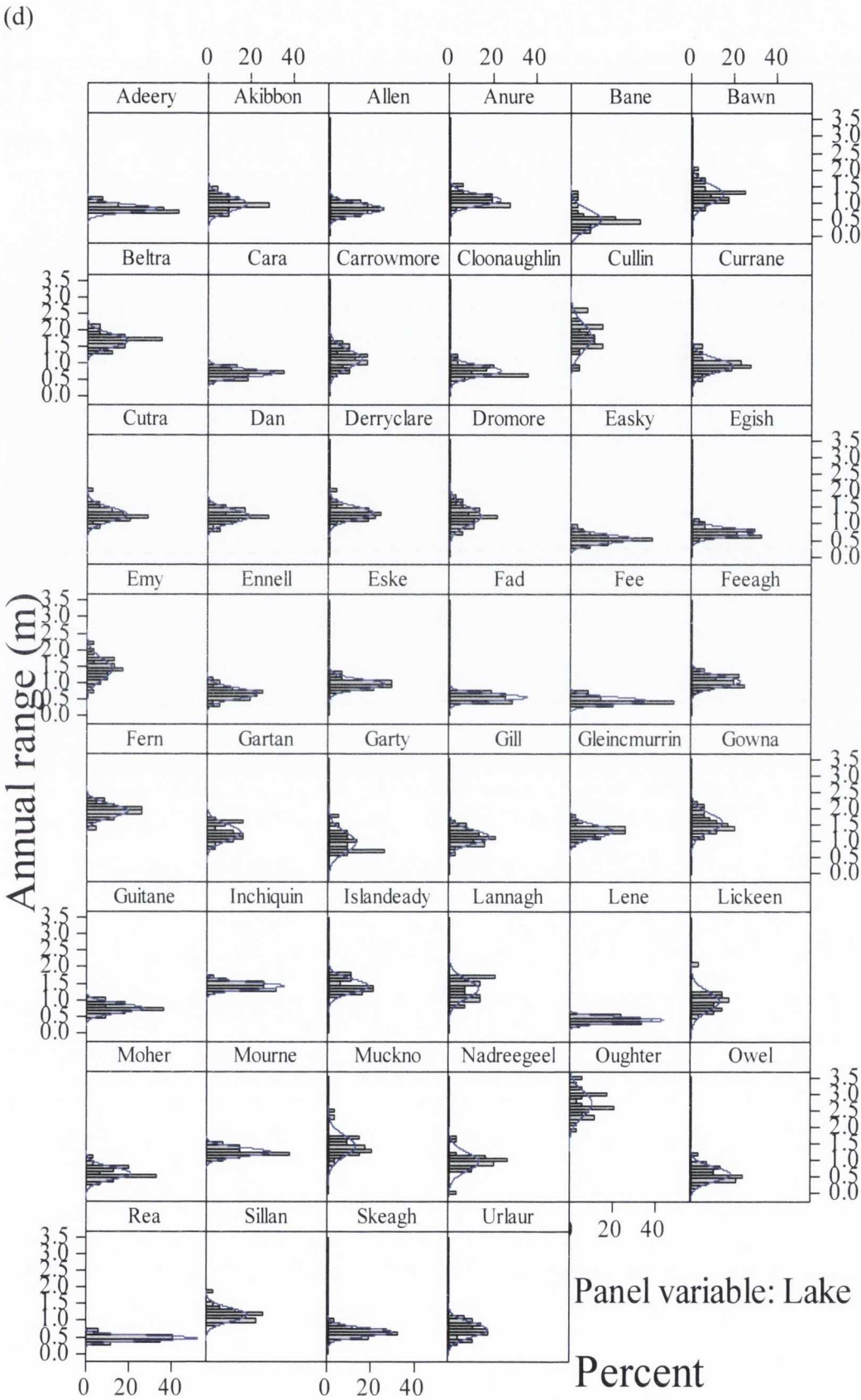


Fig.2.4. Percentage histograms for weekly (a), monthly (b), seasonal (c) and annual (d) water level ranges. All ranges are in meters.

The absolute maximum weekly range recorded was 2.03 m (Lough Cullin). The absolute maximum monthly, seasonal and annual ranges were recorded in Lough Oughter and were, respectively, 2.81 m, 3.47 and 3.47 m. The mean weekly range (WR) varied between 0.02 m in Loughs Lene and Owel and 0.33 m in Lough Fern (Table 2.2). The mean monthly amplitudes (MR) ranged from 0.07 m in Lough Lene to 0.85 m in Lough Fern. The overall mean seasonal (SR) and annual (AR) water level ranges were both lowest in Lough Lene (0.18 and 0.38 m, respectively) and greatest in Lough Oughter (1.57 m and 2.72 m, respectively; Table 2.2).

Table 2.2. Absolute mean range ($\pm$ S.D.) of water level fluctuations and range in the relative contribution (Relative Range, expressed as a percentage) of those values to the annual water level range of analysed lakes.

Timescale	Absolute mean range (m)	Relative range (%)
Weekly	0.02 ($\pm$ 0.14) - 0.33 ($\pm$ 0.26)	3 - 33
Monthly	0.07 ($\pm$ 0.04) - 0.85 ($\pm$ 0.39)	17 - 61
Seasonal	0.18 ($\pm$ 0.08) - 1.57 ($\pm$ 0.61)	44 - 81
Annual	0.38 ($\pm$ 0.09) - 2.72 ($\pm$ 0.38)	NA

The contribution of weekly, monthly and seasonal lake ranges to the annual amplitude differed greatly among lakes (Table 2.2; Fig. 2.5). Overall, the mean weekly range of each lake comprised between 3 and 33% of its annual range (WR_AR) with the extreme case of Lough Cullin where in 1989 it reached 77.5%. However, the largest variability was found at the monthly scale, where the relative contribution of monthly ranges varied between 17 and 61% (Table 2.2).

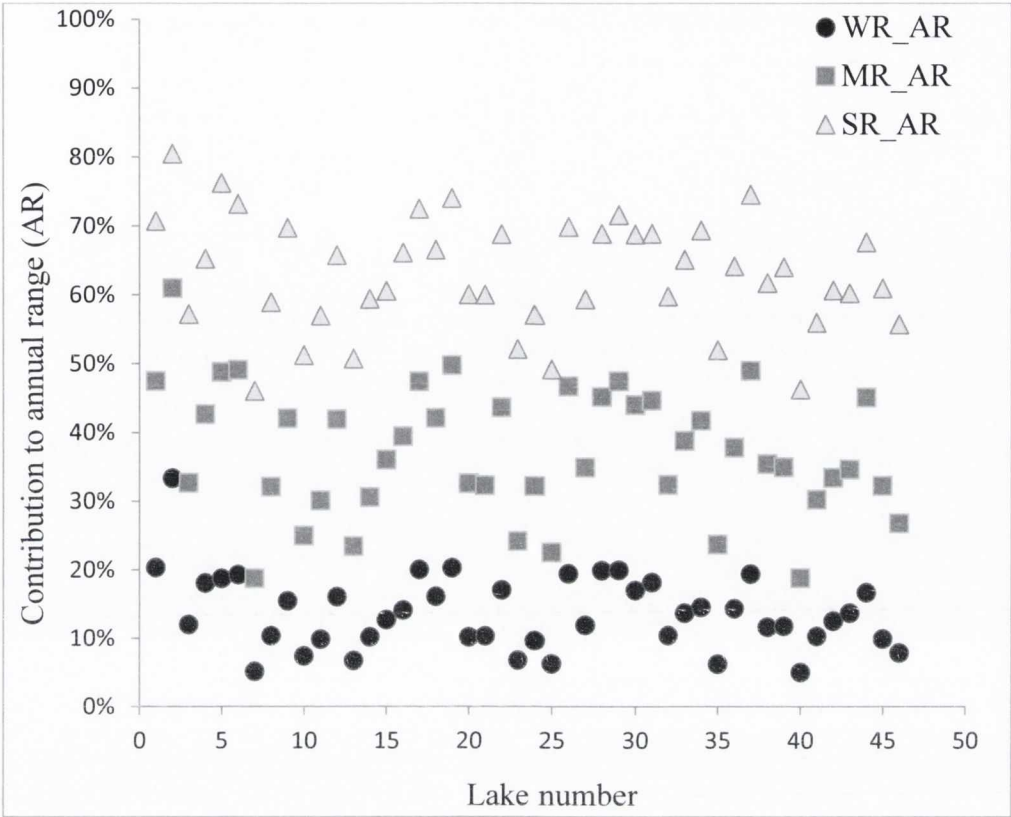


Fig. 2.5. Percent contribution of weekly (black circles), monthly (grey squares) and seasonal (light grey triangles) ranges to the annual range for each lake. Lake numbers are as in Table 2.1.

There was a consistent and pronounced seasonality in mean monthly water level across all lakes, but particularly those lakes that experienced higher water level fluctuations (with mean monthly and annual range in excess of, respectively, 0.45 and 1.00 m, Fig. 2.6).

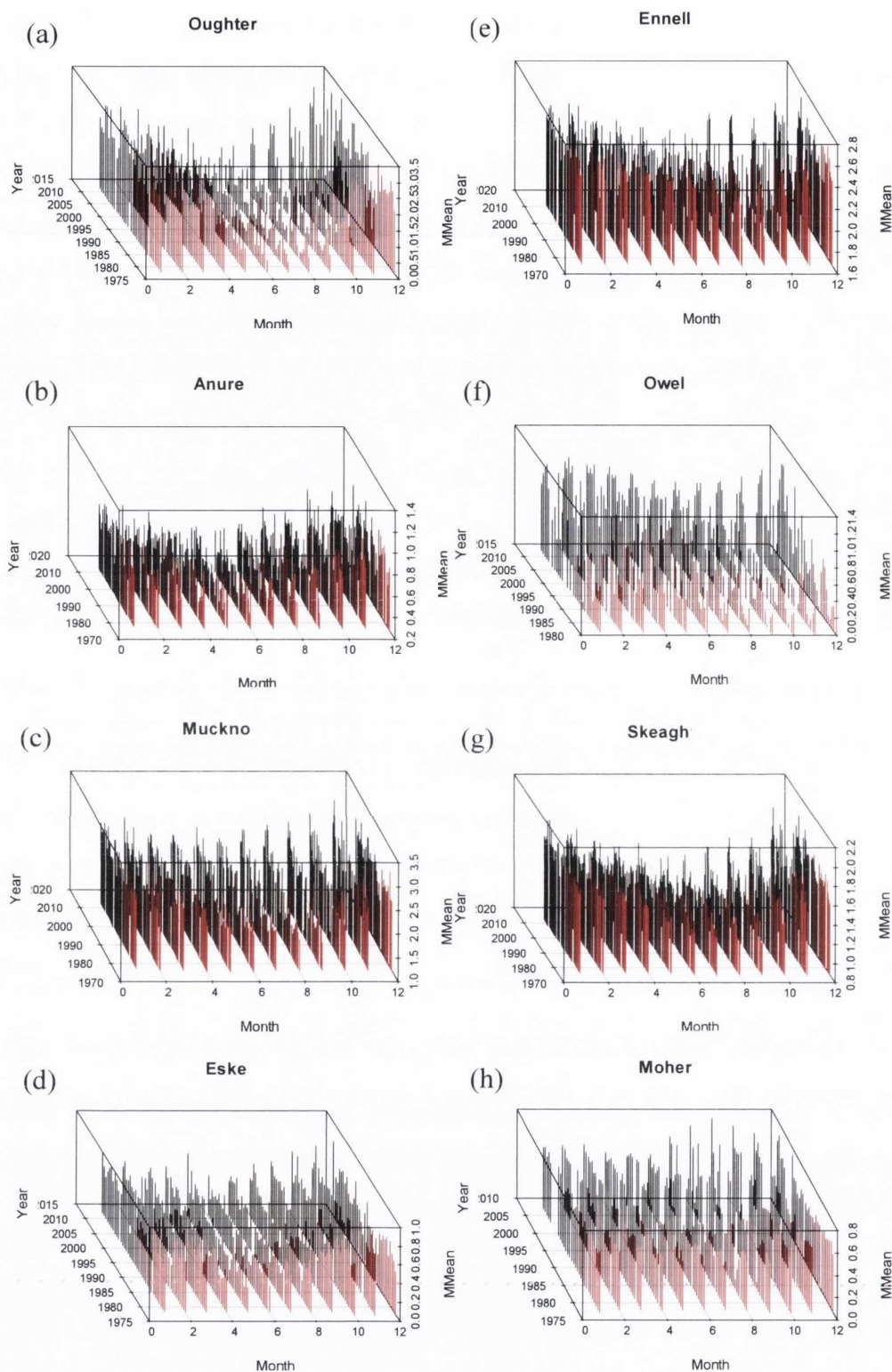


Fig. 2.6. Seasonal patterns in the mean monthly water level (MMean) in lakes experiencing relatively high (a-d) and low (e-h) water level fluctuations. Y-axes are scaled depending on the individual lake gauging stations.

In order to quantify the temporal rate of change water level fluctuations across time I have introduced the slope of the water level ranges, high water level index and low water level index for each of the 46 lakes. It was calculated as the slope of the equation of the mean weekly, monthly, seasonal and annual low or high water level indices, as well as ranges (Fig. 2.7).

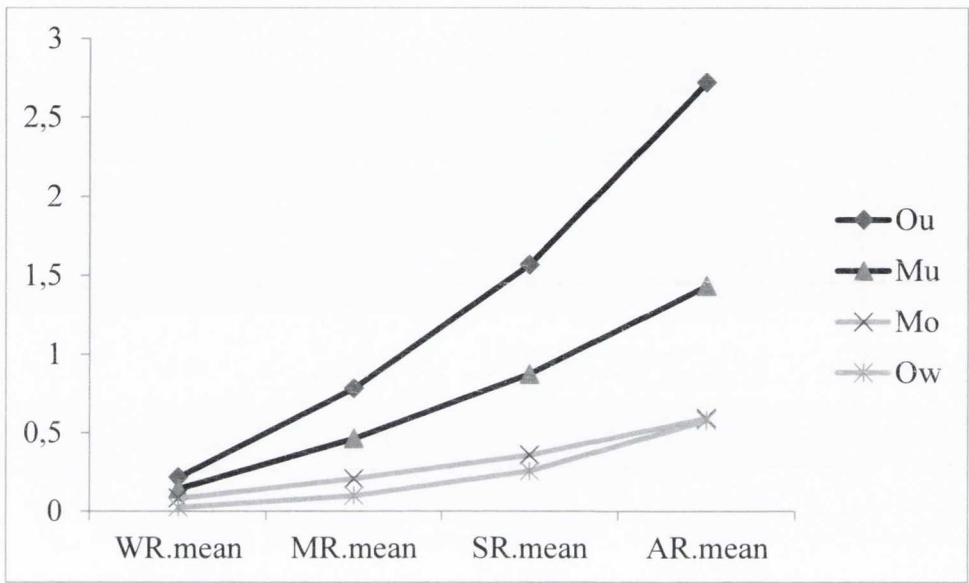


Fig. 2.7. Example of the temporal rate of change of water level ranges for two lakes (Oughter and Muckno) with high water level fluctuations (with black lines) and two lakes with low (Moher and Owel) water level fluctuations (grey lines). WR.mean; MR.mean; SR.mean and AR.mean stand for the mean weekly, monthly, seasonal and annual ranges.

2.3.2. Timing and magnitude of extreme events

The spatial and temporal distribution of water level regimes demonstrated varying degrees of cohesion in terms of reoccurrence of regular temporal patterns. I developed the mean water level index and the range index in order to study the behaviour of monthly and seasonal water level time series (see *Methods*). The mean monthly level typically declined in Spring and reached its lowest level in Summer (Appendix 2.4). Minimum was the mean monthly index in Lough Beltra for the months of June and July when the mean monthly water level was reduced by,

respectively, 51% and 50%. Highest was the monthly mean water level in winter, typically in December or January (reaching 53% above the average monthly water level in Lough Oughter), with a few exceptions (Appendix 2.4.). The seasonality in different lakes was manifested to a different degree. There were several lakes with great stability in mean monthly water level as demonstrated by relatively minor departures (*i.e.* less than 10 %) from the monthly mean throughout the year. These include Bane (+7% to -10%); Carra ($\pm 1\%$); Ennell (+7 to - 6%); Fee ($\pm 6\%$) and Gill (+9% to -10%) (Appendix 2.4). In general, the maximal monthly range was observed in October or December and the minimum in June or July (Fig. 2.8).

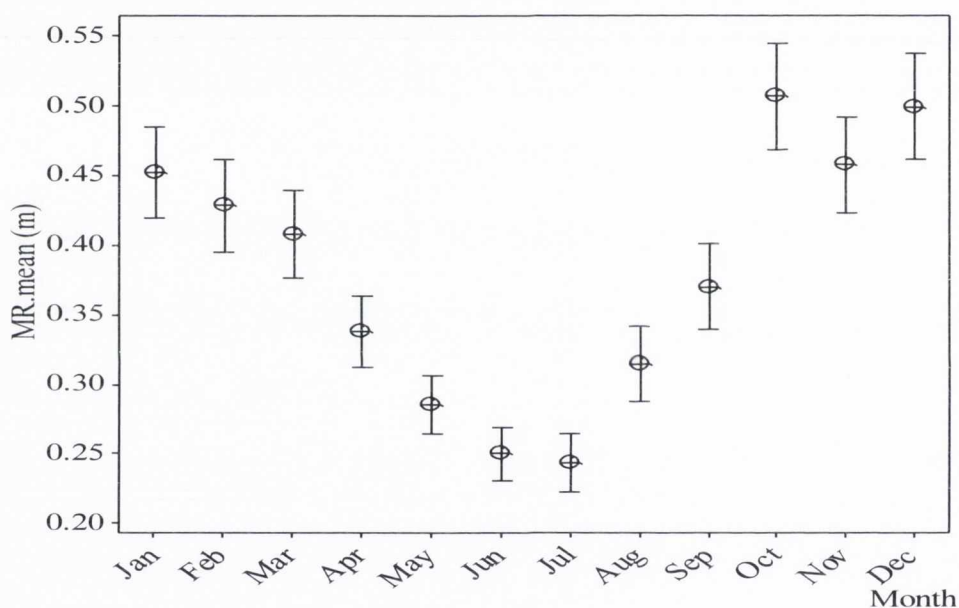


Fig. 2.8. Mean monthly range in water level ($\pm$ SD) across all 46 lakes studied.

For lakes with lower amplitudes of water level fluctuations (Appendix 2.3), the minimum monthly range was recorded also in April or May (Table 2.3). For instance, in Loughs Moher and Easky the mean monthly range index was lowest in April (lower by, respectively, 41% and 25%). In Lough Owel the mean monthly range was lowest in March by 26% on average (Table 2.3.).

Table 2.3. Monthly range index calculated as the ration of each monthly range to the overall mean monthly range. The blue and red colour coding correspond to, respectively, the minimal and maximal monthly range index for each lake.

Lake	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ad	0.99	0.96	1.07	0.80	0.71	0.88	0.96	1.17	1.25	1.11	1.10	1.01
Ak	1.22	1.17	0.97	0.76	0.58	0.55	0.60	0.71	1.22	1.59	1.29	1.30
Al	1.38	1.15	1.17	0.79	0.58	0.64	0.54	0.68	0.87	1.39	1.18	1.47
An	1.03	1.02	0.93	0.83	0.72	0.72	0.95	1.10	1.08	1.29	1.16	1.15
Bel	1.23	1.02	1.12	0.84	0.63	0.55	0.60	0.92	1.08	1.35	1.23	1.36
Bnl	1.03	0.89	0.88	0.81	0.87	0.84	0.98	1.42	1.14	0.91	1.12	1.18
Bw	1.40	1.23	1.20	0.95	0.61	0.54	0.40	0.66	0.75	1.39	1.26	1.63
Cl	1.30	1.11	1.17	0.95	0.80	0.63	0.80	0.82	1.02	1.14	1.05	1.24
Cr	1.27	1.21	1.12	0.95	0.81	0.61	0.65	0.56	0.82	1.41	1.24	1.28
Crw	1.10	1.17	1.06	0.98	0.78	0.55	0.64	0.89	1.04	1.42	1.16	1.23
Cul	1.41	1.33	1.20	0.83	0.68	0.44	0.34	0.65	0.70	1.45	1.33	1.62
Cur	1.20	1.18	1.21	1.17	0.68	0.52	0.82	0.57	0.82	1.12	1.07	1.30
Cut	1.25	1.18	1.09	0.84	0.78	0.65	0.56	0.84	0.99	1.25	1.22	1.35
Dan	1.24	1.20	1.17	0.80	0.84	0.56	0.56	0.80	1.00	1.25	1.20	1.38
Der	1.05	0.97	0.95	0.83	0.85	0.84	0.91	1.00	1.09	1.14	1.18	1.21
Dro	1.29	1.21	1.19	0.98	0.68	0.58	0.41	0.64	0.78	1.50	1.23	1.54
Eas	1.12	1.01	1.01	0.75	0.84	0.86	0.93	0.94	1.11	1.24	1.14	1.07
Eg	1.22	1.15	1.07	1.05	0.83	0.70	0.56	0.65	0.67	1.52	1.12	1.38
Em1	1.08	0.90	0.99	1.07	0.86	0.88	0.82	0.84	0.87	1.19	1.09	1.37
En	1.13	1.09	0.96	0.90	0.81	0.72	0.69	0.80	0.94	1.40	1.36	1.21
Es	1.13	1.07	1.04	0.75	0.74	0.70	0.81	0.97	1.12	1.27	1.17	1.22
Fad	1.11	0.99	0.89	0.77	0.89	0.76	0.83	1.10	1.09	1.30	1.05	1.17
Fee	1.17	0.96	0.97	0.87	0.79	0.77	0.76	0.93	1.12	1.21	1.30	1.15
Fer	1.18	1.22	1.00	0.87	0.65	0.62	0.68	0.88	1.06	1.38	1.19	1.23
Fgh	1.12	1.09	1.08	0.76	0.75	0.65	0.76	0.92	1.16	1.24	1.19	1.30
Gi	1.13	1.18	1.06	0.83	0.87	0.64	0.71	0.83	0.96	1.33	1.20	1.28
Gl	1.07	1.07	0.97	0.85	0.86	0.72	0.77	0.96	1.03	1.23	1.18	1.29
Go	1.14	1.19	1.10	1.06	0.84	0.64	0.51	0.65	0.84	1.46	1.25	1.35
Grn	1.06	1.16	1.07	0.86	0.69	0.71	0.75	0.92	1.17	1.31	1.11	1.21
Gry	1.30	1.14	1.13	1.04	0.67	0.53	0.42	0.67	0.82	1.40	1.15	1.54
Gu	1.18	1.14	1.04	0.82	0.82	0.70	0.46	0.72	1.06	1.29	1.48	1.43
In	1.13	1.07	1.13	0.81	0.66	0.61	0.67	0.93	1.09	1.27	1.23	1.33
Isl	1.25	1.26	1.01	0.88	0.73	0.62	0.46	0.78	0.89	1.54	1.17	1.41
La	1.29	1.48	1.15	0.86	0.51	0.52	0.49	0.66	0.80	1.69	1.35	1.27
Le	1.05	0.81	0.97	0.86	1.10	1.05	1.11	0.94	0.80	0.89	1.22	1.17

Lake	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Li	1.13	1.05	1.08	0.90	0.70	0.64	0.57	0.93	0.99	1.33	1.20	1.48
Mo	1.18	1.10	0.93	0.59	0.73	0.74	0.64	0.90	1.11	1.43	1.38	1.33
Mou	1.33	1.10	1.02	0.85	0.95	0.73	0.65	0.77	1.00	1.12	1.15	1.25
Mu	1.30	1.20	1.20	0.94	0.60	0.61	0.44	0.67	0.88	1.42	1.22	1.48
Na	1.29	1.13	1.03	1.00	0.83	0.62	0.44	0.69	0.77	1.51	1.40	1.18
Ou	1.08	1.16	1.14	1.10	0.86	0.66	0.45	0.78	0.88	1.38	1.19	1.27
Ow	1.38	0.90	0.74	0.83	0.90	0.99	1.08	1.05	0.91	0.90	0.99	1.25
Re	1.34	0.89	0.95	1.03	1.05	0.76	0.60	0.74	0.71	1.59	1.35	1.09
Sil	1.36	1.21	1.24	1.07	0.75	0.65	0.35	0.46	0.60	1.54	1.25	1.45
Sk	1.19	1.11	1.03	1.04	0.79	0.68	0.56	0.74	0.86	1.50	1.21	1.29
Ur	1.22	1.10	1.01	1.02	0.88	0.68	0.51	0.89	0.82	1.52	1.19	1.14

In the majority of the lakes (~80%) the lowest range was recorded in Summer when the seasonal range index was 41% lower overall than the mean seasonal water level, while for more than 90% of the lakes the highest was the seasonal range index in Winter (Table 2.4).

Table 2.4. Within-lake mean range indices at the seasonal temporal scale. The blue and red colour coding correspond to, respectively, the minimal and maximal monthly range index for each lake.

Code	Mean seasonal range index			
	Spring	Summer	Autumn	Winter
Ad	0.93	0.98	1.13	0.96
Ak	0.85	0.60	1.42	1.12
Al	0.91	0.66	1.22	1.17
An	0.87	0.97	1.17	0.99
Bel	0.96	0.75	1.15	1.10
Bn	0.77	1.14	0.98	1.10
Bw	0.95	0.60	1.21	1.25
Cl	1.01	0.81	1.08	1.10
Cr	1.03	0.60	1.34	1.04
Crw	1.02	0.70	1.25	1.04
Cul	1.03	0.48	1.18	1.30
Cur	1.07	0.65	1.08	1.14

Code	Mean seasonal range index			
	Spring	Summer	Autumn	Winter
Cut	0.92	0.75	1.22	1.11
Dan	0.98	0.73	1.14	1.15
Der	0.92	0.96	1.12	1.00
Dro	0.93	0.61	1.25	1.23
Eas	0.91	0.97	1.15	0.97
Eg	0.98	0.65	1.28	1.08
Em	0.99	0.83	1.15	1.03
En	0.83	0.84	1.30	1.04
Es	0.92	0.86	1.17	1.04
Fad	0.91	0.98	1.16	0.94
Fee	0.91	0.85	1.22	1.02
Fer	0.91	0.75	1.25	1.08
Fgh	0.90	0.80	1.18	1.11
Gi	0.99	0.78	1.17	1.05
Gl	0.94	0.89	1.13	1.04
Go	1.04	0.60	1.29	1.07
Grn	0.94	0.78	1.22	1.07
Gry	1.00	0.62	1.18	1.14
Gu	0.92	0.70	1.27	1.14
In	0.96	0.83	1.16	1.05
Isl	0.91	0.67	1.25	1.18
La	0.87	0.51	1.36	1.28
Le	0.98	1.06	0.90	1.05
Li	0.95	0.74	1.26	1.07
Mo	0.77	0.85	1.31	1.10
Mou	1.06	0.81	1.02	1.11
Mu	0.91	0.65	1.26	1.16
Na	1.05	0.56	1.34	1.04
Ou	1.09	0.64	1.20	1.07
Ow	0.74	1.08	0.84	1.32
Re	0.94	0.70	1.40	0.99
Sil	1.03	0.53	1.27	1.17
Sk	0.96	0.68	1.33	1.03
Ur	1.03	0.67	1.28	1.02

Even though the mean index of the seasonal range was generally lowest in Summer, there were a few discrepancies between the mean index of seasonal water level and

range (Appendix 2.5; Table 2.4). In contrast to mean seasonal water level, the seasonal range was highest mostly in Autumn, when it was up to 42% higher than the mean seasonal range (Fig. 2.9).

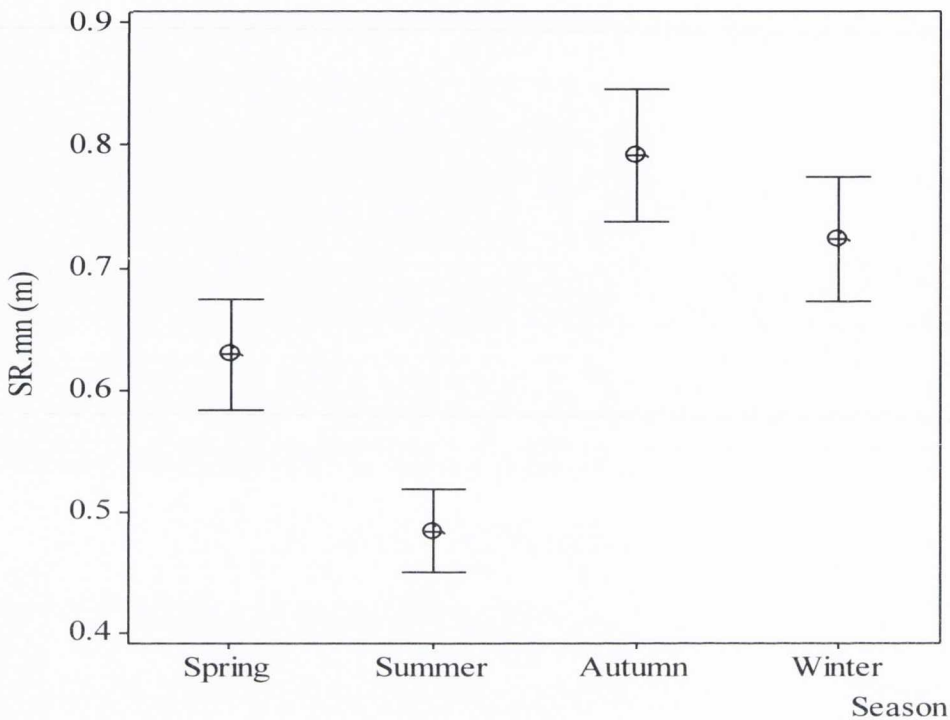


Fig. 2.9. Mean ($\pm$ SD) seasonal range (SR.mn) in water level across the 46 lakes studied.

2.3.3. Identification of key water level metrics

A set of 79 water level metrics, representing all five key components of water level regimes, was identified after excluding metrics with high VIFs and high correlation with other water level metrics. Subsequently, a parsimonious subset comprising 20 hydrological metrics was identified using principal component analysis (PCA). The first two principal components explained 74.3% of the variability in water level regimes among lakes and had eigenvalues higher than one and were, therefore, retained for further analysis. The third PC explained 7% and the fourth only 4% of the total variation and, thus, did not contribute further to the selection of metrics. All selected metrics had eigenvector loadings in excess of 0.7 on either PC1 or PC2 (Table 2.5).

Fifteen variables (representing all five facets) had eigenvector loadings in excess of 0.7 on PC1. All magnitude metrics, except for the monthly spread of the range of water level in December, had negative loadings (Table 2.5). The highest was the contribution of the high water index in Summer and the variation of the high water index in Spring and in Winter (Fig. 2.10). Particularly positive loadings on PC1 included the frequency of extremely high water level events (as defined by the value of the mean daily water level above the 90th percentile) in February (which was also a proxy for the winter season) and the variation in events with extremely low levels annually (below the 10th percentile) and in very rare extremely high annual spells (exceeding the 99th percentile). All of these water level metrics reflect or quantify mostly relatively rapid changes in water level regimes.

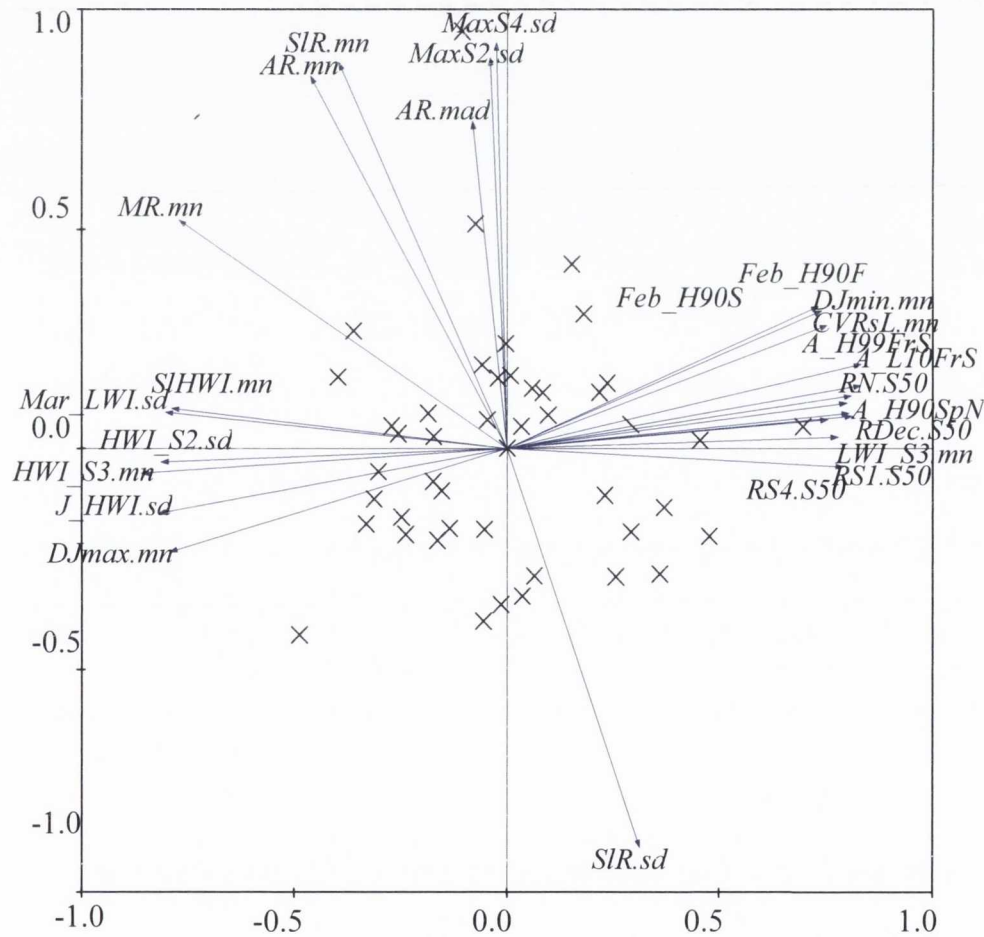


Fig. 2.10. Ordination of the principal component analysis for 46 lakes (crosses) based on the 20 selected water level metrics (vectors). For description and calculations of metrics see Appendix 2.2. Metric abbreviations as in Table 2.5.

Table 2.5. Results of principle component analysis variable reduction procedure for identification of water level metrics best describing water level regimes. The metrics were standardised and centered prior to analysis. Metrics with eigenvector loadings in excess of 0.7 are marked in bold. For description and calculations of metrics see Appendix 2.2.

WL regime component	Water level metric	Eigenvector loading	
		PC1	PC2
Magnitude	Mean monthly range (MR.mn)	-0.77	0.53
	SD of January high water index (J_HWI.sd)	-0.84	-0.14
	SD of March low water index (Mar_LWI.sd)	-0.81	0.08
	Spread of December range (RDec.S50)	0.80	0.10
	SD of maximal Spring level (MaxS2.sd)	-0.04	0.88
	SD of Spring high water index (HWI_S2.sd)	-0.83	-0.02
	Mean Summer high water index (HWI_S3.mn)	-0.88	-0.04
	SD of maximal Autumn level (MaxS4.sd)	-0.05	0.91
	Mean annual range (AR.mn)	-0.46	0.85
Frequency	Frequency of February high water extreme events (Feb_H90Fr)	0.73	0.34
	SD of annual frequency of low water extreme events (A_L10FrSd)	0.79	0.13
	SD of annual frequency of high water extreme events (A_H99FrSd)	0.82	0.15
Duration	CV of mean length of rise events (CVRsL.mn)	0.84	0.22
Timing	Day of the year on which maximum water level occurs (DJmax.mn)	-0.79	-0.26
	Day of the year on which minimum water level occurs (DJmin.mn)	0.75	0.30
	Number of February high water level events (Feb_H90SpN)	0.73	0.36
	Annual number of high water level events (A_H90SpN)	0.80	0.07
Rate	Slope of the mean weekly, monthly, seasonal and annual ranges (SlR.mn)	-0.39	0.88
	Temporal rate of change for high water level index (SlHWI.mn)	-0.83	0.09
	SD of slope of temporal rate of change in ranges (SlR.sd)	0.32	-0.91

The variation explained by PC2 could be attributed mostly to water level metrics related prevalently to the (annual) amplitude of water level regimes and the rate of change (Table 2.5). The variation in seasonal water levels and annual mean range loaded strongly on PC2, as did the temporal rate of change in range as measured by the slope of the ranges (Table 2.5, Fig. 2.10). Thus it could be speculated that PC2 reflects mostly the buffering capacity of the lakes and their water level regimes.

2.3.4. Relating water level regime and catchment characteristics

Mean catchment slope and its standard deviation, as well as catchment area and total length of upstream tributaries were correlated strongly as demonstrated by high variance inflation factors. The standard deviation of mean catchment slope and the total length of upstream tributaries were therefore not considered for the quantile regression models. The AICc-based model selection procedure identified five candidate models with $\Delta_i \leq 2$, relating principal component PC1 to catchment and landscape characteristics (Table 2.6). The ratio between the lake surface area and the area of lake catchment was present in all five candidate models (Table 2.6). The PC1 data supported the first two models as identified by AICc and Akaike weights. In compliance with the parsimony principle and based on evidence ratios, Model 2 was selected as the best model (of this set of models).

There were two potential models with delta $\Delta_i \leq 2$ relating PC2 to landscape and catchment characteristics (Table 2.6). The model most parsimoniously explaining patterns in water level variation, as represented by the second principal component, included lake surface area and catchment area (Table 2.6). Quantile regression models revealed significant direct relationships between PC1 the ratio of lake surface area and catchment area and between PC2 and catchment area. Furthermore, there was a significant inverse relationship between PC2 and lake surface area (Table 2.7).

Table 2.6. Relating water level metrics to catchment characteristics: model selection for PC1 and PC2, based on the corrected Akaike Information Criterion (AICc) and evidence ratio of Akaike weights (ω_i). K denotes the number of parameters included in the model and $\Delta_i = \text{AICc}_i - \text{AICc}_{\min}$. The AICc value for the corresponding null model (*i.e.*, with the overall mean as the only model parameter) is also given in bold for comparison. The most parsimonious models are in italics.

Candidate models	K	AICc	Δ_i	ω_i
PC1 (AICc_{null}= 137.5)				
<u>Model 1</u> : Ratio of lake area to catchment area (SA_CA); Mean catchment slope	3	124.9	0	0.28
<i>Model 2: Ratio of lake area to catchment area</i>	2	<i>125</i>	<i>0.12</i>	<i>0.27</i>
<u>Model 3</u> : Ratio of lake area to catchment area; Lake surface area	3	125.9	0.94	0.18
<u>Model 4</u> : Ratio of lake area to catchment area; Mean catchment slope; Lake surface area	4	126	1.1	0.16
<u>Model 5</u> : Ratio of lake area to catchment area; Catchment area	3	126.9	1.96	0.11
PC2 (AICc_{null}=132.3)				
<u>Model 1</u> : Shoreline length; Lake surface area; Catchment area	4	119.1	0	0.67
<i>Model 2: Lake surface area; Catchment area</i>	3	<i>120.5</i>	<i>1.41</i>	<i>0.33</i>

Table 2.7. Results of quantile regressions testing for an effect of catchment and landscape attributes on water level regimes (quantified through the first two principal components). Quantile models are fit to the selection of explanatory variables based on the best candidate models for each response variable. Significant effects are highlighted in bold.

Response variable	Source of variation	Parameter estimates	<i>t</i> - value	<i>p</i>
PC1	Intercept	-0.779	-2.53	0.015
	Ratio of lake surface area to catchment area	8.380	3.26	0.002
PC2	Intercept	-0.357	-1.28	0.208
	Catchment area	0.0001	3.30	0.002
	Lake area	-0.001	-2.78	0.008

The ranges of water level data across all temporal scales, including the temporal rate of change of ranges, supported models including the ratio between the surface area of individual lakes and their catchment area. Minimal was AICc for models for slope of ranges across time when lake and catchment area were included as well as. In addition, lake and catchment areas appeared in the best models relating monthly and seasonal ranges with catchment attributes, while shoreline length was present in the best model for annual range (Table 2.8).

Quantile regression identified the significance level of regression coefficients for the best models for each of the selected principal components (Table 2.9). The models all revealed significant reverse relationships between lake weekly, monthly, seasonal and annual ranges and the ratio of lake surface area and catchment area. This relationship was bordering on statistical significance for the temporal rate of change in ranges.

Table 2.8. Candidate models relating selected amplitude water level metrics to catchment characteristics. All models presented have $\Delta_i \leq 2$ from the minimal model and > 2 from the null model (given in bold). K denotes the number of parameters included in the model; ω_i - Akaike weights of the i^{th} model and $\Delta_i = AICc_i - AICc_{min}$. The AICc value for the corresponding null model (*i.e.*, with the overall mean as the only model parameter) is also given in bold for comparison. The most parsimonious models are in italics.

Candidate models	K	AICc	Δ_i	ω_i
Weekly range ($AICc_{null} = -96.8$)				
<i>Model 1: Ratio of lake area to catchment area</i>	2	-131.7	0	0.192
<i>Model 2: Ratio of lake area to catchment area; Catchment area</i>	3	-131.1	0.55	0.145
<i>Model 3: Ratio of lake surface area to catchment area; Shoreline length; Catchment area</i>	4	-130.4	1.21	0.105
<i>Model 4: Ratio of lake area to catchment area; Shoreline length</i>	3	-130.2	1.49	0.091
<i>Model 5: Ratio of lake area to catchment area; Catchment area; Lake surface area</i>	4	-130	1.69	0.082
Monthly range ($AICc_{null} = -11.8$)				
<i>Model 1: Ratio of lake area to catchment area; Catchment area; Lake surface area</i>	4	-59.8	0	0.469
Seasonal range ($AICc_{null} = 28.2$)				
<i>Model 1: Ratio of lake area to catchment area; Catchment area; Lake surface area; Shoreline length</i>	5	-29.8	0	0.544
<i>Model 2: Ratio of lake area to catchment area; Catchment area; Lake surface area</i>	4	-27.8	1.98	0.202
Annual range ($AICc_{null} = 61.3$)				
<i>Model 1: Ratio of lake area to catchment area; Catchment area; Lake surface area; Shoreline length</i>	5	-0.4	0	0.726
Slope range ($AICc_{null} = -49.2$)				
<i>Model 1: Ratio of lake area to catchment area; Catchment area; Lake surface area; Shoreline length</i>	5	-93.8	0	0.348
<i>Model 2: Ratio of lake area to catchment area; Catchment area; Lake surface area</i>	4	-93.6	0.14	0.324
<i>Model 3: Ratio of lake area to catchment area; Catchment area; Lake surface area; Mean catchment slope</i>	5	-92.4	1.37	0.175

Table 2.9. Results of quantile regressions testing for an effect of catchment and landscape characteristics on water level ranges at different temporal scales. Quantile models are fit to the selection of explanatory variables based on the best candidate model. Significant effects are highlighted in bold.

Response variable	Source of variation	Parameter estimates	<i>t</i> -value	<i>p</i>
Weekly range (WR)	Intercept	0.201	9.01	≤0.0001
	Ratio of lake surface area to catchment area	-0.839	-3.95	0.0003
Monthly range (MR)	Intercept	0.502	7.55	≤0.0001
	Ratio of lake area to catchment area	-1.601	-4.54	0.002
	Catchment area	0.00001	1.13	0.266
	Lake surface area	-0.00009	-1.35	0.183
Seasonal range (SR)	Intercept	0.712	9.25	≤0.0001
	Catchment area	0.00002	2.71	0.010
	Lake surface area	-0.00022	-2.22	0.032
	Ratio of lake area to catchment area	-1.708	-2.76	0.009
Annual range (AR)	Intercept	1.047	15.03	≤0.0001
	Catchment area	0.00003	3.27	0.002
	Lake surface area	-0.0005	-2.54	0.015
	Ratio of lake area to catchment area	-2.101	-3.35	0.002
	Shoreline length	0.006	1.19	0.239
Slope ranges (SIR)	Intercept	0.291	10.38	≤0.0001
	Catchment area	0.00001	3.74	0.001
	Lake surface area	-0.0002	-2.20	0.034
	Ratio of lake area to catchment area	-0.451	-1.93	0.060

The best model relating the frequency of monthly low (below the 10th percentile) and high (exceeding the 90th percentile) water level events, identified by the minimal

AICc and Akaike weights, included shoreline length, and the ratio between lake surface area and catchment area for the frequency of low water level events (Table 2.10). Three models explained the relationship between the seasonal frequency of extreme low events and catchment characteristics equally well. They included the ratio between lake and catchment area or catchment area, as well as the shoreline length or catchment slope (Table 2.10).

Table 2.10. Candidate models relating selected extreme events water level metrics to catchment characteristics. K denotes the number of parameters included in the model; ω_i - Akaike weights of the i^{th} model and $\Delta_i = AICc_i - AICc_{min}$. The AICc value for the corresponding null model (*i.e.*, with the overall mean as the only model parameter) is also given in bold for comparison. The AICc value for the corresponding null model (*i.e.*, with the overall mean as the only model parameter) is also given in bold for comparison. The most parsimonious models are in italics.

Candidate models	K	AICc	Δ_i	ω_i
Jul_Low10Frequency (AICc_{null}= 216.4)				
<i>Model 1: Ratio of lake surface area to catchment area; Shoreline length</i>	3	209.3	0	0.244
Model 2: Ratio of lake area to catchment area; Lake surface area	3	209.7	0.37	0.203
Model 3: Ratio of lake area to catchment area; Lake surface area; Mean catchment slope	4	210.3	0.93	0.154
Model 4: Ratio of lake area to catchment area; Lake surface area; Shoreline length	4	210.4	1.05	0.144
Model 5: Ratio of lake area to catchment area; Shoreline length; Mean catchment slope	4	210.5	1.14	0.138
Model 6: Ratio of lake area to catchment area; Lake surface area; Shoreline length; Mean catchment slope	5	210.8	1.48	0.117
Dec_High90Frequency (AICc_{null}= 187.5)				
Model 1: Shoreline length; Mean catchment slope	3	181.5	0	0.207
Model 2: Lake surface area; Shoreline length; Mean catchment slope	4	181.8	0.3	0.178
Model 3: Ratio of lake area to catchment area; Shoreline length; Mean catchment slope	4	182.4	0.89	0.133

Candidate models	K	AICc	Δ_i	ω_i
<u>Model 4</u> : Lake surface area; Shoreline length	3	182.7	1.12	0.118
<u>Model 5</u> : Ratio of lake surface area to catchment area; Shoreline length	3	183	1.45	0.1
<u>Model 6</u> : Ratio of lake area to catchment area; Mean catchment slope; Shoreline length; Lake surface area	5	183.2	1.63	0.092
<u>Model 7</u> : <i>Shoreline length</i>	2	183.2	1.63	0.092
<u>Model 8</u> : Ratio of lake area to catchment area; Lake surface area; Shoreline length	4	183.4	1.89	0.08
Summer_Low10Freq (AICc_{null}= 275.8)				
<u>Model 1</u> : Ratio of lake area to catchment area; Shoreline length; Mean catchment slope	4	267.9	0	0.124
<u>Model 2</u> : Ratio of lake area to catchment area; Mean catchment slope; Lake surface area	4	268.7	0.73	0.086
<u>Model 3</u> : Ratio of lake area to catchment area; Catchment area; Mean catchment slope	4	268.8	0.82	0.082
<u>Model 4</u> : <i>Ratio of lake area to catchment area; Mean catchment slope</i>	3	269	1.1	0.072
<u>Model 5</u> : Ratio of lake area to catchment area; Shoreline length	3	269.2	1.23	0.067
<u>Model 6</u> : Catchment area; Mean catchment slope	3	269.5	1.52	0.058
<u>Model 7</u> : Ratio of lake area to catchment area; Shoreline length; Mean catchment slope; Lake surface area	5	269.5	1.57	0.056
<u>Model 8</u> : Ratio of lake area to catchment area; Catchment area	3	269.6	1.62	0.055
Autumn_High90Freq (AICc_{null}= 257.1)				
<u>Model 1</u> : Ratio of lake area to catchment area; Shoreline length; Mean catchment slope; Catchment area; Lake surface area	6	227.8	0	0.188
<u>Model 2</u> : Ratio of lake area to catchment area; Catchment area; Mean catchment slope	4	227.9	0.06	0.188
<u>Model 3</u> : <i>Ratio of lake area to catchment area; Catchment area</i>	3	228	0.25	0.166
<u>Model 4</u> : Ratio of lake area to catchment area; Catchment area; Lake surface area; Shoreline length	5	228.5	0.73	0.131
<u>Model 5</u> : Ratio of lake area to catchment area; Lake surface area; Catchment area; Mean catchment slope	5	228.8	1.02	0.113
<u>Model 6</u> : Ratio of lake area to catchment area; Catchment area; Lake surface area	4	229.5	1.72	0.079

There was an inverse relationship between low water level frequencies in July and the ratio of the lake area to catchment area (Table 2.11). Furthermore, the relationship between shoreline length and the frequency of both extreme low and high water events was consistently positive indicating higher frequency of floods and droughts in lakes with longer shoreline (Table 2.11).

Table 2.11. Results of quantile regressions testing for an effect of catchment and landscape characteristics on water level metrics quantifying the frequency of extreme monthly events. Quantile models are fit to the selection of explanatory variables based on the best candidate model. Significant effects are highlighted in bold.

Response variable	Source of variation	Parameter estimates	t- value	p
Jul_Low10 Frequency	Intercept	7.912	10.87	≤0.0001
	Ratio of lake area to catchment area	-17.718	-1.95	0.057
	Shoreline length	0.029	1.34	0.188
Dec_High90 Frequency	Intercept	6.472	13.32	≤0.0001
	Shoreline length	0.030	1.87	0.068
Summer_ Low10Freq	Intercept	23.833	9.93	≤0.0001
	Ratio of lake area to catchment area	-38.230	-2.03	0.048
	Mean catchment slope	-0.023	-0.07	0.945
Autumn_ High90Freq	Intercept	14.724	15.57	≤0.0001
	Catchment area	-0.0002	-2.44	0.019
	Ratio of lake area to catchment area	-45.111	-6.43	≤0.0001

The results from the quantile regression models for the investigated water level metrics demonstrated that there was a significant relationship between each of the selected nine metrics and the catchment characteristics. Most notable is the importance of the ratio of the lake surface area and catchment area with *p*-values indicating significance in six of the cases and bordering on significance in the other two (Tables 2.9 and 2.11).

2.4. Discussion

Magnitude and variability of water level fluctuations

My results demonstrate great variability in water levels: in some lakes they fluctuate around a mean over long periods of time with gradual changes, while others exhibit considerable short-term or long-term variations. Seasonal patterns were, however, apparent in the monthly and seasonal time series for all lakes. My findings indicate extensive within and among lake variation in water level regimes, which also vary among temporal scales, with amplitudes ranging from 0.02 m per week to 3.47 m per year. Weekly, monthly and seasonal ranges had different contributions to the annual range for each lake with greatest relative variability found at monthly scales. The latter could be ascribed to the notable monthly intra-annual differences identified for most lakes through the monthly range index. In addition, the peakedness of the probability distribution of water level amplitudes could be used as a measure of stability in fluctuations. Lakes with high kurtosis of their ranges were characterised with more stable water level fluctuations. Their ranges were clustered around the mean and rapidly departing from it towards the tails, while flat-toppedness of the probability distribution of the time series demonstrated greater variability in the ranges without a distinct peak in the data. There was no distinct pattern of the peakedness of water level ranges across temporal scales. In some cases, high kurtosis for weekly and annual ranges was associated with low flat-toppedness in monthly and seasonal ranges, while in some lakes the high peakedness in the weekly range was complemented by low kurtosis for annual and seasonal ranges.

These findings highlight a need to acknowledge the importance of variation in water levels at multiple temporal scales. Understanding the link between hydrological processes (changes in water level in particular) and their potential impacts on aquatic systems thus requires an approach that incorporates quantifying hydrological measures across time. The inclusion of metrics representing only one temporal scale could, therefore, yield incomplete and inaccurate conclusions and management decisions, whereas the incorporation of variability at different temporal scales could improve our ability to describe and quantify water level regimes, and thus serve as an important rational basis not only for studying the relationships between hydrology

and lake ecology but also for setting efficient water level management strategies and targets (Kennard et al. 2010b).

Seasonality and extreme events

Regardless of the high variability among lakes, I found pronounced seasonality in water level regimes in all lakes examined. Spatial and temporal distribution of water level regimes demonstrated varying degree of cohesion in terms of reoccurrence of regular temporal patterns. I introduced the mean water level index and the range index in order to study the behaviour of the monthly and seasonal water level time series. Typically, the lowest mean monthly levels and ranges were recorded in Summer and the highest monthly levels in Winter, while the highest monthly ranges occurred in October or December with greatest overall seasonal amplitude taking place in autumn. Monthly and seasonal differences and patterns were more notable in lakes with higher water level fluctuations. These findings may have repercussions for ecosystem health or monitoring programs and scientific field-sampling. Moreover, extreme events may lead to erosion and reduction in the structural variability and habitat availability of benthic substrates (Prus *et al.* 1999, Valdovinos *et al.* 2007) and thus modify lake bed morphology and the physical structure of aquatic environments (Hellsten *et al.* 1996, Lake *et al.* 2000, Nowlin *et al.* 2004). Further, extreme water level fluctuations are known to have detrimental effects on aquatic ecosystems *e.g.* Schmieder *et al.* (2004) demonstrated that extreme flood resulted in loss of approximately $\frac{1}{4}$ of reed beds in Constance lake or of macrophytes in general (Rorslett 1984, Furey *et al.* 2004, Propastin 2008, Deegan *et al.* 2012).

Furthermore, my results have broad implications for risk assessment, water resource management and provision of ecosystem services and maintaining of ecosystem health. For instance, identifying the timing of extreme water levels and maximal amplitudes is crucial for flood control and protection (Fitzpatrick & Bree 2001, Brown *et al.* 2010), and could aid assessment of water availability for agriculture (Kosarev & Yablonskaya 1994) or estimation of fish breeding success (Graynoth 1999, Brunberg & Blomqvist 2003, Okun *et al.* 2005, Okun & Mehner 2005) and thus lead to the reduction of economic and societal risks owing to extreme water level fluctuations. My findings may serve also as a basis for optimising cost-effective

sampling procedures by choosing the most adequate timing or resolution of sampling depending on the study objectives.

Climate change scenarios for Ireland project with high confidence an increase of 20% in rainfall in December and January and decrease or no change for summer months (McGrath et al. 2005), as well as amplification of the seasonal stream flow cycle (Steele-Dunne et al. 2008) and an overall increase of 40% in runoff (Charlton et al. 2001). This, coupled with the greater risk of flooding in winter and intensification in the global water cycle (McGrath et al. 2005, IPCC 2007, Durack et al. 2012), will amplify further existing interannual differences in water levels with important knock-on effects for the integrity of aquatic ecosystems.

Water level metrics

My efforts to characterise lake water level regimes considered measures at different temporal resolutions (from daily to annual) and were based on a robust selection procedure by which, from an initial set of 915 water level metrics (WLM), a non-redundant subset of 20 key metrics were identified. The selected metrics incorporated the five main components of water level regimes and accounted for a vast amount of the variability in water level regimes. Richter *et al.* (1998) while studying the biological implications of river flow regimes, emphasized that each of these key components could elicit particular ecosystem responses. Quantifying (alterations in) water level regimes in this way may, therefore, enable us to independently and explicitly consider the ecological consequences of a particular disturbance altering one or more of the key components of water level fluctuations.

It is important to note that, owing to the fact that all of the 915 metrics were calculated based on the same dataset; the degree of correlation among many variables was very high. Beyond the water level metrics used to describe and quantify water level regimes in the studied lakes, there were other potential water level metrics that could have been included. This suggests that many of the proposed metrics were a proxy for a set of other relevant ones and should be considered only a basis for the selection of hydrological metrics that needs to be used in conjunction with an intuitive and purpose-driven metrics selection approach. These findings therefore

need to be tested using independent data and incorporated in future studies of hydrology of lakes or of the effects of water level fluctuations on lake biota.

This study nonetheless provides important information on which water level metrics could be used to maximise use of available water level data while minimising redundancy in effectively describing and quantifying water level regimes. It highlights the importance of the variation, monthly frequency and timing of extreme events, as well as the water level metrics quantifying flooding events in explaining a considerable proportion of the variation in water level regimes. I proposed an integrated novel measure of temporal rate of change in water level amplitudes which links the range of water level fluctuations across the different temporal resolutions (slope of range), that proved to be of high significance for the grouping of the lakes as demonstrated by the PCA analysis.

Relating water level regimes and the physical attributes of lakes

Freshwater systems are long known to be affected by catchment and landscape in general (Leopold 1941). Catchment is a basic organising unit for understanding and managing ecosystem processes (Brown *et al.* 2010) and conservation efforts need to be aimed at whole-catchment management (Saunders *et al.* 2002). Furthermore, freshwater systems are defined largely by their hydrology, and hydrological regimes could be thought as of result of the complex natural processes which operate on a catchment scale (Smakhtin 2001). Therefore, an important contribution of this study was to elucidate associations between catchment characteristics and the hydrological regimes of lakes. I found highly significant associations between catchment characteristics and each of the five components of lake hydrological regimes (represented by a total of 20 water level metrics). The ratio of lake surface area: catchment area appears to be a particularly important driver of the amplitude of water level fluctuations across a range of temporal scales. The ratio between lake and catchment area could be used as a proxy for the flushiness of the lake or its residence time (Kaste *et al.* 2003), *i.e.* the time required to refill an empty lake with its natural flow. My results indicate that lakes with catchments that are disproportionately large in relation to their surface area are characterised by higher monthly and annual ranges, which is in accordance with the findings of Hill *et al.* (1998). These lakes

could be more sensitive to climatic conditions as they lack the buffering role of larger relative lake area.

Furthermore, the frequency of monthly and seasonal extreme water levels was frequently mediated by shoreline length or catchment slope. This is to be expected as the longer the shoreline and the greater the slope, the more abrupt and pronounced the effects of intensive precipitations and greater runoff. The hydrologic cycle describes the movement of water across the land and, in combination with other geological processes, determines many of the physical characteristics of the habitat (Dodds 2002). Moreover, as water levels are affected by the global water cycle, the expected intensification in the seasonal pattern of water level in lakes might exacerbate considerably the variability of water level fluctuations on a global scale with direct effects on the physical characteristics of lakes and knock-on effects on habitat availability. A potential intensification in seasonal patterns and therefore an increase in annual range will affect not only the physical environment but also breeding and feeding grounds by shifting the terrestrial-aquatic interface in lakes. It might also trigger cumulative local-scale effects such as alteration of sediment loading or the input of detritus, nutrients and organic matter from the riparian zone, modifying the energy pathways at the land-lake interface, affecting benthic littoral communities (Baumgärtner *et al.* 2008, Hofmann *et al.* 2008, Wantzen *et al.* 2008b), and thus affecting whole landscapes.

The number of multi-lake studies on changes in water levels is limited. Smith *et al.* (1987) studied physical conditions, macrophytes and macroinvertebrates in the littoral zones of 27 Scottish lochs with different regimes of water-level variations. There are a few studies focusing on the impact of water levels, rather than on measuring the pressure itself (*e.g.* Beklioglu 2007, Valdovinos *et al.* 2007, Aroviita & Hämäläinen 2008). This is the first multi-lake study that I am aware of that provides comprehensive metric-based quantification of multi-decadal temporal (from daily through weekly, monthly, seasonal and annual) and spatial variability in water level regimes of lakes. In a single-lake study Yin & Yang (2012) investigated the alteration of water level regime using pre- and post-impacted frequency histograms. Their study incorporated only 25 water level metrics as opposed to 915 and was conducted across monthly and annual temporal scales.

In order to protect and manage water resources in Europe in a sustainable manner, the European Parliament has adopted the Water Framework Directive (WFD; 2000/60/EC). It requires the achievement of good ecological and chemical status for all surface waters by 2015. As stated in Annex V of the WFD, the elements of hydromorphology supporting the biological elements comprise hydrological regime and morphological conditions. The procedure proposed in this chapter may serve as a foundation for a solid assessment of disturbances by hydromorphological pressures which is crucial for the achievement of the environmental objectives set by the WFD.

Another novelty of my work is that it pinpoints the underlying relationship between water level regime and landscape characteristics, as well as, it proposes a protocol for the identification of potentially more vulnerable to hydrological stress systems. The recognition of probable risks at an early stage could be crucial for preventing ecosystem degradation and for guiding efforts to restore or maintain ecosystem integrity and biological diversity. The identified water level metrics could be incorporated in lake management and policy making and have the potential to derive a methodology identifying potential risks for the hydrology of lakes based on their lake morphometrics or catchment and landscape characteristics.

3. Amplified Water Level Fluctuations Alter Ecosystem Structure and Functioning



Various stages of the mesocosm experiment

3.1. Introduction

Diminishing global water reserves is rapidly becoming a key driver of water, food and energy insecurity (International Bank for Reconstruction and Development 2010, Vorosmarty *et al.* 2010, Zucco *et al.* 2011). Growing water scarcity is owing not only to increased water demand but also to increased rates of environmental degradation and pollution (Johnson *et al.* 2001). There is, therefore, increasing concern about freshwater availability worldwide (Vorosmarty *et al.* 2000, Gleick 2003). Many factors are driving escalating freshwater demand, including population and economic growth, technological development, urbanization, land conversion and agriculture (Scarsbrook & Townsend 1993, Grimm *et al.* 1997, Sternberg 2006, Rockstrom *et al.* 2007, Palmer 2010, Vorosmarty *et al.* 2010, Porter *et al.* 2011). Humankind is projected to appropriate from 70% to 90% of all accessible freshwater by 2025 (Sophocleous 2004). Over the last five decades, humans have more than tripled water withdrawals (Connor *et al.* 2009). Consequently, human-induced amplification of water level fluctuations is rapidly becoming one of the major disturbances of aquatic ecosystems globally, endangering not only the integrity of ecosystems but also the provision of ecosystem goods and services (Rockstrom *et al.* 2007, Palmer 2010). Moreover, the predicted increase of global mean temperature, coupled with increased climatic variability, in particular higher frequency and intensity of recurring extreme events such as heat waves, heavy precipitation, floods and droughts (Easterling *et al.* 2000, Meehl & Tebaldi 2004, Sophocleous 2004, IPCC 2007), may exacerbate considerably the variability of water level fluctuations on a global scale.

Accessible freshwater accounts for about 0.0001% of the surface of Earth (Shiklomanov & Rodda 2003), nonetheless it contains 9.5% of total animal species (Balian *et al.* 2008). An estimated 12% of all animal species live in freshwater ecosystems, and most other species depend in some way on freshwater ecosystems for their survival (Abramovitz 1996, Johnson *et al.* 2001). Lakes account for 87% of global liquid surface freshwater resources (Shiklomanov & Rodda 2003) and therefore comprise hugely important sources of water and food in both the developed and developing world. Nevertheless, strikingly little is known about the consequences of amplified water level fluctuations for the structure and functioning of standing water ecosystems. Amplified water level fluctuations could potentially alter the

integrity of whole lake systems, affecting them directly through alteration of, for instance, sediment-water interface (*e.g.* Acreman *et al.* 2005, Rorslett 1985, Verneaux *et al.* 2004), water residence times (Brauns *et al.* 2007a) or internal nutrient loading regimes (Zohary & Ostrovsky 2011). However, the negative effects of amplified water level fluctuations are likely to be greatest in littoral zones (Solimini *et al.* 2006, Leira & Cantonati 2008), which provide habitat for the significant majority of biological diversity in lakes (Wetzel 2001, O'Sullivan & Reynolds 2004, Stendera & Johnson 2008, Vadeboncoeur *et al.* 2011). Observational studies have suggested that amplified water level fluctuations may reduce macrophyte diversity and cover, potentially resulting in their complete disappearance from lake systems and consequently reducing considerably the structural diversity of littoral habitats (Rorslett 1984, 1985, Acreman *et al.* 2005). Although benthic (*i.e.* bottom-dwelling) invertebrates tend to be comparatively mobile, their community structure is highly dependent upon lake habitat structure (Tolonen *et al.* 2001, Schindler & Scheuerell 2002, Tolonen 2004, Tolonen *et al.* 2005) and can, therefore, be highly sensitive to anthropogenic impacts on hydrological and morphological lake attributes (Brauns *et al.* 2007b). Importantly, benthic invertebrate consumers form key links in not only whole lake food webs (Carpenter *et al.* 1985, Vander Zanden & Vadeboncoeur 2002) but also in adjacent terrestrial ones (Sabo *et al.* 2009, Wesner 2010, 2011). There is, therefore, a pressing need to examine the effects of amplified water level fluctuations on littoral assemblages, as they have the potential to dramatically alter the structure, functioning and stability of whole lake ecosystems, with knock-on implications for the integrity of associated terrestrial and aquatic systems.

Previous studies investigating the effects of amplified water level fluctuations on lakes and ponds have consistently employed an observational approach. Yet, such an approach cannot distinguish robustly the effects of water level fluctuations from the myriad of confounding factors that are known to affect ecological patterns and processes in lakes. Experiments are therefore needed both to elucidate the effects of water level fluctuations and determine mechanisms in operation. However, replicated experimental manipulation of water level is not feasible in natural field conditions. Accordingly, I constructed outdoor mesocosms which enabled controlled and well-replicated experimental manipulation of water levels. I then established an

experiment to examine the effects of amplified water level fluctuations on the structure and functioning of littoral assemblages. Specifically, I tested whether: (1) water level fluctuations interact with the position of benthic assemblages along the shore (*i.e.* their effects vary along the depth gradient); (2) certain biological traits (*e.g.* dietary preferences or motility) are associated with particular sensitivity or resistance to water level fluctuations; and (3) some established metrics of disturbance in aquatic ecosystems may have the potential to be used as biological indicators of water level fluctuations in lakes.

3.2. Methods

3.2.1. Experimental model system

Sixteen large (*ca.* 800 L) outdoor experimental pond mesocosms were constructed in Trinity College Botanic Gardens, ($53^{\circ}18'44''\text{N}$, $06^{\circ}15'25''\text{W}$). The ponds were triangular in elevation (Fig. 3.1) and exposed to natural climatic variation, thus mimicking as closely as possible the littoral zone of a lake or pond.

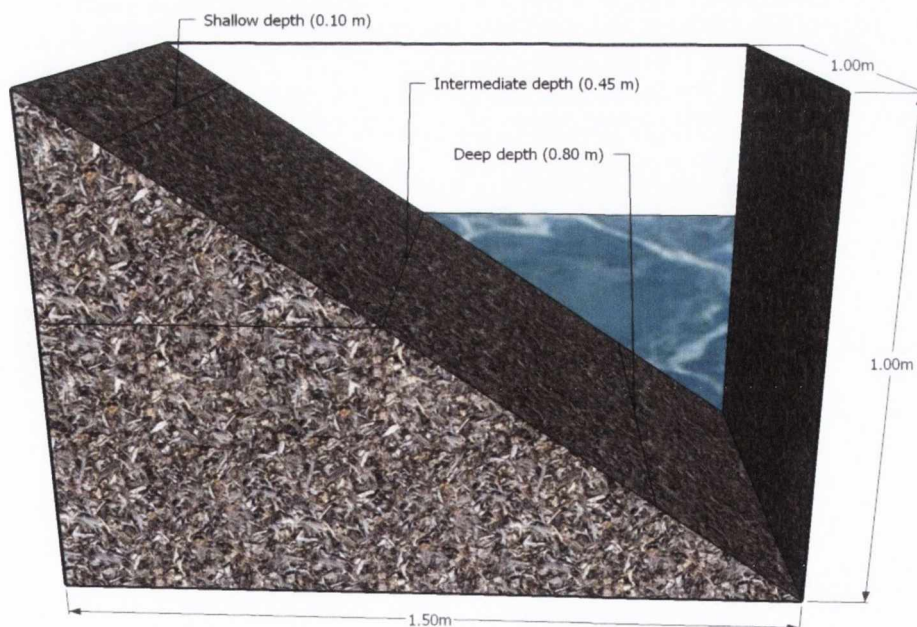


Fig. 3.1. Structure and dimensions of the pond mesocosms with the midpoints of the sampling locations and an indication of the depth to which the water level was dropped.

The slopes of the shoreline in the mesocosms approximated 30 - 35°, were 1.8 m long and faced south. The ponds were lined with under-liner followed by one-millimetre butyl liner and were well insulated as they were dug 1m deep and their sides were not exposed to the sun or atmosphere (Fig. 3.2).

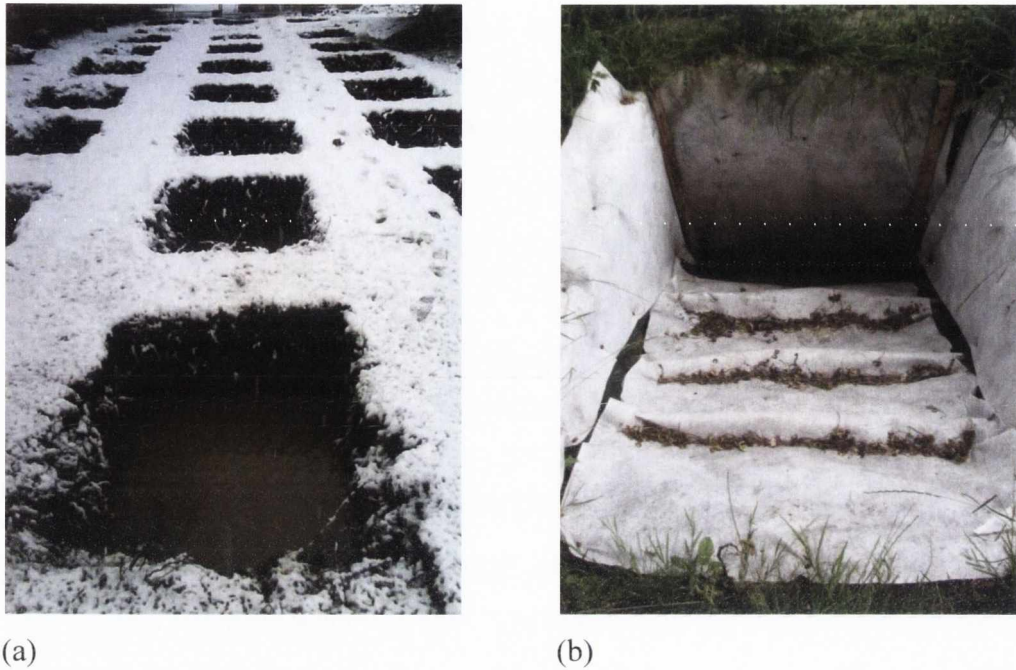


Fig. 3.2. The pond mesocosms (a) during construction and (b) with reinforced sides and under-liner before lining the ponds with one-millimetre butyl liner.

Hard substratum was selected as the sediment oxygen demand by sand, would be greater than the speed with which oxygen from air could be dissolved into the water column (Whitman & Clark 1984). Furthermore, comparison with the findings of the lake field study would be possible as one of the criteria for selection of lake sampling sites was the availability of stony substrate (Chapter 4). The mesocosms substratum comprised a mix of gravel, pebbles and cobbles to a depth of 10 cm. All 16 ponds were filled gradually with tap water that had settled for at least 48 h in two 2600 L tanks and in 16 additionally constructed ponds in order to remove chlorine-based compounds, added during drinking water treatment.

Given that a common criticism of mesocosm experiments is that they tend to include only a few taxa and contain relatively simple assemblages (Giller *et al.* 2004), the

mesocosms were populated with equal volumes of well-mixed inocula from three distinct lakes known to experience no or only very minor water level fluctuations (Loughs Mullagh [53°48'51" N, 06°58'05"W], Ramor [53°49'11" N, 07°03'19"W] and Skeagh [53°56'58" N, 07°00'29"W]). Benthic invertebrates were collected from each lake using a 500 µm pond net and were then pooled and divided equally, and randomly, among each experimental mesocosm over one month prior to the commencement of the experiment to ensure relatively high levels of biodiversity and realistic densities of benthic consumers in the ponds. Two ponds were sampled prior the commencement of the water level manipulation to validate the latter.

3.2.2. Experimental design

The experiment comprised two fixed factors: the presence of water level fluctuations (WLF; two levels: absent and present) and water depth below bankface, *i.e.* relative height on the shoreline; three levels: shallow (0.10 m), intermediate (0.45 m) and deep (0.80 m, Fig. 3.1). A third factor, pond, was incorporated as a random factor and nested within the presence of water level fluctuations. Each WLF treatment comprised seven replicate ponds.

Water levels in the 14 ponds were manipulated experimentally by reducing water depths by 0.45 m (Fig. 3.1), corresponding to the midpoint of the intermediate water depth, at a constant rate over 8 hours. Water levels were then kept at this low level for three days before being returned again at a similar rate to their original maximal height. This pattern, equivalent to a relatively extreme, rapid and short-term fluctuation event in a natural system (Chapter 2), was repeated four times over the duration of the experiment (Fig. 3.3). To remove any potential experimental artefacts associated with the removal and replacement of water, I withdrew water at identical rates from all mesocosms, including those with no experimental water level fluctuations. The water being removed was replaced simultaneously in the ponds of the latter treatment to ensure constant water levels. The water that was removed from the experimental ponds was transferred into the remaining 16 additional mesocosm ponds.

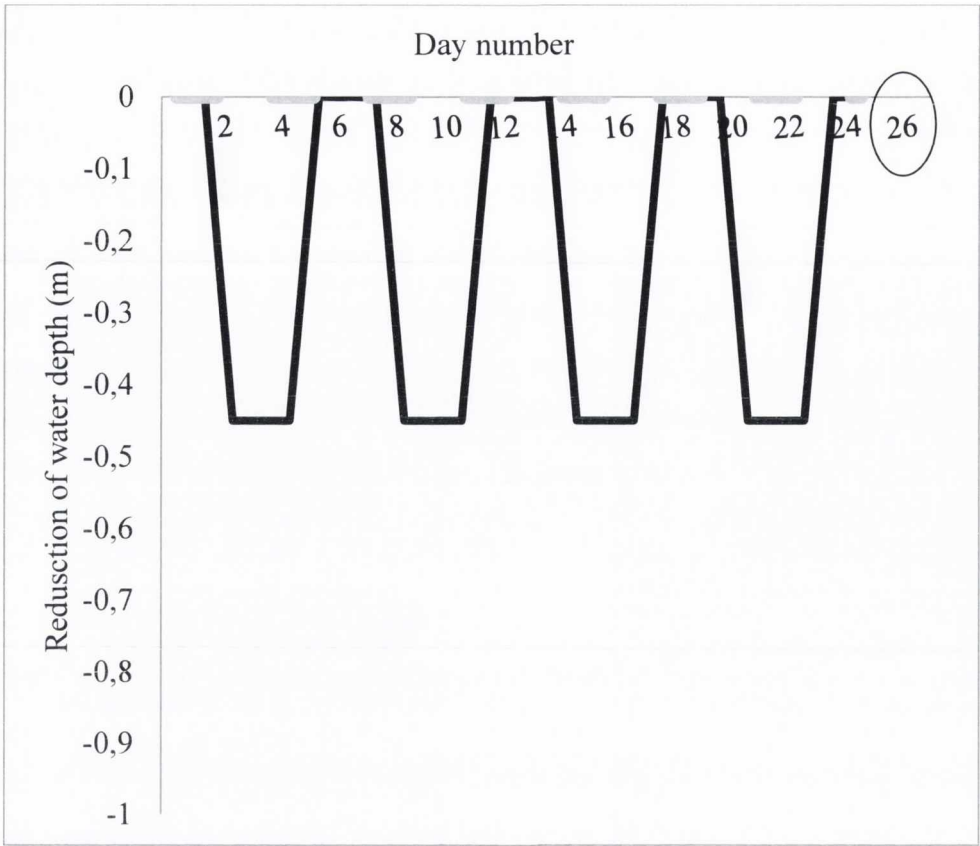


Fig. 3.3. Schedule of water level manipulation in the mesocosms with (black line) and without (grey line) water level fluctuations. The sampling day is marked with a circle.

Ceramic tiles (10 cm x 10 cm) that had been pre-colonised with benthic algae from a nearby lake (Lough Mullagh; 53°48'51" N, 06°58'05" W) were placed at each of the three established sampling depths in each mesocosm. The tiles were colonised in the lake for two weeks at the same depths as they would be placed at in the mesocosms and were then transferred in the ponds together with stones from the lakebed 50 days prior to the commencement of water level manipulation. Evidence accumulated from numerous studies indicates that such tiles support the establishment of assemblages that are qualitatively similar to those on natural hard substrata (e.g. Sladeckova 1962, Clifford *et al.* 1992, Baulch *et al.* 2005).

A series of polyvinyl chloride colonisation traps were placed at each sampling depth in each mesocosm to facilitate quantification of benthic invertebrate assemblages.

The 25 cm diameter open-top traps were 10 cm in height and perforated with 1 cm holes every 4 cm of their surface and were filled with substrate from the ponds two months prior to the commencement of the experiment.

Concentrations of each of total phosphorus, total nitrogen, total and dissolved organic carbon were quantified from the water column of every pond after the commencement of the experiment. Experimental manipulation of water levels had no effect on the water chemistry of the ponds (MANOVA; $F_{1,11} = 0.36$, $p = 0.78$).

3.2.3. Sampling and laboratory analyses

At the end of the experiment, benthic algae were collected by washing the upper surface of the ceramic tiles using a brush and distilled deionised water into a tray. The samples were then filtered in the laboratory through Whatman[®] 47 mm GF/C glass microfibre filters (Whatman[®], Maidstone, UK) for subsequent determination of both algal biomass (measured as chlorophyll *a* and quantified from duplicate samples after methanol extraction following the Standing Committee of Analysts (1983)) and organic matter. The latter was measured after loss on ignition at 550°C for 3.5 hours as ash-free dry mass. I used the autotrophic index (AI), expressed as the ratio of organic matter to chlorophyll *a* concentrations (Clesceri *et al.* 1998), as an indicator of relative periphytic viability. All sampling and collection of data from the mesocosms was done only when water levels were maximal.

Upon completion of the experiment, the benthic invertebrate colonisation traps were removed from the mesocosms and their contents preserved in 75% methylated ethanol. Invertebrates were quantified and identified subsequently in the laboratory to the highest taxonomic level practicable using the following keys: Savage (1989, 1999), Gledhill *et al.* (1993), Richoux (1982), Elliott (1977a), Edington & Hildrew (1995), Fitter & Manuel (1986), Macan (1965, 1970, 1977), Reynoldson & Young (2000), Friday (1988), Nilsson (1997), Wallace *et al.* (2003), Elliott & Mann (1979), Miller (1996), Elliott *et al.* (1988), Croft (1986), Ellis (1962), Fitter & Manuel (1986), Friday (1988), Hynes (1977), Macan & Cooper (1960). Owing to logistical constraints, benthic invertebrates were quantified randomly from six of the seven replicate ponds of each water level treatment.

Macroinvertebrate taxa were assigned to functional feeding groups and categories of locomotive capacity using ASTERICS (Version 3.1.1; AQEM/ STAR Ecological River Classification System; <http://www.fliessgewaesserbewertung.de/en/download/berechnung/>). Based on ingested food, most aquatic insects are effectively polyphagous (Cummins 1973, Lamberti *et al.* 2006) and ranking them by trophic level is a challenging task. The functional feeding group approach was developed by Cummins and Klug (1979) as an alternative to the trophic level approach to improve the understanding of food web relationships. They classified aquatic insects into different functional feeding groups based on feeding mechanisms, category of food ingested and morpho-behavioral adaptations of food acquisition (Cummins 1973, Cummins & Klug 1979). This scheme was further developed and modified by Moog (1995) and was used to construct the AQEM database of species autoecological traits (Ofenböck *et al.* 2004, Furse *et al.* 2006). Ten main classes of functional feeding type are identified under the scheme (Appendix 3.1). In addition, benthic invertebrates found in the mesocosms were assigned to one of six locomotive categories (Appendix 3.2), following Schmedtje and Colling (1996).

3.2.4. Data analyses

I used analysis of variance (ANOVA) to test for effects of water level fluctuations on univariate response variables using DataDesk[®] Version 6.1 (Data Description Inc., Ithaca, New York). Total variation in response variables was partitioned using Type III sum of squares. Least Significant Difference (LSD) post-hoc tests were used to provide pair-wise comparisons among levels of significant terms. Variables were transformed if necessary prior to analysis to meet assumptions of normality and homoscedasticity.

Taxon richness of benthic invertebrates was rarefied to the minimum number of individuals found in a sample ($n = 45$) to remove the confounding influence of abundance on estimates of richness (Sanders 1968, Hurlbert 1971). Shannon's (1948) index of diversity and Pielou's evenness (Pielou 1975) were also used as additional metrics of benthic invertebrate diversity. I examined the effects of water level fluctuations on both phylogenetic and taxonomic richness by quantifying each of the total phylogenetic diversity (PD), taxonomic distinctness (TD) and total taxonomic

distinctness (TTD) of benthic invertebrate assemblages using PRIMER[®] Version 6.1.8 (PRIMER-E Ltd., Plymouth, U.K.). PD is defined as the total length of all phylogenetic branches of the minimum spanning path of the cladogram for a given subset of taxa (Faith 1992). TD is the expected taxonomic distance apart of all pairs of taxa on a taxon list, while TTD is a modification of species richness which incorporates family interrelatedness (Rogers *et al.* 1999, Clarke & Warwick 2001, Salas *et al.* 2006). Hierarchical Linnaean Classification was used as a proxy for cladograms and served as a basis for measuring relatedness. The taxonomic resolution used was family level with equal weights being assigned to each of the seven principal taxonomic levels between family and phylum.

To investigate the potential of established disturbance metrics as indicators of water level fluctuations in lakes, I calculated the richness and percentage of abundance classes of Ephemeroptera, Plecoptera and Trichoptera (EPT scores; Lenat 1988), the Biological Monitoring Working Party (BMWP) score and the average BMWP score per taxon (ASPT). BMWP is based on an individual score for each family according to their sensitivity to various disturbances, while ASPT is the BMWP score divided by the number of families contributing to the score (Armitage *et al.* 1983). These scores are well-established perturbation metrics, used widely in the ecological assessment of running waters (e.g. Barbour *et al.* 1996, Sandin & Johnson 2000, Brabec *et al.* 2004, Hering *et al.* 2004, Furse *et al.* 2006).

Effects of experimental water level fluctuations on the taxonomic, trophic and locomotive structure of benthic invertebrate assemblages were tested using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle & Anderson 2001, Anderson *et al.* 2008), using PRIMER[®] Version 6.1.8 (PRIMER-E Ltd., Plymouth, U.K.) with the PERMANOVA+ add-on. These analyses were based on Bray-Curtis similarity matrices and were done with 9999 permutations of the residuals under a reduced model (Anderson 2005). Invertebrate abundance data were $\log(x + 1)$ -transformed prior to analysis. Similarity percentage species-contributions (SIMPER; Clarke & Gorley 2006) analysis was used to investigate the contribution of individual taxa, functional feeding groups and locomotive types to the pair-wise dissimilarity between treatments.

3.3. Results

3.3.1. Benthic algae

Amplified water level fluctuations reduced benthic algal biomass significantly, irrespective of water depth (ANOVA; $F_{1,24} = 7$, $p = 0.021$; dependent variable was log-transformed; Fig. 3.4a, Table 3.1). Further, although water level fluctuations had no effect on the autotrophic index (Table 3.1), the interaction between water level fluctuation and water depth was close to being statistically significant (ANOVA; $F_{2,24} = 3.09$, $p = 0.064$; Fig. 3.4b).

Table 3.1. Results of ANOVAs testing for an effect of water level fluctuations on (log-transformed) algal biomass and the autotrophic index. Significant effects are highlighted in bold.

Response variable	Source of variation	d.f.	Pseudo- <i>F</i>	<i>p</i>
Algal biomass	WLF	1	7	0.021
	Pond (WLF)	12	0.69	0.74
	Depth	2	0.037	0.96
	WLF*Depth	2	0.724	0.5
	Residual	24		
Autotrophic index	WLF	1	1.53	0.24
	Pond (WLF)	12	2.21	0.05
	Depth	2	0.58	0.57
	WLF*Depth	2	3.09	0.064
	Residual	24		

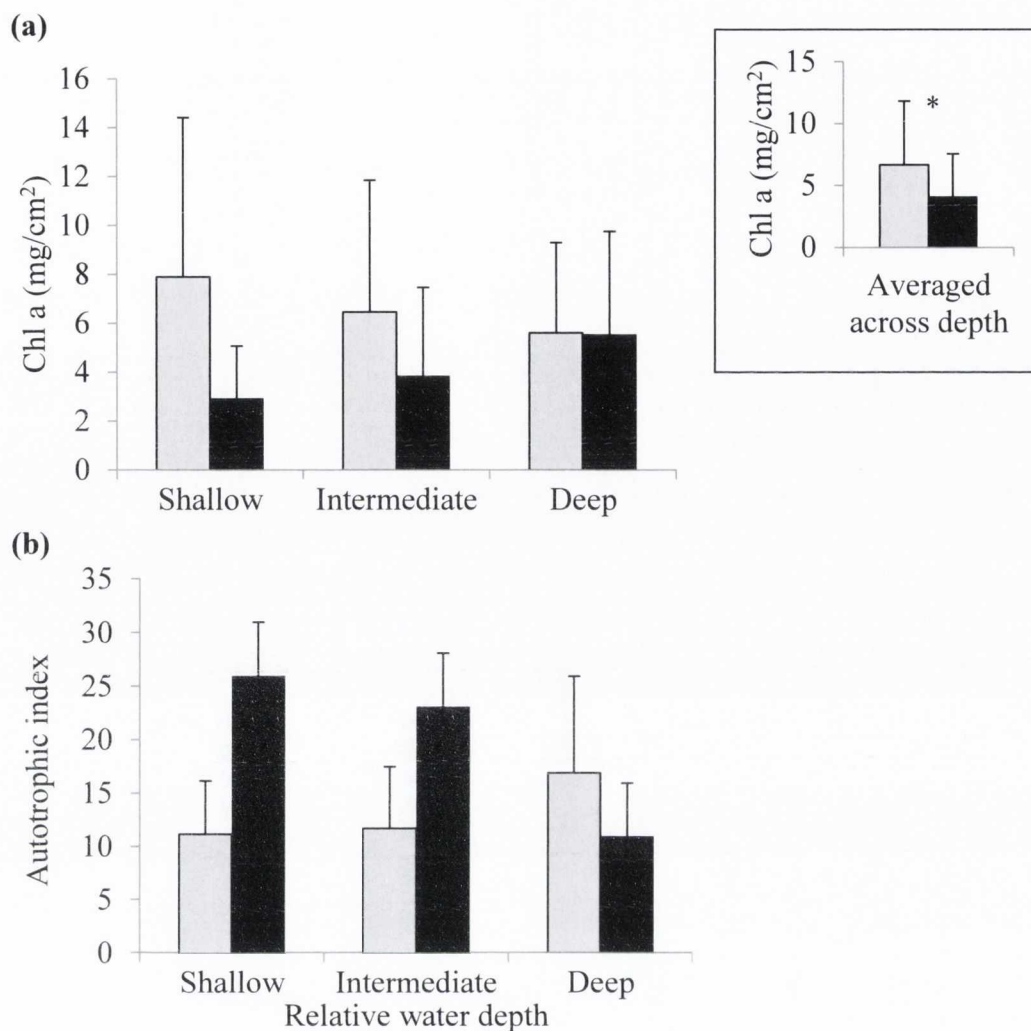


Fig. 3.4. (a) Algal biomass (measured as chlorophyll *a*; mean + s.e, $n = 7$) and (b) the autotrophic index (mean + s.e, $n = 7$) in mesocosms with (black bars) and without (grey bars) water level fluctuations. Untransformed data are shown here for clarity. Inset shows the effect of water level fluctuations across all water depths. Asterisks indicate the level of significance for the individual depths (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

3.3.2. Benthic macroinvertebrates

Fifty-one taxa of benthic macroinvertebrates belonging to 39 families were found in the mesocosms (Appendix 3.3). Water level fluctuations interacted significantly with water depth in their effects on benthic invertebrate density (ANOVA; $F_{2,20} = 22.75$, $p \leq 0.0001$; dependent variable was log-transformed; Table 3.2). Post-hoc tests showed that this was due to an eight-fold reduction in density at the shallowmost depth in the

mesocosms with water level fluctuations ($t = -11.10$, $p \leq 0.0001$; Fig. 3.5a) with no differences found at any of the other depths.

Variations of water level appear to have had a dramatic effect on Trichoptera larvae, as they were found only in the mesocosms that experienced no water level fluctuations. In addition, gastropods were mostly absent from the shallow depth in the ponds with WLF, appearing to have migrated to the intermediate depth where both their absolute (ANOVA; $F_{2,20} = 10.83$, $p = 0.0007$; dependent variable was $\log(x+1)$ -transformed) and relative (ANOVA; $F_{2,20} = 5.24$, $p = 0.015$; dependent variable was $\log(x+1)$ -transformed) densities increased significantly (Fig. 3.5b).

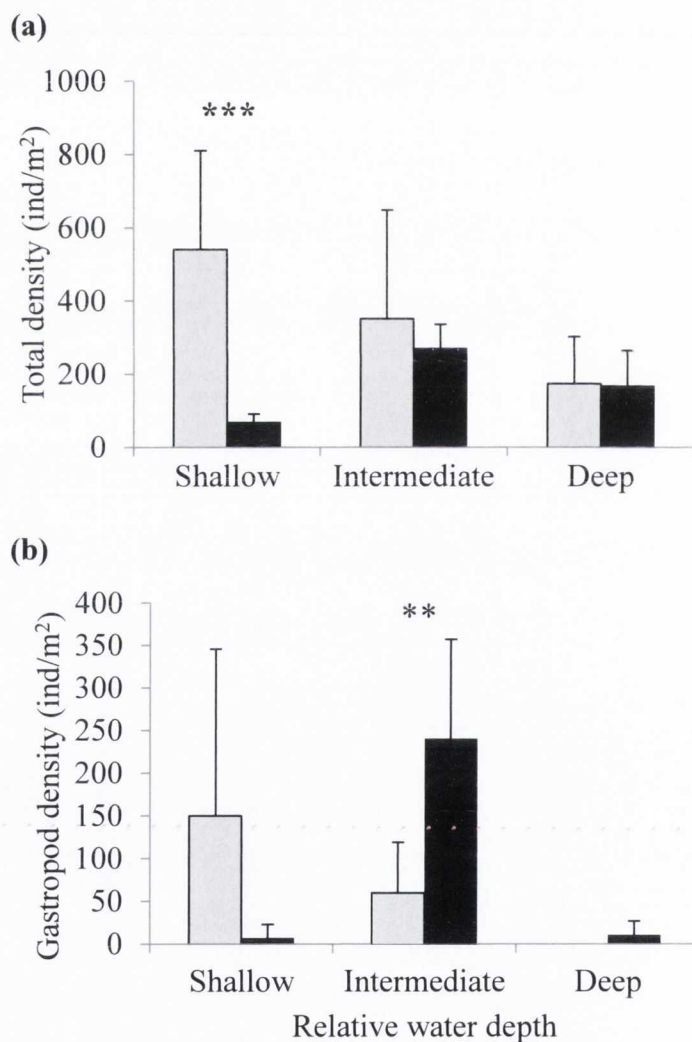


Fig. 3.5. (a) Densities (mean + s.e.m., $n = 6$) of all benthic invertebrates and (b) absolute densities (mean + s.e.m., $n = 6$) of gastropods in ponds with (black bars) and without (grey bars) experimental water level fluctuations. Untransformed data are

shown here for clarity. Asterisks indicate the level of significance for the pair-wise differences between treatments at individual depths (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Moreover, I also observed that terrestrial isopods from the Family Oniscidae, which typically inhabit damp environments, and insects from the Orders Psocoptera and Brachycera and from the Family Platypezidae were found exclusively in the mesocosms with water level fluctuations. The former insect taxon comprises scavengers, while the latter two taxa feed primarily on organic detritus or benthic algae.

Although each of the taxon richness, evenness and Shannon diversity of benthic invertebrate assemblages decreased significantly with increasing water depth (taxon richness: $F_{2,20} = 4.85$, $p = 0.019$; evenness: $F_{2,20} = 4.84$, $p = 0.019$; Shannon diversity: $F_{2,20} = 5.13$, $p = 0.016$), no effect of water level fluctuation was found on any of these measures of benthic invertebrate diversity (Table 3.2; Appendix 3.4).

Table 3.2. Results of ANOVAs testing for an effect of water level fluctuations on the (log-transformed) abundance, (log-transformed) absolute and relative gastropod densities, rarefied taxon richness, evenness and Shannon diversity of benthic invertebrate assemblages. Significant effects are highlighted in bold.

Response variable	Source of variance	d.f.	F-ratio	p
Total invertebrate abundance	WLF	1	6.97	0.025
	Pond (WLF)	10	2.90	0.02
	Depth	2	5.78	0.01
	WLF*Depth	2	22.75	≤ 0.0001
	Residual	20		
Gastropod absolute density	WLF	1	5.52	0.01
	Pond (WLF)	10	0.83	0.52
	Depth	2	16.85	≤ 0.0001
	WLF*Depth	2	10.83	0.0007
	Residual	20		

Response variable	Source of variance	d.f.	F-ratio	p
Gastropod relative density	WLF	1	2.19	0.17
	Pond (WLF)	10	0.98	0.49
	Depth	2	15.39	≤ 0.0001
	WLF*Depth	2	5.25	0.015
	Residual	20		
Taxon richness	WLF	1	1.45	0.26
	Pond (WLF)	10	1.83	0.12
	Depth	2	4.85	0.019
	WLF*Depth	2	1.93	0.17
	Residual	20		
Evenness	WLF	1	1.88	0.2
	Pond (WLF)	10	1.39	0.25
	Depth	2	4.84	0.019
	WLF*Depth	2	2.56	0.1
	Residual	20		
Shannon diversity	WLF	1	0.28	0.61
	Pond (WLF)	10	1.54	0.2
	Depth	2	5.13	0.016
	WLF*Depth	2	0.66	0.53
	Residual	20		

However, water level fluctuations interacted significantly with water depth (Table 3.3) in affecting each of the phylogenetic diversity (ANOVA; $F_{2,20} = 5.99$, $p = 0.009$), taxonomic distinctness (ANOVA; $F_{2,20} = 3.6$, $p = 0.046$) and total taxonomic distinctness (ANOVA; $F_{2,20} = 6.32$, $p = 0.008$) of benthic invertebrate assemblages. Post-hoc tests revealed that phylogenetic structure was altered only at the shallowmost sampling depth, where all three indices were significantly lower in ponds with water level fluctuations (PD: $t = 42.11$, $p = 0.009$; TD: $t = 4.15$, $p = 0.046$; TTD: $t = 76.51$, $p = 0.008$; Fig. 3.6).

Table 3.3. Results of ANOVAs testing for an effect of water level fluctuations on the total phylogenetic diversity (PD), taxonomic distinctness (TD) and total taxonomic distinctness (TTD) of benthic invertebrate assemblages. Significant effects are highlighted in bold.

Response variable	Source of variance	d.f.	F-ratio	p
PD	WLF	1	1.4	0.264
	Pond (WLF)	10	3.31	0.011
	Depth	2	18.64	≤ 0.0001
	WLF*Depth	2	5.99	0.009
	Residual	20		
TD	WLF	1	0.11	0.751
	Pond (WLF)	10	0.81	0.624
	Depth	2	8.74	0.002
	WLF*Depth	2	3.6	0.046
	Residual	20		
TTD	WLF	1	5.05	0.048
	Pond (WLF)	10	2.29	0.055
	Depth	2	19.18	≤ 0.0001
	WLF*Depth	2	6.32	0.008
	Residual	20		

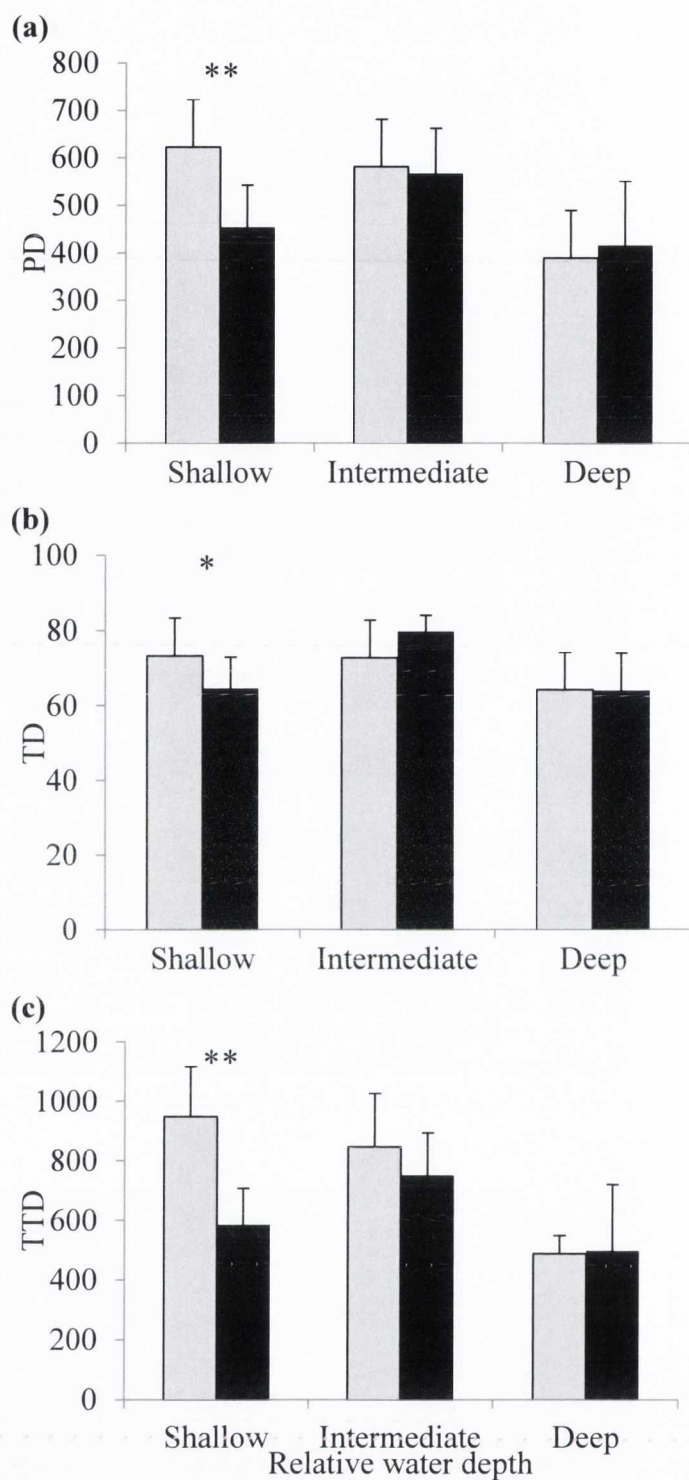


Fig. 3.6. (a) Total phylogenetic diversity (PD), (b) taxonomic distinctness (TD) and (c) taxonomic distinctness (TTD) in mesocosms with (black bars) and without (grey bars) water level fluctuations (mean + s.e., $n = 6$). Asterisks indicate the level of significance for the individual depths (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Water level fluctuations reduced the values of each of the four established metrics of disturbance (*i.e.* BMWP, ASPT and EPT scores) significantly, irrespective of water depth (Table 3.4; Fig. 3.7).

Table 3.4. Results of ANOVAs testing for an effect of water level fluctuations on selected metrics of disturbance in aquatic ecosystems. Significant effects are highlighted in bold.

Response variable	Source of variance	d.f.	F-ratio	p
BMWP score	WLF	1	7.05	0.024
	Pond (WLF)	10	2.48	0.04
	Depth	2	8.76	0.002
	WLF*Depth	2	2.65	0.096
	Residual	20		
ASPT	WLF	1	10.94	0.008
	Pond (WLF)	10	1	0.477
	Depth	2	1.10	0.352
	WLF*Depth	2	0.39	0.679
	Residual	20		
EPT taxa	WLF	1	10	0.01
	Pond (WLF)	10	1.66	0.16
	Depth	2	5.17	0.016
	WLF*Depth	2	3.14	0.065
	Residual	20		
EPT abundance classes [%]	WLF	1	5.48	0.041
	Pond (WLF)	10	2.8	0.024
	Depth	2	0.22	0.802
	WLF*Depth	2	0.3	0.741
	Residual	20		

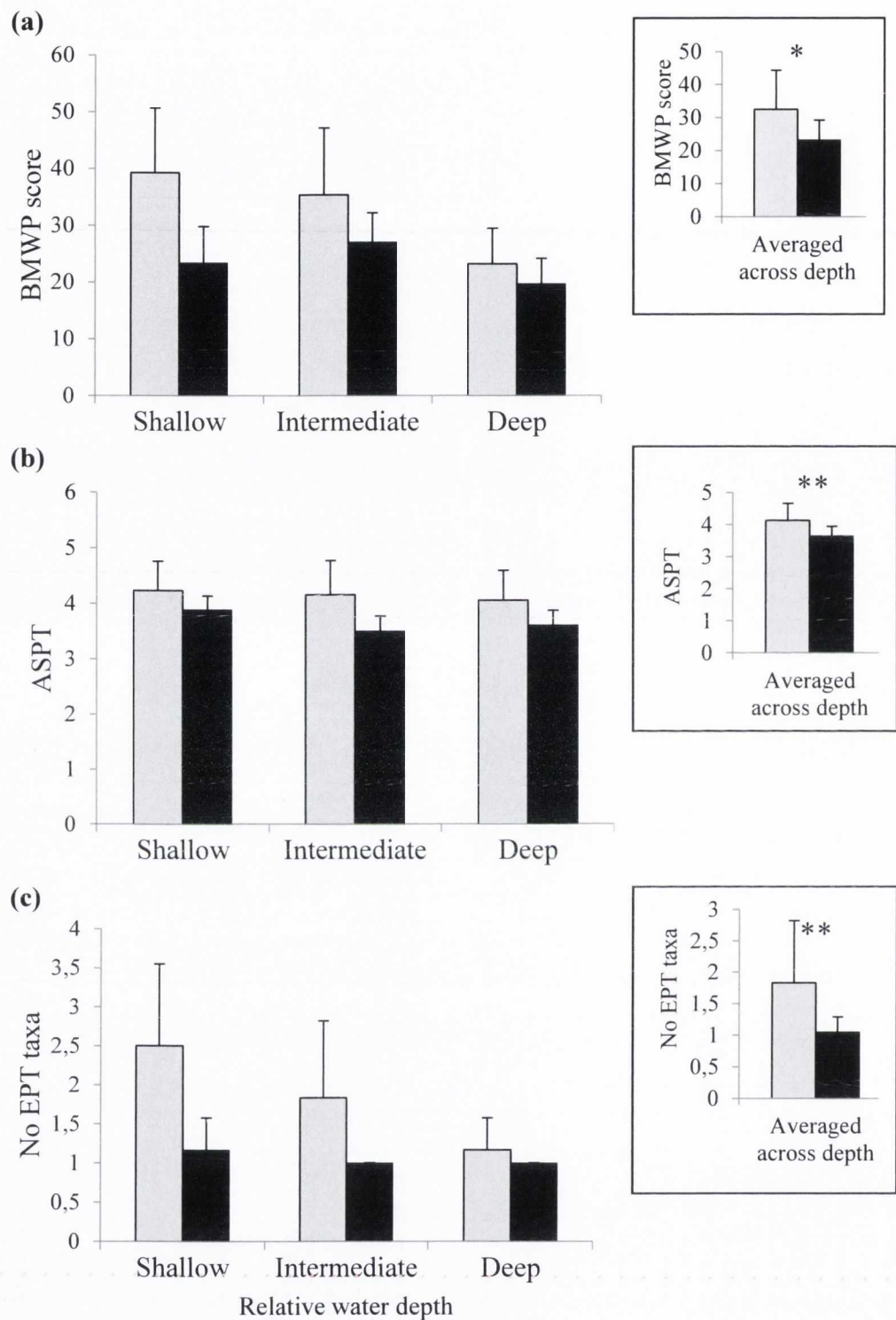


Fig. 3.7. (a) BMWP score, (b) ASPT, (c) number of EPT taxa and (d) percentage of EPT abundance classes (mean + s.e., $n = 6$) of benthic invertebrate assemblages in mesocosms with (black bars) and without (grey bars) water level fluctuations. Insets show the effect of water level fluctuations across all water depths. Asterisks indicate the level of significance for the individual depths (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

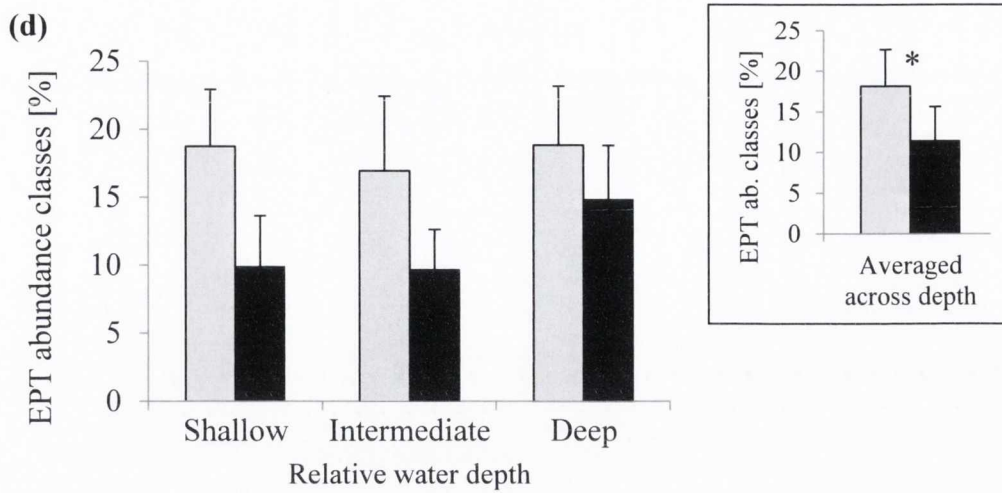


Fig. 3.7. Continued.

Experimental manipulation of water levels significantly altered the taxonomic structure of benthic communities along the depth gradient (PERMANOVA; pseudo- $F_{2,20} = 4.54$, $p \leq 0.0001$; Table 3.5). Benthic invertebrate assemblage structure differed significantly after exposure to water level fluctuations at both the shallow (pseudo- $t = 2.94$, $p = 0.001$) and intermediate (pseudo- $t = 1.27$, $p = 0.049$) water depths, although the magnitude of the effect of WLF decreased consistently with water depth.

Table 3.5. Results of PERMANOVAs testing for an effect of water level fluctuations on the taxonomic, trophic and locomotive structure of benthic invertebrate assemblages. Significant effects are highlighted in bold.

Response	Source of variation	d.f.	Pseudo- <i>F</i>	<i>p</i>
Taxonomic structure	WLF	1	3.16	0.005
	Pond (WLF)	10	2.13	≤ 0.0001
	Depth	2	5.74	≤ 0.0001
	WLF*Depth	2	4.54	≤ 0.0001
	Residuals	20		
Trophic structure	WLF	1	2.94	0.073
	Pond (WLF)	10	2.58	0.005
	Depth	2	3.86	0.004
	WLF*Depth	2	2.56	0.046
	Residual	20		
Locomotive structure	WLF	1	2.75	0.062
	Pond (WLF)	10	2.35	0.006
	Depth	2	2.50	0.039
	WLF*Depth	2	1.52	0.21
	Residual	20		

SIMPER analysis revealed that the taxa contributing most to the dissimilarity between treatments with and without experimental water level fluctuations comprised Chironomidae larvae, *Cloeon dipterum* (Ephemeroptera; Baetidae), and *Asellus aquaticus* (Isopoda; Asellidae), each of which had reduced densities at both the shallowmost and intermediate water depths (Table 3.6).

Table 3.6. Results of SIMPER analysis identifying the five benthic invertebrate taxa that contributed most strongly to the dissimilarity between mesocosms with and without water level fluctuations at the shallowmost and intermediate water depths. Untransformed data are shown for clarity.

Relative water depth	Taxon	Mean abundance		Contribution (%)
		without WLF	with WLF	
Shallow				
	Chironomidae	207.17	27.83	34.06
	<i>Asellus aquaticus</i>	134.17	9.50	24.39
	<i>Cloeon dipterum</i>	115.17	4.33	21.69
	<i>Polycelis nigra/ tenuis</i>	15.83	4.50	3.40
	<i>Gammarus duebeni</i>	14.83	1.50	3.25
Intermediate				
	Chironomidae	215.00	140.50	47.13
	<i>Asellus aquaticus</i>	67.67	55.50	20.73
	<i>Cloeon dipterum</i>	40.33	25.67	13.02
	<i>Potamopyrgus antipodarum</i>	2.00	11.17	3.20
	Oribatei	2.17	8.67	2.76

The effect of experimental water level fluctuations on the trophic structure of benthic invertebrate assemblages interacted significantly with water depth (PERMANOVA; pseudo- $F_{2,20} = 2.56$, $p = 0.046$; Table 3.5). Experimental water level fluctuations caused significant shifts in trophic structure at the shallowmost depth (pseudo- $t = 2.81$, $p = 0.005$) but not at either of the deeper sampling points. This significant shift in trophic structure at the shallowmost depth is attributable primarily to an increase in the relative abundance of predators and filter feeders, and a concurrent reduction in the abundance of shredders, grazers, collector-gatherers and scrapers (Table 3.7).

Table 3.7. Results of SIMPER analyses identifying the five functional feeding groups that contributed most to the dissimilarity between mesocosms with and without water level fluctuations at the shallowmost water depth. Untransformed data are shown for clarity.

Functional feeding group	Mean abundance		Contribution (%)
	without WLF	with WLF	
Predators	9.86	21.40	24.27
Grazers and scrapers	25.79	16.18	43.21
Gatherers and collectors	35.14	26.52	60.52
Filter feeders	8.47	16.02	75.43
Shredders	9.67	5.38	86.29
Parasites	4.09	6.35	91.54

The increase of the percentage of filter feeders in mesocosms with water level fluctuations owes primarily to higher relative abundances of motile Diptera larvae. Further, the magnitude of the effect on benthic invertebrate trophic structure was lower than for taxonomic structure. The main effect of WLF on locomotive structure was bordering on statistical significance (pseudo- $F_{1,20} = 2.75$; $p = 0.062$).

3.4. Discussion

My results demonstrate clearly that amplified water levels alter considerably the structure and functioning of standing water ecosystems. Experimental water level fluctuations reduced algal biomass and invertebrate consumer density, and altered significantly both the taxonomic and trophic structure of benthic invertebrate assemblages. Further, both the phylogenetic diversity and taxonomic distinctness of benthic assemblages were reduced significantly when water levels fluctuated. These results suggest strongly that amplified water level fluctuations have the potential to reduce dramatically the productivity and biological diversity of lake littoral zones. Given that the majority of biodiversity within lakes is found in the littoral zone (Wetzel 2001, O'Sullivan & Reynolds 2004, Strayer & Findlay 2010, Vadeboncoeur

et al. 2011), coupled with the fact that lake littoral provides important food subsidies both to associated aquatic habitats and neighbouring riparian zones (Vander Zanden & Vadeboncoeur 2002, Sabo *et al.* 2009, Wesner 2010, 2011), my findings have important implications not only for lake and pond systems experiencing amplified water level fluctuations, but also for adjacent aquatic and terrestrial ecosystems.

Importantly, for some ecosystem responses the effects of water level fluctuations were mediated by the depth gradient, whereas for others they were not. Values of each of the established disturbance metrics I quantified were reduced significantly by amplified water level fluctuations, irrespective of the depth of sampling. This indicates that these metrics have clear potential to assess the importance of water level regimes in lakes. However, the effect of amplified water level fluctuations on the density, phylogenetic diversity, taxonomic distinctness and the taxonomic and trophic structure of benthic consumer assemblages all varied significantly with water depth, with their effects being strongest within the zone of water level fluctuation. This demonstrates strongly that depth of littoral sampling comprises a key factor that needs to be incorporated explicitly in the assessment of the ecological effects of amplified water level fluctuations in standing water systems.

Several taxa, including Gastropoda and larvae of Trichoptera were entirely absent from the zone of water level fluctuation. Caddis fly larvae (both casebearing and caseless species) were absent even throughout ponds with fluctuating water levels, demonstrating that water level fluctuations may affect biotic assemblages even below the zone of water fluctuation. This finding is consistent with previous observational research (Power *et al.* 2008), implying that Trichoptera larvae are particularly sensitive to fluctuating water levels. These results indicate, therefore, that there is good potential for the identification of useful biological indicators of amplified water level fluctuations. Larvae of Ephemeroptera and Trichoptera appear to have particularly strong potential in this regard. They are known to be sensitive to impairment (Lenat 1988, Barbour *et al.* 1996) and with high discriminatory power to various perturbations including organic pollution, acidity, impoundment and chemical-induced disturbances (Wallace *et al.* 1996, Sandin & Johnson 2000, Hering *et al.* 2004, Ofenböck *et al.* 2004).

Amplified water level fluctuations resulted in increased densities of predators and filter feeders and reductions in grazers and shredders in the zone of water fluctuation in comparison with the ones from mesocosm without water level fluctuations. Predators are known to increase as a result of increased impairment in streams (Rawer-Jost *et al.* 2000) or acidification in lakes (Williamson *et al.* 1999, Fischer *et al.* 2001), thus demonstrating the potential of changes in their abundance to reflect various disturbances in aquatic ecosystems. Predators were probably favoured by the likely high availability of accessible prey in this area, not only because less mobile prey organisms may not have been able to track the rapid draw-down in mesocosm ponds with water level and became easily available when levels returned to their original height, but also because of availability of potential terrestrial invertebrate prey. As the latter were only found in the mesocosms exposed to water level fluctuations, it appears that they migrated into the ponds, when water levels were low, to access previously unavailable food resources (*e.g.* air-exposed benthic algae and dead macroinvertebrates), and were entrapped subsequently by the rising water.

The increase of the percentage of filter feeders in mesocosms with water level fluctuations is attributable primarily to higher relative abundances of the motile larvae of Diptera. These organisms utilize various food sources and employ many distinct feeding strategies, including filter feeding (Cummins 1973, Cummins & Klug 1979). Thus, the increase of filter feeders may not reflect a mechanistic response to water level fluctuations, but rather likely comprises an artefact driven by their categorisation in the functional feeding group database. Fluctuating water levels had adverse effect on grazers not only because they were not able to cope with the rapid decrease in water level, but also owing to the reduced resources availability, for instance periphytic algae. Gastropods, other common grazers that are relatively motile and protected by their shells, found haven from amplified water level fluctuations at the semi-immersed middle depth, where their number increased in the mesocosms with fluctuating water level. In general, specialised feeders, such as grazer and scrapers, are more likely to be sensitive to impairment, while generalists, such as dipteran larvae, tend to be more tolerant, due to accessibility to a wider range of potential food sources (*e.g.* Cummins & Klug 1979, Barbour *et al.* 1996, Furse *et al.* 2006).

Water level fluctuations had no detectable effect on taxon richness or metrics of local-scale (α) diversity. However, all three measures of phylogenetic diversity quantified were reduced significantly by water level fluctuations. This indicates that water level fluctuations impact biological diversity primarily at higher taxonomic levels, causing disproportionately high reductions in overall phylogenetic diversity. Moreover, such loss of higher-level diversity would, in turn, likely result in disproportionate alterations to the functioning of the ecosystem (Faith 1992, Duffy *et al.* 2007). This is supported by the fact that amplified water level fluctuations also triggered significant changes in the trophic structure of benthic invertebrate consumers.

Some authors have suggested that mesocosms have limited relevance for community and ecosystem ecology as they lack the complexity of the whole ecosystem being studied (Carpenter 1996, Schindler 1998). They consider inappropriate the spatial scales for microcosms in terms of including whole communities, and suggest the temporal scale of such studies is too short for accurate assessment of the response of slow-responding organisms and biogeochemical processes (Carpenter 1996, Schindler 1998). My experiment used realistic densities and relatively high levels of biodiversity of benthic assemblages, comparable to those occurring in natural ecosystems. The experiment was conducted in outdoor ponds, exposed to natural environmental fluctuations and the mesocosms mimicked as closely as possible a natural shoreline. Even though careful extrapolation of the results of this mesocosm experiment to ecosystem scale is needed, my findings nevertheless provide important mechanistic insights as to how water level fluctuations affect littoral assemblages along the depth gradient, and helped to identify a number of metrics that may be of use in ecological assessment and for the development of robust ecological indicators of this key and widespread pressure.

Rather than just providing an indication of general ecological integrity, which is the extent of the capability of the many established metrics of aquatic disturbance, I identified a number of specific ways that water level fluctuations appear to modify benthic assemblages along the depth gradient. Measures based on the taxonomic and, to a lesser extent, trophic structure of benthic invertebrate assemblages appear to have most potential in this regard, particularly in littoral areas affected directly by

fluctuating water levels (*i.e.* within the zone of water fluctuation). These distinct shifts in biotic assemblages (*e.g.* doubling of relative predator densities coupled with loss of caddis larvae and dramatic reductions in benthic abundance at shallow depths) have, therefore, the potential to identify amplified WLF as the disturbance responsible for driving those changes. This ability to fingerprint pressures is a key requirement of robust ecological assessment tools, particularly where no quantitative data on potential pressures exists (O'Toole *et al.* 2008).

In conclusion, my results of this experimental study give novel insight into the implications of water level fluctuations for the structure and functioning of standing water ecosystems. Considering the magnitude of the observed effects of water level fluctuations on primary producers and benthic consumers, particularly, but not exclusively, in the zone of water level fluctuation, results of this experiment imply that human-amplified water level fluctuations could have dramatic effects on standing water ecosystems and their integrity. Energy and materials flow within aquatic environments are relatively rapid (*e.g.* Giller *et al.* 2004) and the nature of food-web structure is rather dynamic. Therefore reduction in primary productivity and benthic consumers may result into loss of biomass from lake littoral zones. In addition, benthic invertebrates tend to comprise the significant majority of total prey consumption for many commercially valuable species of fish (Vander Zanden & Vadeboncoeur 2002). Taking into account that the majority of biodiversity within lakes is found in the littoral zone (Strayer & Findlay 2010, Vadeboncoeur *et al.* 2011), in addition to the fact that lake littoral provides important food subsidies both to associated aquatic and terrestrial habitats (Vander Zanden & Vadeboncoeur 2002; Wesner 2010), my findings have important implications not only for lake and pond systems experiencing amplified water level fluctuations, but also for adjacent aquatic and terrestrial ecosystems. Furthermore, a potential increment of the amplitude of WLF in lakes, triggered by the projected climate change and concomitant increase in water abstraction, together with the ensuing dislocation of littoral habitat may evoke further shifts in benthic communities, possibly entailing changes in biodiversity at taxonomic and phylogenetic level or even eliminating the more vulnerable taxa. This could indirectly influence morphological richness and genetic turnover (Clarke & Warwick 2001).

Water Level Fluctuations and their Effects on Lake Ecology

4. Effects of Water Level Fluctuations on the Ecology of Lake Littoral Zones



Collection of benthic invertebrates, water chemistry and in situ quantification of substrate structure using the Stafford frame.

4.1. Introduction

The main threats to the ecological integrity of standing water bodies globally are from nutrient loading and hydromorphological pressures (Bragg *et al.* 2003, Solimini *et al.* 2006, SNIFFER 2008, Wantzen *et al.* 2008b, Donohue *et al.* 2009a, Donohue *et al.* 2009b, Cardinale 2011). Most lakes are subject to natural, mostly seasonal changes in water level, ranging from subtle to sometimes considerable over a longer period of time (Smith *et al.* 1987, Keough *et al.* 1999, Chapter 2). Natural water level fluctuations (WLF) may be essential for the survival of some species and may support both the biodiversity and productivity of lake littoral zones (Gafny & Gasith 1999, Coops & Hosper 2002). However, alteration of natural patterns of water level fluctuations is a key cause of ecological degradation in lake ecosystems (Deegan *et al.* 2012, Yin & Yang 2012). Significantly amplified WLF may have an overriding effect on the ecology, structure, functioning and management of lakes (Coops *et al.* 2003, Schmieder *et al.* 2004, Beklioglu 2007, Wantzen *et al.* 2008b, Chapter 3). Moreover, freshwater ecosystems which are already damaged by the overuse of water (Gleick 2003, Sophocleous 2004, International Bank for Reconstruction and Development 2010) stand to be affected even further by growing population and increasing socio-economic development (Holland *et al.* 2012, Rulli *et al.* 2013).

Biological effects of fluctuating water in lakes are likely to be greatest in littoral zones (Solimini *et al.* 2006), where even small draw-downs can result in the conversion of large areas of standing water to air-exposed habitats (Leira & Cantonati 2008). The importance of littoral zones is unequivocal. Not only does the significant majority of biological diversity in lakes peak in shallow nearshore water (Wetzel 2001, O'Sullivan & Reynolds 2004, Stendera & Johnson 2008, Vadeboncoeur *et al.* 2011), but littoral zones endow with incommensurately important feeding and breeding habitat for the whole-lake ecosystem (Sabo *et al.* 2009, Hampton *et al.* 2011). Thus, impairing lake littoral zones could cause significant alterations to whole lake ecosystem with knock-on consequences for associated terrestrial areas (Wesner 2011, Yin & Yang 2012).

Benthic macroinvertebrates, being less motile and highly dependent on lake habitat structure (Tolonen *et al.* 2001, Schindler & Scheuerell 2002, Tolonen 2004, Tolonen

et al. 2005) are very sensitive to anthropogenic shoreline development and hydrological impacts (Brauns *et al.* 2007b). Littoral invertebrates constitute a taxonomically well-described, ubiquitous, highly abundant and diverse group that respond to a wide range of pressures and can be good indicators of localized conditions and long-term effects (Free *et al.* 2009, Menezes *et al.* 2010). Furthermore, they are very important for freshwater ecosystem functioning, mostly as a result of their intermediate position in energy and matter flow, as well as diverse array of feeding habits (Wallace 1996, Wallace *et al.* 1996). They have, therefore, much potential to be used as bioindicators for investigating in detail the effects of alteration in water level regimes.

Benthic invertebrates are used broadly in stream and river monitoring and quality assessment (Washington 1984, Rosenberg & Resh 1993) and the effects of water level fluctuations on lotic biota has received significant attention (Scarsbrook & Townsend 1993, Poff *et al.* 1997, Townsend *et al.* 1997b, Puckridge *et al.* 1998, Miller *et al.* 2007). Water level fluctuations have been shown to reduce algal biomass, macroinvertebrate diversity and abundance in running waters and alter their trophic structure (Scarsbrook & Townsend 1993, Townsend *et al.* 1997b, a, Marks *et al.* 2000, Miller *et al.* 2007, Power *et al.* 2008). However, little is known about how water level variations affect the ecology of lakes. Unravelling the effects of water level fluctuations on lake littoral assemblages is impeded further by the spatially heterogeneous distribution of lake assemblages due to a great number of natural factors, such as local water chemistry, shore morphology and habitat structure (Tolonen *et al.* 2001, Schindler & Scheuerell 2002, Tolonen 2004, Brauns *et al.* 2007a), sediment size and the presence or absence of macrophytes (Tolonen *et al.* 2005) and biotic interactions like competition and predation (Karjalainen *et al.* 1999, Nystrom *et al.* 2001, Leppä *et al.* 2003).

Changes in lake water level have been shown to lead indirectly to shifts in trophic state through reducing the availability of organic matter (Black *et al.* 2003, Valdovinos *et al.* 2007), altering oxygen, light and temperature regimes or by resuspending bottom sediments, thus increasing both the turbidity and the release of nutrients to the water column (Acreman *et al.* 2005). Furthermore, extreme fluctuations in lake levels may increase sediment erosion and lower macrophyte

diversity, even leading to their disappearance (Rorslett 1984, 1985, Valdovinos *et al.* 2007), and therefore deteriorate habitats and food resources for benthic assemblages. In a study of littoral zones in 27 Scottish lochs, Smith *et al.* (1987) concluded that relatively small changes in water level can be equally destructive to the littoral macrophyte and benthic assemblages. Observational studies by Jurkiewicz-Karnkowska (1989), Prus *et al.* (1999) and Valdovinos *et al.* (2007) suggested that water level fluctuations reduced the abundance and diversity of macroinvertebrates. However, these results contrasted somewhat with the conclusions of Furey *et al.* (2006), who suggested that macroinvertebrate density and biomass can be equal or greater in reservoirs exposed to regular draw-down compared with lakes with natural patterns of WLF. They ascribed these findings to the fact that the effects of water abstraction extended below the exposure zone that was repeatedly desiccated and inundated.

The majority of these investigations were based on one or two water bodies or focused solely on a particular assemblage trait. There is, therefore, a pressing need for studies that focus simultaneously on both biological (*e.g.* feeding preferences and locomotion type) and ecological (*e.g.* habitat preferences and dependence on water chemistry) traits in lakes with contrasting regimes of water level fluctuations, as opposed to mostly taxonomy-based metrics of biotic response. This may help to provide an ‘early warning’ signal of potential structural changes or food-web repercussions before problems are evident in open water and comparatively intractable (Hampton *et al.* 2011).

The aims of the work described in this Chapter are to test the findings of the mesocosm experiment described in Chapter 3 in natural ecosystems and to examine differences in the structure and functioning of biotic assemblages in lakes with contrasting amplitude of water level fluctuations. To the best of my knowledge this is the first observational study investigating the importance of water level regimes in lakes to employ a multi-level, multi-lake (eight lakes) and multi-trait (ecological and biological) approach. The innovations of my study include comparison of a suite of univariate and multivariate community attributes, together with habitat structure in lakes with different regimes of water level fluctuations. The main goals of this study were to investigate: (1) differences in littoral habitat structure in lakes with

contrasting regimes of fluctuating waters; (2) the potential of benthic communities to reflect changes in hydrological regimes of lakes, employing both taxonomy-based and functional trait-based community descriptors and (3) to examine whether effects vary along the depth gradient in natural ecosystems.

4.2. Methods

4.2.1. Lake selection

The selection of lakes to incorporate into this study was based on historical data of mean daily water levels of 63 gauged Irish lakes, together with a number of physico-chemical variables. Thirty-five lakes with active water level recorders (as of January 2009) were selected for further consideration. Annual and monthly ranges were identified as important descriptors of water level regimes and thus the selected groups were chosen to represent two extremes of the spectrum of water level fluctuations (see Chapter 2). In order to reduce environmental noise, lakes with historical data on water column total phosphorus concentrations in excess of $100 \mu\text{g L}^{-1}$ or with alkalinity less than $10 \text{ mg CaCO}_3 \text{ L}^{-1}$ were excluded from further study. As a result, eleven lakes, each with active water level recorders and continuous daily water level measurements in excess of 25 years (Table 4.1), were preselected and visited.

Table 4.1. Baseline information for the lakes preselected for targeted field sampling, with mean ($\pm$ SD) annual (AR) and monthly (MR) ranges; historical data on water chemistry and year in which the water level records begun. Asterisks indicate the eight lakes that were ultimately selected for surveys.

Lake	Mean AR [m]	Mean MR [m]	Records begin	Surface area [ha]	Mean pH	Mean alkalinity [mg CaCO ₃ L ⁻¹]	Mean TP [µgP/L]
Oughter*	2.72 $\pm$ 0.38	0.78 $\pm$ 0.45	1977	658	7.9	70	72
Cullin	1.77 $\pm$ 0.42	0.54 $\pm$ 0.37	1983	1019	8.4	140	41
Inchiquin	1.42 $\pm$ 0.11	0.69 $\pm$ 0.32	1975	107	8.2	142	21
Muckno*	1.43 $\pm$ 0.32	0.46 $\pm$ 0.27	1976	354	8	47	38
Cutra	1.26 $\pm$ 0.21	0.50 $\pm$ 0.25	1975	382	7.6	34	23
Anure*	1.06 $\pm$ 0.17	0.52 $\pm$ 0.21	1976	133	6.8	12	37
Eske*	1.04 $\pm$ 0.07	0.44 $\pm$ 0.16	1977	385	7.5	11	6
Moher*	0.59 $\pm$ 0.19	0.21 $\pm$ 0.12	1977	36	7.3	16	11
Skeagh*	0.65 $\pm$ 0.13	0.16 $\pm$ 0.09	1975	61	7.3	30	40
Ennell*	0.65 $\pm$ 0.17	0.15 $\pm$ 0.10	1979	1151	8.1	154	17
Owel*	0.58 $\pm$ 0.22	0.10 $\pm$ 0.06	1975	1018	8.3	96	10

To minimise the effect of structural habitat heterogeneity, sampling was confined to stony substrates. They were preferred over other substrate type as they are easy and relatively economical to sample; their communities are known to respond to human-induced pressure (Brauns *et al.* 2007a, Donohue *et al.* 2009a, Tolonen & Hämäläinen 2010), including water level regulation (Aroviita & Hämäläinen 2008).

The final lake selection was based on the following criteria, in hierarchical order:

- Presence of active water level data recorders (as of January 2009);
- Record length of water level data - at least 30 years;
- Good data quality - minimal number of missing values for daily water level readings;
- Historical annual and monthly ranges covering the two extreme ranges henceforth referred as low or high fluctuations;
- Availability of stony substrate (Loughs Cullin, Inchiquin and Cutra were excluded).

4.2.2. Lake sampling

I sampled eight lakes (Fig. 4.1), four with high annual (> 1 m) and monthly (0.5 m - 1.5 m) ranges of water level fluctuations and four with relatively small variations in water level (MR < 0.5 m and with AR < 1m, Fig. 4.2). The selected lakes vary in both their physical and chemical characteristics (Tables 4.1). There was, however, no significant difference in overall water chemistry between the lakes with high and low WLF (Table 4.2).

Table 4.2. Results of PERMANOVA testing for differences in water chemistry between lakes with low and high water level fluctuations. The analysis was based on a normalised Euclidian distance matrix, with 9999 permutations of the residuals under a reduced model. Significant effects are highlighted in bold.

Response	Source of variation	d.f.	Pseudo- <i>F</i>	<i>p</i>
Water chemistry	WLF	1	1.17	0.323*
	Lake (WLF)	6	81.69	≤0.0001
	Residual	24		



Fig. 4.1. Locations of sampled lakes belonging to the two water level regime groups: low water level fluctuations (grey circles) and high water level fluctuations (black circles).

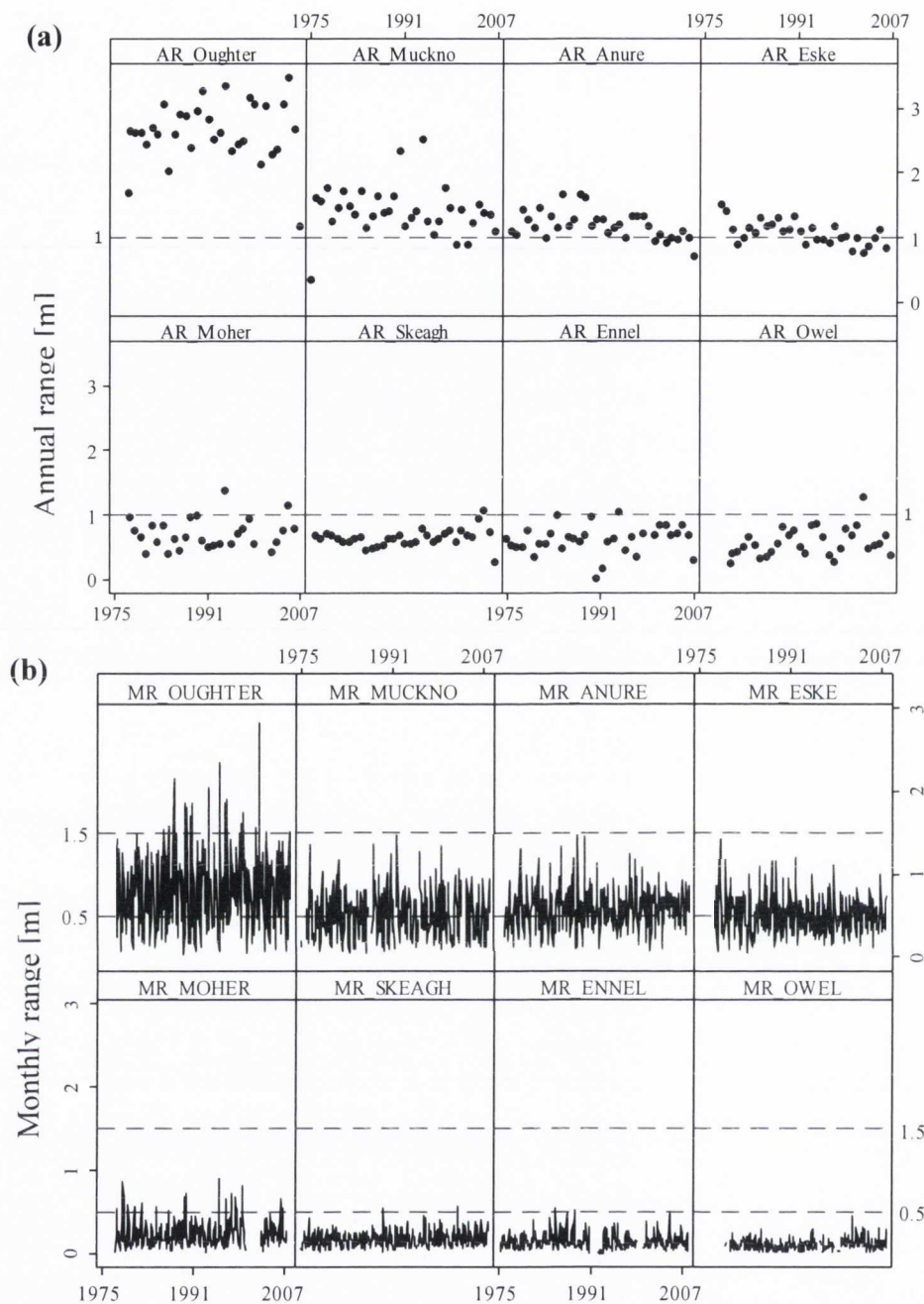


Fig. 4.2. Time series plots of (a) annual (AR) and (b) monthly (MR) ranges for the sampled lakes with time on the X-axis and amplitude of water level in metres on the Y-axis.

Biotic and abiotic sampling of selected lakes was done during an eight week period between late May and July 2009, when water levels were relatively low (Chapter 2) in order to avoid sampling flooded areas. Four straight-line transects orientated

perpendicular to the shoreline and extending to about 1 m water depth, were established in each lake. The slope angle for each transect was measured *in situ*. I quantified habitat structure (inclusive of macrophyte cover) and the structure of both benthic algae and benthic invertebrates at three points along each transect, located at sites at water depths of 0.10 m (shallow site), 0.45 m (intermediate site) and 0.80 m (deep site). Habitat structure was assessed *in situ* using a bathyscope. I estimated the relative (%) coverage of sand and silt, gravel, pebbles, cobbles, boulders, bedrock, coarse woody debris (CWD), soil, flooded grass or roots, leaves or debris, and macrophytes at each sampling point. Habitat characteristics were quantified using a 1 x 1 m Stafford frame consisting of 25 quadrats of equal size. Each frame was positioned in such a way that cell number one in the third row was always located at the target water depth for that sampling site (Fig. 4.3).

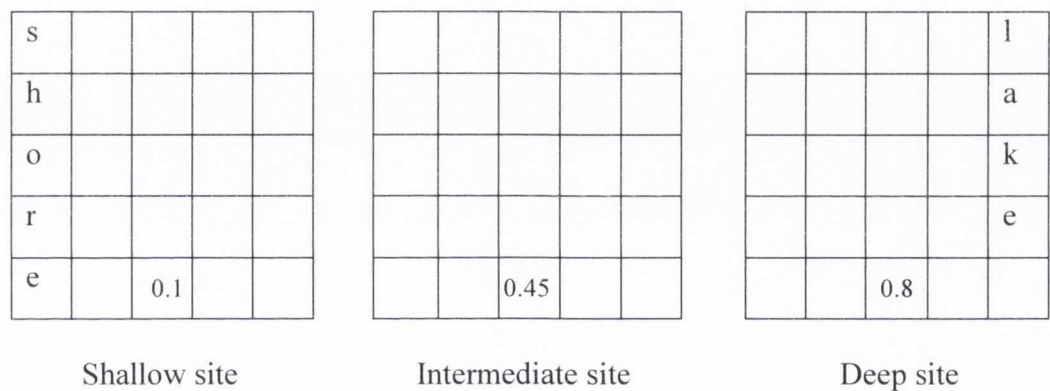


Fig. 4.3. Scheme of the sampling design of each transect with the three sampling depths. Habitat structure was quantified and benthic biota collected from within the three Stafford frames consisting of 25 quadrats with sides of 0.25m and with a total surface area of 1m².

Epilithic diatoms for subsequent quantification of assemblage structure, algal biomass and organic matter content were collected by washing a known area of the upper surface of stones collected from within the frames at each sampling site using a brush and distilled deionised water. Samples for quantification of algal biomass (measured as chlorophyll *a*) were filtered immediately upon collection through Whatman[®] 47 mm GF/C glass microfibre filters and stored in the dark in methanol at < 4 C ° until analysis. Samples for quantification and identification of diatom taxa were preserved

with Lugol's iodine and kept in light resistant glass bottles at $< 4\text{ }^{\circ}\text{C}$ before further processing. Benthic invertebrate samples were collected from each sampling site by kick/ sweep sampling using a hand-held pond net with mesh size $500\text{ }\mu\text{m}$. This involved disturbing the stony substrate with light kicks while moving slowly backwards and sweeping with the net from side to side, ensuring that all dislodged animals passed through the net. Faunal samples were standardized both in area covered and time ($1\text{m}^2/20\text{ sec}$) and were placed in plastic containers and preserved in 90 % methylised ethanol.

Water samples were collected using a weighted 5 L polypropylene bottle thrown lakewards three times from the deepest end of each transect. Water column alkalinity, pH, conductivity, true colour, turbidity, total phosphorus (TP), total nitrogen (TN), dissolved total organic carbon (DTOC) and chlorophyll *a* were quantified from each water sample. All filtering was done using Whatman[®] 47 mm GF/C glass microfibre filter papers immediately upon collection using a hand vacuum pump.

4.2.3. Laboratory analyses

Water conductivity ($\mu\text{S cm}^{-1}$) was determined with a LF 196 WTW GmbH Microprocessor conductivity meter. Water turbidity (NTU) was quantified with 2100P Hach[®] turbidimeter (Loveland, Colorado, USA) and pH was measured using a Jenway 3030 pH meter. Alkalinity was quantified following Clesceri *et al.* (1998) as $\text{mg CaCO}_3\text{ L}^{-1}$ after titration with sulphuric acid. True colour was measured at wavelength 550 nm with a Hach[®] DR5000 spectrophotometer. A known volume of sampled water was filtered and chlorophyll *a* subsequently quantified after methanol extraction following the Standing Committee of Analysts (1983) as described in Chapter 3. Total nitrogen and dissolved organic carbon were quantified using a Vario TOC Cube, Elementar Analysensysteme GmbH (Hanau, Germany). Total phosphorus was quantified in triplicate following Eisenreich *et al.* (1975). Independent laboratory controls with known concentrations were examined together with the samples for TP and TN as a means of quality control (QC).

Benthic algal chlorophyll *a* and organic matter concentrations were analysed following, respectively, the Standing Committee of Analysts (1983) and Clesceri *et*

al. (1998, see Chapter 3). The autotrophic index (AI), expressed as the ratio of organic matter to chlorophyll *a* concentrations was calculated after Clesceri *et al.* (1998, see Chapter 3). Epilithic diatoms were identified to as high a taxonomic resolution as possible (generally to species level) by Dr. Martyn Kelly of Bowburn Consultancy, Durham, UK.

I sorted and identified whole macroinvertebrate samples without subsampling to minimise the variability attributable to laboratory processing (Clarke *et al.* (2006). I identified invertebrates to the highest taxonomic level practicable using the following keys: Croft (1986), Edington & Hildrew (1995), Elliott (1977a), Elliott & Mann (1979), Elliott *et al.* (1988), Ellis (1962), Fitter & Manuel (1986), Friday (1988), Gledhill *et al.* (1993), Hynes (1977), Macan (1965,1970, 1977), Macan & Cooper (1960), Miller (1996), Nilsson (1997), Reynoldson & Young (2000), Richoux (1982), Savage (1989, 1999), Wallace *et al.* (2003). Macroinvertebrate taxa were assigned to functional feeding groups and categories of locomotive capacity as described in Chapter 3 (see Appendix 3 for details) using ASTERICS (Version 3.1.1; AQEM/STAR Ecological River Classification System, <http://www.fliessgewaesserbewertung.de/en/download/berechnung/>). Owing to logistical constraints, benthic algae and invertebrates were identified from a random subset of three of the four transects in each lake.

4.2.4. Data analyses

All statistical analyses incorporated two fixed factors; amplitude of water level fluctuations (WLF; two levels: low and high) and water depth (three levels: shallow [0.1 m], intermediate [0.45 m] and deep [0.8 m]). Lake was incorporated as a random factor and nested within WLF, while transect number was incorporated as a random factor and nested within lake. Mixed analysis of variance (ANOVA) models based on Type III sums of squares were used to test for differences in univariate response variables among lakes experiencing high and low WLF on univariate response variables with DataDesk[®] Version 6.1 (Data Description Inc., Ithaca, New York). Least Significant Difference (LSD) post-hoc tests were used to provide pair-wise comparisons among levels of significant terms. Variables were transformed if necessary prior to analysis to meet assumptions of normality and homoscedasticity.

Taxon richness was rarefied to the minimum number of individuals found in a sample ($n = 27$) to remove the confounding influence of abundance on estimates of richness (Sanders 1968, Hurlbert 1971). Shannon's (1948) index of diversity and Pielou's evenness (Pielou 1975) were also used as additional metrics of benthic assemblage diversity. I examined the dissimilarities in both phylogenetic and taxonomic richness of algal and invertebrate assemblages in lakes experiencing low and high water level fluctuations. These were quantified through the total phylogenetic diversity (PD), taxonomic distinctness (TD) and total taxonomic distinctness (TTD) using PRIMER[®] Version 6.1.8 (PRIMER-E Ltd., Plymouth, U.K.). PD is defined as the total length of all phylogenetic branches of the minimum spanning path of the cladogram for a given subset of taxa (Faith 1992). TD is the expected taxonomic distance apart of all pairs of taxa on a taxon list, while TTD is a modification of species richness which incorporates family interrelatedness (Clarke & Warwick 2001, Salas *et al.* 2006). Hierarchical Linnaean Classification was used as a proxy for cladograms and served as a basis for measuring relatedness. The taxonomic resolution used was genus level for benthic algae and family level for the invertebrates with equal weights being assigned to each of the principal taxonomic levels.

Effects of water level fluctuations on habitat structure and the taxonomic (for diatoms and invertebrates), trophic and locomotive structure (benthic invertebrates only) of benthic assemblages were examined using mixed permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle & Anderson 2001, Anderson *et al.* 2008) based on the same model structure as the univariate analyses. The PERMANOVA analysis of habitat structure was based on Euclidean distance, while Bray-Curtis similarity matrices were used for analyses of benthic assemblages. The relative abundance of diatoms and invertebrates was $\log(x+1)$ -transformed prior to analysis. Similarity percentage species-contributions (SIMPER; Clarke & Gorley 2006) analyses were used to identify habitat types, taxa of benthic algae and invertebrates, or invertebrate functional feeding groups or locomotive types that contributed most to the pair-wise dissimilarity between lakes with low and high water level fluctuations. All multivariate analyses (PERMANOVA and PERMDISP) were based on 9999 permutations of the residuals under a reduced model and were done with the PERMANOVA+ add-on of PRIMER[®] Version 6.1.8 (PRIMER-E Ltd., Plymouth, U.K.). When the number of possible unique permutations was less than

100, p -values were estimated using Monte Carlo simulations (Anderson 2005, Anderson *et al.* 2008) and are marked with asterisks in the tables.

4.3. Results

4.3.1. Habitat structure

Littoral habitat structure varied significantly (Fig. 4.4) with water level fluctuations along the depth gradient (PERMANOVA; pseudo- $F_{2,20} = 3.09$, $p = 0.003$; Table 4.3). Post-hoc tests revealed that habitats differed significantly between lakes with low and high WLF at the shallowmost sampling depth (pseudo- $t = 2.18$, $p = 0.003$), while differences at the intermediate sampling depth were bordering on statistical significance (pseudo- $t = 1.58$, $p = 0.073$). No differences in habitat structure were, however, found between lakes with low and high water level fluctuations at the deepest sampling sites.

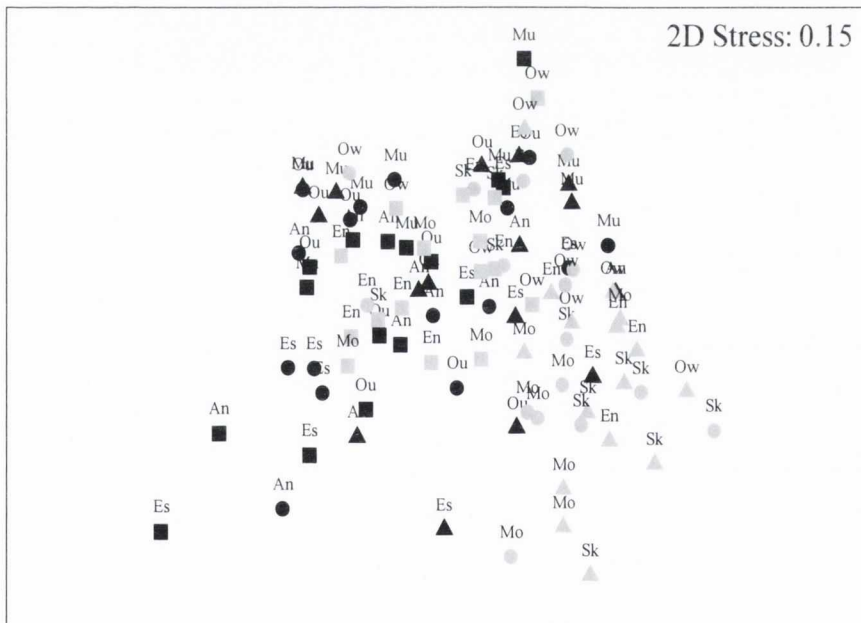


Fig. 4.4. Non-metric multi-dimensional scaling illustrating differences in habitat structure along the depth gradient (shallow sites: triangles; intermediate sites: circles; deep sites: squares) in lakes with low (grey symbols) and high (closed symbols) water level fluctuations. Labels are as follows: Ou- Oughter; Mu- Muckno; An- Anure; Es- Eske; Mo- Moher; Sk – Skeagh; Ow – Owel; En – Ennel.

Table 4.3. Results of PERMANOVA testing for differences in the littoral habitat structure in lakes experiencing low and high water level fluctuations. Significant effects are highlighted in bold.

Response	Source of variation	d.f.	Pseudo- <i>F</i>	<i>p</i>
Habitat structure	WLF	1	3.60	0.029
	Depth	2	8.24	≤0.0001
	Lake (WLF)	6	2.14	0.003
	WLF*Depth	2	3.09	0.003
	Transect(Lake(WLF))	24	2.01	≤0.0001
	Residual	60		

SIMPER analysis (Table 4.4) revealed that lakes with high amplitude of water level fluctuations had greater proportions of pebble, cobble, boulders and bedrock at the shallowmost sampling depth coupled with less gravel and macrophyte cover than lakes with low water level fluctuations.

Table 4.4. Results of SIMPER analysis identifying the contribution (%) of different aspects of littoral habitat structure to the dissimilarity between lakes with low and high amplitudes of water level fluctuations at the shallowmost water depth.

Habitat type	Mean %		Contribution (%)	Cumulative contribution (%)
	Low WLF	High WLF		
Gravel	46.3	17.8	32.54	32.54
Pebble	27.5	40.2	19.84	52.38
Cobble	5.23	17.7	17.62	70.00
Macrophytes	7.57	2.63	8.56	78.56
Soil	3.41	0.66	4.52	83.08
Bedrock	0	4.08	4.49	87.58
Boulder	0	5.95	4.12	91.70
CWD/debris	4.05	2.22	3.12	95.10

4.3.2. Benthic algae

Two hundred and twenty-two diatom algal taxa were recorded in total from the sampled lakes (Appendix 4.1). Of these, 11 were documented in all eight lakes and 71 were found only in a single lake. Fifty-four taxa were found only in lakes with low WLF and 28 in the lakes with high WLF. The percentage abundance of motile diatom taxa varied significantly with water level fluctuations along the depth gradient (ANOVA; $F_{2,70} = 5.86$, $p = 0.006$; Table 4.5).

Table 4.5. Results of ANOVA testing for differences in the (log-transformed) percentage abundance of motile benthic algae in lakes experiencing low and high water level fluctuations. Significant effects are highlighted in bold.

Response	Source of variation	d.f.	F-ratio	p
Motile diatoms	WLF	1	0.84	0.394
	Depth	2	2.93	0.064
	Lake (WLF)	6	13.05	≤ 0.0001
	WLF*Depth	2	5.86	0.006
	Transect(Lake(WLF))	16	2.139	0.024
	Residual	43		

Post-hoc tests revealed that the relative abundance of motile diatoms was significantly greater at the shallowmost ($t = 3.47$, $p = 0.01$) and intermediate ($t = 6.80$, $p \leq 0.0001$) sampling depths in lakes with high WLF (Fig. 4.5).

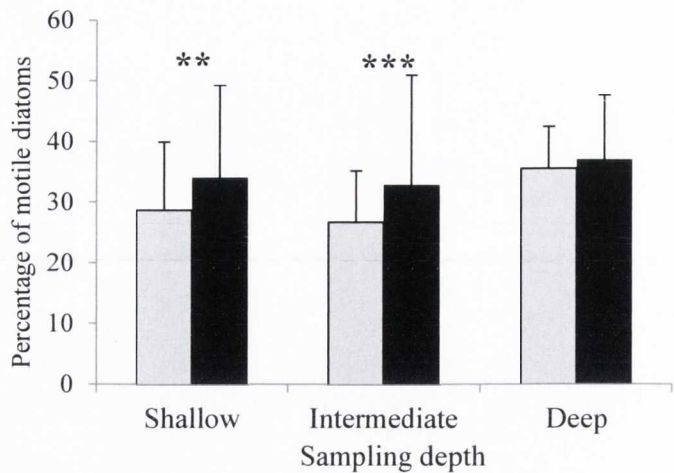


Fig. 4.5. Percentage of motile diatoms (mean + s.e., $n = 4$) in lakes with low (grey bars) and lakes with high (black bars) water level fluctuations. Untransformed data are shown here for clarity. Asterisks indicate the level of significance for the individual depths (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

I found no significant main or interactive effects of water level fluctuations on any of periphyton biomass, the autotrophic index or any measure of algal diversity (taxonomic or phylogenetic). However, the interaction between water level fluctuations and depth on diatom assemblage structure was bordering on statistical significance (PERMANOVA; pseudo- $F_{2,44} = 1.37$, $p = 0.064$; Table 4.6; Fig. 4.6).

Table 4.6. Results of PERMANOVA testing for differences in the taxonomic structure of benthic algae (log (x+1) transformed relative abundance) in lakes experiencing low and high water level fluctuations. Significant effects are highlighted in bold. Asterisks * indicate Monte Carlo obtained p -values.

Response	Source of variation	d.f.	Pseudo- F	p
Taxonomic structure	WLF	1	0.49	0.85*
	Depth	2	2.69	≤ 0.0001
	Lake (WLF)	6	9.16	≤ 0.0001
	WLF*Depth	2	1.37	0.064
	Transect(Lake(WLF))	16	1.65	≤ 0.0001
	Residual	44		

The taxonomic structure of benthic algae was rather affected by water chemistry than differences in water level regimes and was similar in lakes with higher mean total phosphorus such as Oughter, Muckno and Skeagh (Table 4.1; Fig. 4.6).

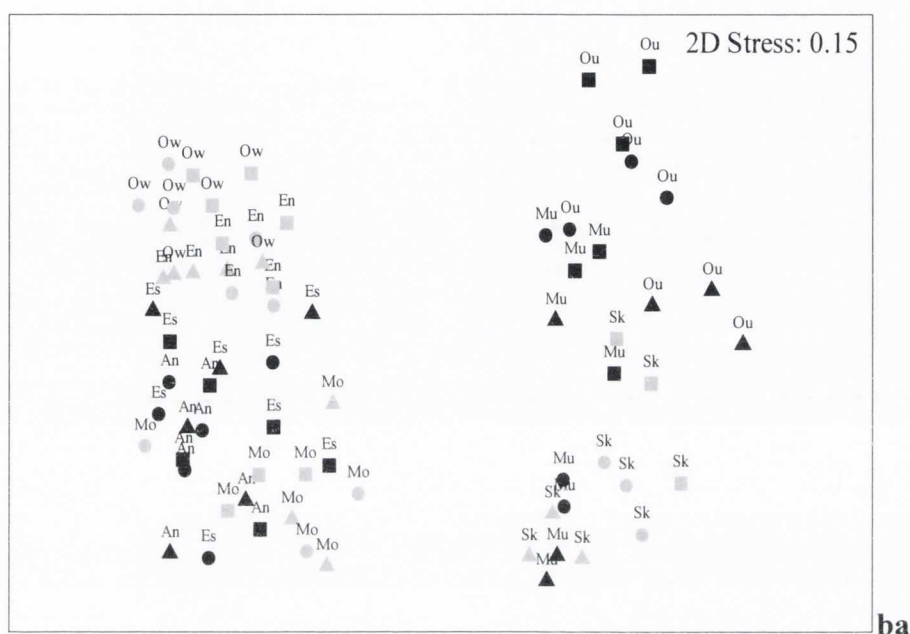


Fig. 4.6. Non-metric multi-dimensional scaling illustrating differences in the structure of benthic algae along the depth gradient (shallow sites: triangles; intermediate sites: circles; deep sites: squares) in lakes with low (grey symbols) and high (closed symbols) water level fluctuations. Labels are as follows: Ou- Oughter; Mu- Muckno; An- Anure; Es- Eske; Mo- Moher; Sk – Skeagh; Ow – Owel; En – Ennel.

4.3.3. Benthic invertebrates

One hundred and twenty-nine taxa of littoral benthic invertebrates were recorded in total from the eight surveyed lakes (Appendix 4.2). Of these, nine were common to all lakes and 55 taxa were found in only a single lake. Thirty-five invertebrate taxa were found only in lakes with low and thirty-two only in lakes with high water level fluctuations. Noteworthy is the fact that six gastropod species were found only in lakes with low WLF while two species (*Bithynia tentaculata* [Bithyniidae] and *Viviparus viviparus* [Viviparidae]) were recorded only from the intermediate and

deep depths in lakes with high WLF. Both *B. tenatculata* and *V. viviparous* have an operculum. Furthermore, individuals from the inoperculate gastropod species, that were common for the two lake groups, were recorded mostly at the intermediate or deep sampling sites in lakes with high WLF, while they were found in high densities at the shallowmost depth of lakes with low WLF.

There was no difference found between lakes experiencing low and high amplitude of water level fluctuations in the total number of taxa, density, rarefied taxon richness and the taxonomic and phylogenetic diversity of benthic invertebrates or any of the established disturbance metrics (BMWP, ASPT and EPT scores). However, the amplitude of water level fluctuations interacted significantly with depth in their effects on the evenness of invertebrate assemblages (ANOVA; $F_{2,44} = 2.91$, $p = 0.037$; Table 4.7, Fig. 4.7). Pair-wise post-hoc tests were, however, inconclusive.

Table 4.7. Results of ANOVA testing for differences in the evenness of benthic invertebrates in lakes experiencing low and high water level fluctuations. Significant effects are highlighted in bold.

Response	Source of variation	d.f.	F-ratio	p
Evenness	WLF	1	2.09	0.18
	Depth	2	6.184	0.004
	Lake (WLF)	6	3.88	0.002
	WLF*Depth	2	2.91	0.037
	Transect(Lake(WLF))	16	0.45	0.96
	Residual	44		

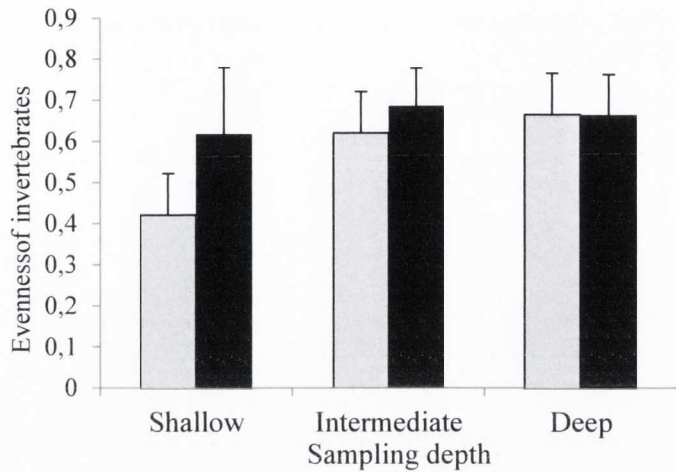


Fig. 4.7. Diversity of benthic invertebrate assemblages (mean + s.e., $n = 4$) measured as Peilou’s evenness in lakes with low (grey bars) and high (black bars) water level fluctuations. Pair-wise post-hoc tests were inconclusive at $p < 0.05$.

I found differences in taxonomic structure of benthic invertebrate assemblages between lakes with low and high water level fluctuations that interacted significantly with water depth (PERMANOVA; pseudo- $F_{1,44} = 2.24$, $p \leq 0.001$; Table 4.8, Fig. 4.8a). The pair-wise post-hoc tests were, however, inconclusive at $p < 0.05$.

Table 4.8. Results of PERMANOVA testing for differences in taxonomic, trophic and locomotive structure of benthic invertebrates (log (x+1) transformed data) in lakes experiencing low and high water level fluctuations. Significant effects are highlighted in bold. Asterisks * indicate Monte Carlo obtained *p*-values.

Response	Source of variation	d.f.	Pseudo- <i>F</i>	<i>p</i>
Taxonomic structure	WLF	1	0.96	0.47*
	Depth	2	5.12	≤ 0.0001
	Lake (WLF)	6	5.07	≤ 0.0001
	WLF*Depth	2	2.24	0.0009
	Transect(Lake(WLF))	16	1.90	≤ 0.0001
	Residual	44		
Trophic structure	WLF	1	4.15	0.043
	Depth	2	10.60	≤ 0.0001
	Lake (WLF)	6	3.99	0.0004
	WLF*Depth	2	1.35	0.249
	Transect(Lake(WLF))	16	1.14	0.309
	Residual	44		
Locomotive structure	WLF	1	2.43	0.14*
	Depth	2	9.62	0.0002
	Lake (WLF)	6	4.48	0.0004
	WLF*Depth	2	2.81	0.045
	Transect(Lake(WLF))	16	1.09	0.380
	Residual	44		

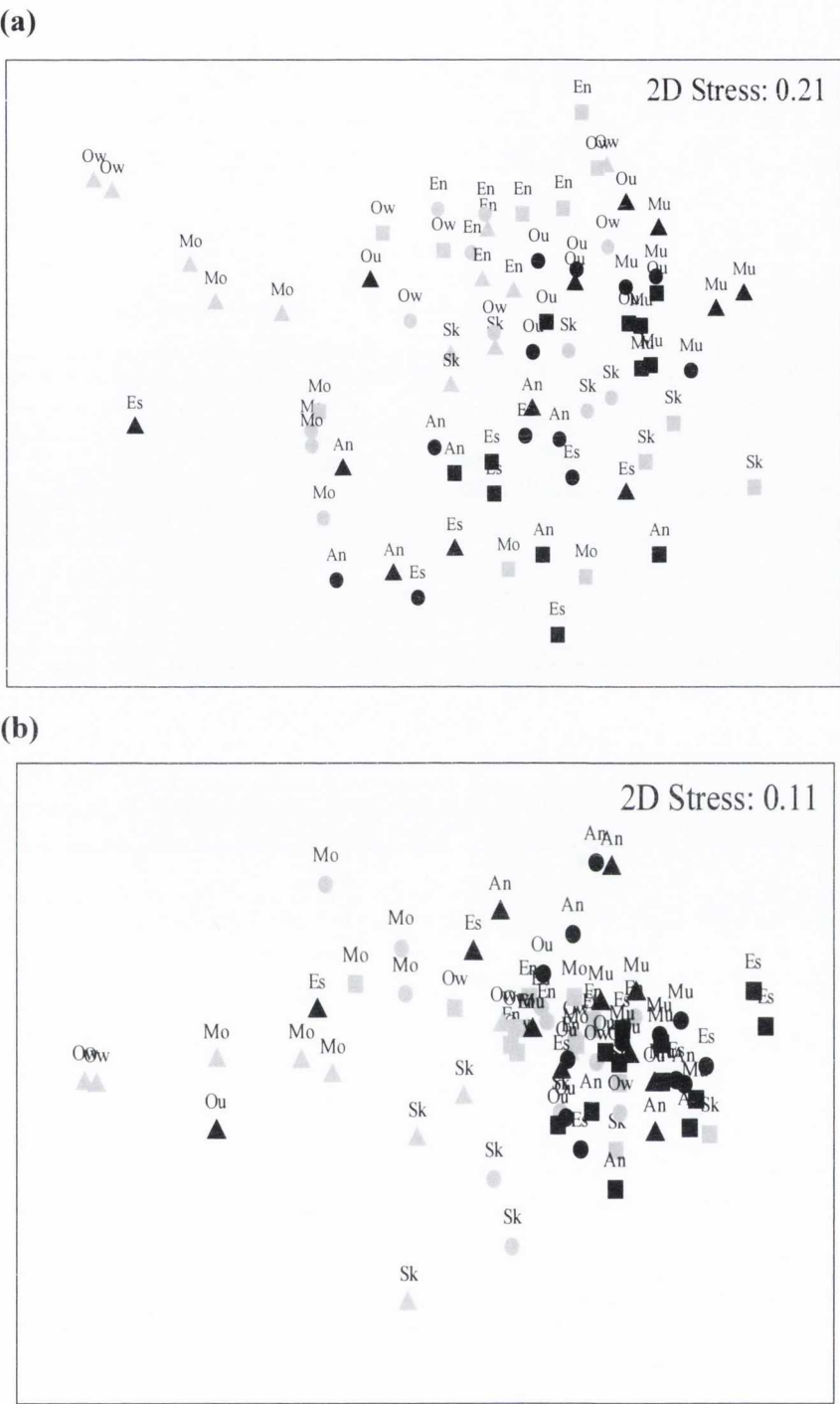


Fig. 4.8. Non-metric multi-dimensional scaling illustrating differences in the (a) taxonomic, (b) trophic and (c) locomotive structure of benthic consumers along the depth gradient (shallow sites: triangles; intermediate sites: circles; deep sites: squares) in lakes with low (grey symbols) and high (closed symbols) water level fluctuations. Labels are as follows: Ou- Oughter; Mu- Muckno; An- Anure; Es- Eske; Mo- Moher; Sk – Skeagh; Ow – Owel; En – Ennel.

(c)

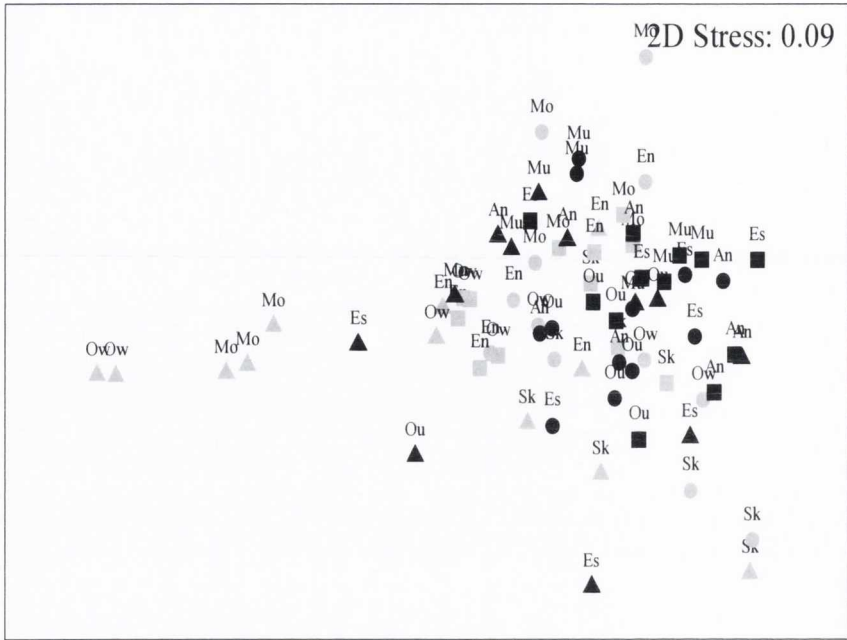


Fig. 4.8. Continued.

SIMPER analysis (Table 4.9) revealed that lakes with high amplitude of water level fluctuations had higher oligochaete and chironomid densities at the shallow and intermediate sampling depths and lower density of crustaceans *Gammarus duebenii* and *Asellus aquaticu* at all depths. Densities increased for *Crangonyx pseudogracilis* at all depths and *G.pulex* at the first two depths.

Table 4.9. Results of SIMPER analysis identifying the five benthic invertebrate taxa that contributed most strongly to the dissimilarity between lakes with low and high water level fluctuations along the depth gradient. Untransformed data are shown for clarity.

Sampling depth	Taxon	Mean abundance		Contribution (%)
		Low WLF	High WLF	
Shallow				
	<i>Gammarus duebeni</i>	47.76	15.94	29.81
	Oligochaeta	16.27	14.37	12.47
	Chironomidae	8.39	19.73	11.43
	<i>Asellus aquaticus</i>	10.56	3.81	8.04
	<i>Gammarus pulex</i>	0.00	8.14	5.48
Intermediate				
	Chironomidae	13.01	27.29	15.33
	Oligochaeta	22.59	20.25	14.03
	<i>Proasellus meridianus</i>	12.79	0.00	9.55
	<i>Asellus aquaticus</i>	10.53	5.78	9.11
	<i>Gammarus duebeni</i>	8.79	4.62	6.21
Deep				
	<i>Asellus aquaticus</i>	18.46	6.29	14.58
	Chironomidae	16.40	29.57	12.49
	Oligochaeta	12.71	23.40	11.39
	<i>Gammarus duebeni</i>	10.56	1.53	8.46
	<i>Radix ampla/labiata</i>	1.80	5.70	5.04

The trophic structure of benthic invertebrate assemblages varied significantly between lakes with low and high water level fluctuations (PERMANOVA; pseudo- $F_{1,44} = 4.15$, $p = 0.043$; Table 4.8). There was a notable decrease in relative abundance of shredders and increase in predators in lakes with high fluctuations in water level (Table 4.10), findings that were highly consistent with the results from my mesocosm experiment (Chapter 3).

Table 4.10. Results of SIMPER analysis identifying the contribution of different trophic groups to the dissimilarity between lakes with low and high water level fluctuations. Untransformed data are shown for clarity.

Functional feeding group	Mean abundance		Contribution (%)
	Low WLF	High WLF	
Shredders	24.05	11.15	28.93
Gatherers/ Collectors	46.45	46.49	26.02
Grazers and scrapers	15.11	17.10	16.71
Predators	6.96	10.02	11.15
Filter feeders	3.87	8.57	9.69

The locomotive structure of benthic invertebrate assemblages varied significantly along the depth gradient in lakes with contrasting water level regimes (PERMANOVA; pseudo- $F_{1,44} = 2.81$, $p = 0.046$; Table 4.8). Pair-wise tests revealed significant differences between the lakes with contrasting water level fluctuations at the deepest sampling sites (pseudo- $t = 2.10$, $p_{MC} = 0.039$) but there was no measurable effect at either the shallow or intermediate sampling depths. This shift in locomotive structure is attributable to a decrease in the relative abundance of swimming and sprawling/ walking species coupled with an increase in the relative abundance of burrowing, boring and (semi) sessile species in lakes with high WLF (Table 4.11).

Table 4.11. Results of SIMPER analysis identifying the contribution of invertebrate locomotive type to the dissimilarity between lakes with low and high water level fluctuations at the deepest sampling sites. Untransformed data is shown for clarity.

Locomotive type	Mean abundance		Contribution (%)
	Low WLF	High WLF	
Swimming	26.38	15.08	27.57
Burrowing/ boring	11.13	21.02	26.98
(Semi) sessile	16.83	23.67	25.16
Sprawling/ walking	45.67	40.23	20.29

My results imply that greater fluctuations in water level may trigger not only significant changes in the taxonomic, trophic and locomotive structure of benthic consumers communities but may also lead to homogenisation along the depth gradient (Fig. 4.8). This effect is particularly noticeable in the zone of water level fluctuations (at the shallow and to a certain extent at the intermediate depths) where the variability in the assemblages appears to be greater among lakes.

4.4. Discussion

My results indicate strongly that there are significant differences in the ecology of lake littoral zones in lakes with contrasting water level regimes, related not only to the structure and functioning of benthic assemblages, but also habitat structure. Notably, some of the recorded responses in lakes with high annual and monthly amplitude of water level fluctuations were mediated by the depth gradient, whereas for others they were not. The findings from my observational study are highly consistent with results from the mesocosm experiment described in Chapter 3. Moreover, they support the potential for the development of a set of metrics based on taxonomic, trophic or locomotive structure of littoral invertebrates, as well as highlighting the impacts of hydromorphological pressures on lake ecosystems.

Littoral substrate significantly different in lakes with lower and higher water level fluctuations and this alteration was mediated by depth. The habitat component that contributed mostly to the dissimilarities (33%) between habitats at the shallowmost depth was the reduced proportion of gravel (a smaller size fraction) in lakes with high monthly and annual amplitudes in water level fluctuations. In addition, the larger size fractions (boulders and bedrock) were recorded at the shallow sampling sites only from lakes experiencing high water level fluctuations. Possible explanation of these differences may be the altered position of the upper littoral zone as a result of a rise (conversion of terrestrial into aquatic habitat) or drop (shift of the littoral zone lakewards) in water level. These findings confirm the speculations of Hofmann *et al.* (2008) that long-term water level fluctuations could induce a slow displacement of the shore line with continuous interplay between short- and long-term water level fluctuations being responsible for shaping shore morphology and determining

sediment grain size distribution. The reduction of gravel cover could trigger changes in lake geomorphology and wave dynamics thus affecting vegetation zonation (Schmieder 2004). My results imply that alterations to the amplitude of water level fluctuations could lead to habitat shifting or loss and modify directly the particle size distribution of benthic substrates in lake littoral zones. Moreover, reducing niche availability through homogenisation or alteration of substrate structure could reduce lake biodiversity and impoverish ecosystems (Weatherhead & James 2001), and therefore reduce their buffering capability against the ecological impacts of other human disturbances such as nutrient pollution (Cardinale 2011). In addition, I found a three-fold reduction in the percentage of macrophytes at the shallow depth in lakes with high water level amplitudes in comparison with lakes with low fluctuations, likely because of direct physical stress. Extreme water level fluctuations have been shown previously to have an adverse effect on macrophytes in lake littoral zones, such as decrease in diversity or even complete disappearance (Rørslett 1984, 1985, Hellsten 2002, Acreman *et al.* 2005, Valdovinos *et al.* 2007).

Variation in water level regimes interacted significantly with water depth in their effects on the abundance of motile diatom species and these effects were bordering on statistical significance for the evenness of benthic invertebrates. Both percentage of motile diatoms and macroinvertebrates evenness were higher in lakes with higher monthly and annual amplitudes. Motile algal species, likely because of being more adaptable and being able to cope with moderate rising of water levels or draw-downs, were found to increase in lakes with greater variations in water level, at both the shallow and intermediate depths. Their prevalence could potentially be ascribed to the increased niche availability as a result of the disappearance or decreased density of less tolerant algal taxa. Littoral invertebrates are known to be dependent on habitat type and availability (Tolonen *et al.* 2001, Schindler & Scheuerell 2002, Hering *et al.* 2004, Tolonen *et al.* 2005, Brauns *et al.* 2007b). Therefore, the increase of evenness of littoral invertebrates could potentially be associated with the significance of water level regimes for habitat structure.

Somewhat surprisingly, greater water level fluctuations alone or interacting with depth had no measurable effect on any of the other univariate taxonomic or phylogenetic diversity metrics of both diatoms and invertebrates. However, the lack

of association could be attributed to the multifactorial interactions and complexity of freshwater bodies that necessitates taking into consideration various abiotic and biotic factors when studying impacts of water level fluctuations (Palomäki 1994, Furey *et al.* 2006, Mastrantuono *et al.* 2008). Moreover, Furey *et al.* (2006) suggested that the effects of water abstraction extended below the exposure zone that was repeatedly desiccated and inundated, thus explaining the equal or greater macroinvertebrate density and biomass in reservoirs subjected to regular draw-down compared with lakes with natural patterns of WLF. Regardless of the absence of significant differences in overall water chemistry between the lakes with high and low WLF, the studied lakes represented a broad range of nutrients and lake size. The effects of amplified water level fluctuations were, therefore, hard to disentangle from the effects of other factors, in particular for algal benthic communities. Miller *et al.* (2007) demonstrated that even though discharge magnitude and duration could potentially affect river macroinvertebrate responses to water withdrawals, hydrological disturbance alone did not have direct, unfavourable impacts. Rather, the synergistic effects of multiple environmental variables shifted the structure and functioning of macroinvertebrate communities substantially and the likelihood of observing detrimental indirect effects increased with the magnitude and duration of low flow events (Miller *et al.* 2007). Noteworthy is the fact that predominantly stony habitats were studied. As shown by Tolonen & Hämäläinen (2010), the assemblage of stony substrate (in comparison with all other substrates) is particularly sensitive to water chemistry (51% of the explained variation was due to human-induced changes in water chemistry) which could further hinder detecting an effect of WLF on univariate metrics.

Smith *et al.* (1987) found that relatively small changes in water level can be equally destructive to the littoral macrophyte and benthic assemblages. Contrasting regimes of water level fluctuations generated a suite of community responses. Their effects could be either direct (physical stress) or indirect (through *e.g.* modifying habitat complexity, resources availability and overall environmental conditions). I found a significant change in taxonomic structure of invertebrates and bordering on significance for diatoms. These findings support the findings from my experimental study. I also found that WLF reduced the extent of variability in the taxonomic, trophic and locomotive structure of benthic invertebrate assemblages with depth.

Thus, my results demonstrate clearly the greater potential in linking fluctuations in water level with multivariate biological responses rather than with univariate metrics. Multivariate analyses are affected by both identity of various units (being species, feeding or locomotion type) simultaneously with their density or percentage, which makes them more sensitive to disturbances (Warwick & Clarke 1993). Moreover, in recent years many studies (Townsend *et al.* 1997b, Statzner *et al.* 2004, Bjelke *et al.* 2005, Céréghino *et al.* 2011) suggest using biological traits might give a greater insight into revealing the impacts of environmental conditions and habitat changes on lake biota.

The shift in community structure of benthic invertebrates in lakes with contrasting water level regimes was mediated by sampling depth. There was an overall decrease of crustacean species at all sampling depths, which was consistent with the findings from the mesocosm experiment. There was a decrease in densities for both native amphipods (*Gammarus pulex*) and isopods (*Asellus aquaticus* and *Proasellus meridianus*) in the lakes with high WLF, while the invasive amphipod *Crangonyx pseudogracilis* increased in density at all sampling depths. *Gammarus pulex*, another alien amphipod (Dick *et al.* 1990, Costello 1993) was recorded only from lakes with higher amplitude of water level fluctuations. Furthermore, alteration of water level amplitudes could be translated into disturbed oxygen regimes (Acreman *et al.* 2005, Hofmann *et al.* 2008) and reduced food availability for macroinvertebrates which aid the replacement of *G. duebenii* by *G. pulex* together with the interguild predation and the more aggressive nature of *G. pulex* (Dick *et al.* 1990, Macneil *et al.* 1997, Dick 2008). As based on these result we could speculate that the settlement of invasive species might be mediated by the hydrological stress or overall decrease in ecosystem resilience (Naeem 2009) and thus affecting functionality rather than only taxonomic structure.

Moreover, greater was the number of gastropod taxa found in lakes with low WLF, from which 6 species were recorded only for this water level group. Inoperculate species were found exclusively in lakes with low fluctuations or on the rare occasions when recorded in lakes with high WLF they were registered at the intermediate or deep depths. In addition to the direct physical disturbance through shifting of the littoral zone, gastropods in lakes with high fluctuations might be subjected to trophic

stress as well. They rely partially on macrophytes as a food source (Cummins & Klug 1979) and as demonstrated here and by other authors (Hill *et al.* 1998, Mastrantuono *et al.* 2008, Wantzen *et al.* 2008b), water level fluctuations could result in decline of macrophytes biomass and diversity. Moreover, the two gastropod species found only in lakes with high WLF had an operculum, which enables the snails to resist desiccation (Gibson 1970) and to survive periods of drought and thus a probable displacement of the littoral zone.

The operculate alien *Potamopyrgus antipodarum* was recorded in greater density at the shallow depth in two transects in Lough Eske, lake with the lowest WLF from the high fluctuation group (see Table 4.1). A few specimens from the same species were also recorded from Lough Anure. It is important to note that the sampling in these two lakes took place after the water receded, immediately following a flooding event. As demonstrated in the mesocosm experiment (Chapter 3), the same gastropod species was found in greater densities at the intermediate depth in mesocosm with amplified WLF, indicating that the specimens might have migrated from the shallow to the intermediate depth during the draw-down periods, and survived there. These results suggest that there is a good potential for utilising gastropods as useful biological indicators of the magnitude and timing of amplified water level fluctuations, as suggested also by Mastrantuono *et al.* (2008). The potential of Trichoptera and Ephemeroptera to respond to WLF was not supported by my findings and thus needs to be examined further in more lakes. As indicated by my results and the findings of Chapter 2, incorporating the timing of extreme events and amplitude of fluctuations at various temporal scales into field sampling programmes, coupled with sampling on more than one occasion, could enhance significantly our knowledge and assist in developing robust metrics for quantifying hydrological disturbances.

The trophic structure of invertebrate assemblages varied significantly among lakes varying in the amplitudes of water level fluctuations, consistent with the results of the mesocosm experiment described in Chapter 3. This was due mostly to a more than two-fold decrease of shredders in lakes with high WLF, which is likely attributable to reductions in food availability. Shredders feed on coarse particulate matter with preferences for the most microbially colonised material (Cummins & Klug 1979). They depend, therefore, on the input of allochthonous matter from the riparian zone

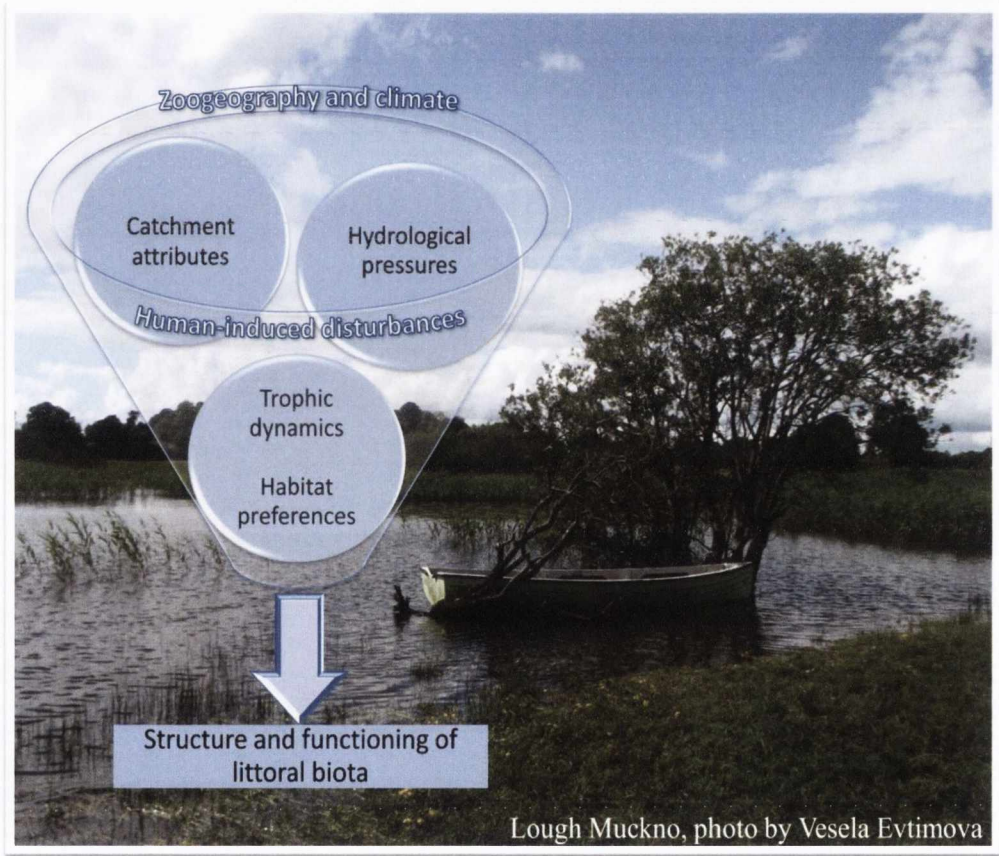
which could be impeded by the shifting of the littoral zone lakewards (Weatherhead & James 2001, Wantzen *et al.* 2008a). Further, these specialised feeders are thought to be more sensitive to perturbations owing to the more restricted range of available food sources (Rawer-Jost *et al.* 2000).

Higher densities of generalist feeders, such as gatherers, collectors and filter feeders, in lakes with high water level fluctuations, could be attributable to the ability of these invertebrates to employ various feeding strategies and tolerate changes in food availability owing to their broad range of potential food sources (Cummins & Klug 1979, Barbour *et al.* 1996). Moreover, the significantly higher percentage of predators in lakes with high water level fluctuations was likely driven by the probable high availability of potential prey, both aquatic and terrestrial. These results are all consistent with the experimental findings from Chapter 3 and with results for rivers (Marks *et al.* (2000). Alteration of trophic structure of macroinvertebrates would not only have important implications for essential ecosystem services that support human well-being, such as fisheries (Menezes *et al.* 2010), but could possibly trigger changes in the whole lake. It is known that littoral invertebrates have intermediate position in energy and matter flow and that lake littoral provides important food subsidies both to adjacent terrestrial habitats and to associated aquatic ecosystems (Vander Zanden & Vadeboncoeur 2002, Sabo *et al.* 2009, Wesner 2010, 2011).

The water chemistry and catchment attributes of the sampled lakes covered a broad range. Nonetheless, the effects of water level fluctuations on littoral assemblages and habitat structure were still detectable. My results are indicative of the capacity of multivariate community metrics to respond to disturbance in water level regime, while other environmental factors might override water level fluctuations as the major causal factor for the univariate response measures of diversity and density. This highlights the importance of taking a multi-trait approach when studying benthic communities in detection of specific impacts of WLF under multiple stressor scenarios and highlights the potential of multivariate community metrics in detecting biological responses to alterations in the environment, supporting the conclusions from other studies (e.g. Warwick & Clarke 1993). My findings have, therefore, important practical implications in monitoring and management. Several studies (*e.g.* Charvet *et al.* 2000, Menezes *et al.* 2010) reveal that biological traits are more

appropriate for detecting human disturbances than taxon abundance- based metrics. Therefore, the sole use of taxon-derived metrics in environmental monitoring and assessment could result in incomplete and inaccurate conclusions and management decisions. On the other hand, benthic invertebrates tend to comprise the significant majority of total prey consumption for many commercially valuable species of fish (Vander Zanden & Vadeboncoeur 2002) and incorporating a functional trait approach could ultimately improve the communication to managers and policy makers of the importance of protecting ecosystem functions (Menezes *et al.* 2010). This study indicates clearly that including both biological traits and sampling depth in existing and in future monitoring programmes could improve significantly our ability to detect and predict effects of amplified water level fluctuations on lake ecosystems.

5. Synthesis and Conclusions



Relationships among large-scale factors that shape the structure and functioning of lake biota.

This study comprises an important step towards improving our ability to quantify water level regimes and our perception of the ecological effects of amplified water level fluctuations and, therefore, towards improving our ability to assess robustly the ecological impacts of this globally important pressure on standing water ecosystems. This task is feasible only after we acquire the knowledge to describe the pressure itself. The novelty of my work comprises the multifaceted approach in defining the potential disturbance as a result of an alteration of water level regimes in lake. The proposed metrics could also be used as a baseline in describing natural water level regimes in lakes. Furthermore, in Chapter 2 I identified the potential risk with respect to the catchment characteristic of the lakes, whereas the mesocosm experiment served to enhance our understanding of the direct effects of amplified water level fluctuations and the mechanisms in operation.

The number of multi-lake studies on changes in water levels is limited. Smith *et al.* (1987) studied physical conditions, macrophytes and macroinvertebrates in the littoral zones of 27 Scottish lochs with different regimes of water-level variations. There are a few studies focusing on the impact of water levels, rather than on measuring the pressure itself: Aroviita & Hämäläinen (2008) compared the effects of water-level regulation in 11 lakes to those in 12 unregulated (reference) lakes for a period of 20 years. Beklioglu (2007) studied WLF in five shallow lakes in Turkey. Valdovinos *et al.* (2007) compared the effects of WLF on benthic macroinvertebrates in regulated and unregulated lakes in the Chilean Andes. My observational study complemented my results through exploring these effects through a multi-level approach, incorporating impacts on the littoral environment, as well as the multi-trait response of primary producers and benthic consumers (Fig. 5.1).

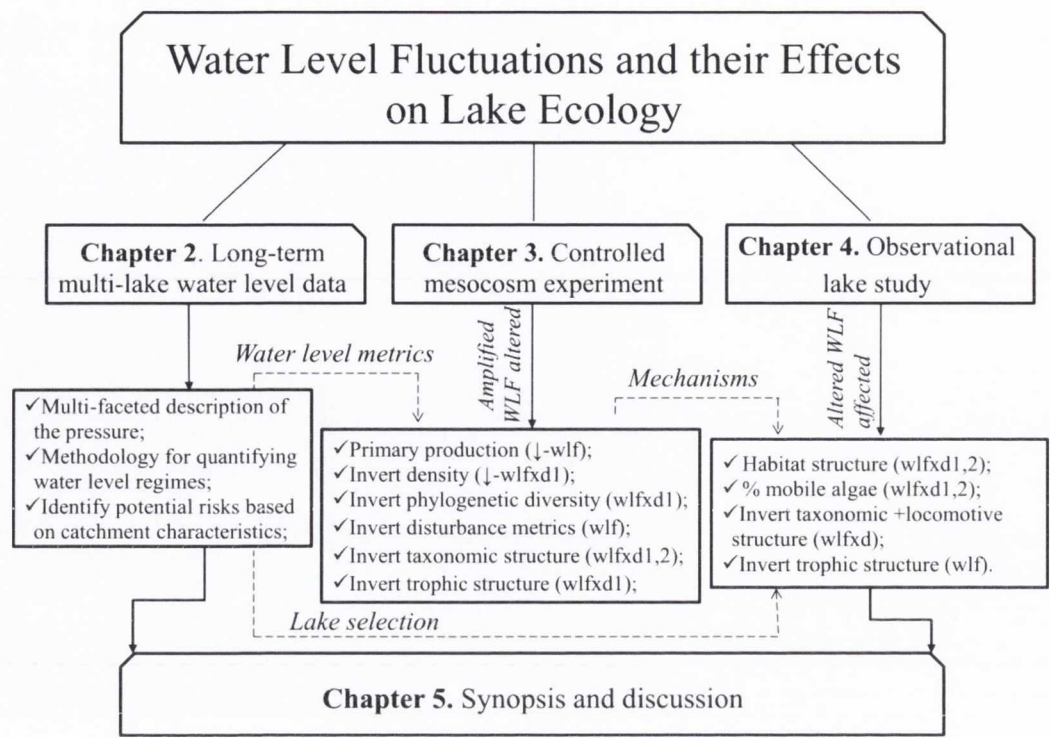


Fig. 5.1. Structure and outline of the thesis with a summary of the main findings.

5.1. Water level regimes

Freshwater availability and the conservation of aquatic resources are key to human well-being (Arthurton *et al.* 2007). Projected global increases in water abstraction triggered by escalating water demand (Palmer 2010, UNESCO 2011), decreases in biodiversity (Abramovitz 1996, McCann 2000, Balian *et al.* 2008) and intensification of ecosystem degradation (Jackson *et al.* 2001, Palmer *et al.* 2004, Sophocleous 2004) are among the leading threats to the sustainability of human populations. Scientists are becoming increasingly aware that freshwater systems are among the most threatened ecosystems (e.g. Johnson *et al.* 2001, Saunders *et al.* 2002, Brown *et al.* 2010, Holland *et al.* 2012) with the main pressures being hydromorphological stress, impacts of nutrient loading and introduction of alien species (Saunders *et al.* 2002, Bragg *et al.* 2003, Solimini *et al.* 2006, Wantzen *et al.* 2008b). Despite its growing prevalence, research on the ecological impacts of changes in water level regimes lags far behind that of other human disturbances (e.g. eutrophication, acidification, etc.).

5.1.1. Water level metrics

Ensuring sustainable water use and maintaining habitat connectivity and natural hydrological regimes are essential to strike a balance between ecosystem and human needs (Palmer *et al.* 2004, Renöfält *et al.* 2010). River flow metrics are being used increasingly to define hydrological variation and compare rivers in efforts to minimize conflicts between these competing demands (Richter *et al.* 1997, Kennard *et al.* 2010a, Kennard *et al.* 2010b). Lake water level regimes have, however, received little attention with this respect. Water level regimes are extremely complex, yet often are over-simplified when analysing biological data with most studies focusing on intra-annual water level fluctuations (White *et al.* 2008). The novelty of my work includes proposing an extensive array of various metrics, describing the magnitude, duration, frequency, timing and rate of change of water level regimes of lakes. Another valuable contribution of this thesis includes the identification of subset of parsimonious metrics for characterising water level regimes. Regardless of their high variability, pronounced seasonality was evident in the monthly and seasonal water level fluctuations of all lakes analysed. Further, the novel measure of temporal rate of change in water level amplitudes, which integrates the range of water level fluctuations across different temporal scales, proved to be a good descriptor of lake water level regimes. My results demonstrate that the inclusion of water level metrics exemplifying only one temporal scale could yield incomplete and inaccurate conclusions and management decisions. This is a key finding since it recognises that the incorporation of temporal variability across scales will not only enhance our ability to describe and quantify water level regimes, but has important practical implications for monitoring programmes and scientific field-studies.

5.1.2. Contribution of landscape attributes

Freshwater ecosystems are defined largely by their hydrology and hydrological regimes reflect the complex natural processes which operate on catchment scales (Smakhtin 2001, Wantzen *et al.* 2008a, Weyhenmeyer 2008). Landscape context is critical for interpreting ecosystem responses to pressures (Donohue *et al.* 2006, Wantzen *et al.* 2008b, Harrault *et al.* 2012) and catchments are recognised as a basic organisational unit for understanding and managing freshwater ecosystem processes (Wantzen *et al.* 2008a, Brown *et al.* 2010). In Chapter 2, I describe how I developed

water level metrics that could be incorporated in lake management and policy development practices. As far as I am aware, this is the first study to investigate the underlying relationship between water level fluctuations and catchment attributes. Models relating hydrological regimes to catchment features were significantly better than the corresponding null models. The results revealed that water level amplitudes across temporal scales were associated significantly with relative ecosystem size and were thus likely a function of lake residence time, while the occurrence of extreme monthly and seasonal events were mediated by shoreline length and catchment slope. These findings suggest strongly that impacts of hydromorphological disturbances on littoral biota may vary in accordance with relative ecosystem size or ecosystem morphometry. This suggests clearly that there is strong potential to derive methodology identifying potential risks for lake hydrological regimes based on their catchment and landscape characteristics. Identifying systems at risk at an early stage could be crucial for adequately preventing ecosystem degradation and for guiding efforts to restore or maintain ecosystem integrity and biodiversity.

5.2. Impacts of amplified water level fluctuations

The multifactorial interactions and complexity of lake ecosystems necessitates taking into consideration many abiotic and biotic factors when studying impacts of water level fluctuations (Palomäki 1994, Furey *et al.* 2006, Mastrantuono *et al.* 2008). Water level fluctuations could potentially affect all physical or biological interactions occurring in a lake, for instance through influencing the input of allochthonous matter, such as leaves or coarse woody debris, which could be washed in from the riparian zone during the Autumn or Winter maximal water levels. The major problem in understanding processes in lake littoral zones comprises, therefore, the interplay between depth, substrate, detritus, plant biomass, predation and macroinvertebrates (Weatherhead & James 2001; Fig. 5.2).

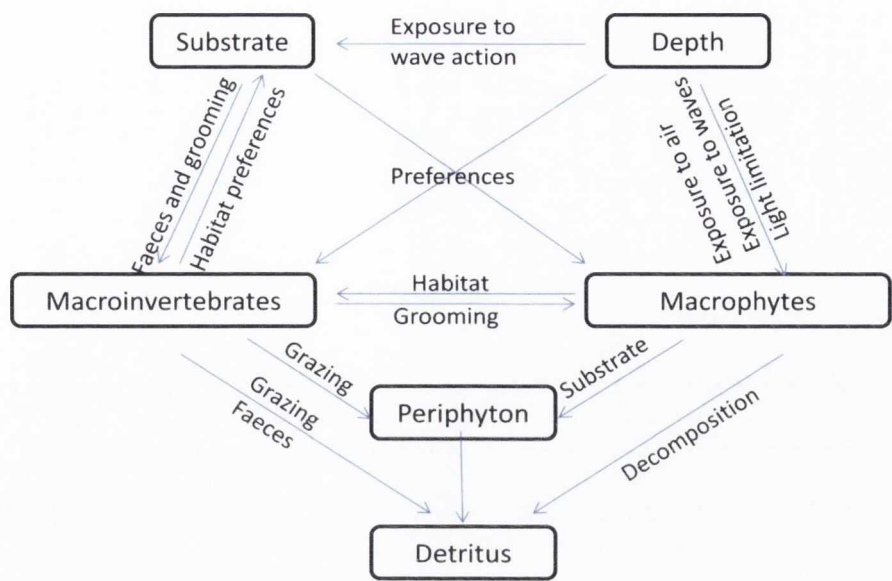


Fig. 5.2. Physical and biological interactions in the littoral zone of lakes (adapted from Weatherhead & James 2001).

5.2.1. Impacts on habitat structure

Littoral habitat structure in lakes experiencing high water level fluctuations differed significantly from those with low fluctuations (Chapter 4). Higher monthly and annual fluctuations were associated with decrease in the percentage of smaller-sized substrate fractions, consistent with the observations of Furey *et al.* (2004). A possible explanation of this is that they were transported from the shore by frequently moving water and also owing to the fact that sampling was conducted when water levels were low. Further, the largest size fractions, such as boulders and bedrock, were recorded at the shallow sampling sites only from lakes experiencing high water level fluctuations. These observations supported the inferences of Hofmann *et al.* (2008), that long-term water level fluctuations could induce a slow shoreline displacement with continuous interplay between short- and long-term fluctuations being responsible for shaping shore morphology and determining sediment grain size distribution. Lake residence times are orders of magnitude longer than that of rivers and therefore multi-annual patterns have a much stronger influence on lake habitat structure than they have on rivers (Wantzen *et al.* 2008a).

My findings highlight the multifaceted nature and complexity of possible impacts of water level fluctuations on littoral zones. They modify directly the particle size distribution of benthic substrates in lake littoral zones and are responsible for the direct physical stress, related habitat displacement and habitat loss. A myriad of environmental factors shape habitat structure (Dodds 2002, Hofmann *et al.* 2008, Chapter 4, Fig. 5.1) and aquatic and nearshore faunal distribution depends largely on habitat, with high diversity of habitats and food resources generating correspondingly diverse littoral communities (Wallace 1996, Weatherhead & James 2001, Schindler & Scheuerell 2002, Stendera & Johnson 2008, Tolonen & Hämäläinen 2010). The reduction of gravel cover and overall alteration in substrate also triggers changes in lake geomorphology and wave dynamics thus affecting vegetation zonation (Schmieder 2004). Observational studies have suggested that amplified WLF may reduce macrophyte diversity and cover, potentially resulting in their complete disappearance from lakes and consequently reducing considerably the structural diversity and productivity of littoral habitats (Rørslett 1984, 1985, Hellsten 2002, Acreman *et al.* 2005, Valdovinos *et al.* 2007). I found a three-fold reduction in macrophyte cover at the shallowmost sampling depth in lakes with high water level fluctuations, likely because of direct physical stress. This likely triggers corresponding reductions in niche availability, through homogenisation or alteration of substrate structure, and food resources and refuge availability through the deterioration of macrophytes, which could further reduce lake biodiversity and impoverish ecosystems, therefore reducing their buffering capability against the ecological impacts of other human disturbances (Cardinale 2011).

5.2.2. Impacts on biota

Experimentally amplified water level fluctuations reduced algal biomass and invertebrate density, and caused high reduction in overall phylogenetic diversity of macroinvertebrates (Chapter 3). Such loss of diversity at higher taxonomic levels would result likely in disproportionate alterations to ecosystem functioning (Faith 1992, Duffy *et al.* 2007). However, no effects were found on taxon richness or metrics of local-scale (α) diversity. Miller *et al.* (2007) found that even though discharge magnitude and duration could affect river invertebrate responses to water withdrawals, hydrological disturbance alone did not have direct, unfavourable impacts. Rather the synergistic effects of multiple environmental variables are more

likely to shift the structure and functioning of macroinvertebrate communities substantially (Miller *et al.* 2007). This is likely the reason why the effects of water level fluctuations on taxon diversity were hard to disentangle from the effects of other factors (Fig. 5.2).

My observational study demonstrated that contrasting regimes of water level fluctuations can generate a suite of both taxonomic and trophic community responses. Overall, gastropod density was greater in lakes and ponds with low water level fluctuations. Some snail species were found only from lakes with low water level fluctuations, revealing the potential of gastropods as useful bioindicators of amplified water level fluctuations, as suggested also by Mastrantuono *et al.* (2008) and Balian *et al.* (2008). Water level fluctuations could result in decline of biomass and diversity of lake producers (Hill *et al.* 1998, Mastrantuono *et al.* 2008, Wantzen *et al.* 2008b, Chapters 3 & 4). Since snails rely on periphytic algae and macrophytes as food sources (Cummins & Klug 1979, Weatherhead & James 2001), water level fluctuations may affect indirectly gastropods in ponds and lakes with high fluctuations, subjecting them to trophic stress owing to reduced resources availability. Moreover, even though benthic (*i.e.* bottom-dwelling) invertebrates tend to be comparatively mobile, their community structure is highly dependent upon lake habitat structure (Tolonen *et al.* 2001; Schindler & Scheuerell 2002; Donohue *et al.* 2009a) and can, therefore, be highly sensitive to anthropogenic shoreline development and altered hydrological conditions (Brauns *et al.* 2007b). Importantly, benthic invertebrate consumers form key links in not only whole lake food webs (Carpenter *et al.* 1985; Vander Zanden & Vadeboncoeur 2002) but also in adjacent terrestrial ones (Wesner 2010). Because of this, benthic invertebrates can comprise key disturbance indicators and form the basis of many established metrics of human perturbations in aquatic ecosystems.

The findings of both the experimental and observational studies showed that the effects on benthic assemblages extended even below the zone of water fluctuations. Maximum density of benthic fauna can occur immediately below the draw-down limit of lakes with high water level fluctuations (Ward 1992). I found some taxa, such as opportunistic chironimids and operculate gastropods, in greater densities at

intermediate depths, indicating that individuals might have been able to migrate with receding water (Cowell & Hudson 1967, McLachlan & McLachlan 1971, Valdovinos *et al.* 2007, Chapters 3 & 4). These findings highlight the need to incorporate sampling depth and timing of extreme water level events when investigating the impacts of water level fluctuations.

Another group that appears to be particularly sensitive to hydrological disturbances is the Trichoptera. Their larvae were absent from entire mesocosms with water level fluctuations, supporting further the assertion that water level fluctuations may affect biotic assemblages even below the zone of water fluctuations. Power *et al.* (2008) found that caddis flies in lotic systems were susceptible to floods. Furthermore, small-bodied predators took advantage of the increased shallow habitats and refugia, thus suppressing the less defended grazers such as mayflies (Marks *et al.* 2000). Such causal pattern of water level fluctuations on Ephemeroptera and Trichoptera larvae was not found for the eight sampled lakes possibly owing to the ability of these taxa to recolonise littoral habitats (Scheifhacken *et al.* 2007), underlying once again the importance of considering seasonality and timing of extreme water level fluctuations when studying their impacts.

In addition, *Gammarus* and *Asellus* are among the taxa responding most sensitively to high water level fluctuations (Hunt & Jones 1972). I found an overall decrease of crustacean densities attributable to reductions in abundance of both isopods and native amphipods in lakes with high WLF, while alien and invasive amphipod species increased in density at all sampling depths in lakes with amplified water level fluctuations. Loss of species of littoral fauna may be followed by recolonisation provided water levels are stable (Hunt & Jones 1972), thus giving the opportunity for new (including alien) species to establish in the ecosystem as a result of freeing-up habitat niches. Invasive non-native plant and animal species are the second greatest threat to biodiversity worldwide after habitat destruction as they can negatively impact on native species, transform habitats and threaten whole ecosystems causing serious environmental and economic problems (Saunders *et al.* 2002, Rudnick & Resh 2005, Brauns *et al.* 2007a, Hebert *et al.* 2008, Naeem 2009, Kadoya *et al.* 2011, Rush *et al.* 2012). Biodiversity losses and species invasions have the potential to

invoke major changes in food-web structure, dynamics and stability (McCann 2000). Anthropogenically altered water level regimes have been associated not only with reduction in plant species richness but also with frequent dominance by invasive plant species (Van Geest *et al.* 2005). Thus, establishment of invasive species might be facilitated by hydrological stress and associated reductions in ecosystem resilience (Naeem 2009).

My findings also indicate clearly that there are likely to be many biological indicators of fluctuating water levels and I have identified a number of distinct ways in which biological communities change along the depth gradient in systems with amplified water level fluctuations. High water level fluctuations caused significant shifts in the trophic structure of benthic invertebrate consumers, attributable to increased densities of predators and filter feeders and reductions in grazers and shredders (Chapter 4). Water level fluctuations affect detritus and organic matter input from the riparian zone and the catchment (Rorslett 1984, Black *et al.* 2003, Valdovinos *et al.* 2007, Wantzen *et al.* 2008a), while animals living in moist environments may migrate to feed on benthic algae or dead animals when water level recedes. Aquatic invertebrate predators were probably favoured by the likely high availability of accessible prey in the littoral area, both aquatic and terrestrial. Changes in water level can, therefore, potentially affect different trophic levels in different ways. Water level fluctuations have also been found to modify shelter availability and to trigger physiological and behavioural responses in fish (Fischer & Ohl 2005). These findings, coupled with the dynamic nature of food-web structure, might have important implications for vital ecosystem services that support human well-being, such as fisheries, and have important economic consequences.

A key finding of both the experimental and observational studies described in this thesis is the fact that sampling depth needs to be taken account of when studying the impacts of hydrological pressures. Depth mediated the response of both primary producer and consumer benthic assemblages and interacted with water level fluctuations in their effects on habitat structure, and therefore needs to be incorporated explicitly in studies on the effects of hydromorphological pressures. The importance of depth pertains to the physical shifting of the littoral zone, resulting

either in the conversion of terrestrial habitats into aquatic, or converting the sublittoral into eulittoral. This is a process, naturally occurring in continental lakes. Nevertheless, potential alteration in the amplitude or seasonality of water level variations not only impacts on ecosystem health and stability, but is essential in flood risk assessment, water management (Fitzpatrick & Bree 2001, Jackson *et al.* 2001, Johnson *et al.* 2001, Baron *et al.* 2002, Brown *et al.* 2010) and ecosystem good and services such as agriculture, water supply, fisheries, recreational activities etc (Kosarev & Yablonskaya 1994, Graynoth 1999, Brunberg & Blomqvist 2003, Okun *et al.* 2005, Okun & Mehner 2005) and thus assist in the reduction of economic and societal risks owing to extreme water level fluctuations.

5.3. Implications and recommendations for future work

My results give novel insight into the impacts of WLF on the structure and functioning of standing water ecosystems. Given that the majority of biodiversity within lakes is found in the littoral zone (Vadeboncoeur *et al.* 2011), coupled with the fact that lake littoral provides important food subsidies both to associated aquatic habitats and neighbouring riparian zones (Vander Zanden & Vadeboncoeur 2002; Wesner 2010), my findings have important implications not only for lake and pond systems experiencing amplified water level fluctuations, but also for adjacent aquatic and terrestrial ecosystems. Moreover, this study confers strong potential for the development of robust ecological indicators of water level fluctuations in standing water ecosystems. Thus important implications for environmental monitoring and mitigation can be drawn from the research described in this thesis. Future research on natural water level regimes and on hydromorphological pressures should consider more detailed multi-metric quantification of water level regimes and incorporate water level metrics that reflect the five main facets of water level regimes: magnitude, frequency, timing, duration and rate of change. This will enable the robust assessment of ecological impacts of hydromorphological disturbances and thus ensure the achievement of the environmental objectives set by the Water Framework Directive, that requires the achievement of good ecological and chemical status for all surface waters by 2015 (WFD; 2000/60/EC). Furthermore, conservation efforts need to be aimed at whole-catchment management (Saunders *et al.* 2002) since it could

potentially improve our understanding of water level fluctuations. In addition, incorporating sampling depth, the timing of extreme events and amplitude of fluctuations at various temporal scales into field sampling programmes, coupled with sampling on more than one occasion, could assist significantly in developing robust metrics for quantifying hydrological disturbances.

All of my findings were based on stony littoral habitats and their communities and need to be tested further for other habitat types, incorporating studies to further disentangle the potential role of Gastropoda, Trichoptera and Ephemeroptera as bioindicators of hydromorphological stress. This thesis and many recent studies (Townsend *et al.* 1997b, Statzner *et al.* 2004, Bjelke *et al.* 2005, Céréghino *et al.* 2011) suggest that using simultaneously both biological (*e.g.* feeding preferences and locomotion type) and ecological (*e.g.* habitat preferences and dependence on water chemistry) traits might give a greater insight into revealing the impacts of environmental conditions and habitat changes on lake biota.

My thesis highlights the importance of examining experimentally the mechanisms behind the responses of littoral biota to hydrological stress. Rarely, however, do disturbances act in isolation in natural systems. Therefore, environmental science and freshwater management could benefit further from experiments aimed at investigating the combined effects of various frequency, timing, duration and magnitude of water level fluctuations, on the one hand, and incorporating different scenarios of nutrient loadings or other forms of human disturbance, on the other.

5.4. Conclusions

This thesis has revealed the multifaceted nature and complexity of the effects of amplified water level fluctuations on lake littoral zones. Moreover, I have proposed the employment of a multi-metric quantification and the inclusion of temporal variability across scales in order to describe and quantify adequately water level regimes. My findings suggest that there is capacity to derive methodology identifying potential risks for lake hydrology based on their catchment and landscape attributes. Detection of possibly more vulnerable systems at an early stage could be crucial for

reducing ecosystem degradation and for guiding efforts to restore or maintain ecosystem integrity and biological diversity.

I found that water level fluctuations have a range of direct and indirect impacts on lakes. They modify directly the particle size distribution of benthic substrates in lake littoral zones and are responsible for the direct physical stress on biota, owing to habitat displacement and habitat loss. Moreover, reducing niche availability, through homogenisation or alteration of substrate structure, and food resources and shelter availability through deterioration of benthic algae and macrophytes, could further reduce lake biodiversity and impoverish ecosystems, as well as reduce their resilience against the ecological impacts of other human disturbances.

Rather than just providing an indication of general ecological integrity, which is the extent of the capability of the many established metrics of aquatic disturbance, I identified a number of specific ways that water level fluctuations appear to modify (Chapter 3) or affect (Chapter 4) benthic assemblages along the depth gradient. Contrasting regimes of water level fluctuations generated a suite of community responses, demonstrating clearly the greater potential in linking fluctuations in water level with multivariate biological responses rather than with univariate biological metrics. My findings suggest that using biological traits might give a greater insight into revealing the impacts of environmental conditions and habitat changes on lake biota. The linkage of trait responses to hydrological disturbance has the capacity to expand biomonitoring approaches beyond traditional taxonomically-based assessments that identify ecological effect, to provide a causal diagnosis and mechanistic linkages of biotic responses to hydromorphological disturbances and environmental conditions, in general. The predicted increase of water demand and global mean temperature, coupled with higher frequency and intensity of extreme events, may intensify considerably the variability of water level fluctuations on a global scale, and thus exacerbate even further the detrimental impacts of extreme water level fluctuations on lake ecology and biodiversity, with significant impacts on the delivery of ecosystem goods and services.

Water Level Fluctuations and their Effects on Lake Ecology

References

- Abrahams, C. 2008. Climate change and lakeshore conservation: a model and review of management techniques. *Hydrobiologia* **613**:33-43.
- Abramovitz, J. 1996. Imperiled waters, impoverished future: The decline of freshwater ecosystems. Worldwatch Institute, Washington, DC.
- Acreman, M. C., M. J. Dunbar, J. Hannaford, A. R. Black, J. S. Rowan, and O. M. Bragg. 2005. Development of Environmental Standards (Water Resources). Stage 1: Identification of Hydro-morphological parameters to which the aquatic ecosystem is sensitive. SNIFFER, Edinburgh.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**:32-46.
- Anderson, M. J. 2005. PERMANOVA. Permutational multivariate analysis of variance: a computer program. Department of Statistics, University of Auckland.
- Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth, UK.
- Anteau, M. J., T. L. Shaffer, M. H. Sherfy, M. A. Sovada, J. H. Stucker, and M. T. Wiltermuth. 2012. Nest survival of piping plovers at a dynamic reservoir indicates an ecological trap for a threatened population. *Oecologia* **170**:1167-1179.
- Armitage, P. D., D. Moss, J. F. Wright, and M. T. Furse. 1983. The performance of a new biological water quality score based on macroinvertebrates over a wide range of unpolluted running-water sites. *Water Research* **17**:333-347.
- Aroviita, J. and H. Hämäläinen. 2008. The impact of water-level regulation on littoral macroinvertebrate assemblages in boreal lakes. *Hydrobiologia* **613**:45-56.
- Arthurton, R., S. Barker, W. Rast, M. Huber, J. Alder, J. Chilton, E. Gaddis, K. Pietersen, and C. Zöckler. 2007. Water. Page 540 in P. Ashton, editor. Global environmental outlook GEO4: environment for development. United Nations Environment Programme, Malta.
- Balian, E., H. Segers, C. Lévêque, and K. Martens. 2008. The Freshwater Animal Diversity Assessment: an overview of the results. *Hydrobiologia* **595**:627-637.
- Barbour, M. T., J. Gerritsen, G. E. Griffith, R. Frydenborg, E. McCarron, J. S. White, and M. L. Bastian. 1996. A Framework for Biological Criteria for Florida Streams Using Benthic Macroinvertebrates. *Journal of the North American Benthological Society* **15**:185-211.
- Baron, J. S., N. L. Poff, P. L. Angermeier, C. N. Dahm, P. H. Gleick, Nelson G. Hairston, Jr., R. B. Jackson, C. A. Johnston, B. D. Richter, and A. D. Steinman. 2002. Meeting Ecological and Societal Needs for Freshwater. *Ecological Applications* **12**:1247-1260.
- Baulch, H. M., D. W. Schindler, M. A. Turner, D. L. Findlay, M. J. Paterson, and R. D. Vinebrooke. 2005. Effects of Warming on Benthic Communities in a Boreal Lake: Implications of Climate Change. *Limnology and Oceanography* **50**:1377-1392.
- Baumgärtner, D., M. Mörtl, and K.-O. Rothhaupt. 2008. Effects of water-depth and water-level fluctuations on the macroinvertebrate community structure in the littoral zone of Lake Constance. *Hydrobiologia* **613**:97-107.

- Baxter, R. M. 1977. Environmental Effects of Dams and Impoundments. *Annual Review of Ecology and Systematics* **8**:255-283.
- Beklioglu, M. 2007. Role of hydrology, nutrients and fish in interaction with global climate change in effecting ecology of shallow lakes in Turkey Pages 583-595 *International River Basin management Congress Book*. General directorate of state hydraulic works, Antalya.
- Bjelke, U., I. M. Bohman, and J. Herrmann. 2005. Temporal niches of shredders in lake littorals with possible implications on ecosystem functioning. *Aquatic Ecology* **39**:41-53.
- Black, A. R., G. M. Barlow, and A. T. Scholz. 2003. Carbon and nitrogen stable isotope assessment of the Lake Roosevelt aquatic food web. *Northwest Science* **77**.
- Brabec, K., S. Zahrádková, D. Němejcová, P. Pařil, J. Kokeš, and J. Jarkovský. 2004. Assessment of organic pollution effect considering differences between lotic and lentic stream habitats. *Hydrobiologia* **516**:331-346.
- Bragg, O. M., R. W. Duck, J. S. Rowan, and A. R. Black. 2003. Review of the methods for assessing the hydromorphology of lakes. *SNIFFER*, Edinbrugh.
- Brauns, M., X.-F. Garcia, and M. Pusch. 2008. Potential effects of water-level fluctuations on littoral invertebrates in lowland lakes. *Hydrobiologia* **613**:5-12.
- Brauns, M., X.-F. Garcia, M. T. Pusch, and N. Walz. 2007a. Eulittoral macroinvertebrate communities of lowland lakes: discrimination among trophic states. *Freshwater Biology* **52**:1022-1032.
- Brauns, M., X.-F. Garcia, N. Walz, and M. T. Pusch. 2007b. Effects of human shoreline development on littoral macroinvertebrates in lowland lakes. *Journal of Applied Ecology* **44**:1138-1144.
- Brown, L. E., G. Mitchell, J. Holden, A. Folkard, N. Wright, N. Beharry-Borg, G. Berry, B. Brierley, P. Chapman, S. J. Clarke, L. Cotton, M. Dobson, E. Dollar, M. Fletcher, J. Foster, A. Hanlon, S. Hildon, P. Hiley, P. Hillis, J. Hoseason, K. Johnston, P. Kay, A. McDonald, A. Parrott, A. Powell, R. J. Slack, A. Sleight, C. Spray, K. Tapley, R. Underhill, and C. Woulds. 2010. Priority water research questions as determined by UK practitioners and policy makers. *Science of The Total Environment* **409**:256-266.
- Brunberg, A.-K. and P. Blomqvist. 2003. Recruitment of *Microcystis* (Cyanophyceae) from lake sediments: the importance of littoral inocula. *Journal of Phycology* **39**:58-63.
- Burnham, K., P. and D. Anderson. 2002. Models selection and multimodel inference: a practical information-theoretic approach. 2nd edition. 488
- Burton, T. M., C. A. Stricker, and D. G. Uzarski. 2002. Effects of plant community composition and exposure to wave action on invertebrate habitat use of Lake Huron coastal wetlands. *Lakes & Reservoirs: Research and Management* **7**:255-269.
- Cardinale, B. J. 2011. Biodiversity improves water quality through niche partitioning. *Nature* **472**:86-89.
- Carlson, S. M. and T. P. Quinn. 2007. Ten years of varying lake level and selection on size-at-maturity in sockeye salmon. *Ecology* **88**:2620-2629.
- Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* **77**:677-680.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**:634-639.

- Céréghino, R., B. Oertli, M. Bazzanti, C. Coccia, A. Compin, J. Biggs, N. Bressi, P. Grillas, A. Hull, T. Kalettka, and O. Scher. 2011. Biological traits of European pond macroinvertebrates. *Hydrobiologia*:1-11.
- Charlton, R., S. Moore, J. Sweeney, and R. Fealy. 2001. Climate change and water resources in Ireland: Initial investigations using downscaled GCMs and hydrological modelling techniques. *Cuadernos de Investigacion Geografica* **27**:125-135.
- Charvet, S., B. Statzner, P. Usseglio-Polatera, and B. Dumont. 2000. Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. *Freshwater Biology* **43**:277-296.
- Chow-Fraser, P. 2005. Ecosystem response to changes in water level of Lake Ontario marshes: lessons from the restoration of Cootes Paradise Marsh. *Hydrobiologia* **539**:189-204.
- Clarke, K. R. and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition, Plymouth
- Clarke, R., A. Lorenz, L. Sandin, A. Schmidt-Kloiber, J. Strackbein, N. Kneebone, and P. Haase. 2006. Effects of sampling and sub-sampling variation using the STAR-AQEM sampling protocol on the precision of macroinvertebrate metrics. *Hydrobiologia* **566**:441-459.
- Clesceri, L. S., A. E. Greenberg, A. D. Eaton, and M. A. H. Franson. 1998. Standard methods for the examination of water and wastewater. 20th edition. American Public Health Association American Water Works Association Water Environment Federation, Washington, DC
- Clifford, H. F., R. J. Casey, and K. A. Saffran. 1992. Short-Term Colonization of Rough and Smooth Tiles by Benthic Macroinvertebrates and Algae (Chlorophyll a) in Two Streams. *Journal of the North American Benthological Society* **11**:304-315.
- Connor, R., J.-M. Faurès, J. Kuylenstierna, J. Margat, P. Steduto, D. Vallée, and W. v. d. Hoek. 2009. Evolution of water use. The United Nations World Water Development Report 3: Water in a Changing World (WWDR-3) UNESCO, Paris.
- Coops, H., M. Beklioglu, and T. L. Crisman. 2003. The role of water-level fluctuations in shallow lake ecosystems – workshop conclusions. *Hydrobiologia* **506-509**:23-27.
- Coops, H. and S. H. Hosper. 2002. Water-level management as a tool for the restoration of shallow lakes in the Netherlands. *Lake and Reservoir Management* **18**:292-297.
- Coops, H., J. T. Vulink, and E. H. van Nes. 2004. Managed water levels and the expansion of emergent vegetation along a lakeshore. *Limnologica - Ecology and Management of Inland Waters* **34**:57-64.
- Costello, M. J. 1993. Biogeography of Alien Amphipods Occurring in Ireland, and Interactions with Native Species. *Crustaceana* **65**:287-299.
- Cowell, B. C. and P. L. Hudson. 1967. Some environmental factors influencing benthic invertebrates in two Missouri River reservoirs. Pages 541-555 in C. E. J. Lane, editor. Reservoir fishery resources symposium. American Fisheries Society, Washington, D.C., Athens, GA.
- Cryer, J. D. and K.-S. Chan. 2008. Time Series Analysis with Applications in R. 2nd edition. Springer Science+Business Media, LLC, New York, USA.491
- Cummins, K. W. 1973. Trophic relations of aquatic insects. *Annual Review of Entomology* **18**:183-206.

- Cummins, K. W. and M. J. Klug. 1979. Feeding Ecology of Stream Invertebrates. *Annual Review of Ecology and Systematics* **10**:147-172.
- Deegan, B. M., S. D. White, and G. G. Ganf. 2012. Nutrients and water level fluctuations: A study of three aquatic plants. *River Research and Applications* **28**:359-368.
- Desgranges, J.-L., J. Ingram, B. Drolet, J. Morin, C. Savage, and D. Borcard. 2006. Modelling Wetland Bird Response to Water Level Changes in the Lake Ontario – St. Lawrence River Hydrosystem. *Environmental Monitoring and Assessment* **113**:329-365.
- Dick, J. T. A. 2008. Role of behaviour in biological invasions and species distributions; lessons from interactions between the invasive *Gammarus pulex* and the native *G. duebeni* (Crustacea: Amphipoda). *Contributions to Zoology* **77** 91-98.
- Dick, J. T. A., R. W. Elwood, and D. E. Irvine. 1990. Displacement of the Native Irish Freshwater Amphipod *Gammarus duebeni* by the Introduced *Gammarus pulex*. *The Irish Naturalists' Journal* **23**:313-316.
- Dinka, M., E. Ágoston-Szabó, Á. Berczik, and G. Kutruicz. 2004. Influence of water level fluctuation on the spatial dynamic of the water chemistry at Lake Fertő/Neusiedler See. *Limnologica - Ecology and Management of Inland Waters* **34**:48-56.
- Dodds, W. K. 2002. *Freshwater ecology: concepts and environmental applications*. Academic Press, San Diego, California, USA. 569
- Donohue, I., L. A. Donohue, B. N. Ainín, and K. Irvine. 2009a. Assessment of eutrophication pressure on lakes using littoral invertebrates. *Hydrobiologia* **633**:105-122.
- Donohue, I., A. L. Jackson, M. T. Pusch, and K. Irvine. 2009b. Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. *Ecology* **90**:3470-3477.
- Donohue, I., M. L. McGarrigle, and P. Mills. 2006. Linking catchment characteristics and water chemistry with the ecological status of Irish rivers. *Water Research* **40**:91-98.
- Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* **10**:522-538.
- Dunbar, M. J., M. Warren, C. Extence, L. Baker, D. Cadman, D. J. Mould, J. Hall, and R. Chadd. 2010. Interaction between macroinvertebrates, discharge and physical habitat in upland rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**:S31-S44.
- Durack, P. J., S. E. Wijffels, and R. J. Matear. 2012. Ocean Salinities Reveal Strong Global Water Cycle Intensification During 1950 to 2000. *Science* **336**:455-458.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate Extremes: Observations, Modeling, and Impacts. *Science* **289**:2068-2074.
- Eisenreich, S. J., R. T. Bannerman, and D. E. Armstrong. 1975. A Simplified Phosphorus Analysis Technique. *Environmental Letters* **9**:43-53.
- Extence, C. A., D. M. Balbi, and R. P. Chadd. 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. *Regulated Rivers: Research & Management* **15**:545-574.
- Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**:1-10.

- Faria, J. C., P. Grosjean, and E. Jelihovschi. 2011. Resources of Tinn-R GUI/Editor for R Environment. *in* UESC, editor. Universidade Estadual de Santa Cruz - UESC/BA/BRASIL, Ilheus, Bahia, Brasil.
- Fischer, J. M., T. M. Frost, and A. R. Ives. 2001. Compensatory dynamics in zooplankton community responses to acidification: measurement and mechanisms. *Ecological Applications* **11**:1060-1072.
- Fischer, P. and U. Ohl. 2005. Effects of water-level fluctuations on the littoral benthic fish community in lakes: a mesocosm experiment. *Behavioral Ecology* **16**:741-746.
- Fitzpatrick, J. and T. Bree. 2001. Flood risk management through reservoir storage and flow control. *in* National Hydrology Seminar 2001, Tullamore, Ireland.
- Folke, C. 2003. Freshwater for Resilience: A Shift in Thinking. *Philosophical Transactions: Biological Sciences* **358**:2027-2036.
- Free, G., A. Solimini, B. Rossaro, L. Marziali, R. Giacchini, B. Paracchini, M. Ghiani, S. Vaccaro, B. Gawlik, R. Fresner, G. Santner, M. Schönhuber, and A. Cardoso. 2009. Modelling lake macroinvertebrate species in the shallow sublittoral: relative roles of habitat, lake morphology, aquatic chemistry and sediment composition. *Hydrobiologia* **633**:123-136.
- Furey, P. C., R. N. Nordin, and A. Mazumder. 2004. Water level drawdown affects physical and biogeochemical properties of littoral sediments of a reservoir and a natural lake. *Lake and Reservoir Management* **20**:280-295.
- Furey, P. C., R. N. Nordin, and A. Mazumder. 2006. Littoral benthic macroinvertebrates under contrasting drawdown in a reservoir and a natural lake. *Journal of the North American Benthological Society* **25**:19-31.
- Furse, M. T., D. Hering, K. Brabec, A. Buffagni, L. Sandin, P. F. M. Verdonshot, A. Schmidt-Kloiber, W. Graf, A. Lorenz, and O. Moog. 2006. The AQEM/STAR taxalist — a pan-European macro-invertebrate ecological database and taxa inventory. Pages 325-342 *in* K. Martens, editor. *The Ecological Status of European Rivers: Evaluation and Intercalibration of Assessment Methods*. Springer Netherlands.
- Gafny, S. and A. Gasith. 1999. Spatially and temporally sporadic appearance of macrophytes in the littoral zone of Lake Kinneret, Israel: taking advantage of a window of opportunity. *Aquatic Botany* **62**:249-267.
- Garcia Molinos, J. and I. Donohue. 2010. Interactions among temporal patterns determine the effects of multiple stressors. *Ecological Applications*:1794-1800.
- García Molinos, J. and I. Donohue. 2011. Temporal variability within disturbance events regulates their effects on natural communities. *Oecologia* **166**:795-806.
- Gibbs, L. M. 2006. Valuing Water: variability and the Lake Eyre Basin, central Australia. *Australian Geographer* **37**:73-85.
- Gibson, J. S. 1970. The Function of the Operculum of *Thais lapillus* (L.) in Resisting Desiccation and Predation. *Journal of Animal Ecology* **39**:159-168.
- Giller, P. S., H. Hillebrand, U.-G. Berninger, M. O. Gessner, S. Hawkins, P. Inchausti, C. Inglis, H. Leslie, B. Malmqvist, M. T. Monaghan, P. J. Morin, and G. O'Mullan. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* **104**:423-436.
- Gizinski, A. and N. Wolnomiejski. 1982. Zoobenthos of Koronowo Dam Reservoir in its 10th and 15th year of existence. *Acta Universitatis Nicolai Copernici* **52**:35-50.

- Gleick, P. H. 1998. Water in Crisis: Paths to Sustainable Water Use. *Ecological Applications* **8**:571-579.
- Gleick, P. H. 2003. Global Freshwater Resources: Soft-Path Solutions for the 21st Century. *Science* **302**:1524-1528.
- Graynoth, E. 1999. Recruitment and distribution of juvenile salmonids in Lake Coleridge, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **33**:205-219.
- Grimm, N. B., A. Chacon, C. N. Dahm, S. W. Hostetler, O. T. Lind, P. L. Starkweather, and W. W. Wurtsbaugh. 1997. Sensitivity of aquatic ecosystems to climatic and anthropogenic changes: the Basin and Range, American Southwest and Mexico. *Hydrological Processes* **11**:1023-1041.
- Groom, A. P. and A. G. Hildrew. 1989. Food Quality for Detritivores in Streams of Contrasting pH. *Journal of Animal Ecology* **58**:863-881.
- Håkanson, L., A. Parparov, and K. D. Hambright. 2000. Modelling the impact of water level fluctuations on water quality (suspended particulate matter) in Lake Kinneret, Israel. *Ecological Modelling* **128**:101-125.
- Hall, R. B. W. and P. A. Harcombe. 1998. Flooding alters apparent position of floodplain saplings on a light gradient. *Ecology* **79**:847-855.
- Halls, A. S. and R. L. Welcomme. 2004. Dynamics of river fish populations in response to hydrological conditions: a simulation study. *River Research and Applications* **20**:985-1000.
- Hampton, S. E., S. C. Fradkin, P. R. Leavitt, and E. E. Rosenberger. 2011. Disproportionate importance of nearshore habitat for the food web of a deep oligotrophic lake. *Marine and Freshwater Research* **62**:350-358.
- Harrault, L., B. Allard, M. Danger, F. Maunoury-Danger, A. Guilpart, and G. Lacroix. 2012. Influence of food-web structure on the biodegradability of lake sediment. *Freshwater Biology* **57**:2390-2400.
- Hebert, C. E., D. V. C. Weseloh, A. Idrissi, M. T. Arts, R. O'Gorman, O. T. Gorman, B. Locke, C. P. Madenjian, and E. F. Roseman. 2008. Restoring piscivorous fish populations in the Laurentian great lakes causes seabird dietary change. *Ecology* **89**:891-897.
- Hellsten, S. 1988. Environmental factors related to water level regulation — a comparative study in northern Finland. *Boreal Environment Research*:345-367.
- Hellsten, S. 2002. Aquatic macrophytes as indicators of water-level regulation in Northern Finland. *Verh. Internat. Verein. Limnol.* **28**:601-606.
- Hellsten, S., M. Marttunen, R. Palomäki, J. Riihimäki, and E. Alasaarela. 1996. Towards an ecologically based regulation practice in Finnish hydroelectric lakes. *Regulated Rivers: Research & Management* **12**:535-545.
- Hering, D., O. Moog, L. Sandin, and P. Verdonschot. 2004. Overview and application of the AQEM assessment system. *Hydrobiologia* **516**:1-20.
- Hill, N. M., P. A. Keddy, and I. C. Wisheu. 1998. A Hydrological Model for Predicting the Effects of Dams on the Shoreline Vegetation of Lakes and Reservoirs. *Environmental Management* **22**:723-736.
- Hofmann, H., A. Lorke, and F. Peeters. 2008. Temporal scales of water-level fluctuations in lakes and their ecological implications. *Hydrobiologia* **613**:85-96.
- Holland, R. A., W. R. T. Darwall, and K. G. Smith. 2012. Conservation priorities for freshwater biodiversity: The Key Biodiversity Area approach refined and tested for continental Africa. *Biological Conservation* **148**:167-179.
- <http://hydronet.epa.ie/>. 2012. Environmental Protection Agency HydroNet site

- Huh, S., D. A. Dickey, M. R. Meador, and K. E. Ruhl. 2005. Temporal analysis of the frequency and duration of low and high streamflow: years of record needed to characterize streamflow variability. *Journal of Hydrology* **310**:78-94.
- Hunt, P. C. and J. W. Jones. 1972. The effect of water level fluctuations on a littoral fauna. *Journal of Fish Biology* **4**:385-394.
- Hurlbert, S. H. 1971. The Nonconcept of Species Diversity: A Critique and Alternative Parameters. *Ecology* **52**:577-586.
- Hutchinson, E. 1975. *A Treatise on Limnology: Geography, physics, and chemistry. Geography and physics of lakes.* John Wiley, New York
- International Bank for Reconstruction and Development. 2010. *Sustaining Water for all in a Changing Climate: World Bank Group Implementation Progress Report.* Washington.
- IPCC. 2007. *Climate Change 2007: Synthesis Report.* Cambridge.
- Jackson, R. B., S. R. Carpenter, C. N. Dahm, D. M. McKnight, R. J. Naiman, S. L. Postel, and S. W. Running. 2001. Water in a Changing World. *Ecological Applications* **11**:1027-1045.
- Jalali, M. B. 2011. Quantile regression due to skewness and outliers Quantile regression due to skewness and outliers **5**:1947 - 1951.
- Johnson, N., C. Revenga, and J. Echeverria. 2001. Managing Water for People and Nature. *Science* **292**:1071-1072.
- Johnson, R. K., T. Wiederholm, and D. M. Rosenberg. 1993. Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. Pages 40-159 in D. M. Rosenberg and V. H. Resh, editors. *Freshwater Biomonitoring and Benthic Macroinvertebrates.* Chapman & Hall, New York, London.
- Jowett, I. G. and M. J. Duncan. 1990. Flow variability in New Zealand rivers and its relationship to in-stream habitat and biota. *New Zealand Journal of Marine and Freshwater Research* **24**:305-317.
- Jurkiewicz-Karnkowska, E. 1989. Occurrence of molluscs in the littoral zone of the Zegrzyński Reservoir and in the pre-mouth and mouth zones of supplying rivers. *Ekologia Polska* **37**:319-336.
- Juutinen, A. M. S. 2001. Effects of spring flood and water level draw-down on methane dynamics in the littoral zone of boreal lakes. *Freshwater Biology* **46**:855-869.
- Kadoya, T., M. Akasaka, T. Aoki, and N. Takamura. 2011. A proposal of framework to obtain an integrated biodiversity indicator for agricultural ponds incorporating the simultaneous effects of multiple pressures. *Ecological Indicators* **11**:1396-1402.
- Kalchev, R. 2012. Water transparency, chlorophyll-a and plankton primary production in the course of Srebarna Lake recovery. Pages 57-68 in Y. Uzunov, B.B. Georgiev, E. Varadinoiva, N. Ivanova, L. Pehlivanov, V. Vasilev, editor. *Ecosystems of the Biosphere Reserve Srebarna Lake.* Professor Marin Drinov Academic Publishing House, Sofia.
- Kalchev, R., V. Vasilev, G. Khiebaum, V. Tsavkova, and L. Pekhivanov. 2007. Recovery of Srebarna lake: experience and perspectives. *Journal of Balkan Ecology* **10**:117-130.
- Karjalainen, J., M. Leppä, M. Rahkola, and K. Tolonen. 1999. The role of benthivorous and planktivorous fish in a mesotrophic lake ecosystem. *Hydrobiologia* **408-409**:73-84.
- Kaste, Ø., J. L. Stoddard, and A. Henriksen. 2003. Implication of Lake Water Residence Time on the Classification of Norwegian Surface Water Sites into

- Progressive Stages of Nitrogen Saturation. *Water, Air, & Soil Pollution* **142**:409-424.
- Kennard, M. J., S. J. Mackay, B. J. Pusey, J. D. Olden, and N. Marsh. 2010a. Quantifying uncertainty in estimation of hydrologic metrics for ecohydrological studies. *River Research and Applications* **26**:137-156.
- Kennard, M. J., B. J. Pusey, J. D. Olden, S. J. Mackay, J. L. Stein, and N. Marsh. 2010b. Classification of natural flow regimes in Australia to support environmental flow management. *Freshwater Biology* **55**:171-193.
- Keough, J. R., T. A. Thompson, G. R. Guntenspergen, and D. A. Wilcox. 1999. Hydrogeomorphic factors and ecosystem response of wetlands of the Great Lakes. *Wetlands* **19**:821-834.
- Koenker, R. 2012. Quantreg: Quantile Regression. Page R package version 4.81.
- Koenker, R. and V. d'Orey. 1994. Remark AS R92: A Remark on Algorithm AS 229: Computing Dual Regression Quantiles and Regression Rank Scores. *Journal of the Royal Statistical Society. Series C (Applied Statistics)* **43**:410-414.
- Koenker, R. W. and V. D'Orey. 1987. Algorithm AS 229: Computing Regression Quantiles. *Journal of the Royal Statistical Society. Series C (Applied Statistics)* **36**:383-393.
- Kosarev, A. N. and E. A. Yablonskaya. 1994. *The Caspian Sea*. SPB Academic Publishing, Hague
- Krzyżanek, E. 1991. The formation of bottom macrofauna communities in three dam reservoirs in Silesia (southern Poland) from the beginning of their existence. *Acta Hydrobiologia* **33**:265-305.
- Lake, P. S., M. A. Palmer, P. Biro, J. Cole, A. P. Covich, C. Dahm, J. Gibert, W. Goedkoop, K. Martens, and J. Verhoeven. 2000. Global change and the biodiversity of freshwater ecosystems: impacts on linkages between above-sediment and sediment Biota. *BioScience* **50**:1099- 1107.
- Lamberti, G. A., J. W. Feminella, and C. M. Pringle. 2006. Methods in stream ecology. Pages 535-560 *in* R. Hauer and G. A. Lamberti, editors. *Methods in Stream Ecology*, 2nd Edition Elsevier, Indiana, Montana, U.S.A.
- Leira, M. and M. Cantonati. 2008. Effects of water-level fluctuations on lakes: an annotated bibliography. *Hydrobiologia* **613**:171-184.
- Lenat, D. R. 1988. Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. *Journal of the North American Benthological Society* **7**:222-233.
- Lenat, D. R. and L. A. P. Smock, D L. 1980. Use of benthic macroinvertebrates as indicators of environmental quality. Pages 97-112 *in* D. L. Worf, editor. *Biological monitoring for environmental effects*. Heath, Lexington, MA.
- Leopold, A. 1941. Lakes in relation to terrestrial life patterns. Pages 200-203 *in* E. J. Kormondy, editor. *Readings in ecology*. Prentice- Hall, Englewood Cliffs, New Jersey.
- Leppä, M., H. Hämäläinen, and J. Karjalainen. 2003. The response of benthic macroinvertebrates to whole-lake biomanipulation. *Hydrobiologia* **498**:97-105.
- Liermann, R. C. A., J. D. Olden, T. J. Beechie, M. J. Kennard, P. B. Skidmore, C. P. Konrad, and H. Imaki. 2012. Hydrogeomorphic classification of Washington state rivers to support emerging environmental flow management strategies. *River Research and Applications* **28**:1340-1358.
- Macneil, C., J. T. A. Dick, and R. W. Elwood. 1997. The trophic ecology of freshwater *Gammarus* spp. (Crustacea:Amphipoda): problems and

- perspectives concerning the functional feeding group concept. *Biological Reviews* **72**:349-364.
- Marks, J. C., M. E. Power, and M. S. Parker. 2000. Flood Disturbance, Algal Productivity, and Interannual Variation in Food Chain Length. *Oikos* **90**:20-27.
- Mastrantuono, L., A. Solimini, P. Nöges, and M. Bazzanti. 2008. Plant-associated invertebrates and hydrological balance in the large volcanic Lake Bracciano (Central Italy) during two years with different water levels. *Hydrobiologia* **599**:143-152.
- McArdle, B. H. and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82**:290-297.
- McCann, K. S. 2000. The diversity-stability debate. *Nature* **405**:228-233.
- McEwen, D. C. and M. G. Butler. 2009. The effects of water-level manipulation on the benthic invertebrates of a managed reservoir. *Freshwater Biology* **55**:1086-1101.
- McGrath, R., E. Nishimura, P. Nolan, T. Semmler, C. Sweeney, and S. Wang. 2005. Climate change : regional climate model predictions for Ireland (2001-CD-C4-M2). 1840951664 (pbk.), Environmental Protection Agency, Johnstown Castle, Co. Wexford.
- McLachlan, A. J. 1970. Some Effects of Annual Fluctuations in Water Level on the Larval Chironomid Communities of Lake Kariba. *The Journal of Animal Ecology* **39**:79-90.
- McLachlan, A. J. and S. M. McLachlan. 1971. Benthic Fauna and Sediments in the Newly Created Lake Kariba (Central Africa). *Ecology* **52**:800-809.
- Meehl, G. A. and C. Tebaldi. 2004. More Intense, More Frequent, and Longer Lasting Heat Waves in the 21st Century. *Science* **305**:994-997.
- Menezes, S., D. J. Baird, and A. M. V. M. Soares. 2010. Beyond taxonomy: a review of macroinvertebrate trait-based community descriptors as tools for freshwater biomonitoring. *Journal of Applied Ecology* **47**:711-719.
- Miller, S. W., D. Wooster, and J. Li. 2007. Resistance and resilience of macroinvertebrates to irrigation water withdrawals. *Freshwater Biology* **52**:2494-2510.
- Montgomery, D. C. and E. A. Peck. 1992. Introduction to linear regression analysis. John Wiley & Sons, New York.
- Moog, O. 1995. Fauna Aquatica Austriaca - a comprehensive species inventory of Austrian aquatic organisms with ecological data., Wien
- Moon, H. P. 1935. Flood Movements of the Littoral Fauna of Windermere. *The Journal of Animal Ecology* **4**:216-228.
- Moss, B. 2010. Ecology of freshwaters: a view of the twenty-first century. Fourth edition. 470
- Naeem, S. 2009. Ecology: Gini in the bottle. *Nature* **458**:579-580.
- Nowlin, W. H., J.-M. Davies, R. N. Nordin, and A. Mazumder. 2004. Effects of Water Level Fluctuation and Short-Term Climate Variation on Thermal and Stratification Regimes of a British Columbia Reservoir and Lake. *Lake and Reservoir Management* **20**:91-109.
- Nystrom, P., O. Svensson, B. Lardner, C. Bronmark, and W. Graneli. 2001. The Influence of Multiple Introduced Predators on a Littoral Pond Community. *Ecology* **82**:1023-1039.
- O'Sullivan, P. E. and C. S. Reynolds. 2004. Limnology and limnetic ecology. Blackwell Publishing. 699

- O'Toole, C., I. Donohue, S. Moe, and K. Irvine. 2008. Nutrient optima and tolerances of benthic invertebrates, the effects of taxonomic resolution and testing of selected metrics in lakes using an extensive European data base. *Aquatic Ecology* **42**:277-291.
- Ofenböck, T., O. Moog, J. Gerritsen, and M. Barbour. 2004. A stressor specific multimetric approach for monitoring running waters in Austria using benthic macro-invertebrates. *Hydrobiologia* **516**:251-268.
- Økland, J. 1992. Effects of acidic water on freshwater snails: results from a study of 1000 lakes throughout Norway. *Environmental Pollution* **78**:127-130.
- Okun, N., W.-C. Lewin, and T. Mehner. 2005. Top-down and bottom-up impacts of juvenile fish in a littoral reed stand. *Freshwater Biology* **50**:798-812.
- Okun, N. and T. Mehner. 2005. Distribution and feeding of juvenile fish on invertebrates in littoral reed (*Phragmites*) stands. *Ecology of Freshwater Fish* **14**:139-149.
- Olden, J. D. and N. L. Poff. 2003. Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications* **19**:101-121.
- Ostendorp, W., K. Schmieder, and K. Jöhnk. 2004. Assessment of human pressures and their hydromorphological impacts on lakeshores in Europe. *International Journal of Ecohydrology and Hydrobiology* **4**:229-245.
- Palmer, M., E. Bernhardt, E. Chornesky, S. Collins, A. Dobson, C. Duke, B. Gold, R. Jacobson, S. Kingsland, R. Kranz, M. Mappin, M. L. Martinez, F. Micheli, J. Morse, M. Pace, M. Pascual, S. Palumbi, O. J. Reichman, A. Simons, A. Townsend, and M. Turner. 2004. Ecology for a Crowded Planet. *Science* **304**:1251-1252.
- Palmer, M. A. 2010. Water resources: Beyond infrastructure. *Nature* **467**:534-535.
- Palomäki, R. 1994. Response by macrozoobenthos biomass to water level regulation in some Finnish lake littoral zones. *Hydrobiologia* **286**:17-26.
- Petkov, N. 2012. Habitat characteristics assessment of the wetlands with breeding Ferruginous Duck *Aythya nyroca* and Pochard *A. ferina* in Bulgaria. *Acrocephalus* **32**:127-134.
- Pielou, E. C. 1975. *Ecological Diversity* Wiley, New York
- Pincebourde, S., E. Sanford, J. Casas, and B. Helmuth. 2012. Temporal coincidence of environmental stress events modulates predation rates. *Ecology Letters* **15**:680-688.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The Natural Flow Regime. *BioScience* **47**:769-784.
- Poff, N. L., J. D. Olden, D. M. Pepin, and B. P. Bledsoe. 2006. Placing global stream flow variability in geographic and geomorphic contexts. *River Research and Applications* **22**:149-166.
- Porter, J. R., L. Deutsch, D. Dumaesq, and R. Dyball. 2011. How will growing cities eat? *Nature* **469**:34-34.
- Power, M. E., M. S. Parker, and W. E. Dietrich. 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecological Monographs* **78**:263-282.
- Probst, W., S. Stoll, L. Peters, P. Fischer, and R. Eckmann. 2009. Lake water level increase during spring affects the breeding success of bream *Abramis brama* (L.). *Hydrobiologia* **632**:211-224.

- Propastin, P. A. 2008. Simple model for monitoring Balkhash Lake water levels and Ili River discharges: Application of remote sensing. *Lakes & Reservoirs: Research & Management* **13**:77-81.
- Prus, T., M. Prus, and P. Bijok. 1999. Diversity of invertebrate fauna in littoral of shallow Myczkowce dam reservoir in comparison with a deep Solina dam reservoir. *Hydrobiologia* **408-409**:203-210.
- Puckridge, J. T., F. Sheldon, K. F. Walker, and A. J. Boulton. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* **49**:55-72.
- R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Radford, D. S. and R. Hartland-Rowe. 1971. A Preliminary Investigation of Bottom Fauna and Invertebrate Drift in an Unregulated and a Regulated Stream in Alberta. *The Journal of Applied Ecology* **8**:883-903.
- Rapport, D. J., W. G. Whitford, and M. Hildén. 1998. Common Patterns of Ecosystem Breakdown Under Stress. *Environmental Monitoring and Assessment* **51**:171-178.
- Rawer-Jost, C., J. Böhmer, J. Blank, and H. Rahmann. 2000. Macroinvertebrate functional feeding group methods in ecological assessment. *Hydrobiologia* **422-423**:225-232.
- Renöfält, B. M., R. Jansson, and C. Nilsson. 2010. Effects of hydropower generation and opportunities for environmental flow management in Swedish riverine ecosystems. *Freshwater Biology* **55**:49-67.
- Richards, R. P. 1990. Measures of Flow Variability and a New Flow-Based Classification of Great Lakes Tributaries. *Journal of Great Lakes Research* **16**:53-70.
- Richter, B., J. Baumgartner, R. Wigington, and D. Braun. 1997. How much water does a river need? *Freshwater Biology* **37**:231-249.
- Richter, B. D., J. V. Baumgartner, D. P. Braun, and J. Powell. 1998. A spatial assessment of hydrologic alteration within a river network. *Regulated Rivers: Research & Management* **14**:329-340.
- Ripl, W. 2003. Water: The Bloodstream of the Biosphere. *Philosophical Transactions: Biological Sciences* **358**:1921-1934.
- Rockstrom, J., M. Lannerstad, and M. Falkenmark. 2007. Assessing the Water Challenge of a New Green Revolution in Developing Countries. *Proceedings of the National Academy of Sciences of the United States of America* **104**:6253-6260.
- Rogers, S. I., K. R. Clarke, and J. D. Reynolds. 1999. The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic. *Journal of Animal Ecology* **68**:769.
- Rorslett, B. 1984. Environmental factors and aquatic macrophyte response in regulated lakes. *Aquatic Botany* **19**:199-220.
- Rorslett, B. 1985. Death of submerged macrophytes- actual field observation and some implications. *Aquatic Botany* **22**:7-19.
- Rosenberg, D. M., I. J. Davies, D. G. Cobb, and A. P. Wiens. 1997. Protocols for measuring biodiversity: Benthic macroinvertebrates in fresh waters. Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Manitoba.
- Rosenberg, D. M. and V. H. Resh. 1993. *Freshwater Biomonitoring and Benthic Macroinvertebrates*. Chapman and Hall, London

- Rudnick, D. and V. Resh. 2005. Stable isotopes, mesocosms and gut content analysis demonstrate trophic differences in two invasive decapod crustacea. *Freshwater Biology* **50**:1323-1336.
- Rulli, M. C., A. Savori, and P. D'Odorico. 2013. Global land and water grabbing. *Proceedings of the National Academy of Sciences* **110**:892-897.
- Rush, S. A., G. Paterson, T. B. Johnson, K. G. Drouillard, G. D. Haffner, C. E. Hebert, M. T. Arts, D. J. McGoldrick, S. M. Backus, B. F. Lantry, J. R. Lantry, T. E. D. Schaner, and A. T. Fisk. 2012. Long-term impacts of invasive species on a native top predator in a large lake system. *Freshwater Biology* **57**:2342-2355.
- Sabo, J. L., J. C. Finlay, and D. M. Post. 2009. Food Chains in Freshwaters. *Annals of the New York Academy of Sciences* **1162**:187-220.
- Salas, F., J. Patrício, C. Marcos, M. A. Pardal, A. Pérez-Ruzafa, and J. C. Marques. 2006. Are Taxonomic Distinctness measures compliant to other ecological indicators in assessing ecological status? *Marine Pollution Bulletin* **52**:817-829.
- Sanders, H. L. 1968. Marine Benthic Diversity: A Comparative Study. *The American Naturalist* **102**:243-282.
- Sandin, L. and R. K. Johnson. 2000. The statistical power of selected indicator metrics using macroinvertebrates for assessing acidification and eutrophication of running waters. *Hydrobiologia* **422-423**:233-243.
- Sasikala, S., N. Tanaka, H. S. Y. Wah Wah, and K. B. S. N. Jinadasa. 2009. Effects of water level fluctuation on radial oxygen loss, root porosity, and nitrogen removal in subsurface vertical flow wetland mesocosms. *Ecological Engineering* **35**:410-417.
- Saunders, D. L., J. J. Meeuwig, and A. C. J. Vincent. 2002. Freshwater Protected Areas: Strategies for Conservation
Áreas Protegidas de Agua Dulce: Estrategias para la Conservación. *Conservation Biology* **16**:30-41.
- Scarsbrook, M. R. and C. R. Townsend. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology* **29**:395-410.
- Scheifhacken, N., C. Fiek, and K.-O. Rothhaupt. 2007. Complex spatial and temporal patterns of littoral benthic communities interacting with water level fluctuations and wind exposure in the littoral zone of a large lake. *Fundamental and Applied Limnology* **169**:115-129.
- Schindler, D. E. and M. D. Scheuerell. 2002. Habitat coupling in lake ecosystems. *Oikos* **98**:177-189.
- Schindler, D. W. 1998. Whole-Ecosystem Experiments: Replication Versus Realism: The Need for Ecosystem-Scale Experiments. *Ecosystems* **1**:323-334.
- Schmedtje, U. and M. Colling. 1996. Okologische Typisierung der aquatischen Makrofauna., Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft.
- Schmieder, K. 2004. European lake shores in danger -- concepts for a sustainable development. *Limnologica - Ecology and Management of Inland Waters* **34**:3-14.
- Schmieder, K., M. Dienst, W. Ostendorp, and K. Jöhnk. 2004. Effects of water level variations on the dynamics of the reed belts of Lake Constance. *International Journal of Ecohydrology & Hydrobiology* **4**: 469-480
- Shannon, C. E. 1948. A Mathematical Theory of Communication. *Bell System Technical Journal* **27**:379-423.

- Shiklomanov, I. A. 1993. World fresh water resources. Pages 13-24 in P. H. Gleick, editor. *Water in crisis: a guide to the world's freshwater resources*. Oxford University Press for Pacific Institute for Studies in Development, Environment and Security and Stockholm Environment Institute, Oxford.
- Shiklomanov, I. A. and J. C. Rodda. 2003. *World water resources at the beginning of the 21st century*. Cambridge University Press, Cambridge, UK. 452
- Sinclair, D. C. 1965. The effects of water level changes on the limnology of two British Columbia coastal lakes, with particular reference to the bottom fauna. University of British Columbia. 106.
- Sladeckova, A. 1962. Limnological Investigation Methods for the Periphyton ("Aufwuchs") Community. *Botanical Review* **28**:286-350.
- Smakhtin, V. U. 2001. Low flow hydrology: a review. *Journal of Hydrology* **240**:147-186.
- Smith, B. D., P. S. Maitland, and S. M. Pennock. 1987. A comparative study of water level regimes and littoral benthic communities in Scottish lochs. *Biological Conservation* **39**:291-316.
- SNIFFER. 2008. Determining the links between lake ecology and hydromorphology - phase 1. Workshop report. Project WFD92.
- Solimini, A. G., G. Free, I. Donohue, K. Irvine, M. Pusch, B. Rossaro, L. Sandin, and A. C. Cardoso. 2006. Using benthic macroinvertebrates to assess ecological status of lakes current knowledge and way forward to support WFD implementation. Institute for Environment and Sustainability.
- Sophocleous, M. 2004. Global and Regional Water Availability and Demand: Prospects for the Future. *Natural Resources Research* **13**:61-75.
- Standing Committee of Analysts. 1983. The determination of chlorophyll a in aquatic environments. in Her Majesty's Stationery Office, editor., London.
- Statzner, B., S. Dolédec, and B. Hugueny. 2004. Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography* **27**:470-488.
- Steele-Dunne, S., P. Lynch, R. McGrath, T. Semmler, S. Wang, J. Hanafin, and P. Nolan. 2008. The impacts of climate change on hydrology in Ireland. *Journal of Hydrology* **356**:28-45.
- Stendera, S. and R. K. Johnson. 2008. Habitat-specific stability and persistence of benthic invertebrate communities in boreal lakes *Fundamental and Applied Limnology* **171**:311-322.
- Sternberg, R. 2006. Damming the river: a changing perspective on altering nature. *Renewable and Sustainable Energy Reviews* **10**:165-197.
- Strayer, D. and S. Findlay. 2010. Ecology of freshwater shore zones. *Aquatic Sciences - Research Across Boundaries* **72**:127-163.
- Sukhdev, P. 2009. Costing the Earth. *Nature* **462**:277-277.
- Tanner, C. C., J. D'Eugenio, G. B. McBride, J. P. S. Sukias, and K. Thompson. 1999. Effect of water level fluctuation on nitrogen removal from constructed wetland mesocosms. *Ecological Engineering* **12**:67-92.
- Tavast, E. 2009. Changing factors of the coasts of Lake Peipsi, North-Eastern Europe. *Quaternary International* **207**:130-136.
- Timmermans, S. T. A. 2001. Temporal Relations Between Marsh Bird and Amphibian Annual Population Indices and Great Lakes Water Levels: A Case Study from the Marsh Monitoring Program. Bird Studies Canada.
- Tixier, G. and F. Guerold. 2005. Plecoptera response to acidification in several headwater streams in the Vosges Mountains (northeastern France). *Biodiversity and Conservation* **14**:1525-1539.

- Tolonen, K. T. 2004. Patterns in diversity and assemblages of lake littoral macroinvertebrates in relation to abiotic and biotic factors. University of Joensuu
- Tolonen, K. T. and H. Hämäläinen. 2010. Comparison of sampling methods and habitat types for detecting impacts on lake littoral macroinvertebrate assemblages along a gradient of human disturbance. *Fundamental and Applied Limnology* **176**:43-59.
- Tolonen, K. T., H. Hämäläinen, I. J. Holopainen, and J. Karjalainen. 2001. Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. *Archiv fur hydrobiologia* **152**:39-67.
- Tolonen, K. T., I. J. Holopainen, H. Hämäläinen, M. Rahkola-Sorsa, P. Ylostalo, K. Mikkonen, and J. Karjalainen. 2005. Littoral species diversity and biomass: concordance among organismal groups and the effects of environmental variables. *Biodiversity and Conservation* **14**:961-980.
- Townsend, C. R., M. R. Scarsbrook, and S. Doledec. 1997a. The Intermediate Disturbance Hypothesis, Refugia, and Biodiversity in Streams. *Limnology and Oceanography* **42**:938-949.
- Townsend, C. R., M. R. Scarsbrook, and S. Doledec. 1997b. Quantifying Disturbance in Streams: Alternative Measures of Disturbance in Relation to Macroinvertebrate Species Traits and Species Richness. *Journal of the North American Benthological Society* **16**:531-544.
- UNESCO. 2011. The Impact of Global Change on Water Resources: The Response of UNESCO's International Hydrological Programme.
- Usseglio-Polatera, P., M. Bournaud, P. Richoux, and H. Tachet. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology* **43**:175-205.
- Vadeboncoeur, Y., P. B. McIntyre, and M. J. V. Zanden. 2011. Borders of Biodiversity: Life at the Edge of the World's Large Lakes. *BioScience* **61**:526-537.
- Valdovinos, C., C. Moya, V. Olmos, O. Parra, B. Karrasch, and O. Buettner. 2007. The importance of water-level fluctuation for the conservation of shallow water benthic macroinvertebrates: an example in the Andean zone of Chile. *Biodiversity and Conservation* **16**:3095-3109.
- Van De Meutter, F., R. Stoks, and L. D. Meester. 2006. Rapid response of macroinvertebrates to drainage management of shallow connected lakes. *Journal of Applied Ecology* **43**:51-60.
- Van Geest, G. J., H. Coops, R. M. M. Roijackers, A. D. Buijse, and M. Scheffer. 2005. Succession of aquatic vegetation driven by reduced water-level fluctuations in floodplain lakes. *Journal of Applied Ecology* **42**:251-260.
- Vander Zanden, M. J. and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* **83**:2152-2161.
- Vassilev, M. 2006. Lower Danube – the last refuge for surviving of sturgeon fishes in the Black Sea region. *in* Water observation and information sysem for decision support, Ohrid, Macedonia.
- Verzani, J. 2002. SimpleR - Using R for Introductory Statistics. Page 114. CSI Math department.
- Vorosmarty, C. J., P. Green, J. Salisbury, and R. B. Lammers. 2000. Global Water Resources: Vulnerability from Climate Change and Population Growth. *Science* **289**:284-288.
- Vorosmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann, and P. M.

- Davies. 2010. Global threats to human water security and river biodiversity. *Nature* **467**:555-561.
- Wallace, J. B. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Page 862 in R. Merritt, W. and K. W. Cummins, editors. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt Publishing Company.
- Wallace, J. B., J. W. Grubaugh, and M. R. Whiles. 1996. Biotic Indices and Stream Ecosystem Processes: Results from an Experimental Study. *Ecological Applications* **6**:140-151.
- Wantzen, K., W. Junk, and K.-O. Rothhaupt. 2008a. An extension of the floodpulse concept (FPC) for lakes, *REFERENCES. Hydrobiologia* **613**:151-170.
- Wantzen, K., K.-O. Rothhaupt, M. Mörtl, M. Cantonati, L. G.-Tóth, and P. Fischer. 2008b. Ecological effects of water-level fluctuations in lakes: an urgent issue. *Hydrobiologia* **613**:1-4.
- Ward, J. V. 1992. Aquatic insect ecology. 456
- Warwick, R. M. and K. R. Clarke. 1993. Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology* **172**:215-226.
- Washington, H. G. 1984. Diversity, biotic and similarity indices. A review with special relevance to aquatic ecosystems. *Water Research* **18**:653-694.
- Weatherhead, M. A. and M. R. James. 2001. Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. *Hydrobiologia* **462**:115-129.
- Wesner, J. S. 2010. Aquatic predation alters a terrestrial prey subsidy. *Ecology* **91**:1435-1444.
- Wesner, J. S. 2011. Predator diversity effects cascade across an ecosystem boundary. *Oikos*:53-60.
- Wetzel, R. G. 2001. *Limonology. Lake and river ecosystems*. 3rd edition. Academic press
- Weyhenmeyer, G. 2008. Rates of change in physical and chemical lake variables – are they comparable between large and small lakes? *Hydrobiologia* **599**:105-110.
- WFD;. 2000/60/EC. Directive of the European Parliament and of the Council of the European Union establishing a framework for community action in the field of water policy. Page 66 in C. o. t. E. Union, editor., Brussels.
- White, M., M. Xenopoulos, K. Hogsden, R. Metcalfe, and P. Dillon. 2008. Natural lake level fluctuation and associated concordance with water quality and aquatic communities within small lakes of the Laurentian Great Lakes region. *Hydrobiologia* **613**:21-31.
- White, M. S., M. A. Xenopoulos, R. A. Metcalfe, and K. M. Somers. 2010. On the role of natural water level fluctuation in structuring littoral benthic macroinvertebrate community composition in lakes. *Journal Limnology and Oceanography* **55**:2275-2284.
- Whitman, R. L. and W. J. Clark. 1984. Ecological Studies of the Sand-Dwelling Community of an East Texas Stream. *Freshwater Invertebrate Biology* **3**:59-79.
- Williamson, C. E., B. R. Hargreaves, P. S. Orr, and P. A. Lovera. 1999. Does UV play a role in changes in predation and zooplankton community structure in acidified lakes? *Limnology and Oceanography* **44**:774-783.

- World Water Assessment Programme. 2009. The United Nations World Water Development Report 3: Water in a Changing World. UNESCO and Earthscan, Paris and London.
- Yin, X. A. and Z. F. Yang. 2012. A method to assess the alteration of water-level-fluctuation patterns in lakes. *Procedia Environmental Sciences* **13**:2427-2436.
- Zhang, D. D., P. Brecke, H. F. Lee, Y.-Q. He, and J. Zhang. 2007. Global climate change, war, and population decline in recent human history. *Proceedings of the National Academy of Sciences* **104**:19214-19219.
- Zohary, T. and I. Ostrovsky. 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. *Inland Waters* **1**:47-59.
- Zucco, C. A., L. G. R. Oliveira-Santos, and F. A. S. Fernandez. 2011. Protect Brazil's land to avert disasters. *Nature* **470**:335-335.
- Zuur, A. F., E. Ieno, and G. M. Smith. 2007. *Analysing Ecological Data*. 1st edition. Springer

Appendices

Chapter 2

Appendix 2.1. List of the 63 lakes with data on mean daily water levels.

Lake	Easting	Northing	Start date	Last record	Record length
Accormore	57860	305819	21/09/1983	02/08/2011	8217
Adeery	171735	381737	01/01/1977	12/02/1991	5156
Akkibon	206932	418432	29/11/1975	11/05/1997	7835
Allen	133745	104485	21/07/1981	05/01/2010	10396
Altan	193893	425031	25/02/1982	23/01/2012	8389
Anure	182369	417737	28/11/1975	23/01/2012	13206
Bane lower	255485	270697	25/05/2007	14/02/2008	265
Bane	255440	270938	31/03/1978	12/12/2011	12310
Bawn	271420	311412	14/10/1976	14/12/2011	12845
Beltra	105192	297652	22/09/1976	08/01/1994	6318
Carra	118999	272739	01/11/1957	13/04/2010	19157
Carrowmore	83800	325700	29/08/1975	13/12/2011	13256
Cloonaugh	61208	71415	27/12/1953	21/02/1984	11014
Coomnacronia	60557	86037	07/09/1988	22/07/1989	314
Coragh	262006	315238	25/10/1977	26/09/2011	12223
Cullaun	147626	174682	05/11/1981	21/12/1986	1873
Cullin	125146	302486	23/09/1983	21/01/2009	9253
Curramore	110128	61073	25/06/1987	16/09/1990	1177
Currane	52800	66800	18/10/1953	11/06/1986	11925
Cutra	148200	197900	23/09/1976	17/02/2012	12931
Dan	315524	202656	04/06/1952	12/08/1986	12488
Derg	170395	172995	21/02/2002	01/12/2006	1475
Derriana	60243	72633	10/10/1953	01/07/1989	13047
Derryclare	80279	247497	10/04/1979	20/11/2011	11913
Derrygooney	269364	310785	14/10/1976	07/12/2009	12108
Dromore	259781	315130	19/11/1975	02/02/2012	13225
Easky	144806	323780	16/12/1975	30/01/2012	13195
Egish	280334	312753	25/03/1975	14/03/2009	12409
Emy	269150	344725	01/10/1981	19/01/2012	11068
Ennell	241376	246616	27/03/1975	29/01/2012	13458
Eske	196691	382063	28/09/1977	17/02/2012	12561
Fad	239774	443226	23/09/1978	17/02/2012	12201

Lake	Easting	Northing	Start date	Last record	Record length
Fadda	80385	76100	19/10/1987	23/04/1990	916
Fee	78200	262000	13/05/1976	20/11/2011	12975
Feeagh	96776	298416	04/03/1976	26/10/2011	13020
Fern	217477	423040	14/09/1976	04/07/1999	8329
Gartan	206080	417290	29/11/1975	25/07/1999	8640
Garty	227471	297404	18/10/1977	03/09/2000	8357
Gill	171439	333444	21/03/1975	06/02/2012	13472
Gleincmurrin	100206	229686	15/07/1976	16/11/2011	12908
Gowna	230045	290846	25/06/1976	15/02/2012	13019
Guitane	101440	85112	26/08/1975	16/07/1986	3978
Inchiquin	127224	189375	12/11/1976	03/12/2011	12805
Islandeay	109733	288476	26/10/1976	02/05/1996	7129
Lannagh	113639	289979	05/03/1976	11/12/1990	5395
Lene	249500	268500	29/01/1981	31/01/2012	11325
Lickeen	213100	337500	21/01/1976	22/08/2003	10077
Major Ballybay	272255	320292	24/03/1976	02/11/1987	4238
Moher	97630	277284	25/08/1977	19/11/2008	11410
Mourne	206344	389584	21/05/1999	02/02/2012	4641
Muckno	286249	317556	05/04/1975	25/01/2012	13445
Nadreegeel	255178	292925	03/11/1976	15/12/2005	10635
Nahillion	72500	253100	17/07/2003	13/11/2007	1869
Oughter	237166	310018	14/10/1977	11/01/2012	12508
Owel	239173	258173	15/11/1979	23/02/2012	11789
Rea	161553	216481	22/01/1976	30/09/1992	6097
Shannonn Weir	167975	167919	12/04/2002	16/03/2004	705
Sillan	269058	306884	14/11/1974	22/05/2005	11148
Skeagh	265261	300686	13/06/1975	15/02/2012	13397
Skean	185140	312810	12/12/2005	15/01/2008	1099
Urlaur	150946	289283	07/12/1975	01/04/2006	11074
White Cordevlis	267263	318794	13/04/1976	20/02/2008	12291
Whitewood	279068	288325	02/08/1983	05/09/1995	4416

Appendix 2.2. Water level metrics description. The abbreviations used are as follows: MDWL mean daily water level; tp – time period the metric is calculated for; U – unit with 1 denoting meters, 2 – dimensionless, 3 – count. The resolutions used are individual months (January- December) and seasons (S1-4) and averaged water level statistics for the week (W), month (M), season (S) and year (A). Dc denotes complete daily time series.

Water level metrics	Code	U	TSindividual	TSoverall	Lake water level metric definition
1. Magnitude					
Summary mean daily water level	D.mean	1	na	Dc	MDWL averaged across years for the complete time series
Summary median daily water level	D.median	1	na	Dc	Median MWDL for the complete time series
Summary maxima of daily water level	D.max	1	na	Dc	Maximum MWDL for the complete time series
Summary minima of daily water level	D.min	1	na	Dc	Minimum MWDL for the complete time series
Extremely low water level threshold	D.01	1	na	Dc	MDWL below which 1 % of all observations fall
Low water level treshold	D.10	1	na	Dc	MDWL below which 10 % of all observations fall
High water level treshold	D.90	1	na	Dc	MDWL above which 90 % of all observations fall
Extremely high water level treshold	D.99	1	na	Dc	MDWL above which 99 % of all observations fall
Lower margin of stable WL 40th percentile	D.40	1	na	Dc	MDWL below which 40 % of all observations fall
Upper margin of stable WL 60th percentile	D.60	1	na	Dc	MDWL below which 60 % of all observations fall
Spread 80	D.S80	2	na	Dc	Ratio of the difference between D.90 and D.10 and the median MWDL for the complete time series

Water level metrics	Code	U	TSindividual	TSoverall	Lake water level metric definition
Spread 100	D.S100	2	na	Dc	Ratio of the range and the median MWDL for the complete time series
Mean water level range	tpR.mean	1	Jan-Dec, S1-4	W, M, S, A	Difference between the maximum and minimum water levels for the specified time period
Mean water level high water index	tp_HWI.mean	2	Jan-Dec, S1-4	W, M, S, A	Ratio of the highest to the mean water level per time step averaged across years for the series
Mean water level low water index	tp_LWI.mean	2	Jan-Dec, S1-4	W, M, S, A	Ratio of the lowest to the mean water level per time step averaged across years for the series
CV of water level maximum	tpMax.cv	2	Jan-Dec, S1-4	W, M, S, A	Coefficient of variation of the maximum water level for the specified period
CV of water level minimum	tpMin.cv	2	Jan-Dec, S1-4	W, M, S, A	Coefficient of variation of the minimum water level for the specified period
CV of water level mean	tpMean.cv	2	Jan-Dec, S1-4	Dc, W, M, S, A	Coefficient of variation of the mean water level for the specified period
CV of water level range	tpR.cv	2	Jan-Dec, S1-4	W, M, S, A	Coefficient of variation of the range of water level for the specified period
CV of water level high water index	tp_HWI.cv	2	Jan-Dec, S1-4	W, M, S, A	Coefficient of variation of the high water level index for the specified period
CV of water level low water index	tp_LWI.cv	2	Jan-Dec, S1-4	W, M, S, A	Coefficient of variation of the low water level index for the specified period
SD of water level maximum	tpMax.sd	2	Jan-Dec, S1-4	W, M, S, A	Standard deviation of the maximum water level for the specified period
SD of water level minimum	tpMin.sd	2	Jan-Dec, S1-4	W, M, S, A	Standard deviation of the minimum water level for the specified period
SD of water level mean	tpMean.sd	2	Jan-Dec, S1-4	Dc, W, M, S, A	Standard deviation of the mean water level for the specified period
SD of water level range	tpR.sd	2	Jan-Dec, S1-4	W, M, S, A	Standard deviation of the range of water level for the specified period

Water level metrics		Code	U	TSindividual	TSoverall	Lake water level metric definition
SD of water level high water index		tp_HWI.sd	2	Jan-Dec, S1-4	W, M, S, A	Standard deviation of the high water level index for the specified period
SD of water level low water index		tp_LWI.sd	2	Jan-Dec, S1-4	W, M, S, A	Standard deviation of the low water level index for the specified period
Mad of water level mean		tpMean.mad	2	Jan-Dec, S1-4	Dc, W, M, S, A	Median absolute deviation of the mean water level for the specified period
Mad of water level range		tpR.mad	2	Jan-Dec, S1-4	W, M, S, A	Median absolute deviation of the range of water level for the specified period
Mad of water level high water index		tp_HWI.mad	2	Jan-Dec, S1-4	W, M, S, A	Median absolute deviation of the high water level index for the specified period
Mad of water level low water index		tp_LWI.mad	2	Jan-Dec, S1-4	W, M, S, A	Median absolute deviation of the low water level index for the specified period
IQR of water level mean		tpMean.IQR	2	Jan-Dec, S1-4	Dc, W, M, S, A	Difference of the 3rd and 1st quartile of the mean water level for the specified period
IQR of water level range		tpR.IQR	2	Jan-Dec, S1-4	W, M, S, A	Difference of the 3rd and 1st quartile of the range of water level for the specified period
IQR of water level high water index		tp_HWI.IQR	2	Jan-Dec, S1-4	W, M, S, A	Difference of the 3rd and 1st quartile of the high water level index for the specified period
IQR of water level low water index		tp_LWI.IQR	2	Jan-Dec, S1-4	W, M, S, A	Difference of the 3rd and 1st quartile of the low water level index for the specified period
S50 of water level maximum		tpMax.S50	2	Jan-Dec, S1-4	W, M, S, A	Ratio of IQR and the overall median of the maximum water level for the specified period
S50 of water level minimum		tpMin.S50	2	Jan-Dec, S1-4	W, M, S, A	Ratio of IQR and the overall median of the minimum water level for the specified period
S50 of water level mean		tpMean.S50	2	Jan-Dec, S1-4	Dc, W, M, S, A	Ratio of IQR and the overall median of the mean water level for the specified period
S50 of water level range		tpR.S50	2	Jan-Dec, S1-4	W, M, S, A	Ratio of IQR and the overall median of the range of water level for the specified period

Water level metrics	Code	U	TSindividual	TSoverall	Lake water level metric definition
S50 of water level high water index	tp_HWL.S50	2	Jan-Dec, S1-4	W, M, S, A	Ratio of IQR and the overall median of the high water level index for the specified period
S50 of water level low water index	tp_LWL.S50	2	Jan-Dec, S1-4	W, M, S, A	Ratio of IQR and the overall median of the low water level index for the specified period
Skew of water level mean	tpMean.skew	2	Jan-Dec, S1-4	Dc, W, M, S, A	Skewness of the mean water level for the specified period
Skew of water level range	tpR.skew	2	Jan-Dec, S1-4	W, M, S, A	Skewness of the range of water level for the specified period
Skew of water level high water index	tp_HWL.skew	2	Jan-Dec, S1-4	W, M, S, A	Skewness of the high water level index for the specified period
Skew of water level low water index	tp_LWL.skew	2	Jan-Dec, S1-4	W, M, S, A	Skewness of the low water level index for the specified period
Kurt of water level mean	tpMean.kurt	2	Jan-Dec, S1-4	Dc, W, M, S, A	Kurtosis of the mean water level for the specified period
Kurt of water level range	tpR.kurt	2	Jan-Dec, S1-4	W, M, S, A	Kurtosis of the range of water level for the specified period
Kurt of water level high water index	tp_HWL.kurt	2	Jan-Dec, S1-4	W, M, S, A	Kurtosis of the high water level index for the specified period
Kurt of water level low water index	tp_LWL.kurt	2	Jan-Dec, S1-4	W, M, S, A	Kurtosis of the low water level index for the specified period
1st percentile of water level range	tpR1%	1	Jan-Dec, S1-4	W, M, S, A	MDWL below which 1 % of all observations fall
10th percentile of water level range	tpR10%	1	Jan-Dec, S1-4	W, M, S, A	MDWL below which 10 % of all observations fall
40th percentile of water level range	tpR40%	1	Jan-Dec, S1-4	W, M, S, A	MDWL below which 40 % of all observations fall
60th percentile of water level range	tpR60%	1	Jan-Dec, S1-4	W, M, S, A	MDWL below which 60 % of all observations fall

Water level metrics	Code	U	TSindividual	TSoverall	Lake water level metric definition
90st percentile of water level range	tpR90%	1	Jan-Dec, S1-4	W, M, S, A	MDWL above which 90 % of all observations fall
99th percentile of water level range	tpR99%	1	Jan-Dec, S1-4	W, M, S, A	MDWL above which 99 % of all observations fall
Number of readings of water level statistics	NoReadings	3	Jan-Dec, S1-5	Dc, W, M, S, A	Number of readings used to calculate the relevant statistic

2. Frequency of fluctuations

Extremely low water level frequency (<99th percentile)	tp_L1Fr	3	Jan-Dec, S1-4	M,S,A	Mean number of occurrences during which the level remains below an extremely low threshold defined by 99th percentile.
Low water level frequency (<90th percentile)	tp_L10Fr	3	Jan-Dec, S1-4	M,S,A	Mean number of occurrences during which the level remains below a lower threshold defined by 90th percentile.
Extremely high water level frequency (>1st percentile)	tp_H99Fr	3	Jan-Dec, S1-4	M,S,A	Mean number of occurrences during which the level remains above the 1st percentile.
High water level frequency (>10th percentile)	tp_H90Fr	3	Jan-Dec, S1-4	M,S,A	Mean number of occurrences during which the level remains above the 10th percentile.
CV of extremely low water level annual frequency (<99th percentile)	A_L1Fr.cv	2	na	D	CV in number of annual occurrences during which levels remain below the 99th percentiles
CV of low water level annual frequency (<90th percentile)	A_L10Fr.cv	2	na	D	CV in number of annual occurrences during which levels remain below the 90th percentiles
CV of extremely high water level annual frequency (>1st percentile)	A_H99Fr.cv	2	na	D	CV in number of annual occurrences during which levels remain below the 1st percentile
CV of high water level annual frequency (>10th percentile)	A_H90Fr.cv	2	na	D	CV in number of annual occurrences during which levels remain below the 10th percentile
SD of extremely low water level annual frequency (<99th percentile)	A_L1Fr.sd	2	na	D	SD in number of annual occurrences during which levels remain below the 99th percentiles
SD of low water level annual frequency	A_L10Fr.sd	2	na	D	SD in number of annual occurrences during

Water level metrics	Code	U	TSindividual	TSoverall	Lake water level metric definition
(<90th percentile)					which levels remain below the 90th percentiles
SD of extremely high water level annual frequency (>1st percentile)	A_H99Fr.sd	2	na	D	SD in number of annual occurrences during which levels remain below the 1st percentile
SD of high water level annual frequency (>10th percentile)	A_H90Fr.sd	2	na	D	SD in number of annual occurrences during which levels remain below the 10th percentile
3. Duration of water level conditions					
Water level rise length	RL.mean	3	na	D	Mean length of intervals of consecutive days in an year during which water level rises averaged across all years
CV of rise length	CVRsL.mean	2	na	D	Mean of the individual coefficients of variation of the rise length per each year
SD of rise length	SDRsL.mean	2	na	D	Mean of the individual standard deviations of the rise length per each year
Water level drop length	DrL.mean	3	na	D	Mean length of intervals of consecutive days in an year during which water level drops averaged across all years
CV of drop length	CVDrL	2	na	D	Mean of the individual coefficients of variation of the drop length per each year
SD of drop length	DrL.mean.sd	2	na	D	Mean of the individual standard deviations of the drop length per each year
Number of water level readings	NoReadings	3	na	D	Number of water level readings used to calculate the length statistics
4. Timing of fluctuations					
Julian date of annual maximum	DJmax.mean	3	na	D	The mean Julian date of the 1-day annual maximum level over all years
CV Julian date of annual maximum level	DJmax_CV	2	na	D	CV in the Julian date of the 1-day annual maximum level

Water level metrics	Code	U	TSindividual	TSoverall	Lake water level metric definition
SD Julian date of annual maximum level	DJmax_SD	2	na	D	SD in the Julian date of the 1-day annual maximum level
Julian date of annual minimum	DJmin.mean	3	na	D	The mean Julian date of the 1-day annual minimum level over all years
CV Julian date of annual minimum	DJmin_CV	2	na	D	CV in Julian date of the 1-day annual minimum level over all years
SD Julian date of annual minimum	DJmin_SD	2	na	D	SD in Julian date of the 1-day annual minimum level over all years
Extremely low level spell count (<99th percentile)	tp_L1SpellNo	3	Jan-Dec, S1-4	M, S, A	Mean number of occurrences during which the level remains below an extremely low threshold defined by the 99th percentile.
Low level spell count (<90th percentile)	tp_L10SpellNo	3	Jan-Dec, S1-4	M, S, A	Mean number of occurrences during which the level remains below a lower threshold defined by 90th percentile.
Extremely high level spell count (>1st percentile)	tp_H90SpellNo	2	Jan-Dec, S1-4	M, S, A	Mean number of occurrences during which the level remains above the 1st percentiles.
High level spell count (>10th percentile)	tp_H99SpellNo	3	Jan-Dec, S1-4	M, S, A	Mean number of occurrences during which the level remains above the 10th percentiles.

5. Rate of change in levels

Number of reversals	RevNo.mean	3	na	D	Number of negative and positive changes in level from one day to the next
CV of No of reversals	RevNo.cv	2	na	D	Coefficient of variation in the number of negative and positive changes
SD of No of reversals	RevNo.sd	2	na	D	Standard deviation in the number of negative and positive changes
Temporal rate of change in range	SlpR.mean	2	na	M, S, A	Temporal rate (slope) of change in water level amplitudes linking the range across different temporal scales

Water level metrics	Code	U	TSindividual	TSoverall	Lake water level metric definition
Temporal rate of change in HWI	SlpHWI.mean	2	na	M, S, A	Slope of change in high water level index across different temporal scales
Temporal rate of change in LWI	SlpLWLI.mean	2	na	M, S, A	Slope of change in low water level index across different temporal scales
CV in temporal rate of change in range	SlpR.cv	2	na	M, S, A	CV in slope of change in water level ranges across different temporal scales
CV in temporal rate of change in HWI	SlpHWI.cv	2	na	M, S, A	CV in slope of change in high water level index across different temporal scales
CV in temporal rate of change in LWI	SlpLWLI.cv	2	na	M, S, A	CV in slope of change in low water level index across different temporal scales
SD in temporal rate of change in range	SlpR.sd	2	na	M, S, A	SD in slope of change in water level ranges across different temporal scales
SD in temporal rate of change in HWI	SlpHWI.sd	2	na	M, S, A	SD in slope of change in high water level index across different temporal scales
SD in temporal rate of change in LWI	SlpLWLI.sd	2	na	M, S, A	SD in slope of change in low water level index across different temporal scales

Appendix 2.3. Kurtosis statistics of water level amplitudes for the 46 lakes. N denotes the number of readings the calculations were based on.

Lake	Weekly range		Monthly range		Seasonal range		Annual range	
	N	Kurtosis	N	Kurtosis	N	Kurtosis	N	Kurtosis
Adeery	703	-0.42	164	1.77	56	3.68	14	3.6
Akkibon	1073	16.57	253	3.21	86	-0.08	21	-0.26
Allen	1394	3.07	324	0	110	-0.05	28	-0.5
Anure	1846	3.26	427	0.42	145	0.88	36	0.3
Bane	1538	129.41	369	13.94	127	1.98	34	2.36
Bawn	1725	7.92	407	1.35	139	0.38	36	0.48
Beltra	869	7.4	203	0.12	69	0.13	17	-0.22
Carra	1905	22.3	440	2.56	146	0.19	37	-0.58
Carrowmore	1639	16.21	381	3.83	130	0.19	34	-0.73
Cloonaugh	1505	5.86	351	1.37	119	2.09	30	0.33
Cullin	1223	15.91	287	1.58	97	-0.43	27	0.63
Currane	798	12.69	209	1.87	74	2.37	22	2.08
Cutra	1702	4.04	396	0.35	136	2.1	35	3.79
Dan	1606	1.79	391	-0.68	130	-0.05	35	-0.46
Derryclare	1622	1.53	381	0.5	129	1.25	33	2.74
Dromore	1678	6.67	403	1.04	136	0.69	36	-0.11
Easky	1672	4.11	399	1.22	137	1.39	34	0.01
Egish	1652	8.99	391	1.96	133	1.8	34	0.11
Emy	1468	2.49	348	1.85	119	0.94	30	0.13
Ennell	1707	10.99	401	2.47	138	0.23	35	0.58
Eske	1744	3.4	411	1.13	138	1.03	34	0.49
Fad	1396	4.34	328	1.32	118	0.41	31	-1.38
Fee	1771	6.71	412	4.14	139	2.75	35	0.32
Feeagh	1759	3.12	414	0.5	139	0.01	36	-0.53
Fern	1131	2.29	271	-0.19	91	-0.26	23	0.28
Gartan	1211	6.2	283	2	95	0.36	24	-0.99
Garty	1114	9.9	265	1.18	87	0.17	23	0.51
Gill	1845	7.22	434	0.97	147	-0.33	37	-0.32
Gleincmurrin	1762	4.32	411	0.57	139	0.4	35	0.39
Gowna	1762	13.41	405	3.16	137	-0.19	35	-0.18
Guitane	531	2.56	124	0.09	42	-0.15	11	-0.6
Inchiquin	1677	1.31	400	-0.75	138	0.62	34	-0.05
Islandeady	989	3.16	228	-0.54	77	-0.04	19	-1
Lannagh	609	2.47	142	-0.53	50	-0.68	14	-1.21
Lene	1015	10.47	239	2.86	83	-0.65	21	-0.53

Lake	Weekly range		Monthly range		Seasonal range		Annual range	
	N	Kurtosis	N	Kurtosis	N	Kurtosis	N	Kurtosis
Adeery	703	-0.42	164	1.77	56	3.68	14	3.6
Akkibon	1073	16.57	253	3.21	86	-0.08	21	-0.26
Allen	1394	3.07	324	0	110	-0.05	28	-0.5
Anure	1846	3.26	427	0.42	145	0.88	36	0.3
Bane	1538	129.41	369	13.94	127	1.98	34	2.36
Bawn	1725	7.92	407	1.35	139	0.38	36	0.48
Beltra	869	7.4	203	0.12	69	0.13	17	-0.22
Carra	1905	22.3	440	2.56	146	0.19	37	-0.58
Carrowmore	1639	16.21	381	3.83	130	0.19	34	-0.73
Cloonaugh	1505	5.86	351	1.37	119	2.09	30	0.33
Cullin	1223	15.91	287	1.58	97	-0.43	27	0.63
Currane	798	12.69	209	1.87	74	2.37	22	2.08
Cutra	1702	4.04	396	0.35	136	2.1	35	3.79
Dan	1606	1.79	391	-0.68	130	-0.05	35	-0.46
Derryclare	1622	1.53	381	0.5	129	1.25	33	2.74
Dromore	1678	6.67	403	1.04	136	0.69	36	-0.11
Easky	1672	4.11	399	1.22	137	1.39	34	0.01
Lickeen	1330	13.35	311	1.9	107	0.4	28	6.06
Moher	1474	8.63	342	3.2	115	1.64	30	-0.33
Mourne	632	1.19	148	-0.57	50	-0.11	13	-0.3
Muckno	1759	7.91	414	0.28	138	1.9	35	3.41
Nadreegeel	1352	119.58	319	15	111	2.74	29	4.84
Oughter	1737	10.29	405	1.03	138	0.05	34	-0.36
Owel	735	8.35	326	1.78	112	0.43	29	1.33
Rea	865	5.63	200	1.67	67	-0.32	17	2.92
Sillan	1554	7.81	362	1.34	122	1.4	30	4.08
Skeagh	1880	10.06	435	4.22	145	0.73	37	1.16
Urlaur	1379	10.11	322	2.23	111	-0.74	27	-0.7

Appendix 2.4. Mean monthly index for each lake, expressed as the ration of the individual month to the overall monthly mean. The blue and red colour coding correspond to, respectively, the minimal and maximal monthly index for each of the 46 lakes.

Lake	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ad	1.22	1.00	1.12	0.72	0.64	0.67	0.82	0.98	1.11	1.23	1.18	1.22
Ak	1.35	1.20	1.16	0.96	0.74	0.61	0.57	0.70	0.86	1.21	1.29	1.27
Al	1.26	1.15	1.09	0.97	0.83	0.77	0.73	0.77	0.84	1.08	1.20	1.23
An	1.16	1.04	1.03	0.87	0.78	0.76	0.89	0.95	1.00	1.14	1.19	1.17
Bel	1.42	1.11	1.19	0.83	0.57	0.49	0.50	0.80	0.97	1.23	1.35	1.45
Bn	1.04	1.07	1.07	1.07	1.05	1.02	0.98	0.93	0.90	0.92	0.95	0.99
Bw	1.42	1.26	1.14	0.96	0.79	0.68	0.60	0.66	0.74	1.04	1.29	1.43
Cl	1.16	1.13	1.08	0.89	0.87	0.79	0.84	0.90	0.96	1.10	1.12	1.18
Cr	1.01	1.01	1.00	1.00	1.00	0.99	0.99	0.99	0.99	1.00	1.01	1.01
Crw	1.25	1.14	1.09	0.95	0.81	0.73	0.73	0.83	0.92	1.09	1.26	1.24
Cul	1.47	1.27	1.18	0.93	0.77	0.70	0.65	0.70	0.77	0.96	1.21	1.40
Cur	1.31	1.27	1.21	0.86	0.67	0.58	0.61	0.66	0.82	1.12	1.12	1.39
Cut	1.36	1.20	1.10	0.92	0.79	0.69	0.64	0.74	0.83	1.05	1.31	1.35
Dan	1.23	1.15	1.12	0.94	0.92	0.77	0.72	0.79	0.87	1.06	1.16	1.29
Der	1.17	1.06	1.04	0.88	0.81	0.78	0.86	0.96	1.00	1.10	1.19	1.17
Dro	1.32	1.21	1.13	0.98	0.85	0.76	0.67	0.74	0.78	1.01	1.24	1.32
Eas	1.09	1.04	1.04	0.94	0.90	0.87	0.93	0.96	0.98	1.06	1.09	1.08
Eg	1.26	1.20	1.12	1.03	0.91	0.82	0.76	0.75	0.77	0.95	1.13	1.24
Em	1.16	1.14	1.15	1.11	1.00	0.91	0.85	0.82	0.82	0.93	1.02	1.08
En	1.07	1.06	1.03	1.01	0.99	0.97	0.95	0.94	0.94	0.95	1.03	1.06
Es	1.20	1.08	1.07	0.87	0.78	0.74	0.82	0.90	1.02	1.13	1.19	1.19
Fad	1.24	1.12	1.07	0.93	0.79	0.65	0.79	0.86	1.00	1.11	1.20	1.22
Fee	1.06	1.02	1.01	0.97	0.94	0.94	0.95	0.97	0.99	1.04	1.06	1.06
Fer	1.40	1.21	1.15	0.88	0.65	0.56	0.61	0.76	0.88	1.22	1.33	1.31
Fgh	1.27	1.08	1.09	0.84	0.74	0.67	0.74	0.87	0.97	1.19	1.29	1.28
Gi	1.09	1.05	1.04	0.97	0.93	0.90	0.91	0.95	0.97	1.04	1.08	1.09
Gl	1.11	1.07	1.03	0.96	0.91	0.88	0.90	0.94	0.97	1.05	1.10	1.10
Go	1.48	1.40	1.25	1.08	0.84	0.67	0.57	0.57	0.67	0.87	1.23	1.42
Grn	1.25	1.12	1.11	0.91	0.76	0.72	0.81	0.86	0.97	1.14	1.19	1.19

Lake	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Gry	1.16	1.09	1.08	1.02	0.92	0.87	0.83	0.87	0.89	0.98	1.08	1.13
Gu	1.24	1.13	1.14	0.84	0.88	0.78	0.65	0.72	0.82	1.17	1.28	1.44
In	1.29	1.14	1.08	0.86	0.75	0.70	0.69	0.84	0.92	1.09	1.29	1.30
Isl	1.16	1.08	1.06	0.93	0.86	0.83	0.82	0.89	0.95	1.10	1.14	1.17
La	1.19	1.17	1.07	0.91	0.81	0.80	0.80	0.84	0.90	1.14	1.23	1.18
Le	1.19	1.26	1.22	1.19	1.08	0.97	0.86	0.77	0.75	0.76	0.90	1.04
Li	1.10	1.09	1.06	0.99	0.91	0.89	0.87	0.90	0.94	1.02	1.09	1.12
Mo	1.12	1.06	1.04	0.96	0.94	0.90	0.87	0.86	0.94	1.08	1.12	1.13
Mou	1.31	1.11	0.97	0.73	0.76	0.67	0.68	0.78	1.03	1.20	1.32	1.32
Mu	1.12	1.07	1.05	1.01	0.95	0.92	0.89	0.89	0.92	0.99	1.08	1.11
Na	1.13	1.11	1.08	1.04	0.93	0.88	0.84	0.87	0.89	0.99	1.07	1.11
Ou	1.53	1.40	1.25	1.05	0.76	0.57	0.45	0.57	0.67	0.91	1.30	1.49
Ow	1.08	1.30	1.32	1.30	1.20	1.07	0.93	0.79	0.72	0.67	0.76	0.89
Re	1.36	1.28	1.19	1.08	0.94	0.80	0.66	0.63	0.71	0.88	1.21	1.30
Sil	1.43	1.31	1.20	1.03	0.81	0.73	0.59	0.59	0.64	0.95	1.25	1.39
Sk	1.13	1.09	1.05	1.01	0.95	0.91	0.88	0.89	0.91	0.98	1.09	1.13
Ur	1.25	1.19	1.06	0.93	0.79	0.78	0.75	0.80	0.91	1.07	1.22	1.24

Appendix 2.5. Within-lake mean water level at the seasonal temporal scale. The blue and red colour coding corresponds to, respectively, the minimal and maximal seasonal index for each of the 46 lakes.

Code	Mean seasonal water level index			
	Spring	Summer	Autumn	Winter
Ad	0.83	0.83	1.18	1.15
Ak	0.96	0.63	1.12	1.27
Al	0.97	0.75	1.04	1.21
An	0.89	0.87	1.11	1.13
Bel	0.85	0.59	1.17	1.33
Bn	1.06	0.98	0.92	1.04
Bw	0.96	0.64	1.04	1.37
Cl	0.95	0.84	1.06	1.15
Cr	1.00	0.99	1.00	1.01
Crw	0.96	0.76	1.09	1.21
Cul	0.95	0.68	0.99	1.39

Code	Mean seasonal water level index			
	Spring	Summer	Autumn	Winter
Cur	0.92	0.63	1.02	1.36
Cut	0.93	0.70	1.06	1.30
Dan	0.99	0.76	1.03	1.22
Der	0.90	0.86	1.10	1.13
Dro	0.98	0.72	1.02	1.28
Eas	0.96	0.92	1.05	1.07
Eg	1.02	0.78	0.96	1.23
Em	1.09	0.85	0.93	1.13
En	1.01	0.96	0.97	1.07
Es	0.90	0.82	1.11	1.16
Fad	0.92	0.75	1.11	1.21
Fee	0.97	0.95	1.03	1.05
Fer	0.89	0.63	1.15	1.31
Fgh	0.89	0.76	1.14	1.21
Gi	0.98	0.92	1.03	1.07
Gl	0.97	0.91	1.04	1.10
Go	1.05	0.60	0.93	1.44
Grn	0.92	0.80	1.10	1.19
Gry	1.00	0.87	0.98	1.13
Gu	0.95	0.73	1.09	1.27
In	0.90	0.74	1.09	1.25
Isl	0.95	0.85	1.06	1.14
La	0.94	0.80	1.08	1.19
Le	1.17	0.88	0.80	1.15
Li	0.99	0.88	1.02	1.11
Mo	0.98	0.87	1.05	1.10
Mou	0.84	0.71	1.18	1.25
Mu	1.00	0.90	0.99	1.10
Na	1.02	0.86	0.99	1.12
Ou	1.01	0.52	0.97	1.48
Ow	1.27	0.92	0.72	1.08
Re	1.07	0.70	0.92	1.30
Sil	1.02	0.63	0.96	1.38
Sk	1.00	0.89	0.99	1.12
Ur	0.93	0.77	1.06	1.22

Chapter 3

Appendix 3.1. Classification and definitions of functional feeding types of benthic macroinvertebrates according to Moog (1995).

Functional feeding type	Food source
Shredders	Fallen leaves, plant tissue, coarse particulate organic matter (CPOM).
Grazers and scrapers	Endo- and epilithic algal tissues, biofilm, partially particulate organic matter (POM) and tissues of living plants
Miners	Leaves of aquatic plants, algae and cells of aquatic plants
Xylophagus	Woody debris
Active filters	Suspended fine particulate organic matter (FPOM), CPOM, micro prey is whirled
Passive filters	Food brought by flowing water current: suspended FPOM, CPOM, prey
Gatherers/ collectors	Sedimented FPOM
Predators	Invertebrate prey
Parasites	Host invertebrate/ fish
Other	Omnivorous or cannot be classified

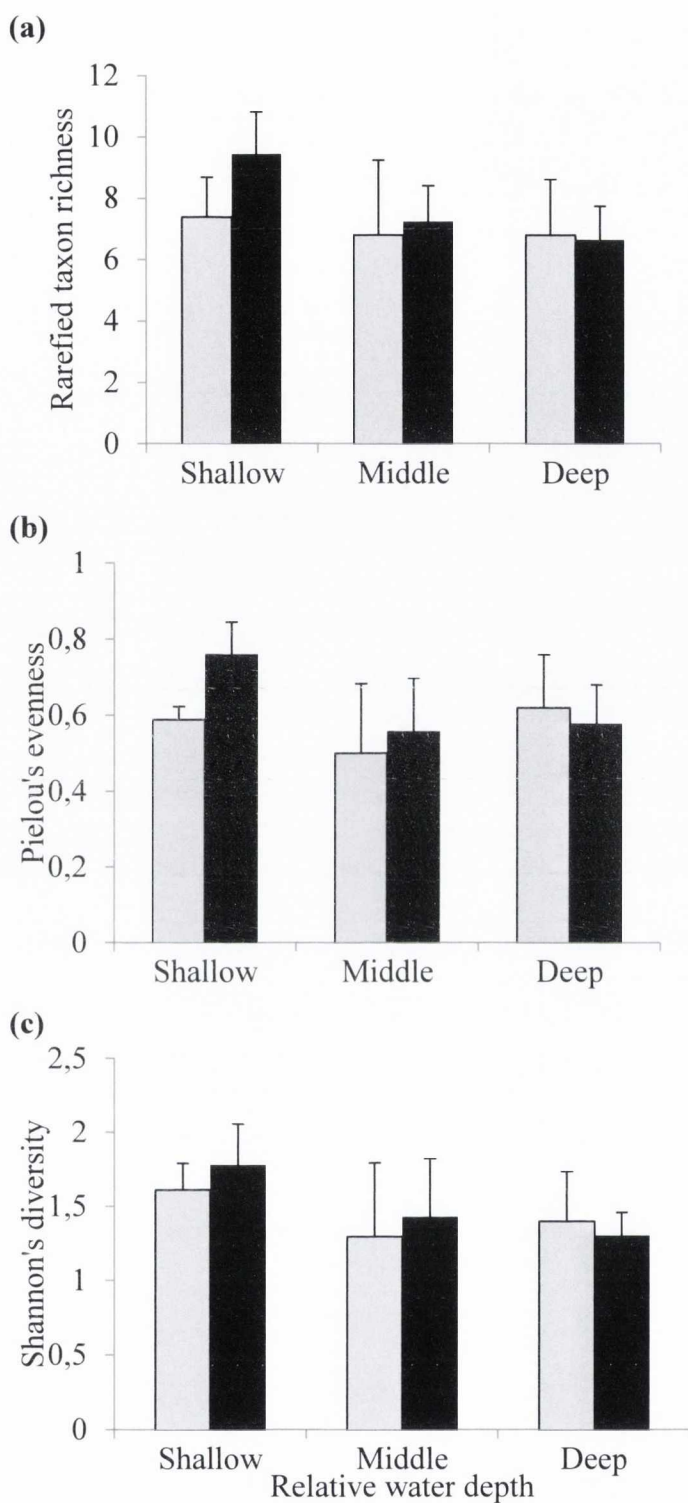
Appendix 3.2. Classification and definitions of benthic macroinvertebrate locomotive capacity according to Schmedtje and Colling (1996).

Locomotion type	Description
Swimming/ skating	Species, which float in lakes or drift in rivers passively
Swimming/ diving	Species, which swim or dive actively
Burrowing/ boring	Species, which burrow in soft substrates or bore in hard substrates
Sprawling/ walking	Species, which sprawl or walk actively with legs, pseudopods or on a mucus
(Semi)Sessile	Species, which are tightened to hard substrates, plants or other animals
Other	Other locomotion type like flying or jumping (mainly outside the water)

Appendix 3.3. Benthic macroinvertebrate taxa found in my experimental ponds at the end of the experiment.

Phylum/Class/ Order	Family	Taxon
Acari		Oribatei
Amphipoda	Crangonycitidae	<i>Crangonyx pseudogracilis</i> Bousfield, 1958
	Gammaridae	<i>Gammarus duebeni</i> Lilljeborg, 1851
		<i>Gammarus pulex</i> (Linnaeus, 1758)
Bivalvia	Sphaeriidae	<i>Pisidium</i> sp. Pfeiffer, 1821
Coelenterate	Hydrozoa	Hydrozoa
Coleoptera	Halipilidae	<i>Brychius elevatus</i> (Panzer, 1794)
	Dytiscidae	<i>Agabus bipustulatus</i> (Linnaeus, 1767)
		<i>Hydroporus planus</i> (Fabricius, 1782)
	Elmidae	<i>Oulimnius tuberculatus</i> (Müller, 1806)
Collembola	Isotomidae	<i>Isotomurus</i> sp. Boerner, 1903
Diptera	Cecidomyiidae	Cecidomyiidae
	Ceratopogonidae	Ceratopogonidae
	Chaoboridae	Chaoboridae
	Chironomidae	Chironomidae
	Culicidae	Culicidae
	Dixidae	Dixidae
	Dolichopodidae	Dolichopodidae
	Stratiomyiidae	Stratiomyiidae
	Diptera Gen. sp.	Diptera Gen.sp.
Ephemeroptera	Beatidae	<i>Cloeon dipterum</i> (Linnaeus, 1761)
Gastropoda	Acroloxidae	<i>Acroloxus lacustris</i> (Linnaeus, 1758)
	Bithyniidae	<i>Bithynia tentaculata</i> (Linnaeus, 1758)
		<i>Myosotella myosotis</i> (Draparnaud, 1801)
	Hydrobiidae	<i>Potamopyrgus antipodarum</i> (Gray, 1853)
	Lymnaeidae	<i>Radix peregra</i> (Müller, 1774)
	Planorbidae	<i>Gyraulus albus</i> (Müller, 1774)
		<i>Segmentina nitida</i> (Müller, 1774)
Hemiptera	Corixidae	<i>Callicorixa praeusta</i> (Fieber, 1848)
		<i>Micronecta poweri</i>
		<i>Sigara distinct</i> (Fieber, 1848)
	Veliidae	Veliidae
Hirudinea	Erpobdellidae	<i>Erpobdella octoculata</i> (Linnaeus, 1758)
	Glossiphoniidae	<i>Glossiphonia complanata</i> (Linnaeus, 1758)
		<i>Helobdella stagnalis</i> (Linnaeus, 1758)

Phylum/Class/ Order	Family	Taxon
Isopoda	Asellidae	<i>Asellus aquaticus</i> (Linnaeus, 1758)
Lepidoptera	Crambidae	<i>Cataclysta lemnata</i> (Linnaeus, 1758)
Nematoda		Nematoda
Oligochaeta		Oligochaeta
Ostracoda		Ostracoda
Plecoptera	Nemouridae	<i>Nemurella picteti</i> Klapalek, 1900
Trichoptera	Leptoceridae	<i>Mystacides azureus</i> (Linnaeus, 1761)
		<i>Mystacides longicornis</i> (Linnaeus, 1758)
	Limnephilidae	<i>Halesus radiates</i> (Curtis, 1834)
	Phryganeidae	<i>Phyrganea bipunctata</i> Retzius, 1783
	Polycentropodidae	<i>Cyrnus flavidus</i> McLachlan, 1864
Turbellaria		<i>Cyrnus trimaculatus</i> (Curtis, 1834)
	Dendrocoelidae	<i>Dendrocoelum lacteum</i> (Müller, 1774)
	Planariidae	<i>Dugesia lugibris</i> (Schmidt, 1861)
		<i>Polycelis nigra</i> (Müller, 1973)



Appendix 3.4. Diversity of benthic invertebrate assemblages (mean + s.e., $n = 6$) measured as (a) rarefied taxon richness, (b) Pielou's evenness and (c) Shannon's diversity in mesocosms with absent (grey bars) and present (black bars) experimental water level fluctuations.

Chapter 4

Appendix 4.1. Benthic algae taxa found in the eight lakes along the depth gradient.

Phylum/Class/Order	Family	Taxon
Achnanthales	Achnanthaceae	<i>Achnanthes</i> Bory de Saint-Vincent, 1822
Achnanthales	Achnanthaceae	<i>Achnanthes exigua</i> Grunow, 1880
Achnanthales	Achnanthaceae	<i>Achnanthes laevis</i> Østrup, 1910
Achnanthales	Achnanthaceae	<i>Achnanthes oestrupii</i> (Cleve-Euler) Hustedt, 1930
Achnanthales	Achnanthaceae	<i>Karayevia oblongella</i> (Østrup) Aboal, 2003
Achnanthales	Achnanthaceae	<i>Planothidium conspicuum</i> (Mayer) Morales, 2006
Achnanthales	Achnanthaceae	<i>Planothidium joursacense</i> (Héribaud-Joseph, 1903) Lange-Bertalot
Achnanthales	Achnanthidiaceae	<i>Achnanthes didyma</i> Hustedt, 1933
Achnanthales	Achnanthidiaceae	<i>Achnanthidium biasolettianum</i> (Grunow) Round & Bukhtiyarova, 199
Achnanthales	Achnanthidiaceae	<i>Achnanthidium minutissimum</i> (Kützing) Czarnecki, 1994
Achnanthales	Achnanthidiaceae	<i>Achnanthidium minutissimum</i> type
Achnanthales	Achnanthidiaceae	<i>Eucocconeis flexella</i> (Kützing) Meister, 1912
Achnanthales	Achnanthidiaceae	<i>Karayevia clevei</i> (Grunow) Bukhtiyarova, 1999
Achnanthales	Achnanthidiaceae	<i>Karayevia laterostrata</i> (Hustedt) Bukhtiyarova, 1999
Achnanthales	Achnanthidiaceae	<i>Kolbesia ploenensis</i> (Hustedt) Kingston, 2000

Phylum/Class/Order	Family	Taxon
Achnanthales	Achnanthidiaceae	<i>Planothidium frequentissimum</i> (Lange-Bertalot) Round & Bukhtiyarova 1996
Achnanthales	Achnanthidiaceae	<i>Planothidium granum</i> (M.H.Hohn & Hellerman) Lange-Bertalot 1999
Achnanthales	Achnanthidiaceae	<i>Planothidium rostratum</i> (Oestrup) Lange-Bertalot, 1999
Achnanthales	Achnanthidiaceae	<i>Psammothidium chlidanos</i> (Hohn & Hellerman) Lange-Bertalot, 1999
Achnanthales	Achnanthidiaceae	<i>Psammothidium</i> sp. Buhtkiyarova & Round, 1996
Achnanthales	Achnanthidiaceae	<i>Rossithidium pusillum</i> (Grunow) Round & Bukhtiyarova, 1996
Achnanthales	Cocconeidaceae	<i>Cocconeis</i> Ehrenberg, 1837
Achnanthales	Cocconeidaceae	<i>Cocconeis pediculus</i> Ehrenberg, 1838
Achnanthales	Cocconeidaceae	<i>Cocconeis placentula</i> Ehrenberg, 1838
Achnanthales	Cocconeidaceae	<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehrenberg) Grunow, 1884
Achnanthales	Cocconeidaceae	<i>Cocconeis placentula</i> var. <i>lineata</i> (Ehrenberg) Van Heurck, 1885
Achnanthales	Cocconeidaceae	<i>Cocconeis placentula</i> var. <i>lineata</i> (Ehrenberg) Van Heurck, 1885
Bacillariales	Bacillariaceae	<i>Cymbellonitzschia diluviana</i> Hustedt 1950
Bacillariales	Bacillariaceae	<i>Denticula tenuis</i> Kützing, 1844
Bacillariales	Bacillariaceae	<i>Grunowia sinuata</i> (Thwaites) Rabenhorst, 1864
Bacillariales	Bacillariaceae	<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow, 1880
Bacillariales	Bacillariaceae	<i>Nitzschia acicularis</i> (Kützing) Smith, 1853
Bacillariales	Bacillariaceae	<i>Nitzschia amphibia</i> Grunow, 1862
Bacillariales	Bacillariaceae	<i>Nitzschia archibaldii</i> Lange-Bertalot 1980

Phylum/Class/Order	Family	Taxon
Bacillariales	Bacillariaceae	<i>Nitzschia capitellata</i> Hustedt, 1922
Bacillariales	Bacillariaceae	<i>Nitzschia dissipata</i> (Kützing) Grunow, 1862
Bacillariales	Bacillariaceae	<i>Nitzschia dissipata</i> var. <i>media</i> (Hantzsch) Grunow, 1881
Bacillariales	Bacillariaceae	<i>Nitzschia filiformis</i> (Smith) Hustedt
Bacillariales	Bacillariaceae	<i>Nitzschia fonticola</i> (Grunow) Grunow, 1881
Bacillariales	Bacillariaceae	<i>Nitzschia frustulum</i> (Kützing) Grunow, 1880
Bacillariales	Bacillariaceae	<i>Nitzschia gracilis</i> Hantzsch, 1860
Bacillariales	Bacillariaceae	<i>Nitzschia hantzschiana</i> Rabenhorst, 1860
Bacillariales	Bacillariaceae	<i>Nitzschia heuflieriana</i> Grunow 1862
Bacillariales	Bacillariaceae	<i>Nitzschia inconspicua</i> Grunow, 1862
Bacillariales	Bacillariaceae	<i>Nitzschia liebetruthii</i> Rabenhorst 1864
Bacillariales	Bacillariaceae	<i>Nitzschia linearis</i> (C.Agardh) Smith, 1853
Bacillariales	Bacillariaceae	<i>Nitzschia nana</i> Grunow, 1881
Bacillariales	Bacillariaceae	<i>Nitzschia palea</i> (Kützing) Smith, 1856
Bacillariales	Bacillariaceae	<i>Nitzschia palea</i> var. <i>debilis</i> (Kützing) Grunow, 1880
Bacillariales	Bacillariaceae	<i>Nitzschia paleacea</i> (Grunow) Grunow, 1881
Bacillariales	Bacillariaceae	<i>Nitzschia perminuta</i> (Grunow) Peragallo, 1903
Bacillariales	Bacillariaceae	<i>Nitzschia pusilla</i> (Kützing) Grunow emend.Lange-Bertalot, 1976
Bacillariales	Bacillariaceae	<i>Nitzschia recta</i> Hantzsch ex Rabenhorst, 1862

Phylum/Class/Order	Family	Taxon
Bacillariales	Bacillariaceae	<i>Nitzschia sigma</i> (Kützing) Smith, 1853
Bacillariales	Bacillariaceae	<i>Nitzschia sociabilis</i> Hustedt, 1957
Bacillariales	Bacillariaceae	<i>Nitzschia</i> sp. Hassall, 1845
Bacillariales	Bacillariaceae	<i>Nitzschia subacicularis</i> Hustedt
Bacillariales	Bacillariaceae	<i>Nitzschia tubicola</i> Grunow, 1880
Bacillariales	Bacillariaceae	<i>Nitzschia valdestriata</i> Aleem & Hustedt 1951
Bacillariales	Bacillariaceae	<i>Nitzschia vermicularis</i> (Kützing) Hantzsch, 1860
Cymbellales	Cymbellaceae	<i>Cymbella affinis</i> Kützing, 1844
Cymbellales	Cymbellaceae	<i>Cymbella cisula</i> (Hemprich & Ehrenberg) Kirchner, 1878
Cymbellales	Cymbellaceae	<i>Cymbella cymbiformis</i> Agardh, 1830
Cymbellales	Cymbellaceae	<i>Cymbella helvetica</i> Kützing, 1844
Cymbellales	Cymbellaceae	<i>Cymbella lanceolata</i> (Agardh) Agardh, 1830
Cymbellales	Cymbellaceae	<i>Cymbella</i> sp. Agardh, 1830
Cymbellales	Cymbellaceae	<i>Cymbopleura amphicephala</i> (Nägeli) Krammer, 2003
Cymbellales	Cymbellaceae	<i>Cymbopleura naviculiformis</i> (Auerswald ex Heiberg) Krammer, 2003
Cymbellales	Cymbellaceae	<i>Cymbopleura subaequalis</i> (Grunow) Krammer, 2003
Cymbellales	Cymbellaceae	<i>Delicata delicatula</i> (Kützing) Krammer, 2003
Cymbellales	Cymbellaceae	<i>Encyonema alpinum</i> (Grunow) Mann 1990
Cymbellales	Cymbellaceae	<i>Encyonema caespitosum</i> Kützing, 1849

Phylum/Class/Order	Family	Taxon
Cymbellaler	Cymbellaceae	<i>Encyonema caespitosum</i> Kützing, 1849
Cymbellaler	Cymbellaceae	<i>Encyonema gracile</i> Rabenhorst, 1853
Cymbellaler	Cymbellaceae	<i>Encyonema minutum</i> (Hilse) Mann, 1990
Cymbellaler	Cymbellaceae	<i>Encyonema perpusillum</i> (Cleve) Mann, 1990
Cymbellaler	Cymbellaceae	<i>Encyonema silesiacum</i> (Bleisch) Mann, 1990
Cymbellaler	Cymbellaceae	<i>Encyonema</i> sp. Kützing, 1834
Cymbellaler	Cymbellaceae	<i>Encyonopsis microcephala</i> (Grunow) Krammer, 1997
Cymbellaler	Cymbellaceae	<i>Navicula clementis</i> Grunow, 1882
Cymbellaler	Cymbellaceae	<i>Navicula faldaisensis</i> Grunow, 1880
Cymbellaler	Cymbellaceae	<i>Placoneis clementioides</i> (Hustedt) Cox 1987
Cymbellaler	Cymbellaceae	<i>Placoneis elginensis</i> (Gregory) Cox, 1988
Cymbellales	Gomphonemataceae	<i>Didymosphenia geminata</i> (Lyngbye) Schmidt, 1899
Cymbellales	Gomphonemataceae	<i>Gomphonema acuminatum</i> Ehrenberg, 1832
Cymbellales	Gomphonemataceae	<i>Gomphonema angustum</i> /pumilum type
Cymbellales	Gomphonemataceae	<i>Gomphonema clavatum</i> Ehrenberg, 1832
Cymbellales	Gomphonemataceae	<i>Gomphonema gracile</i> Ehrenberg, 1838
Cymbellales	Gomphonemataceae	<i>Gomphonema grovei</i> var. <i>lingulatum</i> (Hustedt) Lange-Bertalot, 1985
Cymbellales	Gomphonemataceae	<i>Gomphonema minutum</i> (Agardh) Agardh, 1831
Cymbellales	Gomphonemataceae	<i>Gomphonema olivaceoides</i> var. <i>densistriata</i> Foged, 1963

Phylum/Class/Order	Family	Taxon
Cymbellales	Gomphonemataceae	<i>Gomphonema olivaceum</i> (Hornemann) Brébisson, 1838
Cymbellales	Gomphonemataceae	<i>Gomphonema parvulum</i> (Kützing) Kützing, 1849
Cymbellales	Gomphonemataceae	<i>Gomphonema parvulum</i> var. <i>exilissimum</i> Grunow, 1880
Cymbellales	Gomphonemataceae	<i>Gomphonema</i> sp. Ehrenberg, 1832
Cymbellales	Gomphonemataceae	<i>Gomphonema tergestinum</i> (Grunow) Fricke, 1902
Cymbellales	Gomphonemataceae	<i>Gomphonema truncatum</i> Ehrenberg, 1832
Cymbellales	Gomphonemataceae	<i>Reimeria sinuata</i> (Gregory) Kociolek & Stoermer, 1987
Cymbellales	Rhoicospheniaceae	<i>Rhoicosphenia abbreviata</i> (Agardh) Lange-Bertalot, 1980
Eunotiales	Eunotiaceae	<i>Eunotia arcus</i> Ehrenberg, 1837
Eunotiales	Eunotiaceae	<i>Eunotia arcus</i> var. <i>minor</i> Grunow, 1881
Eunotiales	Eunotiaceae	<i>Eunotia bidentula</i> Smith, 1856
Eunotiales	Eunotiaceae	<i>Eunotia exigua</i> var. <i>tenella</i> (Grunow) Norpel & Alles, 1991
Eunotiales	Eunotiaceae	<i>Eunotia formica</i> Ehrenberg, 1843
Eunotiales	Eunotiaceae	<i>Eunotia implicata</i> Nörpel, Lange-Bertalot & Alles, 1991
Eunotiales	Eunotiaceae	<i>Eunotia incisa</i> Smith ex Gregory, 1854
Eunotiales	Eunotiaceae	<i>Eunotia intermedia</i> (Kraske) Nörpel & Lange-Bertalot, 1993
Eunotiales	Eunotiaceae	<i>Eunotia subarcuatoidea</i> Alles, Nörpel & Lange-Bertalot 1991
Eunotiales	Eunotiaceae	<i>Eunotia</i> sp. Ehrenberg, 1837
Fragilariales	Fragilariaceae	<i>Ctenophora pulchella</i> (Ralfs ex Kützing) Williams & Round, 1986

Phylum/Class/Order	Family	Taxon
Fragilariales	Fragilariaceae	<i>Diatoma ehrenbergii</i> Kützing, 1844
Fragilariales	Fragilariaceae	<i>Diatoma problematicum</i> Lange-Bertalot 1993
Fragilariales	Fragilariaceae	<i>Diatoma</i> sp.
Fragilariales	Fragilariaceae	<i>Diatoma vulgare</i> Bory de Saint-Vincent, 1824
Fragilariales	Fragilariaceae	<i>Fragilaria austriaca</i> (Grunow) Lange-Bertalot, 1980
Fragilariales	Fragilariaceae	<i>Fragilaria bidens</i> Heiberg, 1863
Fragilariales	Fragilariaceae	<i>Fragilaria capucina</i> Desmazières, 1825
Fragilariales	Fragilariaceae	<i>Fragilaria capucina</i> var. <i>mesolepta</i> (Rabenhorst) Rabenhorst, 1864
Fragilariales	Fragilariaceae	<i>Fragilaria capucina</i> var. <i>vaucheriae</i> (Kützing) Lange-Bertalot, 1980
Fragilariales	Fragilariaceae	<i>Fragilaria capucina</i> var. <i>vaucheriae</i> (Kützing) Lange-Bertalot, 1980
Fragilariales	Fragilariaceae	<i>Fragilaria parasitica</i> var. <i>subconstricta</i> Grunow, 1881
Fragilariales	Fragilariaceae	<i>Fragilaria perminuta</i> Lange-Bertalot(2000)
Fragilariales	Fragilariaceae	<i>Fragilaria</i> sp. Lyngbye, 1819
Fragilariales	Fragilariaceae	<i>Fragilaria tenera</i> (Smith) Lange-Bertalot, 1980
Fragilariales	Fragilariaceae	<i>Fragilariforma virescens</i> (Ralfs) Williams & Round, 1988
Fragilariales	Fragilariaceae	<i>Fragilariforma virescens</i> (Ralfs) Williams & Round, 1988
Fragilariales	Fragilariaceae	<i>Meridion circulare</i> (Greville) Agardh, 1831
Fragilariales	Fragilariaceae	<i>Navicula</i> [small species]
Fragilariales	Fragilariaceae	<i>Navicula claytonii</i> Carter 1987

Phylum/Class/Order	Family	Taxon
Fragilariales	Fragilariaceae	<i>Pseudostaurosira brevistriata</i> (Grunow) Williams & Round, 1987
Fragilariales	Fragilariaceae	<i>Pseudostaurosira elliptica</i> (Schumann) Edlund, Morales & Spaulding, 2006
Fragilariales	Fragilariaceae	<i>Pseudostaurosira parasitica</i> (Smith) Morales, 2003
Fragilariales	Fragilariaceae	<i>Staurosira construens</i> Ehrenberg, 1843
Fragilariales	Fragilariaceae	<i>Staurosira oldenburgiana</i> (Hust.) Lange-Bertalot(2000)
Fragilariales	Fragilariaceae	<i>Staurosirella leptostauron</i> (Ehrenberg) Williams & Round, 1987
Fragilariales	Fragilariaceae	<i>Staurosirella pinnata</i> (Ehrenberg) Williams & Round, 1987
Fragilariales	Fragilariaceae	<i>Synedra rumpens</i> var. <i>scotica</i> Grunow, 1881
Fragilariales	Fragilariaceae	<i>Synedra ulna</i> (Nitzsch) Ehrenberg, 1832
Fragilariales	Fragilariaceae	<i>Tabularia fasciculata</i> (C.Agardh) Williams & Round, 1986
Fragilariales	Fragilariaceae	<i>Ulnaria acus</i> (Kützing) Aboal, 2003
Mastogloiales	Mastogloiaceae	<i>Mastogloia smithii</i> Thwaites ex Smith, 1856
Mastogloiales	Mastogloiaceae	<i>Mastogloia</i> Thwaites ex Smith, 1856
Melosirales	Melosiraceae	<i>Melosira varians</i> Agardh, 1827
Naviculales	Amphipleuraceae	<i>Amphipleura pellucida</i> (Kützing) Kützing, 1844
Naviculales	Amphipleuraceae	<i>Frustulia rhomboides</i> (Ehrenberg) De Toni, 1891
Naviculales	Amphipleuraceae	<i>Frustulia saxonica</i> Rabenhorst, 1853
Naviculales	Amphipleuraceae	<i>Frustulia vulgaris</i> (Thwaites) De Toni, 1891
Naviculales	Brachysiraceae	<i>Brachysira brebissonii</i> Ross, 1986

Phylum/Class/Order	Family	Taxon
Naviculales	Brachysiraceae	<i>Brachysira neoexilis</i> Lange-Bertalot, 1994
Naviculales	Brachysiraceae	<i>Brachysira serians</i> (Brébisson) Round & Mann, 1981
Naviculales	Brachysiraceae	<i>Brachysira</i> sp. Kützing, 1836
Naviculales	Brachysiraceae	<i>Brachysira vitrea</i> (Grunow) Ross, 1986
Naviculales	Cavinulaceae	<i>Cavinula cocconeiformis</i> Mann & Stickle, 1990
Naviculales	Diadesmidaceae	<i>Diadesmis contenta</i> var. <i>biceps</i> (Grunow) Hamilton, 1992
Naviculales	Diadesmidaceae	<i>Luticola goeppertiana</i> (Bleisch) Mann, 1990
Naviculales	Diadesmidaceae	<i>Luticola mutica</i> (Kützing) Mann, 1990
Naviculales	Diadesmidaceae	<i>Luticola muticopsis</i> (Van Heurck) Mann, 1990
Naviculales	Diadesmidaceae	<i>Luticola ventricosa</i> (Kützing) Mann, 1990
Naviculales	Diploneidaceae	<i>Diploneis oblongella</i> (Nägeli ex Kützing) Cleve-Euler, 1922
Naviculales	Diploneidaceae	<i>Diploneis ovalis</i> (Hilse) Cleve, 1891
Naviculales	Naviculaceae	<i>Chamaepinnularia</i> sp. Lange-Bertalot & Krammer, 1996
Naviculales	Naviculaceae	<i>Geissleria acceptata</i> (Hustedt) Lange-Bertalot & Metzeltin, 1996
Naviculales	Naviculaceae	<i>Hippodonta capitata</i> (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski, 1996
Naviculales	Naviculaceae	<i>Hippodonta costulata</i> (Grunow) Lange-Bertalot, Metzeltin & Witkowski, 1996
Naviculales	Naviculaceae	<i>Hippodonta lueneburgensis</i> (Grunow) Lange-Bertalot, Metzeltin & Witkowski, 1996
Naviculales	Naviculaceae	<i>Navicula</i> Bory de Saint-Vincent, 1822
Naviculales	Naviculaceae	<i>Navicula capitatoradiata</i> Germain, 1981

Phylum/Class/Order	Family	Taxon
Naviculales	Naviculaceae	<i>Navicula cari</i> Ehrenberg, 1836
Naviculales	Naviculaceae	<i>Navicula cryptocephala</i> Kützinger, 1844
Naviculales	Naviculaceae	<i>Navicula cryptocephala</i> var. <i>veneta</i> (Kützinger) Rabenhorst, 1864
Naviculales	Naviculaceae	<i>Navicula cryptotenella</i> Lange-Bertalot, 1985
Naviculales	Naviculaceae	<i>Navicula difficillima</i> Hustedt 1950
Naviculales	Naviculaceae	<i>Navicula gregaria</i> Donkin, 1861
Naviculales	Naviculaceae	<i>Navicula lanceolata</i> Ehrenberg, 1838
Naviculales	Naviculaceae	<i>Navicula leptostriata</i> Jørgensen, 1948
Naviculales	Naviculaceae	<i>Navicula menisculus</i> Schumann, 1867
Naviculales	Naviculaceae	<i>Navicula pseudolanceolata</i> Lange-Bertalot, 1980
Naviculales	Naviculaceae	<i>Navicula radiosa</i> Kützinger, 1844
Naviculales	Naviculaceae	<i>Navicula reichardiana</i> Lange-Bertalot, 1989
Naviculales	Naviculaceae	<i>Navicula reinhardtii</i> (Grunow) Grunow, 1877
Naviculales	Naviculaceae	<i>Navicula rhynchocephala</i> Kützinger, 1844
Naviculales	Naviculaceae	<i>Navicula tenelloides</i> Hustedt, 1937
Naviculales	Naviculaceae	<i>Navicula tripunctata</i> (Müller) Bory de Saint-Vincent, 1822
Naviculales	Naviculaceae/ sellaphoraceae	<i>Adlafia bryophila</i> (Petersen) Gerd Moser, Lange-Bertalot & Metzeltin, 1998
Naviculales	Naviculaceae/ sellaphoraceae	<i>Adlafia minuscula</i> (Grunow) Lange-Bertalot, 1999
Naviculales	Naviculaceae/ sellaphoraceae	<i>Adlafia suchlandtii</i> (Hustedt) Moser, Lange-Bertalot & Metzeltin, 1998

Phylum/Class/Order	Family	Taxon
Naviculales	Naviculaceae/ sellaphoraceae	<i>Navicula joubaudii</i> Germain, 1982
Naviculales	Naviculaceae/ sellaphoraceae	<i>Navicula minima</i> Grunow, 1880
Naviculales	Neidiaceae	<i>Neidium ampliutum</i> (Ehrenberg) Krammer, 1985
Naviculales	Neidiaceae	<i>Neidium productum</i> (Smith) Cleve, 1894
Naviculales	Pinnulariaceae	<i>Caloneis bacillum</i> (Grunow) Cleve, 1894
Naviculales	Pinnulariaceae	<i>Caloneis limosa</i> (Kützing) Patrick, 1966
Naviculales	Pinnulariaceae	<i>Caloneis</i> sp. Cleve, 1894
Naviculales	Pinnulariaceae	<i>Pinnularia appendiculata</i> (Agardh) Cleve, 1895
Naviculales	Pinnulariaceae	<i>Pinnularia borealis</i> Ehrenberg, 1843
Naviculales	Pinnulariaceae	<i>Pinnularia</i> Ehrenberg, 1843
Naviculales	Pinnulariaceae	<i>Pinnularia gibba</i> Ehrenberg, 1843
Naviculales	Pinnulariaceae	<i>Pinnularia subcapitata</i> Gregory, 1856
Naviculales	Pinnulariaceae	<i>Pinnularia viridis</i> (Nitzsch) Ehrenberg, 1843
Naviculales	Sellaphoraceae	<i>Fallacia helensis</i> (Schulz) Mann 1990
Naviculales	Sellaphoraceae	<i>Fallacia subhamulata</i> (Grunow) Mann, 1990
Naviculales	Sellaphoraceae	<i>Sellaphora pupula</i> (Kützing) Mereschkovsky, 1902
Naviculales	Sellaphoraceae	<i>Sellaphora seminulum</i> (Grunow) Mann, 1989
Naviculales	Sellaphoraceae	<i>Sellaphora</i> sp. Mereschowsky, 1902
Naviculales	Stauroneidaceae	<i>Craticula accomoda</i> (Hustedt) Mann, 1990

Phylum/Class/Order	Family	Taxon
Naviculales	Stauroneidaceae	<i>Stauroneis kriegeri</i> Patrick, 1945
Naviculales	Stauroneidaceae	<i>Stauroneis smithii</i> Grunow, 1860
Pennate undif.		Pennate undif.
Rhopalodiales	Rhopalodiaceae	<i>Epithemia adnata</i> (Kützing) Brébisson, 1838
Rhopalodiales	Rhopalodiaceae	<i>Epithemia sorex</i> Kützing, 1844
Rhopalodiales	Rhopalodiaceae	<i>Rhopalodia gibba</i> (Ehrenberg) Müller, 1895
Surirellales	Surirellaceae	<i>Cymatopleura elliptica</i> (Brébisson) Smith, 1851
Surirellales	Surirellaceae	<i>Surirella minuta</i> Brébisson, 1849
Surirellales	Surirellaceae	<i>Surirella</i> sp. Turpin, 1828
Tabellariales	Tabellariaceae	<i>Tabellaria fenestrata</i> (Lyngbye) Kützing, 1844
Tabellariales	Tabellariaceae	<i>Tabellaria flocculosa</i> (Roth) Kützing, 1844
Thalassiosiphysales	Catenulaceae	<i>Amphora libyca</i> Ehrenberg, 1840
Thalassiosiphysales	Catenulaceae	<i>Amphora ovalis</i> (Kützing) Kützing, 1844
Thalassiosiphysales	Catenulaceae	<i>Amphora pediculus</i> (Kützing) Grunow ex Schmidt, 1875
Thalassiosiphysales	Catenulaceae	<i>Amphora</i> sp. Ehrenberg ex Kützing, 1844
Thalassiosiphysales	Catenulaceae	<i>Halamphora montana</i> (Krasske) Levkov, 2009
Thalassiosiphysales	Catenulaceae	<i>Halamphora oligotraphenta</i> (Lange-Bertalot) Levkov, 2009

Appendix 4.2. Benthic macroinvertebrate taxa found in the eight lakes along the depth gradient.

Phylum/Class/Order	Family	Taxon
Acari		Hydrachnidia Oribatei
Amphipoda	Crangonycitidae Gammaridae	<i>Crangonyx pseudogracilis</i> Bousfield, 1958 <i>Gammarus duebeni</i> Lilljeborg, 1851 <i>Gammarus pulex</i> (Linnaeus, 1758) <i>Pisidium</i> sp. Pfeiffer, 1821 <i>Dreissena polymorpha</i> (Pallas, 1771)
Bivalvia	Sphaeriidae Dreissenidae	Hydrozoa
Coelenterate	Hydrozoa	
Coleoptera	Curculionidae Dryopidae Dytiscidae	<i>Bagous</i> sp. Germar, 1817 <i>Dryops (Dryops)</i> sp. Olivier, 1791 <i>Hydroporus</i> sp. Clairville, 1806 <i>Nebrioporus depressus</i> (Fabricius, 1775) <i>Nebrioporus</i> sp. Régimbart, 1906 <i>Stictotarsus duodecimpustulatus</i> (Fabricius, 1792) <i>Suphrodytes</i> sp. Gozis, 1914 <i>Yola</i> sp Gozis, 1886 <i>Elmis aenea</i> (Müller, 1806)
	Elmidae	

Phylum/Class/Order	Family	Taxon
Collembola		<i>Esolus parallelepipeds</i> (Müller, 1806)
		<i>Limnius volckmari</i> (Panzer, 1793)
		<i>Oulimnius tuberculatus</i> (Müller, 1806)
		<i>Gyrinus</i> sp. Geoffroy, 1762
	Haliplidae	<i>Brychius</i> sp. Thomson, 1859
		<i>Haliphus fulvus</i> (Fabricius, 1801)
		<i>Haliphus</i> (<i>Haliplidius</i>) sp. Guignot, 1928
		<i>Pelodytes</i> sp. Regimbart, 1878
	Helophoridae	<i>Helophorus</i> (<i>Rhopalohelophorus</i>) <i>griseus</i> Herbst, 1793
	Hydraenidae	<i>Hydraena rufipes</i> Curtis, 1830
Decapoda	Isotomidae	<i>Isotomurus</i> sp. Boerner, 1903
	Astacidae	Astacidae
Diptera	Cecidomyiidae	Cecidomyiidae
	Ceratopogonidae	Ceratopogonidae
	Chironomidae	Chironomidae
	Dolichopodidae	Dolichopodidae
	Empididae	Empididae
	Pediciidae	<i>Dicranota</i> sp. Zetterstedt, 1838
	Psychodidae	Psychodidae

Phylum/Class/Order	Family	Taxon
Ephemeroptera	Diptera Gen. sp.	Diptera Gen.sp.
		<i>Centroptilum luteolum</i> (Müller, 1776)
	Beatiidae	<i>Procloeon bifidum</i> (Bengtsson, 1912)
		<i>Procloeon simile</i> (McDunnough, 1924)
		<i>Caenis horaria</i> (Linnaeus, 1758)
		<i>Caenis luctuosa</i> (Burmeister, 1839)
		<i>Serratella ignita</i> (Poda, 1761)
		<i>Ephemera danica</i> Müller, 1764
		<i>Ecchyonurus dispar</i> (Curtis, 1834)
		<i>Electrogena lateralis</i> (Curtis, 1834)
		<i>Heptagenia sulphurea</i> (Müller, 1776)
		<i>Paraleptophlebia wernerii</i> Ulmer, 1920
		<i>Bithynia tentaculata</i> (Linnaeus, 1758)
		<i>Potamopyrgus antipodarum</i> (Gray, 1853)
		<i>Marstoniopsis insubrica</i> (Kuster, 1853)
		Hydrobiidae
Gastropoda	Bithyniidae	
	Hydrobiidae	
	Lymnaeidae	
		<i>Galba truncatula</i> (Müller, 1774)
		<i>Omphiscola glabra</i> (Müller, 1774)
		<i>Radix peregra</i> (Müller, 1774)

Phylum/Class/Order	Family	Taxon
Hemiptera	Neritidae	<i>Theodoxus fluviatilis</i> (Linnaeus, 1758)
	Physidae	<i>Physa fontinalis</i> (Linnaeus, 1758)
	Planorbidae	<i>Ancylus fluviatilis</i> Müller, 1774
		<i>Anisus (Anisus) septemgyratus</i> (Rossmassler, 1835)
		<i>Bathymphalus contortus</i> (Linnaeus, 1758)
		<i>Gyraulus albus</i> (Müller, 1774)
		<i>Armiger crista</i> (Linnaeus, 1758)
		<i>Valvata cristata</i> Müller, 1774
		<i>Valvata macrostoma</i> (Mörch, 1864)
		<i>Viviparus viviparus</i> (Linnaeus, 1758)
	Corixidae	<i>Arctocoris germari</i> (Fieber, 1848)
		<i>Callicorixa praeusta</i> (Fieber, 1848)
		Corixinae
		<i>Micronecta poweri poweri</i> (Douglas & Scott, 1869)
		<i>Sigara distincta</i> (Fieber, 1848)
		<i>Sigara (Sigara) dorsalis</i> (Leach, 1817)
		<i>Sigara falleni</i> (Fieber, 1848)
	Notonectidae	Notonectidae
	Veliidae	Veliidae

Phylum/Class/Order	Family	Taxon
Hirudinea	Erpobdellidae	<i>Erpobdella octoculata</i> (Linnaeus, 1758)
	Glossiphoniidae	<i>Glossiphonia complanata</i> (Linnaeus, 1758)
		<i>Glossiphonia paludosa</i> (Carena, 1824)
		<i>Helobdella stagnalis</i> (Linnaeus, 1758)
		<i>Hemiclepsis marginata</i> (Müller, 1774)
Isopoda	Haemopidae	<i>Haemopsis sanguisuga</i> (Linnaeus, 1758)
	Piscicolidae	<i>Piscicola geometra</i> (Linnaeus, 1758)
	Asellidae	<i>Asellus aquaticus</i> (Linnaeus, 1758)
		<i>Proasellus meridianus</i> (Racovitza, 1919)
		<i>Argulus</i> sp. Müller, 1785
Maxillopoda	Argulidae	
Megaloptera	Sialidae	<i>Sialis morio</i> Klingstedt, 1932
Nematoda		Nematoda
Nematomorpha		Nematomorpha
Nemertini	Tetrastemmatidae	<i>Prostoma</i> sp. Duges, 1828
Odonata	Coenagriidae	Coenagriidae juv.
Odonata	Coenagrionidae	<i>Ischnura elegans</i> (Vander Linden, 1820)
Odonata	Libellulidae	<i>Sympetrum striolatum</i> (Charpentier, 1840)
Oligochaeta		Oligochaeta
Ostracoda		Ostracoda

Phylum/Class/Order	Family	Taxon
Plecoptera	Leuctridae	<i>Leuctra</i> sp. Stephens, 1836
	Nemouridae	<i>Nemurella picteti</i> Klapalek, 1900
Porifera		Porifera
Trichoptera	Ecnomidae	<i>Ecnomus tenellus</i> (Rambur, 1842)
	Glossosomatidae	<i>Agapetus fuscipes</i> Curtis, 1834
	Hydroptilidae	<i>Hydroptila</i> sp. Dalman, 1819
	Hydroptilidae	<i>Oxyethira</i> sp. Eaton, 1873
	Lepidostomatidae	<i>Lepidostoma hirtum</i> (Fabricius, 1775)
	Leptoceridae	<i>Athripsodes albifrons</i> (Linnaeus, 1758)
		<i>Athripsodes bilineatus bilineatus</i> (Linnaeus, 1758)
		<i>Athripsodes cinereus</i> (Curtis, 1834)
		<i>Athripsodes commutatus</i> (Rostock, 1874)
		<i>Ceraclea fulva</i> (Rambur, 1842)
		<i>Mystacides azureus</i> (Linnaeus, 1761)
		<i>Mystacides longicornis</i> (Linnaeus, 1758)
		<i>Oecetis lacustris</i> (Pictet, 1834)
		<i>Oecetis ochracea</i> (Curtis, 1825)
		<i>Oecetis testacea</i> (Curtis, 1834)
		<i>Halesus radiates</i> (Curtis, 1834)
	Limnephilidae	

Phylum/Class/Order	Family	Taxon
Turbellaria	Phryganeidae Polycentropodidae	<i>Limnephilus lunatus</i> Curtis, 1834
		<i>Potamophylax latipennis</i> (Curtis, 1834)
		<i>Agrypnia</i> sp. Curtis, 1835
		<i>Cyrnus flavidus</i> McLachlan, 1864
		<i>Cyrnus trimaculatus</i> (Curtis, 1834)
		<i>Neureclipsis bimaculata</i> (Linnaeus, 1758)
		<i>Polycentropus flavomaculatus</i> (Pictet, 1834)
		<i>Polycentropus irroratus</i> Curtis, 1835
		<i>Psychomyia fragilis</i> (Pictet, 1834)
		<i>Tinodes maculicornis</i> (Pictet, 1834)
		<i>Tinodes waeneri</i> (Linnaeus, 1758)
		<i>Sericostoma personatum</i> (Kirby & Spence, 1826)
		Trichoptera Gen. sp.
		<i>Dendrocoelum lacteum</i> (Müller, 1774)
		<i>Dugesia lugibris</i> (Schmidt, 1861)
		<i>Planaria torva</i> (Müller, 1774)
		<i>Polycelis nigra</i> (Müller, 1973)